Freshwater Mollusk Biology and Conservation

Gains and gaps in knowledge surrounding freshwater mollusk ecosystem functions and services

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REGULAR ARTICLE

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GAINS AND GAPS IN KNOWLEDGE SURROUNDING FRESHWATER MOLLUSK ECOSYSTEM SERVICES

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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 policymakers 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 valuated 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.
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 policymakers 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 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 Išáaxuyi, 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. 2012).

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^3 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 (Atkinson and Vaughn 2015; Strayer 2014; 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; Leiss and Haglund 2007; Vaughn et al. 2008; Bril et al. 2014). Snails (*Elimia* spp.) were an important source of recycled nitrogen in a USA stream, excreting twelve 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 is 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, non-native 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. 2012; 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; Sansom et al. 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 (Sansom et al. 2018a; Constantinescu et al. 2013; 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. 2021). 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 (Augspurger 2003; Wang et al. 2007). Lastly, 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. 2021). 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-Rodriguez et al.

2018; Modesto et al. 2019; Ferreira-Rodriguez et al. 2022). 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 policymakers 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 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 these 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 policymakers 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 valuate these animals and the services they provide as tangible benefits to society.

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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 B.C. 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, *Corbicula*, 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
	Pearl culture	Beads from mussel shells are used as seeds in the pearl industry.	Jiale and Yingsen 2009
Regulating	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
		Non-native snails filter a significant amount of particulates from the water column and their filtration rates rival freshwater bivalves.	Olden et al. 2013
		Freshwater mussel filtration removes coliform bacteria, pharmaceuticals, personal care products, and algal toxins.	Downing et al. 2014; Ismail et al. 2014; 2015; 2016
	Contaminant sequestration	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
	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
Supporting	Nutrient cycling & storage	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

		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
	Denitrification	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; Atkinson et al. 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
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, USA)	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, set water quality criteria, as biomonitors, and to reconnect people to nature.	Augsburger et al. 2003; Wang et al. 2007; Michel et al. 2019

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