

BIOENERGETICS AND HABITAT SUITABILITY MODELS FOR THE CHINESE  
MYSTERY SNAIL (*BELLAMYA CHINENSIS*)

by

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A DISSERTATION

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Doctor of Philosophy

Major: Natural Resource Sciences

Under the Supervision of Professors Kevin L. Pope and Valery E. Forbes

Lincoln, Nebraska

May, 2015

BIOENERGETICS AND HABITAT SUITABILITY MODELS FOR THE CHINESE  
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University of Nebraska, 2015

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Relatively little is known about the invasive Chinese mystery snail (*Bellamya chinensis*). This research aims to elucidate some of the mystery surrounding this species. First, we place the species in context with other invasive freshwater snails of the USA and Canada, identifying current information gaps, categorizing shared characteristics among families and species, and comparing functional roles and ecological effects of freshwater snails. We conclude that more focus needs to be directed to regulating the aquarium, pet, and food trades if we are serious about preventing future invasions. Next, we develop a bioenergetics model for the species by quantifying and comparing consumption, egestion, respiration, and production of the Chinese mystery snail at varying water temperatures. We observed differences in these values across different water temperatures, indicating that temperature affects growth and reproductive strategies of this species. Then we focused on analyzing a specific case study to identify physical, chemical, and biological lake characteristics that help predict where the Chinese mystery snail is found. The top predictor model found that Chinese mystery snail presence is correlated with Secchi depth, latitude, and the presence of other aquatic invasive species. Finally, we use network analysis to develop a method for coupling social and ecological network models so they may be used in tandem to assess how humans aid the movement

of the Chinese mystery snail, as well as how the snail affects an ecosystem after invasion. This was achieved through the adaptation of the framework of infectious disease network modeling.

## Author's Acknowledgments

Where do I start? A PhD is so much more than just this document. To my co-advisors, Dr. Kevin Pope and Dr. Valery Forbes: thank you. There were ups and downs and surprises along the way, and you two guided me through each step with patience and encouragement (and tough love when I needed it). Not only have I changed as a scientist, I've changed as a person as a result of the past 4 years and for that I will always be grateful. Thank you for taking a chance on me. To my committee members, Dr. Chad Brassil, Dr. Amy Burgin, and Dr. Mark Pegg: thank you for enduring the snail ride as it evolved. Your suggestions, thought-provoking meetings, and inspiration were critical to the completion of this project. To Dr. Craig Allen and the IGERT committee: thank you for the unique opportunity of being an IGERT student. This program is an incredible launching pad and opened doors I didn't even know existed. To the University of Nebraska Foundation: thank you for the financial support enabling me to focus on my dissertation full time as a Presidential Graduate Fellow. To Dr. Brian Fath and the IIASA staff: thank you for giving me the opportunity to spend a terrific summer in Austria with a magnificent international team. YSSP was a highlight of grad school, without a doubt.

A very special thank you to the wonderful staff that keeps the NE Coop Unit and IGERT moving forward, especially Valerie Egger and Caryl Cashmere. I will be forever appreciative for the hours of work you both saved me and for your patience when I made things more difficult than they needed to be. Valerie, thank you for all of the help organizing 2 European adventures; I definitely didn't make things easy, but your support resulted in two flawless trips.

I was lucky to join a great group of people comprised of SNR faculty, the NE Coop

Unit, and the IGERT crew. I was even luckier to be part of the Pope Lab, and I cannot thank you guys enough. I am especially grateful to Chris Wiley, Robert Kill, Jason DeBoer, Brian Hammond, Kelly Turek, Luke Kowalewski, Nathan Stewart, Dr. Dustin Martin, and Dr. Chris Chizinski: we had some awesome (and a few not-so-awesome) times and my memories of graduate school will always be dominated by this beautiful, motley crew we were lucky to be a part of. To the Forbes Lab: I loved our talks on science and on life – thank you! To my fellow IGERTs, especially Shelli Hellman, Hannah Birgé, Maggi Swilinski, Ilonka Zlatar, and Noelle Hart: nothing bonds a group faster than being plopped down in a new country where no one speaks the native language. I am continuously inspired by your enthusiasm, optimism, encouragement, and quests for self-improvement, and I am so blessed to be able to call you all friends. To my fellow snailer, Bruce Stephen: thank you for the snail enthusiasm and the endless edits – I would have been lost without your snail expertise! Alec Wong: thank you for all of your dedication to field and lab work! I don't have room to name everyone who contributed to this process but know you are in my heart and I am thankful for the role you played as advisor or friend or combination of the two.

Last, but definitely not least, to my wonderful family, Dad, Mom, and Jonathon: thank you for not forcing me to grow up too fast. I've been able to wander, explore, question, and figure things out as I go, and none of that would be possible without an unbreakable support system. You taught me to keep striving for growth (and to remember there's always room for improvement), while still providing encouragement and unconditional love. And to my friends who became family, Lindsay Schaffner and Jereme Gaeta: thank you for everything you both are (On Wisconsin!).

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## CHAPTER 1: Introduction

Aquatic invasive species are a problem natural resource managers cannot escape. As globalization increases, geographical borders become insignificant, and our job as ecologists is to determine which species are worth the time, energy, and money required for effective management. Only 10-20% of introduced species become invasive in their non-native range (Williamson 1996); an invasive species is one that is introduced into a new ecosystem and ultimately causes ecological or economic harm (Lodge and Shrader-Frechette 2003), and a successful invasion is composed of 5 stages: arrival, establishment, growth and reproduction, the displacement of native species, and community domination (Lockwood et al. 2007). Unfortunately, research efforts typically focus on game or “charismatic” species (Thomsen et al. 2014), and less visible species, such as benthic macroinvertebrates, often go unnoticed until after they have become problematic (surpassing the third stage of invasion), despite being capable of causing huge disruptions in ecosystem processes. Invasive mollusks have gained attention in recent years due to the highly successful zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels, and other aquatic mollusks are following suite (Thomsen et al. 2014). Understanding the life-history characteristics of these lesser-known species allows better predictions of sites susceptible to invasion as well as better predictions of how an ecosystem might respond to an introduction (Thomsen et al. 2014).

One of these species with obvious ecological-knowledge gaps is the Chinese mystery snail (*Bellamya chinensis*). The Chinese mystery snail is native to Asia and was first reported in North America in the 1890s as a live food source imported to the San Francisco food markets (Wood 1892). Since then, it has spread to numerous lakes and

slow-moving rivers throughout the USA and southern portions of Canada (Olden et al. 2013). This prosobranch, freshwater species is large, reaching shell lengths up to 70 mm, lives 4-5 years (Jokinen 1982), has an annual fecundity of 30 juveniles/female (Stephen et al. 2013), and can reach high population densities (Chaine et al. 2012) that fluctuate with environmental conditions (Haak et al. 2013). Adult individuals have a wide temperature tolerance (Wong et al., unpublished data) and are resistant to traditional invasive species chemical management techniques (Haak et al. 2014). All Chinese mystery snails graze on algae and periphyton, but adults > 43 mm are also capable of suspension feeding (Olden et al. 2013). Adults reproduce sexually, and females give birth to live young, brooding an average of 25 juveniles in various stages of development at a time (Stephen et al. 2013).

The Chinese mystery snail has a thick shell and trap-door operculum, allowing isolation from external conditions when environmental conditions are sub-optimal (Solomon et al. 2010). When favorable conditions return, the individual will open and resume feeding. As a result, adults are resistant to desiccation and long periods out of water; larger individuals survived > 9 weeks out of water in laboratory experiments (Unstad et al. 2013). Adults bury themselves in mud and soft substrates (Jokinen 1982), and individuals overwinter in the substrate, migrating to deeper waters around October (Stanczykowska et al. 1972).

Females live a maximum of 5 years, whereas males live a maximum of 4 years (Jokinen 1982). Growth continues throughout an individual's lifespan, so females generally grow larger (Jokinen 1982). The ratio of shell width to height decreases as the shell increases in size; individuals become more elongated with age. Calcium is



necessary for shell growth, and it has been hypothesized that a minimum calcium concentration of 5 mg/L is necessary for the Chinese mystery snail's survival (Jokinen 1982).

Though it is apparent scientists have accumulated basic ecological knowledge about this species, little research exists on how the Chinese mystery snail affects its environment in its non-native range. When present alone, the Chinese mystery snail does not appear to harm native snail abundances (Solomon et al. 2010); however, when the Chinese mystery snail is jointly present with the invasive rusty crayfish (*Orconectes rusticus*), native snail biomasses decrease (Johnson et al. 2009). Mesocosm experiments also revealed that the Chinese mystery snail increases the N:P ratio in the water columns of invaded lakes (Johnson et al. 2009). Advancing our understanding of their influence on invaded ecosystems will offer insights on how to manage this and other mollusk species of concern (Byers et al. 2002).

Ultimately, our goal is to understand how the Chinese mystery snail may disrupt ecological resilience within its introduced range. A resilient ecosystem is one that is capable of absorbing disturbance without undergoing a regime shift to an alternate stable state (Peterson et al. 2008, Folk 2006). A stable state may be undesirable or desirable to humans, so we subjectively decide which state is desirable based on the ecosystem services we want to receive from a system (Scheffer 2009); we want this desirable state to be ecologically resilient so that ecosystem services remain constant over time. Thus, resource managers strive to maintain ecological resilience in the face of new species introductions. To understand how the Chinese mystery snail affects a system, we need to

have a thorough understanding of both the current state of an ecosystem and how a species is likely to affect the ecosystem based on its characteristics (Byers et al. 2002).

## Goals

This research has two main goals: 1) increase our understanding of the ecology of the non-native Chinese mystery snail, and 2) increase our understanding of where the Chinese mystery snail might establish in its introduced range and how this species might influence biotic and abiotic ecosystem processes after introduction.

## Objectives

- 1.) Review existing knowledge of non-native and invasive gastropods in North America.
- 2.) Quantify the components of an energy budget (consumption, elimination, respiration, and production) for adult Chinese mystery snails at varying water temperatures through laboratory experimentation.
- 3.) Identify environmental factors most important to the Chinese mystery snail's survival and development to develop habitat requirements for this species.
- 4.) Couple ecological and social network models to assess how the Chinese mystery snail is likely to spread in Southeast Nebraska and how it will affect the resilience of flood-control reservoirs in this non-native range.

## Overview

This dissertation aims to further our understanding of how aquatic invasive species can affect ecological resilience, using the Chinese mystery snail as the primary

study species. I begin broadly and first review the current status of non-native and invasive gastropods in the USA and Canada (Chapter 2). This synthesis identifies knowledge gaps in our understanding of gastropod ecology and how they potentially alter aquatic ecosystems. Next, I narrow my focus to our primary study species, the Chinese mystery snail. I investigate how the Chinese mystery snail allocates energy and how this affects population dynamics of the species (Chapter 3). Then I identify environmental characteristics necessary for the Chinese mystery snail's survival and establishment and develop an initial habitat suitability model (Chapter 4). In the final research chapter, I use both an existing social network model of boater movement and newly developed, lake-specific ecological network models to simulate the movement of the Chinese mystery snail over time and to assess its effects on ecological resilience within a regional watershed in Southeast Nebraska (Chapter 5). Finally, I conclude with implications for local aquatic invasive species management efforts as well as broader implications for future invasive species management and research (Chapter 6).

## Background information

### *Bioenergetics*

Bioenergetics is the study of the flow and transformation of energy in and between living organisms and between a living organism and its environment (Jobling 1994). To date, no one has investigated bioenergetics or developed an energy budget for the Chinese mystery snail. The main principle of bioenergetics is to identify how much of the energy an organism consumes is metabolizable energy, meaning it is absorbed and can be allocated to respiration and production (Jobling 1994). Quantifying energy content

of inputs and outputs of individuals allows us to then form energy budgets applicable to a population, and this helps us determine how population density may change over time (Kitchell et al. 1977). The basic bioenergetics equation is

$$C - E = P + R,$$

where C = consumption, E = egestion (waste production), P = production (both somatic tissue growth and reproduction), and R = respiration. Consumption refers to all materials ingested by an organism. Egestion refers to the production of fecal material, which is material that has been ingested but eliminated as waste because energy was not extracted from it. Urine output is assumed to exist but is often not measured in aquatic organisms due to the extreme difficulty involved in collecting and measuring it. As a result, the energy content of fecal material is subtracted from the total energy consumed to calculate metabolizable food energy, also referred to as assimilated energy (Lucas 1996).

Assimilated energy is that which is allocated between catabolism (metabolism, or in our case, respiration) and anabolism (personal growth and reproduction).

Catabolism refers to an organism breaking down complex substances into simpler ones, releasing energy in the process (metabolism). It can be measured directly by quantifying the heat produced by an individual or indirectly by measuring respiration, or oxygen consumption (Lucas 1996). For the purpose of clarity, I will refer to catabolism as respiration and use  $R_i$  to depict the respective processes. Maintaining bodily functions requires energy and can be called the standard respiration rate. This is the oxygen consumed during a fasting state and at rest (no motor activity) and is depicted as  $R_s$ . The respiration rate after feeding is  $R_F$ , and the respiration rate after motor activity is  $R_A$ . The

energy cost of digestive processes is also called specific dynamic action (SDA) (Kitchell 1977, Jobling 1994). Typically,  $R_A$  is the maximum respiration rate and  $R_S$  is the minimum respiration rate expected; the difference between the two is called the scope for activity. Thus, respiration rates vary depending on the conditions of the organism and must be explicitly stated. The total respiration requirement is the sum of all components (Lucas 1996):  $R_{total} = R_S + (R_F - R_S) + (R_A - R_S)$ . Using the Chinese mystery snail as our study organism complicates the quantification of catabolism due to its capability of closing itself off from surrounding conditions. Thus, assuming only aerobic respiration and measuring oxygen consumption and then converting these values to energy values may result in a conservative estimate of the energy used during catabolic processes.

Anabolism, or production (P), is the process of taking simple substances and assembling them into more complex ones. Production includes the addition of new somatic tissues, commonly called growth, ( $P_G$ ), the replacement of cells used continuously that need to be replaced ( $P_E$ ), retained residual tissues such as shell growth and shed residual tissues such as mucus ( $P_S$ ), and the development of reproductive products ( $P_R$ ). Thus, total production is the sum of all components (Lucas 1996):  $P_{total} = P_G + P_E + P_S + P_R$ . Specifically, reproduction products are outputs that are eventually eliminated (Lucas 1996), and an individual makes tradeoffs when allocating energy to somatic growth and to reproductive outputs. The Chinese mystery snail has the added requirement of allocating energy to shell formation; the shell, as well as tissues, continues to grow through the entire lifespan of an individual.

All bioenergetics components other than respiration can be measured in biomass (g) or in units of energy (kJ) (Lucas 1996). Regardless of the units used, as long as they

are consistent, three efficiencies can be calculated from the results. Assimilation (A) efficiency is the proportion of consumed energy that is not excreted and is retained as metabolizable energy (A/C). Gross efficiency is the proportion of consumed energy that is allocated to production (P/C). Net efficiency is the proportion of assimilated energy that is allocated to production (P/A) (Lucas 1996).

A critical supporting principle of bioenergetics is the first law of thermodynamics, which states that energy can change forms but it cannot be created or destroyed; the amount of energy going into an organism (consumption, or inputs) will equal the amount of energy expended on respiration and metabolic processes, production, and waste elimination (outputs) (Jobling 1994). For example, if an organism consumes a surplus of energy, it will be capable of reproduction or somatic growth; however, if the organism expends more energy than it consumes, it will have to tap into stored energy reserves and will ultimately lose body mass. If this deficit exists over an extended period, an adult individual will not be capable of reproducing, and a juvenile will not be able to increase its body mass (Jobling 1994). The balance of these inputs and outputs, known as an energy budget, varies with an organism's place in the trophic web, and information on bioenergetics can help us categorize organisms into functional groups (Megrey et al. 2007). Energy budgets also vary due to reasons such as quality and quantity of food, ease of finding and consuming food, an individual's current life stage, and environment-specific stressors such as temperature or predator density (Jobling 1994).

### *Habitat suitability*

The U.S. Fish and Wildlife Service established habitat suitability models as the traditional habitat assessment approach in the early 1980's (USFWS 1981), and models have been completed for a variety of species (NOAA 1997). Original habitat suitability models relied on spatial data, mostly ignoring temporal data (Porzig et al. 2014), and only assessed the effects of individual environmental variables, rather than the cumulative effects of multiple variables (Ahmadi-Nedushan et al. 2006). Using this approach, variables are assessed one at a time and given a suitability value between 0 and 1. Values of 0 indicate conditions are unsuitable for a species' survival and values of 1 indicate conditions are optimal. Individual suitability values can then be multiplied together to calculate a composite suitability index for a pre-defined site (Beecher et al. 2002), but this approach assumes an organism selects a particular variable independently of all other variables. Hence, if a single variable receives a suitability value of 0, the entire site receives a composite score of 0, which may not reflect actual conditions. Original models used by the U.S. Fish and Wildlife Service now serve as research starting points rather than as conclusive models because new computing methods are available.

Currently, the most commonly used type of species distribution model uses species presence data based on the assumptions that all present species are identified at a given site, all absent species are truly absent from a given site, and no dispersal limitations exist (i.e., all suitable habitat is occupied by the species) (Cianfrani et al. 2010). Incorrect assumptions may result in unreliable predictions (Hirzel et al. 2001); predicting a false absence occurs when a model is over-fitted, and predicting a false presence occurs when a model is over-predicted (Guisan and Zimmermann 2000). Thus,

to accurately develop a habitat suitability model for a specific region, it is necessary to have reliable distribution (presence) data.

Identifying sites particularly amenable to supporting Chinese mystery snail populations allows managers to efficiently direct limited resources and increases the likelihood of successful prevention efforts. Shoreline development, distance to population centers, presence of boat landings, species composition, Secchi depth, conductivity, and calcium concentrations have been speculated as critical factors in determining habitat suitability (Solomon et al. 2010), but more research is needed to identify environmental thresholds for this species.

#### *Network analysis*

Ecological network analysis has previously been used to analyze the importance of various ecosystem interactions among species without over-simplifying components of the system (Fath et al. 2007; Zhang et al. 2014). This comprehensive approach is in contrast with conventional modeling techniques, including predator-prey and competition models. As the last research chapter in this dissertation, we take the approach of combining ecological network models with a social network model to analyze the potential spread of the Chinese mystery snail in a regional fishery in Southeast Nebraska. Ecological network models are developed using information compiled from the bioenergetics and habitat suitability research chapters, and we combine these approaches with a real-world case study allowing us to address how the Chinese mystery snail is likely to spread and how it will affect an ecosystem after this spread. This approach enables us to both assess the current ecological resilience of an ecosystem as well as test



new methodologies used to analyze how aquatic invasive species could disrupt ecological resilience, thus providing us with one concrete example of how the results of the first three research chapters can be applied to a real-world problem.

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## CHAPTER 2: Non-native and invasive freshwater snails of the USA and Canada

### Abstract

Many invasive freshwater snail species achieve high population densities following introduction, have the capability to disrupt ecosystem functions and services, and spread by similar means; however, there are gaps in information on their ecology and impacts. In this review, we synthesize available information to identify current information gaps, categorize shared characteristics among families and species of snails, catalog ecosystem effects of introduction, and compare functional roles of threatened or extinct native snails with those of successful invasive snails. Using both peer-reviewed literature and government reports, we identified 16 freshwater snail species listed as exotic to the USA and Canada and 3 species that are native transports within the USA and Canada. After compiling available information, it is clear more focus needs to be directed to regulating the aquarium, pet, and food trades if we want to prevent future invasions.

### Introduction

The number of species introduced into non-native ecosystems is rising, a result of increasing movements of goods and people around the globe. Though not all introductions result in established populations, some non-indigenous species thrive in new environments and harm native species and the ecosystems they inhabit. These invasive species (Lodge *et al.*, 2006)

include both terrestrial and aquatic organisms, though a species classified as invasive in one ecosystem may not have detrimental effects in all ecosystems (Lodge *et al.*, 2006). Many species introductions do not have obvious immediate negative consequences and go unnoticed until after a population is established and successfully reproducing past the point of easy eradication. In the USA alone, there are approximately 50,000 non-indigenous species, 4,300 of which are classified as invasive (Pimentel, Zuniga & Morrison, 2005).

North America is home to the greatest diversity of freshwater mollusks worldwide, and native gastropods often dominate the benthic invertebrate community in streams as the main consumers of primary production, with effects that cascade up through the food web (Johnson *et al.*, 2013). Habitat loss and degradation have jeopardized many native gastropods; of the 703 species native to North America, 74% of them are currently classified as imperiled or extinct (Johnson *et al.*, 2013). Simultaneously, a number of invasive gastropod species are successfully establishing and thriving. Johnson *et al.* (2013) provided a comprehensive review of the conservation status of native gastropods of North America, laying the groundwork for a paper addressing invasive gastropods in the same geographical region.

Many invasive freshwater snail species achieve high population densities following introduction (Lach *et al.*, 2000; Alonso & Castro-Diez, 2008; Chaine *et al.*, 2012), have the capability to disrupt ecosystem processes and services (Carlsson, Bronmark & Hansson, 2004), and spread by similar means (Vander Zanden & Olden, 2008); however, there are gaps in information on their ecology and impacts. Few, if any, studies have compared characteristics

across families or species (Strong *et al.*, 2008). Before we can begin to anticipate potential distributions or effects of invasive snail species, knowledge of their similarities and differences is crucial. Here, we synthesize available information to identify current information gaps, categorize shared characteristics among families and species of snails, catalog ecosystem effects of introduction, and compare functional roles of threatened or extinct native snails with those of successful invasive snails. Knowledge gained from this type of synthesis may be applicable to other freshwater taxonomic groups as well.

## Methods

The geographic range of this review includes snails in the North American countries of the USA and Canada. Using both peer-reviewed literature and government reports, we identified 16 freshwater snail species listed as exotic to the USA and Canada and 3 species that are native transports (native to portions of North America but have expanded their range to include additional regions) within the USA and Canada (Table 1). There are many contradictions and uncertainties in freshwater snail taxonomy that are continuously evolving (Walther *et al.*, 2006), so we include analysis at both the family and species levels.

## Family and species descriptions

The following section provides brief descriptions of each family and the species included in the current review (Table 1). Families are listed alphabetically.

### Ampullariidae

The apple snails are freshwater, prosobranch snails found worldwide in tropical and subtropical regions. They are dextral snails, moderate to large in size (30-80 mm), and are globose with a depressed spire (Burch, 1982). Individuals have a single monopectinate gill and a modified mantle cavity that allows it to act as a lung with a pneumostome (a breathing pore); as a result, they can survive long periods out of water (Burch, 1982). Their operculum is corneous, and sexes are separate. Some species deposit calcareous eggs and others form gelatinous egg masses (Rawlings *et al.*, 2007). Apple snail diets include bryozoans, filamentous algae, periphyton, snail eggs, macrophytes, insect larvae, and animal carcasses (Horgan, Stuart & Kudavidanage, 2014). Only one species in the family Ampullariidae is native to North America, the Florida apple snail (*Pomacea paludosa*), and it is distributed across Florida, Georgia, and Alabama (Rawlings *et al.*, 2007).

Apple snails are very common in the pet and aquarium trades, and, generally speaking, are identified as problematic worldwide due to their destruction of agricultural crops (particularly rice) (Cowie, 2002), native plants (particularly bryozoans) (Wood *et al.*, 2005), water quality, and ultimately, wetland functioning (Carlsson, Bronmark & Hansson, 2004). They reduce native



snail densities by disrupting reproduction cycles and increase primary production by altering nutrient cycles. They can carry and transmit angiostrongyliasis and other human and animal diseases (Horgan *et al.*, 2014). Though apple snails are not invasive throughout their entire distributions, the worst effects of invasion are centered in developing countries and regions that are heavily affected by disruptions in human food sources (Horgan *et al.*, 2014).

### *Pomacea diffusa*

The spike-topped apple snail was first reported in Florida in 1966 (Clench, 1966), was introduced as part of the aquarium trade, and is currently established in Florida and Hawaii (Horgan *et al.*, 2014). This species is currently considered a minor threat in the USA and is still legally transported across state lines (Rawlings *et al.*, 2007; Morrison & Hay, 2011). The diet of *P. diffusa* is varied; they may feed on periphyton (Howells, 2002; Morrison & Hay, 2010), on macrophytes, animal carcasses, worms, and eggs of native snails (Aditya & Raut, 2001), or on algae (Burlakova *et al.*, 2009). Egg masses are white upon initial laying, but develop into a tan or salmon color as they mature (Rawlings *et al.*, 2007).

### *Pomacea haustorium*

The titan apple snail is native to Bolivia, Brazil, and Peru and was originally synonymous with *Pomacea canaliculata*; however, it has since been separated into its own species (Rawlings *et al.*, 2007). Introduced into Florida as part of the pet trade (Horgan *et al.*, 2014), *P. haustorium* has yet to establish outside of the state. *Pomacea haustorium* is of little concern as a non-native

species because it has not successfully established outside of its initial sighting, though caution is still recommended as other non-native species have had limited distributions for years before becoming invasive (Rawlings *et al.*, 2007). *Pomacea haustorium* eats filamentous algae, animal detritus, and snail eggs (Horgan *et al.*, 2014), and mature individuals lay bright green egg masses on emergent vegetation above the water line, with individual eggs approximately 3-5 mm in diameter (Rawlings *et al.*, 2007).

#### *Pomacea insularum*

The island apple snail is native to Argentina, Brazil, and Bolivia, though it is likely found in much of South America (Rawlings *et al.*, 2007). Original reasons for introduction included food, commerce (Horgan *et al.*, 2014), and as a form of biological control for non-native plants in Florida; however, due to the species' voracious consumption of native macrophytes (Byers *et al.*, 2013), it is not suitable for future biological control measures (Baker, Zimmanck & Baker, 2010). The current distribution of *P. insularum* in the USA is Texas, Florida, Alabama, Georgia, Louisiana, and South Carolina (Byers *et al.*, 2013, Horgan *et al.*, 2014), and it colonizes all types of aquatic habitats (Byers *et al.*, 2013; Horgan *et al.*, 2014). The species eats water milfoil (Boland *et al.*, 2008), snail eggs, and periphyton (Horgan *et al.*, 2014), reaches 65 mm in total shell length (Byers *et al.*, 2013), and lives up to 4 years (Cowie, 2006). Individuals mature at 1 year (Boland *et al.*, 2008), and lay large pink egg masses above the water line, typically with 1000-2000 eggs per clutch (Byers *et al.*, 2013; Kyle *et al.*, 2013). This species is cold-tolerant

but vulnerable to frosts (Rawlings *et al.*, 2007) and has survived 70-308 days out of water in laboratory experiments (Byers *et al.*, 2013).

*Pomacea canaliculata*

The channeled apple snail is originally from Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Cowie & Thiengo, 2003) and was most likely introduced to North America in the food, commerce, and pet trades (Horgan *et al.*, 2014). Currently, it is found in Arizona, California, Florida, and Hawaii and has been reported in ponds, rivers, aquatic crop fields, streams, and wetlands (Horgan *et al.*, 2014). In laboratory conditions, snails live for 4 years and sexual maturity is reached at approximately 25 mm total shell length, with fecundity positively correlated with the size of the snail (Estebeñet & Cazzaniga, 1992).

*Marisa cornuarietis*

The first record of the giant rams-horn snail in the USA was in 1957 in southern Florida, though its native range is northern South America (Rawlings *et al.*, 2007). Currently, there are established North American populations in Florida and Texas, and they were most likely introduced as a biological control of schistosomiasis hosts and as part of the pet trade (Seaman & Porterfield, 1964; Horgan *et al.*, 2014). They are avid feeders of macrophytes (rather than epiphytes, the common food source of native snails in North America), and individuals are capable of cutting both leaves and stems, effectively clear-cutting them over time (Horne *et al.*, 1992). The species has been reported in lakes, farm ponds, and reservoirs (Horgan, Arsuffi, &

Neck, 2014). Eggs of *M. cornuarietis* are unique for this family in that they are gelatinous throughout development and are laid in the water (Rawlings *et al.*, 2007).

## Bithyniidae

This family of freshwater snails is endemic to Asia, Africa, the Philippines, and Australia. Species in this family are moderate-sized dextral snails with a calcareous operculum. Originally categorized in the family Hydrobiidae, it was decided that these species required a separate family of their own (Burch, 1982), and species in Bithyniidae are capable of both suspension feeding and grazing (Burch, 1982; Brendelberger & Jurgens, 1993).

### *Bithynia tentaculata*

The only North American non-native species in this family is *Bithynia tentaculata*, the faucet snail, a species that often hosts parasites that cause mortalities in waterfowl populations. Individuals grow to 12-15 mm in total shell length, live an average of 18 months (Jokinen, 1982), and have a yellow-green shell that is covered by a thin periostracum (Burch, 1982). In North America, *B. tentaculata* is found in the Great Lakes and St. Lawrence River (Ricciardi, 2001), and it is speculated that Virginia is the southern limit to its range (Pilsbry, 1932). It was introduced to the Great Lakes in shipping packaging, in ballast water, and through aquarium releases (Mills *et al.*, 1993). The species lives in a variety of permanent water bodies and substrate types (Jokinen, 1992). Individuals lay up to 75 eggs per mass and eggs incubate for 3 weeks to 3 months, depending on water temperature (Jokinen, 1992). Sexual maturity is reached

during the first year of life, at approximately 8 mm in length and at water temperatures  $> 20^{\circ}\text{C}$  (Jokinen, 1992). Other than water temperature, the only known environmental limitation is a requirement for high water hardness (Jokinen, 1992). Another name sometimes used for this species is *Bulinus tentaculatus*.

### Hydrobiidae

This family is prevalent in temperate, tropical, and subtropical regions worldwide and contains more than 100 genera (Taylor & Sohl, 1962; Burch, 1982) with a complicated taxonomic history (Kabat & Hershler, 1993). All members are deposit feeders that ingest substrate and assimilate the attached microorganisms (particularly diatoms) (Fenchel, 1975). Individuals are small ( $< 8$  mm), dextral, prosobranch snails with a corneous operculum and typically have a conical shell with few whorls (Burch, 1982; Kabat & Hershler, 1993). Sexes are separate and fertilization is internal (Kabat & Hershler, 1993). Females are usually oviparous but sometimes ovoviviparous and can brood young within the oviduct or produce veliger larvae, depending on the species (Kabat & Hershler, 1993). If oviparous, egg capsules are deposited one at a time on the substrate (Hershler, 1994). All species can tolerate wide ranges of water temperature, prolonged periods of desiccation, fresh and brackish waters, and waters with low dissolved oxygen concentrations (Fenchel, 1975). Despite having similar feeding styles, multiple Hydrobiidae species have been known to successfully coexist in the same habitat (Fenchel, 1975).

*Potamopyrgus antipodarum*

In North America, one species from this family is of particular concern, the New Zealand mud snail (*Potamopyrgus antipodarum*). Originally from New Zealand (Winterbourn, 1970), the species first appeared in North America in the Middle Snake River of Idaho, USA in 1987 and was thought to have escaped from a nearby fish farm after hitchhiking on fish stocked from overseas (Bowler, 1991). Current population densities in Idaho have been reported to be as high as 299,999 individuals/m<sup>2</sup> (Kerans *et al.*, 2005). The New Zealand mud snail is now also found in Lake Superior (Grigorovich *et al.*, 2003), Lake Ontario (Zaranko, Farara & Thompson, 1997), and Lake Erie (Levri, Kelly & Love, 2007); introduction to the Great Lakes was a result of international shipping and ballast water exchanges (Levri *et al.*, 2007), and population densities in the Great Lakes are considerably lower than in the Western USA, peaking at around 5,600 individuals/m<sup>2</sup> (Zaranko *et al.*, 1997).

The New Zealand mud snail lives on macrophytes, clay, sand, and mud (Heywood & Edwards, 1962) and may establish in oligotrophic or eutrophic lakes and streams (Dorgelo, 1987). In the Great Lakes, *P. antipodarum* lives in water depths ranging from 4 to 25 m (Zaranko *et al.*, 1997) and burrows in the substrate during dry or cold periods (Duft *et al.*, 2003). This species is a deposit feeder, consuming the microorganisms in the substrate, including green algae, diatoms, and periphyton (Haynes & Taylor, 1984).

In its native range of New Zealand, maximum shell lengths are 3 to 12 mm (Winterbourn, 1970), but in its non-native ranges shell lengths are 4 to 6 mm (Ponder, 1988; Zaranko *et al.*,

1997). One individual is capable of producing more than 200 juveniles per year, resulting in 1-6 new generations each year (Richards, 2002). Though both sexual and asexual reproduction is common in its native region (Jokela *et al.*, 1997), most, if not all, non-native populations are parthenogenetic, consisting only of females (Gangloff, 1998). Adults brood offspring in a pouch (Jokela *et al.*, 1997), and highest growth rates occur at a water temperature of 18°C (Dybdahl & Kane, 2005). Despite this optimal temperature, *P. antipodarum* populations survive water temperatures fluctuating between 0 and 28°C (Winterbourn, 1969; Hylleberg & Siegismund, 1987). *Potamopyrgus antipodarum* does possess a relatively thin operculum, yet the species seems able to withstand desiccation fairly well (Levri *et al.*, 2007). The New Zealand mud snail is resistant to predation (Zaranko *et al.*, 1997), alters carbon and nitrogen cycles (Hall, Tank, and Dybdahl, 2003), and is rheotactic (capable of moving upstream against a current) (Haynes, Taylor & Valery, 1985).

### Lithoglyphidae

The gravel snails are small- to medium-sized, globose snails. They were introduced to Europe from tributaries of the Black Sea but some species are native to North America. Sexes are separate, and females lay a single egg at a time. Individuals breathe through gills and have an operculum (Burch, 1982). They are most commonly found in slow-moving bodies of freshwater but require high concentrations of both oxygen and calcium to survive; they are not tolerant to degraded water quality conditions or high levels of pollution (Burch, 1982).

### *Gillia altilis*

The buffalo pebble snail is native to the Eastern USA (Jokinen, 1992; Mills *et al.*, 1993) and most likely migrated through the Erie Canal to reach the Great Lakes (Mills *et al.*, 1993). In addition to lakes, the species can withstand the high flow velocities and silty substrates of streams (Thompson, 1984), as well as sites with dense macrophytes and mud (Kart *et al.*, 2005). *Gillia altilis* primarily grazes periphyton and detritus (Thompson, 1984). Individual shell lengths range from 6 to 8 mm in total length (Jokinen, 1992). There are separate sexes, and females lay eggs on the leaves and stems of macrophytes or in stones and leaf litter (Thompson, 1984). There have not been any reports of serious negative impacts of introduction or spread.

### Lymnaeidae

This family of pond snails is found worldwide, though most of its species are found in North America (Burch, 1982). Snails have thin shells and are typically found in wetlands and marshlands and are dextral with high spires; none of the species have planispiral shells (Burch, 1982). Species within this family range in sizes from 2-40 mm (Soldanova *et al.*, 2010; Zimmermann *et al.*, 2014) and are very popular in the aquarium trade. Individuals breathe through lungs, lack a respiratory pseudobranch, and are hermaphroditic (Burch, 1982).

### *Radix auricularia*

The European ear snail, or big-ear radix, originates from Europe and Asia (Jokinen, 1992) but has been introduced to and established patchy populations in the Great Lakes and the



eastern and western coasts of the USA (Dundee, 1974; Mills *et al.*, 1993). The initial introduction vector was hitchhiking on plants imported to North American greenhouses, but there have been additional introductions by intentional aquarium dumping (Mills *et al.*, 1993). *Radix auricularia* typically prefers lentic waters such as lakes, ponds, mud-bottomed rivers, or water bodies with silty substrate; however, it can tolerate some high-flow environments (Clarke, 1981; Jokinen, 1992).

