Clearing up cloudy waters: A review of sediment impacts to unionid freshwater mussels.

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Abstract:

Freshwater unionid mussels are among the most imperiled fauna in North America, and their decline has been partially attributed to sediment from anthropogenic activities. However, there remains a debate regarding the role played by sediment in mussel declines due to a lack of field and laboratory evidence. If sediment is responsible for mussel declines, then a lack of information will likely impede efforts to mitigate species declines and protect remaining habitat. However, if the impacts of sediment are overstated, time and resources may be wasted on a threat that has little bearing on mussel declines or habitat loss. Given this knowledge gap, the purpose of this paper is to review the literature focused on the potential impact of suspended sediment and sedimentation on freshwater mussels. We focused our search on suspended sediment, expressed either as suspended sediment concentration (SSC) or total suspended solids (TSS), and sediment deposition and scour. We found increases in suspended solids could impact mussels by decreasing food availability, physically interfering with filter feeding and respiration, and impeding various aspects of the mussel-host relationship. We also found mussel-sediment thresholds, wherein certain concentrations of sediment caused significant declines in population performance, which could serve as reference points for ecological research and management. Specifically, we found clearance rates (a measure of feeding) were negatively impacted by TSS concentrations > 8 mg/L, and respiratory stress occurred at ~600 mg/L. Declines in fertilization success and glochidial (i.e., mussel larvae) development were observed at TSS values of 15 mg/L, and reproductive failure occurred at 20 mg/L. Impacts on host fish attachment and glochidial encystment occurred at TSS concentrations of 1,250 – 5,000 mg/L. Impacts on fish varied depending on the biological endpoint but typically occurred at TSS values ranging from 20 – 5,000 mg/L. We also found mussels were sensitive to smothering and mortality occurred at depths as low as 0.6 – 2.5 cm of substrate. Finally, we found relative shear stress (RSS) values > 1, which is a measure of substrate stability in response to scour and entrainment, resulted in significant declines in mussel biodiversity.

[1]Supplementary Data are available with the data through the journal Website

Key Words: sedimentation, freshwater mussels, unionids, population performance, North America, anthropogenic activities

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Introduction

Sediment is composed of inorganic (sand/silt/clay) and organic (biological material) particulate matter which forms through varying processes including weathering of geological features, fluvial processes, wind/wave/or ice action, tectonic uplift, and/or earthquakes. Sediment is introduced to streams and rivers through natural processes such as gully and river channel erosion (Wasson et al. 1996), precipitation runoff (i.e., rain, snow, and ice; Mount 1995; Hastie et al. 2001), and wind transport (Bagnold 1979), which in total account for 30% of the sediment load in aquatic systems. Human land-use activities such as agriculture (Peacock et al. 2005), logging (Beschta 1978), mining (Seakem Group et al. 1992), urbanization (Guy and Ferguson 1963), and hydrological alteration (Black 1995; Hastie et al. 2001) are responsible for the remaining 70% of the total sediment load (Du Plessis 2019). Urban and agriculture runoff, industrial spills, air pollution and polluted groundwater can contaminate sediments (Karickhoff et al. 1979). The U.S. Environmental Protection Agency lists sediment as the most common pollutant in rivers, streams, lakes, and reservoirs (USEPA 2005). Sediment pollution has been estimated to cause $16 billion dollars of damage every year (Du Plessis 2019) based on the economic impacts due to loss of habitat for wildlife, recreation, and the cost of treating water to make it safe for human consumption.

All streams carry sediment, but excessive sediment loads can negatively affect aquatic ecosystems through impacts on channel formation and stream productivity (USEPA 2007), which in turn can degrade freshwater biota (Gammon 1970; Junoy and Viéitez 1990). The channel is shaped by water flow and sediment load (Gordon et al. 2004), so changes in either factor can lead to changes in habitat as the stream channel attempts to establish equilibrium (Frissell et al. 1986; Gordon et al 2004). For example, Anderson et al. (1998) examined the impacts of pipeline construction on channel morphology and found that increased sedimentation due to construction activities elevated the channel bed, which led to steepening of the channel over time and impacted aquatic communities. Stream productivity is also shaped by sediment load via changes in turbidity (Ryan 1991; Hall et al. 2015). This phenomenon occurs

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because suspended particles increase the path length of individual photons of light, which in turn increases the likelihood of absorption by dissolved matter and water itself, which reduces light penetration within the water column. Reduced light penetration can decrease photosynthetic production (Van Duin et al. 2001), which in turn can have cascading effects on ecosystem structure and function (Pace et al. 1999; Heath et al. 2014). Atkinson et al. (2008) examined the influence of suspended sediment on gross primary productivity (GPP) in southeastern Australia and found that sand overlay from sedimentation reduced GPP. Ryan (1991), in an earlier study, made a similar observation and noted the extent to which photosynthetic production is affected by suspended or deposited sediment is dependent on the source of energy to a given stream/river system. For example, headwater streams or those with dense forest canopies rely on energy inputs partially derived from outside sources (i.e., allochthonous), such as leaf packs and woody debris (Vannote et al. 1980), which are subsequently broken down by stream invertebrates. In large systems or those without complete canopy coverage, photosynthetic production is the primary source of energy [i.e., autochthonous] (Vannote et al. 1980). These systems are likely disproportionately impacted by sediment compared to those that rely on allochthonous inputs.

