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Review Paper

Ecosystem services provided by freshwater mussels

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Abstract Ecosystem services are the benefits that humans derive from ecosystems. Freshwater mussels perform many important functions in aquatic ecosystems, which can in turn be framed as the ecosystem services that they contribute to or provide. These include supporting services such as nutrient recycling and storage, structural habitat, substrate and food web modification, and use as environmental monitors; regulating services such as water purification (biofiltration); and provisioning and cultural services including use as a food source, as tools and jewelry, and for spiritual enhancement. Mussel-provided ecosystem services are declining because of large declines in mussel abundance. Mussel propagation could be used to restore populations of common mussel species and their ecosystem services. We need much more quantification of the economic, social, and ecological value and magnitude of ecosystem services provided by mussels, across species, habitats, and environmental conditions, and scaled up to whole watersheds. In addition, we need tools that will allow us to value mussel ecosystem services in a way that is understandable to both the public and to policy makers.

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Humans derive many benefits from ecosystems. These benefits, known as ecosystem services, include provisioning services obtained directly from the ecosystem such as water, food, and timber; regulating services such as water purification, climate control, carbon storage, and pollination; supporting services such as nutrient recycling and storage; and cultural services, which are the benefits that people obtain through tourism and recreation, aesthetic experiences, or spiritual enrichment (Daily et al., 1997). Freshwater systems contribute to many important ecosystem services such as provisioning of clean water, recreation, and ecotourism (Brauman et al., 2007; Dodds et al., 2013). While ecosystem services can be categorized in different ways, this review follows the designations of the United Nations Millennium Ecosystem Assessment (http://www.millenniumassessment.org/en/index.html).

Freshwater mussels (hereafter mussels) perform many important functions in aquatic ecosystems, which have been well described (Vaughn & Hakenkamp, 2001; Strayer, 2008; Vaughn et al., 2008; Haag, 2012). Mussel functions in ecosystems can in turn be framed as the ecosystem services that they provide or contribute towards (Fig. 1; Table 1). Ecosystem services to which mussels contribute

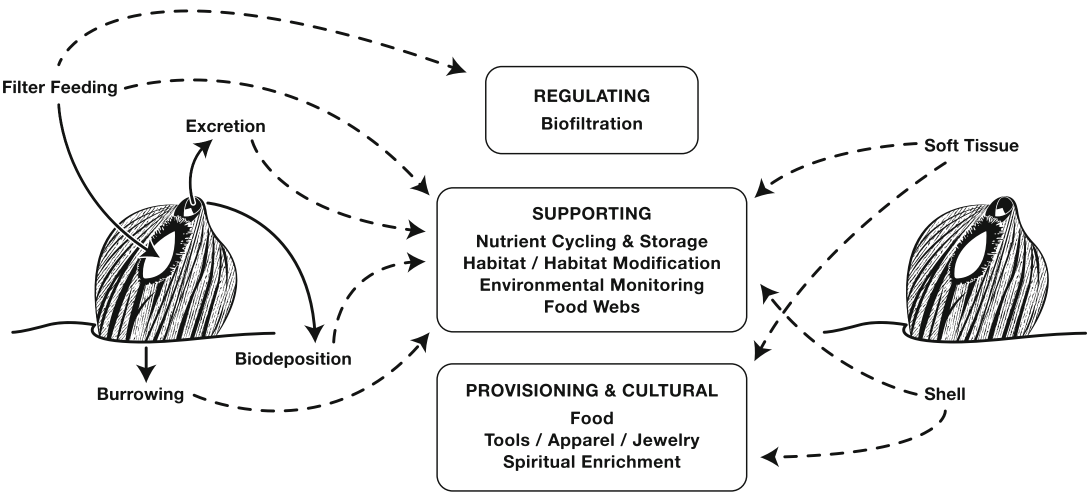

Fig. 1 Mussel tissue and activities that mussels perform can be translated into ecosystem services that are beneficial to humans

Table 1 Ecosystem service classes, mussel-provided ecosystem services, and the benefits that they provide for humans

Ecosystem service class	Mussel-provided ecosystem service	Benefits for humans
Regulating	Biofiltration	Water quality
Supporting	Nutrient cycling and storage	Water quality
	Habitat/habitat modification	Fish habitat
	Environmental monitoring	Water quality
	Food webs	Biodiversity
Provisioning	Food for other species	Biodiversity
	Food for humans	Food provisioning
	Products from mussel shells	Pottery, jewelry, art
Cultural	Cultural value	Spiritual benefits
	Existence value	Conservation value

include the regulating service of water purification (biofiltration); supporting services such as nutrient recycling and storage, structural habitat, and substrate and food web modification; and provisioning and cultural services including use as a food source, as tools, jewelry and art, and for spiritual enhancement (Table 1). This review deals mainly with mussels in the order Unionoida, although I include some references to the invasive Asian clam, *Corbicula fluminea*, which in many ways functions similarly to unionids (Vaughn & Hakenkamp, 2001). This review concentrates on North American mussels, because most of the literature is for this region, but I have included information from other regions where it is available.

Regulating services: mussels as biofilters that purify water

Mussels are powerful filter feeders that remove particles from both the water column and interstitial sediments (Fig. 1) (Vaughn et al., 2008). While it was long thought that mussels fed principally on phytoplankton, recent advances for tracking nutrient assimilation, such as stable isotopes and fatty acids, have shown them to be omnivores whose diet varies with habitat and food availability (Christian et al., 2004; Vaughn et al., 2008; Newton et al., 2013). For example, mussels in small temperate streams feed on a mixture of bacteria and suspended/re-suspended algae (Raikow & Hamilton, 2001), while mussels in large productive rivers feed primarily on phytoplankton (Thorp et al., 1998).

Biofiltration by mussels can remove significant quantities of particles from the water column. In a classic example, Welker & Walz (1998) found that high densities of unionids could remove enough phytoplankton to cause "biological oligotrophication" in the River Spree, Germany. Recently, Pigneur et al. (2014) estimated a 70% loss of phytoplankton biomass and a 61% decline in annual primary production in areas where invasive *Corbicula* have reached high densities in the River Meuse. Chowdhury et al. (2016) found that mussels in a Bangladesh Lake filtered the lake margins in 21 h, supporting high water clarity despite high nutrient levels. While this is an area of active research, most studies are lab-based, and simply applying laboratory filtration estimates to real mussel assemblages in heterogeneous habitats can be inaccurate. For example, Vanden Byllaardt & Ackerman (2014) found that unionid clearance rates could vary over an order of magnitude in the field depending on hydrodynamic conditions and algal flux. More work assessing filtration rates of natural mussel assemblages under varying conditions is needed.

