

## TROPHIC ROLES AND ECOLOGICAL SERVICES PROVIDED BY A MULTI-SPECIES ASSEMBLAGE OF FRESHWATER MUSSELS

### Goals of Research

Clean, freshwater is a necessity to sustain human life. Maintenance of freshwater biodiversity is critical to sustain vital ecological functions, such as biofiltration, that promote clean water. In addition to clean water, functionally intact and biologically complex freshwater ecosystems also provide many other economically valuable services and long-term benefits to human societies such as food supply, flood control, habitat for animal and plant life and the adaptive capacity to respond to future environmental alterations such as climate change (Baron et al. 2002, Loreau et al. 2002). Our understanding of the influence of biodiversity on ecosystem goods and services is incomplete (Naidoo et al. 2008), but it has been proposed that greater biodiversity in the form of greater functional diversity can “insure” that ecosystem functions and processes continue in the wake of environmental fluctuations (Naeem and Li 1997, Yachi and Loreau 1999, Naeem and Wright 2003, Balvanera et al. 2006). The implications of species losses for sustaining water quality are poorly understood. Thus, we need a stronger understanding of the linkages between biodiversity and ecosystem services in freshwaters.

Maintenance of ecosystem services provided by diverse communities of biota in aquatic ecosystems is essential. High levels of biodiversity found within natural environments provide multiple pathways of resource utilization such as energy transformation and nutrient interception and storage (Walker 1995). Water quality is generally enhanced by breakdown of organic matter and biofiltration during ecological processes such as consumption of detritus and filter feeding among numerous species of invertebrates and microbes (Loreau et al. 2002). Unfortunately, despite their importance in sustaining ecosystem function, the loss of freshwater species continues at a higher rate than in any other type of ecosystem (Dudgeon et al. 2005, Sala and Jackson 2006). Many freshwater species are imperiled: 48.5% of North American freshwater mussels (Turgeon et al. 1988, Bogan 1996), 32.7% of crayfishes (Taylor et al. 1996), 22.8% of freshwater gastropods (Neves et al. 1997), and 21.3% of freshwater fishes (Williams et al. 1989). Results from biodiversity–ecosystem function research indicate that ecosystem processes performed by biota are higher for more diverse biological communities (Cardinale et al. 2002, Balvanera et al. 2006, Cardinale et al. 2006). Continued species loss and degradation of habitats will likely lead to further changes in ecosystem function (Carpenter et al. 1985, Schindler 1989, Power 1990, Lhomme and Winkel 2002). Such losses may result in reduced capacity for sustaining processes of self-purification of natural freshwater ecosystems.

Freshwater mussels (*Bivalvia*: *Unionoida*) are natural “biofilters” known for their ability to filter large amounts of water (Strayer et al. 1994, Strayer et al. 1999). Kreeger et al. (2010) estimated that the collective filtration ability of bivalves in the Delaware Estuary watershed exceeds 100 billion liters per hour. Additionally, Vaughn et al. (2004) found that mussels in the Kiamichi River could process the water overlying them 10 times before it passed through a river reach. The North American fauna of freshwater mussels are the most diverse in the world, with approximately 308 native species (Turgeon et al. 1988), but are the most threatened group of fauna in North America. Although they occur in most types of freshwater habitats, mussels are most abundant and diverse in medium to large rivers where they typically occur as dense, multi-

species assemblages called mussel beds (Strayer et al. 2004). Within these beds, mussel biomass can exceed that of other benthic organisms by an order of magnitude and annual production (in terms of dry mass produced per year) can equal that of other macrobenthos (Negus 1966, Strayer et al. 1994). Mussels perform important functions in rivers (Vaughn and Hakenkamp 2001). Living mussels and their spent shells provide habitat for other organisms (Howard and Cuffey 2006, Spooner and Vaughn 2006, Vaughn and Spooner 2006b). Through the process of filtering suspended matter, mussels link benthic and pelagic compartments by transferring energy and nutrients from the water column to the sediment, biodepositing organic matter, and excreting nutrients (Vaughn and Hakenkamp 2001, Vaughn et al. 2004, Howard and Cuffey 2006, Elderkin et al. 2008). The effects of these energy and nutrient subsidies provided by mussels cascade up food webs and stimulate both algal and macroinvertebrate production (Howard and Cuffey 2006, Spooner and Vaughn 2006, Vaughn and Spooner 2006b, Vaughn et al. 2007, Vaughn et al. 2008).

Diverse aquatic communities enhance nutrient cycling and water quality naturally by supporting various processes. Although we know that mussels perform important ecological functions, we need to expand our knowledge of the roles of individual species, and how environmental changes affect these roles to make quantitative predictions about mussel ecosystem services. This will allow us to manage mussel populations to maximize water quality and other services. Thus, my dissertation research is focusing on the functions that mussels perform (nutrient recycling), under what environmental conditions mussels provide ecosystem services, and their bottom-up trophic effects on stream food webs.