Freshwater mussels of the family Unionidae (hereafter mussels) historically dominated the benthic biomass of many rivers in Eastern North America (Parmalee and Bogan 1998; Graf and Cummings 2007; Vaughn et al. 2008; Hoellein et al. 2017) but are now among the most imperiled groups in the world due to human impacts (Bogan 1993). The United States is a biodiversity hotspot for freshwater mussels, with approximately 300 species currently recognized (Williams et al. 1993; Régnier et al. 2009; Strayer and Dudgeon 2010; Haag and Williams 2014). However, twenty-nine of these species have become extinct within the past 100 years, and an additional 66% are considered endangered, threatened, vulnerable or otherwise imperiled (USFWS 2012). These declines will have long-term negative consequences for freshwater ecosystems because mussels influence primary and secondary productivity through their filter feeding, waste excretion, and burrowing activities (Vaughn and Hakenkamp 2001; Spooner et al. 2011). Mussels also enhance habitat through their physical presence

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(Gutiérrez et al. 2003; Zimmerman and De Szalay 2007; Spooner and Vaughn 2008) and are an important food source for birds, mammals, and fish (Haag 2012).

Mussel declines have been partially attributed to sediment stemming from anthropogenic activities. However, evidence demonstrating causal relationships between sediment and mussel losses remains poorly understood. Brim Box and Mossa (1999) reviewed sediment impacts to unionid mussels and found that it may lead to smothering, reduced fish abundance, and declines in feeding and/or respiration. This led Brim Box and Mossa (1999) to conclude that suspended and/or deposited sediments could negatively affect mussel growth, survivorship and reproduction, which overtime may lead to changes in diversity. Haag (2012) in a later review argued that most of the studies referenced in Brim Box and Mossa (1999) lacked controls or focused primarily on the effects of sudden sedimentation rather than the subtle, gradual accumulations of sediment typically seen in free-flowing systems. Haag (2012) concluded that because of this, there is little to no supporting evidence that suspended or deposited sediment is the main driver of long-term mussel decline in lotic systems. Given the uncertainty as to whether sediment negatively affects mussels, the objective of this paper is to review the current knowledge of the effects of sediment on unionid mussels. In our review, we focus on suspended sediment concentration (SSC), total suspended solids (TSS) and sediment deposition and scour on mussel population performance (i.e., growth, survivorship, and reproduction). We also aim to identify mussel-sediment thresholds wherein certain concentrations of sediment caused significant declines in population performance, which could serve as reference points for ecological research and management.

Approach

To evaluate the effects of sediment on freshwater mussels, we reviewed grey literature and peer-reviewed papers. Literature searches were conducted using the Texas A&M library search engine, which pulled articles from various databases, including Google Scholar, EBSCO HOST, and JSTOR. We

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limited our search to within the past 40 years (1980 to present), except for Ellis (1936), which is the first published observation supporting sediment as a cause of mussel declines and serves as a point of controversy between Brim Box and Mossa (1999) and Haag (2012). Search key words included sedimentation, SSC, TSS, scour, burial, burrowing, bed stability, freshwater mussels, unionids, North America, and population performance phrases (i.e., growth, reproduction, and survival). For inclusion in the review, studies had to meet the following criteria: (1) related to sediment effects on freshwater mussels; and/or (2) contain information on the impact of sediment on population performance of freshwater mussels (i.e., reproduction, growth, and survival).

It is important to note that suspended sediment concentration (SSC) and total suspended sediment (TSS) are used interchangeably in the literature to describe methods to measure suspended solids in the water column. However, SSC and TSS quantify different types of particles in the water column and because of this each one is analyzed differently. SSC refers primarily to inorganic particles in the water column (i.e., sand, silt, clay), whereas TSS refers to both inorganic (non-food) and organic particles, and because of this these two measures are generally not comparable (Gray et al. 2000). In this review, we have attempted to distinguish SSC from TSS, although in some cases it was unclear exactly what the authors were measuring. Finally, sedimentation and sediments are often used interchangeably in the literature, which may or may not be the case depending on the study. In this review, we define sedimentation as settled sediments whereas sediment refers to suspended sediments.

Findings and Discussion

Our literature search returned 1,290 articles, of which 115 were included in the review (Table S1[1]. The remaining papers were excluded because they either only addressed issues affecting aquatic invertebrates in general, did not include information detailing the impacts of sediment to the population performance (i.e. growth, reproduction, and survival) of freshwater mussels (Bivalvia: Unionidae), or did

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not discuss the impact of sediment on associated host-fish populations. All papers reviewed and included in our study reported evidence of impact from sediment on either growth, reproduction, or survival on freshwater mussels and/or associated host-fish populations (Table S1[1]). In addition to these papers, we also included three articles (2.59%) reporting impacts to marine mussels because they discussed impacts to population performance that we deemed relevant to this review. The papers reviewed were published between 1936 and 2019, with about 86% of the articles published within the past 40 years. Of the articles reviewed, only one (0.9%) reported complete lack of impact from sediment on freshwater mussels.

