

## **Gains and Gaps in Knowledge Surrounding Freshwater Mollusk Ecosystem Services**

Authors: Atkinson, Carla L., Hopper, Garrett W., Kreeger, Danielle A., Lopez, Jonathan W., Maine, Alexa N., et al.

Source: Freshwater Mollusk Biology and Conservation, 26(1) : 20-31

Published By: Freshwater Mollusk Conservation Society

URL: <https://doi.org/10.31931/fmbc-d-22-00002>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

REGULAR ARTICLE

# GAINS AND GAPS IN KNOWLEDGE SURROUNDING FRESHWATER MOLLUSK ECOSYSTEM SERVICES

Carla L. Atkinson<sup>1\*</sup>, Garrett W. Hopper<sup>1</sup>, Danielle A. Kreeger<sup>2</sup>,  
Jonathan W. Lopez<sup>3</sup>, Alexa N. Maine<sup>4</sup>, Brandon J. Sansom<sup>5</sup>, Astrid Schwalb<sup>6</sup>,  
and Caryn C. Vaughn<sup>3</sup>

<sup>1</sup> Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487 USA

<sup>2</sup> Partnership for the Delaware Estuary, Wilmington, DE 19801 USA

<sup>3</sup> Oklahoma Biological Survey and Department of Biology, University of Oklahoma, Norman, OK 73019 USA

<sup>4</sup> Confederated Tribes of the Umatilla Indian Reservation, Fisheries Program, Freshwater Mussel Research and Restoration Project, Pendleton, OR 97801 USA

<sup>5</sup> U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO 65201 USA

<sup>6</sup> Department of Biology, Texas State University, San Marcos, TX 78666 USA

---

## ABSTRACT

Ecosystems provide essential services to people including food, water, climate regulation, and aesthetic experiences. Biodiversity can enhance and stabilize ecosystem function and the resulting services natural systems provide. Freshwater mollusks are a diverse group that provide a variety of ecosystem services through their feeding habits (e.g., filter feeding, grazing), top-down and bottom-up effects on food webs, provisioning of habitat, use as a food resource by people, and cultural importance. Research focused on quantifying the direct and indirect ways mollusks influence ecosystem services may help inform policy makers and the public about the value of mollusk communities to society. The Freshwater Mollusk Conservation Society highlighted the need to evaluate mollusk ecosystem services in their 2016 National Strategy for the Conservation of Native Freshwater Mollusks, and, while significant progress has been made, considerable work remains across the research, management, and outreach communities. We briefly review the global status of native freshwater mollusks, assess the current state of knowledge regarding their ecosystem services, and highlight recent advances and knowledge gaps to guide further research and conservation actions. Our intention is to provide ecologists, conservationists, economists, and social scientists with information to improve science-based consideration of the social, ecological, and economic value of mollusk communities to healthy aquatic systems.

**KEY WORDS:** restoration, conservation, social valuation, provisioning, regulating, cultural, biodiversity

---

## INTRODUCTION TO ECOSYSTEM SERVICES

Human societies obtain essential goods and services from natural ecosystems, including timber, food, water, and climate regulation, which are known as “ecosystem services” (Millennium Ecosystem Assessment 2005; Mace et al. 2012). Ecosystems provide such services in ways, both direct and

indirect, that underpin human well-being. For example, there is value in a clean river that can be used for human consumption while also providing habitat for fish communities and a place for people to recreate. Ecosystem services can be divided into four main categories, each of which can be valued to draw comparisons with human-engineered infrastructure and services to inform policy and decision makers (Millennium Ecosystem Assessment 2005).

(1) *Provisioning services* are those that provide goods such as food and water.

---

\*Corresponding Author: Carla.L.atkinson@ua.edu

This article has been contributed to by US Government employees, and their work is in the public domain in the USA.

- (2) *Regulating services* are those that control various processes, such as water purification, flood control, climate regulation, or suppression of disease outbreaks.
- (3) *Supporting services* are those that maintain material and energy balances, such as nutrient recycling.
- (4) *Cultural services* are those that provide spiritual or aesthetic benefits.

A large body of work shows that higher biodiversity can enhance and stabilize ecosystem functioning (Tilman et al. 2001; Naeem and Wright 2003; Loreau and de Mazancourt 2013; Oliver et al. 2015), thus providing critical services. Therefore, biodiversity is considered an ecosystem service that is subject to valuation (Mace et al. 2012). Human-induced declines in biodiversity and biomass raise concerns about the deterioration of ecosystem functions and associated ecosystem services (Dirzo et al. 2014; Young et al. 2016). As such, the ecosystem service framework can improve understanding of how the existence of communities of abundant and diverse organisms enhances ecosystems.

Freshwater ecosystems and the organisms that inhabit them contribute to many important ecosystem services including provisioning of clean water, nutrient processing, recreation, and tourism (Brauman et al. 2007; Dodds et al. 2013). Freshwater mollusks (i.e., gastropods and bivalves) in rivers and lakes provide supporting services such as nutrient recycling and storage, provisioning services by acting as food for humans and other organisms, regulating services like water purification, and cultural services such as jewelry and art (FMCS 2016; Vaughn 2018; Zieritz et al. 2022; Table 1). Due to their ecological importance and potential role in provisioning ecosystem services, using mollusks to restore or establish desirable ecosystem services has been proposed (Strayer et al. 2019; Wood et al. 2021). Research that quantifies the direct and indirect ways mollusks provision ecosystem services is key to properly valuating these services and informing policy makers and the public about the value of mollusk communities to society (FMCS 2016). The Freshwater Mollusk Conservation Society identified understanding the role of freshwater mollusks and their habitats on ecosystem services as a high-priority need (FMCS 2016). Zieritz et al. (2022) recently synthesized knowledge on the services provided by and disrupted by bivalve mollusks. We expand on this synthesis by including freshwater bivalves and gastropods and identifying future research needs. We briefly review the status of native freshwater mollusks, assess the current state of knowledge regarding their ecosystem services, and highlight recent advances and knowledge gaps to guide further work describing and quantifying the role of these animals in sustaining ecosystem services. Our intention is to provide ecologists, conservationists, economists, and social scientists with information to improve science-based consideration of the social and economic values of mollusk communities and functioning aquatic systems.

## FRESHWATER MOLLUSKS—A HIGHLY IMPERILED GROUP OF ORGANISMS

Freshwater mollusks are distributed globally, occurring on all continents except Antarctica (Graf and Cummings 2007; Strong et al. 2008). They provide valuable ecosystem services by improving water quality, enhancing nutrient cycling, and playing critical roles in aquatic food webs. However, biodiversity is declining at a greater rate in freshwaters globally than in terrestrial systems (Reid et al. 2019), and mollusks represent one of the most diverse aquatic groups with more than 6,000 species (Böhm et al. 2021). Extinction rates for North American freshwater fauna are estimated to be as high as 4% per decade, five times greater than species losses in terrestrial systems (Ricciardi and Rasmussen 1999). For example, of the species comprising potentially the most diverse freshwater mollusk assemblage in the world (the Mobile Basin in the southeastern USA), one-third are now extinct due to flow regulation and habitat alteration (Williams et al. 2008). More broadly, 44% of European (Cuttelod et al. 2011), 29% of African (Seddon et al. 2011), and 17% of Indo-Burman (Köhler et al. 2012) freshwater mollusks are threatened with extinction. Rates for less-studied regions and faunas may be as high or higher (Dudgeon et al. 2006; Böhm et al. 2021). Mollusk populations are extirpated or severely reduced in many freshwater systems globally due to significant and emerging anthropogenic stressors including habitat modification (e.g., dams and urbanization) and degraded water quality (Benson et al. 2021; Böhm et al. 2021). Globally, 40% of freshwater bivalves are considered threatened, with gastropods likely being more threatened, but this is probably an underestimate given the lack of data for many regions (Lopes-Lima et al. 2018; Böhm et al. 2021). In North America alone, an estimated 72% of freshwater mussels and 74% of freshwater gastropods are imperiled (Johnson et al. 2013). Therefore, it is critical to understand their role in the functioning of freshwater ecosystems and the resulting ecological services associated with them. Despite these and other anthropogenic pressures, some native freshwater mollusk populations remain intact or are being restored, and ecosystem services are a goal of some restoration efforts (FMCS 2016; Strayer 2017).

## STATE OF OUR KNOWLEDGE REGARDING FRESHWATER MOLLUSK ECOSYSTEM SERVICES

### Provisioning Services

Humans have used mollusks for food and as tools for millennia. Evidence of freshwater mollusks serving as a human food source dates to ~6000 years BP in northern Europe and to greater than 2800 years BP in North America (Haag 2012; Meadows et al. 2014; CTUIR 2020). The presence of large shell middens at human habitation sites shows that freshwater mussels were used as food extensively in prehistory by people in North America, Australia, Europe, and likely elsewhere (Parmalee and Klippel 1974; Nicodemus

Table 1. Examples of ecosystem services provided by freshwater mollusks. C = carbon, N = nitrogen, P = phosphorus.

