Freshwater Mussel Nutrient Reduction Literature Review and Assessment

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Introduction

Freshwater mussel populations have declined across the Chesapeake Bay watershed over the past 200 years due to a variety of factors, including dam-related impacts, habitat destruction, poor water quality and other likely more minor factors such as disease and competition from invasive species (Wood et al 2021). Despite these losses, mussels remain an important component of aquatic ecosystems, providing valuable services such as removal of particulates from the water column, reduction of pollutants in the water and sediment stabilization. Understanding and restoring these functions has become increasingly relevant as Pennsylvania advances its nutrient reduction goals within the Chesapeake Bay watershed.

This report supports the Pennsylvania Department of Environmental Protection's (DEP's) efforts to develop a roadmap for future nutrient reduction strategies, evaluate the potential for crediting mussel-mediated denitrification and nutrient cycling, and identify opportunities to restore or expand mussel populations in priority areas. To inform these objectives, Tetra Tech conducted a literature review and an assessment of ongoing research, with particular emphasis on studies published since the Chesapeake Bay Scientific and Technical Advisory Committee (STAC) developed their workshop report, Incorporating Freshwater Mussels into the Chesapeake Bay Restoration Efforts (STAC Report) (Wood et al. 2021). Outreach to universities, hatcheries, and research partners provided additional insight into current work on mussel populations, distribution, propagation, and nutrient reduction efficiencies.

The goals of this project were to synthesize scientific findings since the STAC Report was published, evaluate newly available data sources, document uncertainties, make recommendations for advancing the body of knowledge on freshwater mussel nutrient removal quantification, and consider whether there is sufficient data to make recommendations for one or more freshwater mussel best management practices to provide nutrient crediting mechanisms for mussel restoration activities in the watershed. Collectively, these efforts address key data gaps and strengthen the scientific foundation for future conservation and nutrient management decisions in Pennsylvania's portion of the Chesapeake Bay watershed. The focus was on assessing the state of knowledge since the STAC report. While the review initially focused on 24 Chesapeake Bay Species provided by the Chesapeake Bay Watershed Region Freshwater Mussel Partnership (Table 1), the paucity of data necessitated expanding to a national focus.

Table 1. Unionid Freshwater Mussel Taxa List for the Chesapeake Bay Watershed (Revised September 2025; source: Chesapeake Bay Watershed Region Freshwater Mussel Partnership)

Species	Common Name
Alasmidonta varicosa	Brook Floater
Alasmidonta marginata	Elktoe
Alasmidonta undulata	Triangle Floater
Anodontoides ferussacianus	Cylindrical Papershell
Atlanticoncha ochracea	Tidewater Mucket
Cambarunio iris	Rainbow
Elliptio lanceolata	Yellow Lance
Elliptio producta	Atlantic Spike
Elliptio angustata	Carolina Lance
Elliptio fisheriana	Northern Lance
Elliptio complanata	Eastern Elliptio
Fusconaia masoni	Atlantic Pigtoe
Lampsilis cariosa	Yellow Lampmussel
Lampsilis cardium	Plain Pocketbook
Lampsilis radiata	Eastern Lampmussel
Parvaspina collina	James Spinymussel
Platynaiassubviridis	Green Floater
Prolasmidontaheterodon	Dwarf Wedgemussel
Pyganodon cataracta	Eastern Floater
Sagittunio nasutus	Eastern Pondmussel
Strophitus undulatus	Creeper
Toxolasmaparvum	Lilliput
Utterbackia imbecillis	Paper Pondshell
Utterbackiana implicata	Alewife Floater

Overview of the STAC Report

STAC serves as the Chesapeake Bay Program's primary source of independent scientific and technical expertise, offering guidance on efforts to restore and protect the Chesapeake Bay. In March 2020, the STAC held a workshop on Incorporating Freshwater Mussels in the Chesapeake Partnership to discuss the current state of freshwater mussel science, ecosystem services and benefits of freshwater mussels, prevalence and species in the Chesapeake Bay watershed, strategies of expanding mussel restoration, and considerations for development of best management practices (BMPs) for freshwater mussels. They subsequently published the STAC Report (Wood et al. 2021).

The STAC report provides a detailed examination of the ecosystem services delivered by freshwater mussels, with particular emphasis on their role in nutrient processing and water quality improvement across the Chesapeake Bay watershed. The report details that mussels act as natural biofilters, removing suspended sediments, organic particles, and associated nutrients from the water column. Through filtration and subsequent biodeposition, mussels transfer nutrient-rich material to sediment, where it can potentially stimulate microbial processes such as denitrification. The report highlights that this coupling between mussel activity and sediment microbial communities has the potential to reduce bioavailable nitrogen, a key driver of eutrophication.

The report presents denitrification values from literature and preliminary calculations of pre-Columbian era net denitrification effect (up to 7.9% of current nitrogen loads) and potential present-day impacts (up to 0.79% of current nitrogen loads), based on historical and present-day mussel densities. The STAC notes that while individual mussels and dense mussel beds can enhance denitrification rates, the magnitude of watershed-scale nutrient reduction remains uncertain due to limited empirical data. The report emphasizes that current estimates should be interpreted as early approximations rather than definitive nutrient reduction values.

The STAC report also includes an assessment of the comparability between oyster nutrient removal capabilities and mussels, noting that it is "informative…but not ideal" due to the differences in population, distribution, sizing and research methods creating challenges to extrapolating from oysters to mussels.

The STAC report also identifies several important considerations that influence the extent of mussel-mediated nutrient processing. These include species-specific differences in filtration rates, the influence of temperature and flow conditions on mussel metabolism, and the spatial configuration of mussel beds within a watershed. The report stresses that environmental context (such as sediment composition, organic matter availability, and hydrologic variability) can significantly affect the degree to which mussels enhance denitrification. As a result, nutrient reduction benefits are unlikely to be uniform across systems and must be evaluated within local ecological settings.

The STAC report explains that significant information gaps still hinder accurate measurement of the ecosystem services provided by freshwater mussels highlighting that there is limited information on how different native mussel assemblages influence nutrient cycling, as most existing studies focus on species found outside the Chesapeake Bay watershed and include a variety of different assessment methods. There is also a lack of comprehensive, up-to-date population surveys across the watershed – many species have experienced long-term declines that remain poorly documented. Additionally, long-term monitoring of mussel driven denitrification in the Chesapeake Bay watershed is non-existent. These gaps constrain the development of nutrient reduction models and hinder efforts to integrate mussels into formal watershed planning frameworks.

To address these limitations and data gaps, STAC outlines several recommended next steps and research recommendations. These include improving population assessments to better estimate the spatial extent of mussel beds, expanding field studies to measure denitrification rates from native species at biologically relevant densities, and quantifying factors essential to mussel habitat.

Mechanisms of nutrient and sediment removal or processing

Nutrients and sediments in freshwater systems can be removed or processed through several biological and biogeochemical mechanisms associated with mussels. Each of these is briefly described below and was considered in the literature review and in interviews with practitioners.

Denitrification

Denitrification is a microbial process, often enhanced in mussel beds and surrounding sediments, in which biologically available nitrogen is reduced to gaseous forms such as nitrogen gas (N_2) or nitrous oxide (N_2O). This process can contribute to permanent nitrogen removal from the aquatic ecosystem by transferring dissolved nitrogen out of the water into the atmosphere.