In the following section we discuss our findings from the literature review based on impacts to reproduction, growth, and survival. For each biological endpoint, we synthesize sediment impacts observed by others, potential mechanisms, and knowledge gaps. The focus of each section is to identify sediment thresholds and their impact on various species and life stages of freshwater mussels. Detailed information on the studies reviewed is presented in Table S1[1]. Outlined information includes: (1) species tested; (2) life stages included in the study; (3) sediment type; (4) sediment size; (5) sediment concentrations; (6) duration of experimental exposure; (7) biological functions tested (e.g. filtration rate, clearance rate, smothering, growth); and (8) overall biological response.

Impact of sediment on reproduction

Life cycle

Unionids have a unique reproductive life history in which the larvae (hereafter glochidia) parasitize fish (Haag 2012). This process begins with spawning, wherein the males release spermatozeugmata (aggregates of individual sperm) into the water column, and females filter the spermatozeugmata out of the water column to fertilize the eggs (McMahon and Bogan 2001). Females brood the fertilized eggs, and then glochidia, in the interbranchial chambers of their gills (marsupia) until the glochidia are mature (Kat 1984; Richard et al. 1991). The timing of spawning and brooding can vary

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by species and can be broadly categorized as either short-term (tachytictic) or long-term (bradytictic) (Watters et al. 2001). In general, short-term brooders spawn in the late winter and early spring, with females brooding for a short period (2-8 wks.) after fertilization. Long-term brooders spawn in the late summer and fall, with females brooding through the winter until spring (Yokley 1972; Weaver et al. 1991; Bruenderman and Neves 1993; Garner et al. 1999; Haag 2012). Following brooding, unionid mussels release their larvae passively into the water column or actively through the use of lures or conglutinates, which mimic fish prey items (Haag 2012). In either case, the released larvae typically attach to the fins or gill filaments of their host fish and undergo transformation into free-living juveniles after several weeks (Barnhart et al. 2008).

Spawning and brooding

Sediment can potentially affect the mussel life cycle in several ways. First, sediment can decrease clearance rates (i.e., volume of water cleared of particles per unit time), which can impact the ability of females to capture sperm from the water column and consequently reduce fertilization success. For example, Gascho Landis et al. (2013) evaluating the effects of elevated suspended solids on the reproduction of *Ligumia subrostrata,* Pondmussel, observed a sharp decline in clearance rates when TSS concentrations were > 8 mg/L. The authors also found the portion of gravid females declined by over 20% when TSS concentrations were above ~15 mg/L, and this proportion was reduced to zero at TSS > 20 mg/L. Based on these results, Gascho Landis et al. (2013) hypothesized that TSS interfered with fertilization via two potential mechanisms: (1) reduced clearance rates decreased the chance of females encountering suspended sperm during filter feeding; and/or (2) high TSS increased production of pseudofeces (i.e., filtered material that is not ingested), which led to sperm being bound in mucous and removed during attempts to clear the gills. Gascho Landis and Stoeckel (2016) examining the stage-specific disruption of reproduction by TSS in *Reginaia ebenus*, Ebonyshell, and *L. subrostrata* found the number of females that brooded glochidia declined with increases in TSS. Specifically, the authors found

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concentrations > 20 mg/L resulted in an 80% decline in the number of gravid *R. ebenus* females, mirroring their earlier findings for *L. subrostrata* (Gascho Landis et al. 2013). The authors found that for *R. ebenus*, fertilization success was not impacted, but subsequent development of embryos to glochidia was reduced. In contrast, fertilization success for *L. subrostrata* was impacted by high TSS, but the development of embryos to glochidia was not impacted. The authors noted that reproductive impairment was the same regardless of whether TSS was dominated by organic or inorganic particles. Gascho Landis and Stoeckel (2016) argued their findings provided further support that high TSS causes physical interference with sperm capture, which they hypothesized could be related to the density of cilia (i.e., hairlike structures for filtering) on the gills. The authors noted that species with low cilia density, which are often lentic taxa (e.g., *L. subrostrata*), may not be physically able to clear their gills and efficiently capture sperm at the same time under high TSS conditions. For species with a high density of gill cilia, which typically occur in lotic conditions (e.g., *R. ebenus*), a high TSS may impact reproduction through an alternative mechanism. Short-term brooders such as *R. ebenus* use all four gills to brood glochidia, which differs from *L. subrostrata*, which use only the outside gills. High suspended sediment is then more likely to cause respiratory stress for short-term brooders, particularly during brooding, as a female mussel attempts to meet respiratory demands for herself plus her brood, which could lead to subsequent declines in condition for both (Gascho Landis and Stoeckel (2016).