### **Proposed questions for doctoral research:**

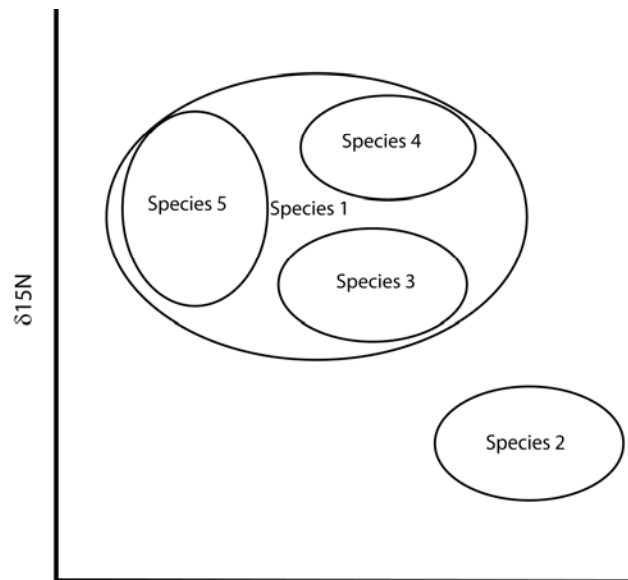
#### **Q1: Do species of co-occurring freshwater mussels occupy different trophic niche spaces (filtering different components)?**

Human alteration of freshwater habitats is changing the composition and availability of food resources for aquatic organisms. While freshwater mussels have traditionally been assigned to the same trophic guild (primary consumers filtering algae from the water column), recent studies indicate that mussels may feed at multiple trophic levels (i.e. bacteria, phytoplankton, zooplankton), and from both the water column and sediment (reviewed in Vaughn et al. 2008). A niche describes the relational position of a species or population in an ecosystem. Trophic niche space describes the degree of overlap in species' diets (Fig 1). Freshwater mussels typically occur as speciose assemblages (Strayer 2008), and partitioning food resources is one potential mechanism by which multiple species could co-exist. Thus, different species may be filtering various components from the water column. Furthermore, different mussel species may select for different types or sizes of particles, and this might vary with environmental conditions and food availability (Vaughn et al. 2008, Galbraith et al. 2009). If variation in food resource utilization occurs this would lead to a diversity of trophic niche spaces. Studying trophic partitioning is essential to understand coexistence within communities (MacArthur 1958, Werner 1977, Levine and HilleRisLambers 2009). Abundant species may have the ability to utilize a wide array of food resources (generalists), allowing them to persist, while rarer species may be more specialized. Finally, native freshwater mussels must compete with a widespread invasive species, the Asian Clam *Corbicula fluminea* (Strayer et al. 1999, Vaughn and Spooner 2006a).

Recent work indicates that *C. fluminea* may be able to utilize a broader spectrum of food resources than native mussels, allowing them to persist and perhaps out-compete native species (Atkinson 2008, Atkinson et al. 2010). More research needs to investigate biofiltration and the trophic roles of native aquatic fauna in relation to invasive species to fully understand the implications of their introduction to native freshwater mussels and to the rest of the food web. I plan to test the following hypotheses:

**H1.1** Different freshwater mussel species specialize on different sizes and varieties of particles. This partitioning allows for co-existence and leads to higher biofiltration efficiency.

**H1.2** Common freshwater mussel species are opportunistic generalists, while rarer species are specialists. Generalists, given their ability to utilize a greater variety of resources, may be more common in ecosystems than species that are specialists.



**Fig 1:** Species 1 occupies a larger isotopic space allowing one to predict that species is a generalist. Species 2 occupies a smaller isotopic space that does not occupy the same space as species 2. Collectively, species 3, 4, 5 occupy the same space and the same amount of space as species 1. The proposed trophic niche space analysis will utilize stable isotopes as a tool.

## **Q2: Do freshwater mussels control nutrient dynamics in the areas they occupy?**

Nutrient limitation is a key process that structures biotic interactions within ecosystems. This is especially apparent in stream environments in which nutrients are taken up readily and cycled through the system in a downstream trajectory (i.e. nutrient spiralling, Newbold et al. 1982). Biogeochemical cycling is driven by organisms that have specific requirements for different nutrients (Sterner and Elser 2002). Ecological stoichiometry predicts that biogeochemical cycles of different elements are interdependent because the organisms that drive these cycles require fixed ratios of nutrients (Sterner and Elser 2002). Stream ecologists are just beginning to hypothesize how the ratios of dissolved N:P may affect the ratios of N and P uptake rates (Cross et al. 2005). Hooper et al. (2005) suggest that combining knowledge of abiotic and biotic controls of ecosystem functioning is essential for understanding the influence of biodiversity on ecosystem services. Freshwater mussels are model organisms to test these interactions because they occur as dense, speciose aggregates in many streams.