Shell Sequestration

Shell sequestration is the long-term incorporation and storage of nutrients and trace materials into the calcareous shell matrix of a mussel. Shell production and growth locks carbon, calcium, and associated nutrients into relatively inert biomass, and it represents a stable pathway for removing material from short to long term biogeochemical cycling.

Tissue Sequestration

Tissue sequestration is the temporary storage of nutrients in the living soft tissues of mussels, built from assimilated organic matter. This process removes nutrients from the water column and suspended particulate pool and retains them in animal biomass until they are transferred through growth, reproduction, mortality, or predation.

Feces/Pseudofeces Filtration and Deposition

Freshwater mussels remove suspended particles from the water column through filtration, capturing fine sediments, phytoplankton, detritus, and associated nutrients. Material that is ingested is expelled as feces, and non-ingested particles bound in mucus are rejected as pseudofeces. Both are deposited on or near the benthos, shifting suspended nutrients and sediment from the water column to the stream or river bottom.

Excretion

Excretion of ammonia is the release of dissolved nitrogenous waste produced during metabolism and other physiological processes. Because ammonia is readily available for uptake and transformation by microbes and primary producers, mussel excretion can recycle nitrogen within the local aquatic ecosystem rather than removing it permanently.

Summary of Published Findings

The literature review process included a review of materials gathered from the Freshwater Mussels Steering Committee's Zotero catalog of resources, a Google Scholar search, and researchers' publications posted to their academic websites or directly provided.

An initial universe of 97 peer-reviewed articles (and dissertations) was identified as potentially relevant for the purposes of developing nutrient reduction efficiencies and characterizing the state of nutrient processing knowledge of freshwater mussels; many of the articles had already been considered during the development of the STAC report. Thirty-seven of the articles were published between 2019 and 2026 (near and after the STAC report). We focused our search on papers published after the STAC report to avoid duplication and focus on new science and data that could be used to develop nutrient reduction efficiencies and characterize nutrient dynamics related to freshwater mussels. Papers addressing locations outside of North America were excluded from further consideration, since the focus of the evaluation is intended to be on native species, local to the Chesapeake Bay watershed.

The literature review followed two paths: 1) to extract relevant, quantified data about freshwater mussel nutrient and sediment removal and processing, and 2) to better understand the factors impacting freshwater mussel nutrient and sediment removal and processing. The literature was screened to determine whether the research addressed the native species listed in Table 1. The majority of the articles did not address native species and none of the research took place within the Chesapeake Bay watershed. Seventeen papers were found that had potentially relevant, quantifiable data about the nutrient processing mechanisms (Table 2). One of the significant findings from the quantifiable data extraction component of the literature review is that a wide range of metrics are being collected, but there is relatively little overlap in the type of metrics collected among studies, leading to challenges with comparability across studies. Given the low number of studies and the unique metrics across studies, the data have been provided as ranges, as summary statistics (mean, median, etc.) would be uninformative since they would only contain a handful of data points.

Table 2. Summary of Physical and Chemical Processes Data

Category	Metric	Range	Incl. Ches. Bay Species	Citation
Clearance Rate	Areal Clearance Rate	0.4-2.3 L/m^2/h	No	van Ee et al. 2022
	Mass Specific Clearance Rate	0.07-1.57 L/ g dry tissue weight/h	Yes	Gentry 2024
	Mass Specific Clearance Rate	0.004-0.02 L/g wet mass/h	Yes	Goldsmith et al. 2021 Hills et al. 2020
	Clearance Rate	0.2-1.1 L/ mussel/h	No	Todd 2024
Denitrification	Mass Specific	0.01-0.45 µmol/kg/h	No	Kubala et al. 2024b
	Areal Rate	0.007-0.017 µmol N2-N/m^2/h	No	Lodato et al. 2026
Total N Removal		0.02-0.5 µmol kg/h	No	Kubala et al. 2024b
Nitrogen Excretion Rate	NH4 excretion rate	0.221359-10.7235 µmol/hr	No	Hopper et al. 2021a
	Mass-specific NH4 excretion rate	15-30 NH4-N g/h	No	Atkinson et al. 2021
	Areal NH4+ excretion rate	110-160 umol NH4/m^2/h	No	Atkinson et al. 2021
	Mass specific NH4+-N flux	1.25-2.18 µmol/g/h	No	Lodato et al. 2026
	Aereal NH4+-N flux (dark conditions)	18.69-120.78 µmol/m^2/h	No	Lodato et al. 2026
	Aereal NH4+-N flux (light conditions)	-30.42 – (-)6.82 µmol/m^2/h	No	Lodato et al. 2026
	NH3 excretion rate	2.09-6.43 µmol NH3/g mussel/hr	No	Atkinson and Forshay 2022
	Nitrogen excretion rate	1.35-2.24 µmol/g/h	No	Kubala 2022
	Areal N excretion rate	0.158-117.0 µmol/m^2/h	Yes	Hopper et al. 2023 Kubala et al. 2024b
Phosphorus Excretion Rate	PO4 excretion rate	0.07-0.27 µmol PO4/g mussel/h	No	Atkinson and Forshay 2022
	Mass-specific phosphorus excretion rate	2-3 µmol PO4-P g/h	No	Atkinson et al. 2021
	Areal PO4 excretion rate	15-28 µmol PO4 m^2/h	No	Atkinson et al. 2021
	Aereal Phosphorus Excretion Rate	2.0-235.0 µmol m^2/h	No	Kubala 2024b Van Ee et al. 2022
	Phosphorus excretion rate	0.07-0.08 µmol g/h	No	Kubala 2022
	Soluble Reactive Phosphorus	0.000571-0.874655 µmol/h	No	Hopper et al. 2021a

Category	Metric	Range	Incl. Ches. Bay Species	Citation
Dissolved Organic Carbon Excretion Rate	DOC excretion rate	0.064427-51.87971 μmol/hr	No	Hopper et al. 2021a
Mean Excretion Stoichiometric Ratio	N:P	22.28-50.78 molar ratio N:P	No	Atkinson et al. 2020
NH_3 release	NH_3 release	~100-140 μg/L/m^2 (following mass mortality event)	Yes	DuBose et al. 2019
SRP release	SRP release	~120-160 μg/L/m^2	Yes	DuBose et al. 2019
Filtration Rate	Total phosphorus filtration rate	13.5% of TP load	Unknown	Bakshi et al. 2023
	Filtration rate	2.75 L/h per mussel	No	Bakshi et al. 2023
	Mass Specific Filtration Rate	0.4-16.9 mg/h/g dry tissue weight	No	Gentry 2024
Carbon Biodeposition Rate	Mass Specific carbon biodeposit rate	27.04-90.15 μmol C/g/h	No	Atkinson and Forshay 2022
	Mass Specific carbon deposition rate	0.34-1.3 μmol/g/h	No	Kubala 2022
	Areal carbon biodeposition rate	6.8-15.7 μmol m^2/h	No	Kubala 2022
Nitrogen Biodeposition Rate	Nitrogen biodeposit rate	2.66-6.77 μmol N/g/h	No	Atkinson and Forshay 2022
	Nitrogen biodeposition rate	0.05-0.17 μmol/g/h	No	Kubala 2022
	Areal nitrogen biodeposition rate	0.9-2.2 μmol m^2/h	No	Kubala et al. 2024a Kubala et al. 2024b
	Particulate Organic Nitrogen biodeposition rate	10-130 ug/mussels h	No	Todd 2024
Phosphorus Biodeposition Rate	Biodeposition (% of TP load)	>60% of TP load	Unknown	Bakshi et al. 2023
	Mass-specific Phosphorus biodeposition rate	0.03-0.12 μmol/g/h	No	Kubala et al. 2024a
	Aereal phosphorus biodeposition rate	0.5-1.8 μmol m^2/h	No	Kubala et al. 2024b
Mean biodeposit stoichiometric ratios	C:N	5.74-66.93 molar ratio C:N	No	Atkinson et al. 2020
	C:P	2.39-561.88 molar ratio C:P	No	Atkinson et al. 2020

