Small Creatures, Big Challenge: A review of current knowledge and assessment of research needs to inform water withdrawal management for the Duck River's freshwater mussel fauna

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Cooperator Science Series # 176-2026

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Contractual References:

This document (USGS IPDS #: IP-180724) was developed in conjunction with the U.S. Geological Survey, Tennessee Cooperative Fishery Research Unit in collaboration with the funding partner, The Nature Conservancy.

Recommended citation:

Womble, K.I. and A.E. Rosenberger. 2026. Small Creatures, Big Challenge: A review of current knowledge and assessment of research needs to inform water withdrawal management for the Duck River's freshwater mussel fauna. U.S. Department of Interior, Fish and Wildlife Service, Cooperator Science Series FWS/CSS-176-2026, Washington, D.C. https://doi.org/10.3996/css87791634

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January 2026

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[1] DISCLAIMER: Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Live vertebrates were not part of the research being reported.

Executive Summary

The Duck River is a remarkable national resource, boasting outstanding biodiversity (Ahlstedt et al. 2017). It contains 151 fish species, over 60 mussel species, and 22 snail species, many of which are federally listed (Etnier and Starnes 1993; Johnson et al. 2013; Ahlstedt et al. 2017; Womble and Rosenberger 2025a). The Duck River watershed is at a pivotal time in its management and ecological history due to significant growth in human population and economic activity. The consequent increase in surface water demand presents challenges for sustainable water resource management. The Tennessee Department of Environment and Conservation (TDEC) has permitted or proposed to permit eight water utilities to withdraw over 77 million gallons per day (mgd) from the Duck River, representing > 40% increase from previously permitted amounts (USFWS 2025). On November 20, 2024, Tennessee Governor Bill Lee signed Executive Order No 108 to ensure long-term stability of the Duck River watershed through balancing economic growth, water resource management, and environmental conservation. Some primary components of this plan are the creation of a Comprehensive Regional Drought Management Plan, the development of a Habitat Conservation Plan, and the establishment of the Duck River Watershed Planning Partnership (DRWPP). Although the planning partnership is not focused on a sole aspect of the Duck River, but the watershed as a whole, the mussel assemblages of the Duck River have been a particular focus due to their importance in providing ecosystem services, sensitivity to water quality, conservation status, and sensitivity to periodic drought conditions in this system.

With multiple state and federal agencies involved in managing the Duck River's unique water resources, a focused review on how future water management could affect the freshwater mussel communities in the Duck River will contribute to this process.

Our objectives of this review are to:

1. Review the effects of changing flow regimes on mussels, with emphasis on the effect of droughts/low flows, highlighting key processes/factors affecting mussels.
2. Highlight critical data gaps that could allow future, evidence-based water management decisions in this system.
3. Propose research topics to address critical data gaps and enable evidence-based water management decisions that consider the needs of freshwater mussels.

Freshwater mussels are a critical component of riverine ecosystems, providing ecosystem services including water filtration, nutrient cycling, and habitat provision (Vaughn et al. 2004; Haag 2012) that benefit human communities. Environmental flows, also referred to as ecological or e-flows, refer to the quantity, timing, and quality of water flows necessary to maintain the ecological health of rivers, wetlands, and other aquatic ecosystems (Acreman and Dunbar 2004; Acreman 2016). For freshwater mussels, environmental flows include maintaining a flow regime and associated water quality regimes that are favorable for both juveniles and adults while also seasonally supporting host fish and the survival of settling glochidia (i.e., larval mussels) in suitable environments (Gates et al. 2015). Freshwater mussels are adapted to the

natural flow regime of their native streams, including seasonal variability in flows. As sedentary filter feeders, mussels require adequate water flow to provide oxygen and food (Allen and Vaughn 2009); however, they also require periods of low flow to increase access to fish hosts and to ensure juveniles are not displaced (Gates et al 2015). Mussels are sensitive to water quality conditions, including pollutants, sedimentation, and artificial alterations of temperature and pH (Strayer and Malcom 2012). Mussel community characteristics, including presence, abundance, and species richness, generally increase with stream size (e.g., stream order); however, responses to changes in flow conditions are often species-specific, and the magnitude and timing of extreme flow conditions have more predictive power for mussel community response than general changes in flow (Lopez and Vaughn 2021). Complex hydraulic variables, such as relative shear stress and Reynolds number, can be strong predictors of mussel community responses because they combine simple hydraulic variables (e.g., velocity, depth) with stream channel characteristics, such as substrate composition and dynamics.

Droughts directly and indirectly affect mussels by influencing their physiology, behavior, reproduction, and ecosystem roles. Mass mussel die-offs during droughts and low water conditions are widely documented (Vaughn et al. 2015; Sousa et al. 2018; Dubose et al. 2019). Droughts can also lead to a shift in mussel community composition, with drought-tolerant species becoming more dominant while more sensitive species experience declines (Galbraith et al, 2010; Lopez et al. 2022; Vaughn and Atkinson 2025). Droughts affect mussels through direct mortality from stranding as well as physiological stress from altered water temperature and quality, reduced habitat and food availability and quality, increased predation and competition, disruption of reproductive cycles, and increased susceptibility to disease and pathogens. Although the effects of droughts, water withdrawals, and low flow conditions on mussels are an increasing area of study, there is a general paucity of data-driven consensus regarding optimal mitigation approaches and strategies (Cushway et al. 2024). Long-term management decisions regarding water withdrawals, particularly during extended or multi-year drought conditions, may consider factors beyond direct mortality such as the sublethal effects of drought and low flow conditions on freshwater mussels for a comprehensive understanding of the effects of prolonged low flows on freshwater mussels and aquatic communities.

The high levels of diversity and endemism in the Duck River have led wildlife, conservation, and academic entities to prioritize the river for conserving freshwater biodiversity. Over 70 species of freshwater mussels were reported historically from the Duck River watershed, over 60 of which are extant. The Duck River harbors 15 federally listed mussel species and hosts the most viable remaining populations of species such as the Slabside Pearlymussel (*Pleuronaia dolabelloides*), the Birdwing Pearlymussel (*Lemiox rimosus*), and the Cumberland Rockshell (*Theliderma intermedia*). Mussel populations in Duck River are critical for state-wide mussel propagation and reintroduction efforts. While the river harbors critical aquatic resources, the portion containing the most diverse and abundant mussel populations is restricted to the area between Columbia and Lillard Mill, which is approximately 50 river miles.

Extreme droughts were recorded in the Duck River watershed in the fall of 2000, 2007, 2016, 2023, and 2024 (USFWS 2025). An exceptional drought occurred in the Duck River watershed in 2007, characterized by prolonged, below-average precipitation and record-high temperatures. This drought demonstrated that severe drought conditions can occur in the Duck River regardless of Normandy Lake's elevations, highlighting the need for flow-based drought triggers to protect aquatic communities in the mainstem Duck River (TRDRA 2013a). Drought conditions occurred in the Duck River watershed in 2024, during which time several mussel stranding events were documented (Hubbs 2024). The observation of hundreds of fresh dead mussels, including federally listed species, highlights conservation concerns given the likelihood of future drought conditions in the watershed.

Generally, wetted channel width and direct mortality from stranding are the primary considerations when assessing the effects of droughts and low flows on freshwater mussel populations. Although direct mortality from stranding or thermal stress is relatively straightforward to observe (though we likely only measure a small portion of stressed, moribund, or fresh-dead individuals during these events), the long-term effects of compromised individual, population, or assemblage-level viability are complex to measure and poorly understood. Although each discrete decision about water withdrawals or flow alterations may appear to have limited ecological consequences when evaluated in isolation, our review suggests that these incremental changes can compound over time. Comprehensive assessment of flow alterations would benefit from considering multiple components of the flow regime (magnitude, frequency, duration, timing, and rate of change), complex hydraulic variables (such as shear stress and Reynolds number), geomorphological processes, water quality parameters, thermal regimes, food resource availability, host fish interactions, and life-stage specific requirements of mussels. An integrated, evidence-based approach that incorporates this ecological complexity will provide a more robust understanding of how flow regime modifications influence the persistence and resilience of the Duck River's mussel fauna, particularly during periods of drought. This multifaceted perspective aligns with our review, which offers a foundation for more comprehensive flow management considerations.

Creating a process for understanding the effects of drought and low flows on the ecology and ecosystem services of the Duck River would allow members of the Tennessee Duck River Development Agency (TDRDA) to develop a rapport for water managers, researchers, and conservationists about the ecological resources of the basin and how they could be considered in tandem with other essential ecosystem services for planning for drought and low flow conditions (Rack et al. 2024). This would be a collaborative process incorporated into the updated drought management plan under development by the TDRDA. Based on the feedback from the working group at the 2025 Tennessee Endangered Mollusk Committee meeting and our results, evidence-based flow thresholds could be established to trigger mitigation of low flow events, alteration of water use in the basin, or other actions to mitigate drought before harm to the Duck River and the ecosystem services it provides takes place.

Based on our review, we identify the following research and information needs: comprehensive and regularly updated spatial description of freshwater mussels in the Duck River, investigations of flow-water quality relationships along the Duck River (depth, temperature, dissolved oxygen, ammonia, alkalinity/calcium carbonate ions, algae and fine particulate matter, and heavy metals), instream flow studies specific to the Duck River that complement existing work underway by the Tennessee Wildlife Resources Agency (TWRA), and investigation of water quality thresholds for freshwater mussels. Prioritizing research needs for the Duck River system would benefit from open and consistent communication among all agencies and stakeholders to ensure that information needs are addressed in a manner that reflects both agency and public priorities, is feasible, and directly benefits the Duck River watershed. The DRWPP provides an opportune collaborative pathway to ensure that expert opinion regarding these research needs is both communicated and incorporated into future endeavors, such as the upcoming Habitat Conservation Plan. Knowledge gained from understanding the relationship between flow management and mussel conservation in the Duck River could inform approaches in other watersheds facing similar water demand and conservation needs.

Acknowledgments

We thank The Nature Conservancy for funding this research and ongoing support from Tennessee Tech University, notably the Center for the Management, Utilization, and Protection of Water Resources (Water Center). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank Rob Bullard with The Nature Conservancy and two anonymous reviewers for their thoughtful comments on the manuscript. We also thank Rheda Rosenberger for their ideas and artwork for our conceptual watershed model (Figure 10).

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Acronyms and Abbreviations

ARAP = Aquatic Resource Alteration Permit
BO = Biological Opinion
cfs = cubic feet per second
CPWS = Columbia Power and Water Systems
CRMRC = Cumberlandian Region Mollusk Restoration Committee
CWA = Clean Water Act
DNA = deoxyribonucleic acid
DRM = Duck River Mile
DRUC = Duck River Utility Commission
DRWPP = Duck River Watershed Planning Partnership
eDNA = environmental DNA
EO = Executive Order
ESA = U.S. Endangered Species Act
HEC-RAS = Hydrologic Engineering Center's River Analysis System
HUC = Hydrologic Unit Code
LTWSP = Long-Term Water Supply Program
MGD = million gallons daily/millions of gallons per day
NCDENR = North Carolina Department of Environment and Natural Resources
NLAA = not likely to adversely affect
RWSP = Regional Water Supply Plan (Comprehensive Regional Water Supply Plan)
SCI = Stream Conditions Index
TDEC = Tennessee Department of Environment and Conservation
TDRDA = Tennessee Duck River Development Agency
TN = Tennessee
TVA = Tennessee Valley Authority
TWRA = Tennessee Wildlife Resources Agency
USACE = U.S. Army Corps of Engineers
USEPA = U.S. Environmental Protection Agency
USFWS = U.S. Fish and Wildlife Service
USGS = U.S. Geological Survey
WIFIA = Water Infrastructure Finance and Innovation Act

1. Introduction and Content of this Document

The Duck River is a remarkable national resource, boasting outstanding biodiversity (Ahlstedt et al. 2017) (Figure 1). It contains 151 fish species, over 60 mussel species, and 22 snail species, many of which are federally listed as threatened or endangered (Etnier and Starnes 1993; Johnson et al. 2013; Ahlstedt et al. 2017; Womble and Rosenberger 2025a). However, this natural legacy is under increasing urban and agricultural pressures, including providing drinking water for 250,000+ people (Webbers 2003; USACE 2018). Surface water withdrawals, mainly for public water supply, are anticipated to increase significantly with regional population growth (USACE 2018). High water demands during drought conditions could significantly alter an otherwise hydrologically and ecologically resilient system (Knight et al. 2012). This situation is further complicated by a backdrop of climate projections that portend greater variability in hydroclimate and water availability (Naz et al. 2016; U.S. Global Change Research Program 2014). With multiple state and federal agencies involved in managing the Duck River's water resources (USACE 2018), access to quality-controlled, regionally and topically relevant information will assist in understanding how the unique biodiversity of the Duck River may respond to changing water availability.

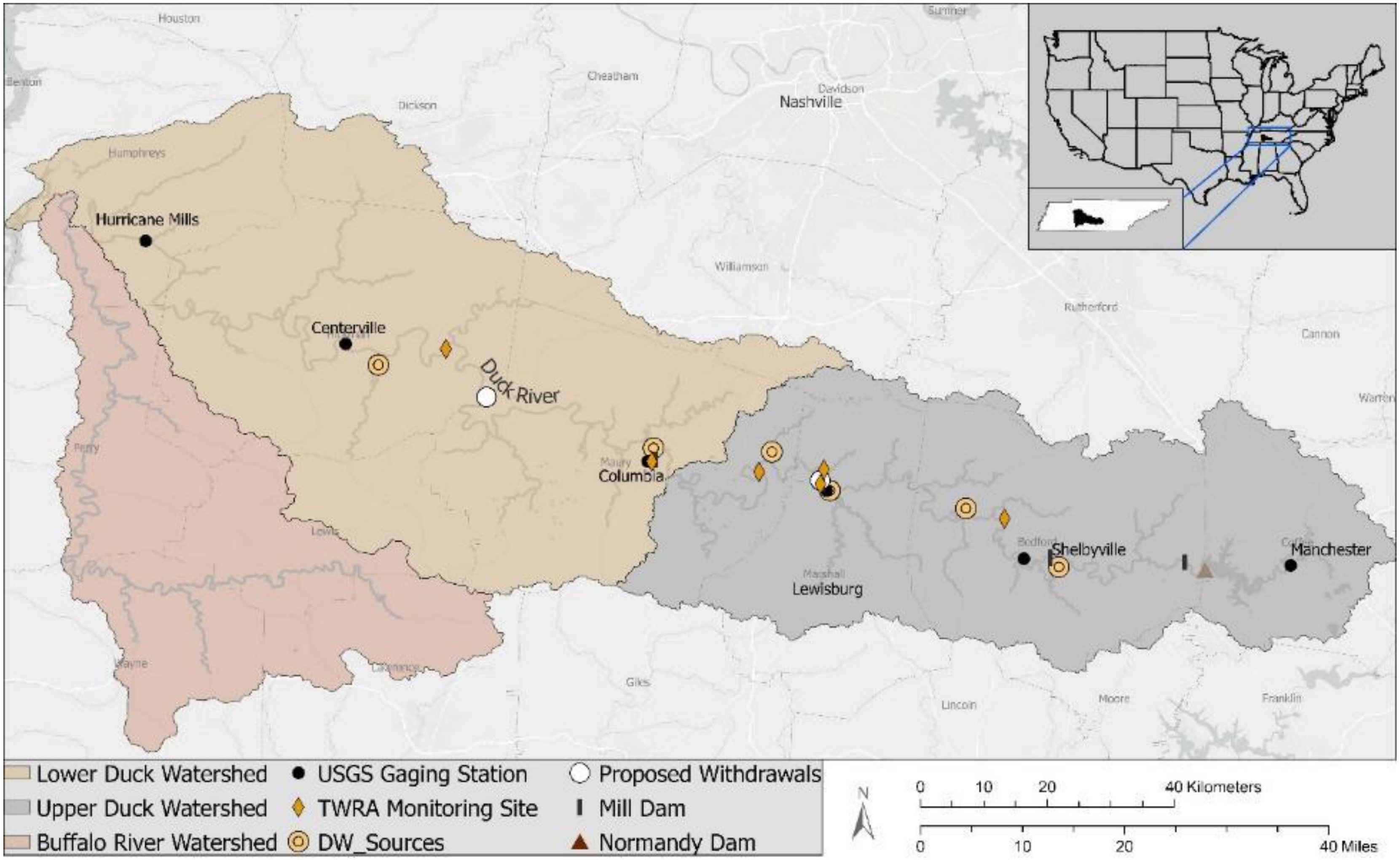

Figure 1. The Duck River watershed in Central Tennessee, including the Lower Duck (beige), Upper Duck (gray), and Buffalo (pink) watersheds, indicating locations of U.S. Geological Survey (USGS) gauging stations (black dots), Tennessee Wildlife Resources Agency (TWRA) mussel monitoring sites (diamonds), Drinking Water (DW) Sources (circles), and Normandy Dam (triangle).

Despite improvements in the region that contributed to increases in mussel ranges and numbers (e.g., the Tennessee Valley Authority [TVA]'s Reservoir Release Improvement program in 1991; Ahlstedt et al. 2017; USACE 2018), water management remains a critical factor for maintaining the unique species richness and abundance of Duck River freshwater mussels. This report summarizes the current state of knowledge on how changes in riverine flow regimes affect freshwater mussels, with a primary focus on droughts and sustained low flows. We emphasize factors most likely to affect the ongoing diversity, abundance, and recovery of mussel assemblages in the Duck River. Relevant studies were identified through searches of databases including Web of Science, Scopus, and Google Scholar using targeted combinations of the following search terms: ("freshwater mussel*" OR "unionid*" OR "bivalve*") AND ("flow*" OR "discharge" OR "hydrolog*") AND ("drought" OR "low flow*" OR "drying"). We also reviewed studies investigating the effects of upstream flow changes on hyporheic or groundwater processes that may be important for delivering mineral resources and nutrients to downstream mussel populations in the Duck River. These terms included: ("hyporheic" OR "groundwater" OR "interstitial") AND ("flow" OR "discharge" OR "hydrolog*" OR "drying" "drought", "low flow*") AND ("nutrient*" OR "mineral*" OR "geochem*") AND ("mussel*" OR "bivalve*" OR "unionid*") AND ("upstream" OR "downstream"). We searched reference lists of highly relevant papers for additional studies. Titles and abstracts of records returned by searches were screened for inclusion based on relevance to the effects of flow alterations on mussels. Studies focused on species, families, and river systems relevant to the Duck River were prioritized.

We begin the review by covering the significance of freshwater mussels to aquatic ecosystems, including their taxonomic uniqueness, life cycle, habitat requirements, and the ecosystem services they provide. This is followed by a summary of what is understood about mussels and environmental flows, starting with existing reviews in the literature that suggest anthropogenic water management practices have led to the current conservation status of most freshwater mussel species. Alterations include isolation or inundation of centers of biological diversity through the construction of dams, river channelization, changed flow regimes, and poor or untargeted management of water quality in tailwaters and other parts of the river. This is followed by a more detailed review of our current state of knowledge on how low flow conditions affect freshwater mussels, whether human-induced through water withdrawals, low water releases, or natural drought.

Our focus then shifts to the Duck River in particular, where we discuss the significance of this river system for freshwater mussel diversity worldwide and in Tennessee, a state renowned for its extraordinary biodiversity. We describe its current fauna and spatial distribution, as well as historical and current threats and potential synergistic interactions. We conclude this section by summarizing the overall effects of flow alteration on this system, including the operations of Normandy Dam, ongoing and proposed water withdrawals, future droughts, and potential interactions between water management and land-use changes. Considering the effects of changing flow regimes on the Duck River mussel fauna, we highlight data gaps and unknowns that may inform evidence-based, adaptive, and flexible water management to achieve desired management outcomes. Our review ends with a proposed outline and structure for a decision support model for environmental flows, highlighting data gaps and remaining research questions. This may serve as a conceptual blueprint for approaching management and withdrawals in the Duck River in an evidence-based and adaptable manner, serving as a transferable approach for Tennessee and beyond.

Objectives of the Review

With acknowledgment of existing reviews, we aim to:

1. Review the effects of changing flow regimes on mussels, with emphasis on the effect of droughts/low flows, highlighting key processes/factors affecting mussels.
2. Highlight important data gaps that could allow future, evidence-based water management decisions in this system.
3. Propose research priorities to address the identified data gaps and enable evidence-based water management decisions that consider the needs of freshwater mussels.

1A. Significance of freshwater mussels in aquatic ecosystems

Wendell Haag thoroughly and expertly covers the extraordinary natural history, ecology, and conservation of North American freshwater mussels in his textbook (Haag 2012). It is not our wish to re-cover topics already well summarized and reviewed therein; however, we provide a short overview of the ecology of freshwater mussels and their significance to aquatic ecosystems to provide a backdrop for our targeted review of the effects of changing flows on the freshwater mussel fauna of the Duck River, a unique and critical part of Tennessee's natural heritage.

Freshwater mussels native to North America belong primarily to the Order Unionida. With six families under this order, the Family Unionidae is the most diverse, boasting around 900 species distributed across North America, Eurasia, and Africa (Lopes-Lima et al. 2018). Five North American species are in the family Margaritiferidae (Haag 2012). Although taxonomic revisions can change species counts from region to region, North America is a hotspot for freshwater mussel diversity, hosting approximately 300 species (FMCS 2025). Of these, a disproportionate number of mussel species are found in the southeastern United States, and a disproportionate number of southeastern species are found in Tennessee (141 species). Historically, the Duck River in Tennessee contained over 70 species of freshwater mussels. To put this in perspective, the Duck River alone contains more than three times the number of mussel species than all of Europe combined. This diversity is a source of pride and natural heritage for all Tennesseans.

The life cycle of freshwater mussels is unique and complex, involving a parasitic larval stage, primarily on fishes (one species is known to use salamanders), yielding a diverse array of mussel-host relationships. Generally, male mussels discharge sperm into the water during spring and early summer; for some species, this sperm is released in hollow spherical aggregates called spermatozeugmata (Coe 1931; Barnhart and Roberts 1997; Waller and Lasee 1997). Female mussels then take in sperm to fertilize their eggs, which brood into glochidia (larval mussels) in marsupial gills (Haag 2012). The evolutionary advantage of brooding within the female to the glochidia stage, followed by a parasitic phase, is to avoid the purely downstream movement of free-floating, planktonic larvae and allow upstream dispersal of a species with limited adult mobility (Haag 2012). To attract a host on which to place their glochidia, female freshwater mussels may employ a variety of subterfuges, including mimicry to attract fish hosts, such as mantle lure displays, the release of food-shaped masses of glochidia called conglutinates, and lure-and-capture of smaller fish (Barnhart et al. 2008; Haag 2012). After several weeks, the juvenile mussels detach from the fish and settle into the substrate, initiating their benthic life stage (Strayer 2008). Mussel species vary tremendously in life history and lifespan (6–100+ years) but are long-lived compared to many aquatic organisms (Haag 2012). Delayed sexual maturity (3-9 years for most species; Woody and Holland-Bartels 1993; Haag and Staton 2003; Haag 2012), low survival from the glochidia stage to adulthood (Yeager et al. 1994; Jones and Neves 2011), and variable recruitment rates mean that recovery after faunal loss may be slow. Mussel species, especially host fish specialists, may experience occasional complete losses of entire year classes due to this complex life history (Payne and Miller 1989).