Mussel-host fish interactions

Suspended sediment may further impact the mussel life cycle by preventing successful attachment (i.e., encystment) of glochidia on the gills, fins, or body of an appropriate host fish. Beussink (2007) evaluating glochidia attachment of *Lampsilis siliquoidea*, Fatmucket, to young-of-the-year *Micropterus salmoides*, Largemouth Bass, which had been previously exposed to elevated sediment, found that suspended montmorillonite clay at concentrations between 1,250 and 5,000 mg/L resulted in reduced attachment and metamorphic success. Beussink (2007) hypothesized that these findings could be

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explained by the following: (1) abrasion by suspended sediment to gill tissues lead to changes in gill morphology that provide less suitable area for glochidia attachment; (2) increases in mucus secretion to protect the gills from abrasion inhibited glochidia attachment; (3) coughing induced by sediment may have dislodged loosely attached glochidia before encapsulation occurred; and (4) declines in keratocytes, which are found in the surface epithelium and play a role in encapsulation of glochidia, became diminished due to wound healing in response to sediment-induced damage to the gills. Because of this, glochidia were not properly encapsulated, which lead to declines in metamorphic success. In addition to reducing glochidia attachment and metamorphic success, elevated sediment may entirely prevent mussel-fish interactions (Brim Box and Mossa 1999). This is because some mussel species use lures or conglutinates, which mimic prey items, to transfer glochidia to their hosts (Barnhart et al. 2008; Haag 2012). For these mussel species, declines in fish visibility due to sediment (Zamor and Grossman 2007) could lead to decreases in the ability of their host fish to locate and then attempt to feed on their lures or conglutinates. For mussels that release free glochidia or mucous webs, it is unknown whether elevated suspended solids could interfere with host fish coming in contact with glochidia. To date, there have been no studies that have tested disruption of host fish infection strategies by sediment.

Host fish survival and behavior

Fishes in streams can be affected by sediment in several ways, which in turn can potentially disrupt the mussel life cycle. First, foraging behavior of fish exposed to high levels of suspended sediment may be impaired, particularly for sight-feeding fish. Chapman et al. (2014) reviewed 18 studies involving sediment impacts on freshwater fish and noted that feeding behavior declined in turbidity-tolerant [*Esox lucius*, Northern Pike, and *M. salmoides*], moderately tolerant [*Onchorhynchus tshawytscha*, Chinook Salmon, and *Oncorhynchus mykiss*, Rainbow Trout] and intolerant [*Salvelinus fontinalis*, Brook Trout] fishes. Sweka and Hartman (2003) made a similar observation, noting that the reactive distance of *Micropterus dolomieu*, Smallmouth Bass, decreased with increases in turbidity, which

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led to reduced prey consumption and subsequent growth. Berry et al. (2003) found similar results, observing that larval *Morone saxatilis*, Striped Bass, reduced their feeding rate when exposed to 200 mg/L sediment (Breitburg 1988).

Second, elevated suspended sediment can cause changes in fish movement as individuals attempt to avoid sediment plumes. For example, Carlson et al. (2001) examining the response of salmonids to sediment in the Columbia River showed that monitored fish avoided the discharge plumes from dredging activities. Birtwell (1999) observed similar results, noting that juvenile *O. tshawytscha* avoided suspended solids at concentrations > 20 mg/L. Berli et al. (2014) showed that swimming performance for *O. mykiss*, Rainbow Trout, in Raven Creek declined across three concentrations of calcium carbonate powder ($CaCO_3$, calcite; low – 110 mg/L; medium – 220 mg/L; and high – 440 mg/L), while swimming performance for *O. mykiss* in Allison Creek declined at medium and high concentrations. In contrast, *Salmo trutta*, Brown Trout, were observed to increase their swimming performance at low concentrations and remained unaffected at medium concentrations but then decreased their swimming performance at high concentrations.

Third, high sediment may result in increased mortality, which could affect population persistence and fish community structure. Kjelland et al. (2015) summarized sediment mortality rates for a range of fish species and found that mortality, depending on species, could occur at TSS concentrations as low as 300 mg/L. Gammon (1970) found that heavy solid input from a limestone quarry significantly reduced the standing crop of fish (total biomass within a particular area at a given time) when heavy solids were greater than 120 mg/L. Both of these studies suggest that the onset of mortality can occur soon after the sediment load increases; however, it is likely that impacts on individual fish occurred before the onset of death (Portner 2001). For example, Buck (1956) found that adult *M. salmoides*, Largemouth Bass, exposed to 62.5 mg/L of sediment lost 50% of their weight, and at 144.5 mg/L, individuals showed stunted growth and impaired reproduction. Sutherland (2005) examined the effects of SSC on *Erimonax monachus*, Spotfin Chub, and found that cortisol (a primary stress hormone) increased when individuals

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were exposed to 50 and 100 mg/L SSC. The author also noted that at SSC equal to 100 mg/L, growth rate was reduced 3-fold below that of the controls.