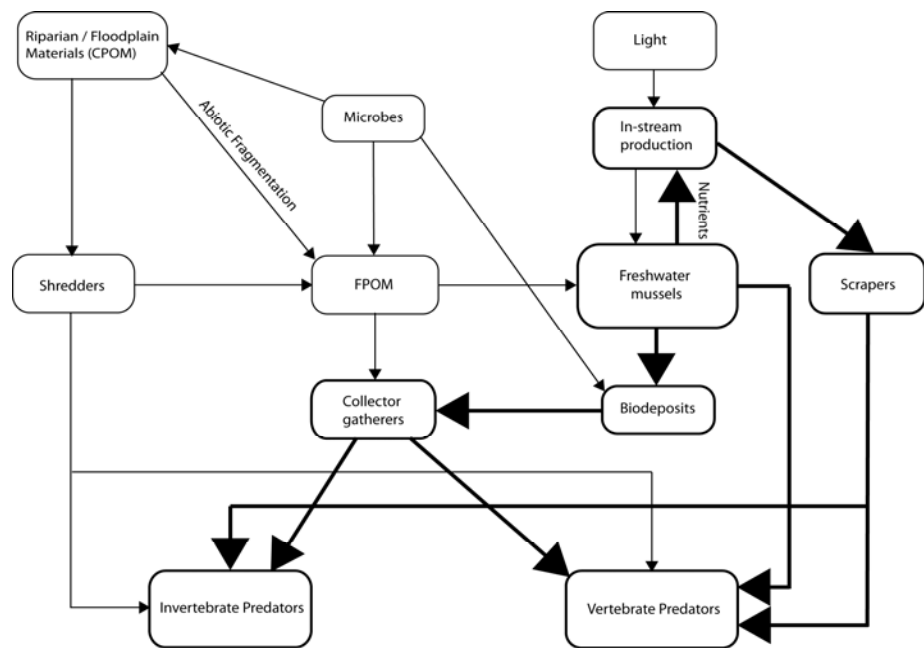
Because all mussels are sedentary filter feeders, they traditionally have been assigned to the same guild and assumed to perform equivalent ecosystem roles. In reality, mussel species vary in multiple traits, ranging from overall size and shell morphology to the spacing of cilia on the gills (Vaughn et al. 2008, Galbraith et al. 2009). Differences are likely to be reflected in the nutrient cycling processes of various species of mussels. Mussels influence nutrient dynamics

of mussels. Mussels influence nutrient dynamics through preferential assimilation and excretion of nutrients (Spooner and Vaughn 2006, Vaughn 2010). Consumers that are at relatively high densities have the potential to influence stream nutrient dynamics through differential excretion of limiting and non-limiting nutrients (Small et al. 2009). Due to their high densities in rivers of southeastern Oklahoma, mussels have the potential to exert large effects on aquatic ecosystems. A breakdown in the feedback of limiting nutrients could drastically alter the ecosystem and cause further loss of species. For example, changes in N:P excretion could influence algal species composition, changes in the food web, and hypoxia in the water column due to algal blooms. Understanding the role of mussels on nutrient cycling dynamics is essential for conserving these systems.

**H2.1:** In areas where mussels are very abundant, they cause changes in the limiting nutrients in the benthic environment. Through differential uptake and excretion of nutrients, freshwater mussels change what nutrients are limiting algal productivity in rivers, thus influencing water quality.

**Q3: How do native mussels influence stream food webs? Are materials provided by mussels energetically linked to other organisms and/or higher trophic levels (e.g. fish, turtles)?**

Food webs link ecosystems through the movement of nutrients and energy (Odum 1969, Polis et al. 1997). The well-documented abundance of bivalves and their high filtration rates suggest that bivalves can potentially exert large effects on stream food webs (Vaughn et al. 2008). The ecological functions performed by mussels (e.g., filter-feeding, nutrient excretion, biodeposition, bioturbation) impact both primary producers and consumers through direct and indirect pathways. Recent studies have shown that mussels, by filtering the water column and releasing nutrients and biodeposits,



**Fig 2:** Conceptual diagram to depict freshwater mussels' role in a stream food web. Bolded arrows denote process that will be studied. Freshwater mussels exert bottom-up trophic effects. Freshwater mussels directly effect in-stream production and excrete biodeposits that influence benthic production. These direct effects indirectly enhance secondary productivity of scrapers and collector gatherers, and continue up the food web.

stimulate both water column and benthic primary production (Vaughn et al. 2007, Vaughn et al. 2008), which in turn is correlated with higher abundance and richness of benthic invertebrates (Howard and Cuffey 2006, Spooner and Vaughn 2006, Vaughn and Spooner 2006b, Vaughn et al. 2008). This bottom-up trophic cascade may be linked further up the food web, influencing secondary consumers such as fishes and turtles (Fig. 2). I will test the following hypothesis:

**H3.1** The nutrients and biodeposits released by mussels are assimilated by benthic algae and these subsidies are then transferred up the food web to higher consumers. This transfer of nutrients and energy maintains a healthy and biodiverse ecosystem.