Freshwater mussels provide a variety of influential ecosystem services. As filter feeders, mussels remove suspended particles, algae, and bacteria from the water column, with a single mussel capable of filtering up to 40 liters (about half the volume of a mini fridge) of water per day (Vaughn and Hakenkamp 2001; Vaughn et al. 2004). This filtration process can improve water clarity and quality. Mussels also contribute to nutrient cycling in aquatic ecosystems through filtering activities and excretion (Atkinson et al. 2014). They transfer nutrients from the water column to the benthos, making these nutrients available for other organisms through the release of digestive products, including both feces and pseudofeces (Atkinson et al. 2018). The mussels themselves are a food source for multiple aquatic and terrestrial predators, including fish, turtles, muskrats, and raccoons (Haag 2019). Fish and invertebrates also consume glochidia and juvenile mussels (Barnhart 2006). In addition to water filtration and nutrient cycling, mussels provide structure—substrate and shelter—for algae, aquatic insects, and juvenile fish (Spooner and Vaughn 2006). The presence of mussels can also increase the diversity and abundance of macroinvertebrates in aquatic habitats (Vaughn et al., 2008). This can result in both increased food availability and stability for freshwater fish that consume macroinvertebrate drift (Brown and Lawson 2010; Leung and Dudgeon 2011).

Habitat requirements of freshwater mussels: implications for instream flow

As adults, many freshwater mussels occur in multispecies aggregates, loosely termed mussel beds (Vaughn 1997), which can contain both widespread and rare species (Spooner and Vaughn 2009; Lueckenhoff 2015). However, not all species universally inhabit beds, and individual mussels can be scattered throughout aquatic environments where they settle and grow. Dense mussel beds can serve as a valuable unit for habitat studies (Key et al. 2021) and conservation efforts (Bouska et al. 2018). Although the tendency for mussel species to aggregate suggests a habitat preference or limitation shared among multiple species (Key et al. 2021), beds occur across a wide range of aquatic habitats, including rivers, streams, lakes, and ponds (Vaughn 2018). In rivers, mussels occur on or over a variety of substrate sizes, typically where the channel is stable or where smaller substrates, such as sand or gravel, are protected by flow refugia provided by instream structures or larger substrates, such as cobble (i.e., armored streams). In these habitats, mussels anchor themselves to the bottom with their foot to maintain their position in the water column (Geist and Auerswald 2007). Freshwater mussels are adapted to the natural flow regime of their native streams, including seasonal variability in flows. As filter feeders, mussels require adequate water flow to provide oxygen and food (Allen and Vaughn 2009); however, they also require periods of low flow to increase access to fish hosts and to ensure juveniles are not displaced (Gates et al. 2015). Mussels are sensitive to changes in water quality, including elevated pollution and sedimentation and shifts in temperature and pH beyond their acclimated ranges (Strayer and Malcom 2012).

One factor that bears significant consideration when assessing the habitat requirements of freshwater mussels is their limited mobility as adults. Unlike their more mobile faunal counterparts, adult mussels cannot readily "track" optimal habitat conditions over any significant distance (> several meters), nor can they move or migrate considerable distances to avoid unfavorable events. Therefore, the occurrence of mussels in an area may reflect a favorable or tolerable habitat 'regime' over time in a fixed area rather than *in situ* habitat conditions measurable at a single point in time (Key et al. 2021). This provides a particular challenge for researchers seeking to understand the effects of changing flow regimes on this taxonomic group (Layzer et al. 1995).

Freshwater mussels have developed behavioral adaptations to cope with adverse events, such as low flows and drought, as well as associated or separate incidents of turbidity, low oxygen levels, or rapid changes in water flow. In response to receding flows, mussels may move short distances laterally, slowly track receding waters, or bury (Gough et al. 2012). They may sometimes close their shells altogether, ceasing gill ventilation or feeding to survive for short periods (Haag 2012; Gough et al. 2012). Additionally, some species of freshwater mussels can bury themselves deeper into the substrate to avoid exposure to unfavorable conditions, finding both water and thermal refugia (Watters 1994; Schwalb and Pusch 2007). However, these adaptations are only effective for short-term disturbances, and prolonged or chronic exposure to adverse conditions can lead to mortality or recruitment failure (Strayer and Malcom 2012).

1B. Environmental flows and freshwater mussels: An overview

Environmental flows are a way to preserve elements of the flow regime that has been altered in many rivers of North America that support freshwater mussels. It is undeniable that the riverine landscape of North America has been profoundly altered by impoundments, channelization, and water withdrawals, resulting in artificial flow, geomorphological, and water quality regimes that have caused a decline in the abundance and diversity of freshwater mussels (Layzer et al. 1993; Heinricher and Layzer 1999; Aldridge et al. 2023). The demand to preserve remnant mussel faunas downstream of impoundments and water withdrawals has sparked increased interest in establishing environmental flow regimes favorable for the persistence and survival of mussel assemblages (Gates et al. 2015; Khan et al. 2020). Environmental flows, also referred to as ecological or e-flows, refer to the quantity, timing, and quality of water flows necessary to maintain the ecological health of rivers, wetlands, and other aquatic ecosystems (Acreman and Dunbar 2004; Acreman 2016). These flows are important for sustaining biodiversity, ecosystem services, and human well-being that depend on these natural systems (Acreman et al. 2008; Arthington et al. 2018). For freshwater mussels specifically, environmental flows maintain flow and associated water quality regimes that are favorable for both juveniles and adults while also seasonally supporting host fish and the survival of settling glochidia in suitable environments (Gates et al. 2015).

Given freshwater mussels' general imperilment and sensitivities to flow alterations, environmental flows may best be defined for whole assemblages. However, the complexity of accommodating multiple life histories and habitat requirements of a diverse fauna may necessitate separating environmental flow recommendations by guild or biological trait (Gates et al. 2015). Numerous studies have emphasized the importance of hydraulic, flow-sensitive parameters in defining the distribution of freshwater mussels (Hardison and Layzer 2001; Gangloff and Feminella 2007; Steuer et al. 2008; Zigler et al. 2008; Allen and Vaughn 2010). This emphasis suggests that the natural flow regime, often considered the "master parameter" for riverine ecosystem health, is a crucial focus (Sofi et al. 2020). A favorable flow regime for mussels should contain low flows that maintain hydrological bed stability, host concentration, and water clarity for lure display. It should also include sufficient moderate and high flow events to prevent stranding or burial of mussels in fine sediment, create critical habitats and favorable river geomorphology, and maintain suitable water quality conditions (Vannote and Minshall 1982; Hartfield and Ebert 1986; Strayer 1993, 1999).

Artificially high or prolonged high or peak flows may harm freshwater mussels by causing dislodgement, disrupting the food supply, or scouring their shells. These effects may be particularly problematic for juveniles or smaller species (Strayer 1999). During artificially high or prolonged high-flow events, scour, potentially down to bedrock, could alter the composition or remove suitable river substrates, making riverbeds uninhabitable (Layzer and Madison 1995). In highly degraded streams where pristine habitats are limited, high flows may accelerate mussel mortality by moving individuals out of remnant, suitable habitats into areas incapable of supporting mussels (Karatayev et al. 2020). Sustained high flows could result in extended periods of behavioral avoidance for freshwater mussels, incurring an energetic cost without the opportunity to feed and replenish physiological reserves. Moreover, even a short-term but poorly timed single flood event during juvenile settling may cause recruitment failures (Neves and Widlak 1987; Holland-Bartels 1990; Hardison and Layzer 2001).

Artificially low or extreme drought-level flows can reduce available habitat for mussels, leading to exposure, stranding, or overcrowding (Allen et al. 2013; Dubose et al. 2019). In remnant channels, elevated temperatures, low oxygen levels, and concentrated toxins can cause stress and mortality for freshwater mussels that escape stranding; this issue is expected to worsen with prolonged drought. Additionally, shallow, clear pools could expose mussels to terrestrial predators (Golladay et al. 2004; Haag and Warren 2008). During low flows, mussels may face a severe energetic deficit; receding waters could force energetic expenditure to avoid stranding (by elevated temperatures and forced movement) while simultaneously depriving mussels of the quantity and quality of food that is otherwise provided by moving water.

Although single events may have only temporary deleterious effects, prolonged or repeated drought events could lead to significant population declines and local extirpation (Randklev et al. 2016). Just as artificially high or sustained flow events can scour favorable sediment to bedrock, extended, artificially low flow regimes could result in the settlement of fine sediments, potentially smothering mussel beds. However, low flows are not universally deleterious to freshwater mussels. Temporary or seasonal low flows may concentrate fish hosts, improve water clarity for mussels that use visual lures to attract hosts, and allow juvenile and glochidial mussels to settle in the sediment in permanently watered habitats during periods of glochidia release.

Although flow is a "master variable" that remains an essential focus for ecological flows, concurrent shifts in water quality in tailwater and downstream, regulated river reaches highlight other effects of impoundments and water withdrawals on mussel assemblages. Alteration of water quality downstream of impoundments poses a significant threat to freshwater mussels. Persistent hypolimnetic, cold-water releases in tailwaters reduce overall metabolic activity in mussels, alter host fish communities, and decrease growth while eliminating the reproductive season. These effects can lead to the presence of non-reproducing, "living dead" assemblages where once diverse beds were present (Miller et al. 1984; Lydeard and Mayden 1995; Vaughn and Taylor 1999). Even without cold-water releases, any alteration or artificial stabilization of the temperature regime could theoretically shift mussel community composition, favoring specific thermal tolerances or adaptations over others (Archambault et al. 2014). While sufficient oxygen levels are essential for mussel survival, other components of water quality may be altered by changing flow regimes, such as mineral content, algae composition, or the transport of fine particulate organic matter. The effects of these alterations are unknown but potentially determine the growth and biological health of resident mussel assemblages.

Finally, the potential of compounding effects of flow alterations on fish hosts and their corresponding effects on mussels cannot be ignored (Smith 1985; Benson et al. 2018). Altered flow regimes can decrease the species richness and abundance of fish communities (Gore and Bryant 1986; Kinsolving and Bain 1993; Scheidegger and Bain 1995). Even if fish can persist under an altered flow regime, the interaction between fish and their mussel hosts could be disrupted. Given the complex and variable sensitivities of mussels and their host fish to flow alterations created by impoundment releases, the most effective way to support diverse, successful, and resilient assemblage of freshwater mussels may be to implement flows that closely mimic a river's natural flow regime in timing, magnitude, duration, and rate of change (Poff et al. 1997; Richter and Richter 2000). This natural regime, at least in theory (or, as historical records may show), once sustained a healthy mussel assemblage. The optimal degree of adherence to the natural flow regime remains uncertain, mainly because historical river behavior may no longer accurately predict future conditions, given the potential effects of climate change and watershed development on river flow. Addressing these uncertainties may necessitate regionally specific research tailored to the unique ecological assemblages of individual river systems, such as those found in the Duck River. This targeted approach could help determine the most effective flow management strategies for maintaining biodiversity and ecosystem health in specific waterways.

The focus of the following detailed and targeted review is to provide an update on the current state of knowledge regarding the effects of water withdrawal and drought on freshwater mussels, as well as the establishment of minimum flows that enable the survival and, ideally, the ongoing resilience and robustness of the Duck River fauna. The general review of freshwater mussel ecology, habitat requirements, and reliance on river flow regimes provided by the previous sections establishes the knowledge baseline from which we pursue specifics for how droughts and low flows may affect freshwater mussels in the Duck River system.

2. Effects of Changes in Flow Regimes on Freshwater Mussels

2A. Natural flow regimes and their components

The natural flow regimes of rivers consist of dynamic processes that shape ecological conditions and support biodiversity. The five components of natural flow regimes are magnitude, frequency, duration, timing, and rate of change of flow (Poff et al. 1997). Magnitude refers to the volume (i.e., discharge) of water moving through a system at any given time. Frequency indicates how often flow events of a certain magnitude occur in a river system, such as floods or droughts. Duration describes the length of time that particular flow conditions persist, and the ecological response of aquatic organisms can vary depending on the value of this component. Timing refers to the seasonality of flow events, and this factor is important for aquatic organisms whose life cycles are aligned to natural seasonal patterns of flow conditions. The rate of change of flow describes how quickly discharge changes between magnitudes. Gradual flow fluctuations provide aquatic organisms with time to adjust to new conditions, thereby minimizing physiological stress and mortality risk. In contrast, rapid fluctuations (i.e., "flashiness") may hinder survival in extreme cases (i.e., outside of the predicted range of expected flows). Rivers rely on these components to maintain flow patterns that support nutrient cycling, sediment transport, and native biodiversity (Poff et al. 1997). Freshwater mussels are relatively sessile organisms with complex life cycles that are adapted to natural flow regimes that support and sustain healthy assemblages. The effects of flow regime changes on freshwater mussel communities are complex and not yet comprehensively understood; however, the following section summarizes current knowledge on the topic.

Review of flow metrics and response of mussels

A recent literature review summarized current knowledge on the effect of multiple flow metrics on freshwater mussels (Lopez and Vaughn 2021). Here, we provide an overview of their findings, but we recommend using their publication for a comprehensive compilation of relevant literature on the effects of hydrodynamic variables on freshwater mussels.

Freshwater mussels are adapted to the flow regimes of their origin rivers, including the natural variability of seasonal flows. Mussels require summer flows sufficient to support the transfer of food resources and oxygen, as well as spring and winter flows that are low enough to prevent sediment scour and displacement (Allen and Vaughn 2010; Steuer et al. 2008). Mussel assemblage traits, such as species richness, presence, and abundance, tend to increase as stream size increases (Gangloff and Feminella 2007; Atkinson et al. 2012; Ford et al. 2016). The timing and magnitude of extreme flow events may have a more negative effect on freshwater mussels than general changes in overall flow (Lopez and Vaughn 2021). The effects of flow variation on mussel communities vary depending on the life stage, season, and evaluation metric assessed. For example, summer high flows are more strongly associated with mussel survival than spring and winter high flows in Georgia (Peterson et al. 2011). In contrast, mussel recruitment in the same study was positively correlated with winter and spring flows.

Lopez and Vaughn (2021) assessed the effects of both simple and complex hydraulic variables on mussel community parameters, including presence, abundance, and species richness. Although simple hydraulic variables (e.g., depth, discharge, velocity) are the easiest to measure and, therefore, the most reported, they are typically not strong predictors of mussel community response. Simple hydraulic variables are limited in their utility for understanding mussel ecology; however, one study indicated that high-flow water depth was positively related to juvenile settling rates (Daraio et al. 2010). Discharge is generally positively associated with mussel community responses, although some exceptions have been noted (Chiavacci et al. 2018; Holcomb et al. 2018). Velocity, more closely related to complex hydraulic forces, is a stronger predictor of mussel community responses than discharge and depth; however, the relationship is not consistent between studies (Lopez and Vaughn 2021).

Complex hydraulic variables that combine substrate and geomorphic channel characteristics with simple hydraulic variables are better predictors of mussel community response. Froude number, Reynold's number, and shear stress are examples of complex hydraulic variables that alter mussel community dynamics. Both Froude number (ratio of inertial to gravitational forces) and Reynolds number (ratio of inertial to viscous forces) are positively correlated with the density of mussels at low flows but not at high flows, indicating that the effects of these variables depend on discharge (Layzer and Madison 1995; Randklev et al. 2019). Shear stress, the horizontal force of friction on substrate, is a critical hydraulic variable for mussels (Gangloff and Feminella 2007; Addy et al. 2012; Randklev et al. 2019). When shear stress is too high, mussels are at risk of dislodgement, which can lead to stranding or displacement to unsuitable habitats. Reynold's number is particularly significant for mussels at the boundary layer, which is the area mussels typically occupy. Specifically, higher turbulence levels between the water and the boundary layer increase diffusion, allowing for proper food resource allocation and waste removal (Lopez and Vaughn 2021; Vogel 1981). Many studies conclude that hydraulic preferences can be species-specific, which warrants investigation when assessing how a mussel community responds to alterations in flow and hydraulic conditions. Hydraulic changes in the Duck River may disproportionately affect certain mussel species; therefore, some species, including federally listed species, may be differentially affected by flow regime changes compared to the general mussel community.

Freshwater mussels are particularly vulnerable to mortality during their larval and juvenile stages; larval mussels must settle into suitable habitats for smaller, vulnerable individuals. Although field studies of larval settling are challenging, modeling results indicate that the optimal location for larval settling is downstream from localities in which shear stress is below that required for substrate mobilization, typically characterized by lower velocities. Contrastingly, juvenile abundance is higher in areas of higher velocities, although this relationship could be driven by Reynold's number (which is positively associated with velocity; Lopez and Vaughn 2021). Further research is warranted to enhance the understanding of species-specific responses to hydraulic changes, and current studies suggest that mussels require distinct hydraulic conditions for each life stage.

2B. Effects of low flows and drought on freshwater mussel communities

Due to their relatively sessile nature and complex life history strategies, freshwater mussels are vulnerable to drought and low flow conditions. Droughts directly and indirectly affect mussels by influencing their physiology, behavior, reproduction, and ecosystem roles. Drought-induced stressors and changes to water quality, such as high temperatures and low dissolved oxygen levels, can compromise physiological condition or cause mussel mortality, thereby reducing the ecosystem services these animals provide. Mass mussel die-offs during droughts and low water conditions are widely documented (Vaughn et al. 2015; Sousa et al. 2018; Dubose et al. 2019), and may be accompanied by increases in ammonia, which may compromise aquatic life downstream (Cherry et al. 2005). Droughts can also lead to a shift in mussel community composition, with more drought-tolerant species becoming more dominant while more sensitive species experience declines (Galbraith et al. 2010; Lopez et al. 2022; Vaughn and Atkinson 2025). The extent of mussel declines in response to drought is affected by pre-drought mussel abundance; therefore, denser mussel aggregations may be more resilient to extirpation than areas with low abundance (Haag and Warren 2008; Mitchell et al. 2021). Although the effects of droughts, water withdrawals, and low flow conditions on mussels are an increasing area of study, there is a general paucity of data-driven consensus regarding optimal mitigation approaches and strategies (Cushway et al. 2024).

Stranding, mortality

Physical stranding occurs when a mussel is exposed out of the water column for an extended period, whether due to substrate dislodgement during high-flow events, handling by a predator, or receding water levels. Mussels are particularly vulnerable to stranding during prolonged periods of low flow. Although mussels can track receding water levels through vertical and horizontal movement, these movement behaviors can be erratic during dewatering events (Schwalb and Pusch 2007; Galbraith et al. 2015). Mussels may be particularly susceptible to stranding during rapid dewatering events when their movement behaviors are insufficient to avoid emersion, such as during dam removal (Galbraith et al. 2015; Sethi et al. 2004). Movement behaviors during dewatering events can vary based on mussel size, population density, and habitat conditions (Burlakova and Karatayev 2007; Lymbery et al. 2021; Curley et al. 2022). Movement responses can be species-specific and influenced by shell shape and size and life history; therefore, certain species may be more susceptible to stranding and subsequent mortality than others (Gough et al. 2012; Gates et al. 2015; Newton et al. 2015; Mitchell et al. 2018). The extent of stranding depends on the duration of low flows, rate of dewatering, and species composition; however, prolonged drought can lead to community-wide stranding events. A stranding mortality event was documented in the Duck River in 2008 during prolonged drought conditions. Thirty mussels of eight species were found dead near the water's edge, representing species of varying sizes and life history strategies (TWRA 2008; Haag 2012). These numbers likely represent a small portion of the actual mortality from this event in the Duck River (Waller and Cope 2019). Similar stranding events were observed throughout the Duck River in 2024 (Hubbs 2024). Although mortality from stranding is often used as a metric to assess drought effects on mussel communities, it does not encompass the breadth of effects that drought conditions have on mussel community health.

Effects on water quality

Although the effects of drought and reduced flows on water quality are complex, this section outlines some primary mechanisms through which freshwater mussels are affected by these conditions. During drought and low flow events, reduced water volumes may elevate temperatures, decrease dissolved oxygen levels, and concentrate pollutants (Mosley 2015), with corresponding effects on freshwater mussels (Haag and Warren 2008; Galbraith et al. 2010). Thermally sensitive mussel species may be particularly vulnerable to deteriorating water quality (Ganser et al. 2015; Wagner et al. 2024), with increased temperatures potentially compromising their immune systems and increasing their susceptibility to contaminants (Falfushynska et al. 2014). The upper lethal thermal tolerances of mussels are understudied and known for only 9.3% of the North American fauna (Fogelman et al. 2023). For mussel species that have been assessed for thermal tolerance, all are currently living in habitats that experience temperatures at or near the upper lethal limits, the effects of which will be exacerbated during drought conditions. The negative effects of low dissolved oxygen on freshwater mussels are well-documented, and droughts can exacerbate these effects (Haag and Warren 2008; Ganser et al. 2015; Cushway et al. 2024). Low flow conditions intensify the effects of nutrient loading from livestock operations and agricultural fertilizers (Hornbach et al. 2021). In extreme cases, mass mussel die-offs during drought conditions can release significant amounts of ammonia and other nutrients into the water, further compromising water quality and triggering cascading ecological effects downstream (Cherry et al. 2005; DuBose et al. 2019). Together, these interacting water quality factors create complex stressors that can lead to both acute mortality and chronic sublethal effects on reproduction, growth, and long-term population viability of freshwater mussels (Cushway et al. 2024).

Reduced habitat availability

Droughts and low flow conditions can significantly decrease habitat availability, therefore increasing abiotic and biotic stressors for aquatic communities (Lake 2000; Magoulick and Kobza 2003). Specifically, droughts can reduce the complexity of aquatic habitats by reducing depth or eliminating the presence of riffles. Low flow conditions can further reduce habitat diversity by exposing stream margins, aquatic vegetation, and submerged woody debris, harming species that occupy these microhabitats by increasing risk of emersion. Emersion can affect the filter-feeding rates of mussels and reduce growth rates (Kelemen et al. 2017; Andre et al. 2021). A reduction in habitat availability may also increase competition for limited resources among native freshwater mussels.

Reduced food availability and quality

Drought reduces water levels and flow rates, which can limit the transport of organic material and nutrients in the water column. Freshwater mussels are sessile filter filters that rely on this transport. Drought conditions, such as low flow and elevated water temperatures, can increase sedimentation and pollutant concentrations in the water column, thereby reducing food quality. Suspended solids, which can become concentrated during low flow periods, can decrease food quality and interfere with filter feeding (Goldsmith et al. 2021). Valve closure is a defensive behavioral response of mussels to thermal and hypoxic stress during drought conditions, enabling them to reduce evaporative water loss; however, this behavior inhibits food acquisition (Kumar et al. 2013; Haney et al. 2020). Occasional valve closure in response to worsening water quality may exacerbate the effects of reduced food consumption and availability (Haney et al. 2020).

Increased predation and competition

Drought-induced low water levels, particularly those resulting in emersion, increase predation risk on mussels (Morales et al., 2011; Walters and Ford, 2013; Karlin et al., 2017;). Various mammals and birds prey on mussels during drought conditions (Sandaas et al. 2004; Burlakova and Karatayev 2007; Morales et al. 2011; Walters and Ford 2013), and this consumption can make up a large percentage of mussel mortality during drought events. Smaller individuals may be more susceptible to predation during emersion (Morales et al. 2011; Lymbery et al. 2021).

Droughts may exacerbate competition between native mussels due to decreased habitat and food availability, especially when invasive *Corbicula* densities are high. *Corbicula* clams have higher reproductive rates than native mussels, and high clam densities can limit habitat and food availability for native species (Sousa et al. 2008; Ferreira-Rodríguez et al. 2018a). Competition with high densities of *Corbicula* clams at high water temperatures may reduce the metabolic functions of native mussels, such as food acquisition and feces production (Ferreira-Rodríguez and Pardo 2017). This competition may be exacerbated during prolonged periods of elevated water temperatures resulting from low flow conditions.