Biofiltration capacities of mussel assemblages can vary substantially with mussel abundance, species composition, and with environmental conditions such as discharge, temperature, and productivity (Spooner & Vaughn, 2008; Vaughn, 2010). Individual mussel filtering rates are governed by mussel physiology and food availability, among other factors. Mussel species have different, temperature-dependent filtration rates (Spooner & Vaughn, 2008). Thus, the biofiltration capacity of a mussel assemblage can vary substantially with assemblage composition and seasonally with temperature. In addition, mussels adjust their feeding rates based on food concentrations (Bril et al., 2014). Disturbance can also influence biofiltration capacity: Lorenz et al. (2013) found that shear stress from boats can reduce daily filtration rates by up to 7%. Finally, biofiltration capacity is heavily dependent on mussel biomass and the volume and residence time of the overlying water (Strayer et al., 1999). For example, mussel assemblages in a small U.S. river (Kiamichi River, Oklahoma) can process the overlying water multiple times before it flows over them during periods of low summer discharge, but can process only a fraction of the water column during high spring and winter flows (Vaughn et al., 2004; Vaughn, 2010).

Human-engineered systems often lack "natural" ecosystem services. A solution is to reintegrate natural ecosystem services into engineered systems. There is a growing interest in using the natural filtering capacity of mussels to pretreat water for human use. For example, Newton et al. (2011) estimated that mussels in a 480-km reach of the Mississippi River filter approximately 53 million m^{-3} day^{-1}, while a Minneapolis-St. Paul wastewater treatment plant produces wastewater flows for 0.7 million m^{-3} day^{-1}. This interest extends to using mussels and other freshwater bivalves to selectively remove disease organisms and contaminants from water supplies, and this is a rapidly growing area of inquiry (Li et al., 2010; Izumi et al., 2012). For example, Faust et al. (2009) found that *Corbicula fluminea* can remove avian influenza viruses from the water, and reduce infectivity. Ismail et al. (2014) found that *Anodonta californiensis* and *Corbicula fluminea* can remove pharmaceuticals, personal care products, herbicides, and flame retardants from the water and either biodeposit or store them in their tissue. This research group also discovered that mussels can actually remove hydrophobic trace organic compounds that cannot be fully removed by conventional wastewater treatment such as ibuprofen and beta blockers. *Anodonta californiensis* also can remove significant amounts of *E. coli* from lake water (Ismail et al., 2015). There is also increasing interest in using mussel biofiltration to augment aquaculture. The mussel *Diplodon chilensis* was used to reduce nutrient loads from salmon farming (Soto & Mena, 1999). Othman et al. (2015) found that filtering mussels reduced bacterial populations by greater than 85% and led to higher growth and lower mortality of farmed Nile tilapia. Of course, while mussels remove contaminants and store them in their tissues or biodeposit them, we know relatively little about the effects of these contaminant burdens on the mussels themselves.

Supporting services: nutrient cycling and storage

Mussels feed on particulate nutrients and convert these nutrients into soft tissue and shell, biodeposits (feces and pseudofeces), and dissolved nutrients (Fig. 1) (Strayer, 2014). Thus, where mussel biomass is high, mussels play an important role in nutrient recycling, translocation and storage, can alter water quality, and potentially can play a role in nutrient abatement.

Mussels excrete soluble nutrients to the water column (Vaughn & Hakenkamp, 2001). These nutrients are readily taken up by algae and heterotrophic bacteria (Fig. 2) (Vaughn et al., 2008; Bril et al., 2014), and cascade up aquatic food webs (see discussion of food webs below). Mussels have been shown to alleviate nutrient limitation and alter algae communities in streams, impacting water quality (Atkinson et al., 2013a). For example, in three rivers in the southern U.S., sites without mussels were nitrogen-limited with approximately 26% higher relative abundance of N-fixing bluegreen algae, while sites with high mussel densities were co-limited (N and P) and dominated by diatoms (Atkinson et al., 2013b). Mussel roles in water column nutrient dynamics are described more thoroughly in Atkinson & Vaughn (2015), Vaughn & Hakenkamp (2001), and Vaughn et al. (2008).

We understand mussel roles in water column nutrient dynamics much better than we understand their role in sediment nutrient dynamics. Mussels couple the water column and sediment compartments by removing particulate materials from the water column and depositing them to the sediment as feces and pseudofeces (Figs. 1, 2). Mussel biodeposition rates can be quite high. Strayer (2014) has estimated that rates of unionid biodeposition, averaged over an entire lake or river, may be as high as 1–300 mg C m^{-2} day^{-1}, 0.1–30 mg N m^{-2} day^{-1}, and 0.03–100 mg P m^{-2} day^{-1}. However, amounts are likely to be quite variable and we know little about the overall chemical composition of biodeposits. Most biodeposits are likely to be initially concentrated around mussel aggregations (Fig. 2), but then are dispersed downstream depending on sediment and hydrologic conditions. Thus, biodeposits likely represent an important nutrient translocation flux from mussel beds to other stream areas (Strayer, 2014). However, we have a poor understanding of the role and importance of these biodeposits in nutrient dynamics and food web support, and much more research is needed in this area.

Mussel effects on nutrient dynamics are highly context-dependent. First, as with biofiltration, mussels have species-specific, temperature-dependent excretion rates. These differences mean that species composition of mussel assemblages can have large effects on nutrient recycling and storage rates at the scale of river reaches and even entire rivers (Vaughn, 2010; Atkinson et al., 2013b; Atkinson & Vaughn, 2015). Secondly, also like biofiltration, mussel effects are much stronger at baseflow than under high discharge conditions (Atkinson & Vaughn, 2015). Finally, Strayer (2014) suggested that mussels should have

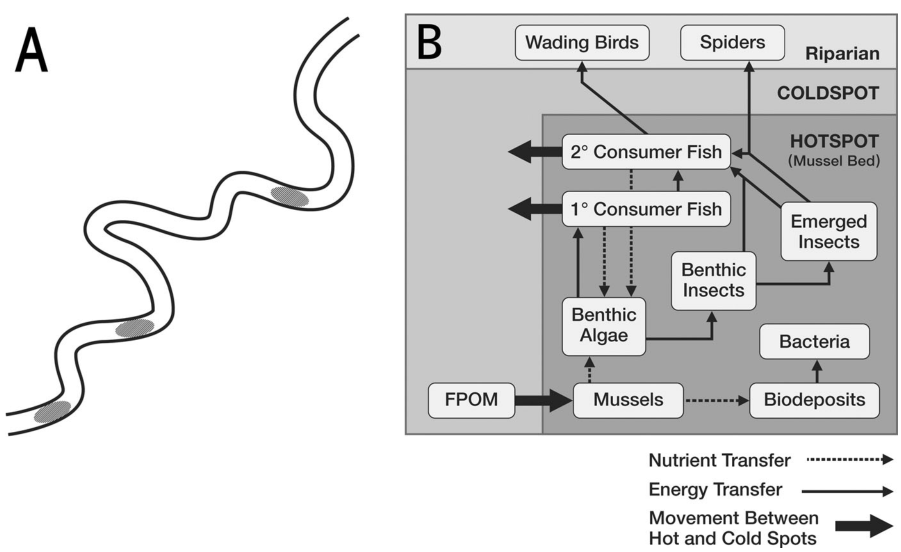

Fig. 2 **A** Schematic showing that mussel beds are patchily distributed in rivers, separated by areas with no mussels or low mussel abundance. In many rivers, mussel beds will be further apart than shown here. **B** Potential fluxes in and out of mussel beds (hotspots of biological activity) and other river areas (coldspots)

much stronger effects in more "pristine" systems, where nutrients are limiting, and this does indeed seem to be the case. In the relatively undeveloped, nitrogen-limited rivers of southeastern Oklahoma, U.S., mussels alleviate nitrogen limitation, shorten nutrient spirals, and mussel-derived nutrients can account for up to 40% of nutrient demand (Atkinson et al., 2013b, 2014c). Spooner et al. (2013) examined how nutrients from mussels affected algae and macroinvertebrates across 14 streams in Ontario that varied in background nutrient loads. In more pristine areas, mussels had strong effects, increasing algal and macroinvertebrate biodiversity. In areas with high nutrient loads, these effects were diminished or lost. In an experiment with *Corbicula*, Turek & Hoellein (2015) found that these bivalves increased ammonium flux more than N_2 production under low nutrient conditions. Under high nutrient loads, bivalves significantly increase both ammonium and N_2 flux out of the sediments, either through increased nitrification–denitrification or enhanced exchange of nutrients between the water column and sediments via bioturbation.

