

# Surviving global change: a review of the impacts of drought and dewatering on freshwater mussels

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## ABSTRACT

The increase in the frequency and intensity of droughts and heatwaves caused by climate change poses a major threat to biodiversity. In aquatic systems, sedentary species such as freshwater mussels are generally considered more vulnerable to changes in habitat conditions than mobile species such as fish. As mussels provide important ecosystem services, understanding the impacts of drought on freshwater mussels is of particular importance for the management of overall functioning of aquatic ecosystems. We used a comprehensive literature search to provide a systematic overview of direct and indirect effects of drought on freshwater mussels (Bivalvia: Unionida) and an evaluation of mitigation strategies. We found that drought studies were concentrated mostly in the USA, with a focus on the Unionidae family. Topics ranged from the physiological effects of high temperatures, emersion, and hypoxia/anoxia to behavioural and reproductive consequences of drought and the implications for biotic interactions and ecosystem services. Studies spanned all levels of biological organization, from individual responses to population- and community-level impacts and ecosystem-wide effects. We identified several knowledge gaps, including a paucity of trait-based evaluation of drought consequences, limited understanding of thermal and desiccation tolerance at the species level, and the synergistic effects of multiple drought stressors on mussels. Although we found many studies provided suggestions concerning management of populations, habitat conditions, and anthropogenic water use, a systematic approach and testing of recommended mitigation strategies is largely lacking, creating challenges for managers aiming to conserve freshwater mussel communities and populations in light of climate change.

*Key words:* global change, temperature, freshwater biodiversity, unionid mussels, mitigation.

## CONTENTS

I. Introduction	2
II. Materials and methods	2
III. Results and discussion	3
(1) Results of the literature search	3
(2) Mortality and physiological responses	5
(a) Thermal stress	6
(b) Emersion and desiccation stress	13
(c) Hypoxia and anoxia	13
(3) Behavioural responses to drought	14
(4) Effects on reproduction and recruitment	14
(a) Adult reproductive success, fertilisation, and host attraction	14
(b) Larval health and host infestation	16
(c) Juvenile metamorphosis and survival	17

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(5) Population and community-wide responses to drought	17
(a) Population responses	17
(b) Community-wide responses	17
(c) Effects of habitat conditions on mussel distribution and range	18
(6) Biotic interactions	18
(a) Predation	19
(b) Invasive species	19
(7) Effects on ecosystem services	20
(8) Mitigation strategies	25
IV. Conclusions	26
V. Acknowledgements	26
VI. References	26
VII. Supporting information	33

## I. INTRODUCTION

Climate change is considered one of the most important threats for biodiversity, especially in freshwater habitats (Heino, Virkkala & Toivonen, 2009; Woodward, Perkins & Brown, 2010; Reid *et al.*, 2019; Sabater *et al.*, 2023). This includes extreme events such as droughts (i.e. prolonged periods of drier than normal conditions, often coupled with increased temperatures). Although not expected to increase ubiquitously, the frequency and magnitude of droughts is predicted to continue to increase in many parts of the world. Coupled with increasing anthropogenic water use, drought conditions will further exacerbate critical situations in associated freshwater ecosystems, particularly since the symptoms of drought in river systems can act synergistically (Wild, Nagel & Geist, 2023). Also, management practices and hydrological alterations due to irrigation can cause artificial drought conditions and can lead to extirpations (Peterson *et al.*, 2011; Araujo & Álvarez-Cobelas, 2016). Hydrological alterations were recently identified as one of the most concerning emerging threats to freshwater mussel conservation (Aldridge *et al.*, 2023).

Drought may impact freshwater organisms directly by causing mortality and altering physiology in response to high temperatures and desiccation, or more indirectly through changes in interspecific interactions (e.g. predator–prey interactions, competition, etc.; Fig. 1). Species-specific responses to these impacts are influenced by physiological, morphological, and behavioural traits. For instance, a species' mobility may influence its ability to seek refuge areas in drought-impacted streams (Magoulick & Kobza, 2003). Species such as freshwater mussels (Bivalvia: Unionida) are typically less mobile and thus more vulnerable to local changes in habitat conditions and recurrent droughts. Hence, knowledge of how drought and dewatering impacts vulnerable organisms like freshwater mussels is essential for developing effective management and conservation strategies. Since many species of freshwater mussels can be considered keystone species of aquatic systems (Geist, 2010, 2011) that provide important ecosystem services (Vaughn, 2018; Zieritz *et al.*, 2022), understanding the impacts of drought on this group is of particular importance for overall ecosystem functioning.