## **Rationale**

Complex interactions within communities maintain the processes that insure ecosystem services. Without these complex, multi-step pathways the flux of nutrients and material are left unchecked. Historically, filter-feeding bivalves were the dominant invertebrate, in terms of biomass, in many eastern North American streams (Parmalee et al. 1998, Strayer 2008). Maintaining mussel biodiversity would ensure biofiltration and other processes were maintained under varying environmental conditions. Preserving natural capita may lead to economic savings to humans by having cleaner water available. Consequently, research on freshwater mussels has significant implications for the conservation of this highly endangered group that are key ecological players in stream ecosystems. Topics in ecological research in recently have been (1) to quantify the relationship between biodiversity and ecosystem function (Loreau 2004, Hooper et al. 2005), (2) to understand how ecosystems are linked by resource subsidies (Polis et al. 2004), and (3) to identify the role of species traits on ecosystem processes (Vaughn et al. 2007, Spooner and Vaughn 2008, 2009). This research will link these three research areas and provide information that can be used in the conservation and management of freshwater mussels (Unionidae). Species loss, habitat alteration, and climate change are causing dramatic changes in the diversity and function of ecological communities. Although mussels are one of the most imperiled faunal groups, conservation efforts are hampered by a lack of knowledge about the consequences of their decline (Strayer et al. 2004). Consequently, understanding how biodiversity influences ecosystem processes, such as biofiltration and the trophic transfer of nutrients and energy, is a critical research need.

## **Approach**

### Overview:

The proposed research will be conducted in southeastern Oklahoma in the Kiamichi, Little, and Mountain Fork River watersheds (Fig. 3). Our laboratory has long-term data on mussel communities and landowner permission to conduct experiments in these catchments (for example, see Vaughn et al. 2007). The Ouachita mountain region is a center of speciation for both terrestrial and aquatic organisms, with a high number of endemic species (Gordon 1980, Mayden 1985). These rivers are major tributaries of the Red River and support healthy and diverse mussel communities (Vaughn et al. 1996, Vaughn and Taylor 1999). However, these rivers are also under threat due to future water extractions by Oklahoma City (<http://www.owrb.ok.gov/supply/ocwp/ocwp.php>) and dam construction (Vaughn and Taylor 1999). In the streams of the Ouachita Uplands in southeastern Oklahoma, mussel beds often

contain over 20 mussel species at densities over 100/m<sup>2</sup> and biomass can exceed 20 kg/m<sup>2</sup> (Vaughn and Taylor 2000). These streams are home to diverse mussel assemblages (31-35 species), making the systems ideal for studying species diversity – ecosystem services hypotheses.

### Synergies with ongoing research

Prior studies in southeastern Oklahoma streams have examined ecosystem processes related to freshwater mussels (Vaughn et al. 2004, Vaughn and Spooner 2006b, Vaughn et al. 2007, Spooner and Vaughn 2009), the consequences of species traits on ecosystem function (Vaughn et al. 2007, Spooner and Vaughn 2008), interactions and varying functional roles of native mussels and invasive species (Vaughn and Hakenkamp 2001, Vaughn and Spooner 2006a), diversity – density effects of burrowing by native mussels (Allen and Vaughn 2009, 2010), and status of rare and endangered mussels (Galbraith et al. 2008).



My research will fill a critical gap by investigating ecological functions and ecosystem services provided by freshwater mussels. EPA STAR funding will help me with my dissertation research - investigating how freshwater mussels influence the environment through biofiltration and preferential uptake and excretion of nutrients, effects of different species on ecosystem services, and their role within stream food webs. Relationships that will be focused upon in detail are shown by the bolded arrows in Fig. 2. I am especially interested in nutrient cycling roles and the involvement and impact of freshwater mussels in stream food webs.

### **Q1: Do species of co-occurring freshwater mussels occupy different trophic niche spaces (filtering different components)?**

#### Proposed approach to testing trophic niche space:

Quantifying diet is essential for understanding the functional role of species in regard to energy processing, transfer, and storage within ecosystems. Naturally occurring stable isotopes are potentially a very powerful approach in determining patterns of energy flow and food web linkages in ecosystems (Peterson and Fry 1987, McCutchan and Lewis 2002). Stable isotopes have been used to assess the food items assimilated by organisms. Additionally, newly proposed statistical techniques allow the comparison of not only the mean isotopic signatures for distinct groups of individuals, but also the degree of dispersion in their signatures, indicating the width of their trophic space (Bearhop et al. 2004, Atkinson 2008, Atkinson et al. 2010). Stable isotope

compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of several common native freshwater mussel species (*Actinonaias ligamentina*, *Amblema plicata*, *Quadrula pustulosa*) and an invasive species (*Corbicula fluminea*) will be measured. The central tendency and dispersion of these signatures will be assessed using a multi-response permutation procedure, which allows analyses of bivariate data. Then, follow-up descriptive statistics (Van Valen's test and bootstrapping) will be used for a discrete dissection of the central tendency and dispersion of the data. This will allow me to understand the overlap of trophic niche space, quantified via stable isotopes, and will allow determination of niche partitioning.