Mussels accumulate nutrients in both their soft tissue and shell as they grow. These nutrients are then released as reproductive products (sperm, larvae, and structures that support larvae), via excretion as the result of protein breakdown (catabolism) under stress, via soft tissue decomposition at death, and through long-term shell dissolution (Strayer, 2014). As described above, mussels have different temperature tolerances that affect physiological rates. Thermally sensitive species will catabolize their tissue under high temperatures, leading to higher excretion rates and increased nutrient cycling (Spooner & Vaughn, 2008). Nutrients stored in mussel soft tissue are released at death through decomposition. If mussel deaths occur at a regular interval throughout the year, nutrient release from tissue breakdown may be offset by nutrient uptake by growing animals ("capacitance," Strayer, 2014). However, mussels are long-lived, and in many cases deaths are synchronous and catastrophic (Haag, 2012). In these cases, mussel death can result in very large nutrient pulses into the ecosystem (Sousa et al., 2012; Bódis et al., 2014; McDowell et al., 2016). Mussels also store significant amounts of nutrients in their shells (Atkinson et al., 2014b; Vaughn et al., 2015), which are released slowly into the ecosystem as shells dissolve (Strayer & Malcom, 2007). These stored nutrients can have important and long-term effects on both aquatic and terrestrial systems. For example, recent work has shown that marine shell middens created by Canadian First Native groups in British Columbia act like a "slow release" fertilizer, increasing calcium and phosphorus in the soil, decreasing soil acidity, and leading to increased forest growth (Trant et al., 2016), and there is no reason to expect that this might not also occur in freshwater mussels. However, whether mussels serve as a short-term nutrient capacitors or longer-term nutrient sinks, these nutrients are retained in the ecosystem and incorporated into food webs rather than being transported downstream (Fig. 2) (Atkinson et al., 2014c). Although nutrients retained in this manner in one river may seem insignificant, summed across multiple watersheds this biological nutrient retention could help mitigate the effects of nutrient pollution (FMCS, 2016).

Mussels should have strong effects on coupled nitrification–denitrification by biodepositing organic material, thus increasing rates of both processes and by bioturbating sediments as they move. Denitrification is a particularly important ecosystem service, because it converts organic nitrogen to molecular nitrogen, moving it back into the atmosphere in an inorganic form. Marine bivalves, freshwater zebra mussels, and *Corbicula* have all been shown to increase denitrification, depending on the environmental conditions (Bruesewitz et al., 2009; Hoellein & Zarnoch, 2014; Turek & Hoellein, 2015). The effects of dense mussel assemblages on denitrification are an overlooked and potentially significant component of nitrogen removal from aquatic systems (Turek & Hoellein, 2015).

Supporting services: mussels as habitat and habitat modifiers

On a global basis, mollusks add physical structure to the environment via their shells, resulting in biogenic habitat such as oyster reefs (Gutierrez et al., 2003). Freshwater mussel shells provide habitat for other organisms as well as play a role in biogeochemical cycling (Strayer & Malcom, 2007). Rates of shell production and decay depend on the amount of accumulated spent shell material, but can exceed

(>10 kg dry mass m^{-2}) (Strayer & Malcom, 2007; Ilarri et al., 2015a, b).

Aggregations of mussels can support more abundant and diverse macroinvertebrate communities than similar habitat without mussels (Beckett et al., 1996; Howard & Cuffey, 2006; Vaughn & Spooner, 2006; Aldridge et al., 2007). Shells themselves provide habitat in otherwise soft sediments, and crevices on shells provide protection from flow and predation. Live mussels support different communities on their shells than dead mussels or stones (Spooner & Vaughn, 2006; Vaughn et al., 2008; Bódis et al., 2014; Ilarri et al., 2015a, b). Algae grow on mussel shells, which attract grazing invertebrates (Francoeur et al., 2002; Allen et al., 2012; Spooner et al., 2012) and cascade up the food web. This phenomenon is described more thoroughly in the section below on mussels' roles in food webs.

Mussels tend to occur in areas that are more stable under high flows (Strayer, 1999; Gangloff & Feminella, 2007; Zigler et al., 2008; Allen & Vaughn, 2010). Strayer (1999) characterized river reaches with abundant mussels as areas that are protected from severe disturbance by floods with return periods of three to 30 years, and suggested that the patchiness of flow refugia in space therefore causes the patchiness of mussel beds in rivers. Do mussels simply proliferate in these areas or do mussels function as ecological engineers that actively modify sediments to make them more stable, such as been found for other animals such as salmon and caddisflies (Moore, 2006)? It has long been suggested that freshwater mussels stabilize sediment, decreasing downstream transport of labile sediments, and making sediments more favorable for other organisms. Yet, there are not good quantitative data demonstrating this phenomenon. In a mesocosm study, Zimmerman and de Szalay (2007) found that sessile mussels increased sediment cohesion and thus sediment stability, but burrowing activities increased erosion and destabilized sediments. However, Allen & Vaughn (2011), in a flume study, found that increasing mussel species richness increased sediment erosion at both low and high mussel densities. It is possible that observations of mussel–sediment interactions in small mesocosm and flume studies may not scale up well to large, dense mussel beds. We need much more research on this topic, particularly at the scale of whole mussel beds and river reaches (Allen et al., 2014).