Service Type	Use	Example	Selected References
Provisioning	Food	Freshwater mussels have been a food source as far back as the Stone Age in Europe and 800 BP for Native Americans.	Meadows et al. 2014; CTUIR 2020
		Mollusks are an important food commodity in southeast Asia.	Bolotov et al. 2014; Dee et al. 2019
	Medicinal uses	Freshwater clams, <i>Corbicula</i> , are used to treat liver disease and side effects of alcoholism.	Bai et al. 2020; Zieritz et al. 2022
	Buttons	Mussels were used extensively in the North American button industry from the mid-1800s to the mid-1990s.	Haag 2012; Strayer 2017
Regulating	Pearl culture	Beads from mussel shells are used as seeds in the pearl industry.	Jiale and Yingsen 2009
	Water purification	Water filtration: Freshwater mussels clear an extensive volume of water, but it depends on their density and the stream discharge.	Vaughn et al. 2004; Vaughn et al. 2015
		Nonnative snails filter a significant amount of particulates from the water column, and their filtration rates rival freshwater bivalves.	Olden et al. 2013
	Contaminant sequestration	Freshwater mussel filtration removes coliform bacteria, pharmaceuticals, personal care products, and algal toxins.	Downing et al. 2014; Ismail et al. 2014, 2015, 2016
		Contaminants that are removed are sequestered by mollusks in the soft tissue and shell.	Mersch and Johansson 1993; Zhang et al. 2012; Giari et al. 2017; Archambault 2020
Supporting	Algal control	Benthic grazing snails can remove and control algal biomass, including nuisance and toxic algae.	Lamberti et al. 1987; Hill et al. 1992; Rosemond et al. 1993; Fervier et al. 2020
		Filter-feeding mollusks can clear and control algal blooms including algal toxins.	Hwang et al. 2021
		Mussel soft tissue and shell act as long-term storage of nutrients such as C, N, and P as well as micronutrients.	Strayer and Malcolm 2007; Atkinson and Vaughn 2015; Atkinson et al. 2018; Hopper et al. 2021b
	Denitrification	Aggregations of mussels act as biogeochemical hotspots of dissolved organic matter and N and P.	Atkinson and Vaughn 2015; Vaughn et al. 2015; Hopper et al. 2021a
		Algal grazing and excretion by freshwater gastropods enhance primary production and nutrient uptake rates.	Hall et al. 2003; Hill and Griffiths 2017
		Mussels contribute to the permanent removal of N from aquatic ecosystems by enhancing denitrification rates.	Hoellein et al. 2017; Trentman et al. 2018; Nickerson et al. 2019
	Habitat provisioning	Mussels improve and create habitat by enhancing hydrodynamic habitat complexity and decreasing turbulent shear stresses	Sansom et al. 2018a, 2018b, 2020; Wu et al. 2020
		Mollusk shells provide habitat for algae, macrophytes, macroinvertebrates, and fish.	Francoeur et al. 2002; Vaughn et al. 2002; Spooner and Vaughn 2006; Vaughn and Spooner 2006; Abbott and Bergey 2007; Lukens et al. 2017; Hopper et al. 2019
	Food web support	Mussel excreta was found to support biomass accrual of primary producers and aquatic insects.	Atkinson et al. 2014, 2018
		Mussels enhance sediment organic matter and increase macroinvertebrate abundance and diversity.	Howard and Cuffey 2006; Spooner and Vaughn 2006; Simeone et al. 2021
		Mollusks comprise the diet of many organisms including crayfish, fish, turtles, and muskrats.	Crowl and Covich 1990; Alexander and Covich 1991; Brown and Lydeard 2010; Haag 2012; Atkinson 2013

Table 1, continued.

Service Type	Use	Example	Selected References
Cultural	Ornamentation for rituals	Beads and other ornaments made from shells have been used in rituals and ceremonies.	Claassen 2008; CTUIR 2020
		Shells are used to ornament burial sites.	Haag 2012
	Heritage and sense of place	Locations with high abundances of mussels have been used in the names of locations within streams (e.g., Muscle Shoals, Alabama).	Haag 2012; Hunn et al. 2015; Vaughn 2018
		There are multiple archeological and historical values from midden piles that have been discovered across Europe and North America.	Parmalee and Klippel 1974; Bērziņš et al. 2014
	Education and research	Mollusks have been used to study water pollution, to set water quality criteria, to be set as biomonitors, and to reconnect people to nature.	Augspurger et al. 2003; Wang et al. 2007; Michel et al. 2019

2011; Haag 2012; Garvey 2017). Columbia Plateau tribes in northwestern North America, such as the Confederated Tribes of the Umatilla Indian Reservation (CTUIR), historically harvested mussels in association with harvest of other food resources (e.g., salmon and plants; Quaempts et al. 2018; CTUIR 2020). The Umatilla named a site on the Columbia River Iśáaxuyi, which means “covered with mussel shells,” due to the high abundance of mussels (Hunn et al. 2015). Freshwater mussels are still considered a first food, a food of significant cultural and ecological importance, by the CTUIR and are actively managed and protected (Quaempts et al. 2018; CTUIR 2020). Freshwater mollusks remain an important food resource in other parts of the world, especially Southeast Asia (Zieritz et al. 2018), where both freshwater mussels and gastropods are a common commodity in markets (Bolotov et al. 2014; Dee et al. 2019). Mollusks are also used for medicinal purposes, mainly in eastern Asia. For example, in its native range, *Corbicula fluminea* has long been a part of traditional Chinese medicine used to treat liver disease and the effects of alcoholism (Bai et al. 2020).

Historically, mollusk shells were important for tools, jewelry, and other uses. Native American tribes used mussel shells for tools and ground them to powder to temper pottery (Rafferty and Peacock 2008). In the Pacific Northwest, tribes collected mussels seasonally, stored shells in large piles, and later worked them into hooks, spoons, and adornment (Brim Box et al. 2006; CTUIR 2020; Peacock et al. 2020). Beginning in the mid-1800s and lasting through the mid-1900s, the mollusk shell button industry was a lucrative business in North America (Coker et al. 1919; Haag 2012). During the peak harvest in 1912, 50,000 tons of mussels were removed from North American rivers, and between 1897 and 1963, the total value of buttons was approximately \$6 billion U.S. dollars (Haag 2012; Strayer 2017). Subsequently, the Japanese pearl industry used beads made from freshwater mussel shells as nuclei to produce cultured pearls in marine bivalves (Haag 2012). Cultured pearls are also produced in freshwater mussels, and this is a large industry in Asia (Jiale and

Yingsen 2009). Additionally, many freshwater bivalves and gastropods have been harvested in Thailand for jewelry and artwork (Nagachinta et al. 2005; Allen et al. 2012a).

## Regulating Services

**Water filtration.**—Through their filter feeding and grazing, mollusks provide important regulating services such as water purification and regulation of algal communities. Freshwater mussels are filter feeders that remove particles and associated nutrients from the water column and interstitial sediments, which can in turn decrease water treatment costs and improve water quality (Vaughn et al. 2008; Newton et al. 2011; Kreeger et al. 2018). Where mussel biomass is high in comparison to water volume, or where hydrologic residence times are long, mussels can filter a substantial amount of water (Vaughn et al. 2004). For example, mussels were able to clear the entire volume of a 440,000 m<sup>3</sup> lake in less than a day, resulting in enhanced water clarity (Chowdhury et al. 2016). Efforts are underway to restore freshwater mussel filtration capacity to U.S. mid-Atlantic watersheds with the goal of improving water clarity and quality (Kreeger et al. 2018). Some groups of gastropods (e.g., Viviparidea and Bithynidae) also function as filter feeders in aquatic ecosystems (Brown and Lydeard 2010), thus likely providing similar benefits to water clarity (see Olden et al. 2013) and particulate nutrient removal. Future research on snail filtration capacity and their effects on water quality could broaden our understanding of the ecosystem services gastropods provide. Freshwater mussels also improve drinking water quality by filtering pathogens or contaminants such as coliform bacteria, pharmaceuticals, personal care products, and algal toxins (Mersch and Johansson 1993; Downing et al. 2014; Ismail et al. 2014, 2015; Hwang et al. 2021) and sequestering these contaminants in their soft tissue and shell (Giari et al. 2017; Archambault 2020). Less is known about filter-feeding gastropods, but based on work on bivalves (Roditi et al. 2000; Baines et al.

2005), we hypothesize that gastropods may be able to remove dissolved organic matter as well as materials such as heavy metals. Further work is needed to understand what mollusks can filter from the environment, what they sequester, the ultimate fate of sequestered materials, and how these aspects of filtration vary among species and environmental contexts.

**Biofilm grazing.**—Snails are important grazers that can substantially reduce algal and biofilm biomass (Lamberti et al. 1987; Hill et al. 1992; Rosemond et al. 1993). Nuisance and toxic algal blooms negatively affect wildlife and human health (Wurtsbaugh et al. 2019). Some work has shown that freshwater snails can help control algal blooms including nuisance cyanobacteria and toxic algae (Zhang et al. 2012; Groendahl and Fink 2017). More research is needed to better understand snails' ability to control algal blooms and their other functional roles in freshwater systems, particularly for detritivorous and filter-feeding snails.