In addition to literature discussed above, Maryland Department of Natural Resources (MDNR) provided a dataset of tissue and shell nutrient analysis that the department conducted as part of a demonstration project to estimate nutrient reduction potential from assimilation into tissue and shell to support augmentation of wild populations with propagated freshwater mussels to contribute to water quality improvements. The data are from whole, propagated animals. The data presented in Table 3 are from two species, *Elliptio complanata* (ELCO) and *Lampsilis radiata* (LARA) collected from three sites: Deer Creek, UT Sassafras River, and the Anacostia River. Data interpretation was not provided along with the raw data, but the nutrient content appears relatively similar between species, with expected higher amounts of C, N and P in the tissues as compared to the shells. The exception was the phosphorus content of the shells of the ELCO from UT Sassafras River, which stood out as an order of magnitude higher than both the ELCO from Deer Creek and the LARA from Anacostia River.

Table 3. Chesapeake Bay-specific freshwater mussel tissue and shell nutrient content data (MDNR)

Species	Location	Mean Length (mm)	Type	Mean %C	Mean % N	Mean %P	C g/DW	N g/DW	P g/DW
Shell									
ELCO	Deer Creek	58.76	Shell	12.55	0.62	0.01	0.130	0.006	0.000
ELCO	UT Sassafrass River	79.50	Shell	11.64	0.61	0.60	0.120	0.006	0.006
LARA	Anacostia River	48.03	Shell	12.78	0.46	0.02	0.132	0.005	0.000
Tissue									
ELCO	Deer Creek	58.76	Tissue	37.96	8.49	2.10	0.392	0.087	0.022
ELCO	UT Sassafrass River	79.50	Tissue	36.79	8.15	2.76	0.380	0.084	0.029
LARA	Anacostia River	48.03	Tissue	37.37	7.07	2.24	0.386	0.073	0.023

Factors Impacting Nutrient Removal and Processing

Species-Specific Nutrient Processing

Across the literature, species identity emerges as one of the strongest determinants of mussel nutrient processing. Different unionid species vary in excretion, biodeposition, and stoichiometry, and these differences scale up to alter denitrification and broader nutrient cycling at the patch and stream reach scale (Atkinson et al. 2021; Atkinson and Forshay 2022; Kubala et al. 2024a; Kubala et al. 2024b). Atkinson et al. (2021) found that species composition controlled the stoichiometry within a patch. That same study found statistically significant species-specific variability in mass-specific NH4 excretion rates but did not find significant differences in PO4 excretion rates. N:P excretion was statistically significant while biodeposit rates varied by two orders of magnitude but were not statistically different across species. In addition, Hopper et al (2021a) found significant effects of species and species × body size variability contributed to N and P excretion rates, with r^2 values > 0.60.

Interspecies differences repeatedly explained variation in both direct nutrient fluxes and indirect sediment processes. In mesocosm and field studies, different mussel species produced distinct mass-specific excretion and biodeposition rates. Kubala et al. (2024a) found that mass-specific N excretion was statistically different among species although mass-specific P excretion rates were not statistically different. Similarly, Lodato et al. (2026) found that while NH4+-N excretion and organic matter biodeposition rates differed among species, microbial N2 fluxes were only negligibly effected by species differences. Mass-specific SRP excretion did not differ among species, although scaled SRP excretion did (Lodato et al. 2026). Atkinson and Foreshay (2021) note that species-specific burying behavior and depth can impact physical bioturbation and denitrification. They found that across species 39% to 78% of soft tissue biomass was completely below the sediment surface, allowing for N excretion and biodeposition near the oxic-anoxic redox boundary allowing for microbial denitrification. Similarly, Kubala et al. (2024b) found that there were species specific differences in burrowing behavior and biodeposition rates and ratios.

Size, Growth, and Lifespan

Body size and life history shape nutrient removal mainly by controlling biomass-specific fluxes and the duration of sequestration. Larger individuals contribute more to areal nutrient processing simply because they represent more biomass (Atkinson et al. 2021). Lifespan is especially important for shell and tissue sequestration: many species of mussels are long-lived, slow-growing animals, with some species living up to a century, and shells can remain relatively intact for decades, so nutrients locked into shell and soft tissue may remain removed from rapid cycling for prolonged periods (Bakshi et al. 2023; Atkinson et al. 2023). Annual shell rings indicate that shell growth records cumulative environmental exposure and long-term storage dynamics (Bakshi et al. 2023).

Life history also matters because it covaries with tissue stoichiometry, growth rate, and longevity. Hopper et al. (2021b) showed that shell elemental composition ratios of C:P and C,Ca:P vary by species. Species with faster growth tended to have lower shell P, and fast growing species had relatively high shell C:P and C,Ca:P. The authors hypothesized that fast growing mussels allocate more P to soft tissues than slower growing mussel species, however, further research is needed. Similarly, van Ee et al. (2022) found that differences across species explained significant variability in clearance rates, respiration, N excretion, and P excretion rates, partially due to differences in body size but also differing tissue stoichiometric requirements, with faster growing species having a high P demand.

Several papers reported body size, biomass, or life history effects directly. In the Hopper et al. (2021a) study of 54 species across 14 aggregations in the Lower-Middle Tennessee basin and the Mobile basin, the combination of body size and species of individuals was a strong predictor of N and P excretion rates and the ratio of N:P. Body size alone was a significant predictor of dissolved organic carbon excretion. Atkinson and Forshay (2022) also noted that body size impacts biodeposition both among and within phylogenetic tribes.

Hydrologic Conditions: Flow, velocity, turbulence, and sediment interaction

Hydrology strongly regulates filtration, biodeposition, and the degree to which mussels influence benthic processes. Clearance rates are observed to generally rise with increasing water velocity until feeding saturation is reached, after which particle rejection and pseudofeces production increase and filtration efficiency can decline (Todd 2024). High velocity conditions can also cause excess bed shear stress leading to a decline in feeding or dislodgement of the mussel (Todd 2024). Todd (2024) found that clearance rates increased 260% as flow increased from 0 to 25 cm/s; however, beyond 25 cm/s clearance rates declined.

Todd (2024) also reported that particulate organic nitrogen (PON) biodeposition increased with water velocity before declining again as velocity increased further, indicating a non-linear relationship between hydrodynamics and particulate processing. At lower velocities (up to 5 cm/s) the PON biodeposits contained proportionally more organic matter than biodeposits under higher flow conditions (15-25 cm/s). The mass of PON per total biodeposit mussel hour also increased between 0 cm/s and 5cm/s before declining again at 15 cm/s and higher. This pattern held across all starting TN concentrations (10 µg/L – 1,000 µg/L).

van Ee et al. (2022) found that mussels contributed more to nutrient turnover at low flows, and that turnover distance varied jointly with discharge and temperature. This indicates that a mussel bed exerts the strongest influence where contact time between water and the bed is long enough for excretion and filtration products to accumulate relative to ambient nutrient concentrations.