Taken together, sediment impacts on fish movement, foraging behavior and survivorship could negatively impact mussel reproduction by decreasing the likelihood of physical interaction between host fish and gravid females. To date, no studies have tested this hypothesis; however, mussel declines due to loss of host fish have been documented for some species (Kelner and Sietman 2000; Fritts et al. 2012; Hart et al. 2018; Dudding et al. 2019), and sediment is considered a main contributor to fish declines in freshwater and estuarine fish (Henley et al. 2000; Berry et al. 2003; Chapman et al. 2014; Kjelland et al. 2015). Thus, it is entirely plausible that sediment impacts on host fish could result in cascading effects to mussels.

Impact of sediment on growth

Overview of mussel filter feeding

Unionid mussels acquire food, respire, excrete waste, and obtain gametes through filter feeding (Haag 2012). Individuals filter feed by generating water current via ciliary action of ctenidia on the gills through the incurrent aperture, which passes through pores in the gills and exits through the excurrent aperture. Food and other particles passing through the gills are captured by ctenidia, partially sorted, and then passed towards the labial palps for final sorting and then to the mouth for ingestion (Nichols et al. 2005; Cummings and Graf 2010). The rate at which this occurs is related to the gape of the aperture openings, life stage, and energetic needs (Rodland et al. 2009; Haag 2012). Environmental stressors such as increased suspended sediments can affect these factors, resulting in decreases in feeding and respiration, which in turn can negatively affect energy metabolism (Dimock and Wright 1993; La Peyre et al. 2019).

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Feeding

Sediment can interfere directly with filter feeding by physically impeding the amount of material an individual can filter and ingest (i.e., mg of particles passing into the mouth per unit time; Kat 1984; Aldridge et al. 1987). This is because as suspended solids increase, clearance rates, which is the hypothetical volume of water completely cleared of particles per unit time, likely decreases to prevent clogging of gill filaments (Bayne and Newell 1983). For water that is passed through the gills for feeding, mussels remove nonfood particles such as sediment prior to ingestion, which comes with an energetic cost (Madon et al. 1998). Under high suspended sediment concentrations, it is likely that mussels may encounter scenarios where feeding gains are outweighed by the energetic costs of sorting food vs. nonfood (Bayne and Widdows 1978; Madon et al. 1998). For example, Tokumon et al. (2015) evaluated the tolerance of *Limnoperna fortunei*, Golden Mussel, an invasive mussel species, to inorganic suspended solids by measuring chlorophyll *a* before and after each experiment to estimate both filtration (i.e., volume of water cleared of particles per unit time; FR, in ml g Total Dry Weight (TDW)$^{-1}$ h^{-1}) and grazing rate (i.e., consumption of phytoplankton; GR, in μg Chl *a* g TDW^{-1}h^{-1}). The authors found that filtration rates were maximized at sediment concentrations between 0 and 100 mg/L but then decreased by 50% at 1,000 mg/L and ~75% at 2,000 mg/L. Grazing rates followed a similar pattern with the highest rates occurring at 0 mg/L and decreasing by 50% at 1,000 mg/L and ~75% at 2000 mg/L. Tokumon et al. (2015) concluded that concentrations of inorganic suspended solids exceeding 1,000 mg/L may suppress feeding and therefore growth, which overtime could negatively impact survivorship. Tuttle-Raycraft and Ackerman (2019) made a similar observation evaluating the effects of TSS and velocity on the clearance rates (i.e., volume of water cleared of particles per unit time) of two populations of *Lampsilis siliquoidea* (turbid vs. clear water) by measuring chlorophyll *a* before and after experiments. The authors found clearance rates significantly declined in both treatments when TSS was greater than or equal to 20 mg/L and declines were greater for the clear water population (~83%) compared to the turbid water population (57%). Finally, Bucci et al. (2008) evaluating valve gape response to 3 levels of turbidity [baseline (0 to

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20 NTU); peak (20 NTU to 50% of the maximum for the experiment); and chronic (50% of the maximum for the experiment to the end of the experiment)] in two freshwater bivalves (*Corbicula fluminea*, Asian clam, and *Lampsilis radiata*, Eastern Lampshell) found *C. fluminea* had a greater valve gape during the peak turbidity and during periods of chronic turbidity displayed extended valve closure. *Lampsilis radiata* on the other hand showed no significant difference in valve gape activity between the three periods.