## Supporting Habitat Services

**Nutrient storage and cycling.**—Mollusks provide important supporting services such as nutrient recycling, translocation, and storage, and they may influence nutrient abatement (i.e., nutrient removal). As mollusks filter feed or graze, they convert energy and associated nutrients in their food into soft tissue, shell, and biodeposits (feces and pseudofeces), and they release bioavailable dissolved nutrients that support primary producers (Spooner and Vaughn 2006; Strayer 2014; Atkinson and Vaughn 2015) and detritus-based food webs (Atkinson et al. 2021; Hopper et al. 2021a).

Nutrient storage by mollusks is an overlooked, but potentially valuable, ecosystem service for nutrient abatement. For example, nitrogen (N)-trading programs in estuarine settings estimate the value of nitrogen assimilated by oysters at \$50 to \$181/kg N/year (Rose et al. 2021). Currently, similar programs to mitigate nutrient loading in freshwater environments do not exist, but they are being considered (Strayer et al. 2019; Wood et al. 2021). Freshwater mollusks assimilate nutrients into both their soft tissues and shells and can store kilograms of carbon (C), N, and phosphorus (P), as well as micronutrients, at a river reach (Atkinson and Vaughn 2015; Hopper et al. 2021b). Additionally, many species are relatively long-lived, and their shells can persist for decades (Strayer and Malcolm 2007; Atkinson et al. 2018), possibly providing long-term storage of nutrients such as calcium. Thus, long-term storage and sequestration via burial could be an important, but often overlooked, ecosystem service provided by freshwater mollusks.

Nutrients that are not assimilated into soft tissue and shell are egested as biodeposits or excreted as bioavailable dissolved nutrients (Strayer 2014; Atkinson and Vaughn 2015; Hopper et al. 2021a). Soluble nutrients excreted into the water column by mollusks are readily taken up by algae and heterotrophic bacteria (Evans-White and Lamberti 2005; Liess and Haglund 2007; Vaughn et al. 2008; Bril et al. 2014).

Snails (*Elimia* spp.) were an important source of recycled nitrogen in a U.S. stream, excreting 12 times more nitrogen than they accumulated in biomass during spring growth, and assimilating and excreting up to 50% of the nitrogen initially taken up by autotrophs and leaf microbes (Hill and Griffiths 2017). Thus, where mollusk biomass is locally high, mollusks can create “biogeochemical hotspots” where nutrient recycling and material flux are increased, leading to concentrations of nutrients that can exceed background ambient concentrations of bioavailable nutrients (Hall et al. 2003; Strayer 2014; Atkinson and Vaughn 2015; Hopper et al. 2021a). Mollusks also can affect nutrient cycling of entire ecosystems. In a small North American stream, nonnative New Zealand mud snails (*Potamopyrgus antipodarum*) dominated carbon sequestration and nitrogen excretion because of their high biomass and ubiquitous distribution (Hall et al. 2003). If bioavailable nutrients are limiting, fertilization by mollusk excreta can lead to spatial variation in algal community assemblages (Atkinson et al. 2013) and increases in biomass of benthic algae, macroinvertebrates, fishes, and riparian invertebrates and vertebrates (Allen et al. 2012b; Atkinson et al. 2014; Lopez et al. 2020; Simeone et al. 2021). Grazing by snails also can reduce macrophyte biomass. Most work on this topic focused on impacts of invasive snails on native aquatic plants (Yang et al. 2018; Bissattini et al. 2021), but native snails also can control invasive plants (Baker et al. 2010). Mollusks also have bottom-up food web effects as prey for other organisms such as crayfishes (Crowl and Covich 1990; Alexander and Covich 1991), fishes (Brown and Lydeard 2010), muskrats (Tyrrell and Hornbach 1998; Haag 2012), and turtles (Atkinson 2013).

Mollusks also have indirect effects on nutrient cycles by modifying biogeochemical reactivity, microbial communities, and redox gradients. Their interactions with the sediments alter oxygen profiles and fluxes of nutrients from the sediment and water column (Matisoff et al. 1985; Boeker et al. 2016). Due to their interactions with the benthic sediments and their high ammonia excretion and biodeposition rates, freshwater mussels enhance denitrification and anaerobic ammonium oxidation (anammox) rates in benthic sediments (Hoellein et al. 2017; Trentman et al. 2018; Nickerson et al. 2019; Atkinson and Forshay 2022). This is beneficial for water quality because denitrification results in the removal of nitrogen from the ecosystem; this service has received considerable attention in marine settings with oysters and other marine mollusks (Newell et al. 2005; Kellogg et al. 2018; Rose et al. 2021). Additional work examining how freshwater mollusks influence microbially mediated processes could increase our understanding of the breadth of ecosystem services mollusks provide. Such effects could be substantial given the high biomass of mollusks in some ecosystems and their important roles in nutrient cycling.

**Habitat engineering.**—Stream-dwelling organisms must cope with high flows (Lopez and Vaughn 2021). Mollusks physically engineer ecosystems through their shell production and movements across and within the benthic substrate, provisioning habitat for other organisms. Mollusk shells

generate complexity in benthic habitats that influence processes across trophic levels (Gutiérrez et al. 2003). Both living shells and spent shells enhance habitat complexity and provide a hard substrate for the settlement and establishment of organisms, including microscopic and macroscopic algae (Francoeur et al. 2002; Abbott and Bergey 2007; Lukens et al. 2017), macrophytes (Vaughn et al. 2002), macroinvertebrates (Spooner and Vaughn 2006; Vaughn and Spooner 2006; Simeone et al. 2021), and fishes (Hopper et al. 2019). Freshwater mussel aggregations can modulate near-bed velocities and turbulence in rivers over decadal time scales, which may enhance bed stability and create habitat for other stream-dwelling organisms by decreasing flow force and velocity (Sansom et al. 2018a, 2018b, 2020). As water flows past mussels, low-velocity refugia form behind them (Kumar et al. 2019), decreasing the hydrodynamic forces on the streambed downstream. Moreover, horseshoe vortices or complex wake structures are created around partially exposed mussels (Constantinescu et al. 2013; Sansom et al. 2018a; Wu et al. 2020), and such features are further modified when mussels are filtering (Wu et al. 2020). These hydraulic modifications can have important implications for other stream-dwelling organisms with specific microhabitat hydraulic preferences (e.g., Davis 1986; Bouckaert and Davis 1998). Overall, mussel aggregations have a reciprocal influence on near-bed flow because they both influence, and are constrained by, hydrodynamic forces at the streambed (Lopez and Vaughn 2021). In addition, shells provide spawning sites and serve as refugia for some fishes (Etnier and Starnes 1993; Aldridge 1999; Wisniewski et al. 2013). Locally high densities of shells, such as at mussel beds, increase the potential for strong hydraulic effects over extended spatial (tens to hundreds of meters) and temporal (decadal) scales (Strayer 2020). Much less is known about whether snails provide hydrodynamic refugia and/or stabilize sediments, but small stream invertebrates, such as caddisflies, can alter stream sediment dynamics and hydraulics when densities are high (Albertson and Allen 2015; Maguire et al. 2020; Mason and Sanders 2021; Mason et al. 2022). Thus, it is reasonable to expect that gastropods, with their sturdy shell, gripping foot, and mucus trails, also might stabilize sediment.

Beyond the obvious direct habitat provisioning of the shell, mollusks can increase habitat availability through their grazing and bioturbation activities. Filter-feeding bivalves increase the photic zone in lakes and rivers and enhance benthic substrate organic matter, allowing colonization by benthic macrophytes and aquatic insects (Strayer 2020). Grazing by invasive snails (*Pomacea canaliculata*) can have strong top-down effects by reducing biomass of aquatic plants, especially in shallow lakes with high nutrient loads (Gao et al. 2021; Liu et al. 2021), possibly leading to shifts from clear to turbid stable states. State shifts such as this can reduce light penetration in littoral zones and visibility for sight-feeding predators, with cascading effects on food webs. Overall, mollusks appear to have varied and sometimes strong effects on stream and lake habitats, which likely influence many other aquatic organisms.

## Cultural Services

Freshwater mollusks provide many cultural services to humans. Large, durable freshwater mussel shells are particularly important for these services. Archaeological studies have shown that in Neolithic northern Europe, large mussel shell middens were used seasonally by pottery-using hunter-gatherer communities to temper pottery (Bērziņš et al. 2014). In North America, beads and other ornaments made from shells were used in rituals and ceremonies (Claassen 2008; CTUIR 2020). For example, the Winnebago tribe in Wisconsin, USA, used shell beads in rituals, produced utensils and fishing hooks from shells, and used powdered shell to temper pottery (Kuhm 2007). Currently, mollusk shells are sometimes used to ornament graves in the southern USA (Haag 2012). In the USA, the abundance of mussels in some areas invoked a sense of place that was translated into names of river reaches (e.g., Muscle Shoals and Išáaxuyi; Haag 2012; Hunn et al. 2015; Vaughn 2018). Living mollusks also bring humans enjoyment and are commonly sold internationally in the aquarium and ornamental pet trade (Ng et al. 2016; Patoka et al. 2017). In some cases, this practice has resulted in accidental introductions of mollusks into new ecosystems (Karatayev et al. 2009). Additionally, mollusks' regulating services (e.g., filtration, grazing) improve human perceptions of freshwater ecosystems by enhancing water clarity and other characteristics. For example, grazing by snails (*Haitia acuta*) reduces the occurrence of large algal mats (Parr et al. 2020), which can be unsightly to humans. Mollusks are also used in education and research to improve understanding of ecosystem health, and they are used as biomonitors for contaminants and pathogens (Mersch and Johansson 1993; Giari et al. 2017). Extensive toxicology research has evaluated mollusks' sensitivities to various contaminants, which have been used to evaluate water quality criteria (Augsburger 2003; Wang et al. 2007). Last, the bequest or existence value of mollusks is an important cultural service because people derive satisfaction from preserving the natural environment for future generations (Turner and Schaafsma 2015; Strayer 2017).