In a paper by Sansom et al. (2020), the Reynolds number (R_e) is cited as a significant hydrologic variable that influences feeding efficiency and protects against dislodgement potential. R_e is a seemingly important "feed-back" trait that dense mussel assemblages intrinsically possess, particularly mussel beds of mixed taxa, mixed age class, and mixed shell sizes, wherein the flow regime (i.e. water velocity) at the stream bed interface tends to be favorably influenced by the aggregated presence of other mussels – especially, large mussels that both protrude above the stream bed surface and remain "anchored" within the substrate. Sansom et al. cite a density of ~25 individuals m^{-2} as a possible threshold for which R_e could become a significant phenomenon, which one could infer makes R_e a trait important enough to consider for its implications in the long-term viability/stability of local populations.

Hydrologic habitat also matters because mussel burial depth and proximity to the oxic-anoxic boundary affect whether excreted nutrients and biodeposits reach microbial hotspots where denitrification can occur (Atkinson and Forshay 2022; Kubala et al. 2024b).

Initial Nutrient Concentrations, Nutrient Limitation

Background nutrient concentrations and pollution levels are central to how mussels affect nitrogen removal and how mussels themselves respond to environmental stress. Denitrification responses are not linear across nutrient gradients: mussel density can reduce denitrification in N-limited sediments, but enhance it when sediments are amended with nitrogen, indicating strong dependence on initial nutrient limitation status (Todd 2024; Kubala et al. 2024b). On the stress side, mussels are highly sensitive to ammonia, nitrate, and other pollutants, and high nutrient loads can indirectly increase toxicity by stimulating algal growth, raising pH, and increasing the fraction of unionized ammonia (Bakshi et al. 2023). Thus, initial pollutant concentration shapes both the ecological function of mussels and their physiological viability.

In Atkinson and Forshay (2022), denitrification increased with mussel biomass, but the authors and the studies they cite also emphasize that nutrient limitation can reverse or reshape that relationship. Trentman et al. (2018), as discussed in Kubala et al. (2024b), found that in an N-limited stream, denitrification decreased with increasing mussel density, whereas N addition caused denitrification to increase with mussel density.

Temperature

Temperature affects both mussel metabolism and the microbial pathways that mediate nutrient removal. Temperature was a consistent physiological driver across the reviewed papers. Elevated temperatures increase oxygen consumption and ammonia excretion in mussels, and several studies note that higher water temperatures can worsen physiological responses and affect survival, growth, and reproduction (Bakshi et al. 2023). Temperature also modifies ammonia toxicity, with unionized ammonia becoming more harmful as temperature rises, especially when combined with elevated pH (Bakshi et al. 2023). Warmer conditions may also alter mussel activity and burrowing behavior, which in turn can influence bioturbation and sediment N-removal potentials (Kubala et al. 2024b).

van Ee et al. (2022) found that temperature explained the greatest amount of variation in clearance, respiration, and excretion among the 11 species examined, with species × temperature interactions indicating that taxa respond differently across the thermal gradient. In general, rates increased from 10 to 30°C, but the magnitude of increase differed among species and was partly structured by body size and thermal guild. Notably van Ee et al. (2022) found that thermally sensitive species contributed a greater fraction of ecosystem function than their total community biomass alone would predict, especially at warmer temperatures and lower flows; however, this was theorized to be related to excess metabolic stress.

Light Impacts

Light was identified as an important modifier to mussel nutrient cycling. Lodato et al. (2026) showed that mussels directly influenced NH_4^+–N and SRP fluxes, but these effects were detectable primarily in dark incubations. Under light conditions the relationship between excreted and accumulated nutrients was not significant. The authors interpret this as evidence mussel excretion stimulates benthic photoautotrophic activity and thus mussels are impacting sediment nutrient cycling.

Light influences also extend to filtration behavior. Hills et al. (2020) found that clearance rates differed between light and dark conditions and that the response was species-specific. The study investigated Asian clam (*Corbicula fluminea*) and paper pondshell (*Utterbackia umbecillis*), both species present in the Chesapeake Bay watershed, although *C. fluminea* is a non-native. During light conditions both species had relatively similar clearance rates (50 ± 18 mL/g/h and 41± 10 mL/g/h), but in dark conditions *C. fluminea* filtration doubled (110 ± 15 mL/g/h), while the *U. umbecillis* filtration rate was cut nearly in half (24 ± 6 mL/g/h). While primarily focused on invasive species, earlier studies cited by Hills et al. showed that light-related gaping, movement and light avoidance were often species-specific.

Sediment Properties and Bioturbation

Sediment characteristics influence how mussels couple the water column to benthic N removal. Mussel burrowing can increase oxygen penetration and disrupt the oxic–anoxic interface, potentially suppressing denitrification in some settings while promoting microbial turnover in others (Kubala et al. 2024a). Sediment depth, substrate type, and the degree to which mussels reside below the surface all influence nutrient deposition and microbial access to labile C and N (Atkinson and Forshay 2022; Kubala et al. 2024b).

Several papers converge on the idea that mussels influence nutrient removal not only by releasing nutrients but also by changing sediment structure and microbial access. Atkinson and Forshay (2022) argued that mussel patches translocate suspended particulates into benthic sediments and create heterogeneity that can facilitate denitrification. As previously noted, they observed that a substantial fraction of soft tissue biomass was buried below the sediment surface, which supports close coupling between mussels and sediment microbes. Kubala et al. (2024b) similarly found that mussels enhanced sediment nitrogen removal potentials and altered bacterial communities via nutrient release and bioturbation.

Bioturbation appears to be a particularly important link between excretion and denitrification. By transporting organic matter and dissolved nutrients into the sediment, mussels can create hotspots of coupled nitrification-denitrification, but the effect is contingent on oxygen penetration, burial depth, and vertical movement. Lodato et al. (2026) suggest that vertical movement may also introduce oxygen into the sediment and thereby dampen the influence of mussels on denitrification. Not every mussel-driven increase in sediment disturbance will enhance N removal; the direction depends on whether the disturbance creates favorable oxic-anoxic interfaces or oxygenates the sediment too thoroughly.

Water Chemistry

Water chemistry strongly modifies both mussel physiology and the downstream consequences of nutrient cycling. Low dissolved oxygen, low hardness, and high pH are all associated with greater stress or toxicity risk for mussels, and these conditions can coincide with eutrophication and high nutrient loading (Bakshi et al. 2023). The literature also notes that ammonia toxicity is especially severe under high pH and elevated temperature, while low-flow summer conditions in lakes and slow streams can intensify exposure to pollutants (Bakshi et al. 2023). These conditions matter for nutrient removal because stressed mussels may filter less efficiently, alter excretion chemistry, or experience mortality that reduces long-term sequestration potential.

Shell and Tissue Sequestration as Longer-Term Storage Pools

The reviewed papers also emphasize that nutrient removal is not limited to short-term fluxes. Shell and soft tissue act as storage pools that can sequester C, N, and P over different timescales. Atkinson et al. (2023) explicitly framed mussel tissues and shells as long-term reservoirs, noting that shells can persist for decades and thereby represent a lasting sink for nutrients and minerals. Lopez et al. (2026) expand on this by noting that shell calcification and decomposition contribute to carbon and nutrient cycling through both short and long-term pathways with shells requiring decades to release N and P back into the ecosystem, while in the short-term N and P from tissue can be made bioavailable during mass mortality events (DuBose et al. 2019 in Lopez et al. 2026)

Therefore, shell sequestration can be treated as a form of delayed nutrient retention and tissue sequestration as a short time scale, but meaningful sink, that can be exported from active cycling for the lifespan of the organism.