As scrapers, *Radix auricularia* ingest detritus, algae, and sand grains (Adam and Lewis, 1992). Individuals live one year and are hermaphroditic. Oogenesis occurs in early- to mid-summer and spermatogenesis occurs in late summer or early fall, so adults reproduce once, producing 30-80 oval eggs laid in clutches on stones or aquatic plants between July and September (Adam & Lewis, 1992; Jokinen, 1992). Eggs incubate between 2 and 3 weeks (Adam & Lewis, 1992) but will fail at temperatures  $> 36^{\circ}\text{C}$  (Salih *et al.*, 1981). Adults can grow to 30 mm in total shell length (Jokinen, 1992), though most only reach about 15 mm (Clarke, 1981), and they are larger than many native freshwater snails (Mills *et al.*, 1993). Their preferred water temperature is  $19^{\circ}\text{C}$  (Rosetti, Rosetti & Cabanac, 1989). The species is also called *Lymnaea auricularia*.

## Physidae

Members of the family Physidae have thin shells, lack an operculum, and are hermaphroditic. They tend to be small to moderate in size with high-spined shells, breathe air with a modified lung containing a pneumostome, and are very tolerant to a range of water quality

conditions. As a result, species in this family are highly adaptable to a variety of environmental conditions and are the most abundant freshwater gastropods in North America (Burch, 1982). Most species in this family are endemic to North America; only a few species occur in Eurasia and Africa (Burch, 1982). There are over 40 species of physids currently recognized in the USA (Dillon *et al.*, 2002).

### *Physa acuta*

*Physa acuta* is most likely native to North America but it is now commonly found worldwide (Dillon *et al.*, 2002). It dispersed through aquarium releases and by the intentional introduction of aquatic macrophytes (Van Leeuwen *et al.*, 2013), and it reaches maximum densities in lentic waters, especially those that are disturbed and eutrophic (Dillon *et al.*, 2002).

*Physa acuta* feed on dead plant and animal matter, epiphytic vegetation, and macrophytes (Dillon *et al.*, 2002). Maximum shell length is only about 17 mm, but they have high fecundity, producing between 20-400 eggs per week; eggs incubate for approximately 20 days. In laboratory conditions, sexual maturity is reached within 6-8 weeks, though in wild populations, it has been reported to take as long as 17 to 18 months (Wethington & Dillon, 1993). Sexual reproduction is preferred, but the species is capable of self-fertilization (Facon, Ravigne & Goudet, 2006). Mature adults are capable of storing allosperm for long periods of time when necessary but may also produce up to 2 generations per year (Wethington & Dillon, 1991, 1997).

*Physa acuta* reportedly spread through water currents (Van de Meutter, De Meester & Stoks, 2007), attached to plants that are transported between lakes by recreational boaters

(Albrecht *et al.*, 2009), and by water birds (McAtee, 1914; Roscoe, 1955). The mucus produced by both juveniles and adults allows them to easily attach to macrophytes or other substrates (Van Leeuwen *et al.*, 2013). *Physa acuta* is preyed on by fishes, crayfishes, and wildlife (Dillon *et al.*, 2002, Van Leeuwen *et al.*, 2013). The species is also called *Physella acuta* and *Physella heterostropha*.

## Planorbidae

Planorbidae, the ram's horn snails, are found in freshwater habitats worldwide and individual species grow to variable shell lengths. They are a dominantly freshwater family and are planispiral with discoidal spires, though some species are more globose with raised spires (Burch, 1982). Some species in this family have hemoglobin, giving them a red hue. Planorbids breathe air and have a mantle cavity that is modified into a lung with a pneumostome (Burch, 1982). They do not have an operculum, and they are hermaphroditic.

### *Biomphalaria glabrata*

*Biomphalaria glabrata*, the blood fluke planorb, is native to the Caribbean and South America (Pointier, David & Jarne, 2005) but is now found in Florida (Burch & Tottenham, 1980) and in fish hatchery ponds in Idaho (Bowler & Frest, 1992), USA. The aquarium plant trade is most likely responsible for dispersal (Pointier *et al.*, 2005), though spread may also have occurred through man-made infrastructure such as canals, irrigation networks, and dams (Pointier *et al.*, 2005). *Biomphalaria glabrata* eat decaying macrophyte tissue, live macrophytes,

epiphytes, epiphytic algae, neuston on surface films, and fecal strings (Thomas, Nwanko & Sterry, 1985). Individuals live for 2 years and mature at a shell length of 7-11 mm, which is typically reached around 10 weeks of age (Pimentel, 1957). Eggs are laid on hard surfaces and incubate for 6-10 days at a water temperature of 25°C (Pimentel, 1957).

*Biomphalaria glabrata* tolerate water temperature  $\leq 35^{\circ}\text{C}$  and have reportedly recovered from natural disasters quickly (Pimentel, 1957). This species is also capable of regenerating worn-out mandibles (Thomas *et al.*, 1985). When present with the invasive *Marisa cornuarietis*, *B. glabrata* densities typically decrease due to competition between the two invasive species, and *M. cornuarietis* has been intentionally introduced because of this (Horgan *et al.*, 2014). The species may also be referred to as *Planorbis glabratus*, *Australorbis glabratus*, or *Taphius glabraus*.

#### Pleuroceridae

Members of the Pleuroceridae family are gill-breathing snails that possess an operculum (Burch, 1982). They are native to North America and Asia, but their greatest diversity is in the Southeastern USA (Minton & Lydeard, 2003); however, they are also one of the most imperiled groups of native gastropods in North America (Johnson *et al.*, 2013). Shell lengths span from 1 to 5 cm and morphology varies by species (Burch, 1982; Johnson *et al.*, 2013). Individuals mature within the first year and live anywhere from 2 to 6 years, also depending on species (Brown, Lang & Perez, 2008). Sexes are separate, and reproduction takes place when females

attach egg capsules to substrates where they can then be fertilized by males (Whelan, Johnson & Harris, 2012).

### *Elimia virginica*

Native to North America, the Virginia river snail is not exotic to the USA; rather, it is a native transport. Originally from the Eastern USA (Smith, 1980; Pennak, 1989), it has since been introduced to the Great Lakes watershed (Mills *et al.*, 1993). The development of the Erie Canal allowed individuals to move from the Atlantic drainage to the Lake Ontario drainage (Mills *et al.*, 1993). *Elimia virginica* prefer large rivers, small streams, and northern lakes with hard, rocky substrates (Harman, 1972; Jokinen, 1992) and is an efficient grazer of epilithic periphyton (Harman, 2000).

Average longevity of *Elimia virginica* is 5 years, with individuals reaching a maximum shell length of 27-33 mm (Smith, 1980). Sexual maturity occurs between 1 (Smith, 1980) and 2 (Dazo, 1965) years, and eggs are deposited on hard substrates from spring to mid-summer in masses of 2-15 (Smith, 1980; Jokinen, 1992). In contrast to most invasive species, *E. virginica* undergoes slow population growth (Hamilton, 1980). Adults tolerate water temperatures as high as 27.5°C, so Virginia is probably the southern limit of this species' range (Smith, 1980). Hybridization with *Elimia livescens* has also been reported (Bianchi, Davis & Strayer, 1994).

### Thiaridae

Thiaridae is a tropical family of freshwater snails that are typically large with high spires. Species in this family were originally classified in the Melaniidae family, but eventually they were separated because of differing biological characteristics (Burch, 1982). Individuals have an operculum with a central nucleus and are parthenogenetic (only females), brooding their young in a pouch. A distinguishing morphological characteristic is the presence of fleshy papillae on the mantle edge (Burch, 1982). Species from this family are commonly found in the aquarium and pet trades.

#### *Tarebia granifera*

*Tarebia granifera*, the quilted melania, is native to India, the Philippines, Hawaii, and Japan (Abbott, 1952); however, it has been introduced to most of the USA (Lachner, Robins & Courtenay, 1970) with established populations in Florida (Chanotis *et al.*, 1980c) and Texas (Murray, 1964). *Tarebia granifera* prefer small pebble substrates in calm waters with depths < 0.5 m (Abbott, 1952, Chanotis *et al.*, 1980a) and their diet is dominated by small particulate organic matter (Oglesby, 1977) and epiphytic algae (Chanotis *et al.*, 1980a). Individuals typically live at least 1 year (Appleton & Nadasan, 2002), averaging 25 mm in total shell length (Abbott, 1952).

*Tarebia granifera* is usually parthenogenetic (Chanotis *et al.*, 1980b); females brood young in a pouch and have between 1 and 30 juveniles developing at any given time (Appleton & Nadasan, 2002). Juveniles are released at shell lengths between 2.5 and 6 mm (Chanotis *et al.*, 1980a). Sexual maturity occurs around 122 days between 6 and 12.5 mm in length (Chanotis

*et al.*, 1980a; Abbott, 1952). This species' lower lethal temperature limit is 7°C and its upper lethal temperature limit is 40°C (Chaniotis *et al.*, 1980b); however, *T. granifera* is rarely found in water > 18°C (Abbott, 1952). It is tolerant of water pollution but not high salinities (Chaniotis *et al.*, 1980a).

In Florida, *Tarebia granifera* was introduced by an aquatic plant dealer who used infested tubs during plant collections (Abbott, 1952); other introductions were likely due to the pet and aquarium trades (Oglesby, 1977). In Africa, individuals survived desiccation for 1 week (Appleton & Nadasan, 2002). The species may also be referred to as *Thiara granifera*, *Melania granifera*, or *Tarebia lateritia*.

#### *Melanoides tuberculatus*

*Melanoides tuberculatus*, the red-rimmed melania, is native to Northern and Eastern Africa, the Middle East, and Southern Asia but is now found throughout the USA (Rader, Belk & Keleher, 2003). During daylight hours, *Melanoides tuberculatus* burrows into the substrate to stay cool (Subda Rao & Mitra, 1982). When exposed at night, individuals feed on algae (mainly diatoms) and plant and animal detritus (Subda Rao & Mitra, 1982; Rader *et al.*, 2003).

In its native range, *M. tuberculatus* lives 2-3.5 years (Berry & Kadri, 1974) and grows to a maximum shell length of 20-40 mm (Brown, 1991). In the USA, extremely thick shells make individuals resistant to predation (Brown, 1991), and maximum shell lengths of 80 mm have been recorded (Murray, 1975). *Melanoides tuberculatus* is parthenogenetic and iteroparous; it is

unknown if invasive populations are capable of sexual reproduction (Rader *et al.*, 2003). Sexual maturity begins at shell lengths between 10-12 mm and individuals may reproduce during their first summer (Berry & Kadri, 1974, Rader *et al.*, 2003). One to 90 eggs incubate for 300-350 days (Rader *et al.*, 2003), and young are released late in the year (Pointier *et al.*, 1991). Thermal tolerances range from 18 to 31°C (Murray, 1971; Neck, 1985), and *M. tuberculatus* survives acute desiccation, though mortality increases rapidly after 18 days (Dudgeon, 1982). This species is also called *Melanoides tuberculata* or *Nerita tuberculata*.

#### Valvatidae

Species from this family are found in the northern hemisphere and are rare, typically residing in permanent standing and flowing fresh waters (Burch, 1982). Only 20 species have been identified (Burch, 1982). Snails are small and dextral with a discoidal spire and have a single bipectinate gill and a thin, circular, corneous operculum. They are hermaphroditic and deposit eggs to develop on substrate (Burch, 1982).

#### *Valvata piscinalis*

*Valvata piscinalis*, the European stream valvata (also called European valve snail), is native to Europe, Western Siberia, and Central Asia but has been introduced to the Great Lakes and St. Lawrence River in North America (Grigorovich *et al.*, 2005). Introduction to Lake Ontario occurred when *Valvata piscinalis* hitchhiked in shipments of straw and marsh grasses from Europe (Mills *et al.*, 1993); since the initial introduction, dispersal has been both natural



and human-mediated (Grigorovich *et al.*, 2005). As generalists, *V. piscinalis* is found in lentic and lotic water bodies, in deep and shallow water, with mud, silt, or sand substrate, and with or without macrophytes (Fretter & Graham, 1978; Van den Berg *et al.*, 1997, Grigorovich *et al.*, 2005). *Valvata piscinalis* both grazes on epiphytic algae and detritus and filter-feeds in eutrophic environments (Grigorovich *et al.*, 2005). Additionally, *V. piscinalis* possesses chemosensory perception that allows them to detect predators and close the operculum when threatened (Kelly & Cory, 1987).

In its native range, *V. piscinalis* grows to a maximum shell length of 7 mm (Fretter & Graham, 1978), but in the species' invasive range, a maximum shell length of 5 mm has been reported (Grigorovich *et al.*, 2005). The species is hermaphroditic (Fretter & Graham, 1978), and sexual maturity is reached after approximately 1 year, when mature individuals lay up to 150 eggs on vegetation and then die between the ages of 13 and 21 months (Grigorovich *et al.*, 2005). Eggs incubate for 15-30 days (Fretter & Graham, 1978).

## Viviparidae

The Viviparidae family is composed of moderate- to large-sized dextral snails with a chitinous operculum. Members of this family are found worldwide and are distributed throughout the USA and Canada in North America (Burch, 1982); however, most are found in the northern hemisphere, in both temperate and tropical regions. Individuals have a single gill, and most are omnivorous or detritivorous, though some species are capable of filter feeding.

They have separate sexes, and females are ovoviviparous, carrying developing juveniles in the oviduct and giving birth to live young (Burch, 1982).

### *Viviparus viviparus*

*Viviparus viviparus*, the river snail, is native to Northern Europe (Kerney, 1999) but has established populations on the East Coast of the USA after being imported by the aquarium trade (Van Damme *et al.*, 2012). *Viviparus viviparus* prefers large, slow-moving, permanent, oligotrophic or mesotrophic bodies of water and usually resides in muddy substrates; this species is not tolerant to pollution or eutrophication (Van Damme *et al.*, 2012). *Viviparus viviparus* is a bottom-dwelling suspension feeder that lives up to 10 years (Van Damme *et al.*, 2012), reaching a maximum shell length of 6-29 mm (Yanygina, 2012).

### *Viviparus georgianus*

*Viviparus georgianus*, the banded mystery snail, is native to the Eastern and Gulf Coast regions of the USA (Jokinen, 1992). It is a native transport that is now found throughout the Northern Midwest (USA) and Great Lakes regions (Clench, 1962). This species prefers lakes and slow-moving rivers (Lee *et al.*, 2002) with silt, mud, or sand substrates, and either hard or soft water (Duch, 1976; Jokinen, 1992). *Viviparus georgianus* grazes on diatom clusters found in the silt and mud and is capable of filter feeding (Duch, 1976).

Sexes are separate, and breeding takes place in macrophyte beds found in shallow waters during spring and fall (Jokinen, 1992). Females brood eggs for 9-10 months (Jokinen *et al.*,

1982; Rivest & Vanderpool, 1986) and produce an average of 11 juveniles per breeding season (Jokinen, 1992). They are also capable of brooding more than one batch of young at a time, with batch size being positively correlated with body size (Vail, 1977). Adults reach a maximum total shell length of 45 mm (Jokinen, 1992). *Viviparus georgianus* was introduced to the Hudson River by a conchologist who released approximately 200 individuals that dispersed following this introduction event (Jokinen, 1992; Mills *et al.*, 1993).

### *Bellamya chinensis*

*Bellamya chinensis*, the Chinese mystery snail, is native to Asia and Japan (Pace, 1973; Jokinen, 1982; Solomon *et al.*, 2010). First documented in North America in the 1890's, it was imported as a live food source to the San Francisco food markets (Wood, 1892). Since then, it has spread to at least 34 states in the USA as well as southern portions of Canada (Havel, 2011), though populations are more abundant in the southern portions of the invaded range (Solomon *et al.*, 2010). Historically, preferred habitat for *B. chinensis* is muddy, soft substrates appropriate for burrowing (Jokinen, 1982), but recent reports document populations living on artificial rip-rap substrate as well as on submerged vegetation (Chaine *et al.*, 2012). All life stages of *B. chinensis* graze periphyton (Johnson, Olden & Vander Zanden, 2009), but larger individuals are also capable of filter-feeding (Olden *et al.*, 2013). Adults live between 3 and 4 years and reach maximum shell lengths of 65-70 mm (Jokinen, 1982).

Sexes are separate and females give live birth, continuously releasing live young during May-October (Havel, 2011). Females have an average of 25 juveniles at different stages of

development at any given time (Stephen *et al.*, 2013). In temperature-controlled laboratory experiments, reproduction takes place year-round (personal observation). *Bellamya chinensis* has a wide temperature tolerance: adults survived acute heating to approximately 45°C, and they survived freezing water temperatures for > 24 hours (Wong *et al.*, unpublished data). Adult snails, which have a thick shell and operculum, were able to survive a 9-week desiccation experiment in the laboratory (Unstad *et al.*, 2013). This species may also be referred to as *Cipangopaludina chinensis malleata*, *Viviparus malleatus*, or *Viviparus chinensis malleatus*.

#### *Bellamya japonica*

*Bellamya japonica*, the Japanese mystery snail, is often confused with *Bellamya chinensis* but is its own species (Smith, 2000). The Japanese mystery snail is native to Asia and Japan (Jokinen, 1982), and is invasive in North America, similar to the Chinese mystery snail (Smith, 2000). The first documented report of Japanese mystery snails in North America was also in the San Francisco food markets in the 1890's (Wood, 1892). Populations mainly reside in lakes, and individuals graze periphyton (Jokinen, 1982). The shell shape is more elongated than that of *B. chinensis* (Soes *et al.*, 2011), reaching a maximum length of 50 mm (Wolfert & Hiltunen, 1968). For both *Bellamya* species, it is unclear if further dispersion is due to natural causes, human movement (mainly recreation), or because of merit releases (intentional releases meant to establish a human food-source population) (Vidthayanon, 2005). This species may also be referred to as *Cipangopaludina japonica/japonicus*, *Cipangopaludina chinensis japonica/japonicus*, *Viviparus japonica/japonicus*, or *Viviparus chinensis japonica*.

## **Characteristics and diversity**

### **Native and invasive ranges**

No central database exists for tracking global species movements, either native or invasive. Lack of consistent distribution and occurrence records as well as taxonomic ambiguity make it difficult to accurately define species locations. The 16 species listed as exotic to North America have native ranges from all over the world (Table 1). Six of the species (37.5%) originated in South or Central America, three (18.75%) originated from Europe, two (12.5%) originated from Eurasia, two (12.5%) originated from Asia, one (6.25%) originated in New Zealand, one (6.25%) originated in the South Pacific, and one (6.25%) originated from Eastern and Northern Africa and the Middle East. Current invasive ranges span across the USA and Southern Canada, though many of the species reported in Canada are limited to the Great Lakes, bordered by the two countries. Three species classified as native transports all originated on the Eastern Coast of the USA and have expanded their ranges to include the Great Lakes and surrounding region.

### **Dispersal mechanisms**

Generally speaking, aquatic invasive species dispersal is primarily attributed to human activity and is passive from the perspective of the organism (Cowie & Robinson, 2003). Primary introductions are initial introductions of the species to a new location. Once a population has established, subsets of the population may disperse to additional sites – a movement known as

secondary invasion (Vander Zanden & Olden, 2008). The 6 dominant dispersal mechanisms for aquatic invasive species are the aquarium trade (Padilla & Williams, 2004), aquatic plant trade (Mills *et al.*, 1993), food trade (Lach *et al.*, 2000), international shipping and ballast water dumping (Henningsen *et al.*, 2010), human recreational activities (Grigorovich *et al.*, 2005), and transport by other wildlife (De Kock & Wolmarans, 2008); these mechanisms can be vectors of both primary and secondary invasions.

Spread via the aquarium trade involves supplying organisms for use by both scientific researchers and hobbyists (Dillon *et al.*, 2002). When private owners tire of their aquariums, they may dump the contents into the nearest water body (Mills *et al.*, 1994); these trends were documented by enthusiast magazines such as *The Aquarium* and *Aquariana* as early as the 1990's (Mills *et al.*, 1994; Olden *et al.*, 2009) and, through continued practice, may lead to multiple introductions, increasing propagule pressure. The apple snail species *Pomacea diffusa*, *P. haustrum*, *P. canaliculata*, *P. insularum*, and *Marisa cornuarietis* were all, in part, introduced to North America as part of the aquarium pet trade (Horgan *et al.*, 2014). *Bithynia tentaculata* was introduced to the Great Lakes when hobbyists dumped personal aquariums into adjacent waterways (Mills *et al.*, 1993). *Radix auricularia* populations have continued to disperse after their initial introduction through aquarium dumping (Mills *et al.*, 1993), and *Physa acuta* have spread worldwide as part of the aquarium trade (Dillon *et al.*, 2002). *Tarebia granifera* is commonly sold for aquarium algae control (Oglesby, 1977), and *Melanoides tuberculatus* was imported to the USA as part of the aquarium industry in the 1930's (Murray, 1971). *Viviparus*

*viviparus*, *Bellamya chinensis*, and *Bellamya japonica* are all sold and spread in the aquarium trade as well (Karatayev *et al.*, 2009; Olden *et al.*, 2009; Haak *et al.*, 2013).

Aquatic plants sold for use in private aquariums can carry hitchhikers across borders (Mills *et al.*, 1994; Samadi *et al.*, 1999; Dillon *et al.*, 2002), and the movement of game fish for recreation, aquaculture, or food has similar ramifications. *Bithynia tentaculata* spread from Europe to North America as hitchhikers in packing materials made of straw and marsh grasses used to protect breakables (Mills *et al.*, 1993). *Radix auricularia* was introduced on plants imported to North American greenhouses (Mills *et al.*, 1993). A Florida aquatic plant dealer used contaminated collecting tubs in the field and subsequently introduced *Tarebia granifera* (Abbott, 1952).

In the food trade of aquatic snails, live products offer the freshest food (Wood, 1892), and individuals may escape during transport or upon arrival (Lach *et al.*, 2000). Aquaculture increases the risk of unintentional introductions; without careful control, snails may escape (Cowie & Robinson, 2003). *Pomacea canaliculata* and *Pomacea insularum* were both introduced as potential food sources (Kyle *et al.*, 2013, Horgan *et al.*, 2014), and *P. insularum* escaped captivity (Kyle *et al.*, 2013). *Bellamya chinensis* and *Bellamya japonica* were both initially introduced to North America in a live-food market in San Francisco and subsequently spread (Wood, 1892).

Shipping and ballast water dumping is a well-documented introduction vector of a number of invasive species into the Great Lakes (Henningsen *et al.*, 2010). Species that survive

transport in harsh ballast conditions have wide physiological tolerances to environmental conditions, increasing the likelihood of successful establishment upon arrival in a new environment (Padilla & Williams, 2004). *Bithynia tentaculata* arrived in the Great Lakes in contaminated shipping materials and through ballast water dumping (Mills *et al.*, 1993). *Potamopyrgus antipodarum* was also initially introduced into the Great Lakes through international shipping (Levri, Kelly & Love, 2007). *Elimia virginica* and *Gillia altilis*, both native transports, used the man-made Erie Canal to migrate into the Lake Ontario watershed (Mills *et al.*, 1994).

Human recreational activities and movement also play an important role in moving species. *Bellamya japonica* was released in the Great Lakes as a food source for channel catfish (a population sport fish) in Lake Erie (Mills *et al.*, 1993). *Valvata piscinalis* spreads through human-mediated dispersal (Grigorovich *et al.*, 2005), and *Viviparus georgianus* was introduced to the Hudson River by a conchologist who released 200 individuals (Jokinen, 1992; Mills *et al.*, 1993). In the Western USA, *Potamopyrgus antipodarum* was likely introduced as a hitchhiker on fish that were stocked from overseas (Bowler, 1991). Finally, transportation by other types of wildlife (e.g., attached to the surface of waterfowl or shore birds) is a form of secondary spread of invasive species but is not often reported as a form of initial introduction.



## Effects of invasion

### Native freshwater snails

Native snail populations are often disrupted by the arrival of non-native snails through indirect and direct competition for food and habitat. Many native snails have geographically restricted ranges, sometimes a single watershed or stream; thus, one introduction event could lead to extinction of one or more native species (Johnson *et al.*, 2013). The apple snail species *Pomacea diffusa* reduces native planorbid snail densities in its invaded range (Aditya & Raut, 2001), and *Pomacea canaliculata* consumes the eggs of native snails (and other invertebrates) (Rawlings *et al.*, 2007). *Pomacea insularum* threatens the native apple snail *Pomacea paludosa* in the USA (Rawlings *et al.*, 2007). *Bithynia tentaculata* co-exists with native snails when foraging as grazers, but they out-compete the same species when functioning as suspension-feeders, (Harman, 1968; Clarke, 1981; Brendelberger & Jurgens, 1993), especially in eutrophic water bodies (Clarke, 1979). *Bellamya chinensis* displaces native snails when present with other invasive species, such as the rusty crayfish (*Orconectes rusticus*) (Solomon *et al.*, 2010). *Potamopyrgus antipodarum* (Riley *et al.*, 2008), *Valvata piscinalis* (Grigorovich *et al.*, 2005), *Tarebia granifera* (Appleton & Nadasan, 2002), and *Bellamya japonica* (Smith, 2000) all out-compete native snail species for food and habitat in invaded areas. The large body size of *Melanoides tuberculatus* combined with reported population densities up to 6,500 individuals/m<sup>2</sup> (Rader *et al.*, 2003; Rabelo & Loureiro, 1995) allow populations to outcompete native hydrobiid

snails (Grigorovich *et al.*, 2005), and the large size of *Viviparus viviparus* helps it dominate the zoobenthos community (Yanygina, 2012).

#### Non-snail species

More commonly reported are the impacts invasive snails have on other (non-snail) species in invaded ecosystems. Being voracious herbivores, snails can establish large populations after invasion and dominate secondary production in benthic zones by out-competing other benthic macroinvertebrates (Kerans *et al.*, 2005; Hall *et al.*, 2006). The apple snails *Pomacea insularum*, *Pomacea cornuarietis*, and *Marisa cornuarietis* cause declines in abundance of other species relying on native vegetation (Cowie, 2002; Carlsson & Bronmark, 2006; Byers *et al.*, 2013), and *P. insularum* has induced changes in the adult snail kite diet, resulting in energetic deficiencies in juvenile birds (Cattau *et al.*, 2010). *Marisa cornuarietis* preys on eggs of the endangered fountain darter (Phillips *et al.*, 2010). If necessary, apple snails will also consume animal carcasses, worms, and eggs of other snails, resulting in direct competition with crayfish, shrimp, and fish (Rawlings *et al.*, 2007). The large population densities of *Potamopyrgus antipodarum* result in a high consumption rate of primary producers (Mills *et al.*, 1993) and reduce the colonization capability of other invertebrates (Ponder, 1988; Kerans *et al.*, 2005). Since *Viviparus georgianus* expanded its range, mallard ducks (*Anas platyrhynchos*) have adapted their diets to include *V. georgianus* in New York, USA; additionally, *V. georgianus* preys upon eggs of largemouth bass (*Micropterus salmoides*) (Eckblad & Shealy, 1972).

#### Vectors of disease: wildlife

Freshwater snails, in general, often serve as intermediate hosts to various trematode species (Gerard & Le Lannic, 2003; Lively, 1989); all trematode species use mollusks as intermediate hosts (Poulin, 2006). When a snail is infected, the trematode fluke reproduces inside it and releases free-swimming cercariae that leave the snail to find a new host to repeat the process. In the case of blood flukes (e.g., family Schistosomatidae), the next host is usually a vertebrate such as birds or humans (Poulin, 2006; Hechinger & Lafferty, 2005). For example, *Bithynia tentaculata* hosts *Schistosoma* species that are responsible for waterfowl mortalities in the Upper Mississippi River Basin, USA (Mills *et al.*, 1993; Henningsen *et al.*, 2010). In its native range, *Radix auricularia* preys on eggs of the parasitic nematode *Ascaris suum*, which then pass through its gut and distribute widely, in some cases causing ascariasis in pigs (Asitinskaya, 1975). In other parts of the world, Lymnaeidae species, including *R. auricularia*, host a Digenea trematode that ultimately causes fascioliasis in livestock (Srihakim & Pholpark, 1991; Remigio, 2002; Aladesanmi, 2007; Dung *et al.*, 2013).

*Valvata piscinalis* is a first intermediate host to *Echinoparyphium recurvatum* (McCarthy, 1990), an intestinal fluke of waterfowl and mammals (Sohn, 1998). *Melanoides tuberculatus* and *Tarebia granifera* are intermediate hosts to the exotic trematode *Philophthalmus gralli*, which infects waterfowl, and the gill trematode *Centrocestus formosanus*, which infects piscivorous birds and fish including the endangered fountain darter (*Etheostoma fonticola*) (Mitchell *et al.*, 2005; Karatayev *et al.*, 2009; Benson, 2012). *Bellamya japonica* may be a host to *Aspidogaster conchiocola*, a parasite that commonly infects freshwater clams (Michelson, 1970).

Identifying parasitic species that are transported with snails is critical; certain species of Planorbidae can shed trematodes for as many as 82 days after becoming infected (Goodchild & Fried, 1963). Interestingly, not all introduced snails transport their native parasite species with them; *Bellamya chinensis*, *Radix auricularia*, *Physa acuta*, *Pomacea canaliculata*, and *Potamopyrgus antipodarum* (Gerard *et al.*, 2003) have all been introduced and show no evidence of transporting their native parasites to their introduced environments (Mastitsky *et al.*, 2010). However, there is evidence that both *Bithynia tentaculata* and *Melanoides tuberculatus* introduced parasites that caused mass mortalities in their invaded range, despite having low impact in their native range (Mastitsky *et al.*, 2010).

#### Vectors of disease: humans

In addition to harming native biota, introduced snails may also carry parasites that infect humans (Madsen & Frandsen, 1989; Hollingsworth *et al.*, 2006). Many trematode species, such as *Schistosoma*, directly harm fish, waterfowl, and humans who rely on fish or waterfowl for food (Nwoke *et al.*, 2004). Trematodes, or flukes, exist in a number of forms, and humans can be infected by blood, liver, intestinal, lung, and pancreatic flukes (Nwoke *et al.*, 2004). Snails ingest trematode eggs when feeding and host the parasite until it becomes free-swimming. Free-swimming individuals then encyst into the flesh of freshwater fish (or humans). If humans ingest an infected fish or other animal, they become a definitive host and carrier and continue the cycle by releasing eggs in their urine and feces (World Health Organization (WHO), 2012). Parasites can also be ingested by drinking contaminated water or by eating food that came in contact with

an infected organism and has not been properly disinfected (WHO, 2012). These parasites cause a myriad of damage in humans; at least 56 million people worldwide suffer from food or waterborne trematode infections, mainly in Southeast Asia and South America (WHO, 2012).

Apple snails, including *Pomacea canaliculata* are intermediate hosts to nematodes, particularly from the genera *Parastrongylus* and *Angiostrongylus*, which infect humans causing eosinophilic meningoencephalitis and abdominal angiostrongyliasis (Rawlings *et al.*, 2007; Lv *et al.*, 2009b; Byers *et al.*, 2013). *Pomacea canaliculata* also hosts *Schistosoma* species harmful to humans (Lv *et al.*, 2009a; Hollingsworth *et al.*, 2006). *Biomphalaria glabrata* is the main host of *Schistosoma mansoni*, a trematode causing human intestinal schistosomiasis, in the species' native range, and it is capable of creating hybrids with other *Biomphalaria* species; the hybrids are also carriers of *S. mansoni* (Pointier *et al.*, 2005). *Elimia virginica* (Huffman & Fried, 1985), *Tarebia granifera* (Chaniotis *et al.*, 1980a), *Valvata piscinalis* (Grigorovich *et al.*, 2005), *Viviparus georgianus* (Wade, 1985), and *Melanooides tuberculatus* (Murray & Haines, 1969) also host various trematode species harmful to humans. More research needs to be done to assess if *Bellamya chinensis* and *Bellamya japonica* host parasites harmful to humans (or wildlife) (Michelson, 1970).

#### Co-existence of invasive species

In addition to native species, invasive species are likely to co-exist with one another in introduced environments. For example, common carp have been used as a biological control for *Pomacea canaliculata* in Japan; however, the fish ultimately added nutrients that helped the snail

grow even faster (Ichinose & Tochiavra, 2003). When *P. canaliculata* is present with *Pomacea insularum*, the combined herbivory can instigate a regime shift of the entire water body, often to a cyanobacteria-dominated regime (Byers *et al.*, 2013).

Sometimes species are intentionally introduced as biological controls for other invasive species. *Marisa cornuarietis* was introduced as a control for invasive weeds (Seamann & Porterfield, 1964), eventually dispersing and becoming invasive itself. Similarly, *Melanoides tuberculatus* (Pointier *et al.*, 1993) and *Tarebia granifera* (Gomez *et al.*, 1990) were introduced to control *Biomphalaria glabrata* populations (Pointier *et al.*, 1993; Dillon, 2000). It is believed that *Viviparus georgianus* is better adapted for fast-moving waters than *Bithynia tentaculata*, giving *V. georgianus* a competitive advantage when both species are present (Vincent, 1979). *Elimia virginica* is largely out-competed by *Bithynia tentaculata* in its invaded range (Mills *et al.*, 1993), though it is also adapted to withstand predation from invasive crayfish (Smith, 1980).

*Bithynia tentaculata* interacts with other invasive species often. The species is preyed upon by common carp (Ricciardi *et al.*, 2001), can be found living on milfoil (*Myriophyllum spicatum*) (Vincent *et al.*, 1981), and may have additive effects on the environment when found in tandem with *Valvata piscinalis* (Grigorovich *et al.*, 2005). It also has a mutualistic relationship with zebra mussels (*Dreissena polymorpha*). Zebra mussel shells provide ample grazing area and house a variety of microfauna (Ricciardi *et al.*, 1997), as well as refuge from predators (Stewart *et al.*, 1999); in turn, the snail provides nutrients and detritus for the zebra mussels (Ricciardi *et al.*, 1997). *Viviparus viviparus* is another species that co-exists with zebra mussels for the same

reasons listed above (Zaiko *et al.*, 2009). Zebra mussels are environmental engineers, and *V. viviparus* invasions are especially successful after the mussels are already established; the disturbed ecosystem aids their establishment (Zaiko *et al.*, 2009). In Wisconsin, USA, *Bellamya chinensis* causes declines in native snail populations when present with the invasive rusty crayfish (*Orconectes rusticus*) but co-exists with native snails when the rusty crayfish is absent (Johnson *et al.*, 2009). *Bellamya chinensis* also likely spreads with the human-mediated movement of aquatic plants (Havel, 2011).

#### Ecosystem services

Despite countless successful invasions, we know relatively little about the disruptions invasive freshwater snails cause to ecosystem services, partially because they are difficult to measure (Parker *et al.*, 1999; Strayer *et al.*, 2006; Simberloff, 2011). As the structure and functioning of an ecosystem changes, the ecosystem services provided by the system also changes. Ecosystem services are benefits that humans receive from the processes that take place in ecosystems (Costanza *et al.*, 1997; Hooper *et al.*, 2005). Apple snails pose a large threat to ecosystem services, specifically to food (Carlsson *et al.*, 2004, Rawlings *et al.*, 2007). In Southeast Asia, apple snails cause immense harm to wetlands and agricultural land, reducing biodiversity and disrupting rice and taro production (Rawlings *et al.*, 2007). The heavy grazing by *Pomacea canaliculata* results in a regime shift from a macrophyte-dominated system to a phytoplankton-based system (Pejchar & Mooney, 2009). Rawlings *et al.* (2007) warn about a similar fate if apple snails spread to the Southeast USA: crops may be harmed and food

production disrupted. Specifically of concern are *Pomacea insularum* and *P. canaliculata*, as damage to crops in the Philippines alone cost farmers an estimated US\$425-1,200 million in 1990 (Pejchar & Mooney, 2009).