## The Conundrum of Services and Disservices by Invasive Mollusks

The role of invasive mollusk species in providing ecosystem services has received attention primarily in terms of their negative effects or "disservices," but they can also enhance services (Charles and Dukes 2008; Limburg et al. 2010; Walsh et al. 2016; Zieritz et al. 2022). Invasive species often do not provide provisioning or cultural services in their introduced range because they have not been used traditionally for those purposes in the new area. However, some species may be introduced because of provisioning or cultural services they provide in their native range or elsewhere. For example, the bivalve *Corbicula fluminea* is thought to have been introduced into the USA in the 1930s by Chinese immigrants who used the species as a food item in its native range (Counts 1986). Thiarid snails have invaded freshwaters globally, and

they frequently are introduced through the aquarium trade, where their grazing services are used to keep aquaria clean (Padilla and Williams 2004; Preston et al. 2022). However, despite their use in the aquarium trade, invasive snails often provide disservices, as many are intermediate hosts for trematodes and other parasites that negatively affect the health of fishes, birds, and humans (e.g., Pinto and de Melo 2011; Lv et al. 2018; Valente et al. 2020).

Filtering and nutrient recycling by invasive mussels can provide important regulating and supporting services. Nutrient fluxes from high densities of *Corbicula* exceeded or equaled those from native mussels in two North American rivers (Hopper et al. 2022). Invasive dreissenid mussels can drastically change energy and nutrient fluxes in a system (Li et al. 2021; Zieritz et al. 2022). At high densities, their filtering activity reduces phytoplankton and redirects nutrients and energy from the water column to the benthos, causing a decrease in pelagic production and an increase in benthic production (Higgins and Vander Zanden 2010; Karatayev et al. 2015). This includes an increase in benthic algae and macrophytes, which are often perceived as nuisances that inhibit boating, swimming, and other recreational uses in lakes and reservoirs. Fouling of native mussels by dreissenid mussels causes high native mussel mortality through resource competition (Haag et al. 1993; Karatayev et al. 2015; Beason and Schwalb 2022), and *Corbicula* clams also are suspected to negatively affect native mussels (Ferreira-Rodríguez et al. 2018, 2022; Modesto et al. 2019). Both invasive species diminish ecosystem services provided by native mussels, but they also provide important benefits, especially in areas where the native mollusk filter-feeding community has been lost or severely degraded. For example, *Dreissena* can be used as biofilters to clear bioavailable contaminants from effluents before discharge (Binelli et al. 2015), and invasive *Corbicula* in Portugal assist in the remediation of acid mine drainage and other contaminants (Ismail et al. 2014; Rosa et al. 2014). Understanding how invasive mollusks provide and alter ecosystem services can give additional insight about services provided by native mollusks and how replacement of native species by invasive species ultimately affects ecosystem structure and long-term function.

## DIRECTIONS FORWARD

A large body of work shows the foundational role of mollusks in freshwater ecosystems (Vaughn and Hakenkamp 2001; Vaughn and Hoellein 2018; Zieritz et al. 2022), but many research gaps and questions remain. Here we discuss research and information needed to better conceptualize mollusks in an ecosystem services framework, which will assist future conservation and management initiatives globally.

- Baseline information for ecosystem services. Information on the species richness, composition, and density of historical mollusk communities is needed to establish a baseline to guide restoration of ecosystem services. Generating this

information is especially important in understudied regions and likely will require combining reference site studies with modeling carrying capacity potential.

- Quantitative comparisons of the biomass distribution and ecosystem services provided by co-occurring native and invasive mollusks.
- Standardized methods that can be used to quantify ecosystem services of mollusks globally. For example, a standardized method for estimating filtration rates among and within species would help guide evaluation of the capacity for mollusks to influence water clarity. This gap could be addressed by globally coordinated research networks.
- The role of gastropods in provisioning ecosystem services. Snails can dominate benthic stream communities (Hawkins and Furnish 1987) and comprise >50% of invertebrate biomass in many systems (Brown et al. 2008; Brown and Lydeard 2010), but, apart from the effects of their grazing, little is known about their role in ecosystem processes. Quantitative assessments of gastropod abundance, functional feeding group status (algivorous and detritivores), nutrient excretion, and other physiological rates are needed.
- Understanding and acknowledging the role of traditional ecological knowledge in maintaining and restoring ecosystem services (e.g., Michel et al. 2019). Traditional knowledge regarding the distribution of mollusks and their uses is necessary for documenting their importance to ecosystem services.
- Understanding how factors such as carrying capacity and habitat suitability constrain mollusk populations and the ecosystem services they provide.
- Understanding how ecosystem services provided by mollusks vary along environmental gradients (e.g., eutrophic-oligotrophic), systems (e.g., river, lake, etc.), and both time and spatial scales.

In addition to research priorities, it is crucial that policy makers and the public recognize the value of and support restoration of mollusk-provided ecosystem services (“ecosystem service goals”; Wood et al. 2021). Disseminating research results and outreach is necessary to build this support, and outreach efforts should be focused on regions where mollusks are diverse and abundant or where they could be used to create a sense of place based on mollusks (e.g., areas where mollusks were once abundant). Building broad recognition of the value of mollusks is a major goal of the Freshwater Mollusk Conservation Society (FMCS 2016). We propose the following actions to meet these outreach and policy goals:

- Apply knowledge from work on ecosystem services provided by marine mollusks (i.e., successes and failures) to inform management and public outreach for freshwater mollusks.
- Examine how environmental, monetary, and institutional factors can both constrain and create opportunities for the

conservation and restoration of freshwater mollusks and the ecosystem services they provide.

- Increase outreach efforts to various stakeholders in regions where mollusks are diverse and abundant to create a sense of place within freshwater ecosystems and value for natural communities.
- Determine if research and management investments are being distributed to address actual needs (i.e., where people live and where services are needed) for enhanced ecosystem services. This could be determined using population census records coupled with evaluations of environmental degradation and public hearings and surveys.
- Encourage collaboration between biologists, social scientists, economists, outreach specialists, and policy makers to develop valuation guidelines for ecosystem services provided by freshwater mollusks and incorporate these guidelines into resource-management planning.

## CONCLUSION

The loss of biodiversity is an urgent concern, one that threatens the ecological integrity of ecosystems along with the essential services they provide (Dudgeon et al. 2006; Oliver et al. 2015). Biodiversity loss is disproportionately high in freshwaters, particularly for mollusks (Lopes-Lima et al. 2018; Reid et al. 2019). Given their high diversity, global distribution, and, in some places, astounding biomass, it is critical to understand how restoration of mollusks fits into the framework of ecosystem services. Research that quantifies the functional importance of freshwater mollusks in ecosystems within a societal and policy context creates opportunities to value these animals and the services they provide as tangible benefits to society.

## ACKNOWLEDGMENTS

We appreciate the input and discussions about this manuscript from members of the Freshwater Mollusk Conservation Society Ecosystem Service committee.