Summary

Overall, the reviewed papers indicate that native freshwater mussels in the Chesapeake Bay watershed should be described as multi-pathway nutrient processors whose removal effects depend on species, assemblage composition, body size, hydrologic residence time, ambient nutrient limitation, light, temperature, and sediment properties. Their strongest and most repeatable impacts occur where biomass is high, nutrients are limiting but not exhausted, and flow conditions allow excreted and biodeposited materials to interact with the sediment-water interface. Under those conditions, mussels can increase sediment denitrification potential, alter microbial community structure, and retain nutrients in shell and tissue pools over ecologically relevant timescales. At the same time, some research make clear that these effects are not universal: light can suppress the detectability of direct nutrient accumulation, high flow can reduce turnover distance, thermal stress can change excretion and clearance, and nutrient limitation can reverse the direction of biomass denitrification relationships.

Summary of discussions with researchers

Several interviews were conducted with researchers from universities, hatcheries, and other state and federal agencies. These included Dr. Carla Atkinson (University of Alabama), Dr. Dave Strayer (Cary Institute), Dr. Lance Butler (Philadelphia Water Department), Dr. Jonathan Lopez (University of Mississippi), Dr. Jess Jones (Virginia Tech/U.S. Fish and Wildlife Service), Mattew Ashton and Megan Kubala (Maryland Department of Natural Resources), Dr. Daniel Allen (Penn State University), and Dr. Sally Entrekin (Virginia Tech). Main findings from these discussions with these researchers are summarized below:

Dr. Carla Atkinson

Dr. Carla Atkinson (University of Alabama) noted that while freshwater mussels have clear potential as nutrient removal tools, there are still major knowledge gaps related to filtration rates, growth rates, biodeposition, species-specific differences, and how these functions vary under different field conditions such as background nutrient levels. She emphasized that population estimates are needed before reduction efficiencies can be quantified and applied with confidence, and that this will require better coordination among state and regional partners, so existing datasets can be integrated and identified data gaps can be filled. She also noted that everyone has different data formatting (e.g., units, methods), so researchers need to find a way to standardize that data to be able to coordinate.

A major theme of the conversation was hatchery propagation and reintroduction. Dr. Atkinson recommended careful consideration of genetic and ecological fit when sourcing mussel broodstock, preferably using those sourced from the same waterbody where reintroduction is planned. She noted that long-term success depends on whether introduced mussels can survive, reproduce, and become self-sustaining, which may take a decade or more. She also noted that hatchery-based efforts could provide useful data for tracking individuals, estimating secondary production, and quantifying ecosystem fluxes, including nutrient assimilation into tissue and shell.

The discussion also highlighted that mussel-based nutrient reduction credits will likely depend on species and site conditions. Dr. Atkinson explained that sequestration and denitrification rates are highly variable across species and settings, and that some locations may offer greater benefits than others depending on flow, background nutrient concentrations, and other waterbody conditions. She also pointed out that increased residence time may increase interactions between mussels and the water column, potentially improving denitrification; however, very low-flow conditions could also create stress and reduce filtration activity.

Dr. Dave Strayer

Dr. Strayer, a retired scientist who previously worked at the Cary Institute, emphasized that the strongest ecological effect of mussels is not necessarily long-term nutrient removal through soft tissue or shell sequestration, but rather the interaction between mussel biology and hydrology. He noted that sequestration in soft tissue is likely limited for long-term nutrient removal, unless mussels are harvested and removed from the system, which does not generally apply to unionids.

Dr. Strayer also emphasized that biodeposition outcomes depend heavily on the hydrologic setting, with retained sediments and nutrients occurring more often in reservoirs or similar environments than in free-flowing rivers where material is likely to be resuspended or transported downstream. Dr. Strayer suggested that any crediting approach should focus first on hydrologically favorable sites, possibly including reservoirs, rather than assuming that the presence of mussels alone will generate measurable reductions. Dr. Strayer also noted that using oysters as a model could be informative for mussels nutrient recycling and for nutrient crediting.

The discussion also highlighted important knowledge gaps. Dr. Strayer noted that much of the literature focuses on feeding and clearance rates, but far less is known about the fate of feces, pseudofeces, and biodeposits after they are produced. He pointed out that bacterial mineralization could quickly convert retained biodeposits back into dissolved nutrients if the material is not hydrologically isolated, limiting any real water quality benefit. Overall, the discussion with Dr. Strayer reinforced that a nutrient crediting system for mussels will likely need to account for system-specific hydrology, and temporary sequestration during population buildup.

Dr. Lance Butler

Dr. Lance Butler (Philadelphia Water Department) emphasized that while there is substantial literature recognizing freshwater mussels as providers of ecosystem services, the field has historically lacked funding, coordination, and a management framework that treats mussels as a BMP, particularly compared to marine systems where ecosystem service valuation is more advanced. His work reflects a growing shift toward addressing these gaps, including research conducted at a state-of-the-art facility examining mussel performance in novel urban habitats. Dr. Butler's research focuses on three Bay species (eastern elliptio, alewife floater, and eastern pondmussel), evaluating clearance rates, absorption efficiencies, and net nutrient processing to better understand functional performance under varying environmental conditions. He stressed the importance of distinguishing between clearance and filtration rates and highlighted that factors such as temperature, density, species, and size strongly influence mussel performance. He also observed that ecosystem service benefits increase at densities of approximately 10–20 individuals per square meter.

Dr. Butler highlighted several data gaps, for example net nutrient removal from freshwater mussels, noting that only a limited number of studies quantify net sequestration across tissue, shell, and reproduction. His own work attempts to address this through modeling and empirical measurements. He stressed that habitat context (e.g., stormwater wetlands vs. tidal systems vs. rivers) and hydrology (e.g., retention time and flow) are critical in determining restoration success and nutrient reduction potential of freshwater mussels, noting that "one-size-fits-all" approaches are inappropriate.

Dr. Butler identified several priorities for advancing the field: improving aquaculture technologies and coordination across hatcheries (currently around 12–13 in the U.S., largely focused on endangered species), expanding datasets across species, and strengthening collaboration among researchers and practitioners. While preliminary estimates from his work suggest nitrogen removal rates of around 1 to 5 percent, he emphasized that mussels provide multiple co-benefits beyond filtration, including sediment stabilization and habitat creation, and that understanding these ecosystem services will be critical for future valuation and potential incorporation into nutrient management frameworks.

Dr. Jonathan Lopez

Dr. Jonathan Lopez (University of Mississippi) emphasized that while substantial progress has been made in quantifying freshwater mussel contributions to nutrient cycling, particularly at the species level in the southeastern United States, such as the lower Mississippi River, key gaps remain for applying these findings to management frameworks such as TMDLs. Existing research provides relatively strong estimates of carbon and nutrient storage and recycling rates for well-studied species, but translating these measurements into meaningful ecosystem-scale impacts is challenging without comprehensive information for an entire system using a mass balance framework.

Dr. Lopez noted that much of the current research has been conducted in nutrient limited, biodiverse systems, where mussels primarily function as nutrient recyclers that support primary production. In contrast, management interests, particularly in regions like the Chesapeake Bay, are increasingly focused on nutrient reduction and removal. Emerging work, for example from Dr. Carla Atkinson's lab, is investigating processes such as denitrification from mussels and removal of nitrogen from the system. However, Dr. Lopez noted that this area is still in its early stages.