The findings of Tuttle-Raycraft and Ackerman (2019) along with Bucci et al. (2008) and Tokumon et al. (2015) indicate suspended sediment may affect feeding. However, other studies have shown reductions in clearance rates may not necessarily result in automatic reduction in feeding and/or particles removed. For example, Gascho Landis et al. (2013) evaluating the effects of TSS on *L. subrostrata* found growth (i.e., length and weight) was unrelated to TSS. The authors noted that at 5 mg/L TSS mussel clearance rate (the volume of water cleared of particles per unit time; L g^{-1} wet mass h^{-1}; calculation based on modified methods of Rissgard 2001) was ~ 0.02 L per g wet weight per hour, which means individual mussels were able to remove 0.1 mg particles per g wet weight per hour. At a TSS of 50 mg/L, clearance rate declined to 0.004 L per gram wet weight per hour, which translated to removing 0.20 mg particles per g wet weight per hour. Gascho Landis et al. (2013) findings indicate the mass of particles removed from the water column did not decrease with a decrease in clearance rate, which likely explains why increasing TSS did not cause declines in growth for *L. subrostrata*. Gascho Landis and Stoeckel (2016) examining the impact of TSS in *R. ebenus* and *L. subrostrata* also found no effect of increasing TSS on growth, except at very low concentrations.

Respiration

Freshwater mussels respire through their gills and during periods of elevated suspended solids respiratory distress may occur due to clogging of the gills. Madon et al. (1998) evaluating the effects of sediment and feeding on the respiration of *Dreissena polymorpha*, Zebra Mussel, found that respiration

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rates decreased as TSS concentrations increased from 0 to 10 mg/L across 3 food levels (0.1, 0.5 and 2.0 mg POM/L). The authors also noted clearance and ingestion rates decreased at the same time, which they argued explained the subsequent decreases in respiration. Conversely, Madon et al. (1998) observed that respiration rates increased at sediment levels from 10 to 100 mg/L in the low and medium food treatments but did not change at the high food treatment. The authors found that pseudofeces production, or mucous secretion, also increased at the same time, which they argued allowed mussels to more effectively pass sediment that could potentially clog their gills. Based on these findings, Madon et al. (1998) noted that suspension-feeding bivalves cope with increases in sediment by either reducing particle intake via reduction in clearance rates or maintaining food intake at some level by producing pseudofeces to prevent clogging of gills. Both mechanisms come at an energetic cost reflected in changes in respiration, which could negatively impact individuals over time. Aldridge et al. (1987) examining the effect of suspended solid exposure on the oxygen uptake of *Cyclonaias pustulosa,* Pimpleback, *Fusconaia cerina*, Gulf Pigtoe, and *Pleurobema beadleanum*, Mississippi Pigtoe, found that individuals exposed to elevated turbidity experienced a depression in oxygen consumption. Oxygen uptake is an indicator of metabolic rate, so decreases in respiration may lead to decreases in mussel metabolism (Prosser 1973), which could then impact growth and reproduction.

Metabolism

Declines in feeding and respiration due to sediment may result in shifts in energetic pathways that can negatively affect growth and reproduction. Aldridge et al. (1987) assessing the effects of suspended solids on mussels using two different types of sediment exposure for 9 days (infrequent: averaging ~750 mg/L for 7 minutes every 3 hours; and frequent: averaging ~600 mg/L for 7 minutes every 0.5 hours) found that exposure to sediment affected feeding and respiration in mussels and that frequent exposure led to shifts in energetic pathways. Specifically, mussels infrequently exposed to sediment had reduced clearance rates, and 2 of the 3 tested species (*C. pustulosa* and *P. beadleanum*) showed reduced oxygen

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uptake and nitrogen excretion rates. Mussels frequently exposed to sediment not only reduced their clearance rates and nitrogen excretion rates and oxygen uptake but also shifted their metabolism to nonproteinaceous body stores, which differed from those exposed to the infrequent treatment. Based on these results, Aldridge et al. (1987) argued that changes in catabolism were likely due to starvation, as individuals unable to feed shifted to stored carbohydrates (e.g., glycogen) and lipids. Generally, glycogen and lipids are indicators of physiological health and often change in response to environmental stress before impacts to growth or survival occur (Naimo et al. 1998). Aldridge et al. (1987) made a similar point and hypothesized that observed declines in glycogen and lipids due to sediment would have disproportionate effects on population performance depending on the time of year they occurred. This difference occurs because mussels experiencing metabolic stress can shift energy from growth to reproduction or maintenance. In cases where mortality is high, mussels have been shown prioritize maintenance over reproduction (Jokela and Mutikainen 1995). Thus, reduced mussel filtration rates could affect growth or reproduction, which could have long-term negative consequences to population persistence.

Impact of sediment on Survival

Suspended and deposited sediment influences river channel formation and can cause changes to channel characteristics at temporal and spatial scales ranging from microhabitat to reach systems (Frissel et al. 1986; Hauer et al. 2018). These changes can occur through two main processes: (1) aggradation, wherein the stream's ability to transport sediments is less than that required to move sediments arriving from upstream, which leads to deposition of sediment; or (2) degradation, wherein there is not enough sediment to exceed transport capacity, which results in erosion of the riverbed and/or banks (Gordon et al. 2004). Aggradation and degradation are natural processes but can be exacerbated by anthropogenic changes to the flow or sediment regime due to increases in flooding or changes in land use (Beschta 1978; Seakem Group et al. 1992; Hastie et al. 2001).