## LITERATURE CITED

- Abbott, L. L., and E. A. Bergey. 2007. Why are there few algae on snail shells? The effects of grazing, nutrients and shell chemistry on the algae on shells of *Helisoma trivolvis*. *Freshwater Biology* 52:2112–2120.
- Albertson, L., and D. Allen. 2015. Meta-analysis: abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams. *Ecology* 96:1329–1339.
- Aldridge, D. 1999. Development of European bitterling in the gills of freshwater mussels. *Journal of Fish Biology* 54:138–151.
- Alexander, J. E., and A. P. Covich. 1991. Predator avoidance by the freshwater snail *Physella virgata* in response to the crayfish *Procambarus simulans*. *Oecologia* 87:435–442.
- Allen, D. J., K. G. Smith, and W. R. T. Darwall, compilers. 2012a. The status and distribution of freshwater biodiversity in Indo-Burma. International Union for Conservation of Nature and Natural Resources, Cambridge, UK, and Gland, Switzerland. 158 pp. Available at <https://www.iucn.org/resources/publication/status-and-distribution-freshwater-biodiversity-indo-burma> (accessed January 10, 2023).
- Allen, D. C., C. C. Vaughn, J. F. Kelly, J. T. Cooper, and M. Engel. 2012b. Bottom-up biodiversity effects increase resource subsidy flux between ecosystems. *Ecology* 93:2165–2174.
- Archambault, J. M. 2020. Contaminant-related ecosystem functions and services of freshwater mussels (Unionidae) and public views on nature's contributions to water quality. Doctoral dissertation, North Carolina State University, Raleigh.
- Atkinson, C. L. 2013. Razor-backed musk turtle (*Sternotherus carinatus*) diet across a gradient of invasion. *Herpetological Conservation and Biology* 8:561–570.
- Atkinson, C. L., and K. J. Forshay. 2022. Community patch dynamics governs direct and indirect nutrient recycling by aggregated animals across spatial scales. *Functional Ecology* 36:595–606.
- Atkinson, C. L., H. M. Halvorson, K. A. Kuehn, M. Winebarger, A. Hamid, and M. N. Waters. 2021. Filter-feeders have differential bottom-up impacts on green and brown food webs. *Oecologia* 195:187–198.
- Atkinson, C. L., J. F. Kelly, and C. C. Vaughn. 2014. Tracing consumer-derived nitrogen in riverine food webs. *Ecosystems* 17:485–496.
- Atkinson, C. L., B. J. Sansom, C. C. Vaughn, and K. J. Forshay. 2018. Consumer aggregations drive nutrient dynamics and ecosystem metabolism in nutrient-limited systems. *Ecosystems* 21:521–535.
- Atkinson, C. L., and C. C. Vaughn. 2015. Biogeochemical hotspots: Temporal and spatial scaling of the impact of freshwater mussels on ecosystem function. *Freshwater Biology* 60:563–574.
- Atkinson, C. L., C. C. Vaughn, K. J. Forshay, and J. T. Cooper. 2013. Aggregated filter-feeding consumers alter nutrient limitation: Consequences for ecosystem and community dynamics. *Ecology* 94:1359–1369.
- Augsburger, T., A. E. Keller, M. C. Black, W. G. Cope, and F. J. Dwyer. 2003. Water quality guidance for protection of freshwater mussels (Unionidae) from ammonia exposure. *Environmental Toxicology and Chemistry* 22:2569–2575.
- Bai, J., Y. Chen, Z. Ning, S. Liu, C. Xu, and J.-K. Yan. 2020. Proteoglycan isolated from *Corbicula fluminea* exerts hepato-protective effects against alcohol-induced liver injury in mice. *International Journal of Biological Macromolecules* 142:1–10.
- Baines, S. B., N. S. Fisher, and J. J. Cole. 2005. Uptake of dissolved organic matter (DOM) and its importance to metabolic requirements of the zebra mussel, *Dreissena polymorpha*. *Limnology and Oceanography* 50:36–47.
- Baker, P., F. Zimmanck, and S. M. Baker. 2010. Feeding rates of an introduced freshwater gastropod *Pomacea insularum* on native and nonindigenous aquatic plants in Florida. *Journal of Molluscan Studies* 76:138–143.
- Beason, E., and A. N. Schwalb. 2022. Impact of zebra mussels on physiological conditions of unionid mussels in Texas. *Aquatic Sciences* 84:21. <http://dx.doi.org/10.1007/s00027-022-00853-8>.
- Benson, J. A., B. A. Stewart, P. G. Close, and A. J. Lymbery. 2021. Freshwater mussels in Mediterranean-climate regions: Species richness, conservation status, threats, and conservation actions needed. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31:708–728.
- Bērziņš, V., U. Brinker, C. Klein, H. Lübke, J. Meadows, M. Rudzīte, U. Schmölcke, H. Stümpel, and I. Zagorska. 2014. New research at Rīņukalna, a Neolithic freshwater shell midden in northern Latvia. *Antiquity* 88:715–732.
- Binelli, A., S. Magni, C. Della Torre, and M. Parolini. 2015. Toxicity decrease in urban wastewaters treated by a new biofiltration process. *Science of the Total Environment* 537:235–242.
- Bissattini, A. M., P. J. Haubrock, V. Buono, P. Balzani, N. Borgianni, L. Stellati, A. F. Inghilesi, L. Tancioni, M. Martinoli, and E. Tricarico. 2021. Trophic structure of a pond community dominated by an invasive alien species: Insights from stomach content and stable isotope analyses. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31:948–963.
- Boeker, C., T. Lueders, M. Mueller, J. Pander, and J. Geist. 2016. Alteration of

- physico-chemical and microbial properties in freshwater substrates by burrowing invertebrates. *Limnologia* 59:131–139.
- Böhm, M., N. I. Dewhurst-Richman, M. Seddon, S. E. H. Ledger, C. Albrecht, D. Allen, A. E. Bogan, J. Cordeiro, K. S. Cummings, A. Cuttelod, G. Darrigran, W. Darwall, Z. Fehér, C. Gibson, D. L. Graf, F. Köhler, M. Lopes-Lima, G. Pastorino, K. E. Perez, K. Smith, D. van Damme, M. V. Vinarski, T. von Proschwitz, T. von Rintelen, D. C. Aldridge, N. A. Aravind, P. B. Budha, C. Clavijo, D. Van Tu, O. Gargominy, M. Ghamizi, M. Haase, C. Hilton-Taylor, P. D. Johnson, Ü. Kebapçı, J. Lajtner, C. N. Lange, D. A. W. Lepitzki, A. Martínez-Ortí, E. A. Moorkens, E. Neubert, C. M. Pollock, V. Prié, C. Radea, R. Ramirez, M. A. Ramos, S. B. Santos, R. Slapnik, M. O. Son, A.-S. Stensgaard, and B. Collen. 2021. The conservation status of the world's freshwater mollusks. *Hydrobiologia* 848:3231–3254.
- Bolotov, I., I. Vikhrev, Y. Beshpalaya, V. Artamonova, M. Gofarov, J. Kolosova, A. Kondakov, A. Makhrov, A. Frolov, and S. Tumpeesuan. 2014. Ecology and conservation of the endangered Indochinese freshwater pearl mussel, *Margaritifera laosensis* (Lea, 1863) in the Nam Pe and Nam Long rivers, Northern Laos. *Tropical Conservation Science* 7:706–719.
- Bouckaert, F. W., and J. Davis. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. *Freshwater Biology* 40:77–86.
- Brauman, K. A., G. C. Daily, T. K. Duarte, and H. A. Mooney. 2007. The nature and value of ecosystem services: An overview highlighting hydrologic services. *Annual Review of Environment and Resources* 32:67–98.
- Bril, J. S., J. J. Durst, B. M. Hurley, C. L. Just, and T. J. Newton. 2014. Sensor data as a measure of native freshwater mussel impact on nitrate formation and food digestion in continuous-flow mesocosms. *Freshwater Science* 33:417–424.
- Brim Box, J., J. Howard, D. Wolf, C. O. Brien, D. Nez, and D. Close. 2006. Freshwater mussels (Bivalvia: Unionoida) of the Umatilla and middle fork John Day rivers in eastern Oregon. *Northwest Science* 80:95.
- Brown, K. M., B. Lang, and K. E. Perez. 2008. The conservation ecology of North American pleurocerid and hydrobiid gastropods. *Freshwater Science* 27:484–495.
- Brown, K. M., and C. Lydeard. 2010. Mollusca: Gastropoda. Pages 207–306 in J. H. Thorp and A. P. Covich, editors. *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, Cambridge, Massachusetts.
- Charles, H., and J. S. Dukes. 2008. Impacts of invasive species on ecosystem services. Pages 217–237 in W. Nentwig, editor. *Biological Invasions*. Springer, Berlin, Heidelberg.
- Chowdhury, G. W., A. Zieritz, and D. C. Aldridge. 2016. Ecosystem engineering by mussels supports biodiversity and water clarity in a heavily polluted lake in Dhaka, Bangladesh. *Freshwater Science* 35:188–199.
- Claassen, C. 2008. Shell symbolisms in pre-Columbian North America. Pages 207–306 in A. Antczak, and R. Cipriani, editors. *Early Human Impacts on Megamolluscs*. International Series 1865. British Archeological Reports Archaeopress, Oxford, England.
- Coker, R. E. 1919. Fresh-water mussels and mussel industries of the United States. *US Bulletin of the Bureau of Fisheries* 36:13–89 [Issued separately as US Bureau of Fisheries Document 865].
- Constantinescu, G., S. Miyawaki, and Q. Liao. 2013. Flow and turbulence structure past a cluster of freshwater mussels. *Journal of Hydraulic Engineering* 139:347–358.
- Counts III, C. L. 1986. The zoogeography and history of the invasion of the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). *American Malacological Bulletin* 2:7–39.
- Crowl, T. A., and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* 247:949–951.
- CTUIR (Confederated Tribes of the Umatilla Indian Reservation). 2020. Šáxu Siwáala Seewíʔs: River mussels through time. Lynx Group Publishing, Walla Walla, Washington.
- Cuttelod, A., M. Seddon, and E. Neubert. 2011. European Red List of non-marine Molluscs. Publications Office of the European Union, Luxembourg. Available at <https://portals.iucn.org/library/node/9981> (accessed November 3, 2022).
- Davis, J. 1986. Boundary layers, flow microenvironments and stream benthos. Pages 293–312 in P. De Deckker and W. D. Williams, editors. *Limnology in Australia*. Monographiae Biologicae, vol. 61. Springer, Dordrecht, the Netherlands.
- Dee, K. H., F. Abdullah, S. N. A. Md Nasir, S. Appalasamy, R. Mohd Ghazi, and A. Eh Rak. 2019. Health risk assessment of heavy metals from smoked *Corbicula fluminea* collected on roadside vendors at Kelantan, Malaysia. *BioMed Research International* 2019. <http://dx.doi.org/10.1155/2019/9596810>.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345:401–406.
- Dodds, W. K., J. S. Perkin, and J. E. Gerken. 2013. Human impact on freshwater ecosystem services: A global perspective. *Environmental Science and Technology* 47:9061–9068.
- Downing, A. S., E. H. van Nes, J. S. Balirwa, J. Beuving, P. O. Bwathondi, L. J. Chapman, I. J. Cornelissen, I. G. Cowx, K. P. Goudswaard, and R. E. Hecky. 2014. Coupled human and natural system dynamics as key to the sustainability of Lake Victoria's ecosystem services. *Ecology and Society* 19:31.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status, and conservation challenges. *Biological Reviews* 81:163–182.
- Etnier, D. A., and W. C. Starnes. 1993. *The Fishes of Tennessee*. University of Tennessee Press, Knoxville.
- Evans-White, M. A., and G. A. Lamberti. 2005. Grazer species effects on epilithon nutrient composition. *Freshwater Biology* 50:1853–1863.
- Ferreira-Rodríguez, N., M. Gangloff, G. Shafer, and C. L. Atkinson. 2022. Drivers of ecosystem vulnerability to *Corbicula* invasions in southeastern North America. *Biological Invasions* 24:1677–1688.
- Ferreira-Rodríguez, N., R. Sousa, and I. Pardo. 2018. Negative effects of *Corbicula fluminea* over native freshwater mussels. *Hydrobiologia* 810:85–95.
- Fervier, V., P. Urrutia-Cordero, E. Piano, F. Bona, K. M. Persson, and L. A. Hansson. 2020. Evaluating nutrient reduction, grazing and barley straw as measures against algal growth. *Wetlands* 40:193–202.
- FMCS (Freshwater Mollusk Conservation Society). 2016. A national strategy for the conservation of native freshwater mollusks. *Freshwater Mollusk Biology and Conservation* 19:1–21.
- Francoeur, S. N., A. Pinowska, T. A. Clason, S. Makosky, and R. L. Lowe. 2002. Unionid bivalve influence on benthic algal community composition in a Michigan Lake. *Journal of Freshwater Ecology* 17:489–500.
- Gao, J., C. Yang, Z. Zhang, Z. Liu, and E. Jeppesen. 2021. Effects of co-occurrence of invading *Procambarus clarkii* and *Pomacea canaliculata* on *Vallisneria denseserrulata*-dominated clear-water ecosystems: A mesocosm approach. *Knowledge and Management of Aquatic Ecosystems* 422:1–7.
- Garvey, J. 2017. Australian aboriginal freshwater shell middens from late quaternary Northwest Victoria: Prey choice, economic variability and exploitation. *Quaternary International* 427:85–102.
- Giari, L., F. Vincenzi, E. A. Fano, I. Galdi, F. Gelli, and G. Castaldelli. 2017. Sensitivity to selected contaminants in a biological early warning system using *Anodonta woodiana* (Mollusca). *Water* 43:200–208.
- Graf, D. L., and K. S. Cummings. 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionida). *Journal of Molluscan Studies* 73:291–314.
- Groendahl, S., and P. Fink. 2017. High dietary quality of non-toxic