Dr. Lopez highlighted the need for species-specific data, especially for dominant or restoration-target species in the Mid-Atlantic. While genus-level or regional extrapolations are sometimes used, particularly for rare species, these approaches introduce uncertainty and are not ideal for management applications. He emphasized that BMP development will require direct measurements of key species, along with a better understanding of habitat requirements and the factors controlling restoration success. Overall, priority research needs include expanding species-level datasets, improving ecosystem scale mass-balance modeling, and advancing understanding of denitrification and nutrient removal pathways in eutrophic systems.

Dr. Jess Jones

Dr. Jess Jones (U.S. Fish and Wildlife Service & Virginia Tech) emphasized that research on freshwater mussel nutrient dynamics is both important and highly complex, with variability driven by species differences, size classes, and environmental conditions (e.g., flow, temperature). Dr. Jones highlighted the importance of focusing on dominant species like *E. complanata*, which contribute a lot to filtration in systems due to their abundance, high clearance rates, and long lifespans (often 40–60 years), enabling long-term nutrient sequestration in shell and soft tissue, often for decades. However, he stressed that nutrient removal pathways can vary widely. Denitrification can be significant under certain conditions but inconsistent across systems, while sequestration and biodeposition also play roles that depend on environmental factors such as nutrient availability.

Dr. Jones summarized his team's research efforts on understanding freshwater mussel ecosystem functions, particularly in the Potomac River basin and other rivers in Virginia. His team conducts species-specific clearance rate studies on about half a dozen mussel species, examining how filtration varies across size classes, environmental conditions, and time. His work involves a project at National Harbor, Maryland where mussels are being cultured, grown, and periodically sampled at different sizes to measure filtration dynamics. Dr. Jones and other members of his team are also collaborating with the Resource Protection Group to investigate denitrification and other ecosystem services in restored tributaries, focusing on dominant species like *E. complanata*. This work integrates field studies, restoration monitoring, and experimental approaches to better quantify how mussels contribute to nutrient cycling under real-world conditions. While early findings suggest that mussels can drive denitrification under certain conditions, the project overall highlights substantial variability and complexity, reinforcing the need for long-term, ecosystem-scale data to properly evaluate their role in water quality improvement and restoration outcomes.

Dr. Jones noted that much of the current research and studies may underestimate mussel ecosystem services because traditional laboratory methods fail to replicate natural conditions, particularly the fact that most mussels are buried and feed interstitially rather than as suspension feeders like oysters. This has implications for modeling and BMP development, as mussels may filter and process more material in their natural habitats compared to when measured experimentally. Dr. Jones noted that, while denitrification is likely the most relevant pathway for nutrient reduction crediting in Chesapeake Bay BMP frameworks, focusing exclusively on it risks overlooking broader ecosystem services such as biodiversity support and ecosystem function. He also stressed that restoration and population sustainability are inherently long-term, spatially complex processes and that determining whether mussel populations are self-sustaining can take decades, making near-term evaluation better focused on survival, growth, and reproduction metrics.

Matthew Ashton and Megan Kubala

Matthew Ashton and Megan Kubala (Maryland Department of Natural Resources) emphasized that efforts to quantify ecosystem services from freshwater mussels are often unnecessarily complicated by concerns about biodiversity, species differences, and high-level ecological research. Matthew argued that BMPs for freshwater mussels should focus on straightforward, defensible metrics such as nutrient sequestration in shell and tissue rather than more complex processes like clearance rates or denitrification. Both Matthew and Megan suggested that existing data are likely sufficient or close to sufficient to support crediting frameworks but remain underutilized, often sitting in raw or unpublished form across researchers.

Data gaps mentioned included standardized measurements across species, life stages, and locations, but they noted that these are possible to address with targeted analysis rather than extensive new fieldwork. While data gaps exist, Matthew noted that the biggest barrier is that the Chesapeake Bay Program and regulatory agencies are becoming increasingly conservative about which BMPs they approve. Even with sufficient science, acceptance into the crediting framework is uncertain, which discourages investment and participation.

Matthew highlighted that focusing on shell and tissue nutrient sequestration could enable faster credit adoption compared to more complex pathways, similar to what is already happening with oysters. Maryland Department of Natural Resources is actively working to collect information on shell and tissue sequestration. Initial data collected was summarized in Table 3. The data were collected as part of the state's Freshwater Mussel Propagation Nutrient Assimilation Monitoring program. The propagation activities are focused on augmenting wild populations to improve water quality, rather than on conservation as an end goal. The candidate mussels for *in situ* propagation (and subsequent analysis) included *E. complanata*, *E. fisheriana*, *L. radiata*, and *P. cataracta*. Maryland Department of Natural Resources provided the Quality Assurance Project Plan (QAPP) for the project, which provides standardized protocols for mussel culture, mussel measurement, sample processing and particulate nutrient sample analysis. The monitoring program generates tissue and shell percent particulate carbon, nitrogen and phosphorus content on a dry weight basis. The QAPP provides a standardized methodology, which can be repeated elsewhere.

The discussion also highlighted practical research needs, such as compiling existing datasets, conducting lab analyses on whole-body samples, and leveraging ongoing monitoring efforts. Funding and incentive structures were cited as barriers, since stakeholders are hesitant to invest without guaranteed credits. Overall, the interview highlights that progress depends less on new science and more on mobilizing existing data, simplifying the framing, and committing institutional support to move mussel BMP crediting forward.

Dr. Daniel Allen

Dr. Daniel Allen (Penn State University) described a Chesapeake Bay Trust-funded proposal, developed with the Maryland Department of Natural Resources, aimed at addressing a key data gap in understanding freshwater mussels' role in nutrient dynamics in Maryland's coastal plain streams. If funded, the project will focus on collecting baseline data by comparing nutrient concentrations upstream and downstream of mussel beds, conducting mesocosm experiments, and quantifying nitrogen sequestration in mussel tissue and shells across a gradient of land uses from forested to agricultural systems. Dr. Allen emphasized that this type of work has not yet been conducted in the region and follows broader approaches outlined by other researchers.

Throughout the discussion, Dr. Allen highlighted major uncertainties in the field, particularly around species-specific clearance rates, variability within genera, and nutrient processing pathways such as denitrification and sequestration. Dr. Allen cautioned against making management decisions or assigning BMP credits without sufficient data, stressing the need to understand how mussels function within the system. Dr. Allen suggested that nutrient storage differs by life stage, with juveniles potentially contributing more to sequestration and adults to nutrient cycling, though he underscored that these ideas remain largely untested. He also noted that soft tissue likely stores more nitrogen than shells, though shells provide longer-term storage. He also suggested that restoration or hatchery efforts prioritize species that are easier to propagate. Overall, Dr. Allen reinforced that while freshwater mussels hold promise for nutrient management, substantial foundational data are still needed before their ecological functions can be confidently incorporated into restoration strategies or crediting frameworks.

Dr. Sally Entrekin

Dr. Sally Entrekin (Virginia Tech) discussed ongoing work in restored urban stream systems in northern Virginia, conducted in collaboration with the Resource Protection Group (RPG) and partners including U.S. Geologic Survey, Dr. Jess Jones, and others. The RPG is focusing on two hydraulically restored streams in Reston that have been regraded and reconnected to their floodplains, to evaluate the effects of mussel introductions (primarily *E. complanata)* on nutrient dynamics and macroinvertebrate communities. Dr. Entrekin noted that current flux models are limited by insufficient high-flow data, which is critical for capturing nutrient transport dynamics in these systems.