To date, several papers have reviewed certain aspects of drought in relation to mussels, most recently thermal tolerance (Fogelman *et al.*, 2023) and environmental flows [general and mussel-specific (Gates, Vaughn & Julian, 2015; Arthington *et al.*, 2018)]. Moreover, there are several regional case studies and patchy evidence of single factors, but a systematic overview of direct and indirect effects of drought on freshwater mussels and an evidence-based evaluation of mitigation strategies is currently lacking. Consequently, the objectives of this review were to (i) synthesise current knowledge of direct and indirect impacts of drought on freshwater mussels at different levels of biological organization (individual, population/community, ecosystem) and (ii) summarise and assess existing and suggested mitigation strategies to identify recommendations for future directions based on existing knowledge gaps.

## II. MATERIALS AND METHODS

We conducted an initial literature search using *Web of Science* for papers published prior to April 2024. To identify drought- and drying-related articles associated with freshwater mussels, we used the following four search terms: 'freshwater AND mussel\* AND drought\*', 'freshwater AND mussel\* AND desiccation\*', 'freshwater AND mussel\* AND dewatering\*', and 'freshwater AND mussel\* AND temperature\*'. We evaluated the resulting journal articles for relevance based on their title and abstract and eliminated any articles that were outside of our scope or unrelated to Unionida. We then expanded our literature search to the reference sections of each article, retaining any additional articles that pertained to the order Unionida and contained relevant information associated with drought and drying. We thus collected articles involving drought, desiccation, dewatering, high temperatures, or low dissolved oxygen concentrations. We also included articles that dealt with artificial dewatering such as dam drawdowns that led to emersion or low-water conditions that impacted mussels. Our literature search was limited to



**Fig. 1.** Examples of direct and indirect impacts of drought on freshwater mussels, including loss of suitable habitat due to dewatering at several locations (A–D) in the San Saba River, Texas, emersion and desiccation (E), and host fish mortality (F). Photograph credits: Kiara Cushway, and Tara Lanzer.

peer-reviewed literature that was easily accessible (i.e. freely available online or through Texas State University libraries or Interlibrary Loan) and available in English. In a few cases, we attempted to contact authors regarding inaccessible articles. In addition, a subset of articles provided only the abstract section in English, so our review was limited to the information contained in the abstract. Data analysis was performed using R software (R Core Team, 2023), and trends in the number of articles published over time were analysed using a

Mann-Kendall test from the *Kendall* package in R (McLeod, 2022).

### III. RESULTS AND DISCUSSION

#### (I) Results of the literature search

Our initial literature search on *Web of Science* yielded 2243 unique articles, 211 of which we retained based on relevance.