- cyanobacteria for a benthic grazer and its implications for the control of cyanobacterial biofilms. *BMC Ecology* 17:20.
- Gutiérrez, J. L., C. G. Jones, D. L. Strayer, and O. O. Iribarne. 2003. Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos* 101:79–90.
- Haag, W. R. 2012. North American freshwater mussels: Ecology, natural history, and conservation. Cambridge University Press, New York.
- Haag, W. R., D. J. Berg, and D. W. Garton. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in Western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 50:13–19.
- Hall, R. O., J. L. Tank, and M. F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and the Environment* 1:407–411.
- Hawkins, C. P., and J. K. Furnish. 1987. Are snails important competitors in stream ecosystems? *Oikos* 49:209–220.
- Higgins, S. N., and M. J. Vander Zanden. 2010. What a difference a species makes: A meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs* 80:179–196.
- Hill, W. R., and N. A. Griffiths. 2017. Nitrogen processing by grazers in a headwater stream: Riparian connections. *Freshwater Biology* 62:17–29.
- Hill, W. R., S. C. Weber, and A. J. Stewart. 1992. Food limitation of two lotic grazers: Quantity, quality, and size-specificity. *Journal of the North American Benthological Society* 11:420–432.
- Hoellein, T. J., C. B. Zarnoch, D. A. Bruesewitz, and J. DeMartini. 2017. Contributions of freshwater mussels (Unionidae) to nutrient cycling in an urban river: Filtration, recycling, storage, and removal. *Biogeochemistry* 135:307–324.
- Hopper, G. W., J. K. Buchanan, I. Sánchez González, M. E. Kubala, J. R. Bucholz, M. B. Lodato, J. D. Lozier, and C. L. Atkinson. 2022. Little clams with big potential: Nutrient release by invasive *Corbicula fluminea* can exceed co-occurring freshwater mussel (Unionidae) assemblages. *Biological Invasions* 24:2529–2545.
- Hopper, G. W., S. Chen, I. Sánchez González, J. R. Bucholz, Y. Lu, and C. L. Atkinson. 2021a. Aggregated filter-feeders govern the flux and stoichiometry of locally available energy and nutrients in rivers. *Functional Ecology* 35:1183–1195.
- Hopper, G. W., G. K. Dickinson, and C. L. Atkinson. 2021b. Associations among elements in freshwater mussel shells (Unionidae) and their relation to morphology and life history. *Freshwater Biology* 66:1980–1991.
- Hopper, G. W., T. P. DuBose, K. B. Gido, and C. C. Vaughn. 2019. Freshwater mussels alter fish distributions through habitat modifications at fine spatial scales. *Freshwater Science* 38:702–712.
- 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.
- Hunn, E. S., E. T. Morning Owl, P. E. Cash, and J. Karson Engum. 2015. Čaw Pawá Láakni—They are not forgotten: Sahaptian place names atlas of the Cayuse, Umatilla, and Walla Walla. Tamástslikt Cultural Institute, Pendleton, Oregon.
- Hwang, S.-J., Y.-J. Lee, M.-S. Kim, and B.-H. Kim. 2021. Filter feeding and carbon and nitrogen assimilation of a freshwater bivalve (*Unio douglasiae*) on a toxic cyanobacterium (*Microcystis aeruginosa*). *Applied Sciences* 11:9294.
- Ismail, N. S., H. Dodd, L. M. Sassoubre, A. J. Horne, A. B. Boehm, and R. G. Luthy. 2015. Improvement of urban lake water quality by removal of *Escherichia coli* through the action of the bivalve *Anodonta californiensis*. *Environmental Science and Technology* 49:1664–1672.
- Ismail, N. S., C. E. Müller, R. R. Morgan, and R. G. Luthy. 2014. Uptake of contaminants of emerging concern by the bivalves *Anodonta californiensis* and *Corbicula fluminea*. *Environmental Science and Technology* 48:9211–9219.
- Ismail, N. S., J. P. Tommerdahl, A. B. Boehm, and R. G. Luthy. 2016. *Escherichia coli* reduction by bivalves in an impaired river impacted by agricultural land use. *Environmental Science and Technology* 50:11025–11033.
- Jiale, L., and L. Yingsen. 2009. Aquaculture in China—Freshwater pearl culture. *World Aquaculture* 40:60.
- Johnson, P. D., A. E. Bogan, K. M. Brown, N. M. Burkhead, J. R. Cordeiro, J. T. Garner, P. D. Hartfield, D. A. Lepitzki, G. L. Mackie, and E. Pip. 2013. Conservation status of freshwater gastropods of Canada and the United States. *Fisheries* 38:247–282.
- Karatayev, A. Y., L. E. Burlakova, V. A. Karatayev, and D. K. Padilla. 2009. Introduction, distribution, spread, and impacts of exotic freshwater gastropods in Texas. *Hydrobiologia* 619:181–194.
- Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 2015. Zebra versus quagga mussels: A review of their spread, population dynamics, and ecosystem impacts. *Hydrobiologia* 746:97–112.
- Kellogg, M. L., M. J. Brush, and J. Cornwell. 2018. An updated model for estimating the TMDL-related benefits of oyster reef restoration. Final report to The Nature Conservancy and Oyster Recovery Partnership. Available at [https://www.conservationgateway.org/Documents/Harris\\_Creek\\_Model\\_and\\_Oyster\\_Reef\\_Restoration\\_Benefits.pdf](https://www.conservationgateway.org/Documents/Harris_Creek_Model_and_Oyster_Reef_Restoration_Benefits.pdf) (accessed October 28, 2022).
- Köhler, F., M. Seddon, A. E. Bogan, D. Van Tu, P. Sri-Aroon, and D. Allen. 2012. The status and distribution of freshwater molluscs of the Indo-Burma region. Pages 66–88 in D. J. Allen, K. G. Smith, and W. R. T. Darwall, editors. *The Status and Distribution of Freshwater Biodiversity in Indo-Burma*. IUCN, Cambridge, United Kingdom, and Gland, Switzerland.
- Kreeger, D. A., C. M. Gatenby, and P. W. Bergstrom. 2018. Restoration potential of several native species of bivalve mollusks for water quality improvement in mid-Atlantic watersheds. *Journal of Shellfish Research* 37:1121–1157.
- Kuhm, H. W. 2007. Aboriginal uses of shell. *Wisconsin Archeologist* 17:1–8.
- Kumar, S. S., J. Kozarek, D. Hornbach, M. Hondzo, and J. Hong. 2019. Experimental investigation of turbulent flow over live mussels. *Environmental Fluid Mechanics* 19:1417–1430.
- Lamberti, G. A., L. R. Ashkenas, S. V. Gregory, and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. *Journal of the North American Benthological Society* 6:92–104.
- Li, J., V. Ianaiev, A. Huff, J. Zalusky, T. Ozersky, and S. Katsev. 2021. Benthic invaders control the phosphorus cycle in the world's largest freshwater ecosystem. *Proceedings of the National Academy of Sciences U.S.A.* 118:e2008223118.
- Liess, A., and A. L. Haglund. 2007. Periphyton responds differentially to nutrients recycled in dissolved or faecal pellet form by the snail grazer *Theodoxus fluviatilis*. *Freshwater Biology* 52:1997–2008.
- Limburg, K. E., V. A. Luzadis, M. Ramsey, K. L. Schulz, and C. M. Mayer. 2010. The good, the bad, and the algae: Perceiving ecosystem services and disservices generated by zebra and quagga mussels. *Journal of Great Lakes Research* 36:86–92.
- Liu, Y., H. Liang, S. Hilt, R. Wang, H. Zhang, and G. Gang. 2021. Shallow lakes at risk: Nutrient enrichment enhances top-down control of macrophytes by invasive herbivorous snails. *Freshwater Biology* 66:436–446.
- Lopes-Lima, M., L. E. Burlakova, A. Y. Karatayev, K. Mehler, M. Seddon, and R. Sousa. 2018. Conservation of freshwater bivalves at the global scale: Diversity, threats and research needs. *Hydrobiologia* 810:1–14.
- Lopez, J. W., T. B. Parr, D. C. Allen, and C. C. Vaughn. 2020. Animal aggregations promote emergent aquatic plant production at the aquatic-terrestrial interface. *Ecology* 101:e03126.
- Lopez, J. W., and C. C. Vaughn. 2021. A review and evaluation of the effects of hydrodynamic variables on freshwater mussel communities. *Freshwater Biology* 66:1665–1679.
- Loreau, M., and C. de Mazancourt. 2013. Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters* 16:106–115.
- Lukens, N. R., B. M. Kraemer, V. Constant, E. J. Hamann, E. Michel, A. M.