Supporting services: mussels support food webs

Mussels play important roles in food webs through the bottom-up provisioning of nutrients and energy. In rivers, mussels often occur as aggregations called mussel beds that can be very dense (up to 100 ind m^{-2}) and speciose (10–20 sp.) (Atkinson & Vaughn, 2015). Mussel beds are patchily distributed in streams because they are constrained to stable sediments with low shear stresses (as described above), and mussels recover very slowly from disturbance (Haag, 2012). Thus, mussel beds in streams are usually separated by long reaches where mussels either do not occur or occur in low abundance (Atkinson & Vaughn, 2015; Newton et al., 2011; Fig. 2A). These beds can be hotspots of biological activity that support the rest of the food web by providing habitat, as described above, and through the bottom-up provisioning of nutrients (Fig. 2B). Nutrients excreted and biodeposited by mussels lead to increases in benthic algae (Spooner & Vaughn, 2006, 2012; Vaughn et al., 2007) and subsequently macroinvertebrates (Vaughn & Spooner, 2006; Spooner et al., 2012). In separate laboratory (Allen et al., 2012; Sansom, 2013) and field (Atkinson et al., 2014c) experiments, seston was labeled with a heavy nitrogen isotope (^{15}N), fed to mussels, and then nitrogen derived from mussel excreta was tracked throughout the food web. Mussel-derived nitrogen was found in most food web compartments including benthic algae, benthic macroinvertebrates, macrophytes, and primary consumer fish. Atkinson et al. (2014c) found that mussel excretion could account for 40% of the nitrogen in a nutrient-limited river reach and that mussels supplied up to 19% of the nitrogen in specific food web compartments. Allen et al. (2012) found that once the grazing insect larvae metamorphose into winged adults, this nitrogen moves into the riparian, terrestrial food web as the insects are consumed by spiders. In a different study, Novais et al. (2015) found that die offs of *Corbicula* provided carrion to adjacent terrestrial systems and entered the detrital food web. Thus, mussels are subsidizing both aquatic and terrestrial food webs and linking aquatic and terrestrial ecosystems

Supporting services: mussels as environmental monitors

Freshwater mussels have the potential to serve as important sentinels or biomonitors of environmental change, revealing past conditions and monitoring future change. Because they are sessile filter feeders, they bioaccumulate particles, allowing measurement of stressor levels in their soft tissues. They are widespread, often occur at high densities and are relatively long-lived, allowing repeated sampling over time (Green et al., 1985; Rocha et al., 2015). Finally, geochemistry of shells can reveal past physical and chemical conditions, over both large spatial and temporal scales (Brown et al., 2005).

Shells incorporate and retain patterns of the chemical and physical environment long after the animal's death, and thus can act as historical archives to reveal long-term environmental change. First, simple patterns of aragonite deposition, revealed as growth lines in the shell similar to tree rings, can reflect past temperature, flow, and other conditions under which mussels grew (Schone et al., 2004; Dunca et al., 2005; Geist et al., 2005; Rypel et al., 2009; Black et al., 2010; Fritts et al., 2017). Trace metals incorporated into shell tissue can be used to uncover past pollution events (Jamil et al., 1999; Brown et al., 2005) and upwelling periods (Langlet et al., 2007). Isotopic signatures of O_{18} and C_{13} in mussels have been used to reveal climatic conditions as far back as the Miocene (Blazejowski et al., 2013).

Mussel soft tissue can be used to assess environmental conditions over shorter time scales. Chemical content in mussel hemolymph, mantle, and/or foot tissue can be used as sublethal biomarkers to monitor water quality, by stress or immune responses (Newton & Cope, 2007; Fritts et al., 2015; Goodchild et al., 2015; Jasinska et al., 2015; Kolarevic et al., 2016). Pharmaceuticals bioaccumulate in mussels at higher levels than many other aquatic organisms including fish (Du et al., 2014). Nitrogen signatures in mussel soft tissue reflect background nutrient conditions (Wen et al., 2010), in particular residential and agricultural land use (McKinney et al., 2002), and net nitrogen loading could be used as a bioassessment tool for tracking agricultural nitrogen sources (Atkinson et al., 2014a). Finally, the stable isotope composition of the periostracum on the outside of the shell can also be used to track environmental change and understand historical food web conditions (Delong & Thorp, 2009; Fritts et al., 2017).

Mussels have become an important indicator organism in ecotoxicology studies (Cope et al., 2008). Juvenile mussels are particularly useful because they are endobenthic and important for examining groundwater toxicity, and a great deal of recent work has gone into establishing water quality criteria using juveniles (Augspurger et al., 2007; Wang et al., 2007). Juvenile mussels are more sensitive to ammonium than any other freshwater organism studied to date (Newton & Bartsch, 2007), and this sensitivity resulted in the U.S. Environmental Protection Agency revising the water quality criteria for ammonia (FMCS, 2016). Finally, mussels are becoming a viable option to detect "real time" changes in water quality by monitoring physiological responses such as gape (shell opening and closing), variations in heart rate, and changes in filtration and behavior (Hauser, 2015; Goodchild et al., 2016; Hartmann et al., 2016).

Provisioning and cultural services

Mussels are prey for other organisms such as muskrats (Tyrell & Hornbach, 1998) and turtles (Atkinson, 2013). Prehistoric humans ate mussels and used their shells as ornaments, tools, and utensils. In the U.S., archeological data indicate that Native Americans harvested mussels for food as long as 10,000 years ago (Haag, 2012). Most present-day western cultures do not utilize mussels as food, although they are considered a Native American traditional ("first food") by tribes in the Pacific Northwest (Brubaker et al., 2009) and mussel harvest is a reserved treaty harvest right for some Native American tribes (Brim Box et al., 2006). Mussels and *Corbicula* are commonly eaten in many southeast Asian regions (Bolotov et al., 2014), and recent work documents their overexploitation there (Ziertitz et al., 2016, 2017).

Native Americans in the southeastern U.S. used mussel shells for wood working, as digging tools, and ground them to powder to temper pottery (Rafferty & Peacock, 2008). Extensive harvest of mussels for freshwater pearls and for the pearl button industry began in the 1850s (Humphries & Winemiller, 2009). During the peak button harvest year of 1912, 50,000 tons of mussels were removed from North American rivers (Haag, 2012). A second wave of mussel harvest occurred following World War II and up until the mid 1990s. In this case, beads made of heavy pieces of shell were used as seeds for the Japanese cultured pearl industry (Haag, 2012). Freshwater pearl farming is still a large industry in China (Jiale & Yingsen, 2009).

Mussels played an important role in early Native American and white culture. Beads and other ornaments made from shells played a significant role in Native American rituals and ceremonies (Claassen, 2008). Some tribes, such as the Choctaw Nation in Oklahoma, have active programs to revive these cultural traditions (Choctaw Nation, 2016). In areas where mussels were historically very abundant, they invoked as "sense of place" that was translated into names of creeks and even as ornaments on graves (Haag, 2012). Historic and current human exploitation and cultural use of North American mussels are thoroughly reviewed by Haag (2012).

Losses, restoration and valuation

Freshwater mussels are one of the most imperiled groups of organisms globally (Lydeard et al., 2004; Lopes-Lima et al., 2014). Approximately 30 North American taxa have become extinct over the past century, and 65% of the remaining 300 North American species are considered vulnerable to extinction (Haag & Williams, 2014). Ricciardi & Rasmussen (1999) predict that we will lose as many of 50% of the remaining species in the next century. In addition, mussel declines include not only species losses but also large declines in the abundance and biomass of once common species (Haag & Williams, 2014). These losses of common species are undoubtedly leading to large losses in mussel-provided ecosystem services.

The Kiamichi River in southeastern Oklahoma, U.S., provides a case study of the link between mussel losses and declines in ecosystem services. My students and I sampled mussel communities in this river over a 20-year period where drought-induced changes in flows and poor water management from a tributary reservoir led to large declines in mussel biomass (Galbraith et al., 2010; Allen et al., 2013; Atkinson et al., 2014b). We used laboratory derived physiological rates and river-wide estimates of species-specific mussel biomass to estimate ecosystem services provided by mussels. We found that biofiltration, nitrogen and phosphorus cycling, and nitrogen, phosphorus and carbon storage provided by mussels declined almost 60% over this time period (Vaughn et al., 2015).