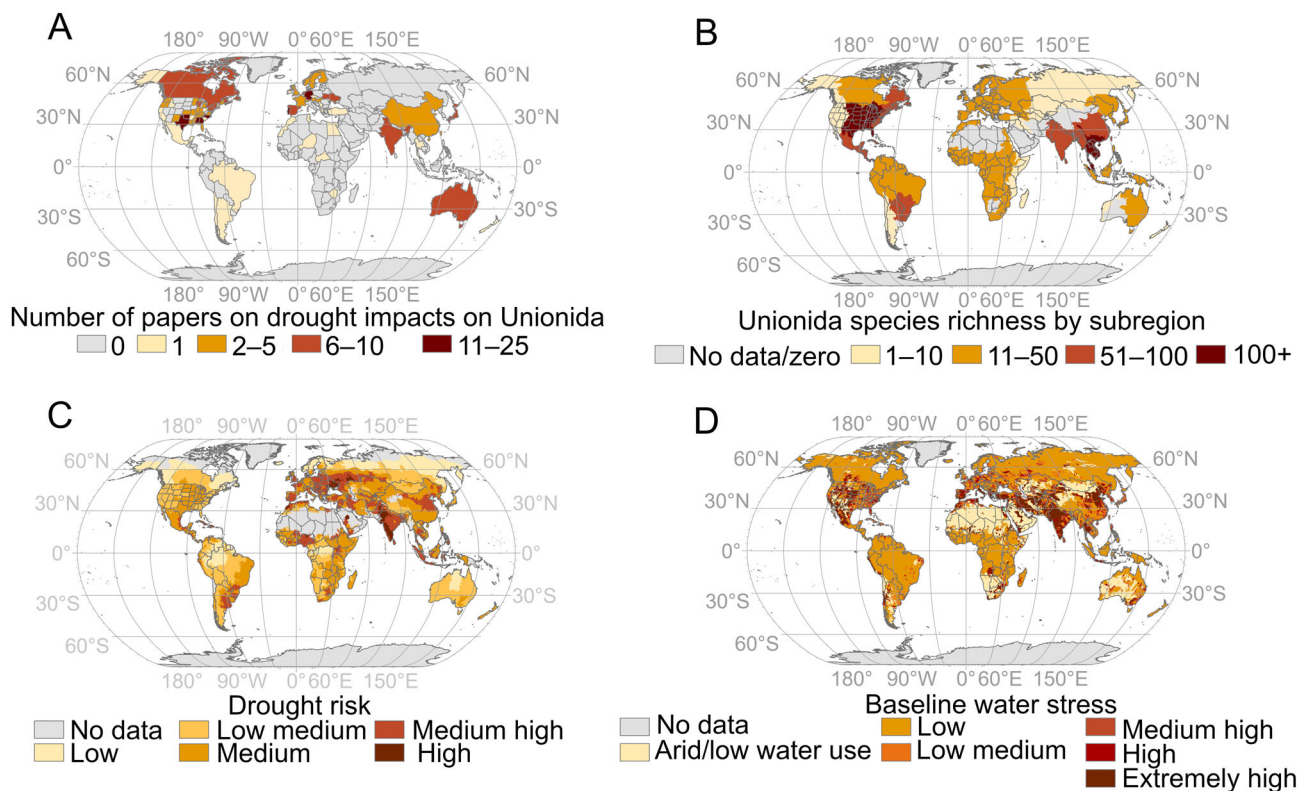
We obtained an additional 50 articles from the reference sections of the initial articles, providing a total of 261 articles. Of these, eight articles were evaluated based (solely) on their abstract because the rest of the article was not in English. Ten articles were excluded because of accessibility issues, but given the large number of articles identified, we feel that our review accurately covers the relevant knowledge regarding drought impacts. Our final literature review included the 251 articles that were determined to be both relevant and accessible (see online Supporting Information, Table S1).

Most studies were conducted in North America ( $N = 136$ ), which aligns with the high levels of diversity on this continent (Graf & Cummings, 2021). North America was followed by Europe ( $N = 75$ ), Asia ( $N = 21$ ), Oceania ( $N = 9$ ), Africa ( $N = 5$ ), and South America ( $N = 3$ ). In addition (not included in the counts above), one study was a global assessment that used data from North America, South America, Asia, Africa, and Europe (Pfister *et al.* 2019). A second study (also not included in the counts above) with an abstract in English compared populations in

Europe (Spain) and Russia but did not specify the region of Russia (which spans both Europe and Asia; Ziuganov, 2004).

Within North America, most studies were conducted in the USA ( $N = 128$ ), and more specifically, in Texas ( $N = 25$ ), Oklahoma ( $N = 18$ ), and North Carolina ( $N = 14$ ; Fig. 2). After the USA, Germany and Portugal had the most studies ( $N = 11$  each, respectively), followed by Spain ( $N = 10$ ; Fig. 2). Areas of southern and eastern Asia (e.g. India, China, and Thailand) have high Unionida richness and high drought and baseline water stress, but few studies were conducted in these areas (Lehner & Grill, 2013; Graf & Cummings, 2021; Kuzma *et al.*, 2023; Figs 2 and S1).

Most studies addressed mussels in the families Unionidae ( $N = 195$ ) or Margaritiferidae ( $N = 31$ ) only, with a limited number of studies focused on mussels from the Hyriidae ( $N = 10$ ), Iridinidae ( $N = 1$ ), and Mycetopodidae ( $N = 1$ ) families. The remaining 13 studies addressed multiple families, with only one study including the family Etheriidae (Table S2). Within these families, the specific impacts of drought and drying were examined for 128 individual species



**Fig. 2.** Maps showing (A) number of papers related to drought impacts on Unionida per country or per state in the USA; (B) Unionida species richness by subregion; (C) global drought risk; and (D) global baseline water stress. Subregions in B were based on Graf & Cummings (2021), adapted from <http://www.feow.org> (Abell *et al.*, 2008). Drought risk (C) and baseline water stress (D) categories were based on baseline annual data from 1979 to 2019 available from the World Resources Institute Aqueduct 4.0 (Lehner & Grill, 2013; Kuzma *et al.*, 2023). Drought risk is a measure of drought likelihood and exposure and vulnerability of populations/assets (Kuzma *et al.*, 2023). Baseline water stress is a measure of water demand *versus* available water resources that are renewable (Kuzma *et al.*, 2023). If the state or country a study was conducted in was not specified, it was assigned to the state or country of the first author at the time of publication.