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Burial and scouring

Localized bed aggradation can lead to scenarios where suitable mussel habitat becomes inundated with unconsolidated material, often fine sediment, which can lead to smothering depending on the mussel species. For example, Ellis (1936) examining the effects of silt deposition on 4 unionid mussel species from the Trinity River, Texas, found that silt accumulations of 0.6-2.5 cm in depth resulted in ~90% mortality for all species over a 14-month period in raceways. The author observed that *Lampsilis teres*, Yellow Sandshell, was the most sensitive of the species tested, whereas *Obliquaria reflexa*, Threehorn Wartyback, *Quadrula apiculata,* Southern Mapleleaf, and *Quadrula nobilis*, Gulf Mapleleaf, were the least sensitive. Imlay (1972) evaluating the response of 3 mussel species to smothering in aerated jars found that *Pyganodon grandis*, Giant Floater, was the least sensitive (emerged individuals: 100%) to 7.62 cm of detritus overlay followed by *Ligumia recta*, Black Sandshell, (~40%) and then *Fusconaia flava*, Wabash Pigtoe (20%). Marking and Bills (1980) determined the depth of silt or sand overlays that could be lethal to 3 species, *F. flava, L. siliquoidea*, and *Lampsilis cardium*, Plain Pocketbook, over 96 hours and observed that 50% of the individuals of *L. cardium* and *L. siliquoidea* were able to emerge from ~21 and 18 cm of silt, respectively. In contrast, only 50% of the individuals of *F. flava* were capable of emerging from 10 cm of silt. Colden and Lipcius (2015) examining the lethal and sublethal effects of sediment burial on *Crassostrea virginica*, Eastern Oyster, quantified the effects of partial and complete burial (i.e., 0, 50, 70, 90, and 110% of oyster shell height). The authors found survival declined when 90% or more of the oyster was buried. The authors hypothesized mortality following burial was due to disruption of feeding, mirroring observations for unionid mussels, which suggests a general sensitivity by bivalves to smothering. Bed aggradation can also lead to increases in turbidity (see previous discussion on sediment effects to filter feeding and mussel-host interactions) and increased embeddedness. The latter occurs when fine sediment fills the interstitial spaces between coarse particles, which could prevent mussels from burrowing and consequently increase their susceptibility to predation or entrainment during floods (see discussion below) (Zimmerman 2003; Nicklin and Balas 2007; Addy et al. 2012).

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Embeddedness can negatively impact certain fish species, which could affect mussels by eliminating their host fish. For example, Sullivan and Watzin (2010) examining the effect of sediment aggradation on fish community structure found that increased embeddedness led to decreases in body condition for *Semotilus atromaculatus*, Creek Chubs, and *Catostomus commersoni*, White Sucker, which feed on the stream bottom. The authors reasoned that embedded substrate reduced habitat for benthic macroinvertebrates or sunlit space for periphyton and, as a consequence, reduced food availability for these benthic feeding fish.

Localized bed degradation can also impact mussels under scenarios where suitable habitat is scoured, which can lead to individuals being washed away or elimination of habitat. Allen and Vaughn (2010) evaluating how bed stability affected mussel diversity in the Little River in southeastern Oklahoma found that mussel species richness and abundance were maximized in areas where the potential for bed movement and particle entrainment was low. The authors determined this by calculating relative shear stress (RSS; a measure of bed mobility) and found that richness and abundance were maximized when RSS was less than 1. Randklev et al. (2019) examining the role of substrate stability on mussels in the Brazos and Trinity River basins of central Texas observed similar results, noting that mussel diversity was maximized at RSS values of 1 or less. The authors also found that some species (i.e., *Potamilus* and *Lampsilis*) were able to persist at higher RSS values (i.e., greater bed mobility) than others (i.e., *Amblema*, *Cyclonaias*, *Quadrula*). Randklev et al. (2019) attributed differences in occupancy within stable vs. unstable habitats to differences in species traits (burrowing, morphology, and life history) between the two groups, which they demonstrated using a series of trait-based analyses.

Implications for Conservation and Future Studies

Although suspended and/or deposited sediment is frequently cited in the peer-reviewed literature as a main contributor to freshwater mussel decline, the idea has not received widespread acceptance due to lack of experimental evidence demonstrating this causal relationship. Much of the available evidence