Disruption of reproductive cycles

Drought conditions affect each stage of the complex life cycle of freshwater mussels. Droughts affect freshwater mussel reproduction through changes in flow, temperature, and the availability of fish hosts. Prolonged drought conditions disrupt mussel reproduction cycles by inhibiting or reducing reproduction behaviors when energy reserves are instead needed for maintaining homeostasis and survival (Ganser et al. 2015). Low flow conditions may hinder fertilization by reducing sperm transport and inhibiting the proper filtration of sperm by female mussels (Gough et al. 2012; Mosley 2012). If droughts lead to elevated temperatures and hypoxic stress, female mussels may abort glochidia to increase oxygen uptake by increasing gill surface area (Aldridge and McIvor 2003; Schneider et al. 2018; Khalloufi et al. 2019; Sangsawang et al. 2019; Fluharty et al. 2023). Furthermore, these conditions can alter the timing of spawning events, which could affect mussel reproduction success if glochidia release does not overlap with host fish contact (Hastie et al. 2003; Osterling 2015; Schneider et al. 2018). Drought conditions can also alter host attraction methods; females may switch from a mantle lure to a conglutinate release, presumably to preserve energy for other physiological needs (Gascho Landis et al. 2012).

Drought conditions can affect the success of glochidia metamorphosis and cause physiological stress for juvenile mussels, primarily through increased water temperature and reduced dissolved oxygen concentrations (Clarke 2010; Taeubert et al. 2014). Low flow conditions and elevated temperatures can reduce juvenile mussel byssal production, which may limit their dispersal abilities (Archambault et al. 2013). If temperature conditions cause an early release of glochidia by females, juvenile metamorphosis would be completed earlier, and the benthic life phase may begin before optimal environmental conditions are present for survival and growth (i.e., beginning benthic phase in late winter or early spring) (Hastie and Young 2001; Osterling 2015). Prolonged low flows and high temperatures may increase the prevalence of hermaphrodism in mussels, which can reduce the genetic diversity of mussel communities (Xu et al. 2022; Cushway et al. 2024).

Freshwater mussel species are often long-lived, and documenting recruitment may require several years of monitoring (Haag 2012). Additionally, methods for detecting juveniles (e.g., substrate excavation and sieving) are more labor-intensive than conventional survey techniques and are less frequently employed (Miller and Payne 1988; Haag 2012). Therefore, the effects of drought conditions on freshwater mussel reproduction are extensive and complex, and reductions in recruitment success may not be immediately apparent in monitoring.

Susceptibility to disease and pathogens

Drought conditions can increase the susceptibility of mussels to disease and pathogens both directly and indirectly. Reduction of water levels can concentrate bacteria, pathogens, and viruses, and increased temperatures from reduced flows could promote pathogen and parasite growth, thereby increasing exposure risk for mussels at a time when their immune response may already be compromised. For example, increased temperatures may decrease lysosomal membrane stability, which can hinder prevention of bacterial and viral infections during droughts (Falfushynska et al. 2014; Ferreira-Rodríguez et al. 2018b). Additionally, temperature stress can lead to hyalinocyte mortality, which may degrade immune response (Beggel et al. 2017). Mussel beds may become isolated in pools during low water conditions; subsequently, pathogen transmission may increase due to overcrowding and poor water quality conditions.

2C. Consequences of altered flow regimes that increase drought and low water frequency on mussel populations

Watershed management decisions that alter flow regimes for human purposes can exacerbate the effects of drought conditions on freshwater mussels. Hydrological alterations are a substantial threat to the conservation of mussels (See Section 1B). Flow management that establishes minimum flows can protect mussel communities during drought conditions, although variable rate management strategies such as percent-of-flow regime thresholds may be more beneficial for aquatic organisms (Allen et al. 2013; Driver et al. 2020). Environmental flows mitigate the adverse effects of anthropogenic flow regime alterations, such as increased impervious surfaces in the watershed and water withdrawals, by maintaining the ecological integrity of rivers (Section 1B); however, species-specific survival thresholds for abiotic factors, including water temperature, dissolved oxygen, and contaminants are poorly understood. These knowledge gaps may limit the success of environmental flows for maintaining mussel communities when water management decisions occur during drought. Despite the wide variety of mitigation efforts currently in practice or proposed, research on the synergistic effects of the complex effects that drought conditions have on freshwater mussels is limited. This review emphasizes the importance of an evidence-based approach to mussel conservation under drought conditions, particularly considering anticipated increases in the frequency and severity of droughts (Strzepek et al. 2010).

In summary, mussel community characteristics, including presence, abundance, and richness, generally increase with stream size (e.g., stream order); however, responses to changes in flow conditions are often species-specific, and the magnitude and timing of extreme flow conditions have more predictive power for mussel community response than general changes in flow. Hydrologic variables are limited in their ability to predict finer-scale local mussel community responses but are helpful when assessing landscape-level and basin-wide changes in mussel community structure. Velocity, discharge, and depth are crucial for mussel communities; however, their effect varies depending on the species and discharge level, and their predictive power by metric is limited. Complex hydraulic variables, such as relative shear stress and Reynolds numbers, are stronger predictors of mussel community responses because they combine simple hydraulic variables (e.g., velocity) with stream channel characteristics, such as substrate composition and dynamics. Freshwater mussels are highly vulnerable to droughts and low flow due to their complex life cycles and limited mobility. These conditions affect their physiology, behavior, reproduction, and survival; further, droughts can shift community structure toward a dominance of drought-tolerant species, which has direct conservation implications due to loss of sensitive species. Although mortality from stranding is often the primary indicator used to assess the effects of droughts on mussels, the compounded effects of the complex factors summarized in this section threaten the long-term viability of mussels and the ecosystem services they provide. Long-term management decisions regarding water withdrawals, particularly during extended or multi-year drought conditions, could consider the sublethal effects of drought and low flow conditions on freshwater mussel communities, in addition to direct mortality.

3. The Duck River and Ecological Flows

3A. Geographic and hydrological characteristics of the Duck River

The Duck River watershed lies entirely within Tennessee, spanning 284 miles and draining over 2,100 square miles. The river originates from a spring in Coffee County and flows into the Tennessee River (Kentucky Lake) in Humphreys County. The watershed primarily falls within two physiographic provinces: the Highland Rim and the Central Basin. The Highland Rim, characterized by broad valleys and rolling hills, includes the Lower Duck and Buffalo Rivers. In contrast, the Central Basin features steeper valleys and karst topography, and the central portion of the Duck River watershed is located in this province. The upper and middle watershed is primarily composed of Ordovician limestone, gradually changing into Mississippian age formations below Columbia, resulting in thicker chert and clay soils (Knight and Kingsbury 2007). Hydrologically, the watershed is divided into three eight-digit hydrological units: the Lower Duck River (HUC 06040003), which drains 1,548 square miles; the Upper Duck River (HUC 06040002), which drains 1,182 square miles; and the Buffalo River (HUC 06040004), which drains 763 square miles.

The Duck River's flow is influenced by both tributary contributions and groundwater, particularly in the Upper Duck River watershed, where limestone and karst features—such as caves, underground streams, and sinkholes—are prevalent. Historical streamflow data indicate the section of river between Shelbyville and Columbia may lose up to 30% of flow during extended baseflow conditions, and water returns to the river through groundwater recharge at Columbia (Knight and Kingsbury 2007; TDRDA 2011) (Figure 2). Fountain Creek contributes a significant portion of flow to the Lower Duck River, and the geology changes below Columbia result in a shift from Ordovician limestone to thicker chert and clay soils, accompanied by a reduction in karst influence. Karst, although providing unique chemical qualities within its surface water system that are favorable for instream water quality, may also render the river particularly vulnerable to low flow and drought periods through reduced surface water availability (Stueber and Criss 2005; Ford and Williams 2007). Groundwater management is crucial for effective surface water management in these environments, as understanding the influence of groundwater is vital for maintaining a stable, high-quality surface water supply, especially when surface water resources are limited (Priyan 2021). Groundwater filtration through karst topography may provide dissolved calcium and bicarbonate ions to downstream systems, thereby buffering surface water against pH changes and supporting aquatic life (Allan et al. 2021). The calcium carbonate cycle in the Duck River may help support its distinctive ecological features (e.g., stable pH, calcium for shell-building organisms like snails and mussels, and support for specialized beneficial algal and bacterial communities that are the food base for freshwater mussels). The concentration of the most diverse and abundant mussel communities in the Duck River immediately downstream of zones where these geochemical processes dominate warrants further investigation into potential causal relationships between water chemistry and mussel community resilience, health, abundance, and structure.

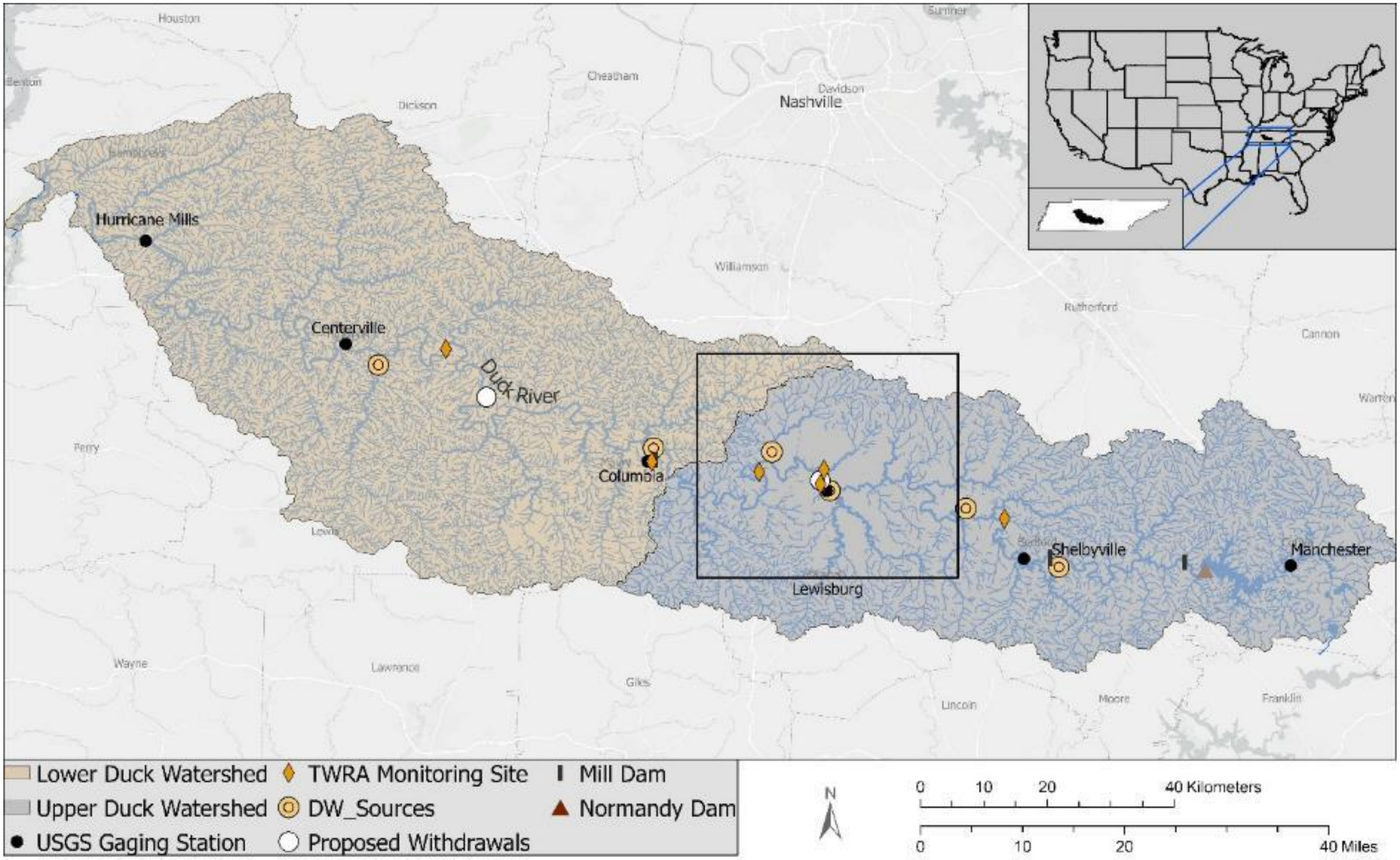

Figure 2. The Duck River in Central Tennessee, flowing east to west, including the Lower (beige) and Upper (gray) watersheds, indicating locations of U.S. Geological Survey (USGS) gaging stations (black dots), Tennessee Wildlife Resources Agency (TWRA) mussel monitoring sites (diamonds), DW Sources (circles), and Normandy Dam (triangle). Surface water availability in the Duck River drainage shows a relative decrease in surface waters in the middle part of the drainage (box inset), which is underlain by the karst topography of the Nashville Basin.

3B. Importance of the Duck River system for freshwater mussels

The Duck River is a haven for aquatic life, particularly for freshwater mussels. The system has high levels of endemism and harbors many federally listed species, including 15 mussel species. A substantial portion of the Duck River is designated as critical habitat for endangered mussels (69 FR 53136, 78 FR 57076, 78 FR 59556, 85 FR 61384). This system harbors the most viable remaining populations of several federally listed species, including the Slabside Pearlymussel (*Pleuronaia dolabelloides*), the Birdwing Pearlymussel (*Lemiox rimosus*), and the Cumberland Rockshell (*Theliderma intermedia*). Over 60 miles of the river are included in the Tennessee Scenic Rivers Program, which aims to "preserve and protect the free-flowing, unpolluted and outstanding scenic, recreational, geologic, botanical, fish, wildlife, historic or cultural values of selected rivers or river segments in the state" (TDEC 2025, in reference to the Tennessee Scenic Rivers Act of 1968; Title 11, Chapter 13). The Duck River is recognized as a priority watershed for biodiversity and conservation by government and non-governmental organizations operating at national and global levels and was designated as one of America's most endangered rivers in 2024 (Smith et al. 2002; American Rivers 2024). In a separate project funded by the U.S. Fish and Wildlife Service, the authors of this report compiled all known and reliable data for the Duck River into a single database, from which details on the spatial distribution of freshwater mussel species through time can be obtained (Womble and Rosenberger 2025a; Womble and Rosenberger 2025b).

The high levels of diversity and endemism in the Duck River have led wildlife, conservation, and academic entities to prioritize the river for conserving freshwater aquatic species biodiversity. Over 70 species of freshwater mussels were reported historically from the Duck River watershed, over 60 of which are extant (Womble and Rosenberger 2025b). Several drainage-wide surveys have been conducted in the Duck River and Buffalo River watersheds (Ortmann 1924; Isom and Yokley 1968; Ahlstedt et al. 2017; Irwin and Alford 2018; Reed et al. 2019), and freshwater mussel populations are quantitively monitored at six locations every five years by the TWRA (Hubbs 2010, 2015; Wisniewski 2020). The Cumberlandian Region Mollusk Restoration Committee identified the Duck River as a high-priority stream for reintroducing 16 mussel species in their 2010 Cumberlandian population restoration and conservation plan (CRMRC 2010). A critical component of freshwater mussel conservation is species propagation and reintroduction. Successful propagation enables the augmentation of extant mussel populations and the reintroduction of mussels into historical habitats from which they have been extirpated. The Duck River is central to these activities in Tennessee and surrounding states. Some populations serve as the sole brood stock for propagation efforts, and the Duck River's habitat offers suitable areas for species reintroductions due to the presence of healthy mussel beds.

Malacologists survey freshwater mussels using various methodologies, and some significant collection events in the Duck River are represented by shell material only. Although the Duck River has been more thoroughly surveyed compared to other watersheds in Tennessee, a lack of consistency in survey methodology prohibits statistically robust comparisons of species richness through time on a drainage-wide scale. Additionally, freshwater mussels are notoriously difficult to detect, and a lack of observation may not indicate the true absence of a species. However, we can assess what available data indicate regarding spatial and temporal changes in freshwater mussel diversity in the Duck River. Available historical data (early 1800s-present) suggest that the highest mussel diversity in the Duck River watershed is between the city of Columbia (46 species) and Lillard Mill (57 species) (Figure 3) (Womble and Rosenberger 2025b). Several additional historically diverse sites are located between these two localities, such as Leftwich, Venable Spring, Hardison Mill, and Hooper Island (Figure 4).

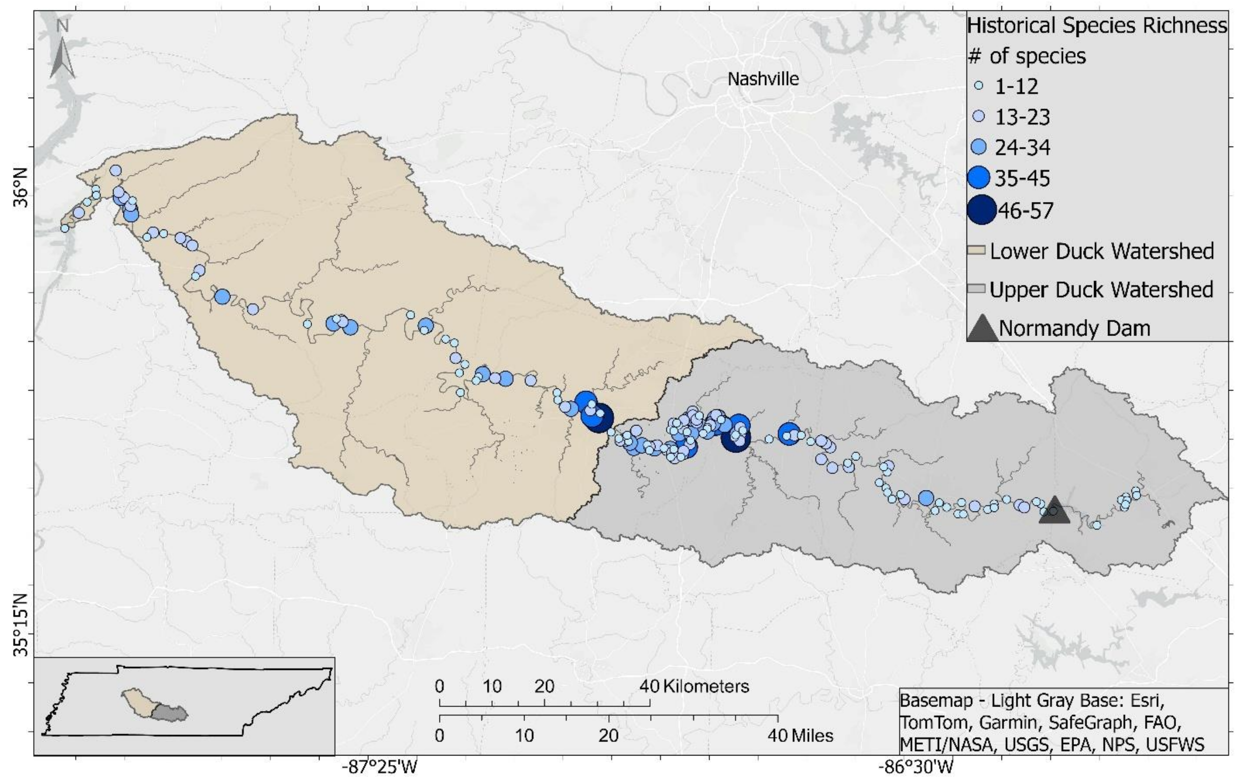

Figure 3. Historical freshwater mussel species richness documented in the Duck River (Womble and Rosenberger 2025b). Records were reported from the early 1800s to 2023. Note that Normandy Dam was constructed in 1976.

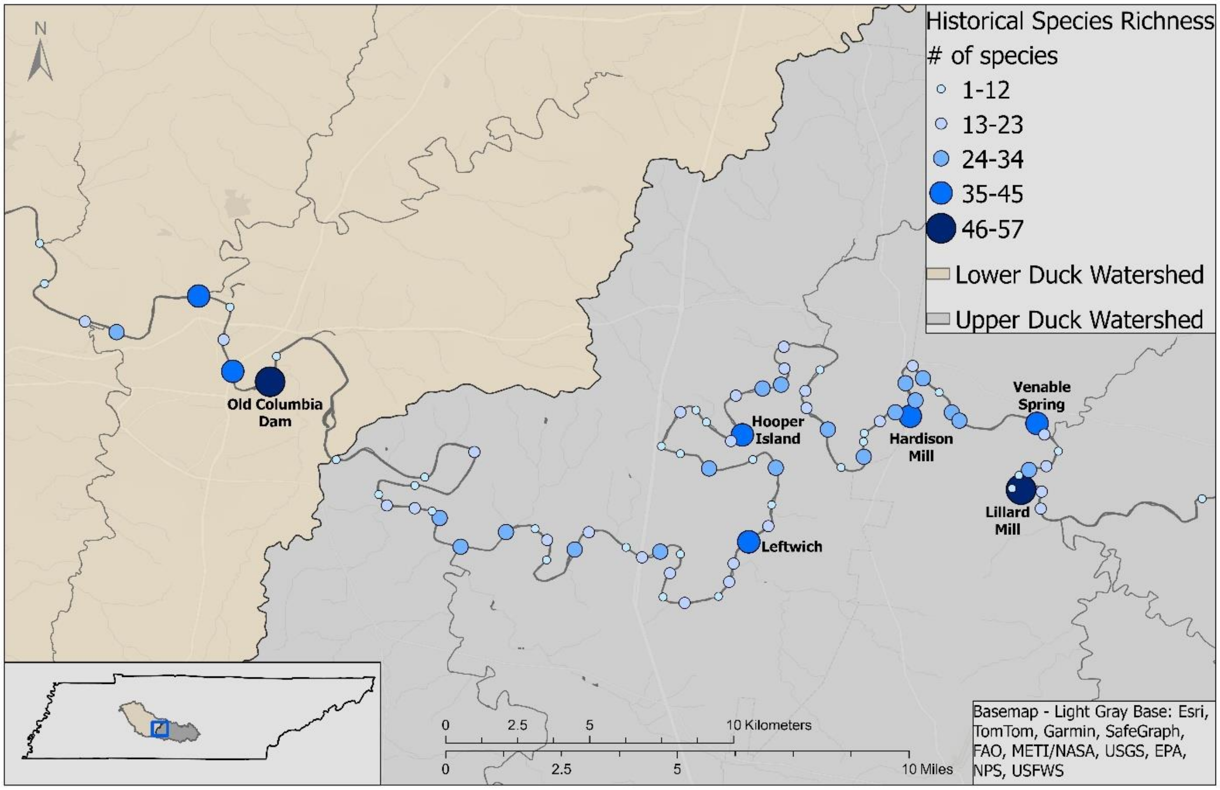

Figure 4. The core area of historical freshwater mussel species richness in the Duck River, Tennessee (Womble and Rosenberger 2025b).

Recent mussel records offer valuable insights into changes in species richness throughout the Duck River's history. For this assessment, "recent records" refer to confirmed observations of live individuals or fresh-dead shells (intact tissue and shiny nacre) collected between 2000 and 2023. Both live mussels and fresh-dead shells are indicative of a species' continued presence in an area and are commonly combined in mussel survey analyses (e.g., Ahlstedt et al. 2017; Reed et al. 2019). An assessment of recent freshwater mussel collections in the Duck River reveals that the core area of diversity has generally persisted. Lillard Mill (DRM 179.2) remains the most diverse site, with a richness of 46 species. While the core area of diversity persists in the Duck River, available data indicate that mussel richness has declined here and throughout the drainage (Figure 5). Reported species richness has declined at 85% of surveyed sites, including Lillard Mill and Columbia, which have decreased by 14 and 11 species, respectively.