(Table S3). Studies spanned all life-history stages, with most addressing adults ( $N = 194$ ; note that if life-history stage was unspecified in a study, we assumed that mussels were in the adult life stage), followed by juveniles ( $N = 14$ ), and larvae (i.e. glochidia or lasidia;  $N = 7$ ). The remaining 36 studies addressed multiple life stages (Table S4).

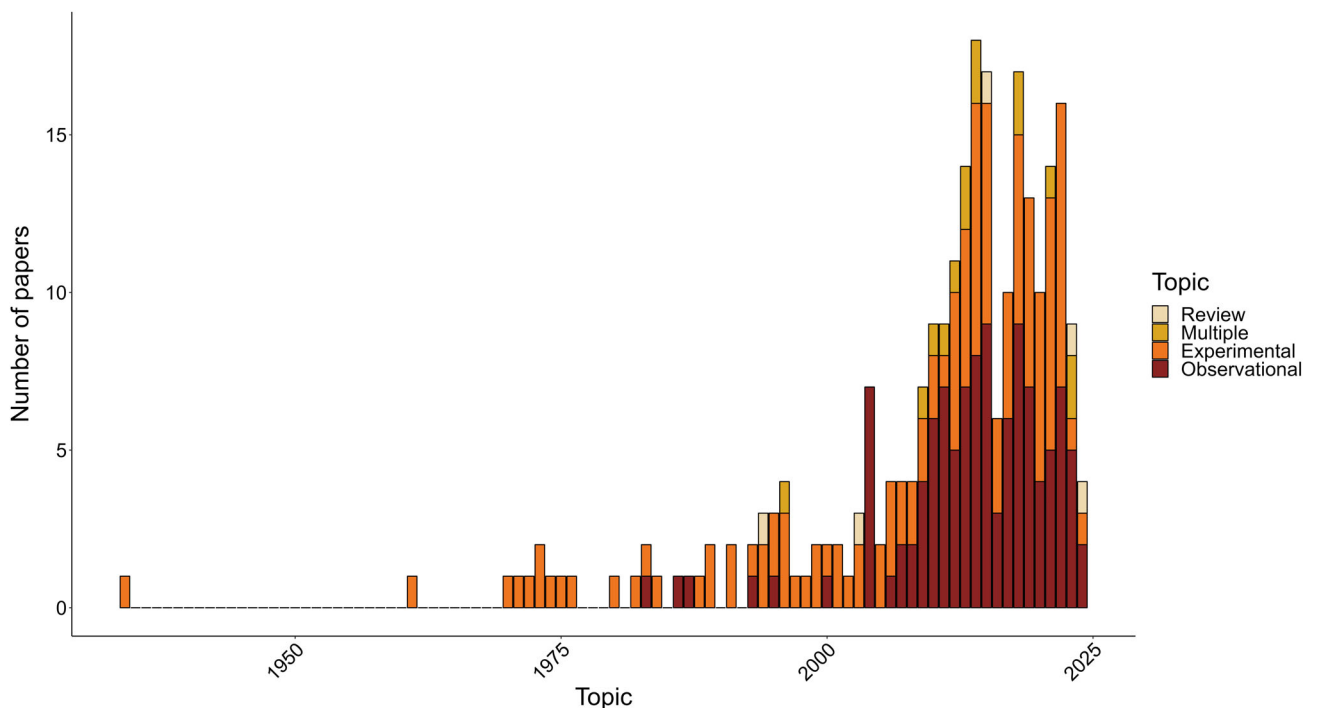
There were slightly more studies with solely experimental ( $N = 120$ ) components than observational ( $N = 112$ ) components, 13 studies that included both observational and experimental components, and one study that contained observational, experimental, and review components. Five additional studies were literature reviews (Fig. 3). Of the 246 non-review studies, 108 had solely laboratory or mesocosm components, 84 had solely field components, 14 used shell chronologies, 10 used solely modelling techniques, five were solely meta-analyses, and 25 studies used multiple approaches (including genetic techniques not discussed above) (Table S5). The number of studies increased over time according to a Mann-Kendall test ( $\tau = 0.73$ ,  $P \ll 0.001$ ), with most studies published since 2000, including peaks in 2014, 2015 and 2018 (Fig. 3).