**Q2: Do freshwater mussels control nutrient dynamics in the areas they occupy?**

Proposed assessment of mussel driven nutrient affects:

Over the summer of 2010, nutrient diffusing substrates were placed at 18 sites (12 replicates at each site) across three different watersheds, with half of the sites containing high mussel densities and the other half having no mussels or very low densities. Preliminary results indicate differences in the limiting nutrients in areas with high mussel densities versus areas with low mussel densities (Table 1). In addition, field excretion experiments were performed to determine excretion rates and the composition of excreted biodeposits and soluble nutrients (C, N, P). Tissue samples were also collected from 10 individuals of common species for determination of tissue stoichiometry (C:N:P). Collectively, these data will allow me to infer the role mussels play in stream nutrient cycling.

Site Type	Site	River	Limiting Nutrients
High Mussel Densities	KM1	Kiamichi	Co-limitation
	KM2	Kiamichi	Nitrogen
	KM3	Kiamichi	Co-limitation
	LM1	Little	Co-limitation
	LM2	Little	Co-limitation
	LM3	Little	Co-limitation
	MFM1	Mountain Fork	Co-limitation
	MFM2	Mountain Fork	Co-limitation
	MFM3	Mountain Fork	Co-limitation
Low Mussel Densities	KNO1	Kiamichi	Nitrogen
	KNO2	Kiamichi	Nitrogen
	KNO3	Kiamichi	Nitrogen
	LNO1	Little	Nitrogen
	LNO2	Little	Nitrogen
	LNO3	Little	Nitrogen
	MFNO1	Mountain Fork	Phosphorus
	MFNO2	Mountain Fork	Co-limitation
	MFNO3	Mountain Fork	Nitrogen

**Table 1:** Results from a nutrient-diffusing substrate experiment done June-July 2010. Substrates (12 replicates of each treatment) were at each site for a total of 18 days.

To further understand the roles of individual species, mesocosm studies utilizing similar methods are planned. Nutrient diffusing substrates (no nutrients, +N, +P, +NP) will be placed in mesocosms with varying species compositions of mussels and sham mussels (control) to determine the nutrients limiting algae growth in the presence and absence of mussels. This study will allow me to determine how mussels influence nutrient cycling dynamics within streams.

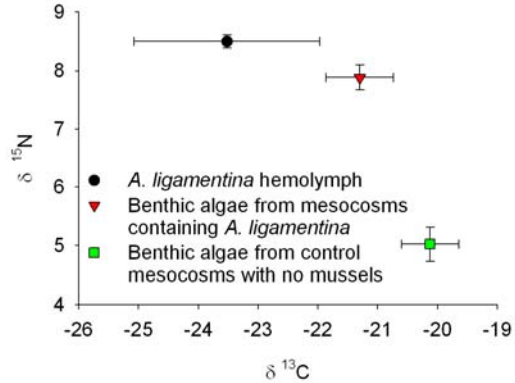
**Q3: How are native mussels influencing stream food webs? Are materials provided by mussels energetically linked to other organisms and/or higher trophic levels (e.g. fish, turtles)?**

Proposed stable isotope studies:

Stable isotopes have been used in many aquatic ecology studies to study food webs, trophic structure, and to understand energetic relationships between organisms and their food sources (Vander Zanden and Rasmussen 1999, Finlay 2001, Post 2002). Understanding how resources vary in a system is necessary to understand the dynamics of the ecosystem and the multiple sources consumers are utilizing. Stable isotope enrichment ( $\delta^{15}\text{N}$ ) has been used as a tool to determine nutrient cycling and food web relationships in multiple studies (Hughes et al. 2000, Galvan et al. 2008, Drake et al. 2009). Relationships that will be focused upon in detail are shown by the bolded arrows in Fig. 2. Dan Allen, a fellow lab member, has successfully enriched adult mussels with heavy nitrogen ( $^{15}\text{N}$ ) in the laboratory (Fig. 4) and has shown the enrichment to last over eight weeks after feeding of enriched algae was discontinued. Juvenile mussels (>300 individuals) will be grown for ~1 year on a  $\delta^{15}\text{N}$  enriched diet in the Aquatic Research Facilities on the University of Oklahoma campus. After enrichment, mussels will be placed in mesocosms with aquatic insects, snails, and fish to measure enrichment of a stream food web by mussels under a controlled environment. Mussels will be introduced to the upper Little River system during the late spring. It has been shown that mussels have greater impact on primary and secondary productivity during low flow conditions, so sampling of the food web will occur under these conditions. Primary producers (benthic algae and river weed, *Podostemnon*), primary consumers (macroinvertebrates), omnivores (crayfish), and predators (invertebrate predators, and razorback musk turtles, *Sternotherus carinatus*) will be sampled to quantify the bottom-up affects of freshwater mussels. Additionally, the isotope information gathered will allow us to describe and quantify interactions within the food web.