When an introduced snail becomes invasive, it may dominate the secondary production in the invaded environment (Hall *et al.*, 2006). Once dominant, the invader may be highly productive and have no effect on native production, thus amplifying the ecosystem's total production, or it may be highly productive and eliminate native production, not changing the amount of total production by the ecosystem (Hall *et al.*, 2006). (It also might fall somewhere in between those two extremes.) The amount and type of secondary production in an ecosystem can have cascading effects through the rest of the food web (Carpenter *et al.*, 1985). For example, *Potamopyrgus antipodarum* achieves high population densities (>500,000 individuals/m<sup>2</sup> (Moore *et al.*, 2012)) in streams in the Western USA, and this dominance reduces native snail populations and alters the carbon cycle, directly affecting the distribution of carbon throughout the rest of the food web (Hall *et al.*, 2003, 2006).

*Bellamya chinensis* alters nutrient cycling in invaded water bodies, excreting less phosphorus than native snails (Johnson *et al.*, 2009). *Tarebia granifera* increases nitrogen concentrations when in habitats with direct sunlight (Moslemi *et al.*, 2012). *Elimia virginica* alters energy flows in streams where the population achieves high density (Dillon, 2000). Other negative effects, like clogging municipal water pipes or beach fouling, are reported for *Bithynia tentaculata* (Mills *et al.*, 1993) and *Potamopyrgus antipodarum* (Moore *et al.*, 2012).



## Synthesis

Worldwide, there are 26 gastropod families that live exclusively in freshwater (Strong *et al.*, 2008), and there are 16 families of freshwater snails native to North America (Johnson *et al.*, 2013). Invasive species included in this review span 11 families, 9 of which overlap with the 16 native North American families, as well as 2 families not native to North America (Johnson *et al.*, 2013) (Table 2). This means there are 7 families, despite having representatives found worldwide, that do not have any established invasive species in North America. Are there characteristics of these species' families that explain what makes particular taxonomic clades successful colonizers? Or perhaps, characteristics that make a taxonomic clade vulnerable to displacement by invasive species?

Of these 7 families non-invasive in North America, 4 are from the prosobranch, small-shelled super family Rissooidea: Amnicolidae, Assimineidae, Cochliopidae, and Pomatiopsidae (notably the same super family as Hydrobiidae, Bithyniidae, and Lithoglyphidae) (Strong *et al.*, 2008). Amnicolidae has approximately 1000 species distributed worldwide, with 18 in North America (Johnson *et al.*, 2013). This family is used as an indicator species; individuals are very sensitive to slight ecological changes and typically live in clean water. Assimineidae has only 20 species found worldwide in estuaries, freshwater rivers and streams, and springs in temperate and tropical regions (Strong *et al.*, 2008). Only 2 species are confirmed in North America, both of which have extremely limited ranges (Johnson *et al.*, 2013). Cochliopidae has approximately 250 species distributed worldwide, with 48 in North America (Johnson *et al.*, 2013). They are

distributed in rivers, streams, swamps, and lakes (Strong *et al.*, 2008) and also have very restricted geographical ranges, making them susceptible to disturbance (Johnson *et al.*, 2013). Pomatiopsidae has 170 species worldwide, 6 of which are found in North American rivers, permanent wetlands, streams, and some saline springs and lakes (Johnson *et al.*, 2013; Strong *et al.*, 2008). Members of this family are amphibious (Strong *et al.*, 2008).

The Semisulcospiridae family is composed of 11 species of prosobranch snails native to North America (Johnson *et al.*, 2013). Individuals are > 40 mm in length and populations can reach high densities in streams (Johnson *et al.*, 2013). All 11 species are classified as imperiled (Johnson *et al.*, 2013). This family is included with Thiariidae and Pleuroceridae in the order Sorbeoconcha and super family Cerithioidea (Zeng *et al.*, 2014).

The family Neritidae is in a separate taxonomic clade of gastropods. It is classified in the super family Neritoidea in the order Neritimorpha. Approximately 110 families are found worldwide, mainly in coastal rivers and streams as well as estuaries. Historically, this family has been found in both freshwater and marine habitats (Strong *et al.*, 2008), with 3 of the 5 native North American species endemic to Hawaii (Johnson *et al.*, 2013). Similar to the Rissooidea super family, members are gill-breathing and have an operculum (Strong *et al.*, 2008).

Acroloxidae is a pulmonate snail in the order Hygrophiiia, notably with Lymnaeidae, Planorbidae, and Physidae (Strong *et al.*, 2008). Only 40 species have been identified worldwide (Strong *et al.*, 2008), and only 1 is found in mountain lakes in Western North America (Johnson *et al.*, 2013). Species are small and hermaphroditic (Johnson *et al.*, 2013).

According to Strong *et al.* (2008), pulmonates are generally the most successful invaders. These include Physidae, Lymnaeidae, Planorbidae, and Thiaridae (Strong *et al.*, 2008). Additionally, Strong *et al.* (2008) grouped families based on historical geographical range. The ancient families with the broadest ranges were Viviparidae, Bithyniidae, Hydrobiidae, Planorbidae, and Lymnaeidae (Strong *et al.*, 2008), demonstrating moderate overlap with their list of successful North American invaders. Acroloxidae is a family with a historically restricted range, and two families, Neritidae and Assimineidae, have been found in freshwater, marine, and brackish waters throughout history (Strong *et al.*, 2008). Finally, Thorp & Covich (2009) suggest members from Hydrobiidae and Pleuroceridae with fragmented populations are most at risk when there is an environmental disturbance. Species with limited geographical range and low tolerance to environmental variability are most susceptible to disturbances (Pimm *et al.*, 2006); of the 66 extinct gastropod species in North America, 61 (~92%) occurred in a single water body, while the remaining 5 species occurred in multiple water bodies (Johnson *et al.*, 2013). There are 637 native gastropod species remaining, though many are endangered or threatened (Johnson *et al.*, 2013).

In contrast to the family-level generalizations of Strong *et al.* (2008) and Thorp & Covich (2009), two of the most dominant families of invaders in North America are members of Ampullariidae (5 species) and Viviparidae (4 species). Both are large-bodied, prosobranch (with operculum) families classified in the order Architaenioglossa (Strong *et al.*, 2008), though their establishment success is patchy and often geographically limited. It is their potential harm to ecosystem services that draws (or deserves) attention. The New Zealand mud snail (Hydrobiidae)

is another species that has received a lot of attention as an invasive. As small prosobranchs capable of both active and passive dispersal, as well as asexual reproduction, this family encompasses the characteristics typical of a successful invader (Strong *et al.*, 2008; Thorp & Covich, 2009). Furthermore, the New Zealand mud snail is capable of achieving high population densities that disrupt ecosystem functioning, and thus, ecosystem services.

Simberloff *et al.*, (2005) identify three types of invasive species management: preventing introductions, eradicating populations, and maintaining populations at manageable levels. When trying to prevent the spread of invasive freshwater snails, more focus needs to be directed to regulating the aquarium, pet, and food trades. While other species, such as the zebra mussel, have highlighted the importance of regulating ballast water and international shipping, little attention has gone to preventing the introduction of gastropods by managing their main introduction vectors (Padilla & Williams, 2004). Due to the nature of the introduction pathway, species introduced through the aquarium, pet, and food trades disperse much farther than those initially introduced to a single water body through ballast water (Padilla & Williams, 2004). While effective policy is necessary to offer true prevention, the scientific community seems to agree that prevention is critical; once a species is established, it is almost impossible to eradicate, and costs of management vastly outweigh costs of prevention efforts (Lodge *et al.*, 1998; Leung *et al.*, 2002; Pimentel *et al.*, 2005; Simberloff *et al.*, 2005; Keller *et al.*, 2007; Vander Zanden & Olden, 2008).

## Directions for future research

This review of 19 freshwater snail species categorized as invasive (or as native transports) within North America highlights life-history traits and effects of introduction, as well as identifies existing gaps in ecological knowledge regarding freshwater gastropods. Species information is scattered and incomplete, and it is difficult, if not impossible, to manage (or prepare for) populations that are not completely understood. Compounding this problem is the fact that most freshwater snail introductions go unnoticed until a reproducing population is established. At a minimum, basic life history and ecology of many of these species should be elucidated. Once we understand the biology of these organisms, we will be able to more fully assess how they affect ecosystem structure and functioning. Due to the dynamic nature of aquatic ecosystems, it is impossible to completely predict where an invasive species will thrive and how it will impact structure and processes in the new system, but we can begin to reduce this uncertainty and make more well-informed management decisions by investigating some of these questions.

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Table 2-1. Taxonomy and native ranges of the invasive freshwater snail species included in this review, as well as the number of species from each family native to the USA and Canada. An \* indicates a “native transport” rather than an exotic species.

Subclass	Order	Family	Number of Species Native to USA/ Canada	Species Name	Common Name(s)	Native Range
Caenogastropoda	Architaenioglossa	Ampullariidae	1	<i>Pomacea diffusa/bridgesii</i>	Spiketop apple snail	South/Central America (Rawlings et al. 2007, Horgan et al. 2014)
				<i>Pomacea haustorium</i>	Titan apple snail	South/Central America (Rawlings et al. 2007, Horgan et al. 2014)
				<i>Pomacea canaliculata</i>	Channeled apple snail	South/Central America (Rawlings et al. 2007, Horgan et al. 2014)
				<i>Pomacea insularum/maculata</i>	Island apple snail	South America (Rawlings et al. 2007)
				<i>Marisa cornuarietis</i>	Giant rams horn	South/Central America (Rawlings et al. 2007)
	Sorbeoconcha	Viviparidae	21	<i>Viviparus viviparus</i>	River snail	Northern Europe (Kerney 1999)
				<i>Viviparus georgianus*</i>	Banded mystery snail	Eastern USA and southern Gulf Coast (Jokinen 1992)
				<i>Bellamya chinensis</i>	Chinese mystery snail	Asia (Jokinen 1982, Solomon et al. 2010)
				<i>Bellamya japonica</i>	Japanese mystery snail	Asia and Japan (Jokinen 1982)
		Thiaridae	0	<i>Tarebia granifera</i>	Quilted melania	India to Philippines and Hawaii, Japan (Abbott 1952)
				<i>Melanooides tuberculatus</i>	Red-rimmed melania	Northern/Eastern Africa, Middle East, Southern Asia
		Pleuroceridae	162	<i>Elimia virginica*</i>	Virginia river snail	Eastern USA (Smith 1980, Pennak 1989)
	Hypsogastropoda	Bithyniidae	0	<i>Bithynia tentaculata</i>	Mud bithynia	Europe (Ricciardi 2001)
		Hydrobiidae	185	<i>Potamopyrgus antipodarum</i>	New Zealand mud snail	New Zealand (Winterbourn 1970)
		Lithoglyphidae	73	<i>Gillia altilis*</i>	Buffalo pebblesnail	Eastern USA (Jokinen 1992, Mills et al. 1993)
Heterobranchia	Mesogastropoda	Valvatidae	10	<i>Valvata piscinalis</i>	European stream valvata	Europe, Caucasus, Western Siberia, and Central Asia (Grigorovich et al. 2005)
Pulmonata	Basommatophora	Lymnaeidae	61	<i>Radix auricularia</i>	European ear snail	Europe and Asia (Jokinen 1992)
		Planorbidae	52	<i>Biomphalaria glabrata</i>	Blood fluke planorb	Caribbean and South America (Pointier et al. 2005)
		Physidae	47	<i>Physa acuta</i>	European physa	North America (Dillon et al. 2002) OR Europe



Table 2-2. Taxonomy of both native and non-native gastropods of North America.

Subclass	Order	Super Family	Family
Caenogastropoda	Architaenioglossa	Ampullarioidea	Ampullariidae
		Viviparoidea	Viviparidae
		Cerithioidea	Thiaridae
	Pleuroceridae		
	Semisulcospiidae		
	Hypsogastropoda		Amnicolidae
			Assimineidae
			Bithynidae
			Cochliopidae
		Hydrobiidae	
	Lithoglyphidae		
	Pomatiopsidae		
Heterobranchia	Mesogastropoda	Valvatoidea	Valvatidae
Pulmonata	Basommatophora	Acroxoidea	Acroxidae
		Lymnaeoidea	Lymnaeidae
		Planorboidea	Planorbidae
			Physidae
Neritomorpha		Neritoidea	Neritidae

## CHAPTER 3: Carbon budget of the adult Chinese mystery snail (*Bellamya chinensis*) at various water temperatures

### Abstract

Bioenergetics modeling helps bridge the gap between individual energy requirements and population-level growth trends; however, baseline bioenergetics models are lacking for many aquatic invasive species. The objectives of the current study were to 1) quantify consumption, egestion, respiration, and production of the invasive Chinese mystery snail (*Bellamya chinensis*), and 2) evaluate the influence of water temperature on the values of these components and differences among them. We used laboratory experiments to measure somatic growth, oxygen consumption, waste production, and reproduction for adult Chinese mystery snails at 12°, 20°, and 27°C. Snails at the coldest water temperature allocated more energy to maintenance and growth than to offspring production, whereas snails at the warmest water temperature allocated more energy to production of offspring but experienced the highest mortality. We observed differences in the carbon budgets of adult Chinese mystery snails across different water temperatures.

### Introduction

Bioenergetics models can serve as the link between individual energy use and population-level growth trends (Sokolova et al. 2012). Once a baseline understanding of how an organism allocates energy is known, it is then possible to assess the physiological effects of environmental stressors and changes on an organism (van Haren et al. 1994, Benke 2010). When trying to develop management methods for invasive species, it is beneficial to have a thorough understanding of the species' energetic needs so that a

complete range of options can be considered. For example, understanding how water temperature affects the energetics of the invasive rainbow smelt (*Osmerus mordax*) in Northern Wisconsin enabled a whole-lake manual-mixing experiment that solely targeted the troublesome smelt and not the native fish (Gaeta et al. 2012). This approach eliminated the need for adding chemicals such as rotenone into the water, thus eliminating the need to re-stock the native fish community.

Understanding an organism's energetics also helps identify habitats and environmental conditions where an invasive population can survive (Sokolova et al. 2012). Having the ability to predict potential sites susceptible to invasion prior to a species introduction is invaluable for natural resource managers (Ng and Gray 2009). Unfortunately, baseline bioenergetics models for invasive invertebrates are limited in comparison to those of invasive vertebrates such as fish (Benke 2010).

In the current study, we apply the bioenergetics theory described in Kitchell et al. (1977) and Jobling (1994) to the invasive freshwater Chinese mystery snail (*Bellamya chinensis*, Reeve 1863). The Chinese mystery snail is a large (~70 mm), freshwater prosobranch currently found throughout the USA (Jokinen 1982, Solomon et al. 2010). Despite this species' vast introduced range, little is understood about how individuals allocate consumed energy between somatic growth and reproduction. This species has separate sexes, and individuals grow throughout their entire lifespan, with females living 4-5 years and males living 3-4 years (Havel 2011); as a result, females tend to be larger in size. Females brood developing young and give live birth; during the breeding season (Havel 2011), a female may have upwards of 100 juveniles at varying stages of development (Crabb 1929, Stephen et al. 2013). The objectives of this study were to 1)

quantify consumption, egestion, respiration, and production of individual Chinese mystery snails, and 2) evaluate the influence of water temperature on the values of these components. We specifically measured carbon because it can be measured for each component of our equation, allowing for an eventual comparison across water temperatures (Adams and Breck 1990, Kitchell et al. 1977).

## Methods

### *Sample collection*

Chinese mystery snails were collected in mid-August 2012 from Wild Plum Lake (40.614° N, 96.902° W), Lancaster County, Nebraska, approximately 27 km southwest of Lincoln. Snails were transported in a 19-L bucket of lake water back to the laboratory at the University of Nebraska-Lincoln and held in aerated tanks filled with de-chlorinated tap water maintained at room temperature. Snails were fed TetraVeggie™ sinking algae wafers three times per week while housed in the laboratory. Laboratory experiments began in May 2013.

### *Experimental design*

Individuals were scrubbed using wire mesh screening to remove algal growth on shells without scouring the actual shell. Total shell length (mm) was measured, each individual was labeled with an identification number (Wong et al. 2013), and snails were randomly assigned to one of three temperature categories: 12°C (N=30), 20°C (N=36), and 27°C (N=30). Annual average water temperatures for Nebraska reservoirs are typically within this range (12-27°C) during both “normal” and “drought” years (Olds et

al. 2011), though reservoirs will undergo periods of colder and warmer water temperatures at certain points of the year.

Once assigned a temperature, snails were further divided into sets of 10 and placed into floating plastic bins with holes drilled around the perimeter, allowing water to flow through the bin while preventing waste and juveniles from escaping into the surrounding water bath. These floating bins were placed into mesocosms equipped with recirculating filtration systems, and temperature was maintained with the use of a heater or chiller. Snails assigned to the 12°C or 27°C temperature categories were placed into the mesocosm at room temperature (20°C) and gradually heated or cooled to the experimental temperature at a rate of approximately 1°C/hour. Previous temperature tolerance experiments indicated that this rate of heating or cooling would not harm adult snails (Wong et al. unpublished data), and all snails were allowed one week of acclimation time before experiments began. Water lost to evaporation was replaced once every two weeks by adding de-chlorinated tap water to the centrally located filtration tubs (Figure 3-1). All of the following measurements were repeated for snails in each of the water temperature groups.

### *Growth*

Before the experiment started, a subsample of 16 snails (total length: 22.4 – 62.5 mm) were dissected so the total carbon and total nitrogen composition of shells and body tissue could be analyzed and compared across different snail sizes. For experimental snails, total shell length (mm) and wet mass (g) were measured weekly for each snail. Total shell length was measured using a Carrera Precision CP98060TF Titanium Digital Caliper (0.01 mm), and wet mass was measured using an OHAUS electronic scale (0.1

g). If an individual died between measurements, a final total length was taken at the point it was removed from the tank. Only growth data from individuals that survived the entire 8-week experiment were used in final analyses. At the end of the experiment, all surviving snails were dissected to remove body tissue from shell. Wet tissue and shell weights were acquired for each, and then samples were dried for 48 hours at 90°C, crushed into homogenous samples, re-weighed to acquire a dry mass, and analyzed for total carbon and total nitrogen. Carbon and nitrogen were measured in the Ecosystems Analysis Laboratory in the School of Biological Sciences, University of Nebraska-Lincoln using dry combustion gas chromatography on a COSTECH Analytical Elemental Combustion System 4010. Mucus production was not independently measured; however, all material, including mucus remaining on body tissues after dissection, was scraped off of drying tins after drying and included in gas chromatography analysis.

### *Reproduction*

Determining sex of Chinese mystery snail individuals is difficult without dissection (Smith 2000), so juveniles were collected weekly at the same time growth measurements were taken. Adults were grouped in sets of 10, so a mean number of young could be calculated for each group and averaged across the number of surviving adults. Assuming a 1:1 sex ratio (Stephen et al. 2013), and based on the observation that snails had been reproducing at room temperature since their introduction to the laboratory in August 2012, we anticipated reproduction would still occur during the experiment. At the end of the experiment, all surviving snails were dissected so individual fecundity could be calculated and sex of individuals could be determined based on the presence or absence of developing juveniles and confirmation of sex organs. Collected juveniles were

dried and weighed before being crushed into homogenous samples for total carbon and total nitrogen analysis. Juvenile tissues and shells were kept together due to the difficulty of adequately separating them. Additionally, all juveniles extracted from a specific adult at the end of the experiment were grouped together for analysis.

### *Respiration*

Oxygen consumption under resting conditions was measured for each snail using the Qubit Systems Q-Box AQUA Aquatic Respirometry Teaching Package (Qubit Systems, Kingston, Ontario, Canada). This is an intermittent-flow system specifically designed to measure respiration of aquatic organisms and allows recording of multiple measurements without disturbing the study organism. The measurement system is self-contained and includes a water pump, a dissolved oxygen sensor, and LoggerPro (Qubit C901) software, allowing consistent measurements at any water temperature while also taking atmospheric pressure into consideration.

The oxygen sensor (Qubit S122) was calibrated twice per day while in use to ensure current environmental variables were included in measurements. Fresh filter paper, Teflon membrane, and potassium chloride were applied, and the system was allowed to run for 30 minutes before experiments started (per manual recommendation). The calibration process included taking two measurements. First, 10 mL of de-oxygenated water treated with the provided sodium sulphite solution was pumped through the oxygen sensor to achieve a zero measurement. The system was flushed with fresh water and then a second measurement was taken by injecting 10 mL of aerated experimental water and entering water temperature and atmospheric pressure values into the software to achieve a maximum oxygen concentration based on environmental

conditions. At the end of each day, the sensor was dismantled, cleaned, and dried to prevent corrosion from occurring. When necessary, the metal electrode was buffed gently with sandpaper to remove any build-up.

Prior to measurements, snails fasted for 24 hours. Volume of each individual was recorded by measuring displaced water in a graduated cylinder before the snail was placed into the 0.22-L respiration chamber. The chamber was closed and submerged in a water bath of experimental water, keeping water temperature constant. Tubing and respiration chamber volume and organism volume were entered into the software before beginning. Circulation time was set to 30 minutes and flushing time was set to 3 minutes, meaning oxygen consumption was measured for 30 minutes before a 3 minute flushing period pumped fresh water into the chamber and tubing before an additional 30-minute circulation period took place, resulting in 2 oxygen consumption measurements per individual. The first circulation period did not begin until the snail was observed to have opened its operculum and emerged from its shell.

Raw output provided oxygen-consumption curves for each individual. Slopes of the curves from each of two measurements were calculated and entered into the equation:  $VO_2 = DO \text{ slope} * (V_r - V_a) * 3600/m$ , where,  $VO_2$  = oxygen consumption (mg  $O_2$ /kg/hour),  $DO \text{ slope}$  = rate of decrease of  $DO$  (mg  $O_2$ /L/sec),  $V_r$  = respirometer volume (chamber and tubing),  $V_a$  = volume of experimental animal (L),  $m$  = animal mass (kg), resulting in two oxygen consumption rates for each individual. These rates were averaged to obtain one value for each individual. The respiration chamber was small enough that the snail's movement was restricted, ensuring that the measurement was taken at rest and while the snail was fasting.



### *Egestion*

A stock population of diatoms (*Navicula*) was ordered from Carolina Biological Supply and cultured in the laboratory using Alga-Gro® medium. Every seven days, a subculture was taken by removing 10 mL of mixed diatoms and medium from the stock population and transferring to a separate 1-L glass jar to ensure healthy diatoms would be available throughout feeding experiments. Subculture jars included 1 L of room-temperature Carolina™ spring water and 10 mL of Alga-Gro® growth medium. Diatoms were kept under fluorescent light for 24 hours a day to facilitate growth.

Individual glass-fiber filters (GF/F nominal pore size 0.7 µm) were weighed using an OHAUS Discovery balance (0.01 mg) and prepared immediately before each feeding trial. First a dry weight was recorded. Then, 100 mL of deionized water was filtered, and the filter was weighed again to acquire a wet weight. Next, 100 mL of mixed diatom and growth medium solution was filtered before a third filter weight was recorded. Filters were labeled, stored in separate Petri dishes, and kept in a dark cooler while transported back to the laboratory to start feeding trials. This method allowed a diatom weight to be calculated before feeding trials commenced, though values were recorded without drying. Five control filters were prepared each time using the same method to compare control weights before and after a feeding trial.

Food was withheld from snails for the 24 hours preceding feeding experiments. Snails were individually placed into 1-L jars of water from the mesocosm water baths containing one freshly prepared filter with diatoms. Jars were suspended in groups of 6 in floating Styrofoam racks, so that each jar was submerged to its rim at the same water temperature at which snails were housed, while simultaneously preventing snails from

escaping. Each snail was allowed to feed on the provided filter for 8 hours. After 8 hours, filters were removed and a wet weight was taken. Filters were then dried for 48 hours at 90°C before further analysis. Snails remained in each jar for an additional 24 hours before being removed and returned to their original bins. After 24 hours, all waste material was siphoned out of each jar and dried in labeled aluminum weigh tins for 48 hours at 90°C. Once dried, fecal material was crushed into homogenous samples, weighed, and analyzed for total carbon and total nitrogen. Gas chromatography requires a minimum sample size to analyze for carbon and nitrogen, and many of the dried fecal matter samples were too small to run. As a result, some samples within the same temperature group were pooled together and analyzed. After filters used in feeding experiments dried for 48 hours, a dry weight was recorded and filters were placed in a muffle furnace at 500°C for 1 hour. All organic material was burned off during this time and a final ash-free dry weight was recorded for each filter.

#### *Model development*

To develop an approximate carbon budget for the Chinese mystery snail, we used the equation presented in Kitchell et al. (1977):

(Equation 1) 
$$C = E + P + R,$$

where  $C$  is consumption (amount of food, or energy, consumed),  $E$  is egestion (production of fecal matter),  $P$  is production (including both somatic growth and reproductive output), and  $R$  is respiration rate (at rest). Our laboratory experiments successfully calculated  $E$ ,  $P$ , and  $R$  values (as described above), and we then used Equation 1 to estimate  $C$  for snails at each water temperature. Before balancing the

equation, units of all values were converted to specific rates of mg Carbon/gram body mass/day).

### *Statistical analyses*

Snails were grouped by water temperature, and growth, oxygen consumption, fecal material production, and reproduction were compared using one- or two-way analysis of variance (ANOVA) and a post hoc comparison test (Tukey HSD). Percent survival, carbon, and nitrogen concentrations were compared using one way ANOVA . To analyze differences in reproduction, we used a t-test assuming unequal variances because snails only reproduced in two of the water temperatures.

### Results

Only individuals with initial lengths  $> 22.4$  mm were included in analyses because no individuals  $< 22.4$  mm were observed carrying young. As a result of this threshold, three surviving individuals were removed from the 12°C treatment, one individual was removed from the 20°C treatment, and two individuals were removed from the 27°C treatment, resulting in starting sample sizes (N) of 27, 35, and 28, respectively. After the 8-week experiment, 24 snails remained at 12°C (89% survival), 23 snails remained at 20°C (66% survival), and 13 snails remained at 27°C (46% survival) (Table 3-1). Survival differed significantly among water temperatures ( $df=2$ , 87,  $F=4.93$ ,  $p=0.009$ ). Specifically, snails at 12°C had significantly higher survival than those at 20° and 27°C, but there was no significant difference between survival of snails at 20° and 27°C ( $p > 0.05$ ).

Preliminary analysis comparing carbon and nitrogen composition of body tissues and shells across a range of sizes yielded no differences in carbon or nitrogen content

regardless of snail size. This was done by grouping snails into sub-categories of 10-mm total length ranges and an ANOVA compared percent carbon and nitrogen content across size groups. Body tissue carbon content across size groups was not significantly different ( $df=2, 13, F=2.0, p=0.16$ ), nor was body tissue nitrogen content ( $df=2, 13, F=2.8, p=0.08$ ). Adult body tissue had a mean ( $\pm$  SD) carbon content of 34.3 (4.6)% and a mean ( $\pm$  SD) nitrogen content of 8.5 (1.9)%. Shell carbon content across size groups was not significantly different (ANOVA,  $df=2, 13, F=3.23, p=0.06$ ), nor was shell nitrogen content (ANOVA,  $df=2, 13, F=2.83, p=0.08$ ). Adult shells had a mean ( $\pm$  SD) carbon content of 14.2 (1.2)% and a mean ( $\pm$  SD) nitrogen content of 0.8 (0.4)% (Table 3-2).

Additionally, a simple linear regression was used to analyze the relationship between shell length and tissue dry mass, and shell length (mm) was related to tissue dry mass (g) by the equation:  $y=0.025x-0.558$  ( $p<0.01, r^2=0.77$ ). Shell length (mm) was related to shell dry mass (g) by the equation:  $y=0.189x-4.706$  ( $p<0.0001, r^2=0.92$ ). Thus, because carbon and nitrogen content did not vary with snail size, and shell length could be used as a determinant of dry shell mass, no additional snail shells were analyzed using gas chromatography. Grinding each snail shell into a homogenous sample adequate for gas chromatography was very difficult and required twice as many samples, so for the remainder of the study, only body tissue of adults was analyzed for carbon and nitrogen.

### *Growth (P)*

Mean initial shell lengths among the three water temperatures were not significantly different ( $df=2, 57, F=0.123, p=0.88$ ); however, mean growth rates among temperature treatments after the 8-week experiment were significantly different ( $df=2,$

57,  $F=7.34$ ,  $p=0.001$ ). Individuals in the 12°C and 20°C temperature treatments grew significantly more than individuals at 27°C (12°C and 27°C:  $df=1$ , 35,  $F=19.52$ ,  $p=0.00009$ ) (20°C and 27°C:  $df=1$ , 34,  $F=5.20$ ,  $p=0.03$ ), though there was no statistical difference in growth between 12°C and 20°C ( $df=1$ , 45,  $F=2.85$ ,  $p=0.09$ ) (Table 3-1).

### *Reproduction (P)*

No juveniles were born during the 8-week experimental period from the snails at 12°C, 212 juveniles were birthed at 20°C, and 418 juveniles were birthed at 27°C (Table 3-1). The mean number of juveniles birthed per live adult was calculated each week based on the number of adults still alive and the number of juveniles removed from the tank. This value ranged between 0.17 and 2.29 at 20°C, and went up and down throughout the experiment. In contrast, at 27°C the mean number of juveniles birthed per live adult peaked at 6.04 the first week and steadily decreased each week to 0 (Figure 3-2). Though the reproduction patterns over the 8-week experiment varied among groups, and snails at 20° and 27°C birthed significantly more juveniles than snails at 12°C, there was no significant difference in the mean number of juveniles birthed per live adult between 20° and 27°C (t-test assuming unequal variances,  $df=8$ ,  $t=1.86$ ,  $p=0.27$ ). There was also no difference in mean carbon composition of juveniles birthed at 20° and 27°C ( $df=8$ ,  $t=2.16$ ,  $p=0.97$ ).

Individual fecundity was measured at the end of the experiment by dissecting each snail and counting the number of developing embryos in each female. Surviving females at 12°, 20°, and 27°C had 377, 121, and 2 developing embryos, respectively; thus, mean fecundity values were 15.7, 5.3, and 0.15 (per remaining adult), respectively

(Figure 3-3). In addition to monitoring reproduction in the laboratory, 35 randomly chosen individuals from the same field collection (water temperature was approximately 28°C) were immediately dissected to assess fecundity. Snails ranged in shell length from 22.7 to 60.1 mm, and 17 (47%) had developing embryos at the time of collection, with a mean fecundity of 22.4 embryos/female (Figure 3-4).

#### *Respiration (R)*

Mean ( $\pm$  SD) rates of oxygen consumption were 173.19 ( $\pm$  107.59), 187.88 ( $\pm$  48.72), and 73.99 ( $\pm$  121.89) mg O<sub>2</sub>/kg/hr for snails at 12°, 20°, and 27°C, respectively (Table 3-1), which are significantly different (ANOVA df=2, 54, F=6.83,  $p$ =0.002). Both 12° and 20°C snails had higher mean oxygen consumption rates than snails at 27°C (12°C and 27°C: df=1, 34, F=15.89,  $p$ =0.0003) (20°C and 27°C: df=1, 32, F=6.17,  $p$ =0.02).

#### *Consumption (C) and egestion (E)*

The experimental design for measuring consumption was determined to be inadequate, as some consumption values were calculated to be less than 0. The dry mass of the diatoms was too small to adequately measure changes in biomass on the filters, particularly because dry weight measurements pre-feeding were not possible. Even using the control filter mean values as a comparison, a number of results reported negative consumption, which is not possible. However, because we have values for the other components of Eq. 3-1, we can estimate the consumption requirements of adult snails (Table 3-1).

Mean ( $\pm$  SD) fecal matter production (mg) was 4.73 ( $\pm$ 2.81), 4.15 ( $\pm$ 2.86), and 4.26 ( $\pm$ 1.17) for snails at 12°, 20°, and 27°C, respectively (Table 3-1); these values were

not statistically different ( $df=2, 32, F=0.17, p=0.84$ ). The mean ( $\pm$  SD) carbon content of fecal material was 30.93 ( $\pm$  4.14), 25.63 ( $\pm$  6.73), and 22.00 ( $\pm$  5.83)% for snails at 12°, 20°, and 27°C, respectively (Table 3-2), and was significantly different among groups ( $df=2, 32, F=5.9, p=0.006$ ). The mean ( $\pm$ SD) nitrogen percentage of fecal material was 3.31 ( $\pm$ 0.79), 3.19 ( $\pm$ 0.89), and 2.79 ( $\pm$ 0.887)% for snails at 12°, 20°, and 27°C, respectively (Table 3-2), and was not significantly different among groups ( $df=2, 32, F=1.00, p=0.38$ ).

### *Carbon budget*

After estimating egestion, respiration, somatic growth, and reproduction for snails at each water temperature, we used Equation 1 to calculate the energy consumption requirements for snails at each temperature. Snails at the coldest water temperature had the highest consumption requirements (2.48 mg Carbon/g body mass/day), and snails at the warmest water temperature had the lowest consumption requirements (1.12 mg Carbon/g body mass/day). The end result is an energy budget produced from the mean values measured at each water temperature (Table 3-3). In all water temperatures, the largest energy expenditure was by far oxygen consumption (our proxy for resting metabolic rate). This information aids the development of energy curves for these snails (Figure 3-5).

### Discussion

This research provided baseline bioenergetics information for Nebraska populations of the invasive Chinese mystery snail, which adds to the growing knowledge base of the Chinese mystery snail's ecology and life-history strategies. Carbon allocation

among growth, maintenance and reproduction is influenced by water temperature. Snails at the coldest temperature had the highest survival among all three groups, higher growth and respiration rates than the snails at the warmest temperature, and they appear to have slowed or paused reproduction during the experimental period. More energy was allocated to maintenance and growth than to offspring production.

Snails at the warmest water temperature exhibited the least amount of individual growth and had the lowest resting oxygen consumption rate. Though they gave birth to the greatest number of juveniles, fecundity peaked during week one and subsequently declined to zero. Post-experiment dissections discovered only 2 embryos in the surviving females. Adult snails at this temperature had lower survival rates than snails at the coldest water temperature. The combination of reduced survival, reduced growth, and reduced oxygen consumption suggest that the snails may have been stressed at the highest temperature. The initial high reproductive output could represent a strategy to maintain fitness in conditions unfavorable for adult survival (Petes et al. 2007); however, to confirm this hypothesis, more research on chronic temperature thresholds for this species is needed.

Snails at 20°C had faster growth rates and higher respiration rates than individuals at the warmest water temperature; however, their average survival was intermediate between snails at the coldest and warmest water temperature. Additionally, they produced more juveniles than snails at the coldest water temperature. Average fecundity was not statistically different between 21°C and 27°C, but snails at 21°C reproduced with less variability around the mean fecundity. Females had significantly more developing



embryos at the end of the experiment in comparison to the 27°C snails, indicating the likelihood of continuing reproduction at 21°C but not 27°C.

These results both agree with and contradict previous research. Current distribution in its non-native range indicates the Chinese mystery snail tolerates water temperatures between 0-30°C (Karatayev et al. 2009); however, no examinations on how water temperature affects the life-history characteristics of this species have been completed. In natural populations, individuals grow throughout their entire life, and reproduction occurs during May-October starting the year after their first winter (Jokinen 1982); in constant laboratory conditions (20°C), mature individuals reproduce year-round (personal observation).

Adult individuals of the Chinese mystery snail survived well at 12°C but did not reproduce. It is probable that females were already developing embryos when the experiment started, as we observed continuous reproduction in pre-experiment conditions at 20°C, but we do not currently have estimates of embryo incubation period for this species. Research on another large, freshwater snail, *Pomacea canaliculata*, discovered that fecundity is density dependent (Tanaka et al. 1999); however, density dependence cannot have explained differences in fecundity in our study since density was the same for each sub-basin used in this experiment, across all three water temperatures.