Despite this, the Duck River remains a stronghold for freshwater mussel populations in the state, maintaining diverse mussel beds that include endangered species such as the Duck River Dartersnapper (*Epioblasma ahlstedti*), Birdwing Pearlymussel (*Lemiox rimosus*), and Slabside Pearlymussel (*Pleuronaia dolabelloides*). High mussel densities can be found at several sites, including Lillard Mill, Venable Spring, and Hooper Island (Wisniewski 2020). While the river harbors critical aquatic resources, the portion containing the most diverse and abundant mussel populations is restricted to the area between Columbia and Lillard Mill, which is approximately 50 river miles. The small spatial extent of these diverse mussel beds is a concern due to ongoing threats in the area, such as increasing water withdrawal demands resulting from human population growth. Additional mussel surveys throughout the entire Duck River watershed could be beneficial to inform future water management decisions.

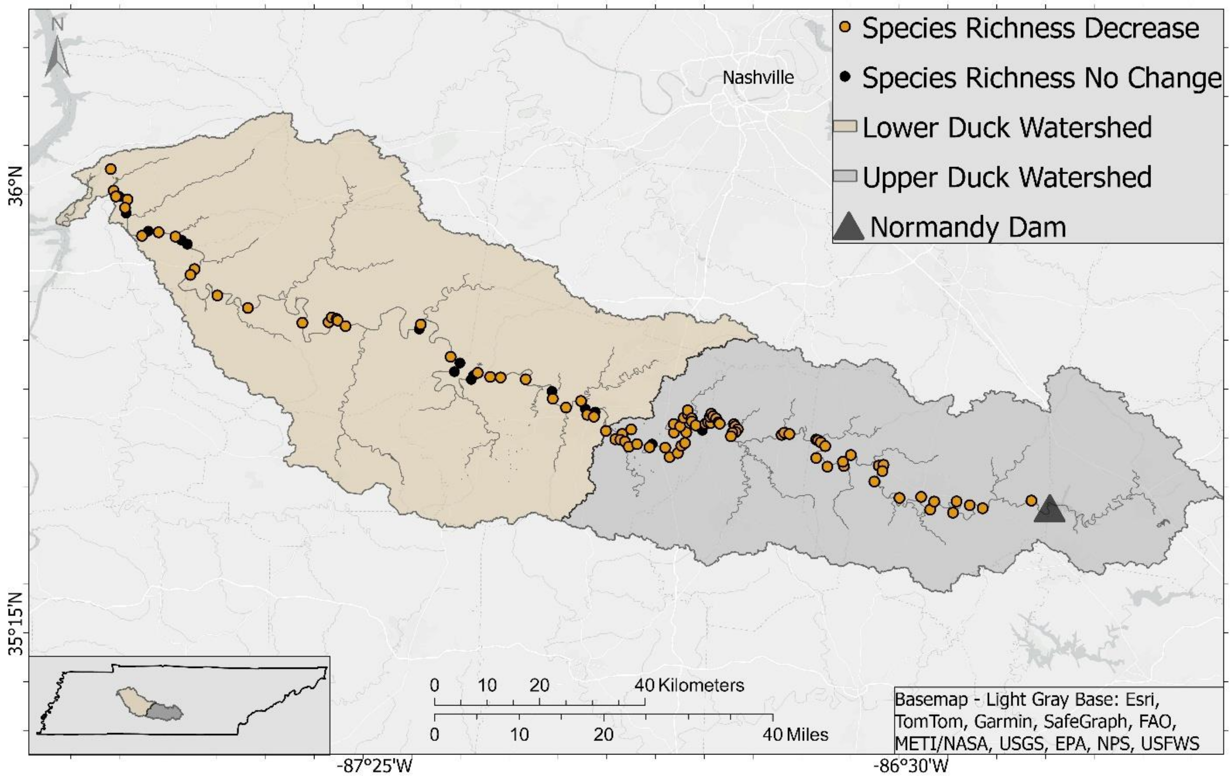

Figure 5. Changes in species richness documented throughout the Duck River (Womble and Rosenberger 2025b). Comparisons are between historical species richness (1800-2024) and recent species richness (2000-2024). Note that Normandy Dam was constructed in 1976.

3C. Historical and current threats to the Duck River system

The ecological value of the Duck River has not shielded it from the widespread effects of anthropogenic modification, and these alterations have directly and indirectly affected freshwater mussel communities. Mill dams were common beginning in the 1800s, with an estimated 25 throughout the watershed at one time (LaForest and Oliveira 1979). Four low-head concrete mill dams persist in the Duck River today: Cortner Mill, Shelbyville, Lillard Mill, and Columbia. Historical phosphate and iron ore mining activities occurred throughout the watershed, and their effects concerned malacologists as early as the 1920s (Otmann 1924). Currently, the Duck River faces threats from development, land use, agricultural practices, water management, and mining, and these factors can increase sediment and nutrient loading and affect water quality (USACE 2018). Point source pollution from agriculture and wastewater is exacerbated by non-point source pollutants that reduce water quality, instigate streambank erosion, and contribute to sedimentation.

Normandy Dam

Normandy Dam was constructed in 1976 on the upper Duck River (DRM 248.6) for flood control, water supply, and recreation. This non-power dam alters the Duck River's natural flow regime, leading to changes in temperature, water quality, and aquatic habitat availability, as well as permanent obstruction of migratory fish passage. Although some mussel species, such as the Giant Floater (*Pyganodon grandis*) and Paper Pondshell (*Utterbackia imbecillis*), can tolerate inundated conditions, most native mussel species in the Duck River are unable to survive in a reservoir environment. Therefore, mussel populations were extirpated from inundated river reaches following construction of the dam. The Tennessee Valley Authority implemented reservoir release improvements in 1991, establishing minimum flows and increasing dissolved oxygen concentrations from Normandy Dam releases. These improvements, in combination with other mitigations, were credited for the improved condition of freshwater mussel populations below the reservoir (Ahlstedt et al. 2017). Normandy Dam plays a vital role in water management in the Duck River, especially during drought conditions. During low flow conditions, releases from Normandy Dam are a primary water source for the Duck River upstream of Columbia. Optimization of these releases has been considered a crucial tool for drought management planning in the watershed (TDRDA, 2011, 2013). The Tennessee Valley Authority has collaborated with various agencies and local municipalities to establish minimum flow requirements from Normandy Dam releases, aiming to meet human population needs while protecting ecosystem resources, including wildlife and recreation (TVA 2025).

Human water use

Water supply planning in the Duck River is a critical component of water resource management in central Tennessee, as the river provides drinking water for over 250,000 people. The Tennessee Department of Environment and Conservation has recently permitted or proposed to permit eight water utilities to withdraw a total of 77 million gallons per day (mgd), representing an over 40% increase in permitted withdrawals (USFWS 2025). Effects of flow regime changes that reduce flows on mussels are multifaceted and complex (see Section 2b). Additionally, increased withdrawals lead to a subsequent increase in released effluents. Wastewater effluent can contain heavy metals and inorganic nutrients, such as ammonia, nitrate, and phosphate, that can negatively affect the health of mussels and host fish (Augspurger et al. 2003; Haag 2012; Nobles & Zhang 2015; Gillis et al. 2017a). As sedentary filter feeders, mussels can bioaccumulate heavy metals, which can lead to DNA damage in hemocytes (invertebrate cells responsible for gas exchange) (Naimo 1995; Khan et al. 2019). Inorganic pollutants can reduce mussel reproductive success and juvenile survival and even lead to local extirpations (Cope et al. 2008; Moore and Bringolf 2018; Gillis et al. 2017b).

Interacting land use effects

Land use in the Duck River watershed is composed of approximately 66.1% forest, 20.5% pasture/hay/grasses, 9.9% cropland, 1.2% commercial/residential, 0.9% woody/emergent wetlands, 0.8% mines/rock/cleared areas, and 0.6% water (USACE 2018). Over 300 stream miles within 40 streams in the Duck River watershed are listed on the Tennessee 303(d) List for biological integrity loss and suspended sediment (TDEC 2024a). Multiple reaches in the Duck River are affected by nutrient enrichment, *Escherichia coli* bacteria, and low dissolved oxygen from multiple human water use activities and agricultural inputs (TDEC 2024a).

Anthropogenic land use has both direct and indirect effects on water quality and physical habitat available for freshwater mussels in the Duck River. Water quality in the Duck River watershed is impaired by high nutrient loading and bacteria counts from livestock waste, failing septic tanks, failing or inadequate wastewater collection systems, and wastewater plant discharges (USACE 2018). Although mussels have evolved behavioral adaptations to avoid short-term physical stressors, their sedentary nature makes them susceptible to the effects of surrounding land use and sensitive to long-term exposure to poor water quality and contaminants. Mussels are more sensitive than other aquatic organisms to contaminants such as ammonia and may be particularly sensitive during the larval or juvenile stage (USEPA 2013; Salerno et al. 2020). Agriculture may have an adverse effect on mussel diversity and abundance; however, it may also have a positive effect on mussel growth (Hornbach et al., 2021). Chronic exposure to herbicides can reduce the growth and survival of juvenile mussels (Bringolf et al. 2007). Excessive nutrients such as phosphate from mining and nitrogen from agricultural practices can lead to algal growth, which, after die-offs, can lower dissolved oxygen levels and harm mussels. Excessive algal growth is widespread in the Lower Duck River, where extensive cropland and a low river gradient lead to higher nitrogen and phosphate inputs. Increased turbidity and suspended solids from erosion and runoff associated with agricultural practices can inhibit the filter-feeding of mussels and negatively affect aspects of their life cycle, including the host-fish relationship (Goldsmith et al. 2021).

The full synergistic effects of these summarized threats on the Duck River mussel fauna are not fully understood. More information is needed regarding the tolerance of Duck River mussel species to flow alterations and various water quality parameters, such as temperature, dissolved oxygen, and contaminants. Filling in these data gaps will ensure that future land use and water management will meet anthropogenic needs while also protecting the ecological integrity of the Duck River and its associated fauna.

3D. Water management and withdrawals in the Duck River system

Historical water management

The Duck River is a vital resource supporting human populations, multiple industries, recreation, and one of the world's most biologically diverse aquatic ecosystems. Sustainable management of this water source requires balancing the consideration of multiple needs, including those of human communities, industry, and aquatic life. Water supply planning in the Duck River represents an important component of water resource management in central Tennessee, as the river currently provides drinking water to over 250,000 people. Areas above Normandy Reservoir receive water from an intake located in the reservoir, and downstream users rely on direct withdrawals from the Duck River at multiple intakes (Figure 1; Figure 2).

The Duck River Development Agency (DRA) was created by the Tennessee General Assembly in 1965 and manages water resources in the Duck River watershed within Bedford, Coffee, Hickman, Marshall, and Maury Counties. The DRA represents seven water utilities (Table 1), primarily in the Upper Duck Watershed; however, water management actions in this region affect those downstream.

Table 1. Water utilities represented by the Duck River Developmental Agency (DRA).

Water Utilities Represented by the DRA
Bedford County Utility District
Columbia Power and Water Systems
Lewisburg Water and Wastewater
Manchester Water Department
Shelbyville Power, Water, and Sewerage System
Spring Hill Water Department
Tullahoma Utility Board

In response to the 2007 drought in the Duck River watershed (see section 3E below), the DRA developed a Comprehensive Regional Water Supply Plan (RWSP), which served as a strategic blueprint for addressing future water needs and potential water shortages (TDRDA 2011). This plan was an open process involving input from the public, elected officials, and both governmental and non-governmental agencies. A hydrologic model, OASIS, was developed to evaluate current and projected water demands under various reservoir (Normandy) and river constraints. The model assessed the need for additional water supply through 2060 and indicated adequate supply for Normandy Reservoir users; however, the model identified a potential deficit of up to 32 mgd for users from Shelbyville to Columbia. Additionally, the DRA analyzed water supply alternatives for the region. Final accepted alternatives included a drought management plan, a water use efficiency plan, optimization of Normandy Reservoir releases and dam improvements, and relocation of Columbia's water withdrawals to a new intake near Williamsport (TDRDA 2011).

As recommended in the 2011 RWSP, the DRA developed a comprehensive drought management plan to establish a regional strategy for drought mitigation and response in the Duck River region (TDRDA 2013a). The plan established a drought response plan for stakeholders using water resources in the Duck River based on drought triggers and phases and outlined how water resources (Normandy Reservoir and the Duck River) are to be managed during drought conditions. The plan established trigger points based on water levels at

Normandy Reservoir and defined four stages of drought response: Monitoring, Alert, Warning, and Emergency (Figure 6). The OASIS model introduced in the RWSP was used to develop forecasts for future conditions during the Alert, Warning, and Emergency stages of drought. Recommended drought response actions primarily involve reducing public water use and adjusting the Shelbyville target flow constraint, which is managed by Normandy releases. Optimizing releases from Normandy Reservoir is a crucial aspect of water resource management in the Duck River region (TDRDA 2013b). During drought conditions, water users upstream of Columbia depend entirely on these releases to meet their water supply needs. The Tennessee Valley Authority (TVA) regulates reservoir releases to maintain the integrity of aquatic ecosystems. A minimum instantaneous flow requirement at Shelbyville was established in 2013: 120 cubic feet per second (cfs) from December through May and 155 cfs from June through November.

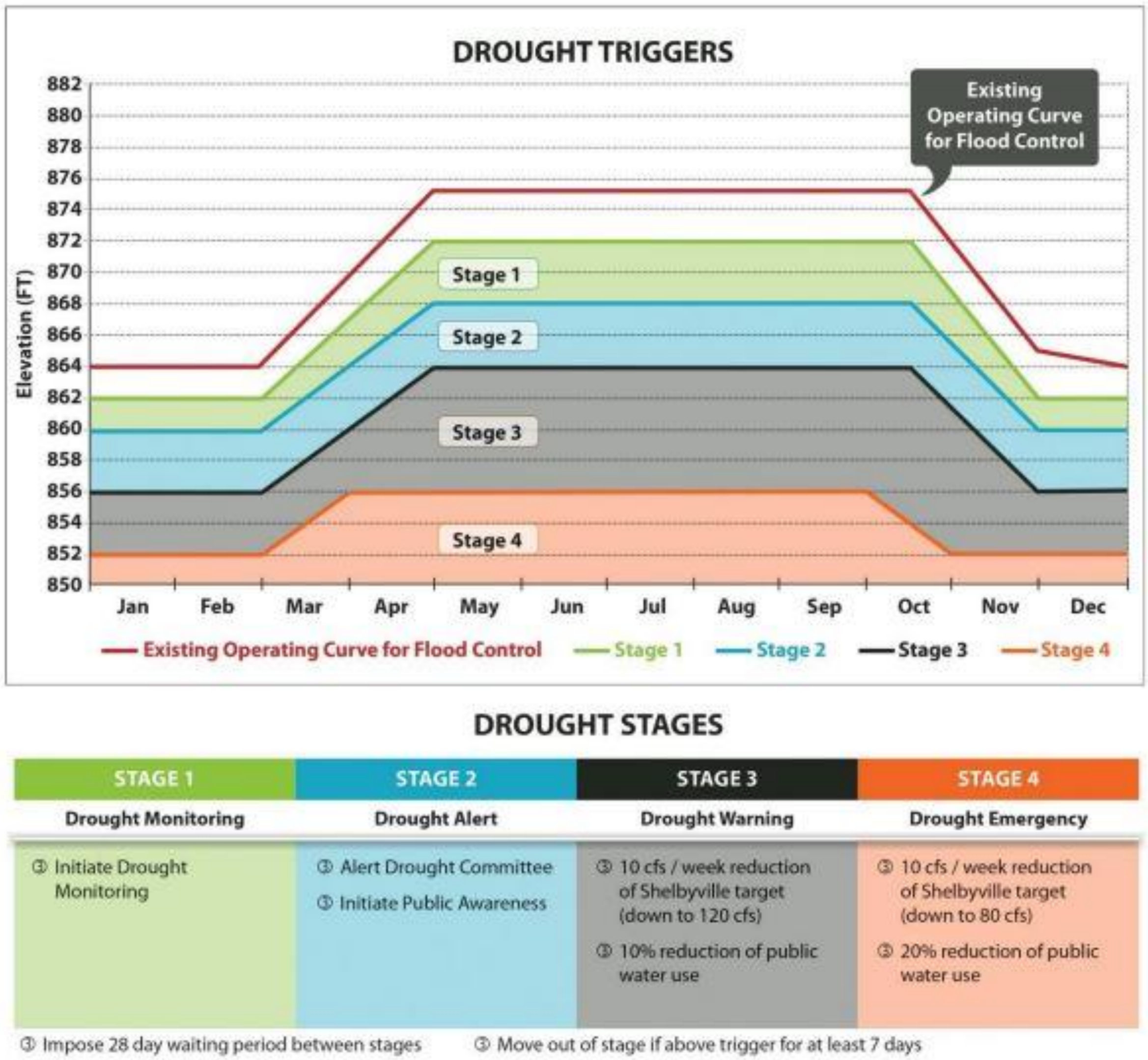

Figure 6. A description of Normandy Reservoir's elevation-based triggers for drought responses, as illustrated by the Duck River Regional Drought Management Plan (edited by Doug Murphy from the Tennessee Duck River Development Agency's Final Report, April 2013).

In 2018, the U.S. Army Corps of Engineers (USACE) developed a watershed plan for the Duck River to address key water resource issues, including water quality, water supply, ecosystem degradation, land use, and flood risk management (USACE 2018). The plan aimed to identify challenges within the watershed and propose mitigation strategies to address them. A central component of the watershed assessment was an ecological model that used a multi-scale approach, incorporating biological and geomorphological data, such as fish, mussels, aquatic macroinvertebrates, and habitat assessments conducted via low-altitude video. These data were used to generate a Stream Conditions Index (SCI), which reflects the overall health of stream and riparian corridors within HUC12 watersheds. The model also served as a tool for prioritizing watersheds for restoration and conservation efforts. The resulting model and watershed plan provided a framework for agencies and organizations to effectively allocate funding and enhance resource management within the watershed. Additionally, the assessment highlighted the need for a drought preparedness plan. The plan also emphasized the importance of regulating environmental flows across smaller watershed segments. Given that the Upper Duck, Lower Duck, and Buffalo watersheds support distinct aquatic communities, segment-specific environmental flow considerations can better inform water management decisions, such as water withdrawal locations and limits (USACE 2018).

Effective water resource management in the Duck River watershed requires a coordinated approach that balances the needs of humans, industry, ecosystem services, and biodiversity. As water demand continues to grow, proactive planning—through drought preparedness strategies, optimized reservoir operations, and environmental flow regulations—will inform efforts to sustain the Duck River and its ecosystem services. The collaborative efforts of agencies such as the Duck River Development Agency, the Tennessee Valley Authority, and the U.S. Army Corps of Engineers have provided a foundation for long-term water security. However, ongoing assessments and adaptive management informed by ongoing research may be necessary to address future challenges.

Current issues in water management

The Duck River watershed is at a pivotal time in its management and ecological history due to significant growth in human population and economic activity. The consequent increase in surface water demand presents challenges for sustainable water resource management. Below we summarize the current events directly affecting mussels in the Duck River.

Water withdrawals

Rapid urban and industrial development in the area south of Nashville poses a threat to the water resources of the Duck River, as the river faces proposed water withdrawals deemed economically necessary (Figure 1, Figure 2). The Tennessee Department of Environment and Conservation (TDEC) has permitted or proposed to permit eight water utilities to withdraw over 77 mgd from the Duck River, representing over a 40% increase from previously permitted amounts (USFWS 2025) (Table 2). Many of these permits, submitted through the Aquatic Resource Alteration Permit (ARAP) program, were appealed by various entities. At the time of this report, TDEC is reviewing public comments for several of these ARAP permits. Reductions in streamflow can affect the integrity of aquatic communities; therefore, TDEC has set minimum flow limitations on permitted withdrawals through the ARAP program. Specifically, withdrawals in the Duck River must not result in a flow below 100 cfs at DRM 133.9 in Columbia or below 175 cfs at the USGS Milltown gage (03599240; U.S. Geological Survey 2022) (Hubbs 2024; USFWS 2025). To investigate the effects of additional water withdrawals, TDEC has partnered with the USACE to conduct hydrologic modeling that will inform how water inputs and outputs affect flows in the Duck River, with a focus on the implications for mussel populations (TDEC 2024b). This hydraulic model, anticipated to be finalized in Summer 2025, was developed with the Hydrologic Engineering Center's River Analysis System (HEC-RAS) and will enable TDEC to assess how a series of alternative water withdrawals will affect water surface elevations and therefore mussel populations (Ryan Wigner, USACE, Nashville District, email comm., 2025).

Additionally, TDEC has initiated a study to assess the relationship between low flows and mussel ecology in the Upper Duck River (AST Environmental 2024).

Table 2. Utilities included recently in Aquatic Resource Alteration Permit (ARAP) program. Asterisk (*) denotes appeals by third-party entities. MGD (millions of gallons per day) refers to proposed or permitted withdrawal amounts, including "grandfathered" withdrawal amounts exempt through Tenn. R. & Regs. 0400-40-07-.02(4).

Permittee Name	**Permit ID**	**MGD**
Duck River Utility Commission*	NRS22.201	12.32
Bedford County Utility Commission*	NRS22.230	4.07
Marshall County Board of Public Utilities*	NRS20.177	6
Shelbyville Power, Water, and Sewerage Systems	NRS21.274	10
Lewisburg Water System	NRS19.148	6
Spring Hill Water System	NRS22.288	6
Maury County Water System	NRS23.098	3
Columbia Power and Water Systems*	NRS23.228	32

The largest proposed withdrawal in the ARAP program is the wastewater treatment plant improvement plan that the U.S. Environmental Protection Agency (USEPA) proposes to fund for the Columbia Power and Water Systems' (CPWS) Long-Term Water Supply Program (LTWSP). CPWS proposes to construct a new primary raw water intake at DRM 100, while maintaining its current intake at DRM 134, thereby increasing the utility's withdrawal capacity from 20 to 32 mgd. Withdrawals at the DRM 134 intake will be primarily for monthly maintenance and will be restricted to when the flow at the USGS Columbia gage exceeds 500 cfs, except in emergencies. TDEC is currently evaluating public comments from a draft permit submitted in March 2025. The USFWS released a combination Biological Opinion/Conference Opinion (BO) for this proposed funding on March 14, 2025 (USFWS 2025). The BO evaluates the effects of the LTWSP on several freshwater mussels: the endangered Birdwing Pearlymussel (*Lemiox rimosus*), Sheepnose (*Plethobasus cyphyus*), and Slabside Pearlymussel (*Pleuronaia dolabelloides*), the threatened Round Hickorynut (*Obovaria subrotunda*) and Rabbitsfoot (*Theliderma cylindrica*), and the proposed for listing as endangered Tennessee Pigtoe (*Pleuronaia barnesiana*) and Tennessee Clubshell (*Pleurobema oviforme*), and relevant designated critical habitats. The aquatic project area assessed in this BO includes 61 river miles from DRM 134 (Columbia) to DRM 73 (below Centerville).

The BO summarizes conservation measures related to the proposed actions, including several measures related directly to flow. Hydrological modeling conducted using the OASIS model (see Section 3C) and the System for Environmental Flow Analysis (Jowett et al. 2023) indicates that the proposed withdrawals will increase the mean annual 7-day low flow by up to 21 cfs in the upstream sections of the aquatic project area where mussels are most abundant.

CPWS will develop an operational plan that minimizes rapid changes in flow and limits the intake operation at DRM 134 to periods of high flow, thereby minimizing the effects on mussels in this area. Additionally, the BO describes a compensatory mitigation plan that includes funding for mussel propagation, a Mussel Salvage Plan, and a Rapid Response Team to address drought events.