**Expected Results**

The results of this experiment will increase our understanding of how interactions between abiotic factors and species roles and the impact of biodiversity on the functioning of the ecosystem. I predict that mussels will have a strong influence on nutrient cycling, and that their bottom-up affects on the ecosystem are important to the food web. Discerning how biodiversity influences ecosystem processes, such as biofiltration and the trophic transfer of nutrients and energy is a critical research need. Organisms affect the rest of the community by their feeding activities and preferential ingestion and assimilation of resources. Due to the high biomass of freshwater mussels in this system, I predict that they exert a large effect on the ecosystem. More research is needed to understand interspecific interactions and the influence of species



**Fig 4:** Results from Dan Allen's isotope experiments. Benthic algae were more enriched in mesocosms that contained enriched mussels (*Actinonaias ligamentina*).



assemblages on ecosystems. This will have immediate applicability to understanding the value of freshwater mussels in the role of supporting higher trophic levels and providing ecosystem services.

#### Scientific significance:

My research aims at linking three major areas of ecological research: the affects of cross-boundary subsidies, the relationship between biodiversity and ecosystem function, and the role of species traits on ecosystem processes. Cross-boundary resource subsidies have been a major focus of ecological research in recent years (see Polis et al. 2004). These subsidies are donor-controlled; prior studies demonstrating that emerging aquatic insects subsidize terrestrial food webs have been approached from the perspective of the recipient system (Nakano and Murakami 2001, Sabo and Power 2002, Sanzone et al. 2003). Freshwater mussels subsidize the benthic compartment of streams through the transfer of energy and nutrients from the water column; this transfer allows materials to be more readily available to most stream consumers. Complex interactions within communities maintain the processes that insure ecosystem services. The diverse assemblages of freshwater mussels provide ecosystem services such as biofiltration. Understanding the roles of highly diverse mussel communities is essential for better knowledge of biodiversity – ecosystem service relationships in freshwater ecosystems. This study is one of the first to investigate the mechanisms that control the rate of cross-boundary subsidies between the water column and benthic areas within the context of aquatic food webs via energy and nutrient transfers.

#### Broader Impacts:

The proposed research project will result in a pioneering study that integrates biogeochemistry and biology to understand how the biotic communities influence nutrient cycling processes and the aquatic food web. My first year of fieldwork was successful and yielded a large amount of data that I am in the process of analyzing. The Ouachita region of southeastern Oklahoma is rural and sparsely populated. In my first year of field work, I lived in the area and conversed with a variety of landowners and local residents on water issues and have given out freshwater mussel identification keys. I plan to bring greater awareness of these aquatic organisms and the importance of freshwater habitats to the communities. In April 2011, I will be assisting with an Earth Day Event in Ada, OK. This will include a display on aquatic biodiversity and the freshwater resources of Oklahoma. I will continue working with local residents and I am planning school programs in the future in order to educate the new generation about sustaining our water resources. Scientific research is essential to understanding our world, yet communicating our knowledge to the community becoming even more critical.

Environmental management will be better informed through a stronger focus on how ecosystem services vary in response to species loss and environmental change, with consideration given to both the magnitude and variability of important process rates. Furthermore, as species are lost to streams, it is essential to understand how underlying environmental processes will be affected. Additionally, this research will provide information that can be used in the conservation and management of freshwater mussels (Unionidae). Understanding how different species of freshwater mussels respond to environmental variability, their ability to be biofilters, and nutrient cycling will allow us to better predict the consequences of their decline. Evaluation of ecosystem services requires knowledge biogeochemical processes, biological communities, and

stream ecology. I aim to assess the influence of biological processing and identify critical communities that influence nutrient water quality.