Additionally, natural populations overwinter by burrowing into the substrate, indicating they can survive prolonged periods at water temperatures around 4°C (Jokinen 1982).

Future bioenergetics studies would benefit by including a water temperature closer to this value, something we were unable to do in the current study due to equipment limitations.

Individuals in the warmest water temperature had the greatest mortality and the slowest growth, consistent with bioenergetics research on the freshwater *Helisoma trivolvis* snail (Eversole 1978, Norton and Bronson 2006). Somatic growth of the freshwater snail *Bulinus globosus* is reported to stop above 28.5°C when reproduction is occurring, and the snails seem to prioritize reproduction over somatic tissue growth at this temperature (O’Keefe 1985). Studies of the invasive *Pomacea canaliculata* (Family: Ampullariidae) observed higher fecundity and lower longevity in warmer water temperatures (Estebenet and Cazzaniga 1992). Previous research on water temperature preferences of freshwater prosobranchs concluded that gill-breathing snails tend to prefer “cool” water conditions, in the range of 19-22°C, rather than colder or warmer temperatures (Van der Schalie and Berry 1973). In contrast, pulmonates had a wider water temperature range in which life processes would continue to take place. However, the general temperature range that freshwater snails function in was reported to be 12-30°C (Van der Schalie and Berry 1973).

Respiration is a common proxy for metabolism (Lampert 1984). Typically, respiration rate increases with temperature until a threshold is reached, after which respiration rate decreases rapidly (Von Brand et al. 1948, Berg and Ockelmann 1959, Calow 1975). Respiration of freshwater snails decreases during starvation (Von Brand et al. 1948), increases during the production of eggs or juveniles, and decreases during the annual post-reproduction phase (Calow 1975). Generally, weight-specific metabolic rates decrease with increasing organism body mass (von Bertalanffy 1957), meaning specific respiration rate decreases as snails grow. In our experiment, snails at the warmest water temperature had the lowest respiration rates. This could imply that the snails were in the

post-reproduction phase, causing a drop in respiration (Callow 1975), or it could imply that the temperature threshold was surpassed. Neither survival nor body sizes varied between snails at 20° and 27°C, and few embryos were removed during post-experiment dissection of snails from the 27°C mesocosms, so it is more likely the snails were no longer reproducing. Thus, snails will not likely reproduce during the entire reported reproduction timeline of May-October in Nebraska, as lake temperatures can reach 25°C in early- to mid-June (NGPC 2014), though this varies with lake depth and microhabitat (Olds et al. 2011). We also observed a decrease in specific respiration rate as body size increased. This species overwinters by burying into lake sediment in deep waters (Jokinen 1982), and no metabolic analysis during this period has been completed. Overwinter analysis of another Viviparidae species, *Viviparus georgianus*, described decreased fecundity during winter months; however, females still had embryos at each sampling period (Browne 1978).

Our results parallel descriptive reports of *Bellamya chinensis* behavior in its non-native range (Jokinen 1982), meaning the Chinese mystery snail populations in Nebraska are not unique. During spring (12°-20°C), individuals prepare for and start the annual reproduction period. When water temperatures rise (>27°C), reproduction slows or stops, but juveniles may be birthed in the fall when water temperatures fall again. In areas where lakes stratify throughout the summer (Solomon et al. 2010, Johnson et al. 2009), snail habitat (as observed from the 1-m bathymetric contour line) is unlikely to warm past 25°C, and if it does, it is for a shorter duration than in Nebraska. It is currently unknown if developing embryos can survive overwintering in utero, but this would be an interesting question for future research. Research comparing populations from different

latitudes would also be useful, particularly if dispersal increases with warmer temperatures.

Unfortunately, we were unable to assess growth and maturity of juveniles. Juvenile mortality increased after handling, and we were unable to successfully rear them longer than 2-3 weeks in laboratory conditions. Consumption experiments proved to be inconclusive due to an inappropriate experimental design, though we can use the primary bioenergetics equation (Equation 1) to estimate consumption needs based on the information we have on waste elimination, respiration, growth, and reproduction. Based on these estimates, individuals at 12°C would need the greatest food consumption rate to produce the observed results. In contrast, individuals at 27°C have the lowest estimated consumption requirements. The estimated range of specific consumption rates for adult Chinese mystery snails was 5.17-11.03 mg C/mg body weight/day. Growth and feeding rates both vary based on nutritional quality of food (Fink and Von Elert 2006), but all snails were fed the same food throughout the experiment. Adult Chinese mystery snails are capable of both grazing periphytic algae and suspension feeding (Olden et al. 2013); they have a siphon that allows them to filter particles out of surrounding water, though this does not appear to start until the snail reaches approximately 42 mm in total length, so further research on food preferences would also clarify differences in consumption of benthic vs. pelagic algae. Finally, independently measuring mucus production would be beneficial in future research, as gastropods require mucus for a number of life activities, and the energetic costs of mucus production may be relatively large (Davies et al. 1992; Ng et al. 2013). It is still debated whether shell calcification is an energetically expensive process or not, though it has been speculated that calcification is not energetically costly

compared to other metabolic costs (Palmer 1992). We did not measure energy required for calcification in our experiments.

When evaluating our current bioenergetics curves (Figure 3-5), we would benefit from including more temperature points. We also need a different method for estimating consumption rates, as the diatom filter experiment did not work as anticipated. A different experimental design that successfully measured consumption would allow us to compare observed values with those calculated in the present model through the bioenergetics equation (Equation 1). Additionally, snails in natural systems eat more than just diatoms, so consumption rates may vary based on the type of food being used in experiments. One disconnect in our experiment was the fact that we fed the snails algal pellets *ad libitum* throughout the study period except during consumption trials, when we fed them diatoms (however, we also only used fecal matter collected during this feeding experiment and allowed the snails to fast before the experiments started). Feeding them the same food throughout the entire experiment would eliminate any adjustment period. Being presented with a new food type suddenly may have affected their feeding rate.

These baseline data can be used for comparison in future studies investigating environmental limitations of the Chinese mystery snail and also pave the way for studies of toxicology, habitat suitability, and effects of varying water chemistry on this species' bioenergetics. Additionally, both the successful and unsuccessful components of our experimental methods can be applied to bioenergetics models of other invasive species, including the New Zealand mudsnail (*Potamopyrgus antipodarum*), apple snails (Ampullaridae spp.), rusty crayfish, Asian clams (*Corbicula fluminea*), and zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis*) mussels. Invasive

gastropods have the capability to disrupt ecosystem processes and services (Carlsson et al. 2004) and spread by similar means (Vander Zanden and Olden 2008); however, there are gaps in information on their ecology and impacts. Bioenergetics information can help fill in these information gaps and allow for a much-needed comparison of characteristics across families and species (Strong et al. 2008).

### Management implications

The development of this bioenergetics framework for the Chinese mystery snail allows us to suggest a number of management options. Based on habitat preferences of the Chinese mystery snail, managers should focus on lakes that have silty or muddy substrates in the littoral zone; Chinese mystery snails require these soft substrates to burrow, allowing them to overwinter successfully in climates that drop below freezing for extended periods of time. However, lakes that freeze completely for most of the winter are not desirable sites for Chinese mystery snails, though more research has to be done exploring their long-term freezing tolerance. It is possible that lowering a reservoir's water level, when possible, and letting the lake completely freeze could be enough to eliminate a snail population.

Chinese mystery snails can survive in water temperatures between 0 and 30°C, though reproductive success varies throughout this range. Lakes with average temperatures between 17 and 22°C during the spring and summer months would make ideal Chinese mystery snail habitat. In these conditions, adult snails are not undergoing thermal physiological stress, and energy can be allocated to somatic growth and reproduction. Patches of rip-rap or rocky substrates may provide refuge for developing

juveniles (and adults), increasing the probability they will reach sexual maturity. This snail also thrives in eutrophic environments where there is abundant diatom and periphyton available for forage.

We know that rotenone and copper sulfate do not effectively control adult Chinese mystery snails (Haak et al. 2014), nor does altering the water's pH (ranging from 4 to 10) (Haak unpublished observations). However, other questions have yet to be explored. Though rotenone and copper sulfate did not help control adult snails, adding a chemical that binds to  $\text{CaCO}_3$  making it unavailable may limit juvenile growth and survival and could slowly decrease population sizes over a period of 4-5 years. We also have not experimented with manual removal. Harvesting the largest individuals (who usually bear a higher number of juveniles each season) could also gradually decrease the Chinese mystery snail population size. This technique successfully decreased the rusty crayfish (*Orconectes rusticus*) population in Sparkling Lake, Vilas County, Wisconsin (Hein et al. 2006).

Finally, educating the public on the ramifications of introducing the Chinese mystery snail into a water body could help prevent future introductions from occurring in the first place. We still do not know if Chinese mystery snails transport parasites from their native range, and some of these parasites can be deadly to humans. In Taiwan, the Chinese mystery snail is an intermediate host for a parasite that causes eosinophilic meningitis in humans (Lv et al. 2009), so educating the public on these possible harms could reduce the number of intentional introductions that take place.

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Table 3-1. Summary data for adult snails at each of 3 water temperatures. Significant differences are indicated by different superscript letters.

	12°C	20°C	27°C
Number surviving snails > 22.4 mm (% of initial snails)	24 (89) <sup>a</sup>	23 (66) <sup>b</sup>	13 (46) <sup>b</sup>
Mean (± SD) initial shell length (mm)	47.39 (5.22) <sup>a</sup>	47.69 (7.71) <sup>a</sup>	46.53 (7.60) <sup>a</sup>
Mean (± SD) shell growth (mm):			
Week 1	0.72 (0.55)	0.47 (0.68)	0.25 (0.19)
Week 2	0.49 (0.49)	0.22 (0.32)	0.12 (0.13)
Week 3	0.21 (0.21)	0.17 (0.24)	0.04 (0.09)
Week 4	0.08 (0.11)	0.02 (0.04)	0.01 (0.02)
Week 5	0.02 (0.06)	0.01 (0.01)	0.08 (0.11)
Week 6	0.01 (0.03)	0.02 (0.05)	0.01 (0.03)
Week 7	0.12 (0.18)	0.07 (0.14)	0.01 (0.02)
Week 8	0.01 (0.03)	0.04 (0.10)	0.00 (0.00)
Total shell growth	1.35 (0.67) <sup>a</sup>	1.00 (0.76) <sup>a</sup>	0.51 (0.18) <sup>b</sup>
Total juveniles birthed	0	212	418
Mean juveniles/live adult	0	0.17-2.29	6.04-0.00
Total embryos collected post-experiment	377	121	2
Mean fecundity of females post-experiment	31.42	12.1	2
Mean (±SD) oxygen consumption rate (mgO <sub>2</sub> /kg/hr)	173.19 (107.59) <sup>a</sup>	187.88 (48.72) <sup>a</sup>	73.99 (121.89) <sup>b</sup>
Mean (±SD) fecal matter production (mg/day)	4.76 (2.81) <sup>a</sup>	4.15 (2.86) <sup>a</sup>	4.26 (1.17) <sup>a</sup>
Estimated consumption (mg C/g body weight/day)	11.03	8.95	5.17

Table 3-2. Mean ( $\pm$ SD) carbon and nitrogen content (%) for adult body tissue, fecal matter, and juveniles produced at each water temperature. Statistically significant differences within each category are indicated by different superscript letters.

	12°C	20°C	27°C
Mean ( $\pm$ SD):			
Body tissue carbon composition (%)	40.65 (2.93) <sup>a</sup>	39.62 (4.01) <sup>a</sup>	38.22 (5.49) <sup>a</sup>
Body tissue nitrogen composition (%)	11.61 (1.68) <sup>a</sup>	10.36 (1.84) <sup>a</sup>	10.92 (2.50) <sup>a</sup>
Fecal matter carbon composition (%)	30.93 (4.14) <sup>a</sup>	25.63 (6.73) <sup>b</sup>	22.00 (5.83) <sup>b</sup>
Fecal matter nitrogen composition (%)	3.31 (0.79) <sup>a</sup>	3.19 (0.89) <sup>a</sup>	2.79 (0.88) <sup>a</sup>
Juvenile carbon composition (%)	-	22.92 (2.09) <sup>a</sup>	21.35 (2.21) <sup>a</sup>
Juvenile nitrogen composition (%)	-	3.79 (0.71) <sup>a</sup>	3.31 (0.78) <sup>a</sup>

Table 3-3. Estimated carbon budget for Chinese mystery snails at each of three water temperatures. Numbers are mean specific rates with units of mg Carbon/gram body mass/day. Egestion values include both unassimilated material as well as excretion.

	12°C	20°C	27°C
Egestion	0.85	0.60	0.41
Respiration	1.56	1.69	0.67
Somatic growth	0.02	0.02	0.04
Reproduction	0.05	0.02	0.04
Consumption	2.48	2.33	1.12

Figure 3-1. Laboratory tank arrangement used for all experiments. Water was re-circulated through tanks and a centralized filter basin within specific water temperatures. Ten adult snails were housed in each floating sub-basin.

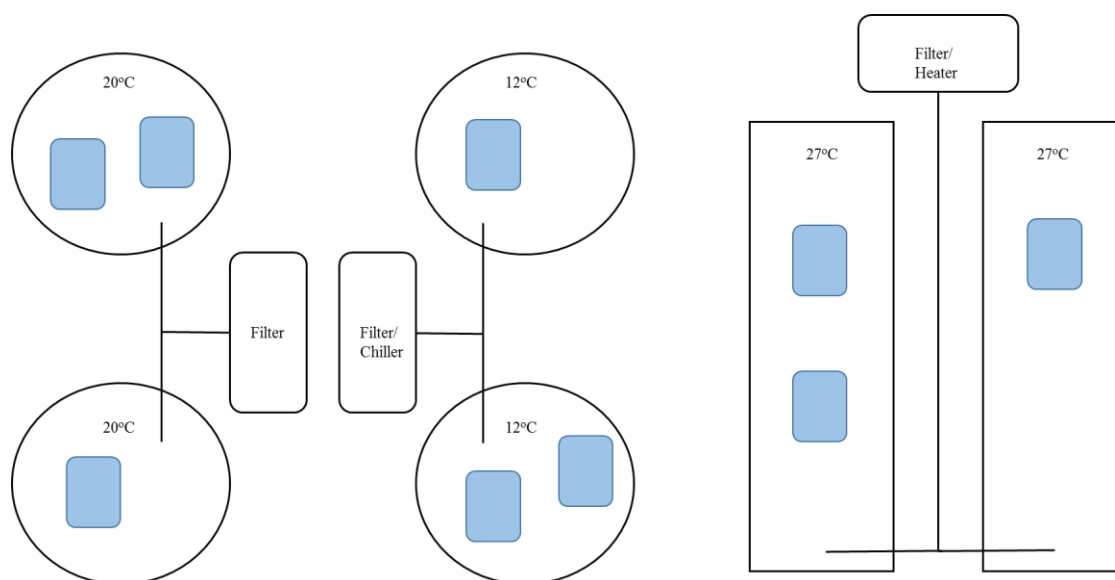




Figure 3-2. Mean number of juveniles birthed each week per live adult snail at each of 3 water temperatures. No juveniles were birthed by snails in the 12°C group.

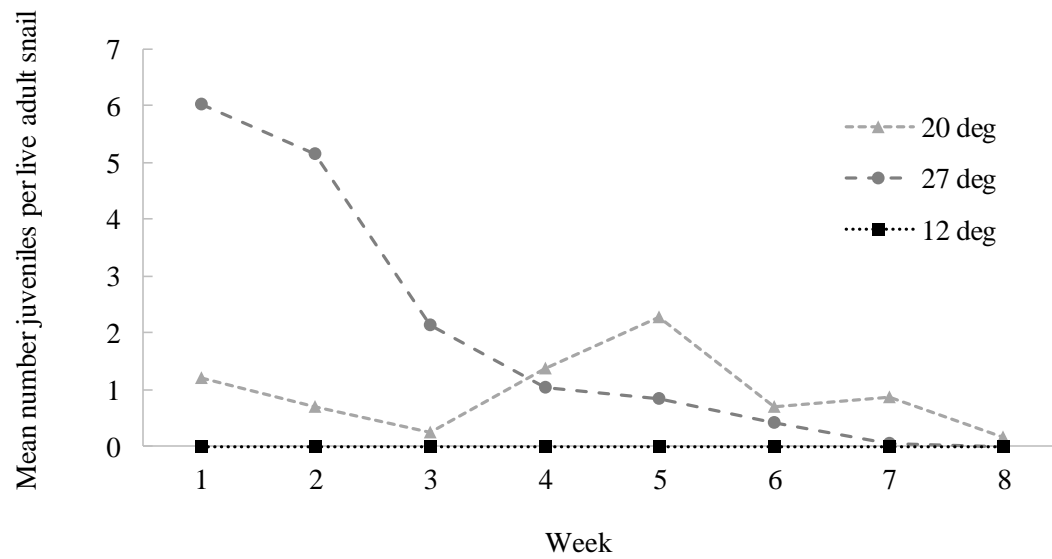


Figure 3-3. Least square regressions between adult female snail shell length (12°C, N=12; 20°C, N=10; 27°C, N=1) and number of developing embryos from females dissected at the end of the laboratory experiment. No line is indicated for 27°C due to a single data point.

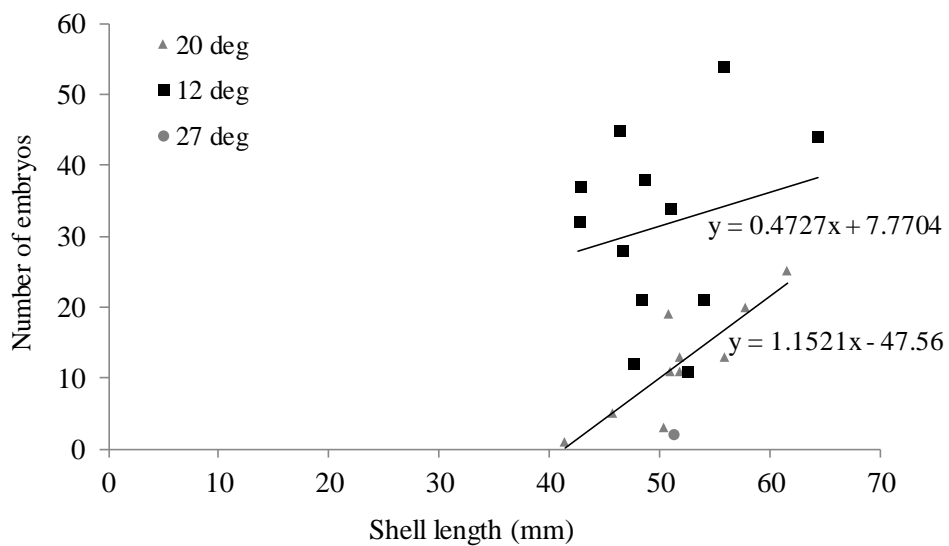


Figure 3-4. Relationship between adult female snail shell length (N=17) and number of developing embryos measured immediately after field collection from Wild Plum Lake, Nebraska. The trendline displayed represents an exponential relationship.

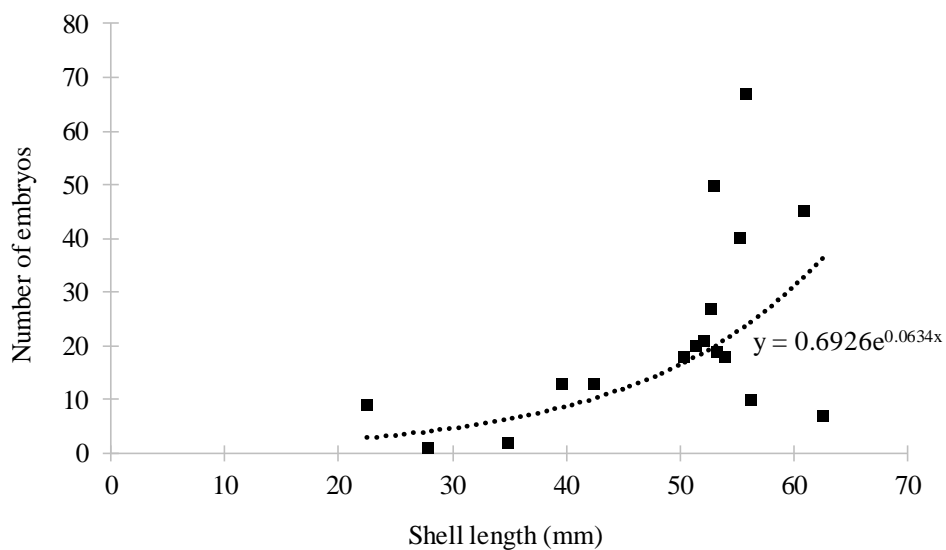
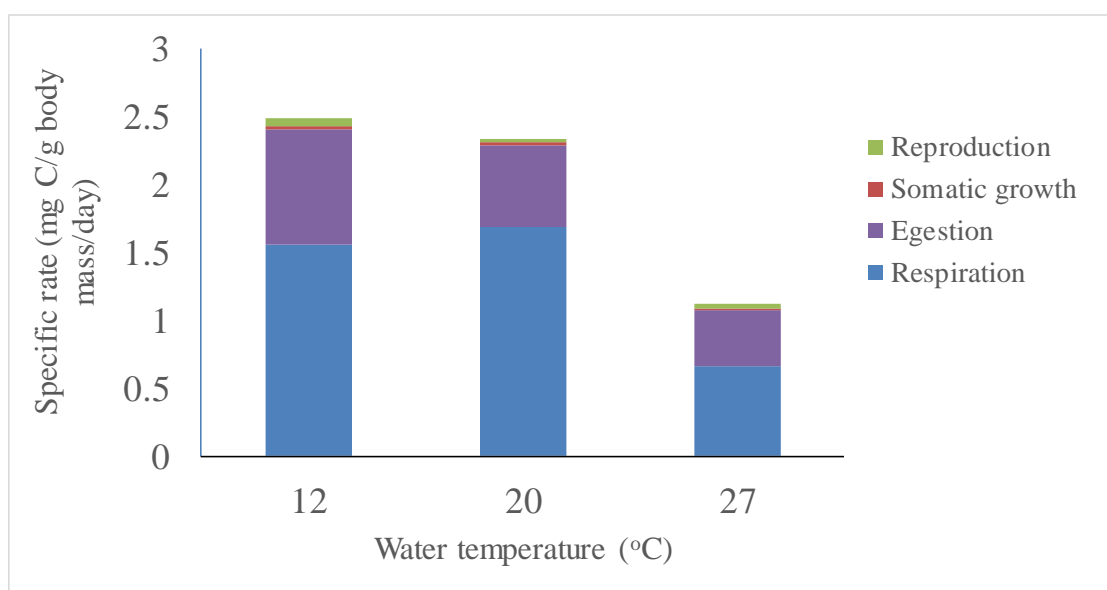


Figure 3-5. Carbon specific rates for the Chinese mystery snail at different water temperatures.



## CHAPTER 4: Identifying environmental predictors of presence or absence of the adult Chinese mystery snail

### Abstract

Habitat suitability models (HSM) predict spatial distributions of a species by statistically relating field observations with physical variables, quantify habitat requirements, and improve understanding of species-habitat relationships. The objective of this analysis was to identify physical, chemical, and biological lake characteristics that help predict where the Chinese mystery snail (*Bellamya chinensis*) is found, using a specific case study. Various data were compiled for 136 lakes that have been surveyed for aquatic invasive species in Vilas County, Wisconsin, and logistic regression was used to identify significant predictor variables of Chinese mystery snail presence. Analyses found lakes with Chinese mystery snails had a shallower mean depth, less Secchi visibility, higher conductivity, greater levels of shoreline development, more aquatic invasive species present, a greater number of boat landings, and lower latitudes. This model may be applicable to other regions with adequate lake-specific physical data.

### Introduction

In this era of globalization, the ability to predict local habitat conditions and biotic communities at a regional scale is critical for sound natural resource management (Zorn et al. 2008). In recent years, habitat suitability models (HSM) have been used at state and regional scales to monitor the spread of invasive species (Crall et al. 2013), as well as to predict potential spread before it happens (Guisan and Zimmerman 2000). Habitat

suitability models predict spatial distributions of a species by statistically relating field observations with physical variables (Hirzel et al. 2006, Porzig et al. 2014), quantify habitat requirements, and improve understanding of species-habitat relationships (Ahmadi-Nedushan et al. 2006). A habitat requirement is an abiotic feature of the environment necessary for the survival and persistence of an individual or population (Ahmadi-Nedushan et al. 2006). The U.S. Fish and Wildlife Service established HSM as the traditional habitat assessment approach in the early 1980's (USFWS 1981), and models have been completed for numerous terrestrial and aquatic species (NOAA 1997).

Original models relied on spatial data, mostly ignoring temporal data (Porzig et al. 2014), and only assessed the effects of individual environmental variables, rather than the cumulative effects of multiple variables (Ahmadi-Nedushan et al. 2006). Using this approach, variables are assessed one at a time and given a suitability value between 0 and 1. Values of 0 indicate conditions are intolerable for a species' survival and values of 1 indicate conditions are optimal. Individual suitability values can then be multiplied together to calculate a composite suitability index for a pre-defined site (Beecher et al. 2002), but this approach assumes an organism selects a particular variable independently of all other variables (Eq. 4-1). Hence, if a single variable receives a suitability value of 0, the entire site receives a composite score of 0, which may not reflect actual conditions.

(Eq. 4-1) 
$$HSI = SI_1 \times SI_2 \times \dots \times SI_n$$

As computing resources improved, HSM become more complex, and the original models used by the U.S. Fish and Wildlife Service serve as research starting points rather than as conclusive tools. Alternative methods include the arithmetic-mean method, the

geometric-mean method, and the lowest suitability index method (Ahmadi-Nedushan et al. 2006). The advantage of these approaches is that they assume one variable can compensate for poor conditions of other variables (Korman et al. 1994). The individual habitat suitability value for each variable is still calculated independently, but the average of all the values is used to calculate the composite score. The physical habitat can be displayed as a grid of individual cells, and the weighted usable area (WUA) within each cell is multiplied by the composite score (Vismara et al. 2001). These approaches to HSM assume that all included environmental variables are equally important to the growth and survival of a species, yet are all still considered independent of one another, with no cumulative interactions (Beecher et al. 2002). This assumption of equal importance can be addressed by using an exponential weighted relative importance value ( $b_n$ ) to an individual variable's suitability score ( $SI_n$ ) (Eq. 4-2). Though these modified HSM are improvements over the original method, organisms likely consider more than one environmental variable at a time; thus, a multivariate approach is more appropriate (Clark et al. 1993).

$$(Eq. 4-2) \quad HSI = SI_1^{b_1} \times SI_2^{b_2} \times \dots \times SI_n^{b_n}$$

Currently, the most commonly used HSM use species presence and absence data and are increasingly used to predict how species distributions might change with changing environmental conditions (Guisan and Zimmerman 2000). When using presence and absence data, a primary assumption is that the modeled species is in pseudo-equilibrium with its environment, meaning that all suitable habitats are occupied (Guisan and Thuiller 2005). Further, presence and absence data are based on the

assumptions that all present species are identified, all absent species are truly absent from a site, and no dispersal limitations exist (i.e., all suitable habitat is occupied by the species) (Cianfrani et al. 2010). Incorrect assumptions may result in unreliable predictions (Hirzel et al. 2001); predicting a false absence occurs when a model is over-fitted, and predicting a false presence occurs when a model is over-predicted (Guisan and Zimmermann 2000).

One application of HSM is to predict sites vulnerable to the establishment of invasive species (Ficetola et al. 2007). In order to construct a model, environmental requirements and thresholds of the modeled species must be known. The Chinese mystery snail (*Bellamya chinensis*) is a non-native gastropod species found in more than 30 states in the USA, as well as southern portions of Canada (Jokinen 1982), but little is known about its habitat requirements. Identifying sites amenable to supporting invasive populations allows managers to efficiently direct limited resources and increases the likelihood of successful prevention efforts. Shoreline development, distance to population centers, number of boat landings, biotic community composition, Secchi depth, conductivity, and calcium concentrations have been speculated as important environmental variables for determining habitat suitability of the Chinese mystery snail (Solomon et al. 2010). The objective of this analysis was to identify physical, chemical, and biological lake characteristics that help categorize where the Chinese mystery snail is found, using a specific case study.



## Methods

We compiled data from existing data sets to evaluate if we could identify trends or commonalities of environmental variables that helped explain the distribution of Chinese mystery snail populations. Lakes in Vilas County, Wisconsin have been intensively researched for > 40 years, and numerous state management and research agencies specifically research aquatic invasive species' distribution and effects in these lakes. Data on 17 variables (Table 4-1) from the North Temperate Lakes Long Term Ecological Research (NTL-LTER) and the Wisconsin Department of Natural Resources (WDNR) were compiled for 136 lakes that have been surveyed for aquatic invasive species. Of these, Chinese mystery snails were present in 56 lakes and absent in 80 lakes (Figure 4-1). Due to incomplete data sets, only variables with data available for > 75% of the lakes were included in subsequent analyses, resulting in 7 remaining variables (Table 4-1). The “glmulti” package in R was used to run a second order Akaike Information Criteria (AICc) to select the best model from a set of models (N=100) including possible combinations of these 7 variables (Akaike 1974). The calculated AICc weights represent the likelihood of a particular model, and this method selects the most parsimonious model while also considering the number of parameters included. The resulting model estimates the probability of a positive response occurring given a set of explanatory variables (Agresti 1996, Jongman et al. 1995). To evaluate the overall model and the individual parameter estimates, a Wald Test statistic was calculated for each variable. Goodness-of-fit was analyzed using a McFadden's  $R^2$  test, which measured the predictive power of our model. Pearson residuals were calculated for each lake, and both leverage and Cook's distance were measured for each.

With presence and absence data, logistic regression with a logit link function is appropriate (Ahmadi-Nedushan et al. 2006). Binomial distributions are assumed for logistic regression (Peng and So 2002). A response curve of a species describes the probability of a species being present,  $p_i$ , as a function of environmental variables (Fladung et al. 2003). The response variable is transformed by the logit link function (Agresti 1996), which transforms bounded probabilities between 0 and 1 to unbounded values using the following equation:

$$(Eq. 4-3) \quad g(x) = \log\left(\frac{p_i}{1-p_i}\right),$$

where  $p_i$  can be the probability of species presence in a cell (in this case a cell equals a lake, as we did not have abundance or within-lake distribution data available) and  $g(x)$  is the linear combination of environmental factors (Garland et al. 2002, Geist et al. 2000). The logit is the natural logarithm of the odds of Y (Peng and So 2002). Transforming the probability to odds removes the upper bounds and taking the logarithm of the odds removes the lower bound (Allison 1999). Thus, logistic regression is expressed as:

$$(Eq. 4-4) \quad \log\left(\frac{p_i}{1-p_i}\right) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n,$$

where  $\alpha$  is the y-intercept,  $\beta$  is slope,  $X_i$  is a predictor variable (data can be continuous or categorical);  $\alpha$  and  $\beta$  values are estimated by the maximum likelihood method (Peng and So 2002). In this case study, the outcome is dichotomous (either the lake has Chinese mystery snails or it does not). The null hypothesis states that all  $\beta$  values are equal to zero. If the null hypothesis is rejected, then there is a relationship between the predictor variables,  $X_i$ , and the outcome.

## Results

Seven variables were included in the AICc model selection: number of boat landings, maximum depth, distance to nearest population center, number of AIS present (Table 4-2), Secchi depth, latitude, and longitude (Table 4-3). The top 100 models (Appendix C) were constructed from these 7 variables and resulted in a top model including 3 variables:

$$CMS \sim \text{Mean Secchi depth} + \text{Number of AIS} + \text{Latitude},$$

with an AICc value of 116.34 and a weight of 0.20. Then, logistic regression was used to measure the relationship between Chinese mystery snail presence and absence and the environmental predictor variables (Table 4-5). McFadden's  $R^2$  test produced an  $R^2 = 0.49$  (Table 4-5). Variance inflation factor (VIF) tested for multicollinearity of each independent variable, and we concluded there was no evidence of multicollinearity (Table 4-5), (i.e., the model inputs were independent of each other) (Ohri 2013). Based on these the Pearson residuals calculated for each lake, no points were flagged as exceeding the influence thresholds (leverage  $> 2$  and Cook's distance  $> 4$ ).

## Discussion

To further our understanding of the Chinese mystery snail habitat requirements, we collected chemical, physical, and biological information from 136 lakes in Vilas County, Wisconsin. Of these lakes, 56 had Chinese mystery snails and 80 did not have Chinese mystery snails documented. After analyzing differences in the environmental variables, we found the top model included Secchi depth, total number of aquatic invasive species, and latitude.

Previous research has linked increases in residential and recreational shoreline development with decreases in littoral habitat quality, increases in invasive species introductions, and increases in fishing pressure (Carpenter et al. 2007). Humans are often responsible for the introduction of invasive species (Litvak and Mandrak 1993, Johnson and Carlton 1996, Johnson et al. 2001, Padilla and Williams 2004, Johnson et al. 2008, Kelly et al. 2013); however, there are conflicting reports on which variables best approximate levels of recreational activity in the absence of specific counts. In Vilas County, the level of shoreline development is positively correlated with lake surface area and negatively correlated with accessibility (defined as travel costs to get to a specific lake) (Schnaiberg et al. 2002). Another study found lake facilities (boat landings, campgrounds, better roads leading to a lake), lake surface area, and social perception of the quality of fishing were significant predictors of the average number of recreational boats on a lake during peak tourist season (July-August) (Reed-Andersen et al. 2000). Lakes without boats were typically hydrologically isolated, high in the landscape, and without public access (Reed-Andersen et al. 2000). In our study, lake surface area was not significantly different between lake groups (lakes with or without the Chinese mystery snail), and multivariate statistics indicated that neither shoreline development nor number of boat landings were significant predictors of presence or absence of the Chinese mystery snail. Perceived quality of recreational fishing was not included in our analysis, but values were estimated post hoc based on lake ratings on the popular fishing website Lake-Link; average lake ratings between lakes with and without the Chinese mystery snail were not significantly different (ANOVA,  $df = 2, 100$ ,  $F = 0.94$ ,  $p = 0.33$ ).

Despite these mixed reports, the total number of aquatic invasive species in a water body is a significant predictor of presence or absence of the Chinese mystery snail in this set of lakes, and while we do not know all vectors of spread for the Chinese mystery snail, we are aware of how some of these other species are spread. Eurasian watermilfoil (*Myriophyllum spicatum*) hitchhikes between lakes attached to recreational boats, trailers, and gear (Madsen 1998). In North America, the rusty crayfish (*Orconectes rusticus*) was initially introduced through legal and illegal stocking in natural waters and moved through man-made canals, but subsequent invasions are increasingly due to aquaculture, the food, aquarium, and pond trades, and use of crayfish as live bait (Lodge et al. 2000). Curly-leaf pondweed (*Potamogeton crispus*) introductions are believed to increase with higher levels of recreational activity and lake disturbance (Nichols 1999). Rainbow smelt (*Osmerus mordax*) spread through legal and illegal introductions, bait bucket dumping, and dispersal through drainage canals (Evans and Loftus 1987). Purple loosestrife (*Lythrum salicaria*) was likely initially introduced in packing materials shipped to North America (Mills et al. 1994), and through the horticulture industry, marketed as a desirable “wildflower” (Thompson et al. 1987). All of these other aquatic invasive species have strong human vectors of spread, thus it seems reasonable to conclude that humans influence the spread of the Chinese mystery snail, yet none of our proxies of human influence were highly influential predictors of presence or absence of the Chinese mystery snail. Additionally, a similar study looking at 44 lakes in Vilas County not only looked at presence and absence of the Chinese mystery snail, but also looked at abundance and distribution within lakes and found that the number of boat landings and the distance from the lake to the town of Minocqua, Wisconsin were both

significant predictors of increased Chinese mystery snail abundance within a lake (Solomon et al. 2010). Our present study does not include abundance, as that information does not exist for the majority of our included lakes. It is possible that the Chinese mystery snail may be correlated with the presence of other invasive species because of sampling bias – a lake is more likely to be reported to have multiple aquatic invasive species when it is searched specifically for aquatic invasive species, so there would naturally be a correlation among species being found together. Lakes without reports of the Chinese mystery snail may not have been searched for any invasive species.