The BO identifies the North Carolina Department of Environment and Natural Resource's recommendations for establishing ecological flows (NCDENR 2013) as the best available science regarding ecological flow management in the Duck River. Although this strategy has not been fully implemented in North Carolina, it provides a scientifically grounded starting point for ecological flow establishment that involves both flow and biological strategies. The flow component employs a percentage-of-flow strategy, maintaining 80-90% of ambient modeled flows, along with a critical low flow component, beyond which further actions are warranted to protect ecological integrity. The biological response strategy evaluates the effects of flow changes on fish and invertebrate diversity, where a 5-10% decrease in diversity triggers further review. Applying this framework, the BO calculated that the proposed maximum withdrawal of 32 mgd, or 45.9 cfs, would require a minimum flow of 250 cfs at the USGS Shady Grove gage to maintain an 80% flow-by rate, and 500 cfs to maintain a 90% flow-by rate (USFWS 2025). Since the proposed withdrawal moves the water intake from upstream at Columbia to an area where mussel populations are generally less abundant, and since the original intake will not operate below 500 cfs at Columbia, the BO concludes that the action is not expected to significantly affect mussel habitat. However, if the proposed maximum withdrawal of 32 mgd had occurred during the 2024 drought (see Section 3E below)—when the 3-day low flow at Shady Grove fell to 177 cfs—a flow-by rate of 72% would have resulted. Some nonprofit organizations recommended that withdrawals at both intakes be conditioned for CPWS to regulate withdrawals at both intakes with a percentage-of-flow based on a 90% flow-by and a critical low flow threshold to trigger withdrawal cessation (Harpeth Conservancy 2025; Duck River Conservancy 2025). Dr. Ryan Jackwood (Harpeth Conservancy, written comm., 2025) calculated site-specific 90% flow-by rates and low flow thresholds: for the Columbia intake (DRM 134), a 90% flow-by of 310 cfs and a cutoff of 136 cfs at the Columbia gage; and for the Shady Grove intake (DRM 100), a 90% flow-by of 500 cfs and a cutoff of 187 cfs (Harpeth Conservancy 2025) These recommendations are more conservative than the current CPWS commitment to only operate the intake at DRM 134 when the Columbia gage exceeds 500 cfs.

The BO concludes that the proposed action would not result in the jeopardization of existence for these species or adversely modify or destroy designated critical habitat for Slabside Pearlymussel (*Pleuronaia dolabelloides*), Fluted Kidneyshell (*Ptychobranchus subtentus*), Round Hickorynut (*Obovaria subrotunda*), or the Salamander Mussel (Si*mpsonaias ambigua*). Overall, the proposed action may adversely affect and result in incidental take of 705 Round Hickorynut (*Obovaria subrotunda*), 11,275 Slabside Pearlymussel (*Pleuronaia dolabelloides*), 3,523 Rabbitsfoot (*Theliderma cylindrica*), 700 Sheepnose (*Plethobasus cyphyus*), 3,523 Tennessee Pigtoe (*Pleuronaia barnesiana*), and 705 Tennessee Clubshell (*Pleurobema oviforme*) in the lower reach of the proposed actions. The BO concludes that harm and harassment will only occur for freshwater mussels in the direct vicinity of construction and the reach below the DRM 100 intake. Take will happen in the form of both lethal/harm and harassment and will be offset by a plethora of conservation measures described in the BO. Throughout this review, we have identified data gaps regarding the effects of water withdrawals and drought conditions on mussel community resiliency. The BO acknowledges these gaps and therefore includes an adaptive management plan as a conservation measure. This plan involves CPWS's consideration of funding the USFWS to conduct instream flow studies, develop minimum flows, monitor water quality, conduct mussel physiology and tolerance studies, salvage mussels during droughts, and monitor mussel populations. Due to the uncertainty regarding how the synergistic effects of proposed water withdrawals, karst geology, localized drought conditions, and climate change will affect mussel communities, the effect analyses in the BO are limited to the next six years. It acknowledges that consultation would be reinitiated if new information and science become available.

The proposed >40% in daily water withdrawal has unknown consequences for the Duck River's habitat, fauna, and surrounding agricultural practices. Specifically, knowledge regarding how these increased withdrawals will alter unique freshwater mussel populations in the Duck River is currently limited. Municipal water withdrawals in the Duck River region could consider minimizing the effects of altered flows on aquatic life and habitat. Releases from Normandy Dam have historically controlled minimum flows throughout much of the river; however, the ecological flows required to sustain aquatic life and habitat in the Duck River are not currently known. The methodology proposed by the BO for CPWS is a good starting point; however, the strategies for ecological flows established by NCDENR (2013) would be most beneficial if applied to *all* proposed water withdrawal activities in the Duck River to ensure consistent and science-based water management throughout the entire watershed. Furthermore, additional studies are beneficial to determine if this strategy is sufficient to protect mussel populations. Research on the synergistic effects of altered or reduced flows, such as water quality effects and non-lethal stress of mussels, could be prioritized in tandem with, not following, the Mussel Salvage Plan proposed to monitor mussel loss and ammonia/dissolved oxygen concentrations in response to drought. We acknowledge that data gaps prevent some water management thresholds from fully capturing the effects of withdrawals and alterations on mussel communities. However, we suggest water use managers maintain an open dialogue with all relevant state, federal, academic, public, and private entities to ensure that the best available science informs management decisions as these data gaps are filled.

Normandy Dam release optimization

At the time of this report, TVA has implemented modifications to the Normandy Dam release strategy, which took effect on June 1, 2025 (TVA 2025). The key change involves replacing the current instantaneous flow targets at Shelbyville with a weekly average flow target. This adjustment is intended to provide TVA with greater operational flexibility and enhance water conservation in Normandy Reservoir. The revised targets establish a weekly average flow of 120 cfs from December through May, with a minimum instantaneous threshold of 100 cfs. From June through November, the weekly average flow target increases to 155 cfs, with a minimum instantaneous threshold of 135 cfs. The proposed changes are predicted to increase Normandy's elevation approximately 25% of the time, potentially by up to two feet, compared to previous operations (TVA 2025). The additional water retained in Normandy Reservoir will be available for release during drought conditions, supplementing low river flows and improving conditions for aquatic species by enhancing flow, wetted perimeter, and dissolved oxygen levels, while also reducing water temperatures and chlorophyll concentrations.

To evaluate the potential effects of the proposed alternative on freshwater mussels, TVA modeled wetted width at five locations corresponding to TWRA's long-term mussel monitoring program (Hubbs 2010, 2015; TVA 2025). TVA acknowledges the potential for reductions in wetted width under the proposed operation changes. Specifically, modeled flows suggest a 10 cfs reduction in summer and a 5 cfs reduction in winter compared to current operations. These conditions are projected to occur between 0% to 37% of the year, depending on the location and modeling scenario. Under normal, non-drought conditions, the proposed changes would reduce the 50th percentile wetted perimeter at the five surveyed locations by an average of 0.6 feet (average channel width is 138 feet). During drought conditions, modeling indicates that the proposed changes would reduce wetted perimeters at all locations, with an average reduction of 0.9 feet in summer and 0.4 feet in winter. However, TVA characterizes these changes as small, temporary, and within normal historical variation for the Duck River.

TVA determined that the proposed operation alternative may affect but is not likely to adversely affect (NLAA) mussel species in the Duck River (TVA 2025). They conclude that since reductions in wetted perimeter would be small, temporary, and within historical variation for the Duck River, mussels will not be adversely affected during normal, non-drought conditions because most mussel species occupy the middle of the channel and non-juvenile mussels are capable of moving towards water or burrowing to avoid stranding. For the species that do occupy marginal stream habitats, effects of the proposed alternative are expected to be minimal, gradual, and temporary. Furthermore, under critical drought conditions, the proposed operational alternative is predicted to slightly benefit mussels by making more water available for release downstream, which could improve habitat conditions.

Metrics used to assess effects of the new Normandy Dam operations on mussel communities included wetted width scenarios and the ability of mussels to avoid stranding. This method does not account for the effects of no mussel recruitment (e.g., juvenile survival or sub-lethal stress that could affect mussel health and population dynamics). The literature reviewed in this document suggests that the relationship between flow regimes and freshwater mussel ecology extends beyond the simple metric of wetted width. Additionally, the synergistic effects of altered flows with other stressors, such as temperature changes, water quality degradation, and reduced host fish availability, may compound low flow effects on mussel populations in ways not captured by single-variable analyses.

Proposed Columbia Dam

The proposed Columbia Dam impoundment was initially conceived as part of a multi-dam project in the 1930s and authorized by Congress in 1969 to provide flood control, recreation, water quality enhancement, and water supply (TVA 1979; USACE 2018). Construction began in 1973, and by the time the project was discontinued, it was considered 45% complete. The concrete dam was 90% complete, while the earthen dam was 60% complete (Federal Register 2001), and an estimated $82 million had been invested in its construction (Seattle Times 1999). It was at this point that an economic analysis suggested an unfavorable benefit-cost ratio for the project, which was deemed unjustified for continued federal funding (TVA 1979). This prompted Congress to halt appropriations, and existing structures were removed between 1999 and 2000 (Federal Register 2001).

Endangered freshwater mussels at the location of the proposed dam and reservoir are cited in both official documents and news sources as the cause of the project's elimination (TVA 1979; Seattle Times 1999; What's Up Columbia 2024; TVA 2025). This focus may conceal the underlying complexity of the dam's economic viability, which may have contributed to its delayed initial construction (TVA 1979; Seattle Times 1999; Federal Register 2001). The cessation of the Columbia Dam project may be more accurately portrayed as a convergence of multiple technical and economic challenges in addition to the environmental and regulatory obstacles that rendered the project untenable (Federal Register 2001; USACE 2018; TDRDA 2025). Projections indicated that the river's ability to maintain water supply to the reservoir would be frequently strained, particularly during drought conditions (TDRDA 2011; Strzepek et al. 2010), where the underlying karst conditions would result in continued water loss from the reservoir (Knight and Kingsbury 2007; Knight et al. 2013). Furthermore, water quality concerns arose early in the planning process, with anticipated problems including taste and odor issues associated with water retention and low flows, which would compromise the reservoir's utility for municipal water supply (TVA 1979; USACE 2018; TDRDA 2025). The loss of ecosystem services that resident mussels would provide in the absence of the reservoir would conceivably exacerbate this problem, though to what degree is unknown. The project's flood control benefits were also questioned, as the proposed operational scheme of a 12,000-acre summer pool reducing to a 4,000-acre winter pool would provide limited flood protection (TVA 1979; TDRDA 2025). The evaluation of alternative pool levels in response to these constraints highlighted the project's incompatibility with the geological realities of the site and its environmental regulatory framework (TVA 1979; Knight et al. 2013; TDRDA 2025).

Ultimately, the cessation of the Columbia Dam project serves as a case study of the interplay between geological/ hydrological constraints and natural resource conservation in the Duck River watershed (TDRDA 2025). Although some attributed the project's cessation to the newly created Endangered Species Act at that time, its cancellation also stemmed from fundamental structural, engineering, water quality, and hydrologic/geologic issues that rendered the dam both technically problematic and ecologically destructive, and alternatives more cost-effective (TVA 1979). The proposed reservoir site is above the karst topography of the Central Basin, characterized by sinkholes, losing streams, and reduced surface water availability (Ford and Williams 2007). This karst landscape, underlain by Ordovician limestone, creates a "losing" section of the river where substantial volumes of water are lost to groundwater through permeable bedrock formations (Knight and Kingsbury 2007; Knight et al. 2013) (Figure 2).

The small size and karst topography of the Duck River watershed, while creating unique chemical qualities within its surface water system that are favorable for instream water quality (Stueber and Criss 2005), make this section of the river particularly vulnerable to water loss during impoundment. Maintaining reservoir levels in this geology would place continuous demands on upstream water resources, particularly Normandy Reservoir, effectively transferring drought stress from one location to another rather than addressing regional water supply challenges. The 2007-2008 drought, during which Normandy Reservoir reached 42% capacity, demonstrated the vulnerability of the existing system to climatic variability (TDRDA 2025). Adding another reservoir in a losing reach of the river may exacerbate rather than alleviate these challenges, particularly given that climate projections indicate that droughts will become more frequent and intense (Strzepek et al. 2010).

Paradoxically, the same geological processes that make reservoir maintenance technically challenging may also contribute to the extraordinary biodiversity that makes this section of the Duck River globally significant. Groundwater filtration through karst topography supplies dissolved calcium and bicarbonate ions to downstream systems, buffering surface water against pH changes and supporting aquatic life (Allan et al. 2021). The concentration of the most diverse and abundant mussel communities in the Duck River, located immediately downstream of zones where these geochemical processes dominate, is not coincidental. The calcium carbonate cycle in the Duck River supports its distinctive ecological features, including stable pH conditions and calcium availability for shell-building organisms, such as mussels, while also fostering specialized algal and bacterial communities that are the food base for freshwater mussels. The area between Columbia and Lillard Mill, which the proposed reservoir would inundate, is the most unique, significant, and densely populated section of the river for freshwater mussels, harboring the highest documented mussel diversity in the watershed, with 57 species historically documented at Lillard Mill (Womble and Rosenberger 2025b). Underground flows and upwelling through this karst geography, which may drive, or at least facilitate, this unique diversity, are spatially fixed processes tied to geological formations and groundwater flow patterns that cannot be relocated or replicated. Unlike mobile organisms that might theoretically be relocated, the springs, seeps, and subsurface water-rock interactions that deliver essential minerals and nutrients to support mussel metabolism and shell growth are place-specific. They would conceivably be permanently lost if flooded by a reservoir.

The Columbia Dam case illustrates how geological constraints and ecological values may be intrinsically linked. The karst topography that made the dam economically and technically problematic is the same geological foundation that creates unique biogeochemical conditions supporting the world's most diverse temperate freshwater mussel fauna. This case highlights that geological realities can dictate both engineering feasibility and ecological value, rendering some projects inadvisable on multiple grounds. Modern water resource management in the Duck River has since evolved toward approaches that work within existing geological and ecological constraints (TDRDA 2011, USACE 2018). The Duck River Development Agency's 2011 Comprehensive Regional Water Supply Plan identified multiple alternatives, including drought management planning, water use efficiency programs, optimizing Normandy Reservoir releases, and developing new downstream intakes that avoid the unique middle reaches of the river (TDRDA 2011). These approaches recognize that sustainable water security must incorporate the fundamental geological processes that shape the system.

Executive Order 108: Duck River Watershed Planning Partnership

On November 20, 2024, Tennessee Governor Bill Lee signed Executive Order No 108 (EO 108) (State of Tennessee 2024) to ensure long-term stability of the Duck River watershed through balancing economic growth, water resource management, and environmental conservation. Executive Order 108 orders the continued implementation of TDEC's Comprehensive Permitting Pilot Program in the Duck River Watershed. It sets a water loss reduction goal rate of no more than 20% and grants TDEC the authority to consider and prioritize regionalization and interconnection of water systems within the watershed for withdrawal permitting activities. Additionally, the order requires the development of a Habitat Conservation Plan for the Duck River to ensure compliance with the Endangered Species Act, the creation of a Comprehensive Regional Drought Management Plan, and an update to the Normandy Reservoir Management Plan. The order also calls for the improvement of sustainable river recreation and increased public education on watershed protection.

One primary component of EO 108 is the establishment of the Duck River Watershed Planning Partnership (DRWPP). The DRWPP is comprised of 19 individuals from political, regulatory, and academic entities and is responsible for the following objectives:

- Developing comprehensive watershed management recommendations that balance the needs of water users and economic growth against the need to protect the environmental integrity of the Duck River.
- Advising and providing recommendations to the Governor, the Duck River Development Agency, the Tennessee Department of Environment and Conservation (TDEC), the Tennessee Wildlife Resources Agency (TWRA), and legislative leadership on policies and actions to promote the sustainable use and conservation of water resources in the Duck River Watershed.
- Identifying opportunities for water system regionalization, drought resilience, habitat conservation, and water loss reduction.
- Engaging with local communities, utilities, industries, and conservation organizations to ensure broad participation in watershed planning efforts.

Executive Order 108 highlights the governor's expectation of watershed-wide collaboration to establish water management practices that ensure long-term stability of the Duck River. Our review suggests that sustainable water use management necessitates an understanding of complex ecological processes, and EO 108 requires all parties involved to consider the ecological integrity of the Duck River moving forward. Specifically, the proposed Habitat Conservation Plan will be developed by TDEC and state, federal, and local partners, and will seek to minimize and mitigate threats to mussels while working to regionalize water management and permit water withdrawals. Comprehensive assessment of flow alterations should consider multiple components of the flow regime (magnitude, frequency, duration, timing, and rate of change), complex hydraulic variables (such as shear stress and Reynolds numbers), geomorphological processes, water quality parameters, thermal regimes, food resource availability, host fish interactions, and life-stage specific requirements of mussels. Evidence suggests that mussels respond differently to flow alterations depending on their species traits, life history stages and strategies, and spatial distributions within the river system. An integrated, evidence-based approach that incorporates this ecological complexity may provide a more robust understanding of how flow regime modifications influence the persistence and resilience of the Duck River's significant mussel fauna, particularly during vulnerable periods such as reproduction. This multifaceted perspective aligns with our review, which offers a foundation for more comprehensive flow management considerations.

3E. Historical and projected drought patterns in the Duck River watershed

Extreme droughts were recorded in the Duck River watershed in the fall of 2000, 2007, 2016, 2023, and 2024 (USFWS 2025). An exceptional drought occurred in the Duck River watershed in 2007, characterized by prolonged below-average precipitation and record-high temperatures (TDRDA 2013a). This drought event caused significant issues with the public water supply and had notable effects on water quality and aquatic habitats. For example, reduced flows from water pumps at Normandy Reservoir affected water availability, and elevated raw water temperatures caused taste and odor issues. Water treatment became more difficult, particularly in Columbia and Spring Hill (TDRDA 2013a). The 2011 RWSP identified a potential deficit of up to 32 mgd for Duck River users in 2060 during extreme or prolonged drought conditions. Under drought conditions like those in 2007, a deficit of approximately 4 mgd could occur (TDRDA 2011). The RWSP emphasized the importance of incorporating drought considerations into all water supply planning activities. As a result, drought preparedness has been recognized as a critical component of water management in the Duck River watershed for over a decade. The 2007 drought demonstrated that severe drought conditions can occur in the Duck River regardless of Normandy Lake's elevations, highlighting the need for flow-based drought triggers to protect aquatic communities in the mainstem Duck River (TRDRA 2013a).

Drought conditions occurred in the Duck River watershed in 2024, during which several mussel stranding events were documented (Hubbs 2024) (Figure 7). An extended low flow event was recorded between July 4 and July 16 based on below-median daily flow measurements at the USGS Milltown gage (03599240). Don Hubbs surveyed eight sites near existing or proposed water intakes between Shelbyville and Centerville (DRM 222-51) in July and September 2024 to assess the effects of this low flow event on freshwater mussel populations, and he observed 777 fresh dead individuals of 36 species (Hubbs 2024). Federally protected species were observed throughout the survey reach and accounted for 58.4% of total collected mussels. The Birdwing Pearlymussel (*Lemiox rimosus*, federally endangered) and the Round Hickorynut (*Obovaria subrotunda*, federally threatened) comprised 24.6% and 19.65% of the sample between Shelbyville and Columbia, respectively. Many individuals had soft tissue remaining in their shells, indicating recent mortality (Figure 8). At Venable Spring, a TWRA long-term monitoring site, 277 fresh dead mussels were collected. Mussels were observed stranded or attempting to move horizontally to deeper water within marginal habitats. Numerous live mussels were found in extremely shallow water (less than 4 inches deep), further highlighting their vulnerability during low flow conditions (Figure 9)

Figure 7. Drought conditions during Summer 2024 in the Duck River, Tennessee. Photographs provided by Don Hubbs.

Figure 8. Fresh dead mussel shells collected in the Duck River during mussel stranding surveys in 2024 (Hubbs 2024, pg. 30, Figure 30).

Figure 9. Photographs from Venable Spring site on the Duck River, “looking downstream at 100 flags placed next to live mussels in < 4-inch-deep water over a 40 m stretch of bank along the right descending bank immediately upstream from the spring confluence at the downstream site boundary” (Hubbs 2024, pg. 16, Figure 12).

Climate projections indicate that droughts will become more frequent and intense, and water availability will be further limited by increased evaporation rates resulting from rising temperatures (Strzepek et al. 2010). Models forecast that increased warming will continue through the end of the century for all seasons, with the greatest temperature increases in the summer months in the southeastern United States. This trend is likely to be compounded by continued population growth and economic activity, which will increase water demand and further strain surface water supply. At the time of the 2018 Duck River Watershed Plan, available tools were not capable of accurately estimating the magnitude and effect of climate change on the Duck River watershed. However, overall climate projections indicate that droughts will become more frequent and severe; therefore, future climate changes could be considered in future management decisions when possible (USACE 2018). In its BO on Columbia Power and Water Systems infrastructure upgrades, the USFWS identified that five severe droughts occurred in Maury County, TN from 2000-2024 (USFWS 2025). Based on this pattern, they concluded that another drought is likely within the next six years (USFWS 2025). An updated Comprehensive Regional Drought Management Plan for the Duck River watershed is in development but not yet available at the time of this report.

The Duck River supports dense mussel beds, particularly in the core area of diversity between Columbia and Milltown in the Upper Duck watershed (see Section 3B). However, available data indicate that the densities of these beds have generally declined since 2010 (Hubbs 2010, 2015; Wisniewski 2020). The observation of hundreds of fresh dead mussels, including listed species, highlights conservation concerns given the likelihood of future drought conditions in the watershed. Although the mussel populations in the Lower Duck watershed are generally under-surveyed, available data suggest they are less abundant here than in areas further upstream in the system. This lower abundance may make them more susceptible to drought conditions, as the severity of post-drought declines can depend on pre-drought abundance (Haag and Warren 2008; Mitchell et al. 2021). The documentation of mussel strandings in the Lower Duck River on September 5, 2024, coupled with the fact that the largest proposed increase in withdrawals—from 20 mgd to 32 mgd by CPWS—is planned for this area, underscores the potential for proposed water use to affect mussel populations throughout the entire Duck River, especially during droughts.

This section of our review highlights a broader challenge in water resource management: the cumulative effects of multiple, individually assessed modifications to river systems. Although each discrete decision about water withdrawals or flow alterations may appear to have limited ecological consequences when evaluated in isolation, our review suggests that these incremental changes can compound over time. Drought conditions can further exacerbate the consequences of these flow alterations. A watershed-scale perspective—one that examines the collective influence of all flow alterations, land use changes, and water quality factors—aligns more closely with current ecological understanding of riverine systems and may be warranted for such a globally significant system. An integrated approach, supported by comprehensive data collection and monitoring of key environmental indicators, would provide a stronger foundation for understanding how the unique assemblage of mussel species in the Duck River responds to changing flow conditions across multiple spatial and temporal scales. Evaluating flow modifications within this broader ecological context may reveal threshold effects and interactions that remain obscured when examined through narrower analytical frameworks. This type of approach may serve as a model and transferable example for other southeastern systems that are subjected to flow alterations and drought conditions.