A major theme of the discussion was the challenge of detecting measurable nutrient effects in open systems, particularly in relatively low-nutrient or hydrologically dynamic streams. Dr. Entrekin emphasized that much of the evidence for nutrient removal, including parallels to oyster BMPs, comes from controlled chamber studies rather than field-scale observations. Dr. Entrekin highlighted that system context is critical: oligotrophic systems may show limited removal potential, while more eutrophic systems could produce stronger signals but also introduce physiological stressors for mussels. Her team is also investigating stress thresholds (e.g., salinity impacts) and species-specific responses, while continuing to explore biotic interactions, particularly the relationship between mussels and macroinvertebrate communities.

From a crediting perspective, Dr. Entrekin emphasized a stepwise approach similar to existing BMP frameworks: first establishing predictable per-organism sequestration or removal rates (e.g., from chamber studies), then scaling these to the ecosystem level while accounting for broader ecological responses. She noted that linking mussel restoration to biological condition metrics such as indices of biotic integrity (IBIs) could help connect nutrient dynamics with aquatic life benefits, though this remains challenging. More broadly, Dr. Entrekin emphasized the importance of expanding the narrative around mussel ecosystem services beyond nutrient storage alone to include habitat and ecological function. She also identified the need for improved coordination, including shared data repositories and regional collaboration (e.g., a Mid-Atlantic mussel network), and highlighted the potential for hatchery-based restoration programs to be integrated into incentive or crediting frameworks if better aligned with monitoring and data-sharing efforts.

Findings

Overall General Findings

One of the basic components of understanding and developing possible nutrient reduction credits is the measurement of ecological services that are comparable across species and systems. Therefore, improved standardization of units and measurements (or establishing correlation coefficients between existing measurements) will be needed to fully apply existing measured rates. As noted in many of the researchers' interviews, the data collected to date are largely not standardized in method or units. This is consistent with the data collected from the recently published literature, where each metric was only evaluated by one or two studies, making comparisons or summary conclusions challenging.

A separate finding is that, although much has been done to evaluate nutrient sequestration and denitrification rates for many freshwater mussel taxa, there is a paucity of such data for species endemic to the Chesapeake Bay watershed for which a credit could be developed.

Even the more common species (e.g, *E. complanata*) lack basic sequestration and denitrification rates. On a more positive front, there is ongoing research (see Dr. Jones, Dr. Entrekin, and Matthew Ashton summaries) to look at these factors within the Potomac River watershed. Additionally, Dr. Allen's work, if funded, has the potential to fill in some of the basic gaps for mussels in several Maryland tributaries. Although it is outside the Chesapeake Bay watershed, Dr. Butler's work in ultra-urban waterways may also contribute to the body of knowledge on this topic.

Lastly, environmental variability must be better understood in the role it plays in nutrient dynamics within mussel beds. This includes broad knowledge of system (watershed or tributary) dynamics that include temperature regimes, level of eutrophication, biodiversity of mussels, and life history parameters (age, lifespan, etc). While it is recognized that biodiversity is not a goal of credit development, species overlap does play a role in aquatic metabolism and therefore can be parameterized.

Freshwater Mussels as a BMP

One of the objectives of this project was to evaluate whether there is sufficient data to develop nutrient reduction crediting values for freshwater mussels as a BMP. Given the lack of published data on nutrient removal values for species endemic to the Chesapeake Bay watershed and within the Chesapeake Bay watershed, the authors of this assessment determined there is insufficient new data to advance specific nutrient reduction values for consideration as part of a freshwater mussel BMP. While there is not enough data currently, the most promising options for nutrient crediting are denitrification and sequestration in shells and tissue. With sequestration having the advantage of potentially more straightforward data collection processes and denitrification having the advantage of permanently removing nitrogen from the ecosystem but with more uncertainty about appropriate values and context-dependent variability. Future sequestration BMPs will need to consider the crediting implications if there is a mussel bed die off, which would release nutrients back into the water column, while this would not be an issue for denitrification. Under both mechanisms, regular verification of persistent populations will be required to maintain credits over time.

The remaining components of this assessment focus on the factors that could influence nutrient removal values, identifying data gaps, and making recommendations for advancing the research with a focus on developing one or more freshwater mussel BMPs.

Factors impacting nutrient/sediment removal or processing

Several factors influence how mussels remove nutrients and sediments. These have been alluded to by several of the researcher interviews, in addition to the literature review, but should be noted individually.

Species

It is widely acknowledged that Unionid species span a broad extent of evolutionary lineages and therefore exhibit diverse metabolic traits and sensitivities to environmental variability. Furthermore, growth rates and lifespans vary considerably between species, even within the same genera, making broad estimates of rates of removal impossible between species.

Waterbody hydrology and water quality characteristics

Several authors and interviewees reiterated the need to understand the aquatic environment that mussels inhabit, specifically considering flow and level of eutrophication. Both elements affect the concentrations of nutrients that individual mussels are exposed to, thereby affecting removal rates. Similarly, low flow areas may not carry away excreted metabolites thereby initiating a localized regeneration of the nutrient cycles, depending on microbial community dynamics. van Ee et al. (2020) noted that low river discharge rates impacted ecosystem functioning of the mussel populations. Levels of eutrophication play an outsized role in nutrient dynamics; i.e. greater concentrations of nutrients result in increased removal rates, although these rates plateau at high concentrations. Much of the general body of literature on freshwater mussel nutrient removal processes has focused on oligotrophic streams in the southeastern United States, making those data less translatable to the frequently eutrophic conditions in the Mid-Atlantic.

Light Conditions

As previously noted, light conditions affect nutrient cycling in aquatic systems. Research has demonstrated variability in clearance rates on a diurnal cycle, reflecting increased metabolism during daylight hours. Although not noted as a direct effect in the literature, more natural conditions include well-developed tree canopies in the riparian zone, thus shading streams from passive solar radiation. In this sense, the light regime (or shading) would naturally affect water temperatures, which affect metabolic rates.

Temperature

As with all living organisms, temperature has a large influence on metabolism. It was noted earlier from the literature review how temperature interacts with metabolic processes including NH4 excretion in addition to growth (N, P assimilation in tissues and shells). Waterbodies with known thermal spikes or chronic high temperatures (e.g. those found in urbanized watersheds) should be evaluated for the viability of mussel growth and survival.

Summary of findings

1) Existing data are insufficient to develop Chesapeake Bay freshwater mussel nutrient reduction efficiencies for BMPs.
2) The greatest scientific support currently exists for shell and tissue sequestration pathways.
3) Denitrification remains promising but highly uncertain and context dependent.
4) Species-specific and site-specific variability are major drivers of nutrient processing.
5) Lack of standardized methods and datasets is a major barrier.
6) Several active research efforts may substantially reduce current uncertainties within the next 3-5 years.

Uncertainties and Data Gaps

A number of uncertainties and data limitations currently constrain the ability to quantify the nutrient-reduction benefits of freshwater mussels and to apply these findings consistently across the Chesapeake Bay watershed. One of the most significant challenges is the lack of standardized measurement protocols. Existing studies vary widely in their methods and reporting units, making it difficult to compare results or synthesize findings into a unified set of nutrient-reduction efficiencies. Establishing consistent protocols would substantially improve the reliability and comparability of future research.