Secchi depth is a measure of light penetration into a water body and is one means of quantifying water clarity. Secchi depth may be used as an indicator of water quality and as a proxy for measuring turbidity (a measure of the suspended particles in the water column) due to suspended inorganic particles or phytoplankton biomass. Interestingly, in a previous study of Vilas County lakes, no significant difference in mean Secchi depth was observed between lakes categorized as developed and undeveloped (Carpenter et al. 2007). A similar study reported shoreline development was not correlated with increased turbidity or chlorophyll-a (Stedman and Hammer 2006). Secchi depth likely varies for reasons other than anthropogenic influences in a watershed. Pertaining to aquatic invasive species, an increase in Secchi depth (i.e., greater water clarity) correlates with a higher likelihood of finding rusty crayfish in Vilas County lakes (Olden et al. 2011), but a decrease in Secchi depth is a significant predictor of greater Chinese mystery snail abundance (Solomon et al. 2010). Chinese mystery snails are more likely to be found in lakes with higher non-anthropogenic turbidity, such as lakes with high phytoplankton density, or lakes that were sampled after a storm or snowmelt event.

Latitude was the last indicator of Chinese mystery snail presence and absence, which coincides with results from previous research in the region (Solomon et al. 2010, though their study also included a few lakes in Oneida County, directly to the south of Vilas County). Climate records from around the county provided maximum and minimum air temperature, annual number of growing degree days, and intermittent data on ice-free days for a number of our study lakes. There were no significant differences across latitude, and Vilas County is only approximately 40-50 km from south to north. Most of the larger townships are in southern portions of the county but because of high tourism rates, distribution of permanent residents are not a reliable indicator of lake use. Second homes, cottage rentals, and campgrounds attract many temporary residents and tourists, especially during the summer months. One possible explanation of this effect is the WDNR's use of citizen science volunteers to collect limnological data. Lakes are not randomly selected; rather, a lake is often included in data collection if there is a volunteer who lives on or nearby the lake and has a vested interest in monitoring water quality. It is possible that lakes in the southern portion of the county are biased toward higher likelihood of being monitored; thus, there have been more reports of invasive species in southern lakes. Though our study measured distance to the nearest town, not all towns have equivalent numbers of permanent residents. Previous research linking distance to nearest population center with Chinese mystery snail abundance used Minocqua, Wisconsin as the only population center (Solomon et al. 2010); however, this population center is in Oneida County, not Vilas County. Generally speaking, we find Chinese mystery snails to be more abundant in the southern portions of their invasive range (Solomon et al. 2010), so we would expect a large-spatial-scale trend of snails in southern

portions of a study region; however, we did not find any climatological data available that indicated significant differences between the north and south portions of Vilas County.

Our top model included all three variables – total number of aquatic invasive species, Secchi depth, and latitude – meaning there is an interaction among these variables, providing interesting feedback for natural resource managers. The Chinese mystery snail is more likely to be found in lakes within the southern portion of Vilas County that have documentation of other aquatic invasive species and diminished water clarity. Conveniently, there is an online database tracking Secchi depth in real time, and the Wisconsin DNR has an established aquatic invasive species database for many of the county's lakes. Latitude is static, so this enables managers to identify lakes of concern before even heading out to the field. Identifying these lakes of concern also aids in the creation of a list of lakes that would most benefit from citizen science efforts, and new volunteers can be directed to these water bodies.

While our top model included only three variables, there were a few additional models that provided strong models: number of boat landings, mean lake depth, and distance to the nearest population center. These additional variables have the potential to build upon the top model by providing useful information to managers. The Chinese mystery snail was more often found in lakes with more public boat landings, deeper mean depth, and closer to population centers. In a region that relies heavily on tourism, these variables make logical sense: lakes that are easier to access (by either being geographically close to a population center or having more public access points) receive more human traffic and more opportunities for a species introduction. Deeper lakes tend



to have larger sportfish populations, also attracting boaters (and thus, hitchhiking invasive species). These additional variables allow managers to branch out past the lakes of concern identified using the top model. Conveniently, these metrics are also available for analysis without additional fieldwork.

In summary, we can say with confidence that Secchi depth, the number of aquatic invasive species, and latitude are significantly correlated with Chinese mystery snail presence and absence within Vilas County, Wisconsin lakes. This model may be applicable to other regions with adequate lake-specific physical, chemical, and biological data, though accurate distribution data for many aquatic invasive species are often lacking. Using a method like Ecological Niche Factor Analysis may be beneficial in future research, as this approach only requires presence data, eliminating the effects of false absence reports. Traditional habitat suitability models do not work well for predicting the potential spread of the Chinese mystery snail because the species (at least the adult Chinese mystery snail) has such a wide tolerance of environmental conditions (Appendix D). As a result, we should be trying to glean information from already-invaded sites, so that we may anticipate future sites of spread and make proactive management decisions. Finally, Chinese mystery snails are not the only invasive species we can study using this approach. Similar species, such as the New Zealand mudsnail (*Potamopyrgus antipodarum*), the zebra mussel (*Dreissena polymorpha*), and the apple snails (*Pomacea spp.*) can all be studied using similar models where data are available. Aquatic invasive species will always be an issue with which natural resource managers need to contend, so researchers need to get creative finding methods that can be applied to glean information on a variety of species.

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Table 4-1. Environmental variables collected for each lake in the case study example.

An \* indicates variables that were available for > 75% of lakes and thus, included in all analyses.

Environmental variable	Units
Surface area	ha
Maximum depth*	m
Mean depth	m
Distance from nearest population center*	km
Secchi depth*	m
Conductivity	µS/cm
Alkalinity	µeq/L
Chlorophyll-a	µg/L
Ca <sup>2+</sup> concentration	mg/L
Total phosphorus	µg/L
Latitude*	decimal degrees
Longitude*	decimal degrees
pH	
Number of aquatic invasive species*	
Number of boat landings*	
Lake type <sup>1</sup> :	
Drainage	
Seepage	
Spring	
Shoreline development <sup>2</sup> :	
High	
Medium	
Low	
Dominant substrate type <sup>1</sup> :	
Sand	
Gravel	
Rock	
Muck	

<sup>1</sup>WI DNR Classification

<sup>2</sup>Vilas County Zoning and Planning Department Classification

Table 4-2. Aquatic invasive species present in each lake included in case study. CMS = Chinese mystery snail (*Bellamya chinensis*), BMS = Banded mystery snail (*Viviparus georgianus*), RCF = Rusty crayfish (*Orconectes rusticus*), EWM = Eurasian water-milfoil (*Myriophyllum spicatum*), CLP = Curly-leaf pondweed (*Potamogeton crispus*), FWJ = Freshwater jellyfish (*Craspedacusta sowerbyi*), PLS = Purple loosestrife (*Lythrum salicaria*), RBS = Rainbow smelt (*Osmerus mordax*), SWF = Spiny-water flea (*Bythotrephes longimanus*).

Lake name	CMS	BMS	RCF	EWM	CLP	FWJ	PLS	RBS	SWF
Adams		X							
Allequash	X								
Anderson			X					X	
Anne			X						
Anvil	X	X	X	X					
Arrowhead	X		X	X					
Averill			X						
Baker	X								
Ballard		X							
Big Arbor Vitae	X	X	X		X				
Big Kitten						X			
Big	X	X	X						
Big Muskellunge			X						
Big Portage			X						
Big Sand	X			X	X				
Big St. Germain	X	X	X						
Birch	X		X						
Black Oak			X						
Boulder	X		X						
Brandy	X								
Buckskin	X								
Carpenter	X								
Catfish	X		X	X					
Circle Lily			X						
Clear		X	X						
Constance									
Crab			X						
Crystal								X	
Day									
Dead Pike								X	
Deerskin									
Diamond			X						

Table 4.2. Continued.

Lake name	CMS	BMS	RCF	EWM	CLP	FWJ	PLS	RBS	SWF
Dollar									
Duck	X	X	X	X					
Eagle	X	X	X	X					
East Ellerson									
Escanaba			X		X				
Fawn		X	X						
Fence		X						X	
Finger	X								
Fishtrap	X	X	X						
Forest		X		X					
Found		X							
Grassy									
Gunlock	X						X		
Harris					X				
Haskell									
Helen									
High	X	X	X						
Horsehead									
Hunter	X								
Ike Walton									
Imogene						X			
Island	X	X	X		X				
Jag									
Johnson		X							
Jute									
Kentuck	X	X	X	X	X		X		
Lac Vieux Desert	X	X	X	X	X	X			
Lake Flambeau								X	
Lake Laura		X							
Lake Salsich						X			
Landing									
Little Arbor Vitae	X	X	X						
Little Bass	X								
Little Crawling Stone	X	X	X					X	
Little Crooked			X						
Little Gibson	X								
Little Papoose			X						
Little Portage									
Little Spider	X		X			X			
Little Trout								X	
Long Interlaken	X	X						X	
Long Lake	X			X		X		X	
Loon Lake	X								
Lower Buckatabon	X								
Lynx									
Madeline	X								





Table 4-2. Continued.

Lake name	CMS	BMS	RCF	EWM	CLP	FWJ	PLS	RBS	SWF
Towanda									
Trout	X	X							
Turner		X	X						X
Upper Gresham			X						
Van Vliet	X		X	X					
Watersmeet			X						
West Bay			X	X					
White Sand	X		X						
Whitefish			X				X		
Wildcat									
Wishow	X	X				X			
Wolf									
Yellow Birch									
Zee			X	X					

Table 4-3. Summary statistics for the variables used in model development.

Variable	Minimum	First quartile	Median	Mean	Third quartile	Maximum
Number of boat landings	0.0	0.0	1.0	0.8	1.0	4.0
Maximum depth	1.2	6.8	10.2	11.5	13.8	35.7
Distance to nearest population center	0.0	6.1	10.3	10.9	14.3	34.0
Number of AIS	0.0	1.0	1.0	1.6	2.3	6.0
Secchi depth	1.0	2.1	2.9	3.4	4.0	15.0
Latitude	45.9	46.0	46.0	46.1	46.2	46.3
Longitude	-90.1	-89.8	-89.6	-89.6	-89.3	-89.0

Table 4-4. Top 5 models selected with AICc selection method (from N=100).

Rank	Model	AICc	k	Delta	Weight
1	CMS~Number AIS + Secchi depth + Latitude	116.34	5	0.00	0.20
2	CMS~Number AIS + Secchi depth + Latitude + Max depth	117.58	6	1.24	0.11
3	CMS~Number AIS + Secchi depth + Latitude + Longitude	118.12	6	1.78	0.08
4	CMS~Number AIS + Secchi depth + Latitude + Distance	118.22	6	1.88	0.08
5	CMS~Number AIS + Secchi depth + Latitude + Landings	118.27	6	1.93	0.08

Table 4-5. Summary of logistic regression results for the top model.

	Final model								
Variable	$\beta$		SE( $\beta$ )	Lower 95% CI	Upper 95% CI	Wald statistic	<i>p</i> -value	VIF	Odds ratio
Intercept	359.50	**	116.75	171.61	769.76	9.48	0.002		>1E40
Number of AIS	1.68	***	0.31	1.13	2.41	29.73	<0.001	1.04	5.37
Secchi depth	-0.61	**	0.20	-1.02	-0.06	9.35	0.002	1.00	0.54
Latitude	-7.83	**	2.54	-14.17	-3.04	9.53	0.002	1.04	0.00
AICc	109.91								
Test	Statistic		<i>p</i> -value						
Pearson Chi-square	99.01		0.98						
Likelihood ratio	87.14		<0.001						
Hosmer-Lemshow	12.28		0.14						
McFadden's R <sup>2</sup>	0.49								

\* $p < 0.05$ . \*\* $p < 0.01$ . \*\*\* $p < 0.001$ .

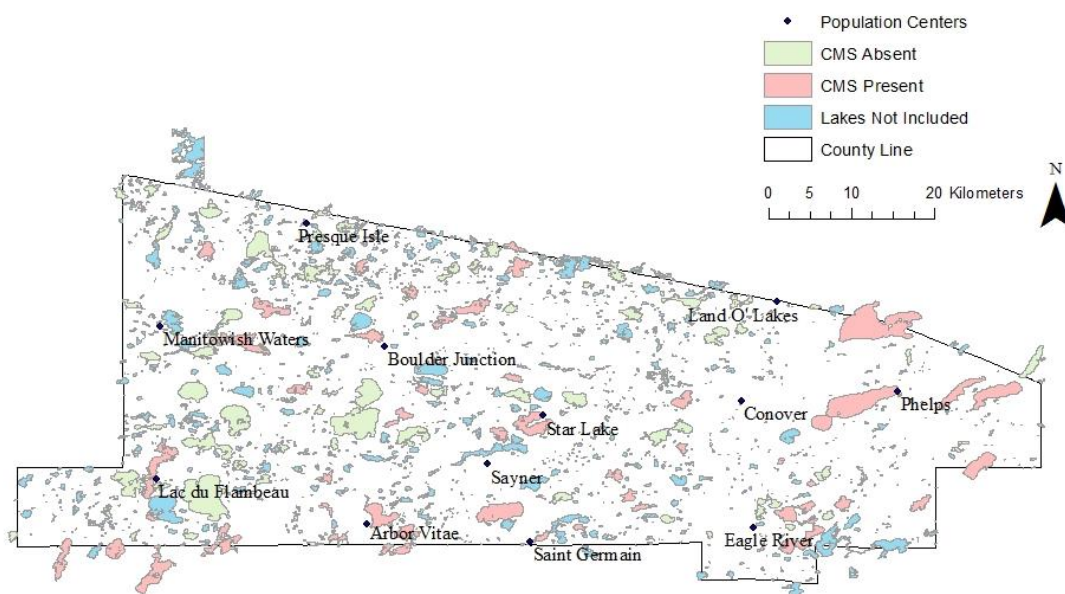


Figure 4-1. Map of named lakes in Vilas County, Wisconsin. Red lakes had Chinese mystery snails (CMS), green lakes did not have Chinese mystery snails, and blue lakes were not included in the analysis. Towns used to determine “distance to nearest population center” are marked.

## CHAPTER 5: Coupling ecological and social network models to assess “transmission” and “contagion” of an aquatic invasive species

### Abstract

Network analysis has been employed to answer a variety of economic, ecological, social, and epidemiological questions, but novel approaches that combine multiple models are needed to better understand how these varied, complex systems are interconnected and influence one another. Understanding how humans use natural resources is critical for effective resource management, and understanding how an ecosystem responds to disturbances, whether intentional (e.g., stocking fish species) or unintentional (e.g., introduction of a non-native species), allows managers to make proactive, rather than reactive, decisions. The objectives of this project were twofold; first, develop a method for coupling social and ecological network models so that they may be used in tandem, and second, use these models to assess both how humans aid the movement of an aquatic species and what effects this species has on an ecosystem after introduction. Here, we adapt the framework of infectious disease network modeling to couple an existing social network model and newly developed ecological network models to develop a working, coupled, dual-aspect model. The Salt Valley region in Southeastern Nebraska, USA, is used as our case study to test this this novel, coupled-model approach. We assess both how angler movement among reservoirs aids in the spread of an invasive species (*Bellamyia chinensis*), and how the introduction of *B. chinensis* affects energy

flows within individual-lake food webs. This case study demonstrates the applicability of combining both social and ecological models to address an interdisciplinary problem within a complex, social-ecological system that can be applied to numerous non-native species.

## Introduction

### *Network analysis*

Network analysis has been employed for economic, ecological, social, and epidemiological research. One method for quantifying how a species may influence its environment is ecological network analysis (ENA). This method is particularly helpful for investigating potential effects before a species has been introduced, allowing managers to be proactive rather than reactive, and it accepts that ecosystems consist of complex networks of interactions and allows for a holistic examination of the system in question (Fath et al. 2007). Rather than investigating how an invasive species impacts one or two species, we can use ENA to assess how energy flows throughout an entire food web are affected; we are not limited to a subset of the ecosystem (Fath et al. 2007). Individual species or functional groups exchange energy with other groups; in network analysis the species or group is represented by a node and the exchanges are represented by connecting edges. Ecosystem resilience can be assessed by adding or removing nodes and observing how the system reacts in a simulated future (Janssen et al. 2006). A number of user-friendly software platforms have been developed specifically for ENA modeling, permitting its application to a variety of ecosystems and questions.



The strong human component embedded in the problem of spreading aquatic invasive species naturally leads to a direct link with social network analysis. Social network analysis is based on graph theory and statistics and prompts the collection of qualitative data relevant to the study system that can then be analyzed using quantitative methods (Janssen et al. 2006). The structural characteristics of networks can be analyzed to help gauge the resilience of the system. Connectivity of a node is the ratio of the number of direct links it has with other nodes to the total number of links in the network. Entrenched in the concept of connectivity is that of reachability, or whether a path exists between two nodes. Nodes that have lower connectivity and require more steps to get to are less likely to be impacted by whatever flow is being measured through the network. In contrast, these less-connected nodes tend to be less resilient to disruptions to the network, whereas well-connected nodes are more resilient to network perturbations because of higher redundancy. Another network characteristic, centrality (Wasserman and Faust 1994), can be used to identify nodes that have a higher-than-average number of connections (i.e., these nodes act as network hubs). High centrality nodes may act as connectors within the system; if they are removed, the network could split into two separate networks (Janssen et al. 2006). Degree centrality measures the number of links a node has, and betweenness centrality measures how influential a node is at reducing the path length between any two nodes (Freeman 1979).

#### *Infectious disease model framework*

Combining ecological and social networks into one working model, while discussed theoretically, has not been successfully implemented, but would allow an

investigation into how ecosystem components are connected by the movement of people. Parallels exist between modeling the spread of invasive species and modeling the spread of infectious diseases (Byers et al. 2009, Floerl et al. 2009, Meentemeyer et al. 2011). Infectious diseases spread through networks via physical contacts of individuals (Meyers et al. 2005). The transmissibility of a disease is the average probability of an infected person (represented by a node) transmitting the disease to a susceptible person through physical contact (represented by an edge) (Meyers et al. 2005). When a host is infected, network analysis allows scientists to calculate how many secondary cases are likely to occur as a result of contact with the primary host (Meyers et al. 2005), as well as the average number of connections for an infected host (Hethcote 2000). Using this same framework, we would like to calculate the probability of a species from an “infected and contagious” primary host reservoir (represented by a node) being “transmitted” (introduced) to a new reservoir as a result of human movement (represented by a directed edge between nodes). Once the species has “infected” a new lake, we can then proceed to calculate how long it takes for the population to become large enough so that the reservoir becomes “contagious” and is capable of acting as a source population. We can also monitor how a species introduction affects biomass and energy flows among groups in the new ecosystem.

#### *Aquatic invasive species*

As global movements of humans and goods increase, so do the number of non-native species introduction events. A non-native species that establishes in a novel environment and then proceeds to disrupt ecosystem structure and functioning is called

an invasive species (Lodge and Shrader-Frechette 2003). Invasive species are expensive to manage, both economically (Pimentel et al. 2005) and ecologically (Byers 2009), and are almost impossible to eliminate once a reproducing population has been established.

Invasive species cost the USA an estimated \$120 billion per year in environmental and economic damages and are responsible for approximately 40% of listed Threatened and Endangered species as a result of direct (e.g., predation) and indirect (e.g., competition for food or habitat) interactions (Pimentel et al. 2005). Herbivores and detritivores are the least studied invasive species groups, despite their potential detrimental effects on biodiversity (Thomsen et al. 2014). Over half of all recent invasive species studies (N=137) focused on species in the USA, predominantly in temperate regions, and only 33 focused on invasive species found in freshwater lakes (Thomsen et al. 2014). Though over 80 mollusk species have been introduced, only three have received ample attention: the zebra mussel (*Dreissena polymorpha*), the quagga mussel (*Dreissena bugensis*), and the Asian clam (*Corbicula fluminea*). Combined, these three species cost the USA approximately \$2 billion in damages each year (OTA 1993, U.S. Army Corps of Engineers 2002, Pimentel et al. 2005). Less represented in research are the effects invasive gastropods have on ecosystems, especially freshwater reservoirs.

### *Resilience theory*

The field of ecology now accepts that ecosystems are dynamic social-ecological systems (Dame and Christian 2006), and researching how an invasive species affects ecosystem structure and functioning allows us to assess the ecosystem's resilience.

According to resilience theory, ecosystems can persist in different stable states, or regimes, based on the structure and functions that take place, and as dynamic systems, a certain amount of perturbation (either natural or anthropogenic) can be “absorbed” before a regime shift takes place (Folke 2006). Incidentally, most aquatic invasive species passively spread through the movement of humans (Vander Zanden and Olden 2008) and are capable of causing a system to undergo a regime shift to a new, often undesirable, dominating stable state. Identifying which species are of most concern with respect to causing these changes should be a priority for natural resource managers. Knowing that eradicating established species is difficult if not impossible, prevention is critical, but with thousands of species and limited resources, identifying which species may cause the most harm is essential (Byers et al. 2002). This necessity is further complicated by the difficulty of quantifying resilience.

### *Objectives*

A geographically focused case study is used in our attempt to demonstrate how social and ecological models can be used together to answer social-ecological questions. The objectives of the current research study are twofold: 1) couple a social network depicting human movement among regional reservoirs with each reservoir’s individual ecosystem network model to assess how perturbations influence biomass and energy flows throughout the entire network, and 2) assess the specific impacts the non-native Chinese mystery snail (*Bellamya chinensis*) would have on the region and estimate its introduction probability to individual reservoirs based on human movement.

## Methods

### *Study area*

The Salt Valley region of southeastern Nebraska, USA comprises 19 reservoirs which were included in the current study (Figure 1). Reservoirs range from 0.048 to 7.28 km<sup>2</sup> in surface area, and have variable fish communities and stocking regimes (Table 1). Some aquatic invasive species are already established in Salt Valley reservoirs (Table 1). Parts of this region are urbanized (around the City of Lincoln), and much of it is rural agricultural land dedicated to row crops and pastures.

### *Social network development*

Members of the Nebraska Game and Parks Commission (NGPC) and Nebraska Cooperative Fish and Wildlife Research Unit (NCFWRU) conducted in-person and mail-return angler surveys between 2009 and 2012. Specifically, data on number of anglers, angling methods, species sought, use of other Salt Valley reservoirs, and demographics were collected and compiled, providing the raw data for the social component of the current research project (Martin 2013). Experimental design, data collection, and results are well-documented (Chizinski et al. 2014, Martin et al. 2014).

Data on reservoir substitutability was obtained from the in-person angler interviews and analyzed using the iGraph package in R. Directed connections between nodes (reservoirs) were normalized to correct for different survey sizes and then weighted to depict the number of anglers who moved between two particular nodes. This provided a social network of how often anglers move between and among reservoirs in the region.

Boat anglers were also asked where they last fished (with their boat), so we were able to create a network depicting where anglers are coming from, including reservoirs and lakes outside of the current study area, a critical piece of information when studying aquatic invasive species that are passively transported due to human movements.

Reservoirs that already have Chinese mystery snails were classified as “infected” nodes and the original 5 are considered primary hosts, whereas reservoirs that do not yet have Chinese mystery snails were classified as “susceptible” nodes. In terms of infectious disease models, the weights of these connections (the number of anglers moving between two reservoirs) represent the transmission rate between nodes. We estimated the maximum percentage of live snails that could successfully be introduced to a new lake via hitchhiking on macrophytes attached to boat trailers was 0.12% (i.e. infection rate) (Johnson et al. 2001). In other words, an introduction of live snails will occur during 0.12% of angler movements from an infected node to a susceptible node, meaning time to infection varies with the number of anglers moving between two specific lakes. This value gives us the propagule frequency, or the average number of possible introduction events over a period of time, but not the propagule size (the number of individuals introduced with each event) (Wittmann et al. 2014). Propagule size is difficult to estimate. Female Chinese mystery snails give live birth, they may be carrying a number of viable juveniles at any given time; when they undergo stress in the laboratory, they tend to give birth rapidly (personal observation). Thus, we assume the introduction of a single individual is adequate to establish a new population.

#### *Model species*

The Chinese mystery snail is native to Asia and was first recorded in North America in 1892 as a live food source imported to the San Francisco food market (Wood 1892). The species has since spread to numerous lakes and slow-moving rivers throughout the USA as well as in southern portions of Canada (Olden et al. 2013). Adult Chinese mystery snails are large, reaching shell lengths of 70 mm, live 4-5 years (Jokinen 1982), have an average annual fecundity of 30 juveniles/female (Stephen et al. 2013), and can achieve high population densities (Chaine et al. 2012) that have been reported to fluctuate with environmental conditions (Haak et al. 2013). Despite these fluctuations, adult individuals have survived desiccation experiments longer than 9 weeks (Unstad et al. 2013), have a wide temperature tolerance (Wong et al., unpublished data), and are resistant to traditional invasive species management techniques (Haak et al. 2014). All Chinese mystery snails graze on algae and periphyton, but adults > 43 mm are also capable of suspension feeding (Olden et al. 2013). Adults reproduce sexually, and females give live birth to young, often brooding juveniles at various stages of development at a time (Stephen et al. 2013).

Limited research exists on the effects Chinese mystery snails have on their non-native environments. When present alone, the Chinese mystery snail does not appear to harm native snail abundance (Solomon et al. 2010); however, when present with the invasive rusty crayfish (*Orconectes rusticus*) (Table 2), native snail biomasses decrease (Johnson et al. 2009). The Chinese mystery snail also increases the N:P ratio in the water columns of invaded lakes (Johnson et al. 2009).

Five (Branched Oak, Pawnee, Wild Plum, Wagon Train, and Holmes) of the 19 Salt Valley reservoirs have established populations of Chinese mystery snails; however no research has examined how (or if) the snails affect energy flows within these flood-control reservoirs. Despite some species causing a great amount of damage to their novel ecosystems, it has been estimated that 80 – 90% of non-native species actually have minimal effects in their introduced range (Williamson 1996). The current lack of information on this species prompted our use of it in this research.

#### *Ecological network development*

If a snail is successfully transported from an infected reservoir to a susceptible reservoir, then what will happen to the newly infected ecosystem? In cases where a reproducing population develops, we wanted to estimate how this disturbance affects the flows of energy within each reservoir. To do this required developing ecosystem network models for each of the 19 study reservoirs. Using the dominant fish community as the basis for each network (Table 1), we were able to identify and compartmentalize species or functional groups critical to the trophic web of each reservoir.

Models were developed using the software Ecopath with Ecosim (Polovina 1984, Christensen and Pauly 1995). The first step is creating a static mass-balanced model of the system in Ecopath, based on current community composition. This requires data on three of four categories for each species or group: biomass (metric tons/km<sup>2</sup>), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), and ecotrophic efficiency (EE) (see Appendix). The production/biomass ratio is equivalent to the total mortality rate for a species or group (Allen 1971), and ecotrophic efficiency is the portion



of production consumed in the system or exported (Walters et al. 1997). Additionally, a diet composition matrix representing proportions of each type of prey in a predator's diet is necessary. These values, combined with the fishing pressure on species within each reservoir (from the NGPC and NCFWRU creel project), were used to develop a mass-balanced model based on Equation 1:

$$\text{Eq. 1} \quad B_i \times (P/B)_i \times EE_i = Y_i + \sum_{j=1}^n B_j \times (Q/B)_j \times DC_{ji}$$

where:  $B_i$  is the biomass of group  $i$  during a given time period;  $(P/B)_i$  is the production/biomass ratio of group  $i$ ;  $EE_i$  is ecotrophic efficiency of group  $i$ ;  $Y_i$  is the yield of group  $i$ , i.e.,  $(Y_i = F_i \times B_i)$ , where  $F_i$  is mortality due to fishing;  $B_j$  is the biomass of consumers or predators;  $(Q/B)_j$  is food consumption per unit of biomass of predator  $j$ ; and  $DC_{ji}$  is the proportion of  $i$  in the diet of  $j$ . Details on the development of this equation can be found in Christensen and Pauly (1992a, b).

Input data were collected from empirical studies on specific reservoirs when available; however, because much of this information has never been measured for these reservoirs, reported values for each were collected from the literature, using values from similar aquatic ecosystems when possible (i.e., reservoirs or small lakes in the Midwestern USA). Confidence in the quality of input variables is calculated using the Pedigree function in Ecopath (see Appendix). After inputs were entered, models did not always mass-balance immediately. To manually balance each model, the diet composition matrix was adjusted (never exceeding  $\pm 10\%$  of the initial value). Once these

options were exhausted, small adjustments were made to input variables for which we had the least confidence (also never exceeding  $\pm 10\%$  of the initial value). Through this process, balanced models were achieved for each reservoir.

A population estimate for Chinese mystery snail was empirically derived (126.75 t/km<sup>2</sup>) for one of the study reservoirs, Wild Plum, in 2011 (Chaine et al. 2012). The subsequent drought of 2012 caused a mortality event, and the population estimate was recalculated to be 38.58 t/km<sup>2</sup> (Haak et al. 2013). To observe what biological community would be necessary to support such a biomass, we developed a second Ecopath mass-balanced model for each lake, adding Chinese mystery snails at this post-drought biomass level, and the two models were compared. Likewise, in the five reservoirs that already had Chinese mystery snail populations, we removed the snails from the lake and developed a new Ecopath mass-balanced model reflecting possible conditions in the absence of snails.

Once all mass-balanced models were developed, Ecosim was used to create dynamic models by re-expressing Equation 1 as a set of differential equations as illustrated by Equation 2 (Walters et al. 1997).

$$\text{Eq. 2} \quad \frac{dB_i}{dt} = f(B) - M_0 B_i - F_i B_i - \sum_{j=1}^n c_{ij}(B_i, B_j)$$

where:  $f(B)$  is a function of  $B_i$  if  $i$  is a primary producer or

$$f(B) = g_i \sum_{j=1}^n c_{ji} \times (B_i, B_j) \text{ if } i \text{ is a consumer (Walter et al. 1997).}$$

Ecosim also reflects prey vulnerability when developing the dynamic model, and adjusting vulnerability estimates dictates whether the model is donor-controlled or “joint limited”. In a donor-controlled model, consumer abundance is ignored when calculating flow from  $i$  to  $j$ , and in a joint-limited model, flows are adjusted based on prey and predator biomasses (Walters et al. 1997). Low vulnerability values create a donor-controlled model, and high vulnerability values create “top-down” models with trophic cascades (Walters et al. 1997, Carpenter and Kitchell 1993). In the current report, we discuss results based on donor-controlled models only.

Dynamic models were developed under two scenarios: 1) the Chinese mystery snail was introduced at a density of  $0.0003 \text{ t/km}^2$  (the lowest value supported by the software, or approximately 8 snails) and projected without biomass forcing and 2) the Chinese mystery snail was introduced at a density of  $0.0003 \text{ t/km}^2$  and a biomass forcing function was loaded to simulate effects resulting from snail biomasses determined by logistic growth (de Vlamar 2006) from the introduced density up to the carrying capacity. Carrying capacity was calculated for each reservoir, using a conservative value of 10% ( $3.838 \text{ t/km}^2$ ) of the empirically calculated post-drought Chinese mystery snail population in Wild Plum of  $38.58 \text{ t/km}^2$  biomass value (described in Langseth et al. 2012).

#### *Coupling social and ecological network models*

Drawing on the framework for infectious disease network modeling, we attempted to insert individual ecological models within the existing social network (Figure 2). As previously mentioned, infectious disease modeling is conceptually similar

to the spread of non-native species. Infectious disease models include primary hosts, transmission rates lag times until an infected individual becomes contagious, and then secondary hosts who get infected and eventually become source populations of the disease (Meyer et al. 2005). In terms of the current research, primary hosts are reservoirs that currently have Chinese mystery snail populations (represented as nodes), transmission rates can be estimated based on the social network depicting angler movement (represented by directed edges between nodes), and lag times can be calculated by using the ecological networks to simulate population growth within a newly invaded reservoir. Finally, we can combine this information to project an invasion timeline within this group of reservoirs while also evaluating how a system's structure (biomass values) and function (energy flows) is affected by the introduction of the Chinese mystery snail. Variations in how a system responds to the disturbance of an added species in the network enables us to begin estimating how resilient an individual reservoir is to stressors on the system.

## Results

### *Social network analysis*

The in-person angler surveys collected information on how anglers view reservoirs as substitutable. Anglers were asked to provide the name of a specific water body when asked where they would go if a reservoir was immediately closed. Of the 4601 anglers interviewed, 3746 (81%) stated they would move to another reservoir within the Salt Valley region. Another 684 anglers (15%) said they would go to a water

body outside of the study area, and 171 (4%) were unsure to which water body they would move.

Using the answers from the anglers who would stay within the Salt Valley, a directed network displaying their responses was developed (Figure 3). Nodes represent each reservoir and the thickness of the edge depicts the percentage of respondents from one reservoir who would move to each of the other reservoirs. No edge connecting two reservoirs signifies that no angler specified they would move to that specific reservoir. Betweenness, closeness, and degree were calculated for each node in the network (Table 3). Betweenness values for East and West Twin Lake and Bowling Lake are zero because no in-person interviews were collected from these two reservoirs. Additionally, while there are only 19 reservoirs, the highest possible degree is 38 due to the directed nature of the network.

Anglers utilizing a boat were asked an additional question on which water body they last fished with their boat; 2582 responses were recorded. Of these, 1908 (74%) had last fished at a Salt Valley reservoir, and 674 (26%) had last fished at a water body outside of the region. A weighted, directed network was developed, depicting boat movement among reservoirs (Figure 4). Similar to the previous network, nodes represent each reservoir, but an additional node is added to represent water bodies outside of the study area. Edge thickness depicts the percentage of respondents who had previously been at a specific reservoir and moved to the reservoir where they were interviewed. Betweenness, closeness, and degree values were calculated for each node within the network (Table 4).

### *Ecological network analysis*

An initial mass-balanced Ecopath model was developed for each of the 19 reservoirs to represent current conditions. Total consumption, export, respiration, production, and throughput values were calculated for each reservoir. A second mass-balanced Ecopath model was developed for each reservoir at the estimated biomass currently found in Wild Plum reservoir (the only empirically-derived population estimate for any of the reservoirs, 38.58 t/km<sup>2</sup>). Total consumption, export, respiration, production, and throughput values were recalculated to determine the physical resources that would be necessary to sustain this set biomass of Chinese mystery snails in each reservoir. These secondary models do not necessarily represent conditions that are ecologically feasible; rather, they are used to quantify the resources that would be necessary to support such a population size. The Wild Plum population biomass was used as the reference point, so Wild Plum was only included in the secondary model and thus excluded from statistical analyses ( $N = 18$ ). The values for the first and second sets of models were averaged together (Figure 5) and compared using paired, two-sample means t-tests (Frisk et al. 2011). All values were statistically different, with  $p$ -values  $< 0.01$  ( $\alpha=0.05$ ).

After running and analyzing these second Ecopath models for the reservoirs, we returned to the initial (first) 14 Ecopath models for reservoirs that do not yet have Chinese mystery snails. Using these initial mass-balanced static models as input, we simulated biomass changes over a 25-year period using the second half of the software, Ecosim. Chinese mystery snails were introduced into each reservoir at the lowest density

allowed by the software ( $0.0003 \text{ t/km}^2$ ), and two scenarios were modeled: one without biomass forcing and one with biomass forcing based on logistic growth. When no biomass forcing function was used, the Chinese mystery snail populations stayed equal to the initial density or even decreased. An ANOVA yielded no significant differences among comparable flow values at model years 0, 10, 15, or 20 ( $p > 0.5$ ).