4. Bringing it All Together: Environmental Flows and Freshwater Mussels

The flow regime is the principal regulator of water quality and quantity in riverine habitats. It controls the physical features of streams (e.g., substrate composition and stability, wood debris, and stream structure) as well as the ecosystem and biological features of streams (e.g., fish communities, food availability, predation, and nutrient cycling). As such, an understanding of the interplay between Duck River mussel communities, instream flow regimes, and watershed management on freshwater mussel populations requires an information-based, conceptual approach that integrates flow dynamics, water quality, geomorphological and watershed processes, and individual/community freshwater mussel responses to provide a holistic view of how changes in flow regimes will affect freshwater mussel communities (Figure 10). This can be incorporated into a broader conservation and management strategy that includes other water uses and instream flow needs for the Duck River (see Section 5). Although the full range of research tools and information required to incorporate all these processes into an environmental flow management plan is not available at the time of writing this report, acknowledging the complexity of the flow-mussel ecology relationship may inform proactive management of this key Tennessee resource.

Water regulation and withdrawals, in concert with watershed development, can fundamentally change natural flow regimes in terms of magnitude, timing, frequency, duration, and rate of change of discharge and flow events (Poff et al. 1997), all of which can affect mussel ecology in ways known and unknown (Section 2). An understanding of the extent of flow alteration that freshwater mussels in the Duck River can tolerate—or from which they can recover—requires not only consideration of human activities that directly remove or add water to the Duck River (e.g., release from Normandy dam, water withdrawals for agriculture or municipal use, treated wastewater release) but also those activities that can affect geochemical and groundwater processes (i.e., groundwater recharge and upwelling) and the rate of delivery of surface water (e.g., increase in impervious surfaces through human development). Further, the source, timing, and rate of change in water delivery to the mainstem Duck River have the potential to alter water quality, which may interact synergistically with water availability to affect freshwater mussels in the Duck River.

Of particular concern during drought conditions are the effects of extremely low flows on freshwater mussels, as evidenced by documented die-offs during past and recent drought conditions. Although direct mortality from stranding or thermal stress is relatively straightforward to observe (though we likely only measure a small portion of stressed, near-dead, or fresh-dead individuals during these events), the long-term effects of compromised individual, population, or assemblage-level viability are complex to measure and poorly understood. An investigation of the effects of drought on freshwater mussels must extend beyond the immediate risks of desiccation and thermal stress to include the effects of altered water quality, as well as the delivery of food and mineral resources, an interruption of which could lead to energetic deficits and reduced resilience to environmental stress, even when mussels remain submerged. Valve closure as a defensive response to adverse conditions, if prolonged, could also compromise the physiological condition of mussels. Finally, reduced surface water-groundwater connectivity during drought conditions (or the disruption of these processes by the construction of impervious surfaces in the watershed) may limit the delivery of essential minerals and nutrients from upstream sources that are crucial for mussel shell growth and metabolism (Allan et al. 2021) or affect the availability of host fishes to disperse young. Finally, the synergistic effects of low flows and drought conditions, combined with other factors such as water quality, invasive species, and habitat changes, are poorly understood. This knowledge gap is particularly relevant for the Duck River, where multiple stressors operate simultaneously within a complex geological and hydrological context (Figure 10).

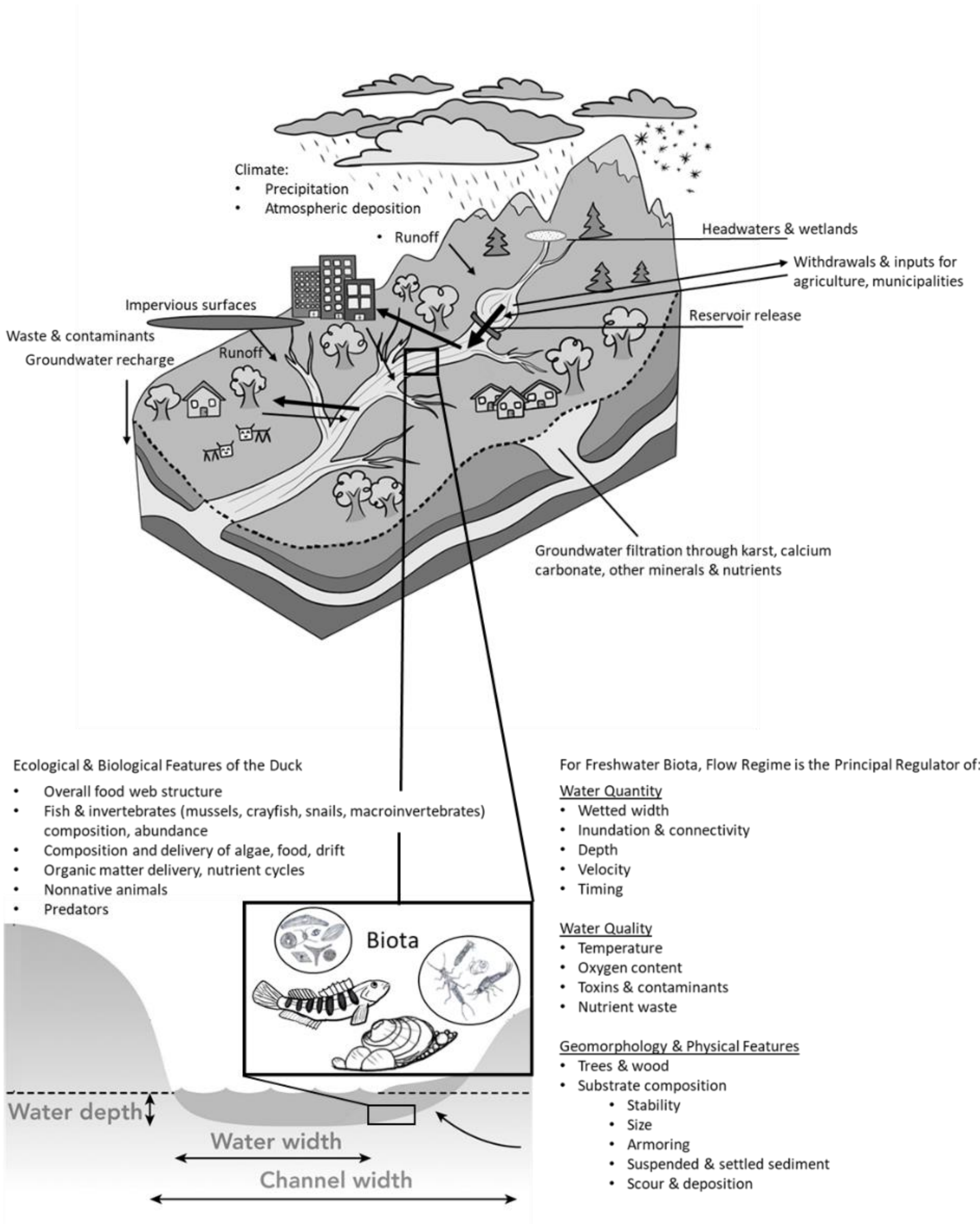

Figure 10. Simplified hydrologic schematic of the Duck River watershed, illustrating primary sources and routing of water, nutrients, and hydrological and hydrogeomorphological processes that could directly affect freshwater mussel habitat. Whole watershed processes are illustrated that affect site-scale water quality and physical habitat features important to individual mussels, mussel assemblages, and mussel metapopulations (Artwork credit: Rheda Rosenberger and Amanda Rosenberger).

Systematic approaches to mitigate the adverse effects of droughts and low flows on freshwater mussels are lacking; however, there is a consensus that successful mitigation requires site-specific management due to heterogeneity in habitat conditions and mussel communities (Cushway et al. 2024). Mitigation may be most successful when it incorporates habitat and water quality management, climate monitoring, and sustainable water use to protect mussel populations. Survey work, such as the long-term monitoring of mussels and their host fish, can inform assessments of the community's response to droughts and facilitate the identification of redundant populations of sensitive or rare species. However, strategies should expand beyond monitoring mussel population conditions to assess the full range of drought effects on mussel communities. For example, studies evaluating the sublethal stress of drought and low flows may inform our understanding of mussel health tolerances, especially for listed species with strongholds in the Duck River. Without research specific to freshwater mussels, managers may also consider incorporating other essential services that the Duck River provides, which are directly related to flow and water supply (See Section 5).

5. Proposed Collaborative Efforts for Establishing Low Flow Thresholds for the Duck River, Tennessee

Rack et al. (2024) described their approach for defining low flow thresholds for the Flint River, Georgia, a free-flowing river important for municipal water supply, recreation, and native biota. The paper first highlights the field of translational ecology as a systematic and evidence-based process that effectively addresses both social and ecological dimensions of environmental problems (Enquist et al. 2017; Golladay et al. 2021). Translational ecology is an emerging field that aims to bridge the gap between scientific research and real-world environmental problem-solving (Enquist et al. 2017; Table 3). It focuses on effectively applying ecological knowledge and scientific findings to address complex environmental challenges while considering their social and ecological dimensions (Golladay et al. 2021). The primary objective of translational ecology is to facilitate the transfer of scientific knowledge into actionable solutions and policies that benefit both society and the environment (Weingart et al., 2021; Figure 11).

Table 3. Key aspects of translational ecology and their descriptions.

Overarching Principles	**Description**	**References**
Interdisciplinary approach	Combines knowledge from various disciplines, such as ecology, social sciences, economics, and policy, to develop a holistic understanding of environmental problems and their potential solutions.	Enquist et al. 2017
Stakeholder engagement	Actively involves stakeholders, including policymakers, practitioners, and local communities throughout the research process. This collaboration ensures that research questions are relevant and that resulting solutions are feasible and acceptable to those affected.	Golladay et al. 2021; Safford et al. 2017
Real-world application	The focus is on developing practical, evidence-based solutions that can be effectively implemented in real-world settings. This involves considering the social, economic, and political contexts in which environmental problems occur.	Weingart et al. 2021
Adaptive management	Recognizes the complexity and uncertainty inherent in environmental systems. It employs adaptive management strategies, which involve continuous monitoring, learning, and adjustment of interventions based on new information and changing conditions, with stakeholder involvement.	Williams 2011; Fujitani et al. 2017
Science communication	Effectively communicates scientific findings to diverse audiences, including decision-makers and the public. This involves presenting information in accessible and compelling ways to facilitate understanding and action.	Enquist et al. 2017; Safford et al. 2017

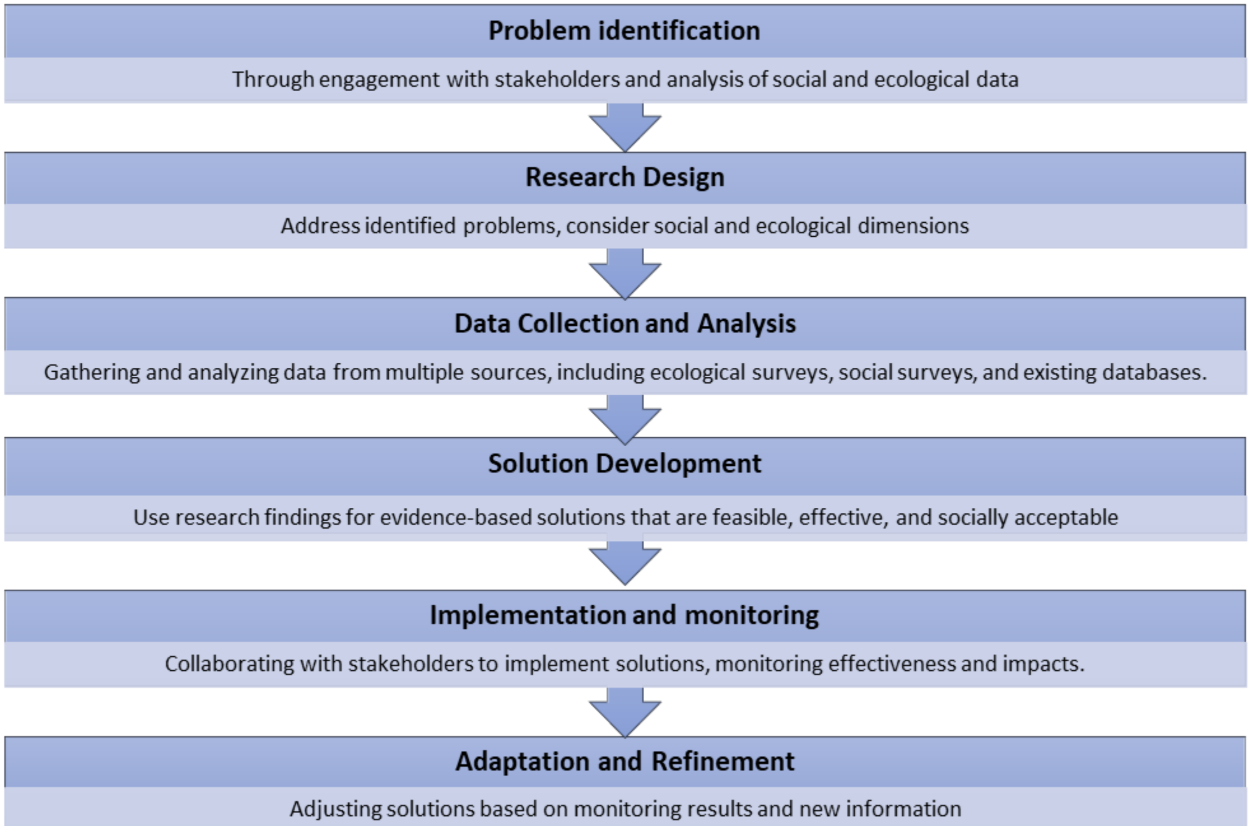

Figure 11. Workflow of the translational ecology process. Figure derived by Amanda Rosenberger.

Table 4. Agencies involved with proposed water withdrawal projects for the Duck River, Tennessee*.

Agency	Role	Agency	Role
TDEC	ARAP/ CWA Section 401 Water Quality Certification Drinking water regulation NPDES regulation of wastewater discharges SRF, land managers and state park and wildlife management areas	TVA	Lead federal agency; consults with USFWS as needed under ESA Section 7 Regulates the intake structure in the river and associated pipelines affecting the river TVA Act Section 26(a) permit for intake structure and limit on water withdrawal
TWRA	No regulatory capacity for water withdrawals Provides data and comments on regulatory actions, land managers and State Park managers	USACE	CWA Section 404 Regulates work and impacts to navigable waters under Section 10 of the Rivers and Harbors Act Falls under ESA Section 7 consultation interagency cooperation
DRA	Regional Planning Organization for the Duck River region Developed Comprehensive Regional Water Supply Plan and Drought Management Plan	EPA	Oversees state water quality standards and any changes to flow criteria under the designated use of Fish and Aquatic Life Administers WIFIA loan program With USACE, administers CWA Section 404, requiring alternatives analysis and may consider water loss
		USFWS	Under ESA Section 7, provides consultation to federal agencies because water withdrawals may impact listed species Provides data and comments on regulatory actions Evaluate ESA Section 10 - take of a listed species in conjunction with a suitable Habitat Conservation Plan May also provide financial assistance to states under ESA Section 6 to fill information gaps and support conservation programs for listed species.

*Acronym definitions:

ARAP: Aquatic Resource Alteration Permit
CWA: Clean Water Act
DRA: Duck River Agency
EPA: U.S. Environmental Protection Agency
ESA: Endangered Species Act
NPDES: National Pollutant Discharge Elimination System
SRF: State Review Framework
TDEC: TN Department of Environment and Conservation
TVA: Tennessee Valley Authority
TWRA: Tennessee Wildlife Resources Agency
USACE: U.S. Army Corps of Engineers
USFWS: U.S. Fish and Wildlife Service
WIFIA: Water Infrastructure Finance and Innovation Act

Creating a collaborative process for understanding the effects of drought and low flows on the ecology and ecosystem services of the Duck River allows members of the TDRDA to develop a rapport—and common language—for water managers, researchers, and conservationists about the ecological resources of the basin and how they could be considered in tandem with other essential ecosystem services for planning for drought and low flow conditions (Rack et al. 2024). Our findings support that a collaborative process be incorporated into the updated drought management plan under development by the TDRDA. Based on the feedback from the working group at the 2025 Tennessee Endangered Mollusk Committee meeting and our results, evidence-based flow thresholds could be established that could trigger mitigation of low flow events, alteration of water use in the basin, or other actions to mitigate drought before harm to the Duck River and the ecosystem services it provides. Furthermore, when evidence is lacking or weak for thresholds, studies can be proposed to provide additional information that managers require to make the most informed decisions. Ideally, these knowledge gaps will be identified and addressed *before* a severe drought occurs in the watershed. In the meantime, the NCDENR 2013 strategy can be implemented for proposed water withdrawals in the Duck River to establish consistent and science-based water management throughout the entire watershed (Table 5). This strategy has been accepted as best available science by several entities (USFWS 2025; Harpeth Conservancy 2025; Duck River Conservancy 2025).

Table 5. Relevant calculations for applying the North Carolina Department of Environment and Natural Resources (NCDENR) 2013 ecological flow guidance to current and proposed water withdrawals in the Duck River. Data provided by Ryan Jackwood (Harpeth Conservancy, written comm., 2025).

Treatment Plant	**Proposed Withdrawal amount (mgd)**	**Proposed Withdrawal amount (cfs)**	**90% FlowBy Value (cfs)***	**80% FlowBy Value (cfs)***
Lewisburg	6	9.282	92.82	46.41
Shelbyville	10	15.47	154.7	77.35
Columbia	32	49.504	495.04	247.52
Columbia	20	30.94	309.4	154.7
DRUC	12.32	19.05904	190.5904	95.2952
Marshall	3	4.641	46.41	23.205
Bedford	4.07	6.29629	62.9629	31.48145
Spring Hill	6	9.282	92.82	46.41

6. Knowledge Gaps and Future Research Directions

Despite summarized research on freshwater mussels and their ecological requirements, knowledge gaps remain that limit our ability to make evidence-based water management decisions for the Duck River system. The interplay between flow regime, water quality, geomorphology/hydrogeomorphology, and mussel ecology suggests the need for an integrated, multidisciplinary research approach. Decisions incorporating the ecosystem consequences of flow management may be informed by comprehensive, regularly updated spatial descriptions of mussel diversity throughout the Duck River system, using both traditional and emerging methodologies, such as environmental DNA (eDNA). Research investigating the relationships between flow and water quality along the entire river is necessary, particularly in areas of geomorphological and geochemical significance for mussel communities. Species-specific thresholds for key flow parameters and their water quality consequences would allow predictions of behavioral responses, physiological stress, and mortality triggers for the Duck River's diverse mussel fauna. Focused studies on population dynamics of both rare and common species in response to flow variation may provide crucial insights for conservation planning. These proposed research priority areas reflect a need for interdisciplinary collaboration among hydrologists, geomorphologists, ecologists, and water resource managers to develop science-based flow management policies that balance human water needs with the conservation of the Duck River's globally significant mussel fauna.

Potential research to inform ecological flows for Duck River freshwater mussels:

- Comprehensive and regularly updated spatial description of freshwater mussel diversity, using a combination of historical and contemporary surveys and a variety of survey approaches, including eDNA. Stream reaches where data gaps exist may be prioritized (Womble and Rosenberger 2025b). In areas of deeper water, diving methodologies should be employed to ensure sufficient detection.
- Investigations of flow-water quality relationships along the length of the Duck River system, with particular focus on areas of high geomorphological interest and geochemical importance, and investigation of those water quality features most likely to affect the individual fitness, population dynamics, and resilience of freshwater mussels. This may require expanded monitoring of the following parameters:
    - Depth
    - Temperature (could incorporate thermal modeling)[2]
    - Dissolved oxygen
    - Ammonia
    - Alkalinity/Calcium Carbonate ions

[2] We acknowledge the suggestions from Fogelman et al. (2023) that call for an improved understanding of mussel thermal ecology and that mussel conservation requires better spatial thermal modeling to predict when water temperatures become lethal for different species, combined with distribution mapping to identify at-risk populations. This research would inform relocation programs and requires more data on species-specific temperature tolerance limits.

    - Algae and fine particulate matter abundance and composition
    - Heavy metals
- Instream flow studies specific to the Duck River (e.g., assessing the sufficiency of the NCDENR 2013 strategy for protecting mussel populations), complementing existing work underway by TWRA investigating population dynamics of mussels under its current flow regime using mark-recapture techniques.
- Investigation of relationships between water quality and mussel behavior, physiological conditions, and performance.
    - Question: What are the species-specific thresholds for water quality parameters such as temperature, dissolved oxygen, and ammonia?
    - Question: What are the species-specific thresholds for key flow parameters (magnitude, duration, timing) that trigger behavioral responses, physiological stress, and mortality in Duck River mussel species?
- Investigation and monitoring of the population dynamics of rare and common mussel species related to instream flow parameters in the Duck River.
    - How do mussel life history traits vary in response to environmental flow recommendations for the Duck River? Life history categories from Haag 2012, Moore et al. 2021, and Hooper et al. 2023 can be used to organize species designations. Again, this complements existing work underway by TWRA using mark-recapture techniques.
- Investigation of flow-habitat relationships, including depth, scour, velocity, sediment dynamics.
- Investigation and monitoring of water quality differences up and downstream of the Nashville Basin.
- Relationship between flow and flow management and invasive species, including the *Corbicula* clam and invasive carp.

To meet the expectations of EO 108, agencies must collaborate to ensure that economic activity and water management are conducted in a manner that sustains the ecological integrity and long-term stability of the Duck River (State of Tennessee 2024). Our review suggests that this necessitates the establishment of suitable ecological flows and sustainable low flow thresholds relevant to freshwater mussels. Since significant data gaps exist, prioritizing research needs for the Duck River system will require open and consistent communication among all agencies and stakeholders to ensure that information needs are addressed in a manner that reflects both agency and public priorities, is feasible, and directly benefits the Duck River watershed. The Duck River Watershed Planning Partnership provides an opportune collaboration pathway to ensure that expert opinion regarding these research needs is both communicated and incorporated into future endeavors, such as the upcoming Habitat Conservation Plan.

7. Conclusions

This review examined the effects of flow regimes on freshwater mussels, with a particular emphasis on the Duck River and ongoing threats to the system. The Duck River harbors over 60 mussel species, more than three times the biodiversity of all European waters combined, making it globally significant for freshwater conservation. The Duck River's status as a refuge for numerous imperiled mussel species, including 15 federally listed species, underscores the importance of evidence-based water management. Our review revealed the complex relationships between flow dynamics and mussel communities, highlighting the importance of magnitude, timing, and variability of flows. Low flow conditions and drought events present challenges to mussel survival, including reduced habitat availability, changes in water quality with unknown consequences, stranding, food limitation, increased predation pressure, disruption of reproductive cycles, and increased susceptibility to disease. The concentration of known peak mussel diversity in a relatively small, 50-mile stretch between Columbia and Lillard Mill creates challenges for sustaining the overall resilience of mussel populations in the Duck River watershed, which is currently at a pivotal time in its management history.

Extreme droughts were recorded in the Duck River watershed in the fall of 2000, 2007, 2016, 2023, and 2024 (USFWS 2025). Mussel stranding events were documented in the Duck River during the exceptional drought of 2007 (TWRA 2008) and more recently following drought conditions in July 2024 (Hubbs 2024). Hundreds of fresh dead shells of mostly listed species were collected in the Duck River's core area of mussel diversity in 2024. Generally, wetted channel width and direct mortality from stranding are the primary considerations when assessing the effects of droughts and low flows on freshwater mussels. Although direct mortality from stranding or thermal stress is relatively straightforward to observe, the long-term effects of compromised individual, population, or assemblage-level viability are complex to measure and poorly understood. While each discrete decision about water withdrawals or flow alterations may appear to have limited ecological consequences when evaluated in isolation, our review suggests that these incremental changes can compound over time and interact with other factors. Climate projections indicate that droughts will become more frequent and severe while human demands on water resources increase; therefore, drought management planning could be considered in future water management decisions in the Duck River watershed to ensure protection of freshwater mussel communities.