Although the importance of mussel-provided ecosystem services is increasingly recognized, there have been few attempts to determine how the loss of these services may affect freshwater ecosystems, and the subsequent social, cultural, and economic benefits for humans FMCS, 2016; Castro et al., 2016b). The value of most mussel-provided ecosystem services cannot be assessed with a traditional marketplace framework, rather we need to encompass non-market and modeling methods (Southwick & Loftus, 2003; Ruffo & Kareiva, 2009; Castro et al., 2016a). Valuation studies of oysters and other marine bivalves can guide these efforts. For example, while oysters are a fishery commodity, they also provide a host of non-market ecosystem services such as biogenic habitat, biofiltration, and nutrient removal (Grabowski et al., 2012). The value of these non-market services can be assessed using the value of engineered structures for water filtration, wastewater treatment costs, replacement costs for sewage treatment plants, and nutrient credit programs (Beck et al., 2011; Grabowski et al., 2012). Along these lines, the American Fisheries Society has produced guidelines for assessing monetary damage from mussel kills that include ecological, use and non-use values, plus restoration costs (Southwick & Loftus, 2003). Because information to accurately estimate non-economic value is rarely available, they recommend using replacement costs as a conservative method for determining restitution for killed mussels.

Valuation of ecosystem services must also consider the social demand for ecosystem services, which can be assessed with metrics such as social perceptions or willingness to pay for services such as biofiltration producing clean water. For example, Castro et al. (2016a, b) used face-to-face surveys to assess multiple stakeholders' social perceptions and willingness to pay for ecosystem services in the Kiamichi watershed. These surveys included showing stakeholders photographs of mussel and fish species and the ecosystem services that they provide. This study found that most stakeholders identified habitat for species and water quality as the most important and economically valuable ecosystem services. Regulating services received the highest willingness to pay value. The study also identified potential conflicts between water user groups depending on whether they lived in the watershed or were distant water users (Castro et al., 2016a, b).

Technology for propagating freshwater mussels has improved greatly over the past 20 years. In the U.S., there are now over a dozen federal and state facilities dedicated mussel to propagation, usually related to restoring listed species (FMCS, 2016). Such facilities could also be used for the large-scale production of common mussel species, which could then be restored to rivers to re-establish lost ecosystem services such as biofiltration and nutrient abatement.

Haag & Williams (2014) suggest that a conservation goal should be to protect mussels for the benefit of stream ecosystems, rather than vice versa. To accomplish this, we need much more quantification of the value and magnitude of ecosystem services provided by mussels, across species, habitats, and environmental conditions, and scaled up to whole watersheds. We need tools that will allow us to value mussel ecosystem services in a way that is understandable to both the public and to policy makers. Achieving this will require collaboration with social scientists, economists, and stakeholders. Sustaining and restoring mussel ecosystem services represent a transdisciplinary challenge, but the benefits will likely far exceed the capital invested in this effort.

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References

Aldridge, D. C., T. M. Fayle & N. Jackson, 2007. Freshwater mussel abundance predicts biodiversity in UK lowland rivers. Aquatic Conservation-Marine and Freshwater Ecosystems 17: 554–564.

Allen, D. C. & C. C. Vaughn, 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. Journal of the North American Benthological Society 29: 383–394.

Allen, D. C. & C. C. Vaughn, 2011. Density-dependent biodiversity effects on physical habitat modification by freshwater bivalves. Ecology 92: 1013–1019.

Allen, D. C., C. C. Vaughn, J. F. Kelly, J. R. Cooper & M. H. Engel, 2012. Bottom-up biodiversity effects increase resource subsidy flux between ecosystems. Ecology 93: 2165–2174.

Allen, D. C., H. S. Galbraith, C. C. Vaughn & D. E. Spooner, 2013. A tale of two rivers: implications of water management practices for mussel biodiversity outcomes during droughts. Ambio 42: 881–891.

Allen, D. C., B. J. Cardinale & T. Wynn-Thompson, 2014. Toward a better integration of ecological principlesinto ecogeoscience research. BioScience 64: 444–454.

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. & 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, 2013a. Native mussels alter nutrient availability and reduce blue-green algae abundance. EPA Science Brief EPA/600/F13/231

Atkinson, C. L., C. C. Vaughn, K. J. Forshay & J. T. Cooper, 2013b. Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. Ecology 94: 1359–1369.

Atkinson, C. L., A. D. Christian, D. E. Spooner & C. C. Vaughn, 2014a. Long-lived organisms provide an integrative footprint of agricultural land use. Ecological Applications 24: 375–384.

Atkinson, C. L., J. P. Julian & C. C. Vaughn, 2014b. Species and function lost: role of drought in structuring stream communities. Biological Conservation 176: 30–38.

Atkinson, C. L., J. F. Kelly & C. C. Vaughn, 2014c. Tracing consumer-derived nitrogen in riverine food webs. Ecosystems 17: 485–496.

Augspurger, T., F. J. Dwyer, C. G. Ingersoll & C. M. Kane, 2007. Advances and opportunities in assessing contaminant sensitivity of freshwater mussel (Unionidae) early life stages. Environmental Toxicology and Chemistry 26: 2025–2028.

Beck, M. W., R. D. Brumbaugh, L. Airoldi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, G. J. Edgar, B. Hancock, M. C. Kay, H. S. Lenihan, M. W. Luckenbach, C. L. Toropova, G. Zhang & X. Guo, 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61: 107–116.

Beckett, D. C., B. W. Green & S. A. Thomas, 1996. Epizoic invertebrate communities on upper Mississippi River unionid bivalves. American Midland Naturalist 135: 102–114.

Black, B. A., J. B. Dunham, B. W. Blundon, M. F. Raggon & D. Zima, 2010. Spatial variability in growth-increment chronologies of long-lived freshwater mussels: Implications for climate impacts and reconstructions. Ecoscience 17: 240–250.

Blazejowski, B., G. Racki, P. Gieszcz, K. Malkowski, A. Kin & K. Krzywiecka, 2013. Comparative oxygen and carbon isotopic records of miocene and recent lacustrine unionid bivalves from Poland. Geological Quarterly 57: 113–122.

Bodis, E., B. Toth & R. Sousa, 2014. Massive mortality of invasive bivalves as a potential resource subsidy for the adjacent terrestrial food web. Hydrobiologia 735: 253–262.

Bolotov, I., I. Vikhrev, Y. Bespalaya, V. Artamonova, M. Gofarov, J. Kolosova, A. Kondakov, A. Makhrov Frolov, S. Tumpeesuwan, A. Lyubas, T. Romanis & K. Titova, 2014. Ecology and conservation of the Indochinese freshwater pearl mussel, *Margaritifera laosensis* (Lea, 18634) in the Nam Pe and Nam Long rivers, Northern Laos. Tropical Conservation Science 4: 706–719.