When forcing biomass using a logistic growth model to estimate population size over time, mean flow values for consumption, exports, respiration, production, flows to detritus, and total system throughput at simulation-year 20 were significantly greater than those of simulation year 0, 10, and 15 (Figure 6). Two-way ANOVAs yielded p-values of 0.0009, 0.001, 0.00003, 0.0001, 0.002, and 0.0002, respectively, and a Tukey HSD analysis specified that all 20 year values were significantly higher than the other values ( $p < 0.01$ ).

Despite having significantly higher flows at simulation-year 20, there were no significant changes in network metrics of connectance index (the number of actual connections in relation to the number of total possible connections), transfer efficiency (the fraction of the total food intake by a trophic level that is transferred to the next highest trophic level), and system omnivory index (a measure of the extent to which a network displays web-like features), even with biomass forcing (two-way ANOVA,  $p > 0.05$ ), though the total system biomass (excluding detritus) significantly increased at year 20 (two-way ANOVA and Tukey HSD,  $p = 0.006$ ).

In general, mid-trophic level fishes, such as crappie, channel and flathead catfish, and bluegill, were most often negatively affected by the introduction of the Chinese

mystery snail, resulting in lower biomass values (Table 5). Predator fish and terrestrial predators increased in biomass after an introduction, as well as zooplankton and autotroph biomass.

### *Coupled social and ecological network models*

Coupling social and ecological models was possible by applying our study system to the framework of infectious disease modeling. Reservoirs with established Chinese mystery snail source populations that can be spread are termed infected and contagious. In terms of infectious disease models, these reservoirs would be the primary hosts from which future infections stem. Reservoirs without the Chinese mystery snail are considered susceptible to infection (an infection is the same as a species introduction event). Using the infection rate of 0.12% and the calculated lag time individual to each reservoir, a map of projected invasion over the next 25 years was developed. Through this method, primary host reservoirs critical to the spread of Chinese mystery snail were identified. Wagon Train, Branched Oak, and Pawnee reservoirs are top three reservoirs in which managers should prevent the snail from being removed. Wildwood and Stagecoach are the two most important reservoirs of which managers should prevent the snail from being introduced. If introduced, Wildwood and Stagecoach act as secondary hubs and allow the snail to spread to peripheral, less-visited reservoirs in the network (Figure 7). At the end of the 25-year simulation, 7 additional reservoirs were infected and contagious, and an additional 3 were infected.

## Discussion

### *Social network analysis*



Resilience theory acknowledges ecosystems are social-ecological systems, and that including social dimensions enhances our understanding of ecosystem dynamics (Folke 2006). Despite this acceptance, social dimensions are typically looked at alone in the context of invasive species, as in, how do humans aid in the transport of invasive species? Though this is, arguably, a very important topic, it only tangentially accepts ecosystems as social-ecological systems.

Data collected from the Nebraska creel project (Martin 2013) were used to develop the directed social networks of angler movement. In-person surveys provided information on how anglers move between reservoirs in the region. Though we have information from both bank and boat anglers, the boat anglers are particularly relevant to the spread of invasive species, so we developed the social network using these answers. Future iterations of this approach could include more detailed angler movement patterns and the use of both categories of anglers. In this research, we have more confidence in the quality of our social network data than our ecological network data.

#### *Ecological network analysis*

To develop the ecological network models, we used the software Ecopath with Ecosim 6.4, which has been consistently updated over the past 25-30 years and used in > 150 peer-reviewed publications (Christensen and Walters 2004); however, as with any model, some limitations exist. Ecopath provides a static “snapshot” of a mass-balanced system; it does not necessarily represent equilibrium conditions. Ideally, long-term time series data are used to fit parameters, but we did not have access to such data. That being said, our models represent starting points based on best current information that can be

adjusted as additional empirical data become available. In fact, these models can be used to identify where the largest gaps in critical data exist. For example, there were almost no lake-specific biomass estimates for any of the species, including sport fish species, despite long-term stocking and fishery management efforts by local agencies.

Additionally, there were few published reports or available data of macroinvertebrate abundance or biomass. Thus, we selected macroinvertebrates most commonly reported in the limited fish-diet data that exists and used biomass estimates from similar Midwestern reservoirs that have published data. As a result, the macroinvertebrate species or functional groups included are taxonomically broad and biased toward species that are consumed by fish species worthy of study and analysis. Future research would benefit from individual lake assessments, increasing the amount of data necessary for this approach to work.

Diet composition matrices are extremely important inputs for the development of Ecopath models, yet these proportions are estimates based on the species and functional groups included in the model. As such, including age stanzas to account for ontological diet changes is beneficial but could not be included in the present analysis due to the uncertainty of the input data. This is another example of an information gap that exists and where future research could be focused to improve the current model.

In Ecosim, the vulnerability values are critical to how the model is structured. Lower vulnerability values stimulate a network based on bottom-up control, and higher vulnerability values stimulate a network based on top-down control (Christensen and Pauly 1998, Christensen and Walters 2004, Ahrens et al. 2012). The vulnerability values

used in the present study were estimated by the software and provide results of a donor-controlled model. Converting the Ecopath models to dynamic models in Ecosim is also complicated by temporal variation. Most likely, actual values of input parameters change over the course of a year, especially in temperate climates, but for simplicity a single value is entered for a period of time of 1 year.

The developers of Ecopath with Ecosim have actively identified strengths and weaknesses of the software as it continues to be developed (Walters et al. 1997, Pauly et al. 2000, Christensen and Walters 2004), and reviews on the strengths and weaknesses of Ecopath with Ecosim, as well as comparisons with other ecological network models, have been published by other groups (Plaganyi and Butterworth 2004, Link et al. 2008, Fath et al. 2013). The major strength of ecosystem network modelling, in general, is the ability to look at the system as a whole rather than limiting investigation to single-species effects; however, some caveats have been provided. When using Ecopath with Ecosim, accepting the default values provided by the software should be discretionary, and users should be cautious against using the software as a “black-box” modelling tool, especially when confidence in the data is limited (Plaganyi and Butterworth 2004). Link et al. (2008) compared Ecopath with another modelling software, EcoNetwrk, and found the results to be similar despite the differences underlying the models. Fath et al. (2013) compared Ecopath with the software NEA and found discrepancies in results between the two models, particularly with the calculated Finn’s Cycling Index. In the current study, we heeded these warnings as much as possible.

After developing initial Ecopath models, we wanted to calculate what ecosystem structure would be necessary to support a given biomass of Chinese mystery snail. To do this, the initial model was duplicated and the Chinese mystery snail was added as a functional group at a biomass of 38.58 t/km<sup>2</sup>, the value empirically derived from Wild Plum reservoir following the 2012 drought (Haak et al. 2013). Input values for other groups were adjusted as little as possible, and biomass values for all groups were recalculated by the software. The resulting models showed that a biomass of this magnitude would greatly disrupt the systems, and many results were not ecologically feasible. Many fish species, including important sport fish like crappie, bluegill, channel catfish, and flathead catfish, were eliminated and eutrophication took place. As a result, we returned to the initial Ecopath models and ran long-term (25 year) simulations.

The simulations that did not force Chinese mystery snail biomass resulted in the snail either staying at a very low biomass or disappearing all together. One possibility is that we did not include all of the vital compartments (species/functional groups) specific to the functioning of that reservoir in the analysis. Nutrient concentrations and the microbial community were both excluded due to extremely low confidence in available data. Though our models fell within the range of number of compartments included in published reports, it is possible that a key species or functional group was missing, ultimately affecting our results. As previously mentioned, little (if any) data existed on macroinvertebrate biomass, and we did not conduct individual lake surveys for each species. This likely affects our ecological models because we had less confidence in the species and functional group estimates for the lower trophic levels. That data were not

available for this region of Nebraska. In contrast, it may also be the case that the reservoirs have enough functional redundancy, allowing changes to ecosystem structure without changes to ecosystem functioning.

It would be informative to adjust vulnerability parameters to assess what would happen if the model was structured with “top-down” control; this is typically when we can fully analyze trophic cascades (Carpenter and Kitchell 1993). Completing a sensitivity analysis of the vulnerability estimates would help clarify this issue (Christensen and Walters 2004) and would allow us to analyze how changes to the stocking regime of predator fish could affect system dynamics.

Little previous research has been reported using ENA models to analyze the effects of invasive species. Miehl et al. (2009a, b) used ENA to compare ecosystems before and after a zebra mussel invasion, but because they had time series data spanning from pre- to post-invasion, they developed two static, mass-balanced models in Ecopath and compared the outputs. In contrast, Langseth et al. (2012) used Ecopath with Ecosim to develop models that mirror species invasions in Great Lakes Michigan and Huron. They too had time-series data from pre- and post-invasions; however, they tested four different methods to determine which introduction method is best when using Ecosim to model a species' introduction to a new ecosystem. Based on the quality of the data available to us, we followed their recommendation to use biomass forcing to assess hypothetical impacts of an invasive species introduction (Langseth et al. 2012). This group also tried introducing the invasive species at a low biomass, but found they had to control the species' dynamics with an artificial fishery, which may also explain why we

did not see major changes to the system when we introduced Chinese mystery snails at low biomasses and did not use biomass forcing (Langseth et al. 2012).

Though the mean flow values of total system consumption, exports, respiration, production, flows to detritus, and total system throughput were significantly higher in simulation year 20, none of the connectivity metrics commonly used to compare ecosystems were significantly different. Additionally, certain fish species were more susceptible to population declines after the introduction of the snail, though not all fish within a calculated trophic level were negatively affected. It appears the Chinese mystery snail causes changes to the distribution of the community's species biomass, but that overall functioning remains relatively constant in lieu of these changes.

#### *Coupled social and ecological network models*

To couple the social and ecological models, a number of assumptions were required. First, we assumed the transmission rate of 0.12% from Johnson et al. (2001) applied to Chinese mystery snail movement on macrophytes attached to boat trailers. Aquatic invasive species are commonly moved by commercial and recreational boating (Schneider et al. 1998, Muirhead and Macissac 2005). This estimate is conservative because it does not take into account other means of introduction, such as movement on wildlife or fishing gear, and it does not include intentional aquarium dumping (Padilla and Williams 2004) or “merit releases” by people who wish to establish a harvestable population as a food source (Vidthayanon 2005).

We also assumed a single female was enough to potentially start a population. Reproduction is sexual, and females give live birth (Jokinen 1982). During the breeding

period, a female will brood multiple juveniles at varying stages of development (Stephen et al. 2013). Females will expel young when stressed, giving birth, and some of these juveniles are viable and survive (personal observation).

Using the transmission rate above, it is assumed snails will be introduced at boat landings, and subsequent populations will be found around these points in a reservoir (Johnson et al. 2001, Vander Zanden et al. 2008, Rothlisberger et al. 2010). Once a lake is infected, there is a lag time before the population density is large enough to begin acting as a contagious source population; this threshold is set at 10% of the estimated carrying capacity of snails in that lake (Fogarty et al. 2011). Finally, we assumed angler movement, fishing pressure, and fish stocking are all constant over time.

Previous reports of applying epidemiological models to ecological research have been discussed in the literature (Mack et al. 2000, Floerl et al. 2009, Meentemeyer et al. 2011, Ferrari et al. 2014). Mack et al. (2000) discuss the theoretical similarities between epidemiological models and invasive species models. Floerl et al. (2009) modeled the spread of a hypothetical invader by hull fouling on recreational yachts in New Zealand. That study (Floerl et al. 2009) was based on the social network of boat movement, and did not incorporate ecological networks or limitations into analysis. Meentemeyer et al. (2011) used spatio-temporal, stochastic epidemiological modeling and geographical modeling to predict the invasion of a forest pathogen. Ferrari et al. (2014) also used epidemiology network theory to develop dynamic network models to simulate the spread of a terrestrial forest pathogen, though the pathogens in each of these examples spread independently and do not require a human social network component for analyzing

changes in the species' distributions. To our knowledge, the present study is the first to apply the epidemiological model framework to an analysis including coupled social and ecological network models.

Admittedly, this coupled approach is difficult to implement due to the data-heavy nature of the method. Having long-term data available on the movement of humans within a region and on the biotic community composition is a difficult task, particularly in an era of budget cuts and limited resources. In the present study, the survey data used to develop the social networks and the data on fishing pressure were collected over a 4-year period as part of a student dissertation (Martin 2013), and not all lakes were included in each aspect of data collection, providing some limitations in the analysis. Stocking records were collected from the Nebraska Game and Parks Commission online database. Input data for the ecological networks were collected from empirical research of specific reservoirs, when possible, but much of the inputs were collected from research on other Midwestern USA reservoirs reported in the literature. Site-specific input data for each reservoir simply does not exist, but we tried to include values from as ecologically similar systems as possible. The resulting models are believed to be as accurate as possible with the constraints of current data availability.

Reservoir prioritization was compiled by assessing both likelihood of introduction as well as ecological effects predicted to occur after introduction. Identifying reservoirs that acted as “hubs” for future invasions allowed us to hypothesize how some of the smaller, less-connected, peripheral reservoirs may become infected. Typically, these smaller reservoirs have fewer species or functional groups represented in the models,



resulting in less functional redundancy in the systems. It has been postulated that a system with less functional redundancy is less capable of absorbing disturbances and thus, is more likely to undergo a regime shift after disturbance (Folke et al. 2004, Nystrom 2006). Based on simulations, three of the reservoirs that currently have Chinese mystery snail population, Wagon Train, Branched Oak, and Pawnee, are the most important sources of new invasions. Preventing outgoing individuals from these reservoirs will greatly limit, or at least slow, the spread of Chinese mystery snails in the region. In contrast, despite having the largest population of Chinese mystery snails, Wild Plum's population is of little importance in the spreading of snails through the network.

If the Chinese mystery snail spreads in the manner suggested by simulations, then two reservoirs, Wildwood and Stagecoach, are most likely to act as invasion hubs, connecting peripheral, less-visited reservoirs to the infected and contagious reservoirs (though the first secondary reservoirs to become contagious do not occur until simulation-year 15). In the current model, anglers from Branched Oak infect Wildwood and anglers from Wagon Train infect Stagecoach, both in simulation-year 2. These reservoirs act as invasion "hubs" and intensify invasions to less-connected, peripheral reservoirs in the system, such as Merganser or Timber Point. For example, if the Chinese mystery snail is introduced into Merganser, simulations predict decreasing channel catfish (an important sport fish species) biomass and a significant increase in common carp and plant biomass, both of which negatively affect ecosystem function. These secondary hubs also amplify the number of secondary introductions (Vander Zanden and Olden 2008) to already-infected reservoirs.

## Future Research

The model developed in the current study should be seen as a starting point rather than a final result or prediction. There are a number of future manipulations that can be modeled, and it is clear there are many data gaps present in this set of reservoirs. Our social data was significantly better than existing ecological data. We used a donor-controlled model, and adjusting the vulnerability values in Ecosim would enable us to estimate how changing fishing pressure or stocking regimes affect the system. This “top-down” control simulates potential trophic cascades that result from changes to the system and may result in different biomass or energy flows. We would also benefit from breaking down the lower trophic level species and groups into more detailed categories; however, this would require the collection of more data if we wanted to include numbers more accurate than an estimation.

Adjusting the transmission rate as Chinese mystery snail biomass increases would also be a fruitful addition. In the present study, we maintained the same transmission percentage once the population density reached the minimum of 10% of the carrying capacity. However, adjusting the transmission rate as snail biomass increases would allow an even more accurate prediction of the potential invasion timeline.

Nebraska is heavily influenced by agriculture, so modeling the impact of nutrient loading would also provide insights in to how landscape use sculpts ecosystem structure in flood-control reservoirs. The present model did not include microbes or nutrients, both of which heavily affect ecosystem functioning. A sensitivity analysis of input parameters would clarify how important confidence in the input variables is. In addition to the

Ecopath inputs, analyzing sensitivity of the vulnerability values in Ecosim would solidify how those values influence model outputs. Vulnerability cannot be directly calculated, yet is critical to model functioning and outputs.

Finally, if the simulated ecological changes did occur, how might anglers adjust which lakes they fish? This is a cyclical question because if anglers alter fishing pressure, the ecological networks will change, further affecting angling pressure. Additional creel data exist on which species anglers sought when fishing, and these data could be used to extrapolate how ecosystem changes affect angler movement based on species-preference of anglers.

#### Conclusions and management implications

The results of this research indicate that network coupling is possible and allows for the assessment of ecological resilience at a regional scale. Our coupled social and ecological network approach enabled us to rank reservoirs in order of prioritization, both in terms of where invasive species outreach should focus on preventing species from leaving and where outreach should focus on preventing species from being introduced. This is a tangible output agencies can use to ensure their efforts are as effective as possible. This framework was implemented using the Chinese mystery snail as a study species, but it has the potential to be applied to any aquatic invasive species that spreads via anthropogenic movement. It also helps managers identify how humans may be affecting the landscape by creating a visual representation of connection patterns that may not otherwise be apparent. Finally, this approach may also be useful in determining

regional effects of intentional (e.g., stocking) and unintentional (e.g., invasive species, natural disasters) disturbances.

In conclusion, though this specific example focused on reservoirs in southeast Nebraska, the specific ecological networks are not the focal point of our research. Rather, the approach we used to couple the social and ecological network models is the emphasis of the study, and we found that social and ecological network models can be used in tandem to answer interdisciplinary questions using the framework of infectious disease models. The case-study's specific results showed that Chinese mystery snails did not cause significant changes to ecosystem functioning in flood-control reservoirs in southeastern Nebraska but did often cause changes in the biotic composition of the community, with mid-trophic-level fishes most often negatively affected. Additionally, after introduction, primary production increases greatly. This may lead to system eutrophication, a management nightmare in itself, and is another area worthy of future research. These results provide local agencies an idea of how they might want to manage the invasive Chinese mystery snail, but a broader subset of natural resource management agencies can benefit from the general approach we presented, using data from their own regions and areas (or species) of concern. If data are lacking, it also helps managers identify where collection efforts should be focused.

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Table 5-1. Name, size, community structure, and established aquatic invasive species of each Salt Valley reservoir.

Reservoir (Year of last renovation)	Area (km <sup>2</sup> )	Dominant fish community*	Established aquatic invasive species
Bluestem	1.320	Bluegill, Largemouth bass, Walleye, Crappie, Flathead catfish, Channel catfish, Common carp	
Bowling (2007)	0.048	Bluegill, <b>Largemouth bass, Channel catfish, Rainbow trout</b>	
Branched Oak	7.280	Bluegill, <b>Largemouth bass, Walleye</b> , Crappie, Flathead catfish, <b>Channel catfish</b> , Blue catfish, Common carp, <b>Hybrid striped bass</b> , White perch	Asian clam, Chinese mystery snail, White perch
Conestoga	0.930	Bluegill, Largemouth bass, <b>Walleye</b> , Crappie, Flathead catfish, Channel catfish, Common carp, Hybrid striped bass, Freshwater drum	
Cottontail (2006)	0.117	Bluegill, <b>Largemouth bass, Channel catfish</b> , Green sunfish	
East/West Twin	1.090	Bluegill, Largemouth bass, <b>Walleye</b> , Muskellunge, Crappie, <b>Channel catfish</b> , Bullhead, Common carp	
Holmes (2004)	0.400	Bluegill, Largemouth bass, <b>Walleye, Channel catfish, Rainbow trout</b>	Chinese mystery snail
Killdeer	0.080	Bluegill, <b>Largemouth bass</b> , Crappie, <b>Channel catfish</b> , Bullhead	
Meadowlark (2007)	0.220	Bluegill, Largemouth bass, Crappie, <b>Channel catfish</b>	
Merganser	0.170	Bluegill, Largemouth bass, <b>Channel catfish</b> , Bullhead	
Olive Creek	0.710	Bluegill, Largemouth bass, <b>Channel catfish</b>	
Pawnee	3.000	Bluegill, <b>Largemouth bass</b> , Sauger, <b>Walleye</b> , White bass, Crappie, Flathead catfish, Channel catfish, Common carp, Freshwater drum, White perch	Chinese mystery snail, White perch
Red Cedar	0.200	Bluegill, Largemouth bass, Crappie, Flathead catfish, Channel catfish	
Stagecoach	0.790	Bluegill, Largemouth bass, <b>Walleye</b> , Crappie, Channel catfish, Common carp, <b>Hybrid striped bass</b>	
Timber Point (2005)	0.110	Bluegill, Largemouth bass, <b>Muskellunge</b> , Crappie, <b>Channel catfish</b>	
Wagon Train	1.270	Bluegill, Redear sunfish, Largemouth bass, <b>Walleye, Muskellunge, Channel catfish</b>	Chinese mystery snail
Wild Plum	0.060	Bluegill, Largemouth bass, Channel catfish	Chinese mystery snail
Wildwood (2003)	0.420	Bluegill, Largemouth bass, <b>Walleye, Channel catfish</b>	
Yankee Hill (2007)	0.840	Bluegill, Largemouth bass, <b>Walleye, Channel catfish</b>	

\* Fish in **bold** are species stocked at least once since January 2010.

Table 5-2. Common and scientific names of all species referenced in manuscript. Species are listed alphabetically by common name.

Common name	Scientific name
Asian clam	<i>Corbicula fluminea</i>
Bluegill	<i>Lepomis macrochirus</i>
Black crappie	<i>Poxomis nigromaculatus</i>
Blue catfish	<i>Ictalurus furcatus</i>
Bullhead	<i>Ameiurus spp.</i>
Channel catfish	<i>Ictalurus punctatus</i>
Chinese mystery snail	<i>Bellamya chinensis</i>
Common carp	<i>Cyprinus carpio carpio</i>
Flathead catfish	<i>Pylodictis olivaris</i>
Freshwater drum	<i>Aplodinotus grunniens</i>
Green sunfish	<i>Lepomis cyanellus</i>
Hybrid striped bass	<i>Morone chrysops x saxatilis</i>
Largemouth bass	<i>Micropterus salmoides</i>
Muskellunge	<i>Esox masquinongy</i>
Quagga mussel	<i>Dreissena bugensis</i>
Rainbow trout	<i>Oncorhynchus mykiss</i>
Redear sunfish	<i>Lepomis microlophus</i>
Rusty crayfish	<i>Orconectes rusticus</i>
Sauger	<i>Sander canadensis</i>
Walleye	<i>Sander vitreus</i>
White bass	<i>Morone chrysops</i>
White crappie	<i>Poxomis annularis</i>
White perch	<i>Morone americana</i>
Zebra mussel	<i>Dreissena polymorpha</i>

Table 5-3. Betweenness, closeness, and degree values for each reservoir in the reservoir substitutability network.

Reservoir	Betweenness	Closeness	Degree
Bluestem	37	0.833	19
Bowling	0	0.003	6
Branched Oak	8	0.725	25
Conestoga	23	0.893	22
Cottontail	15	0.595	19
East West Twin	0	0.003	11
Holmes	14	0.609	23
Killdeer	63	0.962	13
Meadowlark	21	0.625	15
Merganser	13	0.735	12
Olive Creek	21	0.641	27
Pawnee	20	0.481	21
Red Cedar	3	0.676	7
Stagecoach	9	0.549	23
Timber Point	36	0.676	12
Wagon Train	16	0.676	28
Wild Plum	93	0.920	15
Wildwood	42	0.794	31
Yankee Hill	14	0.588	25

Table 5-4. Betweenness, closeness, and degree values for each reservoir in the boater movement network.

Reservoir	Betweenness	Closeness	Degree
Bluestem	0	0.0236	15
Bowling	0	0.0026	4
Branched Oak	36	0.0406	26
Conestoga	20	0.0309	21
Cottontail	8	0.0311	13
East West Twin	0	0.0026	8
Holmes	5	0.0295	20
Killdeer	0	0.0139	4
Meadowlark	0	0.0267	12
Merganser	0	0.0113	7
Olive Creek	46	0.0348	26
Pawnee	17	0.0369	19
Red Cedar	0	0.0026	2
Stagecoach	18	0.0373	25
Timber Point	29	0.0346	18
Wagon Train	25	0.0403	30
Wild Plum	0	0.0249	9
Wildwood	28	0.0365	27
Yankee Hill	28	0.0364	25
Outside Region	0	0.1295	15

Table 5-5. After the simulated introduction, each species or functional group increased, decreased, or had no change in biomass. The last column represents the number of reservoirs, out of 14, that each species or functional group was included in.

Species/functional group	Increase	Decrease	No change	Number of reservoirs included, out of 14
Autotrophs	12	0	2	14
Benthic macroinvertebrates	2	4	8	14
Bluegill	4	3	7	14
Bullhead	1	2	0	3
Channel catfish	5	7	0	12
Common carp	2	0	2	4
Crappie	3	7	1	11
Detritus	8	0	6	14
Flathead catfish	1	2	0	3
Freshwater drum	0	1	0	1
Hybrid striped bass	1	0	0	1
Largemouth bass	12	2	0	14
Muskellunge	2	0	0	2
Pred. birds	9	0	5	14
Rainbow trout	0	0	1	1
Redear sunfish	0	1	0	1
Walleye	4	2	0	6
White bass	0	0	1	1
Zooplankton	12	0	2	14

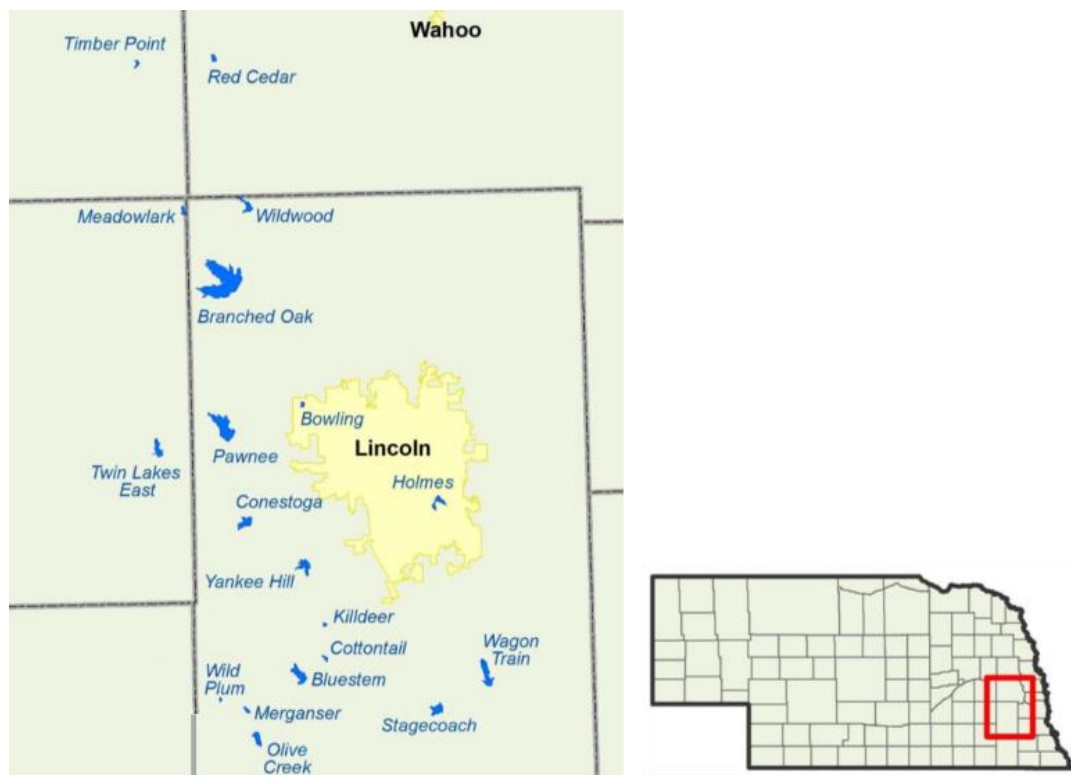


Figure 5-1. Map of reservoirs in Salt Valley region of southeastern Nebraska.



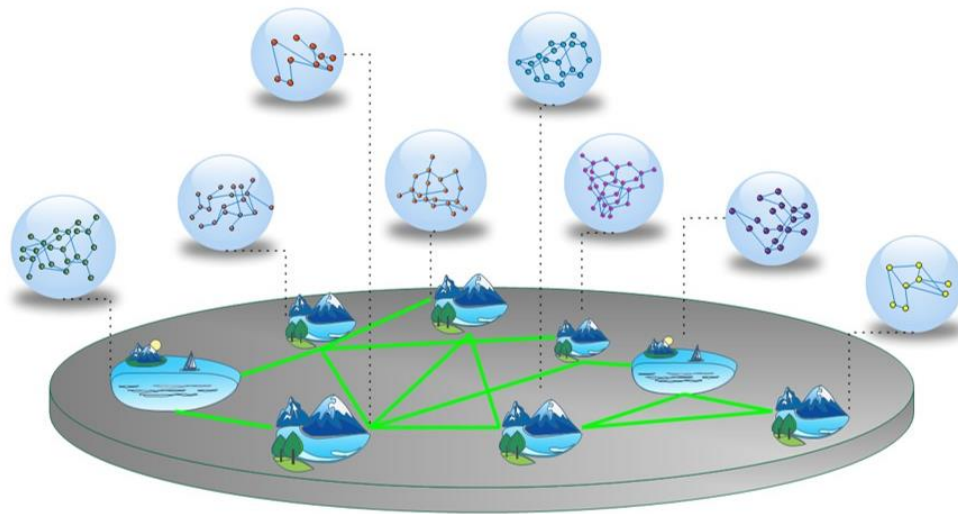


Figure 5-2. Conceptual model of how social and ecological models are coupled in the study system. Reservoirs are distributed across the landscape and connected by humans moving between and among them (social network). Within each reservoir is a unique trophic food web network (ecological network).

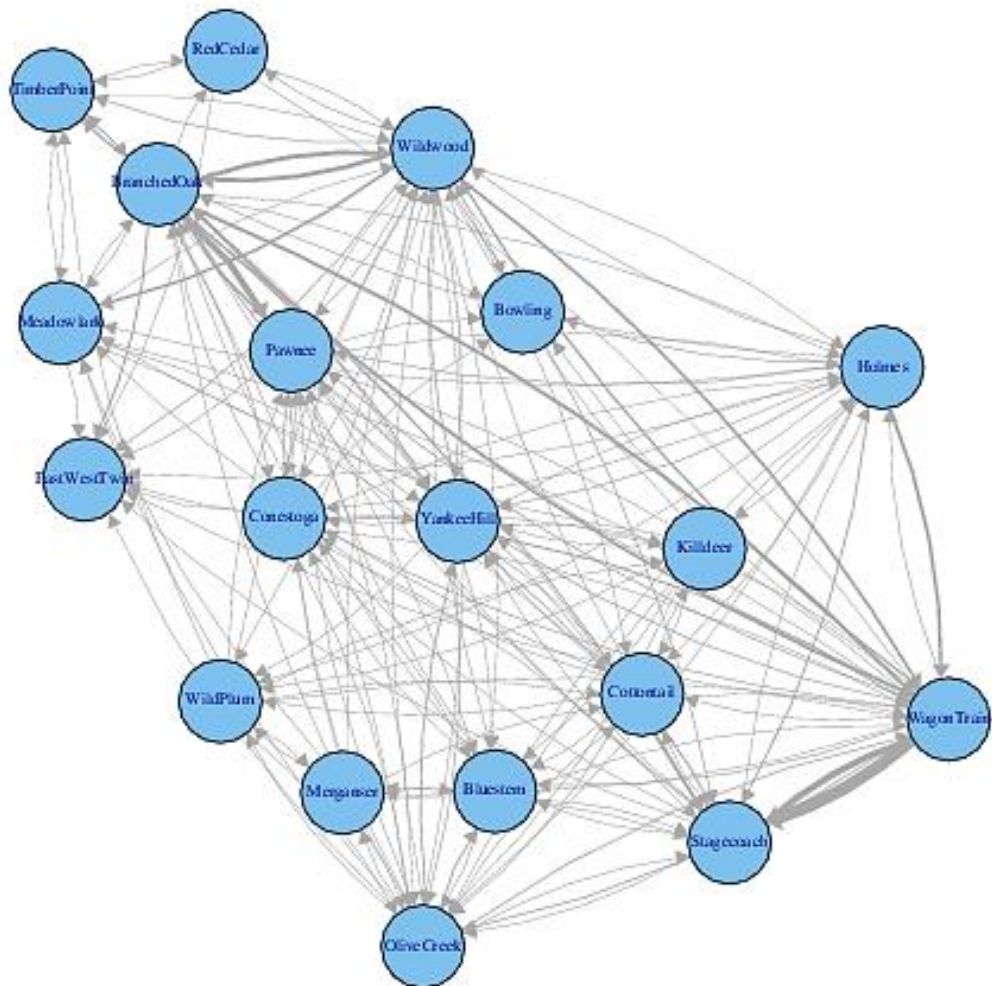


Figure 5-3. Reservoir substitutability of anglers in the Salt Valley of Nebraska. Nodes represent individual reservoirs and weighted, directed edges depict the percentage of respondents who would relocate to a given reservoir if necessary. Network layout approximates reservoir locations on the landscape. Figure made in R using iGraph package.

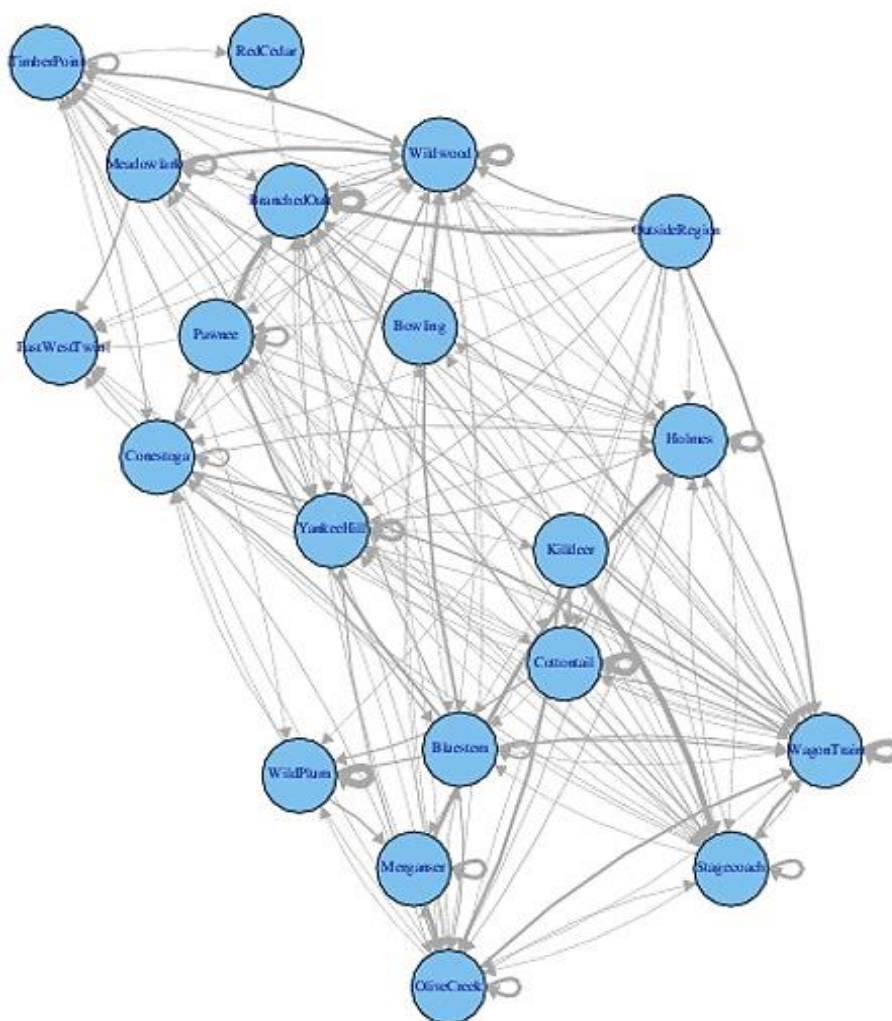


Figure 5-4. Weighted, directed network of boat movement among Salt Valley reservoirs. Nodes represent individual reservoirs and weighted, directed edges depict the percentage of respondents who previously fished at a reservoir before fishing at the reservoir where they were interviewed. Network layout approximates reservoir locations on the landscape. Figure created in R using iGraph package.