## Literature Cited

- Allen, D. C. and C. C. Vaughn. 2009. Burrowing behavior of freshwater mussels in experimentally manipulated communities. *Journal of the North American Benthological Society* **28**:93-100.
- Allen, D. C. and C. C. Vaughn. 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. *Journal of the North American Benthological Society* **29**:383-394.
- Atkinson, C. L. 2008. Food resource quality and its utilization by a native and an invasive bivalve in a Gulf Coastal Plain stream. University of Georgia, Athens, Georgia.
- Atkinson, C. L., S. P. Opsahl, A. P. Covich, S. W. Golladay, and L. M. Conner. 2010. Stable isotope signatures, tissue stoichiometry, and nutrient cycling of a native and invasive freshwater bivalve. *Journal of the North American Benthological Society* **29**:496-505.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* **9**:1146-1156.
- Baron, J. S., N. L. Poff, P. L. Angermeier, C. N. Dahm, P. H. Gleick, N. G. Hairston, R. B. Jackson, C. A. Johnston, B. D. Richter, and A. D. Steinman. 2002. Meeting ecological and societal needs for freshwater. *Ecological Applications* **12**:1247-1260.
- Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* **73**:1007-1012.
- Bogan, A. E. 1996. Decline and decimation: The extirpation of the unionid freshwater bivalves of North America. *Journal of Shellfish Research* **15**:484.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**:426-429.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**:989-992.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**:634-639.
- Cross, W. F., J. P. Benstead, P. C. Frost, and S. A. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. *Freshwater Biology* **50**:1895-1912.
- Drake, D. C., B. J. Peterson, K. A. Galvan, L. A. Deegan, C. Hopkinson, J. M. Johnson, K. Koop-Jakobsen, L. E. Lemay, and C. Picard. 2009. Salt marsh ecosystem biogeochemical responses to nutrient enrichment: a paired N-15 tracer study. *Ecology* **90**:2535-2546.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, and M. L. J. Stiassny. 2005. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**:163-182.
- Elderkin, C. L., A. D. Christian, J. L. Metcalfe-Smith, and D. J. Berg. 2008. Population genetics and phylogeography of freshwater mussels in North America, *Elliptio dilatata* and *Actinonaias ligamentina* (Bivalvia : Unionidae). *Molecular Ecology* **17**:2149-2163.
- Finlay, J. C. 2001. Stable-carbon-isotope ratios of river biota: Implications for energy flow in lotic food webs. *Ecology* **82**:1052-1064.

- Galbraith, H. S., S. E. Frazier, B. Allison, and C. C. Vaughn. 2009. Comparison of gill surface morphology across a guild of suspension-feeding unionid bivalves. *Journal of Molluscan Studies*.
- Galbraith, H. S., D. E. Spooner, and C. C. Vaughn. 2008. Status of rare and endangered freshwater mussels in Southeastern Oklahoma. *Southwestern Naturalist* **53**:45-50.
- Galvan, K., J. W. Fleeger, and B. Fry. 2008. Stable isotope addition reveals dietary importance of phytoplankton and microphytobenthos to saltmarsh infauna. *Marine Ecology-Progress Series* **359**:37-49.
- Gordon, M. E. 1980. Recent Mollusca of Arkansas, U.S.A. with annotations to systematics and zoogeography. *Arkansas Academy of Science Proceedings* **34**:58-62.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* **75**:3-35.
- Howard, J. K. and K. M. Cuffey. 2006. The functional role of native freshwater mussels in the fluvial benthic environment. *Freshwater Biology* **51**:460-474.
- Hughes, J. E., L. A. Deegan, B. J. Peterson, R. M. Holmes, and B. Fry. 2000. Nitrogen flow through the food web in the oligohaline zone of a new England estuary. *Ecology* **81**:433-452.
- Kreeger, D., J. Adkins, P. Cole, R. Najjar, D. Velinsky, P. Conolly, and J. Kraeuter. 2010. Climate change and the Delaware Estuary: three case studies in vulnerability assessment and adaptation planning. *Partnership for the Delaware Estuary* 10-01.
- Levine, J. M. and J. HilleRisLambers. 2009. The importance of niches for the maintenance of species diversity. *Nature* **461**:254-U130.
- Lhomme, J. P. and T. Winkel. 2002. Diversity-stability relationships in community ecology: Re-examination of the portfolio effect. *Theoretical Population Biology* **62**:271-279.
- Loreau, M. 2004. Does functional redundancy exist? *Oikos* **104**:606-611.
- Loreau, M., A. Downing, M. Emmerson, A. Gonzalez, J. Hughes, P. Inchausti, J. Joshi, J. Norberg, and O. Sala. 2002. A new look at the relationship between diversity and stability. Pages 79-91 *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford Univ Press, New York.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**:599-619.
- Mayden, R. L. 1985. Biogeography of Ouachita highland fishes. *Southwestern Naturalist* **30**:195-211.
- McCutchan, J. H. and W. M. Lewis. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography* **47**:742-752.
- Naeem, S. and S. B. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* **390**:507-509.
- Naeem, S. and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6**:567-579.
- Naidoo, R., A. Balmford, R. Costanza, B. Fisher, R. E. Green, B. Lehner, T. R. Malcolm, and T. H. Ricketts. 2008. Global mapping of ecosystem services and conservation priorities. Pages 9495-9500. *Natl Acad Sciences*.

- Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* **98**:166-170.
- Negus, C. L. 1966. A quantitative study of growth and production of unionid mussels in River Thames at Reading. *Journal of Animal Ecology* **35**:513-&.
- Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity. Pages 43-85 *in* G. W. Benz and D. E. Collins, editors. *Aquatic fauna in peril: the southeastern perspective*. Southeastern Aquatic Research Institute, Lenz Design and Communications, Decatur, Georgia.
- Newbold, J. D., R. V. Oneill, J. W. Elwood, and W. Vanwinkle. 1982. Nutrient spiralling in streams - implications for nutrient limitation and invertebrate activity. *American Naturalist* **120**:628-652.
- Odum, E. P. 1969. Strategy of ecosystem development. *Science* **164**:262-&.
- Parmalee, P. W., A. E. Bogan, and A. P. Farms. 1998. *The freshwater mussels of Tennessee*. University of Tennessee Press Knoxville, TN.
- Peterson, B. J. and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* **18**:293-320.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**:289-316.
- Polis, G. A., M. E. Power, and G. R. Huxel. 2004. *Food Webs at the Landscape Level*. University of Chicago Press, Chicago, IL.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**:703-718.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* **250**:811-814.
- Sabo, J. L. and M. E. Power. 2002. River-watershed exchange: Effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* **83**:1860-1869.
- Sala, O. E. and R. B. Jackson. 2006. Determinants of biodiversity change: Ecological tools for building scenarios. *Ecology* **87**:1875-1876.
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank, and N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* **134**:238-250.
- Schindler, D. W. 1989. Biotic impoverishment at home and abroad. *BioScience* **39**:426-426.
- Small, G. E., A. M. Helton, and C. Kazanci. 2009. Can consumer stoichiometric regulation control nutrient spiraling in streams? *Journal of the North American Benthological Society* **28**:747-765.
- Spooner, D. E. and C. C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology* **51**:1016-1024.
- Spooner, D. E. and C. C. Vaughn. 2008. A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. *Oecologia* **158**:307-317.
- Spooner, D. E. and C. C. Vaughn. 2009. Species richness and temperature influence mussel biomass: a partitioning approach applied to natural communities. *Ecology* **90**:781-790.
- Sterner, R. W. and J. J. Elser. 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press.

- Strayer, D. L. 2008. *Freshwater Mussel Ecology: A Multifactor Approach to Distribution and Abundance*. University of California Press.
- Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves. *BioScience* **49**:19-27.
- Strayer, D. L., J. A. Downing, W. R. Haag, T. L. King, J. B. Layzer, T. J. Newton, and S. J. Nichols. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. *BioScience* **54**:429-439.
- Strayer, D. L., D. C. Hunter, L. C. Smith, and C. K. Borg. 1994. Distribution, abundance, and roles of freshwater clams (*Bivalvia*, *Unionidae*) in the freshwater tidal Hudson river. *Freshwater Biology* **31**:239-248.
- Taylor, C. A., M. L. Warren, J. F. Fitzpatrick, H. H. Hobbs, R. F. Jezerinac, W. L. Pflieger, and H. W. Robison. 1996. Conservation Status of Crayfishes of the United States and Canada. *Fisheries* **21**:25-38.
- Turgeon, D. D., A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, C. F. E. Roper, A. Scheltema, F. G. Thompson, and J. D. Williams. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. American Fisheries Society Special Publication:iii-vii, 1-277.
- Vander Zanden, M. J. and J. B. Rasmussen. 1999. Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. *Ecology* **80**:1395-1404.
- Vaughn, C. C. 2010. Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions. *BioScience* **60**:25-35.
- Vaughn, C. C., K. B. Gido, and D. E. Spooner. 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: species roles and effects of abundance. *Hydrobiologia* **527**:35-47.
- Vaughn, C. C. and C. C. Hakenkamp. 2001. The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* **46**:1431-1446.
- Vaughn, C. C., C. M. Mather, M. Pyron, P. Mehlhop, and E. K. Miller. 1996. The current and historical mussel fauna of the Kiamichi River, Oklahoma. *Southwestern Naturalist* **41**:325-328.
- Vaughn, C. C., S. J. Nichols, and D. E. Spooner. 2008. Community and foodweb ecology of freshwater mussels. *Journal of the North American Benthological Society* **27**:409-423.
- Vaughn, C. C. and D. E. Spooner. 2006a. Scale-dependent associations between native freshwater mussels and invasive *Corbicula*. *Hydrobiologia* **568**:331-339.
- Vaughn, C. C. and D. E. Spooner. 2006b. Unionid mussels influence macroinvertebrate assemblage structure in streams. *Journal of the North American Benthological Society* **25**:691-700.
- Vaughn, C. C., D. E. Spooner, and H. S. Galbraith. 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. *Ecology* **88**:1664-1662.
- Vaughn, C. C. and C. M. Taylor. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology* **13**:912-920.
- Vaughn, C. C. and C. M. Taylor. 2000. Macroecology of a host-parasite relationship. *Ecography* **23**:11-20.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* **9**:747-752.

- Werner, E. E. 1977. Species packing and niche complementarity in 3 sunfishes. *American Naturalist* **111**:553-578.
- Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contrerasbalderas, J. D. Williams, M. Navarromendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern - 1989. *Fisheries* **14**:2-20.
- Yachi, S. and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* **96**:1463-1468.