Brauman, K. A., G. C. Daily, T. K. Duarte & 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 & 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 & D. Close, 2006. Freshwater mussels (Bivalvia: Unionoida) of the Umatilla and Middle Fork John Day rivers in eastern Oregon. Northwest Science 80: 95–107.

Brown, M. E., M. Kowalewski, R. J. Neves, D. S. Cherry & M. E. Schreiber, 2005. Freshwater mussel shells as environmental chronicles: geochemical and taphonomic signatures of mercury-related extirpations in the North Fork Holston River, Virginia. Environmental Science & Technology 39: 1455–1462.

Brubaker, M., J. Bell & A. Rollin, 2009. Climate Change Effects on Traditional Inupiaq Food Cellars. Center for Climate and Health Alaska Native Health Consortium, CCH Bulletin No: 1.

Bruesewitz, D. A., J. L. Tank & S. K. Hamilton, 2009. Seasonal effects of zebra mussels on littoral nitrogen transformation rates in Gull Lake, Michigan, USA. Freshwater Biology 54: 1427–1443.

Castro, A. J., C. C. Vaughn, M. Garcia-Llorente, J. P. Julian & C. L. Atkinson, 2016a. Willingness to pay for ecosystem services among stakeholder groups in a south-central US watershed with regional conflict. Journal of Water Resources Planning and Management 142: 05016006.

Castro, A. J., C. C. Vaughn, J. P. Julian & M. Garcia-Llorente, 2016b. Social demand for ecosystem services and implications for watershed management. Journal of the American Water Resources Association 52: 209–221.

Choctaw Nation., 2016. http://www.choctawschool.com/home-side-menu/iti-fabvssa/traditional-uses-of-freshwater-mussels.asp

Chowdhury, G. W., A. Zieritz & 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.

Christian, A. D., B. N. Smith, D. J. Berg, J. C. Smoot & R. H. Findley, 2004. Trophic position and potential food sources of 2 species of unionid bivalves (Mollusca: Unionidae) in 2 small Ohio streams. Journal of North American Benthological Society 23: 101–113.

Claassen, C., 2008. Shell symbolisms in pre-Columbian North America. In Antczak, A. & R. Cipriani (eds), Early Human Impacts on Megamolluscs. International Series 1865. British Archeological Reports, 232–236

Cope, W. G., R. B. Bringolf, D. B. Buchwalter, T. J. Newton, C. G. Ingersoll, N. Wang, T. Augspurger, F. J. Dwyer, M. C. Barnhart, R. J. Neves & E. Hammer, 2008. Differential exposure, duration, and sensitivity of unionoidean bivalve life stages to environmental contaminants. Journal of the North American Benthological Society 27: 451–462.

Daily, G. C., S. Alexander, P. R. Ehrlich, L. Goulder, J. Lubchenco, P. A. Matson, H. A. Mooney, S. Postel, S. H. Schneider, D. Tilman & G. M. Woodwell, 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. Issues in Ecology 2: 1–16.

Delong, M. D. & J. H. Thorp, 2009. Mollusc shell periostracum as an alternative to tissue in isotopic studies. Limnology and Oceanography-Methods 7: 436–441.

Dodds, W. K., J. S. Perkin & J. E. Gerken, 2013. Human impact on freshwater ecosystem services: a global perspective. Environmental Science & Technology 47: 9061–9068.

Du, B., S. P. Haddad, A. Luek, W. C. Scott, G. N. Saari, L. A. Kristofco, K. A. Connors, C. Rash, J. B. Rasmussen, C. K. Chambliss & B. W. Brooks, 2014. Bioaccumulation and trophic dilution of human pharmaceuticals across trophic positions of an effluent-dependent wadeable stream. Philosophical Transactions of the Royal Society B-Biological Sciences 369: 20140058.

Dunca, E., B. R. Schone & H. Mutvei, 2005. Freshwater bivalves tell of past climates: but how clearly do shells from polluted rivers speak. Palaeogeography Palaeoclimatology Palaeoecology 228: 43–57.

Faust, C., D. Stallknecht, D. Swayne & J. Brown, 2009. Filter-feeding bivalves can remove avian influenza viruses from water and reduce infectivity. Proceedings of the Royal Society B-Biological Sciences 276: 3727–3735.

Francoeur, S. N., A. Pinowska, T. A. Clason, S. Makosky & R. L. Lowe, 2002. Unionid bivalve influence on benthic algal community composition in a Michigan Lake. Journal of Freshwater Ecology 17: 489–500.

Freshwater Mollusk Conservation Society, 2016. A national strategy for the conservation of native freshwater mollusks. Freshwater Mollusk Biology and Conservation 19: 1–21.

Fritts, A. K., J. T. Peterson, P. D. Hazelton & R. B. Bringolf, 2015. Evaluation of methods for assessing physiological biomarkers of stress in freshwater mussels. Canadian Journal of Fisheries and Aquatic Sciences 72: 1450–1459.

Fritts, A. K., M. W. Fritts, W. R. Haag, J. A. DeBower & A. F. Casper, 2017. Freshwater mussel shells (Unionidae) chronicle changes in a North American river over the past 1000 years. Science of the Total Environment 575: 199–206.

Galbraith, H. S., D. E. Spooner & C. C. Vaughn, 2010. Synergistic effects of regional climate patterns and local water management on freshwater mussel communities. Biological Conservation 143: 1175–1183.

Gangloff, M. M. & J. W. Feminella, 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, USA. Freshwater Biology 52: 64–74.

Geist, J., K. Auerswald & A. Boom, 2005. Stable carbon isotopes in freshwater mussel shells: environmental record or