Although the effects of droughts, water withdrawals, and low flow conditions on mussels are an increasing area of study, there is a general paucity of data-driven consensus regarding optimal mitigation approaches and strategies (Cushway et al. 2024). This review highlights the substantial knowledge gaps that limit our ability to make evidence-based water management decisions for the Duck River system. Research indicates the need for a multifaceted approach to water management that considers ecological flows and human water needs. Developing flow thresholds informed by mussel ecology could provide benchmarks for water management decisions. Collaborative frameworks involving diverse stakeholders, such as water utilities, government agencies, conservation organizations, and researchers, could facilitate the integration of scientific information into management decisions. Monitoring mussel populations and environmental conditions would support adaptive management as new information becomes available. Long-term monitoring of the mussel communities in the Duck River may provide key information for the continued conservation of the river's biodiversity. The complex effects of drought and flow alteration suggest that water management strategies may be most effective when adaptive, accounting for species- and site-specific responses to changing conditions. Prioritizing research needs for the Duck River system would benefit from ongoing communication among all agencies and stakeholders to ensure information needs are addressed in a manner that reflects both agency and public priorities, is feasible, and directly benefits the Duck River watershed. Knowledge gained from understanding the relationship between flow management and mussel conservation in the Duck River could inform approaches in other watersheds facing similar water demand and conservation needs.

Literature Cited

Acreman, M. 2016. Environmental flows—basics for novices. Wiley Interdisciplinary Reviews (WIREs) Water 3:622-628.

Acreman, M.C., and M.J. Dunbar. 2004. Defining environmental river flow requirements–a review. Hydrology and Earth System Sciences 8:861-876.

Acreman, M.C., M.J.Dunbar, J., Hannaford, O. Mountford, P. Wood, N. Holmes, I. Cowx, R. Noble, C. Extence, J. Aldrick, J. King, A, Black, and D. Crookall. 2008. Developing environmental standards for abstractions from UK rivers to implement the EU Water Framework Directive. Hydrological Sciences Journal 53:1105-1120.

Addy, S., S.L. Cooksley, and I. Sime. 2012. Impacts of flow regulation on freshwater pearl mussel (*Margaritifera margaritifera*) habitat in a Scottish montane river. Science of the Total Environment 432:318-328.

Ahlstedt, S.A., J.R. Powell, R.S. Butler, M.T. Fagg, D.W. Hubbs, S.F. Novak, S.R. Palmer, and P.D. Johnson. 2017. Historical and current examination of freshwater mussels (Bivalvia: Margaritiferidae: Unionidae) in the Duck River Basin, Tennessee. Malacological Review 45(46):163 pp.

Aldridge, D.C. and A.L. McIvor. 2003. Gill evacuation and release of glochidia by *Unio pictorum* and *Unio tumidus* (Bivalvia: Unionidae) under thermal and hypoxic stress. Journal of Molluscan Studies 69:55–59.

Aldridge, D.C., I.S. Ollard, Y.V. Bespalaya, I.N. Bolotov, K. Douda, J. Geist, W.R. Haag, M.W. Klunzinger, M. Lopes-Lima, M.C. Mlambo, N. Riccardi, R. Sousa, D.L. Strayer, S.H. Torres, C.C. Vaughn, T. Zajac, and A. Zieritz. 2023. Freshwater mussel conservation: A global horizon scan of emerging threats and opportunities. Global Change Biology 29(3):575-589.

Allan, J.D., M.M. Castillo, and K.A. Capps. 2021. Stream ecology: structure and function of running waters. Springer Nature, Cham, Switzerland. 436pp.

Allen, D.C., and C.C. Vaughn. 2009. Burrowing behavior of freshwater mussels in experimentally manipulated communities. Journal of the North American Benthological Society 28:93-100.

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

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

American Rivers. 2024. America's most endangered rivers of 2024. A call to action for clean water. Final Report. 24pp. Accessed at: https://www.americanrivers.org/wp-content/uploads/2024/04/v8_AR_2024-Most-Endangered-Rivers-FINAL.pdf.

Andre, C., J.F. Bibeault, and F. Gagne. 2021. Identifying physiological traits of species resilience against environmental stress in freshwater mussels. Ecotoxicology 30:1862-1871.

Archambault, J.M., W.G. Cope, and T.J. Kwak. 2013. Burrowing, byssus, and biomarkers: behavioral and physiological indicators of sublethal thermal stress in freshwater mussels (Unionidae). Marine and Freshwater Behaviour and Physiology 46:229–250.

Archambault, J.M., W.G. Cope, and T.J. Kwak. 2014. Survival and behaviour of juvenile unionid mussels exposed to thermal stress and dewatering in the presence of a sediment temperature gradient. Freshwater Biology 59:601-613.

Arthington, A.H., A. Bhaduri, S.E. Bunn, S.E. Jackson, R. E. Tharme, D. Tickner, B. Young, M. Acreman, N. Baker, S. Capon, A. C. Horne, E. Kendy, M.E. McClain, N.L. Poff, B.D. Richter, and S. Ward. 2018. The Brisbane declaration and global action agenda on environmental flows. Frontiers in Environmental Science 6(45):15pp.

AST Environmental. 2024. Duck River Mussel Survey and Habitat Assessment Report: Slick Shoals, Old Trap Island, Cundiff Island, Carpenter Bridge Shoal, Marshall and Maury Counties, Tennessee. Report prepared for Civil & Env Consultants, Inc. and TDEC. 58pp.

Atkinson, C.L., Julian, J.P., and C.C. Vaughn. 2012. Scale-dependent longitudinal patterns in mussel communities. Freshwater Biology 57(11):2272-2284.

Atkinson, C.L., J.P. Julian, and C.C. Vaughn. 2014. Species identity dominates over environment in shaping the mussel-associated macroinvertebrate community. Freshwater Science 33:675-687.

Atkinson, C.L., C.C. Vaughn, K.J. Forshay, and J.T. Cooper. 2018. Consumer-driven nutrient dynamics in freshwater ecosystems: from individuals to ecosystems. Biological Reviews 93:309-329.

Augspurger, T., A.E. Keller, M.C. Black, W.G. Cope, and F.J. Dwyer. 2003. Water quality guidance for protection of freshwater mussels (Unionidae) from ammonia exposure. Environmental Toxicology and Chemistry 22:2569-2575.

Barnhart, M.C., and A.D. Roberts. 1997. Reproduction and fish hosts of unionids from the Ozark Uplifts. Pages 14–20 in K.S. Cummings, A.C. Buchanan, and L.M. Koch (editors). Conservation and management of freshwater mussels. II. Proceedings of a UMRCC Symposium, 16–18 October 1995, St Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

Barnhart, M. C. 2006. Buckets of muckets: a compact system for rearing juvenile freshwater mussels. Aquaculture 254:227-233.

Barnhart, M.C., W.R. Haag, and W.N. Roston. 2008. Adaptations to host infection and larval parasitism in Unionoida. Journal of the North American Benthological Society 27:370-394.

Beggel, S., M. Hinzmann, J. Machado, and J. Geist. 2017. Combined Impact of Acute Exposure to Ammonia and Temperature Stress on the Freshwater Mussel *Unio pictorum*. Water 9(455): doi:10.3390/w9070455.

Benson, J.A., P.G. Close, B.A. Stewart, and A. Lymbery. 2018. Upstream recolonization by freshwater mussels (Unionoida: Hyriidae) following installation of a fishway. Aquatic Conservation: Marine and Freshwater Ecosystems 28(2):512-517.

Bouska, K.L., A.E. Rosenberger, S.E. McMurray, G.A Linder, and K.N. Key. 2018. State-level freshwater mussel programs: current status and a research framework to aid in mussel management and conservation. Fisheries 42(8):345-360.

Bringolf, R.B., W.G. Cope, C.B. Eads, P.R. Lazaro, M.C. Barnhart, and D. Shea. 2007. Acute and chronic toxicity of technical-grade pesticides to glochidia and juveniles of freshwater mussels (Unionidae). Environmental Toxicology and Chemistry 26(10):2086-2093.

Brown, B.L., and R.L. Lawson. 2010. Habitat heterogeneity and activity of an omnivorous ecosystem engineer control stream community dynamics. Ecology 91:1799-1810.

Burlakova, L.E. and A.Y. Karatayev. 2007. The effect of invasive macrophytes and water level fluctuations on unionids in Texas impoundments. Hydrobiologia 586:291-302.

Cherry, D.S., J.L. Scheller, N.L. Cooper, and J.R. Bidwell. 2005. Potential effects of Asian clam (*Corbicula fluminea*) die-offs on native freshwater mussels (Unionidae) I: water-column ammonia levels and ammonia toxicity. Journal of the North American Benthological Society 24:369-380.

Chiavacci, S.J., A.P. Stodola, and S.A. Douglass. 2018. Natural and anthropogenic factors predict the presence of two freshwater mussels (Bivalvia: Unionidae) in Illinois, USA. Freshwater Science, 37(4):870-884.

Clarke, L.R. 2010. Population density and growth of the freshwater mussel *Anodonta californiensis* in a flow-fragmented stream. Journal of Freshwater Ecology 25:179-192.

Coe, W.R. 1931. Spermatogensis in the California oyster (*Ostrea lurida*). Biological Bulletin 61(3):309-315.

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

Cumberland Region Mollusk Restoration Committee (CRMRC). 2010. Plan for the population restoration and conservation of imperiled freshwater mollusks of the Cumberlandian Region. 144pp.

Curley, E.A.M., R. Thomas, C.E. Adams, and A. Stephen. 2022. Adaptive responses of freshwater pearl mussels, *Margaritifera margaritifera*, to managed drawdowns. Aquatic Conservation: Marine and Freshwater Ecosystems 32:466-483.

Cushway, K.C., J. Geist, and A.N. Schwalb. 2024. Surviving global change: a review of the impacts of drought and dewatering on freshwater mussels. Biological Reviews 100(1):275-307.

Daraio, J.A., L.J. Weber, and T.J. Newton. 2010. Hydrodynamic modeling of juvenile mussel dispersal in a large river: The potential effects of bed shear stress and other parameters. Journal of the North American Benthological Society, 29(3):838-851.

Driver, L.J., J.M. Cartwright, R.R., Knight, and W.J. Wolfe. 2020. Species-Richness Responses to Water-Withdrawal Scenarios and Minimum Flow Levels: Evaluating Presumptive Standards in the Tennessee and Cumberland River Basins. Water 12(5):24pp.

DuBose T.P., C.L. Atkinson, C.C. Vaughn, and S.W Golladay. 2019. Drought-Induced, Punctuated Loss of Freshwater Mussels Alters Ecosystem Function Across Temporal Scales. Frontiers in Ecology and Evolution 7(274):13 pp.

Duck River Conservancy. 2025. Re: Sent via email: Robert.D.Baker@tn.gov Duck River Conservancy Comments on Draft Aquatic Resource Alteration Permit NRS23.228, Columbia Power & Water Systems. Emal sent to Robert D. Baker, Tennessee Department of Environment and Conservation. April 18, 2025. Accessed at: https://dataviewers.tdec.tn.gov/dataviewers/f?p=9034:34001.

Enquist, C.A., S.T. Jackson, G.M. Garfin, F.W. Davis, L.R. Gerber, J.A. Littell, J.L. Tank, A.J. Terando, T.U. Wall, B. Halpern, J.K. Hiers, T.L. Morelli, E. McNie, N.L. Stephenson, M.A. Williamson, C.A. Woodhouse, L. Yung, M.W. Brunson, K.R. Hall, L.M. Hallett, D.M. Lawson, M.A. Moritz, K. Nydick, A. Pairis, A.J. Ray, C. Regan, H.D. Safford, M.W. Schwartz, and M.R. Shaw. 2017. Foundations of translational ecology. Frontiers in Ecology and the Environment 15(10):541-550.

Etnier, D.A., and W.C. Starnes. 1993. The fishes of Tennessee. University of Tennessee Press, Knoxville.

Falfushynska, H., L. Gnatyshyna, I. Yurchak, A. Ivanina, O. Stoliar, and I. Sokolova. 2014. Habitat pollution and thermal regime modify molecular stress responses to elevated temperature in freshwater mussels (*Anodonta anatina*: Unionidae). Science of the Total Environment 500-501:339-350.

Federal Register. 2001. Use of lands acquired for the Columbia Dam component of the Duck River project and future water supply needs in the upper Duck River basin. Tennessee Valley Authority 66:33378. Accessed at: https://www.federalregister.gov/documents/2001/06/22/01-15729/use-of-lands-acquired-for-the-columbia-dam-component-of-the-duck-river-project-and-future-water (May 2025).

Ferreira-Rodríguez, N., and I. Pardo. 2017. The interactive effects of temperature, trophic status, and the presence of an exotic clam on the performance of a native freshwater mussel. Hydrobiologia 797:171-182.

Ferreira-Rodríguez, N., R. Sousa, and I. Pardo. 2018a. Negative effects of *Corbicula fluminea* over native freshwater mussels. Hydrobiologia, 810(1):5-95.

Ferreira-Rodríguez, N., I. Fernandez, M. Leonor Cancela, and I. Pardo. 2018b. Multibiomarker response shows how native and non-native freshwater bivalves differentially cope with heat-wave events. Aquatic Conservation: Marine and Freshwater Ecosystems 28:934-943.

Fluharty, R.S., H.A. Abdelrahman, and J.A. Stoeckel. 2023. Effects of brood viability and rising temperature on oxygen consumption of freshwater mussel glochidia (Bivalvia: Unionidae). Canadian Journal of Zoology 101:859–868.

Fogelman, K.J., J.M. Archambault, E. Irwin, M. Walsh, S. Brewer, and J.A. Stoeckel. 2023. A review of lethal thermal tolerance among freshwater mussels (Bivalvia: Unionida) within the North American faunal region. Environmental Reviews 31(2):278-297.

Ford, D.F., A.D. Walters, L.R. Williams, M.G. Williams, and N.B. Ford. 2016. Mussel assemblages in streams of different sizes in the Neches River Basin of Texas. Southeastern Naturalist, 15(1):26-40.

Ford, D. and P.D. Williams. 2007. Karst hydrogeology and geomorphology. John Wiley & Sons, Chichester, UK.

Freshwater Mollusk Conservation Society (FMCS). 2025. The 2025 FMCS checklist of freshwater mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. Accessed at: https://molluskconservation.org/Library/Committees/Names/Appendix_1_Bivalves_Revised_Names_List_wo_Sphaeriidae_20250803.pdf.

Fujitani, M., A. McFall, C. Randler, and R. Arlinghaus. 2017. Participatory adaptive management leads to environmental learning outcomes extending beyond the sphere of science. Science Advances 3(6):e1602516.

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

Galbraith, H.S., C.J. Blakeslee, and W.A. Lellis. 2015. Behavioral responses of freshwater mussels to experimental dewatering. Freshwater Science 34:42-52.

Gangloff, M.M., and J.W. Feminella. 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, U.S.A. Freshwater Biology 52:64-74.

Ganser, A.M., T.J. Newton, and R.J. Haro. 2015. Effects of elevated water temperature on physiological responses in adult freshwater mussels. Freshwater Biology 60:1705-1716.

Gascho Landis, A.M., T.L. Mosley, W.R. Haag, and J.A. Stoeckel. 2012. Effects of temperature and photoperiod on lure display and glochidial release in a freshwater mussel. Freshwater Science 31:775-786.

Gates, K.K., C.C. Vaughn, and J. P. Julian. 2015. Developing environmental flow recommendations for freshwater mussels using the biological traits of species guilds. Freshwater Biology 60:620-635.

Geist, J. and K. Auerswald. 2007. Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). Freshwater Biology 52:2299-2316.

Gillis, P.L., R. McInnis, J. Salerno, S.R. de Solla, M.R. Servos, and E.M. Leonard. 2017a. Freshwater mussels in an urban watershed: Impacts of anthropogenic inputs and habitat alterations on populations. Science of the Total Environment 574:671-679.

Gillis, P.L., R. McInnis, J. Salerno, S.R. de Solla, M.R. Servos, and E.M. Leonard. 2017b. Municipal wastewater treatment plant effluent-induced effects on freshwater mussel populations and the role of mussel refugia in recolonizing an extirpated reach. Environmental Pollution 225:460-468.

Goldsmith, A.M., F.H. Jaber, H. Ahmari, and C.R. Randklev. 2021. Clearing up cloudy waters: a review of sediment impacts to unionid freshwater mussels. Environmental Review 29:100-108.

Golladay, S.W., P. Gagnon, M. Kearns, J.M. Battle, and D.W. Hicks. 2004. Response of freshwater mussel assemblages (Bivalvia: Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia. Journal of the North American Benthological Society 23:494-506.

Golladay, S.W., K.L. Martin, J.M. Vose, D.N. Wear, A.P. Covich, R.J. Hobbs, K.D. Klepzig, G.E. Likens, R.J. Naiman, and A.W. Shearer. 2021. Achievable future conditions as a framework for guiding forest conservation and management. Forest Ecology and Management 360:80-96.

Gore, J.A. and R.M. Bryant, Jr. 1986. Changes in fish and benthic macroinvertebrate assemblages along the impounded Arkansas River. Journal of Freshwater Ecology 3:333-345.

Gough, H.M., A.M. Landis, and J. A. Stoeckel. 2012. Behaviour and physiology are linked in the responses of freshwater mussels to drought. Freshwater Biology 57:2356-2366.

Graf, D.L., and K.S. Cummings. 2021. A 'big data' approach to global freshwater mussel diversity (Bivalvia: Unionoida), with an updated checklist of genera and species. Journal of Molluscan Studies 87:eyaa034.

Haag, W.R. 2012. North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press, Cambridge, UK.

Haag, W.R. 2019. Reassessing enigmatic mussel declines in the United States. Freshwater Mollusk Biology and Conservation 22:43-60.

Haag, W.R., and J.L. Staton. 2003. Variation in fecundity and other reproductive traits in freshwater mussels. Freshwater Biology 48: 2118-2130.

Haag, W.R., and M.L. Warren Jr. 2008. Effects of severe drought on freshwater mussel assemblages. Transactions of the American Fisheries Society 137:1165-1178.

Haney, A., H. Abdelrahman and J.A. Stoeckel. 2020. Effects of thermal and hypoxic stress on respiratory patterns of three unionid species: implications for management and conservation. Hydrobiologia 847:787-802.

Hardison, B.S. and J. B. Layzer. 2001. Relations between complex hydraulics and the localized distribution of mussels in three regulated rivers. Regulated Rivers: Research and Management 17:77-84.

Harpeth Conservancy. 2025. Re: Comments on Revised Draft Aquatic Resource Alteration Permit NRS23.228, Columbia Power & Water Systems. Email submitted to Robert D. Baker, Tennessee Department of Environment and Conservation and Water.Permits@tn.gov. April 18, 2025. Accessed at: https://dataviewers.tdec.tn.gov/dataviewers/f?p=9034:34001

Hartfield, P. and D. Ebert. 1986. The mussels of southwest Mississippi streams. American Malacological Bulletin 4:21-23.

Hastie L.C. and M.R. Young. 2001. Freshwater pearl mussel (*Margaritifera margaritifera*) glochidiosis in wild and farmed salmonid stocks in Scotland. Hydrobiologia 445:109-119.

Hastie, L.C. P.J. Cosgrove, N. Ellis, and M. Gaywood. 2003. The threat of climate change to Freshwater Pearl Mussel populations. AMBIO: A Journal of the Human Environment 32:40-46.

Heinricher, J.R. and J.B. Layzer. 1999. Reproduction by individuals of a nonreproducing population of *Megalonaias nervosa* (Mollusca: Unionidae) following translocation. The American Midland Naturalist 141:140-148.

Holcomb, J.M., C.P. Shea, and N.A. Johnson. 2018. Cumulative spring discharge and survey effort influence occupancy and detection of a threatened freshwater mussel, the Suwannee moccasinshell. Journal of Fish and Wildlife Management, 9(1):95-105.

Holland-Bartels, L.E. 1990. Physical factors and their influence on the mussel fauna of a main channel border habitat of the upper Mississippi River. Journal of the North American Benthological Society 9:327-335.

Hooper, G.W., J.R. Bucholz, T.D. DuBose, K.J. Fogelman, S.M. Keogh, M.E. Kubala, M.B. Lodato, D.H. Nichols, I.S. Gonzalez, J.M. Pfeiffer, J.A. Stoeckel, J.D. Lozier, and C.L. Atkinson. 2023. A trait dataset for freshwater mussels of the United States of America. Scientific data 10(745):15pp. https://doi.org/10.1038/s41597-023-02635-9.

Hornbach, D.J., H.N. Stutzman, M.C. Hove, J.L. Kozarek, K.R. MacGregor, T.J. Newton, and P.R. Ries. 2021. Influence of surrounding land-use on mussel growth and glycogen levels in the St. Croix and Minnesota River Basins. Hydrobiologia 848:3045-3063.

Hubbs, D., S. Chance, L. Colley, and B. Butler. 2010. 2010 Duck River Quantitative Mussel Survey. Tennessee Wildlife Resources Agency Fisheries Division Report 11-04. 48pp. Accessed at: https://www.tn.gov/content/dam/tn/environment/water/duck-river-watershed-planning-partnership/drwpp_resources-2010-duck-river-quantitative-mussel-survey-twra.pdf

Hubbs, D. 2015. 2015 Duck River Quantitative Survey. Tennessee Wildlife Resources Agency Fisheries Division Report 16-06. 60pp.

Hubbs, D. 2024. Duck River Low Flow Mussel Mortality Survey Bedford, Marshall, Maury and Hickman Counties, Tennessee July 16 – 17, September 5, 2024. Report prepared for the Southern Environmental Law Center. 34 pp.

Irwin, K.L., and J.B. Alford. 2018. Survey of native mussels in the upper Duck and Harpeth River drainages, Tennessee. Unpublished report submitted to the Tennessee Wildlife Resources Agency, Nashville.

Isom B.G., and P. Yokley, JR. 1968. The mussel fauna of the Duck River in Tennessee, 1965. American Midland Naturalist 80(1):34-42.

Johnson, P.D., A.E. Bogan, K.M Brown, N.M. Burkhead, J.R. Cordeiro, J.T. Garner, P.D. Hartfield, D.A.W. Lepitzki, G.L. Mackie, E. Pip, T.A. Tarpley, J.S. Tiemann, N.V. Whelan, and E. Strong. 2013. Conservation status of freshwater gastropods of Canada and the United States. Fisheries 38:247-282.

Jones, J.W. and R.J. Neves. 2011. Influence of life-history variation on demographic responses of three freshwater mussel species (Bivalvia: Unionidae) in the Clinch River, USA. Aquatic Conservation: Marine and Freshwater Ecosystems. 21:57-73.

Jowett, T. Payne, and R. Milhous. 2023. SEFA system for environmental flow analysis software manual version 1.9.

Karatayev, V.A., L.E. Burlakova, A.Y. Karatayev, L. Yang, and T. Miller. 2020. Advection exacerbates population decline from habitat loss: maintaining threatened taxa while restoring natural river flow regimes. Oecologia 193:773-785.

Karlin, A.T., K.R. Buer, and W.J. Stark. 2017. Late-drought survey of freshwater mussels in the Upper Saline and Smoky Hill Rivers with emphasis on the status of the Cylindrical Papershell (*Anodontoides* ferussacianus). Transactions of the Kansas Academy of Science 120:141-156.

Kelemen, Z., D.P. Gillikin, L.E. Graniero, H. Havel, F. Darchambeau, A.V. Borges, A. Yambe´le´, A. Bassirou, and S. Bouillon. 2017. Calibration of hydroclimate proxies in freshwater bivalve shells from Central and West Africa. Geochimica et Cosmochimica Acta 208:41-62.