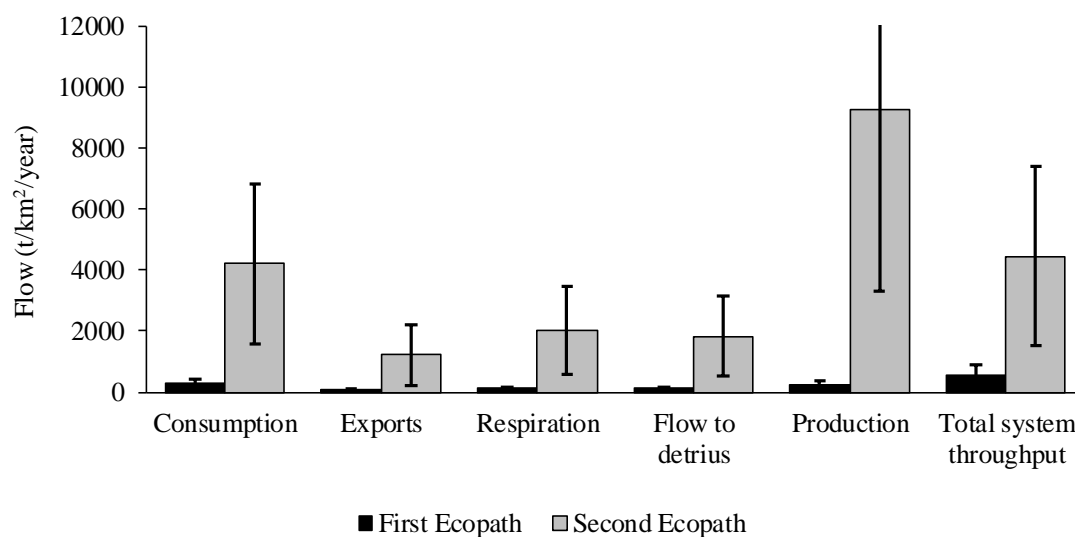


Figure 5-5. Mean ( $\pm$ SD) consumption, export, respiration, detrital, production, and system throughput flows as calculated in first Ecopath models (current-state of system) and in secondary Ecopath models (Chinese mystery snails biomasses were set equal to the current biomass estimate of Wild Plum reservoir, the densest population known in our system).

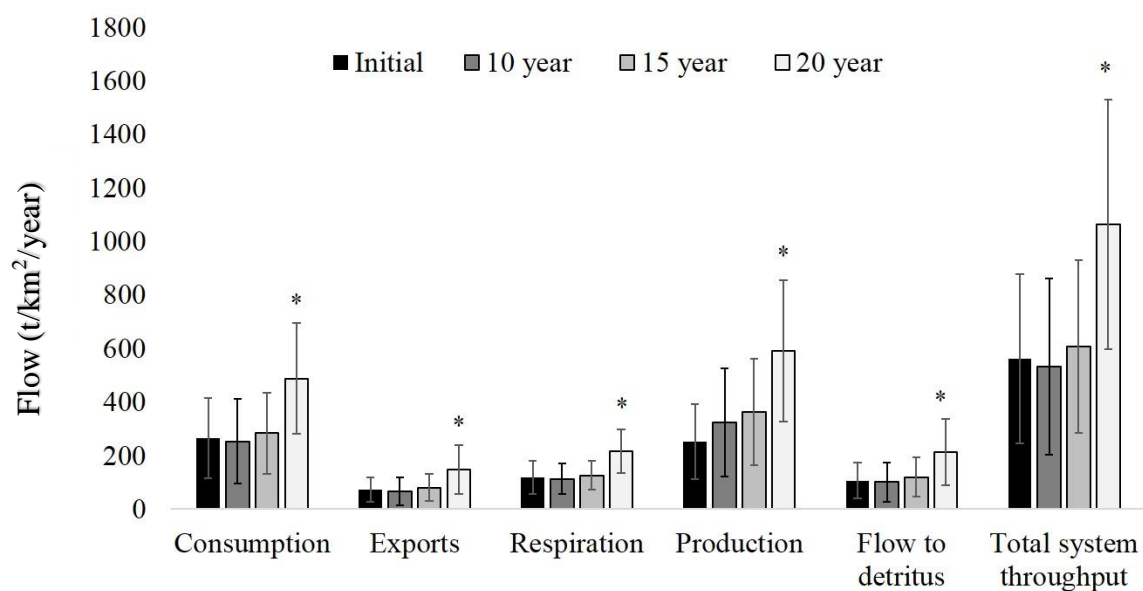


Figure 5-6. Mean ( $\pm$ SD) flow values (t/km<sup>2</sup>/year) of consumption, export, respiration, production, flow to detritus, and total system throughput across reservoirs at the initial time period and at 10 years, 15 year, and 20 years of simulation. Asterisks (\*) are used to denote bars that are statistically different from the other bars in the same category; all results from year 20 of the simulation were significantly higher than previously reported values for that category.

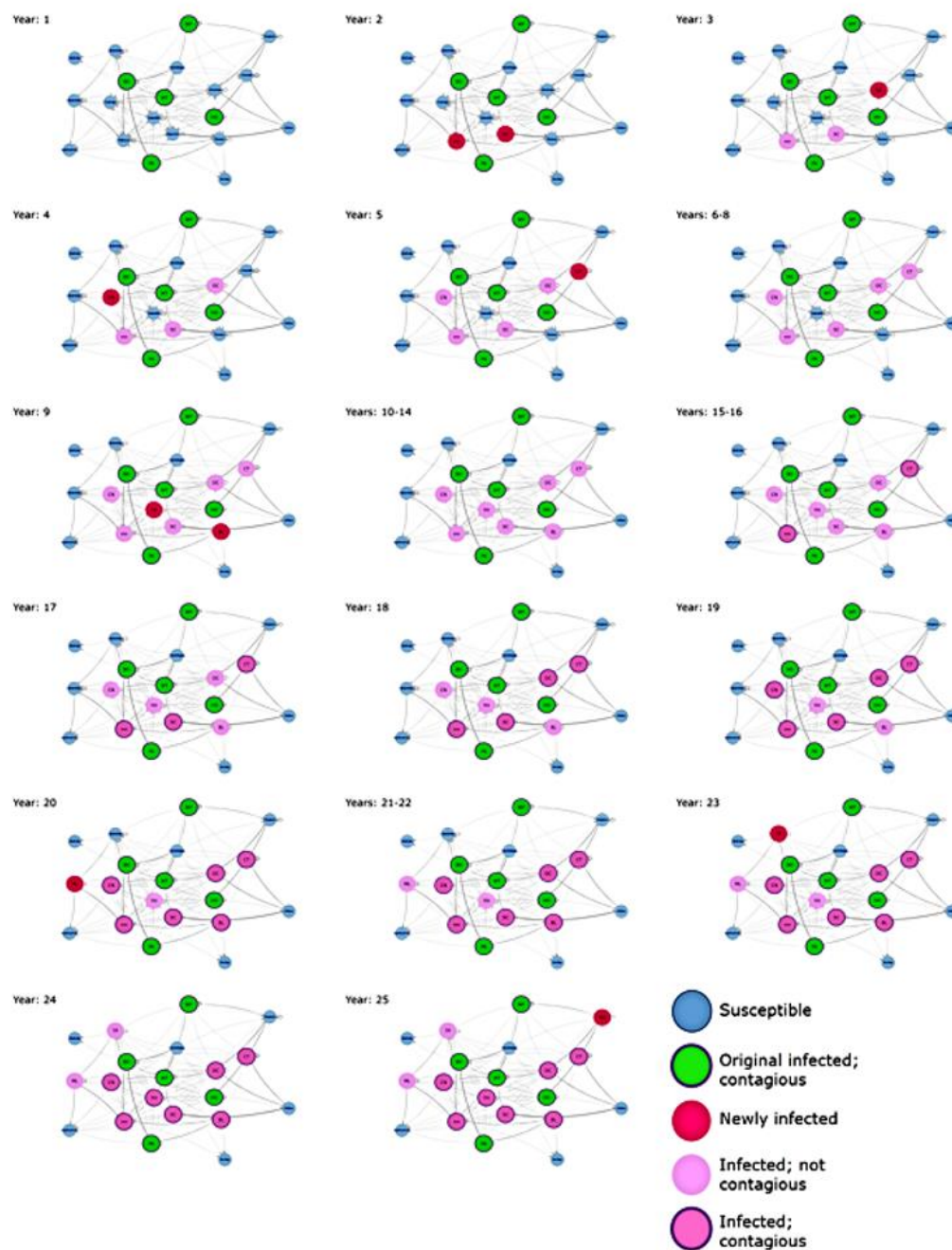


Figure 5-7. Simulated invasion of Chinese mystery snail in the Salt Valley, Nebraska reservoirs. Consecutive years when no changes take place are grouped together.

## CHAPTER 6: Conclusions, management implications, and directions for future research

Successful management of aquatic invasive species is a complex process with no blueprint for success. First, it requires a thorough understanding of the current state of the ecosystem under consideration. It is necessary to have clear objectives of what needs to be managed and why – what is the definition of “successful management?” If we wish to manage for ecological resilience, we have to define resilience of what to what. What ecosystem services are produced from an ecosystem in a desirable stable state? Management objectives are developed based on maintaining these ecosystem services and are thus subjective, based on what humans want. As a result, appropriate management of an invasive species will vary among ecosystems.

Once management objectives have been clarified and agreed upon by stakeholders, it is necessary to know how a particular species is likely to affect an ecosystem after introduction. How does the species of concern compare to similar native and non-native species; what can we learn from information that is already available? What characteristics does the species have that might enable it to thrive in the introduced ecosystem? If the species does thrive, achieving community domination, how will this affect the ecosystem’s biotic community or abiotic components like nutrient cycling? When reviewing the literature on invasive species, there are two dominant themes: preventing introductions and eradicating established populations. In many cases these may be the two most important components of invasive species management, but there may also be introduced species that achieve high population densities and invasive status in some ecosystems but not in others, even within the same geographical region, so

perhaps there is a “middle ground” of management actions available. However, with the increasing numbers of species introductions, it is difficult to gather adequate information for each species and ecosystem under consideration.

This research attempts to help clarify some of this information for the Chinese mystery snail, a species we knew very little about at the onset of the study. We have investigated the species' ecology in laboratory experiments, assessed variables that may be used to predict the species' distribution, and applied this knowledge to a case study focusing on flood-control reservoirs in Southeast Nebraska. We have also developed an initial model for coupling ecological and social network models to help predict where and when the Chinese mystery snail might spread, as well as how it could potentially influence an ecosystem's ecological resilience after introduction.

I had two primary goals for this research: 1) increase our understanding of the ecology of the Chinese mystery snail, and 2) increase our understanding of where the Chinese mystery snail might establish in its introduced range and how it might influence biotic and abiotic ecosystem processes after introduction. Both of these goals have been met and this dissertation adds to our knowledge of the invasive Chinese mystery snail's ecology and potential impacts. Specifically, these goals were met by achieving the objectives listed in Chapter 1. To highlight the most important aspects of this research, I list a number of conclusions, management recommendations, and opportunities for further research.



- Contrary to previous reports categorizing pulmonate gastropods as the most successful invaders with the most prominent negative influences on their introduced ranges (Strong et al. 2008), our review (Chapter 2) identifies prosobranch gastropods as the dominant gastropod invaders in North America with the largest impact on ecosystem processes. Of the 19 species included in the review, 5 species belong to the family Ampullaridae and 4 species (including the Chinese mystery snail) belong to the family Viviparidae. Species from both families are morphologically larger than native North American snails, and the combination of thick shells and the presence of an operculum makes these snails resistant to environmental variation and predation. Further research should assess if these species transport their native parasites to non-native ranges, as there may be important implications to human health.
- If we wish to actively attempt to halt the introductions of invasive gastropods to North America, regulating agencies should focus on the aquarium, pet, and food trades. Though humans may be responsible for moving snail species between lakes on recreational boating and fishing gear, these movements account for secondary introductions (Vander Zanden and Olden 2008). Primary introduction vectors of aquatic gastropods are the aquarium, pet, and food trades, allowing dispersal over much broader spatial scales than human outdoor recreation or natural dispersal (Padilla and Williams 2004). Despite being classified as

“invasive” it is still possible to order Chinese (and Japanese) mystery snails as well as apple snails online for home delivery. By mis-identifying or mis-labeling species on various websites, consumers do not even realize they are aiding in the spread of invasive species. A brief Google search produces a plethora of companies to choose from, all of which take a liberal methodology of classifying snail species or even family. One of the most prevalent errors is the synonymous use of “mystery snails” and “apple snails;” however, we now know that these are the two most problematic families of invasive snails in North America. There is a clear disconnect between organism commerce and regulations preventing the spread of invasive species.

- It will be difficult, if not impossible, to predict potential distribution and effects of gastropod invasions if we do not first have a thorough understanding of the species’ ecology and life-history characteristics. Our review revealed large knowledge gaps for most gastropod species, including knowledge on gastropods in their native ranges as well as their invasive ranges. Basic information such as habitat preferences, reproduction patterns, and parasitology are incomplete for most species. Gastropods have simply not received adequate research attention for us to accurately predict where they might spread or the effects this spread may have on the environment, humans, and wildlife.

- Our bioenergetics research (Chapter 3) identified differences among adult growth and survival and reproduction in varying water temperatures. This has implications when trying to assess the potential invasive range of the Chinese mystery snail, particularly when trying to factor in the role of climate variability on invasion success. Future research should assess a broader range of water temperatures, include juveniles in the analysis, and examine the bioenergetics of adults during periods where reproduction is not occurring.
- Our analysis of abiotic and biotic variables that can be used to predict Chinese mystery snail distribution (Chapter 4) yielded Secchi depth, latitude, and the total number of aquatic invasive species present in a water body as the most important predictor variables to Chinese mystery snail presence or absence. Turbid water bodies in Nebraska make searching for Chinese mystery snails difficult; in contrast, surveys can be conducted visually by snorkeling in the northern Wisconsin lakes included in this analysis. Thus, if the Chinese mystery snail is a species that managers wish to monitor in Southeast Nebraska, new sampling techniques need to be developed. At the current time, we do not have a robust method to determine Chinese mystery snail presence or absence in these flood-control reservoirs. If this type of habitat suitability research is to be repeated for Nebraska reservoirs, a presence-only approach, such as

Ecological Niche Factor Analysis would be more appropriate than an approach requiring both presence and absence data.

- Our research on coupling social and ecological network model types (Chapter 5) investigated a new approach and its application to invasive species management. By adapting the framework of infectious disease network modeling, we developed a novel method that incorporates likelihood of introduction events (caused by human movements) as well as individual-lake Chinese mystery snail population growth based on current ecological conditions within each reservoir. Due to the data-heavy nature of this type of approach, we relied on a number of assumptions for the initial model, but preliminary results show potential for this method to be used in future invasive species research.
- Based on our assumptions and knowledge of the current conditions of Salt Valley, Nebraska reservoirs, we could not conclude that Chinese mystery snails negatively affect ecosystem functioning if they continue to spread to new reservoirs in the region, at least within the temporal scale used in the model (~20 years). Though some mid-trophic level fishes were negatively affected by the hypothetical introduction of the Chinese mystery snail, our model predicted increases in a number of predator fish species as well as increases in primary production. However, this increase in primary production may result in eutrophication, particularly because we know the Chinese mystery snail influences nitrogen and phosphorus cycles after

introduction (Johnson et al. 2009). Lack of consistent, up-to-date water chemistry data for the Salt Valley reservoirs makes it difficult to further analyze these potential effects.

The results of this research elucidated some of the mystery surrounding the Chinese mystery snail; however, future research is necessary to continue examining this species and its effect on ecological resilience. Due to the limited nature of gastropod research, information on the Chinese mystery snail is based on geographically clumped populations. Northern Wisconsin, Southeast Nebraska, and Pacific Northwest populations have been independently studied, but no comparison studies have been conducted. In many scenarios, we are not even sure how long populations have been established in a specific area, making it impossible to make predictions or learn from management successes or failures. Thus, there is still a good deal of mystery surrounding the group called mystery snails.

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## Appendix A.

Table A-1. Wet weight (g) data collected during bioenergetics experiments but not included in analyses. Bold script indicates the final weight for a snail that died before the end of the 8-week experiment.

Temp.	Initial	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Final
20	34.9	36.3	35.1	35.5	35.5	33.8	35.4	35.1	35.3
20	20.1	21.4	19.1	19.3	19.0	19.0	19.1	19.1	18.9
20	26.3	28.5	25.5	25.50	24.9	24.7	<b>24.3</b>	.	.
20	16.3	17.4	15.2	15.0	15.1	15.2	15.2	14.7	15.2
20	24.3	25.4	24.0	23.6	23.1	24	23.2	23.4	23.7
20	18.3	20.2	18.1	17.6	18.0	17.4	<b>18.3</b>	.	.
20	30.2	33.8	29.1	28.9	28.7	27.6	28.4	28.2	28.8
20	21.7	22.0	20.5	20.5	20.3	19.7	20.0	20.3	19.5
20	23.2	24.0	22.2	22.8	22.3	22.6	<b>22.7</b>	.	.
20	32.5	34.5	32.4	32.2	32.4	31.9	31.8	31.8	32.9
20	24.7	24.5	21.7	21.9	21.4	22.1	22.0	22.3	21.7
20	21.1	21.0	18.9	17.6	18.0	18.4	17.8	18.4	17.6
20	21.2	22.1	20.2	19.6	19.8	19.6	19.7	19.6	19.6
20	21.1	21.5	18.8	19.4	19.1	19.5	19.1	18.6	19.2
20	23.2	23.9	23.4	22.9	23.0	<b>22.4</b>	.	.	.
20	14.2	13.1	13.1	12.7	13.4	13	13.2	13.0	12.6
20	21.8	21.4	20.8	21.1	20.5	21.1	21.0	20.9	21.1
20	19.8	19.2	17.7	17.8	17.3	18.2	17.6	17.9	18.1
20	21.3	21.4	20.5	20.4	19.1	20.1	20.8	20.3	20.1

Table A-1.  
Continued.

Temp.	Initial	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Final
20	1.0	1.2	1.2	1.20	1.5	<b>1.6</b>	.	.	.
20	0.4	<b>0.5</b>	.	.	.	.	.	.	.
20	2.8	3.0	3.0	2.7	2.6	2.3	1.8	1.7	1.8
20	3.8	3.9	3.9	3.3	3.3	3.3	3.4	3.4	3.4
20	1.2	<b>1.2</b>	.	.	.	.	.	.	.
20	12.3	12.3	12.3	12.1	12.1	12.4	12.5	12.4	12.3
20	18.1	17.8	16.0	15.0	15.8	15.2	15.8	15.5	15.0
20	27.6	27.0	25.5	24.8	25.1	25.0	<b>25.1</b>	.	.
20	16.9	<b>16.3</b>	.	.	.	.	.	.	.
20	15.2	15.0	13.5	13.3	13.7	13.3	13.4	13.7	13.7
20	28.4	<b>26.9</b>	.	.	.	.	.	.	.
20	16.0	15.6	14.8	13.8	13.9	14.4	14.2	14.4	14.3
20	12.1	11.9	10.1	10.1	10.1	10.0	10.0	10.2	10.4
20	25.4	<b>26.5</b>	.	.	.	.	.	.	.
20	6.3	<b>5.9</b>	.	.	.	.	.	.	.
20	19.8	18.4	20.5	18.1	19.2	17.9	19.0	18.9	17.2
12	15.4	17.4	13.6	13.9	13.2	13.0	13.4	13.8	13.5
12	20.6	21.7	17.7	17.8	17.5	17.5	17.4	17.9	17.8
12	22.6	23.2	20.3	20.3	20.2	20.2	20.6	19.9	20.5
12	24.9	24.5	22.8	23.0	23.0	23.9	23.2	23.5	22.8
12	15.0	15.2	13.8	14.4	13.8	14.0	13.7	14.0	14.6
12	18.2	18.8	16.5	17.1	17.0	16.9	17.1	16.6	16.2
12	17.1	17.9	15.1	15.2	15.2	15.1	15.3	15.1	14.7



Table A-1.  
Continued.

Temp.	Initial	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Final
12	19.9	20.2	17.2	17.6	17.5	17.3	17.5	17.7	17.4
12	16.3	17.4	15.0	15.4	15.2	15.1	15.1	15.1	15.4
12	18.7	19.2	17.0	17.9	17.8	17.4	17.7	17.1	17.8
12	19.9	21.6	15.9	16.6	16.9	16.5	16.4	16.7	16.1
12	20.3	19.8	17.8	17.9	17.7	17.8	17.9	18.1	18.9
12	17.6	18.6	14.5	15.3	14.5	15.1	15.4	15.2	15.3
12	16.1	16.5	13.8	14.4	14.5	14.0	14.1	14.3	14.8
12	18.7	18.8	17.4	18.8	18.4	17.8	18.0	18.5	18.4
12	24.2	24.9	21.8	22.7	22.2	21.5	21.7	21.5	23.8
12	21.3	22.4	16.8	18.0	17.8	17.3	17.3	17.7	18.0
12	2.8	2.8	2.6	2.7	2.7	2.8	2.8	2.8	2.9
12	2.3	2.3	2.2	2.2	2.2	2.3	2.5	2.5	2.8
12	3.5	3.6	3.0	3.2	3.1	3.2	3.2	3.3	3.4
12	15.9	16.0	14.1	14.5	13.8	14.1	14.8	14.2	14.5
12	27.0	27.2	25.7	25.6	24.3	24.3	25.4	24.5	24.4
12	25.8	25.7	22.9	23.2	22.6	23.6	23.9	22.5	23.5
12	24.2	24.0	19.4	19.7	19.6	<b>19.5</b>	.	.	.
12	11.6	11.5	10.1	10.2	9.8	10.1	10.0	10.2	10.2
12	15.4	16.5	<b>14.5</b>	.	.	.	.	.	.
12	13.1	13.8	12.7	12.4	12.4	10.5	<b>7.9</b>	.	.
12	16.2	17.3	15.7	15.8	15.8	16.0	16.0	16.0	16.1
12	16.8	17.8	15.5	15.2	15.0	16.0	15.4	15.5	16.1
12	42.7	42.7	37.9	38.0	38.4	39.1	38.0	38.2	38.5

Table A-1.  
Continued.

Temp.	Initial	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Final
27	29.3	30.1	29.4	29.2	30.2	<b>28.7</b>	.	.	.
27	15.8	16.6	16.7	17.2	17.1	17.3	17.1	<b>17.0</b>	.
27	14.9	15.4	15.6	16.0	15.7	15.2	16.4	15.5	15.7
27	23.0	54.1	23.7	24.3	25.1	24	<b>25.7</b>	.	.
27	19.2	19.9	20.0	20.6	19.7	18.7	21.1	18.5	20.7
27	16.6	18.0	<b>17.8</b>	.	.	.	.	.	.
27	17.0	18.2	18.3	18.2	18.3	18.0	18.4	17.3	18.5
27	23.0	23.4	23.2	24.0	23.3	23.8	25.0	23.0	23.9
27	23.5	26.0	25.4	26.2	26.5	26.7	27.8	24.5	22.2
27	7.3	7.7	7.5	7.9	7.9	8.0	8.6	8.0	8.2
27	21.3	22.2	21.4	20.8	22.3	22.9	23.3	<b>20.6</b>	.
27	19.7	20.2	20.2	19.9	20.2	20.6	20.9	20.6	21.8
27	14.2	15.1	13.8	14.7	14.9	14.8	15.2	<b>15.1</b>	.
27	17.7	19.0	18.4	18.2	18.8	18.6	<b>19.6</b>	.	.
27	<b>14.4</b>	.	.	.	.	.	.	.	.
27	17.4	18.2	18.3	18.4	17.9	18.2	18.4	18.1	18.6
27	14.5	15.4	14.9	15.5	14.9	15.6	15.2	15.9	15.1
27	20.8	22.3	21.9	21.7	21.7	<b>21.6</b>	.	.	.
27	17.9	18.9	18.5	18.0	18.3	18.5	18.9	<b>19.5</b>	.
27	19.8	21.0	20.9	20.9	21.2	21.1	21.2	21.2	21.1
27	22.4	23.9	23.5	23.6	23.4	23.4	<b>23.6</b>	.	.
27	5.1	5.1	5.0	5.2	5.2	5.2	5.5	5.2	5.0
27	16.9	17.6	17.5	17.6	18.4	17.6	<b>18.8</b>	.	.

Table A-1.  
Continued.

Temp.	Initial	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Final
27	9.2	10.0	9.7	9.5	9.9	9.6	10.0	<b>10.2</b>	.
27	11.6	12.1	12.0	12.3	12.0	11.9	12.5	12.3	12.5
27	12.1	12.9	12.7	12.1	12.5	12.6	<b>12.7</b>	.	.
27	12.5	13.7	13.7	13.8	13.5	13.5	14.3	14.0	13.5
27	12.7	13.6	13.4	13.0	13.2	12.6	<b>13.9</b>	.	.
27	1.6	1.8	1.7	1.8	1.9	1.9	2.2	1.9	2.0
27	0.7	0.8	0.7	0.9	0.9	0.8	0.8	0.9	0.6

Appendix B. Dominant fish species found in each water body.

Table B-1. Presence of Chinese mystery snail (CMS) (Y = Yes, N = No) and dominant fish species or groups of species (X = Yes) found in each waterbody (based on WI DNR classification): Panfish = Bluegill (*Lepomis macrochirus*), Yellow perch (*Perca flavescens*), and Crappies (*Pomoxis* spp.), NOP = Northern pike (*Esox lucius*), SMB = Smallmouth bass (*Micropterus dolomieu*), LMB = Largemouth bass (*Micropterus salmoides*), MUE = Muskellunge (*Esox masquinongy*), WAE = Walleye (*Sander vitreus*), Trout = Brown (*Salmo trutta*), Rainbow (*Oncorhynchus mykiss*), and Brook (*Salvelinus fontinalis*) trout.

Lake name	CMS	Panfish	NOP	SMB	LMB	MUE	WAE	Trout
Adams	N	X			X			
Allequash	Y	X	X	X	X	X	X	
Anderson	N	X			X			
Anne	N	X			X			X
Anvil	Y	X	X	X			X	
Arrowhead	Y	X	X	X	X	X	X	
Averill	N	X	X		X	X	X	
Baker	Y	X	X		X			
Ballard	N	X				X	X	
Big Arbor Vitae	Y	X			X	X	X	
Big Kitten	N	X		X	X	X	X	
Big	Y	X	X	X	X	X	X	
Big Muskellunge	N	X	X	X	X	X	X	
Big Portage	N	X		X	X		X	
Big Sand	Y	X	X	X	X	X	X	

Table B-1. Continued.

Lake name	CMS	Panfish	NOP	SMB	LMB	MUE	WAE	Trout
Big St. Germain	Y	X	X	X	X	X	X	X
Birch	Y	X	X	X	X	X	X	
Black Oak	N	X	X	X	X		X	X
Boulder	Y	X	X	X	X	X	X	
Brandy	Y	X	X		X	X	X	
Buckskin	Y	X	X		X	X	X	
Carpenter	Y	X	X	X	X		X	
Catfish	Y	X	X	X	X	X	X	
Circle Lily	N	X	X	X	X	X	X	
Clear	N	X	X	X	X	X	X	
Constance	N	X			X			
Crab	N	X	X	X	X	X	X	
Crystal	N	X	X		X			
Day	N	X		X				
Dead Pike	N	X	X	X	X	X	X	
Deerskin	N	X	X	X	X	X	X	
Diamond	N	X		X	X	X	X	
Dollar	N	X	X		X			
Duck	Y	X	X	X	X	X	X	
Eagle	Y	X	X	X	X	X	X	
East Ellerson	N	X			X			
Escanaba	N	X		X	X	X	X	
Fawn	N	X	X		X	X	X	
Fence	N	X	X	X	X	X	X	X
Finger	Y	X			X		X	

Table B-1. Continued.

Lake name	CMS	Panfish	NOP	SMB	LMB	MUE	WAE	Trout
Fishtrap	Y	X	X	X	X	X	X	
Forest	N	X	X	X	X		X	
Found	N	X	X		X	X	X	
Grassy	N	X	X		X			
Gunlock	Y	X	X	X	X	X	X	
Harris	N	X	X	X	X	X	X	
Haskell	N	X	X		X	X	X	
Helen	N	X	X		X	X	X	
High	Y	X	X	X	X	X	X	
Horsehead	N	X	X	X	X	X	X	
Hunter	Y	X		X	X		X	
Ike Walton	N	X		X	X	X	X	
Imogene	N	X		X	X			
Island	Y	X	X	X	X	X	X	
Jag	N	X		X	X	X	X	
Johnson	N	X						
Jute	N	X		X	X	X		
Kentuck	Y	X		X	X	X	X	
Lac Vieux Desert	Y	X	X	X	X	X	X	
Lake Flambeau	N	X	X	X	X	X	X	
Lake Laura	N	X		X	X	X	X	
Lake Salsich	N	X	X		X			
Landing	N	X	X		X			
Little Arbor Vitae	Y	X			X	X	X	

Table B-1. Continued.

Lake name	CMS	Panfish	NOP	SMB	LMB	MUE	WAE	Trout
Little Bass	Y	X			X			
Little Crawling Stone	Y	X	X	X	X	X	X	
Little Crooked	N	X	X		X	X	X	
Little Gibson	Y	X			X	X		
Little Papoose	N	X			X	X	X	
Little Portage	N	X	X		X	X		
Little Spider	Y	X		X	X	X	X	
Little Trout	N	X		X	X	X	X	X
Long Interlaken	Y	X	X	X	X	X	X	
Long	Y	X	X	X	X	X	X	X
Loon	Y	X		X	X			
Lower Buckatabon	N	X	X	X	X	X	X	
Lynx	Y	X	X	X	X	X	X	
Madeline	Y	X	X		X	X	X	
Mamie	N	X	X	X	X	X	X	
Manitowish	N	X	X	X	X	X	X	
McCullough	N	X	X		X	X	X	
Middle Sugarbush	N	X	X	X	X	X	X	
Moon	Y	X	X	X	X	X	X	
Morton	N	X	X		X	X	X	
Moss	N	X	X	X	X	X	X	
Muskellunge	Y	X	X		X	X	X	
No Mans	N	X			X	X	X	
North Turtle	N	X	X	X	X	X	X	

Table B-1. Continued.

Lake name	CMS	Panfish	NOP	SMB	LMB	MUE	WAE	Trout
Otter	Y	X	X	X	X	X	X	
Oxbow	N	X	X	X	X	X	X	
Palmer	Y	X	X	X	X	X	X	
Pardee	N	X		X	X	X	X	
Partridge	Y	X		X	X	X	X	
Pickerel	Y	X	X		X	X	X	
Pine	Y	X	X		X			
Plum	Y	X	X	X	X	X	X	
Plummer	N	X		X	X	X	X	
Pokegama	Y	X	X	X	X	X	X	
Presque Isle	N	X	X	X	X	X	X	
Razorback	Y	X	X	X	X	X	X	
Sanborn	N	X	X		X			
Scattering Rice	Y	X	X	X	X	X	X	
Shishebogama	Y	X	X	X	X	X	X	
Smoky	N	X		X	X			X
Snipe	Y	X			X	X	X	
South Twin	Y	X		X	X	X	X	
Sparkling	N	X		X	X	X	X	
Spectacle	N	X		X	X		X	X
Spider	Y	X	X	X	X	X	X	
Squash	N	X			X			
Squirrel	Y	X	X	X	X	X	X	
Star	Y	X	X	X	X	X	X	
Stateline	N	X	X		X			



Table B-1. Continued.

Lake name	CMS	Panfish	NOP	SMB	LMB	MUE	WAE	Trout
Stearns	N	X	X	X	X	X	X	
Stone	N	X	X	X	X	X	X	
Stormy	Y	X	X	X	X			X
Sugar Maple	N	X	X	X	X			
Sumach	N	X			X	X	X	
Sunset	N	X	X	X	X	X	X	
Tambling	N	X	X		X		X	
Tenderfoot	N	X	X	X	X	X	X	
Tippecanoe	N	X		X	X	X	X	
Towanda	Y	X	X		X	X	X	
Trout	N	X	X	X	X	X	X	X
Turner	N	X	X		X	X	X	
Upper Gresham	Y	X	X		X	X	X	
Van Vliet	N	X	X		X	X	X	
Watersmeet	N	X	X	X	X	X	X	
West Bay	Y	X	X	X	X	X	X	
White Sand	N	X	X	X	X	X	X	
Whitefish	N	X			X	X	X	
Wildcat	Y	X		X	X	X	X	
Wishow	N	X			X			
Wolf	N	X		X	X	X	X	
Yellow Birch	N	X	X	X	X	X	X	
Zee	N	X			X			

## Appendix C: Assessing pH and calcium requirements of the Chinese mystery snail

The initial objective of our research was to identify how pH and calcium ( $\text{Ca}^{2+}$ ) concentration affect the growth of adult Chinese mystery snails. Both of these variables have been speculated as important for Chinese mystery snail survival (Jokinen 1982, Solomon et al. 2010). Laboratory experimentation was implemented to address this objective, but we found that adult Chinese mystery snails are habitat generalists, so a secondary analysis of an existing dataset was applied as well.

A subset of adult snails was used to assess the effects of varying pH on growth. The pH of water was measured using a LaMotte pH test kit (Code 7514-pH). The control tank (15 L) had de-chlorinated tap water with a pH of 7. Experimental tanks (15 L) were filled with de-chlorinated tap water and adjusted using LaMotte acidity test-kit reagents (Code 7182) until one had a pH of 4.5 and the other a pH of 10. Most natural lakes in the Midwest USA fall within this range of pH values (Rahel and Magnuson 1983, Webster and Brezonik 1995). Five individuals between 30-50 mm in total shell length were individually labeled and randomly assigned to the two experimental tanks and control tank (N=15). Growth of each individual was monitored over 4 weeks, and pH was measured daily and adjusted when necessary.

A separate subset of snails was used to assess the effects of varying calcium ( $\text{Ca}^{2+}$ ) concentration on adult snail growth. Similar to the pH experiment, there were two experimental tanks (15 L) and one control tank (15 L). The LaMotte calcium hardness test was used to estimate the calcium concentration (Model EC-68, Code 3583). The

control tank with de-chlorinated tap water had 60 ppm calcium hardness with no manipulation necessary. It has been hypothesized that Chinese mystery snails require a calcium concentration of 5 ppm for survival (Solomon et al. 2010), and zebra mussels (*Dreissena polymorpha*) require a minimum calcium concentration between 12-20 ppm (Whittier et al. 2008). Though the City of Lincoln tap water falls above this range, we used it as the control tank, because de-chlorinated tap water was used in all Chinese mystery snail experiments and is what the snails acclimated to in the laboratory. Spring water from Carolina Biological Supply (Item #132450) was used in one experimental tank, with a calcium concentration of 6 ppm. Kent Marine 00048 Turbo Calcium was added to de-chlorinated tap water in the second experimental tank until the calcium concentration measured 120 ppm. Five individuals between 30-50 mm in total shell length were individually labeled and randomly assigned to the two experimental tanks and control tank (N=15). Growth of each individual was monitored over 4 weeks, and calcium hardness was measured twice per week and adjusted as needed.