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comes from either Brim Box and Mossa's (1999) review of sediment impacts to mussels, a handful of laboratory/field studies (e.g., Gascho Landis 2013, 2016) or broad generalizations drawn from invertebrates as a whole (Seakem Group et al. 1992; Beschta 1978; Extence et al. 2011; Jones et al. 2012; Buendia et al. 2013). For laboratory and ecological studies that have focused on understanding the linkage between sediment and mussel population performance, there has been little effort to standardize methods, which could help draw better inferences and translate results to other species or geographic regions. For example, SSC, TSS and turbidity are often used interchangeably in the ecological literature to refer to suspended sediment, implying that all 3 measurements are equivalent, which is not correct. There are also no standard methods for determining sediment toxicity thresholds, whether measured as SSC, TSS, or turbidity, to mussels. Because of this limitation, sediment effects, or the lack thereof, cannot be fully realized until experimental bias is better accounted for. Finally, we also found that very few studies actually placed their results within an environmental context, which is critical because results generated from laboratory studies may not translate to real-world scenarios. For studies that do place their results within an environmental context the identified TSS-mussel thresholds may be specific to the species/subpopulation examined and therefore not translate well to other regions. For example, Gascho Landis and Stoeckel (2016) found the number of females brooding glochidia declined significantly when TSS > 20 mg/L. In Texas, where much of our work on mussels has been performed, 20 mg/L TSS is often exceeded during high flows and may be exceeded for some rivers even during normal baseflows. Studies showing negative effects of high suspended solids on unionid mussels also present a conundrum in that healthy populations of many mussel species are often found in turbid systems (see discussion below). Our review of TSS-fish thresholds indicates this may also be an issue for fish. For example, sediment has been observed to have detrimental impacts on fish such as *M. salmoides* (Largemouth Bass), however, M. *salmoides* are often found in turbid systems (Buck 1956).

This review shows that available literature on the impact of suspended sediment on freshwater mussels is insufficient to determine a sediment target for healthy streams. Most of the studies were

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conducted in laboratory conditions and did not emulate conditions that broadly reflect sediment concentration changes in natural streams. It is well known TSS concentrations fluctuate in a stream such that baseflow TSS is usually lower and less variable than stormflow TSS concentrations. However, alterations to the landscape (e.g. increased imperviousness, deforestation or loss of riparian vegetation) can lead to changes in baseflow and stormflow concentrations of TSS, which have the potential to impact mussels and their host fish. However, studies showing negative effects of high suspended solids on unionid mussels present a conundrum in that healthy populations of many mussel species are often found in turbid systems. This may be explained by inter- and intraspecific plasticity in species traits (e.g., palp size which affects particle sorting ability), that allow some species and/or subpopulations to occur in turbid environments. It has long been reported in the marine bivalve literature that palp size is plastic and dependent on sediment loads in the habitat from which mussels are collected (Jorgensen 1990, Kiorboe & Mohlenberg 1981) and similar observations have been recently made for unionids (e.g., Tuttle-Raycraft and Ackerman 2019). This trait may help explain why some species are able to persist in habitats with high suspended sediments. Interspecific variability among palp size or other traits that allow mussels to cope with sediment could explain, in part, why mussel beds are often dominated by only few species. That is, sediment may act as an environmental filter selecting for species that are able to cope with turbid conditions. Finally, the negative effects of high TSS (inorganic + organic) on reproduction may be at least partially offset by the stochasticity of TSS in many river systems (i.e. TSS are not constantly high). For example, in turbid systems, ISS (inorganic suspended solids) could periodically drop below 20 mg/L (or some other experimentally derived reproductive threshold), providing an annual reproductive window for mussels. This may explain why recruitment of many mussel species is low and/or sporadic from year to year even in relatively healthy populations.

Our review shows that sediment is a threat to mussels, but there remains a number of methodological and experimental issues that need to be resolved plus more rigorous testing, across species and among populations, to better understand how sediment impacts population performance and

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to identify species-specific thresholds. Therefore, we provide the following recommendations based on our review, which may help researchers and managers in addressing these knowledge gaps: (1) long-term studies are needed to understand both the short- and long-term effects of sediment on mussels (Norkko et al. 2006). Much of the research conducted to date has focused on short-term effects (i.e., sudden increase in TSS or deposition of sediment), which may be helpful for mitigating acute impacts, but not chronic effects linked to changes in land use; (2) evaluation of other life stages are needed to better understand how sediment affects the entire mussel life cycle. Juvenile and glochidia life stages are known to be especially sensitive to waterborne contaminants (Cope et al. 2008), and our review shows that sediment could potentially impact various aspects of mussel reproduction and habitat where juveniles and adults reside. Currently, it is unknown how sediment affects fully developed glochidia and it remains an enigma how juveniles, which live burrowed in the sediments and pedal feed, could be impacted by sedimentation. Because of this conundrum, we recommend that along with adults, glochidia and juveniles are utilized in experimental methods to understand the full scope of the impact of sediment to these life stages and on the persistence of mussel populations; (3) more studies are needed on the impacts sediment may have on mussel-host fish interactions. Generally, mussel-host infection strategies range from passive release into the water column to actively baiting fish through the use of lures or conglutinates (Haag 2012). For mussels that use lures to infect their host, increases in suspended sediment often result in corresponding declines in visibility, which could decrease the ability of the host fish to locate and then attempt to feed on the lures or conglutinates of mussels (Kjelland et al. 2015). For mussels that passively release free glochidia, it is unknown whether elevated suspended sediment could interfere with host fish encountering glochidia; and (4) there is an urgent need to standardize terms used to describe sediment-related effects on mussels and experimental methods. In our review, we found a variety of terms used to describe solid-phase material suspended in the water-sediment mixture. Because of this variation, it is difficult to translate and compare experimental research or utilize the results to support conservation and management efforts.

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