Key, K.N., A.E. Rosenberger, G.A. Lindner, K. Bouska, and S. E. McMurray. 2021. Riverscape-scale modeling of fundamentally suitable habitat for mussel assemblages in an Ozark River System, Missouri. Freshwater Mollusk Biology and Conservation 24(2):43-58.

Khalloufi, N., C. Aissaoui, and M. Bejaoui. 2019. Growth, reproductive traits and habitat patterns of *Unio ravoisieri* (Mollusca: Bivalvia) from Ichkeul Lake tributaries (Northern Tunisia). Biologia 74:821-834.

Khan, M.I., M. Zahoor, A. Khan, N. Gulfam, and M. Khisroon. 2019. Bioaccumulation of heavy metals and their genotoxic effect on freshwater mussel. Bulletin of Environmental Contamination and Toxicology 102:52–5.

Khan, J.M., J. Dudding, M. Hart, C.R. Robertson, R. Lopez, and C.R. Randklev. 2020. Linking flow and upper thermal limits of freshwater mussels to inform environmental flow benchmarks. Freshwater Biology 65(12):2037-2052.

Kinsolving, A.D. and M.B. Bain. 1993. Fish assemblage recovery along a riverine disturbance gradient. Ecological Applications 3:531-544.

Knight, R.R. and J.A. Kingsbury, 2007, Water resources of the Duck River watershed, Tennessee. U.S. Geological Survey Scientific Investigations Report 2007-5105, 46pp, accessed April 5, 2024 at https://doi.org/10.3133/sir20075105.

Knight, R.R., W.S. Gain, and W.J. Wolfe. 2012. Modelling ecological flow regime: an example from the Tennessee and Cumberland River basins. Ecohydrology 5:613-627.

Knight, R.R., J.C. Murphy, W.J. Wolfe, C.F. Saylor, and A.K. Wales. 2013. Ecological limit functions related to fish community responses to hydrologic departures from the ecological flow regime in the Tennessee River Basin, United States. Ecohydrology 6:155-171.

Kumar, S., R.K. Pandey, S. Das, and V. Krishna Das. 2013. Temperature dependent mortality and behavioral changes in a freshwater mussel *Lamellidens marginalis* to dimethoate exposure. Journal of Environmental Biology 34:165–170.

LaForest, M.J. and L.L. Oliveira. 1979. An inventory of mills on the Duck River. Tennessee Valley Authority, Office of Natural Resources, Knoxville, Tennessee. 31 pp.

Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19:573-592.

Layzer, J.B. and L.M. Madison. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. Regulated Rivers: Research & Management 10:329-345.

Layzer, J.B., M.E. Gordon, and R.M. Anderson. 1993. Mussels: the forgotten fauna of regulated rivers. A case study of the Caney Fork River. Regulated Rivers: Research & Management 8:63-71.

Leung, A.S. and D. Dudgeon. 2011. Scales of spatiotemporal variability in macroinvertebrate abundance and diversity in monsoonal streams: detecting environmental change. Freshwater Biology 56:1193-1208.

Lopes-Lima, M., L.E. Burlakova, A.Y. Karatayev, K. Mehler, M. Seddon, and R. Sousa. 2018. Conservation of freshwater bivalves at the global scale: diversity, threats and research needs. Hydrobiologia 810:1-14.

Lopez, J.W. and C.C. Vaughn. 2021. A review and evaluation of the effects of hydrodynamic variables on freshwater mussel communities. Freshwater Biology 66:1 665–1679.

Lopez, J.W., T.P. DuBose, A.J. Franzen, C.L. Atkinson, and C.C. Vaughn. 2022. Long-term monitoring shows that drought sensitivity and riparian land use change coincide with freshwater mussel declines. Aquatic Conservation: Marine and Freshwater Ecosystems 32: 1571-1583.

Lueckenhoff, L.K. 2015. Development of standardized and validated survey methods for assessing unionid mussel assemblages in Missouri. Master's Thesis: University of Missouri, Columbia, Missouri.

Lydeard, C. and R.L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeast United States. Conservation Biology 9:800-805.

Lymbery, A.J., L. Ma, S.J. Lymbery, M.W. Klunzinger, S.J. Beatty, and D.L. Morgan. 2021. Burrowing behavior protects a threatened freshwater mussel in drying rivers. Hydrobiologia 848:3141-3152.

Magoulick, D.D., and R.M. Kobza, 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48:1186-1198.

Miller, A.C., B.S. Payne, and T. Siemsen. 1984. Description of the habitat of the endangered mussel *Plethobasus cooperianus*. The Nautilus 98:98-101.

Miller, A.C. and B.S. Payne. 1988. "The need for quantitative sampling to characterize size demography and density of freshwater mussel communities. *American Malacological Bulletin* 6:49-54.

Mitchell, Z.A., J. McGuire, J. Abel, B.A. Hernandez, and A.N. Schwalb. 2018. Move on or take the heat: can life history strategies of freshwater mussels predict their physiological and behavioural responses to drought and dewatering? Freshwater Biology 63:1579-1591.

Mitchell, Z.A., L.E. Burlakova, A.Y. Karatayev, and A.N. Schwalb. 2021. Changes in community composition of riverine mussels after a severe drought depend on local conditions: a

comparative study in four tributaries of a subtropical river, Hydrobiologia 848:3015-3029.
Moore, A.P. and R.B. Bringolf. 2018. Effects of nitrate on freshwater mussel glochidia attachment and metamorphosis success to the juvenile stage. Environmental Pollution 242(Part A):807-813.
Moore. A.P., N. Galic, R.A. Brain, D.J. Hornbach, and V.E. Forbes. 2021. Validation of freshwater mussel life-history strategies: A database and multivariate analysis of freshwater mussel life-history traits. Aquatic Conservation: Marine and Freshwater Ecosystems 31(12):3386-3402.
Morales, J., E. Penın, and M. Lizana. 2011. Depredacion ocasional de Sus scrofa L. sobre una metapoblacion relíctica de *Margaritifera margaritifera* L. (Bivalvia: Mollusca) en el río Negro (NO de España). Galemys, Spanish Journal of Mammalogy 23:51–56 (In Spanish with English summary).
Mosley, T. L. 2012. Effects of waterflow, distance, and male density on the fertilization success of freshwater mussels. Master's Thesis: Auburn University, Auburn, Alabama.
Mosley, L.M. 2015. Drought impacts on the water quality of freshwater systems; review and integration. Earth-Science Reviews 140:203-214.
Naimo, T. J. 1995. A review of the effects of heavy metals on freshwater mussels. Ecotoxicology 4:341-362.
Naz, B.S., S.C. Kao, M. Ashfaq, D. Rastogi, R. Mei, and L.C. Bowling. 2016. Regional hydrologic response to climate change in the conterminous United States using high-resolution hydroclimate simulations. Global and Planetary Change 143:100-117.
Neves, R.J. and J.C. Widlak. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. American Malacological Bulletin 5:1-7.
Newton, T.J., S.J. Zigler, and B.R. Gray. 2015. Mortality, movement and behaviour of native mussels during a planned water-level drawdown in the Upper Mississippi River. Freshwater Biology 60:1–15.
Nobles, T. and Y. Zhang. 2015. Survival, growth and condition of freshwater mussels: Effects of municipal wastewater effluent. PLoS One. doi:10.1371/journal.pone.0128488.
North Carolina Department of Environment and Natural Resources (NCDENR). 2013. Recommendations for Estimating Flows to Maintain Ecological Integrity in Streams and Rivers in North Carolina. Report by the North Carolina Ecological Flows Science Advisory Board. 33pp. Accessed at: https://www.researchgate.net/publication/261688695_Recommendations_for_estimating_flows_to_maintain_ecological_integrity_in_streams_and_rivers_in_NC.
Ortmann, A.E. 1924. The naiad-fauna of the Duck River in Tennessee. American Midland Naturalist 9(1):18-62.
Osterling, E.M. 2015. Timing, growth and proportion of spawners of the threatened unionid mussel *Margaritifera margaritifera*: influence of water temperature, turbidity and mussel density. Aquatic Sciences 77:1–8.

Payne, B.S. and A.C. Miller. 1989. Growth and survival of recent recruits to a population of *Fusconaia ebena* (Bivalvia: Unionidae) in the lower Ohio River. American Midland Naturalist 121:99-104.

Peterson, J.T., J.M. Wisniewski, C.P. Shea, and C. Rhett Jackson. 2011. Estimation of mussel population response to hydrologic alteration in a southeastern U.S. stream. Environmental Management, 48(1):109-122.

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.D. Richter, R.E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769-784.

Priyan, K. 2021. Issues and challenges of groundwater and surface water management in semi-arid regions. Pages 1-17 in Groundwater resources development and planning in the semi-arid region. Springer, Cham, Switzerland.

Rack, L.E., M.C. Freeman, B.N. Emanuel, L.S. Craig, S.W. Golladay, C. Yang, and S. J. Wenger. 2024. How low is too low? Partnering with stakeholders and managers to define ecologically based low-flow thresholds in a perennial temperate river. River Research and Applications. 40:1393-1416.

Randklev, C.R., N. Ford, S. Wolverton, J.H. Kennedy, C. Robertson, K. Mayes, and D. Ford. 2016. The influence of stream discontinuity and life history strategy on mussel community structure: a case study from the Sabine River, Texas. Hydrobiologia 770:173-191.

Randklev, C.R., M.A. Hart, J.M. Khan, E.T. Tsakiris, and C.R. Robertson. 2019. Hydraulic requirements of freshwater mussels (Unionidae) and a conceptual framework for how they respond to high flows. Ecosphere, 10(12):19pp.

Reed, M.P., G.R. Dinkins, and S.A. Ahlstedt. 2019. Freshwater mussels (Bivalvia: Margaritiferidae and Unionidae) of the Buffalo River drainage, Tennessee. Southeastern Naturalist 18(2):346-372.

Richter, B.D. and H.E. Richter. 2000. Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. Conservation Biology 14:1467-1478.

Safford, H.D., S.C. Sawyer, S.D. Kocher, J.K. Hiers, and M. Cross. 2017. Linking knowledge to action: the role of boundary spanners in translating ecology. Frontiers in Ecology and the Environment 15(10):560-568.

Salerno, J., P.L. Gillis, H. Khan, E. Burton, L.E. Deeth, C.J. Bennett, P.K. Sibley, and R.S. Prosser. 2020. Sensitivity of larval and juvenile freshwater mussels (Unionidae) to ammonia, chloride, copper, potassium, and selected binary chemical mixtures. Environmental Pollution 256. doi: 10.1016/j.envpol.2019.113398.

Sandaas, K., D. Dolmen, A. Rikstad, and T. Riseth. 2004. Birds feasting on freshwater pearl mussel during the dry summers of 2002 and 2003. Fauna (Oslo) 56:168–171 (In Norwegian with English summary).

Sangsawang, A., U. Kovitvadhi, and S. Kovitvadhi. 2019. The effect of water temperature on the early-life development, growth and survival of the freshwater mussel *Hyriopsis bialata*. Aquaculture 510:311–317.

Scheidegger, K.J. and M.B. Bain. 1995. Larval fish distribution and microhabitat use in free-flowing and regulated rivers. Copeia 1995:125-135.

Schneider, L.D., P.A. Nilsson, and E.M. Österling. 2018. Evaluating temperature- and host-dependent reproduction in the parasitic freshwater mussel *Unio crassus*. Hydrobiologia 810: 283-293.

Schwalb, A.N. and M.T. Pusch. 2007. Horizontal and vertical movements of unionid mussels in a lowland river. Journal of the North American Benthological Society 26:261-272.

Seattle Times. 1999. $83 million later, unfinished dam being dismantled. October 10, 1999. Accessed at: https://archive.seattletimes.com/archive/19991010/2988099/83-million-later-unfinished-dam-being-dismantled (June 2025).

Sethi, S.A., A.R. Selle, M.W. Doyle, E.H. Stanley, and H.E. Kitchel. 2004. Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin (USA). Hydrobiologia 525:157-165.

Smith, D.G. 1985. Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut River system. Freshwater Invertebrate Biology 4:105-108.

Smith, R.K., P.L. Freeman, J.V. Higgins, K.S. Wheaton, T.W. FitzHugh, K.J. Ernstrom, and A. A. Das. 2002. Priority areas for freshwater conservation action: a biodiversity assessment of the southeastern United States. The Nature Conservancy 3.

Sofi, M.S., S.U. Bhat, I. Rashid, and J.C. Kuniyal. 2020. The natural flow regime: a master variable for maintaining river ecosystem health. Ecohydrology 13:e2247.

Sousa, R., M. Rufino, M. Gaspar, C. Antunes, L. Guilhermino, L. 2008. Abiotic impacts on spatial and temporal distribution of *Corbicula fluminea* (Müller, 1774) in the River Minho Estuary, Portugal. Aquatic Conservation: Marine and Freshwater Ecosystems, 18(1), 98–110.

Sousa, R., A. Ferreira, F. Carvalho, M. Lopes-Lima, S. Varandas, and A. Teixeira. 2018. Die-offs of the endangered pearl mussel *Margaritifera margaritifera* during an extreme drought. Aquatic Conservation: Marine and Freshwater Ecosystems, 28(5):1244-1248.

Spooner, D.E. and C.C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. Freshwater Biology 51:1016-1024.

Spooner, D.E. and C.C. Vaughn. 2009. Species richness and temperature influence mussel biomass: a partitioning approach applied to natural communities. Ecology 90(3):781-790.

State of Tennessee, Office of the Governor. 2024. Executive Order No. 108: An order to conserve the Duck River Watershed. Accessed at: https://publications.tnsosfiles.com/pub/execorders/exec-orders-lee108.pdf.

Steuer, J.J., T. Newton and S.J. Zigler. 2008. Use of complex hydraulic variables to predict the distribution and density of unionids in a side channel of the Upper Mississippi River. Hydrobiologia 610:67-82.

Strayer, D.L. 1993. Macrohabitats of freshwater mussels (Bivalvia: Unionacea) in streams of the northern Atlantic Slope. Journal of the North American Benthological Society 12:236-246.

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

Strayer, D.L. 2008. Freshwater mussel ecology: a multifactor approach to distribution and abundance. University of California Press, Berkeley.

Strayer, D.L. and H.M. Malcom. 2012. Causes of recruitment failure in freshwater mussel populations in southeastern New York. Ecological Applications 22:1780-1790.

Strzepek, K., G. Yohe, J. Neumann, and B. Boehlert. 2010. Characterizing changes in drought risk for the United States from climate change. Environmental Research Letters 5:044012.

Stueber, A.M. and R.E. Criss. 2005. Origin and transport of dissolved chemicals in a karst watershed, Southwestern Illinois. Journal of the American Water Resources Association 41:267-290.

Taeubert, J., G. El-Nobi, and J. Geist. 2014. Effects of water temperature on the larval parasitic stage of the thick-shelled river mussel (*Unio crassus*). Aquatic Conservation: Marine and Freshwater Ecosystems 24:231-237.

Tennessee Department of Environmental and Conservation (TDEC). 2024a. List of Impaired and Threatened Waters in Tennessee. April 2024. Accessed at: https://www.tn.gov/content/dam/tn/environment/water/watershedplanning/wr_wq_impaired-waters-list-2024-final.xlsx.

Tennessee Department of Environment and Conservation (TDEC). 2024b. Division of Water Resources Response to Comments: Aquatic Resource Alteration Permit Applications. March 14, 2024. 20pp. Accessed at: https://dataviewers.tdec.tn.gov/dataviewers/f?p=2005:1:15281615887782:.

Tennessee Department of Environment and Conservation (TDEC). 2025. Tennessee Scenic Rivers. Tennessee Department of Environment and Conservation. Accessed at: https://www.tn.gov/environment/program-areas/na-natural-areas/na-sr-scenic-rivers-list.html.

Tennessee Duck River Development Agency (TDRDA). 2025. Duck River region water supply history. Accessed at: https://www.tn.gov/content/dam/tn/environment/water/duck-river-watershed-planning-partnership/drwpp_meeting-05-05-25-duck-river-water-supply-history.pdf (May 2025).

Tennessee Duck River Development Agency (TDRDA). 2011. Duck River Comprehensive Regional Water Supply Plan: Report. 40pp. Accessed at: https://webgen1files1.revize.com/theduckriveragencytn/Document%20Center/Projects%20and%20Programs%20Programs/DuckRiverComprehensiveRegionalWaterSupplyPlanReport.pdf.

Tennessee Duck River Development Agency (TDRDA) 2013a. Duck River Regional Drought Management Plan: Final Report. 38pp. Accessed at: https://www.tva.com/docs/default-source/default-document-library/site-content/environment/environmental-stewardship/environmental-reviews/normanry-drought-management-plan/dmp_report.pdf.

Tennessee Duck River Development Agency (TDRDA) 2013b. Optimization of Normandy Reservoir Releases: Final Report. 17pp. Accessed at: https://www.tva.com/docs/default-source/default-document-library/site-content/environment/environmental-stewardship/environmental-reviews/normanry-drought-management-plan/onrr_report.pdf.

Tennessee Valley Authority (TVA). 1979. Report to OMB on Columbia Dam Alternatives. Tennessee Valley Authority Environmental Review. Accessed at: (https://www2.tntech.edu/wrc/DuckRiverManual/OMBReport.pdf).

Tennessee Valley Authority (TVA). 2025. Normandy Reservoir Optimization of Reservoir Releases: Final Environmental Assessment. 254pp.

Tennessee Wildlife Resources Agency (TWRA). 2008. Memo from David McKinney to Duck River Interagency Project. Subject: Duck River Mussel Stranding, Prior to August 16, 2008, Duck River mile 165.8- Lower Hardison Mill Dam.

U.S. Army Corps of Engineers (USACE). 2018. Duck River Watershed Plan: Final Watershed Assessment. U.S. Army Corps of Engineers, Nashville District, Nashville, Tennessee. 153pp. Accessed at: https://erdc-library.erdc.dren.mil/server/api/core/bitstreams/ce9bdf87-038b-4733-ad3d-d15a56f17d74/content.

U.S. Environmental Protection Agency (USEPA). 2013. Aquatic Life Ambient Water Quality Criteria for Ammonia – Freshwater. EPA 822-R-18-002/EPA-822-R-13-001. 242pp.

U.S. Fish and Wildlife Service (USFWS). 2025. Biological Opinion/Conference Opinion: Environmental Protection Agency Columbia Power and Water System Long-term Water Supply Program, FWS ECOSphere Project Code: 2022-0002767. 106pp.

U.S. Geological Survey, 2022, USGS water data for the Nation: U.S. Geological Survey National Water Information System database, accessed August 20, 2022, at https://doi.org/10.5066/F7P55KJN.

U.S. Global Change Research Program. 2014. National climate assessment. Accessed at: https://nca2014.globalchange.gov/.

Vannote, R.L. and G.W. Minshall. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. Proceedings of the National Academy of Sciences 79:4103-4107.

Vaughn, C.C. 1997. Regional patterns of mussel species distributions in North American rivers. Ecography 20:107-115.

Vaughn, C.C. 2018. Ecosystem services provided by freshwater mussels. Hydrobiologia 810:15-27.

Vaughn, C.C. and C.M. Taylor. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. Conservation Biology 13:912-920.

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

Vaughn, C.C., K.B. Gido, and D.E. Spooner. 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: species roles and effects of abundance. Hydrobiologia 527:35-47.

Vaughn, C.C., D.E. Spooner, and H.S. Galbraith. 2008. Context-dependent species identity effects within functional groups of stream fish. Ecological Applications 18:1072-1084.

Vaughn, C.C., C.L. Atkinson, and J.P Julian. 2015. Drought-induced changes in flow regimes lead to long-term losses in mussel-provided ecosystem services. Ecology and Evolution, 5(6):1291-1305.

Vaughn, C.C. and C.L. Atkinson. 2025. The Importance of Long-Term Data for Understanding How Environmental Change Impacts Mussel Communities and Their Ecosystem Effects. American Malacological Bulletin 41(1):1-10.

Vogel, S. 1981. Life in moving fluids. Princeton University Press. 488pp.

Wagner, A., D. Linke, F. Grunicke, and T.U. Berendonk. 2024. Thermal Tolerance and Vulnerability to Climate Change of a Threatened Freshwater Mussel. Diversity 16:39.

Waller, D.L. and B.A. Lasee. 1997. External morphology of Spermatozoa and Spermaozeugmata of the freshwater mussel *Truncilla truncata* (Mollusca: Bivalvia: Unionidae). The American Midland Naturalist 138(1):220-223.

Waller, D.L. and W.G. Cope. 2019. The status of mussel health assessment and a path forward. Freshwater Mollusk Biology and Conservation 22:26-42.

Walters, A.D. and N.B. Ford. 2013. Impact of drought on predation of a state threatened mussel, *Potamilus amphichaenus*. The Southwestern Naturalist 58:479–481.

Watters, G.T. 1994. Form and function of unionoidean shell sculpture and shape (Bivalvia). American Malacological Bulletin 11(1):1-20.

Webbers, A, 2003, Public water-supply systems and associated water use in Tennessee, 2000. U.S. Geological Survey Water-Resources Investigations Report 03-4264, Nashville, Tennessee, accessed June 6, 2025 at https://pubs.usgs.gov/wri/wri034264/PDF/PublicSupply.pdf.

Weingart, P., M. Joubert, and K. Connoway. 2021. Public engagement with science—Origins, motives and impact in academic literature and science policy. Plos One 16(7):e0254201.

What's Up Columbia. 2024. Columbia Dam proposal gains momentum with unanimous commission vote. Accessed at: https://www.whatsupcolumbia.com/p/issue416 (May 2025).

Williams, B.K. 2011. Adaptive management of natural resources—framework and issues. Journal of Environmental Management 92(5):1346-1353.

Wisniewski, J. 2020. 2020 Duck River quantitative mussel survey. Tennessee Wildlife Resources Agency, Nashville, TN. Fisheries Report 16-06. 38 pp. Accessed at: https://www.tn.gov/content/dam/tn/environment/water/duck-river-watershed-planning-partnership/drwpp_resources-2020-duck-river-quantitative-mussel-survey-twra.pdf.

Woody, C.A. and L. Holland-Bartels. 1993. Reproductive characteristics of a population of the washboard mussel *Megalonaias nervosa* (Rafinesque 1820) in the Upper Mississippi River. Journal of Freshwater Ecology 8:57-66.

Womble, K.I. and A.E. Rosenberger. 2025a. A comprehensive freshwater mussel database for the Duck River Drainage, Tennessee. U.S. Department of Interior, Fish and Wildlife Service, Cooperator Science Series FWS/CSS-166-2025, Washington, D.C. https://doi.org/10.3996/css36499787.

Womble, K.I. and A.E. Rosenberger. 2025b. Historical assessment of freshwater mussel communities in the Duck River, Tennessee: seven decades of change in a biodiversity hotspot. U.S. Department of Interior, Fish and Wildlife Service, Cooperator Science Series FWS/CSS-174-2025, Washington, D.C. Accessed at: https://www.fws.gov/sites/default/files/documents/2025-12/css-174-duck-river-womble-and-rosenberger.pdf.

Xu, H.Q., H.M. Ma, Q. Zeng, B.J. Hu, J.Q. Sheng, and Y.J. Hong. 2022. Temperature on hermaphroditism and sex reversal in freshwater pearl mussel *Hyriopsis schlegelii*. Acta Hydrobiologica Sinica 46:741-753.

Yeager, M.M., D.S. Cherry, and R.J. Neves. 1994. Feeding and burrowing behaviors of juvenile rainbow mussels, *Villosa iris* (Bivalvia: Unionidae). Journal of the North American Benthological Society 13: 217-222.

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