- Socci, Y. Vadeboncoeur, and P. B. McIntyre. 2017. Animals and their epibiota as net autotrophs: Size scaling of epibiotic metabolism on snail shells. *Freshwater Science* 36:307–315.
- Lv, S., Y. H. Guo, H. M. Nguyen, M. Sinuon, S. Sayasone, N. C. Lo, X.-N. Zhou, and J. R. Andrews. 2018. Invasive Pomacea snails as important intermediate hosts of *Angiostrongylus cantonensis* in Laos, Cambodia and Vietnam: Implications for outbreaks of eosinophilic meningitis. *Acta Tropica* 183:32–35.
- Mace, G. M., K. Norris, and A. H. Fitter. 2012. Biodiversity and ecosystem services: A multilayered relationship. *Trends in Ecology and Evolution* 27:19–26.
- Maguire, Z., B. B. Tumolo, and L. K. Albertson. 2020. Retreat but no surrender: Net-spinning caddisfly (Hydropsychidae) silk has enduring effects on stream channel hydraulics. *Hydrobiologia* 847:1539–1551.
- Mason, R. J., S. P. Rice, M. F. Johnson, P. Wood, and D. Vettori. 2022. Aquatic insect bioconstructions modify fine-sediment entrainment and mobility. *Earth and Space Science* 127:e2021JF006399.
- Mason, R. J., and H. Sanders. 2021. Invertebrate zoogeomorphology: A review and conceptual framework for rivers. *WIREs Water* 8:e1540.
- Matisoff, G., J. B. Fisher, and S. Matis. 1985. Effects of benthic macroinvertebrates on the exchange of solutes between sediments and freshwater. *Hydrobiologia* 122:19–33.
- Meadows, J., H. Lubke, I. Zagorska, V. Berzins, A. Cerina, and I. Ozola. 2014. Potential freshwater reservoir effects in a Neolithic shell midden at Rinnukalns, Latvia. *Radiocarbon* 56:823–832.
- Mersch, J., and L. Johansson. 1993. Transplanted aquatic mosses and freshwater mussels to investigate the trace metal contamination in the rivers Meurthe and Plaine, France. *Environmental Technology* 14:1027–1036.
- Michel, P., A. Dobson-Waitere, H. Hohaia, A. McEwan, and D. F. Shanahan. 2019. The reconnection between mana whenua and urban freshwaters to restore the mouri/life force of the Kaiwharawhara. *New Zealand Journal of Ecology* 43:1–10.
- Millennium Ecosystem Assessment (MEA). 2005. Ecosystems and human well-being: Synthesis. Island Press, Washington, DC.
- Modesto, V., P. Castro, M. Lopes-Lima, C. Antunes, M. Ilarri, and R. Sousa. 2019. Potential impacts of the invasive species *Corbicula fluminea* on the survival of glochidia. *Science of the Total Environment* 673:157–164.
- Naem, S., and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6:567–579.
- Nagachinta, A., M. Piamtipmanus, J. Jivaluk, W. Punyaganok, and J. Totanapoka. 2005. Utilization of freshwater mollusks of Thailand. Department of Fisheries, Ministry of Agriculture and Cooperatives, 155 p. (In Thai, not seen; cited by Allen et al. 2012).
- Newell, R., T. Fisher, R. Holyoke, and J. Cornwell. 2005. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. Pages 93–120 in R. F. Dame, and S. Olenin, editors. *The Comparative Roles of Suspension-Feeders in Ecosystems*. NATO Science Series IV: Earth and Environmental Series, vol. 47. Springer, Dordrecht, the Netherlands.
- Newton, T. J., S. J. Zigler, J. T. Rogala, B. R. Gray, and M. Davis. 2011. Population assessment and potential functional roles of native mussels in the Upper Mississippi River. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21:122–131.
- Ng, T. H., S. K. Tan, W. H. Wong, R. Meier, S.-Y. Chan, H. H. Tan, and D. C. J. Yeo. 2016. Mollusks for sale: Assessment of freshwater gastropods and bivalves in the ornamental pet trade. *PLoS One* 11:e0161130.
- Nickerson, Z. L., B. Mortazavi, and C. L. Atkinson. 2019. Using functional traits to assess the influence of burrowing bivalves on nitrogen-removal in streams. *Biogeochemistry* 146:125–143.
- Nicodemus, A. 2011. The Bronze Age and Dacian fauna from new excavations at Pecica Santul Mare. *Analele Banatului, Serie Noua* 19:79–84.
- Olden, J. D., L. Ray, M. C. Mims, and M. C. Horner-Devine. 2013. Filtration rates of the non-native Chinese mystery snail (*Bellamya chinensis*) and potential impacts on microbial communities. *Limnetica* 32:107–120.
- Oliver, T. H., M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A. Hector, C. D. L. Orme, O. L. Petchey, V. Proença, D. Raffaelli, K. B. Suttle, G. M. Mace, B. Martín-López, B. A. Woodcock, and J. M. Bullock. 2015. Biodiversity and resilience of ecosystem functions. *Trends in Ecology and Evolution* 30:673–684.
- Padilla, D. K., and S. L. Williams. 2004. Beyond ballast water: Aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2:131–138.
- Parmalee, P. W., and W. E. Klippel. 1974. Freshwater mussels as a prehistoric food resource. *American Antiquity* 39:421–434.
- Parr, T. B., C. C. Vaughn, and K. B. Gido. 2020. Animal effects on dissolved organic carbon bioavailability in an algal controlled ecosystem. *Freshwater Biology* 65:1298–1310.
- Patoka, J., O. Kopecký, V. Vrabec, and L. Kalous. 2017. Aquarium mollusks as a case study in risk assessment of incidental freshwater fauna. *Biological Invasions* 19:2039–2046.
- Peacock, E., J. Mitchell, and B. Kirkland. 2020. Investigating freshwater mussel (Unionidae) shell diagenesis at an archaeological site on the Tombigbee River, Mississippi, southeastern U.S.A. *Journal of Archaeological Science: Reports* 31:102350.
- Pinto, H. A., and A. L. De Melo. 2011. A checklist of trematodes (Platyhelminthes) transmitted by *Melanoides tuberculata* (Mollusca: Thiaridae). *Zootaxa* 2799:15–28.
- Preston, D. L., E. R. Crone, A. Miller-ter Kuile, C. D. Lewis, E. L. Sauer, and D. C. Trovillion. 2022. Non-native freshwater snails: A global synthesis of invasion status, mechanisms of introduction, and interactions with natural enemies. *Freshwater Biology* 67:227–239.
- Quempts, E. J., K. L. Jones, S. J. O'Daniel, T. J. Beechie, and G. C. Poole. 2018. Aligning environmental management with ecosystem resilience: A First Foods example from the Confederated Tribes of the Umatilla Indian Reservation, Oregon, USA. *Ecology and Society* 23:29.
- Rafferty, J., and E. Peacock. 2008. The spread of shell tempering in the Mississippi Black Prairie. *Southeastern Archaeology* 27:253–264.
- Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon, and S. J. Cooke. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* 94:849–873.
- Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* 13:220–222.
- Roditi, H. A., N. S. Fisher, and S. A. Sañudo-Wilhelmy. 2000. Uptake of dissolved organic carbon and trace elements by zebra mussels. *Nature* 407:78–80.
- Rosa, I. C., R. Costa, F. Gonçalves, and J. L. Pereira. 2014. Bioremediation of metal-rich effluents: Could the invasive bivalve *Corbicula fluminea* work as a biofilter? *Journal of Environmental Quality* 43:1536–1545.
- Rose, J. M., J. S. Gosnell, S. Bricker, M. J. Brush, A. Colden, L. Harris, E. Karplus, A. Laferriere, N. H. Merrill, T. B. Murphy, J. Reitsma, J. Shockley, K. Stephenson, S. Theuerkauf, D. Ward, and R. W. Fulweiler. 2021. Opportunities and challenges for including oyster-mediated denitrification in nitrogen management plans. *Estuaries and Coasts* 44:2041–2055.
- Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: Effects of nutrients and herbivores. *Ecology* 74:1264–1280.
- Sansom, B. J., J. F. Atkinson, and S. J. Bennett. 2018a. Modulation of near-bed hydrodynamics by freshwater mussels in an experimental channel. *Hydrobiologia* 810:449–463.
- Sansom, B. J., S. J. Bennett, J. F. Atkinson, and C. C. Vaughn. 2018b. Long-term persistence of freshwater mussel beds in labile river channels. *Freshwater Biology* 63:1469–1481.