marker for metabolic activity? Geochimica Et Cosmochimica Acta 69: 3545–3554.
Goodchild, C. G., M. Frederich & S. I. Zeeman, 2015. AMP-activated protein kinase is a biomarker of energetic status in freshwater mussels exposed to municipal effluents. Science of the Total Environment 512: 201–209.
Goodchild, C. G., M. Frederich & S. I. Zeeman, 2016. Is altered behavior linked to cellular energy regulation in a freshwater mussel (*Elliptio complanata*) exposed to triclosan? Comparative Biochemistry and Physiology C-Toxicology & Pharmacology 179: 150–157.
Grabowski, J. H., R. D. Brumbaugh, R. F. Conrad, A. G. Keeler, J. J. Opaluch, C. H. Peterson, M. F. Piehler, S. P. Powers & A. R. Smyth, 2012. Economic valuation of ecosystem services provided by oyster reefs. Bioscience 62: 900–909.
Green, R. H., S. M. Singh & R. C. Bailey, 1985. Bivalve molluscs as response systems for modeling spatial and temporal environmental patterns. The Science of the Total Environment 46: 147–169.
Gutierrez, J. L., C. G. Jones, D. L. Strayer & O. O. Iribane, 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, Cambridge.
Haag, W. R. & J. D. Williams, 2014. Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. Hydrobiologia 735: 45–60.
Hartmann, J. T., S. Beggel, K. Auerswald, B. C. Stoeckle & J. Geist, 2016. Establishing mussel behavior as a biomarker in ecotoxicology. Aquatic Toxicology 170: 279–288.
Hauser, L. W., 2015. Predicting episodic ammonium excretion by freshwater mussels via gape response and heart rate. PhD dissertation, University of Iowa.
Hoellein, T. J. & C. B. Zarnoch, 2014. Effect of eastern oysters (*Crassostrea virginica*) on sediment carbon and nitrogen dynamics in an urban estuary. Ecological Applications 24: 271–286.
Howard, J. K. & K. M. Cuffey, 2006. The functional role of native freshwater mussels in the fluvial benthic environment. Freshwater Biology 51: 460–474.
Humphries, P. & K. O. Winemiller, 2009. Historical impacts on river fauna, shifting baselines, and challenges for restoration. Bioscience 59: 673–684.
Ilarri, M. I., A. T. Souza, V. Modesto, L. Guilhermino & R. Sousa, 2015a. Differences in the macrozoobenthic fauna colonising empty bivalve shells before and after invasion by *Corbicula fluminea*. Marine and Freshwater Research 66: 549–558.
Ilarri, M. I., A. T. Souza & R. Souza, 2015b. Contrasting decay rates of freshwater bivalves' shells: aquatic versus terrestrial habitats. Limnologica 51: 8–14.
Ismail, N. S., C. E. Muller, R. R. Morgan & R. G. Luthy, 2014. Uptake of contaminants of emerging concern by the bivalves *Anodonta californiensis* and *Corbicula fluminea*. Environmental Science & Technology 48: 9211–9219.
Ismail, N. S., H. Dodd, L. M. Sassoubre, A. J. Horne, A. B. Boehm & 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 & Technology 49: 1664–1672.
Izumi, T., K. Yagiti, S. Izumiyami, T. Endo & Y. Ituh, 2012. Depletion of *Cryptosporidium parvaum* oocysts from contaminated sewage using freshwater benthic pearl clams (*Hyriopsis schlegeli*). Applied and Environmental Microbiology 78: 7420–7428.
Jamil, A., K. Lajtha, S. Radan, G. Ruzsa, S. Cristofor & C. Postolache, 1999. Mussels as bioindicators of trace metal pollution in the Danube Delta of Romania. Hydrobiologia 392: 143–158.
Jasinska, E. J., G. G. Goss, P. L. Gillis, G. J. Van Der Kraak, J. Matsumoto, A. A. D. Machado, M. Giacomin, T. W. Moon, A. Massarsky, F. Gagne, M. R. Servos, J. Wilson, T. Sultana & C. D. Metcalfe, 2015. Assessment of biomarkers for contaminants of emerging concern on aquatic organisms downstream of a municipal wastewater discharge. Science of the Total Environment 530: 140–153.
Jiale, L. & L. Yingsen, 2009. http://agris.fao.org/agrisearch/search.do?recordID=US201301612025.
Kolarevic, S., M. Kracun-Kolarevic, J. Kostic, J. Slobodnik, I. Liska, Z. Gacic, M. Paunovic, J. Knezevic-Vukcevic & B. Vukovic-Gacic, 2016. Assessment of the genotoxic potential along the Danube River by application of the comet assay on haemocytes of freshwater mussels: the joint Danube Survey 3. Science of the Total Environment 540: 377–385.
Langlet, D., L. Y. Alleman, P. D. Plisnier, H. Hughes & L. Andre, 2007. Manganese content records seasonal upwelling in Lake Tanganyika mussels. Biogeosciences 4: 195–203.
Li, X. N., H. L. Song, W. Li, X. W. Lu & O. Nishimura, 2010. An integrated ecological floating-bed employing plant, freshwater clam and biofilm carrier for purification of eutrophic water. Ecological Engineering 36: 382–390.
Lopes-Lima, M., A. Teixeira, E. Froufe, A. Lopes, S. Varandas & R. Sousa, 2014. Biology and conservation of freshwater bivalves: past, present and future perspectives. Hydrobiologia 735: 1–13.
Lorenz, S., F. Gabel, N. Dobra & M. T. Pusch, 2013. Modelling the effects of recreational boating on self-purification activity provided by bivalve mollusks in a lowland river. Freshwater Science 32: 82–93.
Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Hershler, K. E. Perez, B. Roth, M. Seddon, E. E. Strong & F. G. Thompson, 2004. The global decline of nonmarine mollusks. Bioscience 54: 321–330.
McDowell, W. G., W. H. McDowell & J. E. Byers, 2016. Mass mortality of a dominant invasive species in response to an extreme climate event: implications for ecosystem function. Limnology and Oceanography. doi:10.1002/lno.10384.
McKinney, R. A., J. L. Lake, M. A. Charpentier & S. Ryba, 2002. Using mussel isotope ratios to assess anthropogenic nitrogen inputs to freshwater ecosystems. Environmental Monitoring and Assessment 74: 167–192.
Moore, J. W., 2006. Animal ecosystem engineers in streams. Bioscience 56: 237–246.
Newton, T. J. & M. R. Bartsch, 2007. Lethal and sublethal effects of ammonia to juvenile *Lampsilis mussels* (Unionidae) in sediment and water-only exposures. Environmental Toxicology and Chemistry 26: 2057–2065.

Newton, T. J. & W. G. Cope, 2007. Biomarker responses of unionid mussels to environmental contaminants. In Farris, J. L. & J. H. Van Hassel (eds.), Freshwater Bivalve Ecotoxicology. CRC Press, Boca Raton: 257–284.

Newton, T. J., S. J. Zigler, J. T. Rogala, B. R. Gray & 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.

Newton, T. J., C. C. Vaughn, D. E. Spooner & M. Arts, 2013. Profiles of biochemical tracers in unionid mussels across a broad geographic range. Journal of Shellfish Research 32: 497–507.

Novais, A., A. T. Souza, M. Ilarri, C. Pascoal & R. Sousa, 2015. From water to land: how an invasive clam may function as a resource pulse to terrestrial invertebrates. Science of the Total Environment 538: 664–671.

Othman, F., M. S. Islam, E. N. Sharifah, F. Shahrom-Harrison & A. Hassan, 2015. Biological control of streptococcal infection in Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) using filter-feeding bivalve mussel *Pilsbryoconcha exilis* (Lea, 1838). Journal of Applied Ichthyology 31: 724–728.

Pigneur, L. M., E. Falisse, K. Roland, E. Everbecq, J. F. Deliege, J. S. Smitz, K. van Doninck & J. P. Descy, 2014. Impact of invasive Asian clams, *Corbicula* spp., on a large river ecosystem. Freshwater Biology 59: 573–583.

Rafferty, J. & E. Peacock, 2008. The spread of shell tempering in the Mississippi Black Prairie. Southeastern Archeology 27: 253–264.

Raikow, D. F. & S. K. Hamilton, 2001. Bivalve diets in a midwestern U.S. stream: a stable isotope enrichment study. Limnology and Oceanography 46: 513–522.

Ricciardi, A. & J. B. Rasmussen, 1999. Extinction rates of North American freshwater fauna. Conservation Biology 13: 1220–1222.

Rocha, T. L., T. Gomes, V. S. Sousa, N. C. Mestre & M. J. Bebianno, 2015. Ecotoxicological impact of engineered nanomaterials in bivalve molluscs: an overview. Marine Environmental Research 111: 74–88.