Another major source of uncertainty relates to the environmental conditions in which freshwater mussels are studied. Factors such as stream size, flow variability, temperature, and surrounding land use can strongly influence filtration rates, denitrification, and nutrient sequestration in both tissue and shell. This variability makes it difficult to generalize results across systems or extrapolate findings from one site to another, supporting the need for site-specific or basin-scale studies that account for environmental variability when evaluating the ecological function of freshwater mussels.

There is also a need for more research focused specifically on the factors unique to the Chesapeake Bay and its tributaries. Many existing studies focus on other regions, such as the southeastern United States, and their findings may not fully reflect the environmental conditions such as hydrologic or biogeochemical conditions found in the Chesapeake Bay watershed. Additionally, majority of the studies found focus on species found outside of the Chesapeake Bay watershed.

In addition to better understanding environmental factors particular to the Chesapeake watershed (and its physiographic provinces), there is a singular massive gap in data characterizing the specific ecosystem services provided by endemic species. As noted elsewhere, understanding the basic removal rates of native mussel species are underrepresented in the literature. From interviews and comparisons to other research outside the region, this is likely the primary data gap to be addressed.

A related gap is the limited understanding of what an “unaltered” or reference mussel community looks like in the Chesapeake Bay. While the “Eden” river may not exist, it is important to understand the unaltered dynamics of lotic systems in which mussels evolved. While inferences may be made by studying least-impaired rivers, the gap in understanding a pristine system remains and will likely remain so.

Finally, sediment removal by freshwater mussels remains an understudied aspect of their ecological function. While studies exist that do quantify sediment/total suspended solid removal by mussels, these rates have not been established for species native to the Chesapeake watershed. Uncertainties and data gaps and progress towards closing the gaps are summarized in Table 4.

Table 4. Uncertainties and data gaps

Topic	Status
Standardized metrics and methods	Insufficient
Accounting for site-specific conditions that impact nutrient removal values	Insufficient
Data on Chesapeake Bay-specific species	Developing, but insufficient
Reference conditions in Chesapeake Bay watershed	Insufficient
Impacts on sediment	Insufficient in Chesapeake Bay species

Considerations for BMP Crediting

Biogenic nutrient removal is a recognized BMP but has largely been restricted to plants which sequester nutrients into tissues, either long-term (e.g. trees) or shorter term, but removable (e.g. algae at wastewater treatment plants). One of the few animals used for nutrient credits is the eastern oyster (*Crassostrea virginica*), a bivalve found in coastal waters of eastern North America. Oysters, which inhabit brackish to fully marine waters, are efficient filter feeders that are extremely effective at removing algae from the water column and incorporating the metabolized nutrients into tissue. Additionally, oysters facilitate denitrification through microbial activity. The oyster BMP is often touted as a model for freshwater mussel BMP development. There are differences to consider, however, between the two taxa. Oysters live in tidally mediated systems, so water hydrodynamics are more complicated than those found in lotic systems (where the majority of freshwater mussels are found). Secondly, oysters can be harvested, thereby permanently removing sequestered nutrients from the system. In contrast, freshwater mussels are rarely harvested for human use, therefore the lifespan of the species plays a larger role when calculating BMP temporal impacts.

When considering the development of a mussel BMP, accurate mapping of existing beds will be a critical component when assigning credits. Currently there is variability between the Chesapeake watershed states in terms of mapping mussels. To the extent possible, states should consider updating mussel distribution maps.

Recommendations and Next Steps

To support the effective use of freshwater mussels in nutrient-reduction strategies, researchers will need to work within a more coordinated and standardized framework that promotes consistency across studies. Current variability in sampling approaches, analytical techniques, and reporting units limits the ability to synthesize findings or generate accurate nutrient reduction values.

Future research should also focus more explicitly on the environmental conditions and species relevant to the Chesapeake Bay watershed. As noted prior, nutrient processing functions can vary widely across landscapes, hydrologic regimes, and land use contexts, making it difficult to generalize findings from studies conducted in other regions or under different environmental settings. Targeted, region-specific research is therefore essential for accurately characterizing freshwater mussel nutrient dynamics and for informing restoration, management, and potential crediting frameworks within the Chesapeake Bay context. In addition to conducting research within the Chesapeake watershed, focus must be kept on native species and determining those species-specific parameters. Furthermore, species-specific research should prioritize those species currently propagated in hatcheries as these are the taxa most likely targeted for nutrient credits (e.g., *E. complanata*).

Mussels are ecosystem engineers and play a key role in moving nutrients from the water column to the sediment and interstitial microbial populations. Quantifying denitrification remains a critical research need. Through our literature review, and discussions with experts, very few studies have quantified freshwater mussels' role in denitrification. Improved measurement of denitrification rates, particularly under Chesapeake Bay-specific conditions, would help with understanding the extent to which mussels contribute to permanent nitrogen removal versus nutrient recycling.

Strengthening coordination among hatcheries, researchers, and resource managers will be essential for increasing progress in nutrient reduction. Increased collaboration can support more consistent information sharing, improve propagation and husbandry techniques, and facilitate the exchange of data on survival, growth, and nutrient-processing. A more integrated hatchery network would also help ensure that restoration efforts are aligned with regional conservation priorities and that emerging research is incorporated into management decisions.

Finally, to accomplish these goals, dedicated funding for basic research will be needed. Existing frameworks (e.g. the Freshwater Mussel Partnership) provide an infrastructure that can be exploited for collaboration and expertise already in place. Funding can originate from a wide variety of sources including federal (e.g., EPA, U.S. Fish and Wildlife Service), states (those agencies responsible for BMP credits), and a variety of non-government organizations research funds (e.g. Chesapeake Bay Trust).

Opportunities for taking action on next steps can be discussed by sharing the findings of this state of the science assessment with the Freshwater Mussel Partnership at their next annual meeting and presenting the findings to the Conowingo Watershed Implementation Team. Follow-up should continue with the researchers noted above that have ongoing and potential future relevant research.

The recommended next steps, along with potential general timeframes, are summarized in Table 5.

Table 5. Summary of Recommend Next Step Action Items

Item	Action	Timeframe for Implementation	Notes
1	Share findings of this assessment with Freshwater Mussel Partnership and other organizations and at events throughout the watershed.	Near-term	Potential events include the Virginia Freshwater Mussel Science Symposium (August 2026)
2	Focus on gaining approval for N removal through shell/ tissue sequestration of *E. complanata* for near term CBP approval due to the relative amount of data and active focus on research within at least one jurisdiction.	Medium-term	Requires implementation of action items 3, 4 and 5.
3	Conduct watershed-wide freshwater mussel surveys and establish a commonly formatted structure for an extensive mussel distribution database and coordinate with appropriate agencies to establish most abundant species and most suitable environments.	Near-term	In part, this is carried over from the STAC report recommendation for surveys to establish existing species distribution and abundance.
4	Develop standardized metrics and methodologies for desired parameters	Near-term	

Item	Action	Timeframe for Implementation	Notes
5	Conduct shell/tissue sequestration analysis more widely within the watershed for *E. complanata* and additional hatchery-reared abundant species, using standardized methods and reporting units.	Near-term	Coordinate with hatcheries on abundant species successfully reared in hatcheries Coordinate among state agencies/hatcheries/researchers on standardized reporting units Should follow metrics in item 4.
6	Conduct/fund in situ and mesocosm experiments within the Chesapeake Bay watershed to establish baseline data for determining N denitrification efficiencies for species identified in earlier action items as abundant hatchery species.	Long-term	Should follow metrics in item 4.
7	Leverage ongoing and proposed research initiatives identified in this assessment for additional funding	Near- and long-term	

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