- Sansom, B. J., S. J. Bennett, J. F. Atkinson, and C. C. Vaughn. 2020. Emergent hydrodynamics and skimming flow over mussel covered beds in rivers. *Water Resources Research* 56:1–17.
- Seddon, M., C. Appleton, D. Van Damme, and D. Graf. 2011. Freshwater molluscs of Africa: Diversity, distribution, and conservation. Pages 92–125 in W. Darwall, D. Smith, D. Allen, R. Holland, I. Harrison, and E. Brooks, editors. *The Diversity of Life in African Freshwaters: Underwater, under Threat. An Analysis of the Status and Distribution of Freshwater Species throughout Mainland Africa*. IUCN, Cambridge, United Kingdom, and Gland, Switzerland.
- Simeone, D., C. H. Tagliaro, and C. R. Beasley. 2021. Filter and deposit: A potential role of freshwater mussels in ecosystem functioning associated with enhanced macroinvertebrate assemblage structure in a Neotropical river. *Hydrobiologia* 848:4211–4223.
- Spooner, D. E., and C. C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology* 51:1016–1024.
- Strayer, D. L. 2014. Understanding how nutrient cycles and freshwater mussels (Unionoida) affect one another. *Hydrobiologia* 735:277–292.
- Strayer, D. L. 2017. What are freshwater mussels worth? *Freshwater Mollusk Biology and Conservation* 20:103–113.
- Strayer, D. L. 2020. Non-native species have multiple abundance–impact curves. *Ecology and Evolution* 10:6833–6843.
- Strayer, D. L., J. Geist, W. R. Haag, J. K. Jackson, and J. D. Newbold. 2019. Essay: Making the most of recent advances in freshwater mussel propagation and restoration. *Conservation Science and Practice* 1:10.1111/csp2.53
- Strayer, D. L., and H. M. Malcom. 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. *Freshwater Biology* 52:1611–1617.
- Strong, E. E., O. Gargominy, W. F. Ponder, and P. Bouchet. 2008. Global diversity of gastropods (Gastropoda; Molluska) in freshwater. Pages 149–166 in E. V. Balian, C. Lévêque, H. Segers, and K. Martens, editors. *Freshwater Animal Diversity Assessment*. Springer, Dordrecht, the Netherlands.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Trentman, M. T., C. L. Atkinson, and J. D. Brant. 2018. Native freshwater mussel effects on nitrogen cycling: Impacts of nutrient limitation and biomass dependency. *Freshwater Science* 37:276–286.
- Turner, R. K., and M. Schaafsma, editors. 2015. *Coastal Zones Ecosystem Services: From Science to Values and Decision Making*. Springer International Publishing, Heidelberg.
- Tyrrill, M., and D. J. Hornbach. 1998. Selective predation by muskrats on freshwater mussels in 2 Minnesota rivers. *Journal of the North American Benthological Society* 17:301–310.
- Valente, R., M. R. Robles, and J. I. Diaz. 2020. Gastropods as intermediate hosts of *Angiostrongylus* spp. in the Americas: Bioecological characteristics and geographical distribution. *Memorias do Instituto Oswaldo Cruz* 115:e200236.
- Vaughn, C. C. 2018. Ecosystem services provided by freshwater mussels. *Hydrobiologia* 810:15–27.
- Vaughn, C. C., C. L. Atkinson, and J. P. Julian. 2015. Drought-induced changes in flow regimes lead to long-term losses in mussel-provided ecosystem services. *Ecology and Evolution* 5:1291–1305.
- 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., and T. J. Hoellein. 2018. Bivalve impacts in freshwater and marine ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 49:183–208.
- 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. 2006. 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 B. W. Hoagland. 2002. River weed growing epizoically on freshwater mussels. *Southwestern Naturalist* 47:604–605.
- Walsh, J. R., S. R. Carpenter, and M. J. Vander Zanden. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proceedings of the National Academy of Sciences U.S.A.* 113:4081–4085.
- Wang, N., C. G. Ingersoll, D. K. Hardesty, C. D. Ivey, J. L. Kunz, T. W. May, F. J. Dwyer, A. D. Roberts, T. Augspurger, C. M. Kane, R. J. Neves, and M. C. Barnhart. 2007. Acute toxicity of copper, ammonia, and chlorine to glochidia and juveniles of freshwater mussels (Unionidae). *Environmental Toxicology and Chemistry* 26:2036–2047.
- Williams J. D., A. E. Bogan, and J. T. Garner. 2008. *Freshwater Mussels of Alabama and the Mobile Basin in Georgia, Mississippi, and Tennessee*. University of Alabama Press, Tuscaloosa.
- Wisniewski, J. M., K. D. Bockrath, J. P. Wares, A. K. Fritts, and M. J. Hill. 2013. The mussel–fish relationship: A potential new twist in North America? *Transactions of the American Fisheries Society* 142:642–648.
- Wood, J., P. Bukaveckas, H. Galbraith, M. Gattis, M. Gray, T. Ihde, D. Kreeger, R. Mair, S. McLaughlin, S. Hahn, and A. Harvey. 2021. Incorporating freshwater mussels into the Chesapeake Bay restoration efforts. STAC Publication Number 21-004, Edgewater, Maryland. Available at [https://www.chesapeake.org/stac/wp-content/uploads/2021/07/FINAL-Report\\_Freshwater-Mussels\\_21-004.pdf](https://www.chesapeake.org/stac/wp-content/uploads/2021/07/FINAL-Report_Freshwater-Mussels_21-004.pdf) (accessed October 28, 2022).
- Wu, H., G. Constantinescu, and J. Zeng. 2020. Flow and entrainment mechanisms around a freshwater mussel aligned with the incoming flow. *Water Resources Research* 56:e2020WR027983.
- Wurtsbaugh, W. A., H. W. Paerl, and W. K. Dodds. 2019. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. *WIREs Water* 6:e1373.
- Yang, Q.-Q., S.-W. Liu, C. He, and X.-P. Yu. 2018. Distribution and the origin of invasive apple snails, *Pomacea canaliculata* and *P. maculata* (Gastropoda: Ampullariidae) in China. *Scientific Reports* 8:1185.
- Young, H. S., D. J. McCauley, M. Galetti, and R. Dirzo. 2016. Patterns, causes, and consequences of anthropocene defauna. *Annual Review of Ecology, Evolution, and Systematics* 47:333–358.
- Zhang, J., Z. Wang, Z. Song, Z. Xie, L. Li, and L. Song. 2012. Bioaccumulation of microcystins in two freshwater gastropods from a cyanobacteria-bloom plateau lake, Lake Dianchi. *Environmental Pollution* 164:227–234.
- Zieritz, A., A. E. Bogan, E. Froufe, O. Klishko, T. Kondo, U. Kovitvadhii, S. Kovitvadhii, J. H. Lee, M. Lopes-Lima, and J. M. Pfeiffer. 2018. Diversity, biogeography and conservation of freshwater mussels (Bivalvia: Unionida) in East and Southeast Asia. *Hydrobiologia* 810:29–44.
- Zieritz, A., R. Sousa, D. C. Aldridge, K. Douda, E. Esteves, N. Ferreira-Rodríguez, J. H. Mageroy, D. Nizzoli, M. Osterling, and J. Reis. 2022. A global synthesis of ecosystem services provided and disrupted by freshwater bivalve molluscs. *Biological Reviews* 97: 1967–1998.