In both experiments snails acclimated to the laboratory conditions (de-chlorinated tap water at room temperature ( $20\pm 1^{\circ}\text{C}$ ) over a period of 6 months. Snails were fed TetraVeggie™ sinking algae wafers three times per week. Twice per week 90% of the water was siphoned and replaced with water already at the same pH or calcium concentration. No juveniles were evaluated in any experiments due to the difficulty of rearing them in the laboratory.

In the pH experiment, mean growth (measured by total shell length (mm)) did not vary among experimental tanks and the control tank ( $p = 0.44$ , Table C-1a). Total wet mass (g) was not significantly different among groups ( $p = 0.95$ , Table C-1b). Varying pH did not affect the growth (measured as total shell length) or wet mass of the adult Chinese mystery snails in this experiment. All snails survived the 4-week experiment.

In the calcium concentration experiment, mean growth (measured by total shell length (mm)) did not vary among experimental tanks and the control tank ( $p = 0.71$ , Table C-2a). Total wet mass (g) was also not significantly different among groups ( $p = 0.12$ , Table C-2b). Varying calcium ( $\text{Ca}^{2+}$ ) concentration did not affect the growth (measured as total shell length) or wet mass of the adult Chinese mystery snails in this experiment. All snails survived the 4-week experiment.

Our experiments to assess the influence of varying calcium and pH indicated the adult Chinese mystery snails have general habitat requirements regarding these two variables. One significant disadvantage of this study was the inability to assess influences on juvenile snails. Calcium is a necessary component of shell formation, but we were unable to successfully keep juvenile snails alive in the aquariums throughout all experimental efforts. Additionally, juveniles may be more susceptible to changes in pH. A thinner shell and operculum limit the isolation afforded to adult snails during undesirable environmental conditions; thus, it is possible we would have measured different responses to variable calcium and pH.

Our laboratory results do support previous reports on the generalist nature of Chinese mystery snails. The Chinese mystery snail is capable of surviving desiccation periods  $\geq 9$  weeks in laboratory conditions (Unstad et al. 2013), and their critical upper lethal water temperature limit is 44.2°C (Wong et al., unpublished data). Adults are capable of switching between grazing on periphyton and suspension-feeding from the water column depending on conditions (Olden et al. 2013). Finally, adults are not affected by chemical treatments of copper sulfate or rotenone (Haak et al. 2014).

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Table C-1. Output from single-factor ANOVA analyzing effects of water with pH = 4, 7, and 10 on differences in (a.) total shell length (mm) and (b.) wet mass (g).

a.

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	1.133	2	0.566	0.878	0.440	3.885
Within Groups	7.735	12	0.644			
Total	8.868	14				

b.

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	0.101	2	0.050	0.049	0.951	3.885
Within Groups	12.216	12	1.018			
Total	12.317	14				

Table C-2. Output from single-factor ANOVA analyzing effects of water with calcium (Ca<sup>2+</sup>) concentrations = 6, 60, and 120 ppm on differences in (a.) total shell length (mm) and (b.) wet mass (g).

a.

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	0.294	2	0.147	0.349	0.711	3.885
Within Groups	5.054	2	0.421			
Total	5.348	4				

b.

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	3.137	2	1.568	2.496	0.124	3.885
Within Groups	7.540	12	0.628			
Total	10.677	14				



## Appendix D: Ecological network development

### Ecopath Inputs

#### Basic inputs

Ecopath requires three of the following four categories to be entered for each species or functional group: biomass ( $\text{t}/\text{km}^2$ ), P/B ( $\text{t}/\text{km}^2/\text{year}$ ), Q/B ( $\text{t}/\text{km}^2/\text{year}$ ), and EE. The production/biomass (P/B) ratio is the equivalent to the total mortality rate (Z) (Allen 1971, Merz and Myers 1998) and includes the quantity harvested by fishing (F), predation (M2), net migration (NM), biomass accumulation (BA), and other mortality (M0) (Eq. D-1):

$$\text{(Eq. D-1)} \quad \text{P/B} = \text{Z} = \text{F} + \text{M2} + \text{NM} + \text{BA} + \text{M0}.$$

The consumption/biomass ratios are only entered for secondary consumers; this value cannot be entered for primary producers (Pauly et al. 2000). The ecotrophic efficiency (EE) is a unitless value representing the amount of production that is used or harvested from the system (Pauly et al. 2000). This value cannot be directly measured but varies between 0 and 1, and  $(1 - \text{EE})$  provides the “other mortality” value. By providing three of these values, the fourth can be calculated by the software, using the following generalized formula:  $\text{Production} = \text{Catch} + \text{biomass accumulation} + \text{predation mortality} + \text{net migration} + \text{other mortality}$ .

This predation mortality term is the parameter that links all of the groups to one another (Pauly et al. 2000). Additional inputs include the proportion of the model area where a species occurs. For example, rooted macrophytes are limited to the photic zone

of a lake or reservoir, so this may only be one-third of the total surface area, in which you would enter 0.334 for that species. The production/consumption (P/Q) ratio can be entered if either P/B or Q/B inputs are left blank. In the current analysis, all P/Q values were calculated by the software and not used as inputs in any of the models.

The values for unassimilated consumption were attained from the literature and varied from 0.15 to 0.40, depending on the species or functional group. The default value of 0.2 (Winberg 1956) was used when no estimate from the literature could be found. It was assumed there was detritus import to the system based on the nature of the reservoirs as “flood-control” reservoirs; it is realistic to assume both detritus and sediment are loaded into the system, particularly after precipitation events. An example of the basic input data for the initial Ecopath models can be found in Table D-1.

#### Diet composition

A diet composition matrix was compiled and included all species or groups used in each model. Quantification of diet composition is difficult, so these values were adjusted during the process of balancing each model. The diet for each predator group summed to 1, with the awareness that species or functional groups excluded from the current model may be included in a predator’s diet under natural circumstances. If it is believed these non-included groups are particularly important to a diet, a proportion value was entered in the “import” row for that species. This is one of the problems of modeling open systems where it is not practical to include everything. One example of this is the inclusion of terrestrial insects in the diets of fish like largemouth bass. While terrestrial insects were not included in any of our models, we could account for their importance by

including a percentage in the “input” category for the largemouth bass diets. An example of a diet composition matrix for one reservoir can be found in Table D-2.

#### Other production

Immigration and emigration rates were kept at zero for these initial models. The lakes are not naturally connected, so there is little chance fish are able to move between lakes during natural weather conditions (we ignored the influence of floods in the current research). Biomass accumulation is only possible to estimate when we have more than one biomass estimate for a given species or group. As we relied on single estimate values, we do not include accumulation values; however, with additional site-specific data collection, this would be possible in future adaptations of the model.

#### Fishery

Estimates for catch, harvest, and discard rates were gathered from Martin (2013), as part of the Nebraska state creel project. These values were assumed constant over time, because they represent a “snapshot” of the fishery and we do not have long-term data at this time. However, because the creel project is ongoing, it will be possible to include varying fishery information in future adaptations of the model. All fishing effort in the Salt Valley is recreational rather than commercial, so no values were placed on the recreational fishery regarding market price and profits. The fishery information used in the development of the initial Ecopath models can be found in Table D-3.

#### Pedigree

The input information was collected from a variety of sources with varying degrees of confidence. We used the pedigree function in Ecopath to estimate the overall

confidence of the data for each reservoir. Pedigree information can be used for identifying where future research would be most beneficial when trying to improve these models.

### Initial Ecopath Model Outputs

#### Tables and flow matrices

Once a mass-balanced model has been achieved, Ecopath provides a number of output materials. The first is a summary of the table of input values, including the results of the values calculated by the software (Table D-4). Next is a table with the total flows to detritus (t/km<sup>2</sup>/year), the net efficiency, and the omnivory index for each species or functional group (Table D-5), followed by a table that outlines types of mortality for each group included in the model and a matrix clarifying mortality rates for all predator/prey relationships (Table D-6).

Perhaps most importantly, Ecopath also provides an energy-flow matrix depicting total flows between each predator/prey combination, as well as flows to detritus (Table D-7), and it calculates a table outlining respiration and assimilation values for each species or functional group, as well as respiration/assimilation, production/respiration, and respiration/biomass ratios for each compartment (Table D-8).

#### Flow diagrams and model statistics

To visually understand the characteristics of the model, a flow diagram is produced for each, in which nodes represent each compartment and weighted links indicate how much energy is flowing between these compartments. The nodes placement

in relation to the y-axis signals the calculated trophic level for that compartment, and the size of the node represents the species or functional group's biomass in the system (Figure D-1).

A table of important model statistics includes total values for consumption, exports, respiration, production, flows to detritus, as well as total system throughput for each reservoir as a whole. It also includes important comparative information, including ratios, net system production, and connectivity values (Table D-9).

#### Network analysis

The network analysis tool provides a way to analyze each model in terms of flows among trophic levels. Whereas the initial results described provide information for individual compartments, this aggregation by trophic level is important because species may have different calculated trophic levels depending on each reservoir's specific biotic composition. This type of aggregation allows a different type of comparison between different reservoirs. Absolute flows broken down by trophic levels are shown in Table D-10, and Table D-11 shows the total consumption, export, respiration, flow to detritus, and total throughput aggregated by each trophic level. To help visualize how the flows in Table D-11 are distributed by each trophic level, Lindeman spines are also developed by the software (Figure D-2). Mixed trophic impact matrices elucidate indirect effects species or functional groups have on one another (Figure D-3).

Transfer efficiency is an important metric in network analysis. The transfer efficiency is the ratio of the energy consumed by one trophic level to the amount of energy that is successfully transferred to the next highest trophic level (Pauly et al. 2000)

(Table D-12). Additional metrics included in the network analysis output are keystoneeness of each compartment (Table D-13), ascendancy, and information on the number of cycles and pathways present in each food web (Table D-14). Two keystone indices are given. The first is the keystone index, represented by  $KS_i = \log [\epsilon_i (1 - p_i)]$ , over the relative total impact (Libralato et al. 2006). The second keystone index is the keystone index, represented by  $KS_i = \log [\epsilon_i * 1/p_i]$ , over the relative total impact (Power et al. 1996).

#### Secondary Ecopath Model Outputs

Outputs from the secondary Ecopath models were similar to those generated from the initial Ecopath models, allowing efficient side-by-side comparisons. The same lake was used in all of the following tables and figures for consistency, but each procedure was completed for each of the 19 lakes and was completed multiple times, based on the type of model being analyzed.

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Table D-1. Example of an input data table. Known values are entered and all blank values (depicted with “.”) are calculated by the software.

Group name	Biomass in habitat area (t/km <sup>2</sup> )	Production/ biomass (/year)	Consumption/ biomass (/year)	Ecotrophic efficiency	Other mortality	Production/ consumption	Unassimil/ consumption	Detritus import (t/km <sup>2</sup> /year)
Predatory birds	0.0100	0.30	5.00	.	.	.	0.20	.
Walleye	0.4000	0.90	6.00	.	.	.	0.20	.
Largemouth Bass	1.1000	2.00	6.00	.	.	.	0.20	.
Channel Catfish	1.3500	2.20	8.00	.	.	.	0.20	.
Crappie	0.5000	3.00	8.00	.	.	.	0.20	.
Bluegill	0.6000	3.20	8.00	.	.	.	0.20	.
Freshwater Drum	0.5000	1.00	3.52	.	.	.	0.20	.
Flathead Catfish	0.6000	1.00	3.60	.	.	.	0.20	.
Common Carp	1.4000	3.00	8.00	.	.	.	0.20	.
Chinese Mystery Snail	0.0003	3.00	10.00	.	.	.	0.20	.
Benthic Macroinvertebrates	.	35.00	120.00	0.90	.	.	0.25	.
Copepods	.	20.00	100.00	0.95	.	.	0.30	.
Cladocerans	.	20.00	100.00	0.95	.	.	0.30	.
Autotrophs	.	250.00	.	0.99	.	.	0.00	.
Detritus	2.0000	.	.	.	.	.	0.20	2.00
Sediment	5.0000	.	.	.	.	.	0.00	1.00



Table D-2. Example of a diet composition matrix for a single reservoir. Columns represent predators and rows represent prey.

Each column sums to one, indicating 100% of that predator's diet.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1 Predatory birds	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Walleye	0.050	0.05	0	0	0	0	0	0	0	0	0	0	0
3 Largemouth Bass	0.050	0.05	0.05	0.050	0	0	0	0	0	0	0	0	0
4 Channel Catfish	0.005	0	0	0	0	0	0	0	0	0	0	0	0
5 Crappie	0.050	0.05	0.05	0.050	0	0	0	0	0	0	0	0	0
6 Bluegill	0.050	0.05	0.05	0.050	0.05	0	0	0	0	0	0	0	0
7 Freshwater Drum	0	0.05	0	0	0	0	0	0	0	0	0	0	0
8 Flathead Catfish	0	0	0	0.050	0	0	0	0	0	0	0	0	0
9 Common Carp	0	0	0	0.001	0	0	0	0	0	0	0	0	0
10 Chinese Mystery Snail	0.001	0	0	0	0	0	0	0	0	0	0	0	0
11 Benthic Macroinvertebrates	0.250	0.40	0.30	0.300	0.30	0.30	0.80	0.4	0.4	0	0	0	0
12 Copepods	0.100	0.05	0.10	0	0.20	0.30	0	0	0	0.3	0	0	0
13 Cladocerans	0.100	0.05	0.10	0	0.20	0.30	0	0	0	0.3	0	0	0
14 Autotrophs	0.250	0.10	0.10	0.200	0.05	0.05	0	0.2	0.3	0.3	0.60	1	1
15 Detritus	0	0	0.10	0.100	0	0.05	0.10	0.2	0.2	0.1	0.25	0	0
16 Sediment	0	0	0	0	0	0	0.05	0.1	0.1	0	0.1	0	0
17 Import	0.094	0.15	0.15	0.199	0.20	0	0.05	0.1	0	0	0.05	0	0
18 Sum	1	1	1	1	1	1	1	1	1	1	1	1	1

Table D-3. Example of fishery information used for a single reservoir. Discards represent fish that were caught and then released. Landings are fish that were caught and harvested. Fishing data are from Martin (2013).

Group name	Discards (t/km <sup>2</sup> )	Landings (t/km <sup>2</sup> )
Predatory birds	0	0
Walleye	0	0
Largemouth Bass	0.237	0.011
Channel Catfish	2.475	0.431
Crappie	0	0
Bluegill	0.293	0.0447
Freshwater Drum	0	0
Flathead Catfish	0	0
Common Carp	3.631	0.557
Chinese Mystery Snail	0	0
Benthic Macroinvertebrates	0	0
Copepods	0	0
Cladocerans	0	0
Autotrophs	0	0
Detritus	0	0
Sediment	0	0
Sum	6.636	1.0437

Table D-4. Example of basic estimates output table. Bolded values were calculated by the software.

Group name	Trophic level	Biomass in habitat area (t/km <sup>2</sup> )	Biomass (t/km <sup>2</sup> )	Production/ biomass (/year)	Consumption/ biomass (/year)	Ecotrophic efficiency	Production/ consumption
Predatory birds	<b>2.95</b>	0.0100	0.0100	0.3	5.00	<b>0.00</b>	<b>0.06</b>
Walleye	<b>3.14</b>	0.4000	0.4000	0.9	6.00	<b>0.34</b>	<b>0.15</b>
Largemouth Bass	<b>2.90</b>	1.1000	1.1000	2.0	6.00	<b>0.56</b>	<b>0.33</b>
Channel Catfish	<b>2.83</b>	1.3500	1.3500	2.2	8.00	<b>0.98</b>	<b>0.28</b>
Crappie	<b>2.99</b>	0.5000	0.5000	3.0	8.00	<b>0.66</b>	<b>0.38</b>
Bluegill	<b>2.90</b>	0.6000	0.6000	3.2	8.00	<b>0.80</b>	<b>0.40</b>
Freshwater Drum	<b>2.84</b>	0.5000	0.5000	1.0	3.52	<b>0.24</b>	<b>0.28</b>
Flathead Catfish	<b>2.44</b>	0.6000	0.6000	1.0	3.60	<b>0.90</b>	<b>0.28</b>
Common Carp	<b>2.40</b>	1.4000	1.4000	3.0	8.00	<b>1.00</b>	<b>0.38</b>
Chinese Mystery Snail	<b>2.60</b>	0.0003	0.0003	3.0	10.00	<b>0.06</b>	<b>0.30</b>
Benthic Macroinvertebrates	<b>2.00</b>	<b>0.4947</b>	<b>0.4947</b>	35.0	120.00	0.90	<b>0.29</b>
Copepods	<b>2.00</b>	<b>0.1593</b>	<b>0.1593</b>	20.0	100.00	0.95	<b>0.20</b>
Cladocerans	<b>2.00</b>	<b>0.1593</b>	<b>0.1593</b>	20.0	100.00	0.95	<b>0.20</b>
Autotrophs	<b>1.00</b>	<b>0.3021</b>	<b>0.3021</b>	250.0		0.99	
Detritus	<b>1.00</b>	2.0000	2.0000			<b>0.90</b>	
Sediment	<b>1.00</b>	1.0000	5.0000				

Table D-5. Example of key indices output.

Group name	Biomass accumulation (t/km <sup>2</sup> /year)	Biomass accumulation rate (/year)	Net migration (t/km <sup>2</sup> /year)	Flow to detritus (t/km <sup>2</sup> /year)	Net efficiency	Omnivory index
1 Predatory birds				0.003	0.075	0.477
2 Walleye				0.718	0.188	0.397
3 Largemouth Bass				2.280	0.417	0.398
4 Channel Catfish				2.224	0.344	0.523
5 Crappie				1.308	0.469	0.218
6 Bluegill				1.350	0.500	0.090
7 Freshwater Drum				0.732	0.355	0.134
8 Flathead Catfish				0.492	0.347	0.241
9 Common Carp				2.241	0.469	0.240
10 Chinese Mystery Snail				0.001	0.375	0.240
11 Benthic Macroinvertebrates				16.574	0.389	0.002
12 Copepods				4.937	0.286	
13 Cladocerans				4.937	0.286	
14 Autotrophs				0.755		
15 Detritus	1.083	0.541	-2.000			0.570
16 Sediment			-1.000			0.152

Table D-6. Example of output table outlining different mortality rates for each species/functional group.

Group name	Production/ biomass (Z)	Fishing mortality rate	Predation mortality rate (/year)	Other mortality rate (/year)	Fishing mortality/ total mortality	Proportion natural mortality
Predatory birds	0.30			0.30	0.00	1.00
Walleye	0.90		0.31	0.59	0.00	1.00
Largemouth Bass	2.00	0.23	0.90	0.87	0.11	0.89
Channel Catfish	2.20	2.15	0.00	0.05	0.98	0.02
Crappie	3.00		1.99	1.02	0.00	1.00
Bluegill	3.20	0.56	1.99	0.65	0.18	0.82
Freshwater Drum	1.00		0.24	0.76	0.00	1.00
Flathead Catfish	1.00		0.90	0.10	0.00	1.00
Common Carp	3.00	2.99	0.01	0.00	1.00	0.00
Chinese Mystery Snail	3.00		0.17	2.83	0.00	1.00
Benthic Macroinvertebrates	35.00		31.50	3.50	0.00	1.00
Copepods	20.00		19.00	1.00	0.00	1.00
Cladocerans	20.00		19.00	1.00	0.00	1.00
Autotrophs	250.00		247.50	2.50	0.00	1.00

Table D-7. Example of an output table illustrating energy flow values between predator and prey groups. Predators are in columns and prey are in rows.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	15	16
1 Predatory birds														0.00	
2 Walleye	0.00250	0.12												0.36	0.36
3 Largemouth Bass	0.00250	0.12	0.33	0.54										1.14	1.14
4 Channel Catfish	0.00025													1.11	1.11
5 Crappie	0.00250	0.12	0.33	0.54										0.65	0.65
6 Bluegill	0.00250	0.12	0.33	0.54	0.20									0.67	0.67
7 Freshwater Drum		0.12												0.37	0.37
8 Flathead Catfish				0.54										0.25	0.25
9 Common Carp				0.01										1.12	1.12
10 Chinese Mystery Snail	0.00005													0.00	0.00
11 Benthic Macroinvertebrates	0.01250	0.96	1.98	3.24	1.20	1.44	1.41	0.86	4.48					4.97	11.60
12 Copepods	0.00500	0.12	0.66		0.80	1.44				0.00				1.48	3.46
13 Cladocerans	0.00500	0.12	0.66		0.80	1.44				0.00				1.48	3.46
14 Autotrophs	0.01250	0.24	0.66	2.16	0.20	0.24		0.43	3.36	0.00	35.62	15.93	15.93	0.45	0.30
15 Detritus			0.66	1.08		0.24	0.18	0.43	2.24	0.00	14.84				
16 Sediment							0.09	0.22	1.12		5.94				
17 Import	0.00470	0.36	0.99	2.15	0.80	0.00	0.09	0.22	0.00	0.00	2.97	0.00	0.00	0.00	0.00
18 Sum	0.05000	2.40	6.60	10.80	4.00	4.80	1.76	2.16	11.20	0.00	59.37	15.93	15.93	14.06	24.49

Table D-8. Example of respiration and assimilation output table.

Group name	Respiration (t/km <sup>2</sup> /year)	Assimilation (t/km <sup>2</sup> /year)	Respiration/ assimilation	Production/ respiration	Respiration/ biomass (/year)
Predatory birds	0.04	0.04	0.93	0.08	3.70
Walleye	1.56	1.92	0.81	0.23	3.90
Largemouth Bass	3.08	5.28	0.58	0.71	2.80
Channel Catfish	5.67	8.64	0.66	0.52	4.20
Crappie	1.70	3.20	0.53	0.88	3.40
Bluegill	1.92	3.84	0.50	1.00	3.20
Freshwater Drum	0.91	1.41	0.64	0.55	1.82
Flathead Catfish	1.13	1.73	0.65	0.53	1.88
Common Carp	4.76	8.96	0.53	0.88	3.40
Chinese Mystery Snail	0.00	0.00	0.63	0.60	5.00
Benthic Macroinvertebrates	27.21	44.53	0.61	0.64	55.00
Copepods	7.96	11.15	0.71	0.40	50.00
Cladocerans	7.96	11.15	0.71	0.40	50.00
Autotrophs					
Detritus					
Sediment					

Table D-9. Example of network statistics output table.

Parameter	Value	Units
Sum of all consumption	134.994	t/km <sup>2</sup> /year
Sum of all exports	27.753	t/km <sup>2</sup> /year
Sum of all respiratory flows	63.901	t/km <sup>2</sup> /year
Sum of all flows into detritus	48.187	t/km <sup>2</sup> /year
Total system throughput	274.835	t/km <sup>2</sup> /year
Sum of all production	113.474	t/km <sup>2</sup> /year
Mean trophic level of the catch	2.600	
Gross efficiency (catch/net p.p.)	0.102	
Calculated total net primary production	75.534	t/km <sup>2</sup> /year
Total primary production/total respiration	1.182	
Net system production	11.633	t/km <sup>2</sup> /year
Total primary production/total biomass	9.971	
Total biomass/total throughput	0.028	/year
Total biomass (excluding detritus)	7.576	t/km <sup>2</sup>
Total catch	7.680	t/km <sup>2</sup> /year
Connectance Index	0.332	
System Omnivory Index	0.204	



Table D-10. Absolute flows separated by trophic level. Units for all values are in t/km<sup>2</sup>/year.

Group name / Trophic level	I	II	III	IV	V	VI	VII
Predatory birds	0	0.01	0.02	0.01	0.00	0.00	0
Walleye	0	0.32	1.61	0.45	0.02	0.00	0
Largemouth Bass	0	1.71	4.20	0.67	0.02	0	0
Channel Catfish	0	4.27	4.68	1.77	0.09	0.00	0
Crappie	0	0.26	3.52	0.23	0	0	0
Bluegill	0	0.49	4.31	0	0	0	0
Freshwater Drum	0	0.29	1.47	0	0	0	0
Flathead Catfish	0	1.23	0.93	0	0	0	0
Common Carp	0	6.86	4.34	0	0	0	0
Chinese Mystery Snail	0	0.00	0.00	0	0	0	0
Benthic Macroinvertebrates	0	59.37	0	0	0	0	0
Copepods	0	15.93	0	0	0	0	0
Cladocerans	0	15.93	0	0	0	0	0
Autotrophs	75.53	0	0	0	0	0	0
Detritus	20.75	0	0	0	0	0	0
Sediment	26.35	0	0	0	0	0	0
Total	122.60	106.60	25.09	3.12	0.13	0.00	0

Table D-11. Total import, consumption, export, flow to detritus, respiration, and production flow values separated by trophic level.

Units for all values are in t/km<sup>2</sup>/year.

Trophic level/ Flow	Import	Consumption by predators	Export	Flow to detritus	Respiration	Throughput
VII		0	0	0	0	0
VI		0	0.0003	0.0004	0.0010	0.0020
V		0.002	0.0218	0.0273	0.0611	0.1120
IV		0.108	0.4070	0.6680	1.3440	2.5270
III		2.226	2.1840	5.1670	8.5070	18.0800
II		16.230	2.0970	22.2700	37.1400	77.7400
I	0	74.780	0	0.7550	0	75.5300
Sum	0	93.340	4.7100	28.8900	47.0500	174.0000

Table D-12. Transfer efficiencies per trophic level.

Source\trophic level	II	III	IV	V	VI	VII
Producer	23.6	24.4	20.4	21.0	22	
Detritus	27.1	24.4	20.2	21.1		
All flows	24.5	24.4	20.4	21.0	22	

Proportion of total flow originating from  
detritus: 0.33

Transfer efficiencies (calculated as  
geometric mean for Trophic levels II-IV)

From primary producers: 22.7%

From detritus: 23.7%

Total: 23.0%

Table D-13. Keystone indices for each species or functional group. Keystone indices are described in the text.

Group name	Keystone index	Keystone index #2	Relative total impact
Predatory birds	-0.00132	2.879	1
Walleye	-0.325	0.976	0.5
Largemouth Bass	-0.547	0.36	0.333
Channel Catfish	-0.135	0.699	0.893
Crappie	-0.606	0.604	0.266
Bluegill	-0.409	0.728	0.424
Freshwater Drum	-1.15	0.06	0.0759
Flathead Catfish	-1.174	-0.0368	0.0729
Common Carp	-0.476	0.346	0.411
Chinese Mystery Snail	-2.994	1.409	0.00102
Benthic Macroinvertebrates	-0.245	0.969	0.61
Copepods	-0.503	1.184	0.322
Cladocerans	-0.503	1.184	0.322
Autotrophs	-0.0655	1.351	0.897

Table D-14. Output table on cycles and pathway lengths.

Parameter	Value	Units
Throughput cycled (excluding detritus)	0.45	t/km <sup>2</sup> /year
Predatory cycling index	0.25	% of throughput without detritus
Throughput cycled (including detritus)	13.96	t/km <sup>2</sup> /year
Finn's cycling index	5.2	% of total throughput
Finn's mean path length	2.926	none
Finn's straight-through path length	2.465	without detritus
Finn's straight-through path length	2.774	with detritus

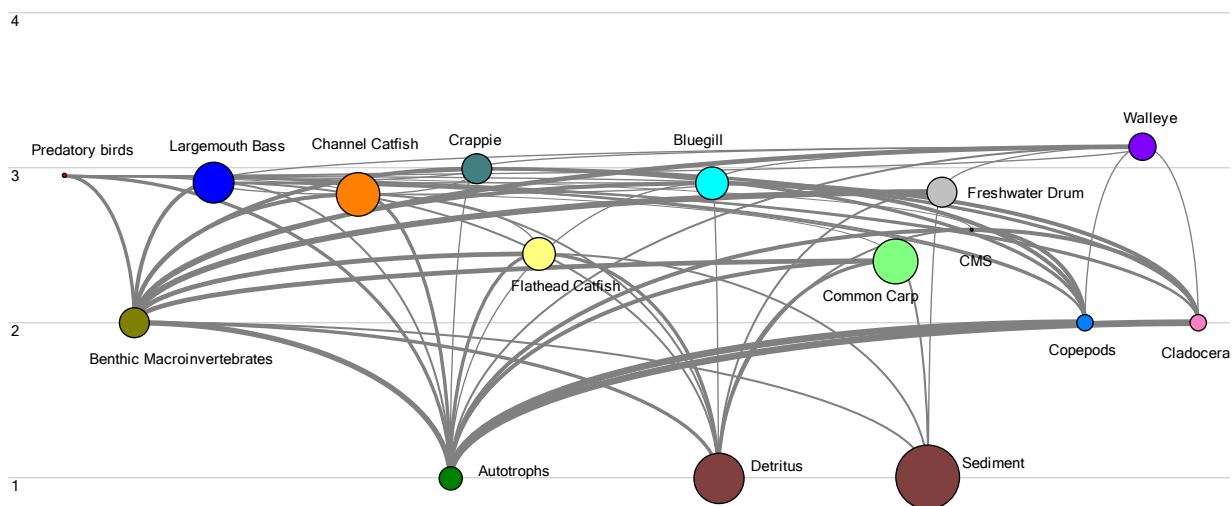


Figure D-1. Example of a flow diagram output. This example is from the same lake as the preceding tables. Calculated trophic levels are on the y-axis, and node size is scaled to that species' biomass. Weighted links between nodes represent the energy flow between nodes.

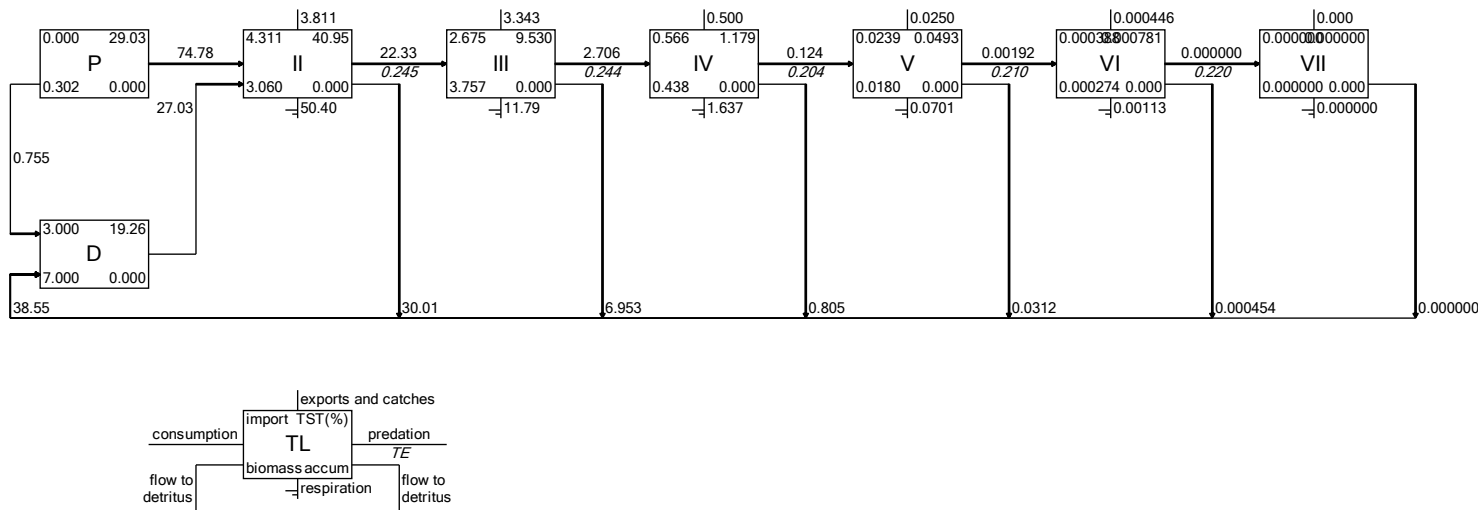


Figure D-2. A Lindeman spine produced for the same lake as the preceding examples. Flow values for consumption, respiration, export, predation, flows to detritus, and imports are given, as well as total system throughput and biomass accumulation values.

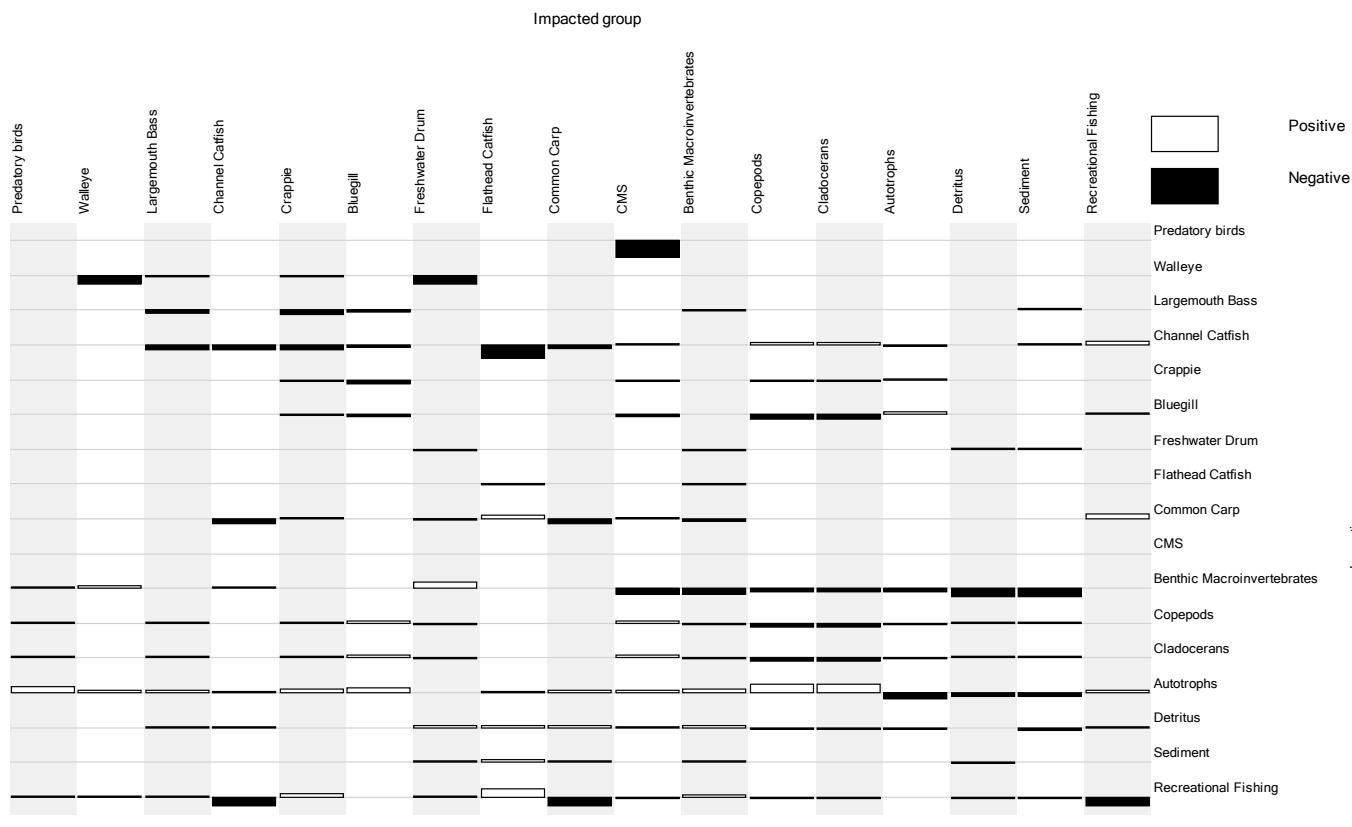


Figure D-3. Mixed trophic impact plot produced for a single lake. The color and size of the rectangle indicates how the group in a given row impacts the group in each column. The larger the box, the greater the impact. Black boxes are negative impacts and white boxes are positive impacts. (Chinese mystery snail is abbreviated as CMS in this figure.)