Ruffo, S. & P. M. Kareiva, 2009. Using science to assign value to nature. Frontiers in Ecology and the Environment 7: 3–3.

Rypel, A. L., W. R. Haag & R. H. Findlay, 2009. Pervasive hydrologic effects on freshwater mussels and riparian trees in southeastern floodplain ecosystems. Wetlands 29: 497–504.

Sansom, B., 2013. The influence of mussels on fish populations. MS thesis, Department of Biology, University of Oklahoma.

Schone, B. R., E. Dunca, H. Mutvei & U. Norlund, 2004. A 217-year record of summer air temperature reconstructed from freshwater pearl mussels (*M. margaritifera*, Sweden). Quaternary Science Reviews 23: 1803–1816.

Soto, D. & G. Mena, 1999. Filter-feeding by the freshwater mussel, *Diplodon chilensis*, as a biocontrol of salmon farming eutrophication. Aquaculture 171: 65–81.

Sousa, R., S. Varandas, R. Cortes, A. Teixeira, M. Lopes-Lima, J. Machado & L. Guilhermino, 2012. Massive die-offs of freshwater bivalves as resource pulses. Annales De Limnologie-International Journal of Limnology 48: 105–112.

Southwick, R. I. & A. J. Loftus (eds), 2003. Investigation and Monetary Values of Fish and Freshwater Mussel Kills. American Fisheries Society Special Publication No. 30. American Fisheries Society, Bethesda

Spooner, D. E. & C. C. Vaughn, 2006. Context-dependent effects of freshwater mussels on the benthic community. Freshwater Biology 51: 1016–1024.

Spooner, D. E. & C. C. Vaughn, 2008. A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. Oecologia 158: 307–317.

Spooner, D. E. & C. C. Vaughn, 2012. Species' traits and environmental gradients interact to govern primary production in freshwater mussel communities. Oikos 121: 403–416.

Spooner, D. E., C. C. Vaughn & H. S. Galbraith, 2012. Species traits and environmental conditions govern the relationship between biodiversity effects across trophic levels. Oecologia 168: 533–548.

Spooner, D. E., P. C. Frost, H. Hillebrand, M. T. Arts, O. Puckrin & M. A. Xenopoulos, 2013. Nutrient loading associated with agriculture land use dampens the importance of consumer-mediated niche construction. Ecology Letters 16: 1115–1125.

Strayer, D. L., 1999. Use of flow refuges by unionid mussels in rivers. Journal of the North American Benthological Society 18: 468–476.

Strayer, D. L., 2008. Freshwater Mussel Ecology: A Multifactor Approach to Distribution and Abundance. University of California Press, Berkeley.

Strayer, D. L., 2014. Understanding how nutrient cycles and freshwater mussels (Unionoida) affect one another. Hydrobiologia 735: 277–292.

Strayer, D. L. & H. M. Malcom, 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. Freshwater Biology 52: 1611–1617.

Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findley & M. L. Pace, 1999. Transformation of freshwater ecosystems by bivalves. BioScience 49: 19–27.

Thorp, J. H., M. D. Delong, K. S. Greenwood & A. F. Casper, 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia 117: 551–563.

Trant, A. J., W. Nijland, K. M. Hoffman, D. L. Mathews, D. McLaren, T. A. Nelson & B. M. Starzomski, 2016. Intertidal resource use over millennia enhances forest productivity. Nature Communications. doi:10.1038/ncomms12491.

Turek, K. A. & T. J. Hoellein, 2015. The invasive Asian clam (*Corbicula fluminea*) increases sediment denitrification and ammonium flux in 2 streams in the midwestern USA. Freshwater Science 34: 472–484.

Tyrell, M. & D. J. Hornbach, 1998. Selective predation by muskrats on freshwater mussels in two Minnesota rivers. Journal of the North American Benthological Society 17: 301–310.

Vanden Byllaardt, J. & J. D. Ackerman, 2014. Hydrodynamic habitat influences suspension feeding by unionid mussels in freshwater ecosystems. Freshwater Biology 59: 1187–1196.

Vaughn, C. C., 2010. Biodiversity losses and ecosystem function in freshwaters: emerging conclusions and research directions. BioScience 60: 25–35.

Vaughn, C. C. & C. C. Hakenkamp, 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshwater Biology 46: 1431–1446.

Vaughn, C. C. & 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., K. B. Gido & 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., D. E. Spooner & H. S. Galbraith, 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. Ecology 88: 1654–1662.

Vaughn, C. C., S. J. Nichols & D. E. Spooner, 2008. Community and foodweb ecology of freshwater mussels. Journal of the North American Benthological Society 27: 41–55.

Vaughn, C. C., C. L. Atkinson & J. P. Julian, 2015. Multiple droughts lead to long-term losses in mussel-provided ecosystem services. Ecology and Evolution 5: 1291–1305.

Wang, N., T. Augspurger, M. C. Barnhart, J. R. Bidwell, W. G. Cope, F. J. Dwyer, S. Geis, I. E. Greer, C. G. Ingersoll, C. M. Kane, T. W. May, R. J. Neves, T. J. Newton, A. D. Roberts & D. W. Whites, 2007. Intra- and interlaboratory variability in acute toxicity tests with glochidia and juveniles of freshwater mussels (Unionidae). Environmental Toxicology and Chemistry 26: 2029–2035.

Welker, M. & N. Walz, 1998. Can mussels control the plankton in rivers? A planktological approachapplying a Langrangian sampling strategy. Limnology and Oceanography 43: 753–762.

Wen, Z. R., P. Xie & J. Xu, 2010. Mussel isotope signature as indicator of nutrient pollution in a freshwater eutrophic lake: species, spatial, and seasonal variability. Environmental Monitoring and Assessment 163: 139–147.

Zieritz, A., M. Lopes-Lima, A. E. Bogan, R. Sousa, S. Walton, K. Rahim, J. J. Wilson, P. Y. Ng, E. Froufe & S. McGowan, 2016. Factors driving changes in freshwater mussel (Bivalvia, Unionida) diversity and distribution in Peninsular Malaysia. Science of the Total Environment 571: 1069–1078.

Zieritz, A., A. E. Bogan, O. Klishko, T. Kondo, U. Kovitvadhi, S. Kovitvadhi, J. H. Lee, M. Lopes-Lima, J. M. Pfeiffer, R. Sousa, D. V. Tu, I. Vikhrev, & D. T. Zanatta, 2017. Diversity, biogeography and conservation status of freshwater mussels (Bivalvia: Unionida) in East and Southeast Asia. *Hydrobiologia* (*in press*)

Zigler, S. J., T. J. Newton, J. J. Steuer, M. R. Bartsch & J. S. Sauer, 2008. Importance of physical and hydraulic characteristics to unionid mussels: a retrospective analysis in a reach of large river. Hydrobiologia 598: 343–360.

Zimmerman, G. F. & F. A. de Szalay, 2007. Influence of unionid mussels (Mollusca: Unionidae) on sediment stability: an artificial stream study. Fundamental and Applied Limnology 168: 299–306.