The endpoints investigated in studies varied across levels of biological organization, with several studies addressing multiple endpoints and multiple levels of biological organization (Fig. 4). At the individual level, most studies considered physiological responses ( $N = 99$ ), mortality ( $N = 75$ ), or behaviour ( $N = 37$ ). Population, distribution, and community-level responses were addressed by 77 studies, of which 50 studies used historical comparisons of pre- and post-drought mussel

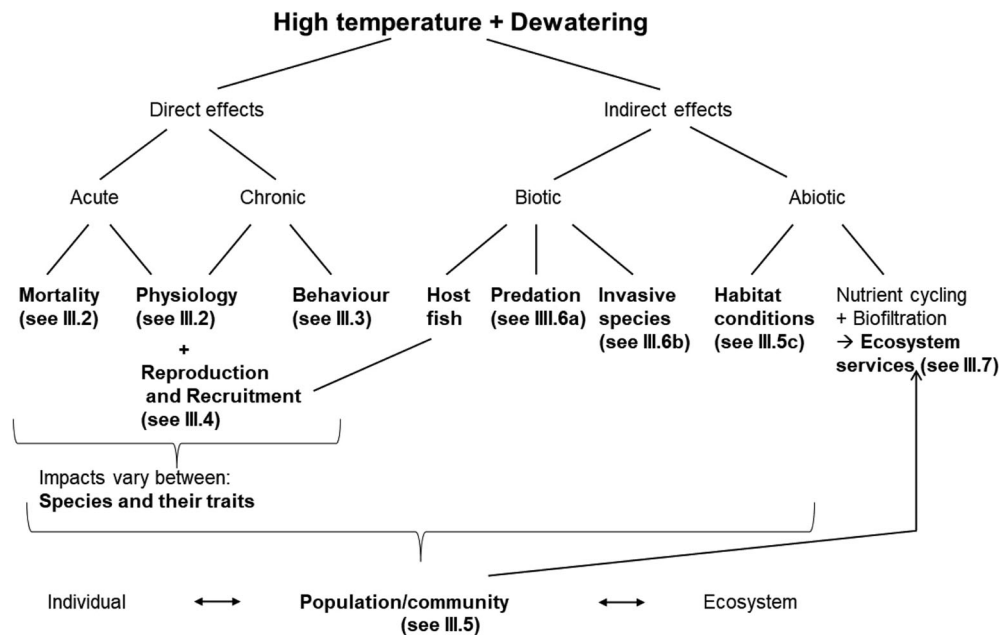
communities. Fifty articles addressed indirect biotic effects such as predation, interaction with invasive species, or recruitment and host fish interactions. Habitat conditions (e.g. low dissolved oxygen concentration, changes in water and sediment chemistry, habitat suitability, etc.) were the most widely addressed topic ( $N = 183$ ) for drought impacts on mussels, which included 99 observational studies, 71 studies with an experimental component, nine studies with both, three review studies, and one study with experimental, observational, and review components. Sixteen studies addressed ecosystem services. Finally, 39% of articles provided suggestions for managing and mitigating drought risk.

## (2) Mortality and physiological responses

The effects of drought on freshwater mussels at the individual level may be lethal (i.e. mortality) or sublethal (i.e. physiology and growth). These include acute (<7 days), medium (7–20 days), or chronic ( $\geq 21$  days) effects (Fogelman *et al.*, 2023). Twenty-two experimental studies examined the lethal effects of drought, 67 examined sublethal effects (e.g. behaviour, physiology, etc.), and 31 studies examined both lethal and sub-lethal effects. Fourteen experimental studies addressed other effects (e.g. host fish survival or habitat suitability). Fifty-eight experimental studies examined the acute effects of drought, 17 examined medium effects, and 17 examined chronic effects. In addition to assessments at single time points, 22 studies addressed effects at two time points, and three studies addressed effects at all three time



**Fig. 3.** Number of articles related to drought impacts on *Unionida* published per year. The proportion of experimental and observational studies, studies using multiple approaches, and reviews are shown in different colours. The number of articles published has increased significantly over time according to a Mann-Kendall test ( $\tau = 0.73$ ,  $P \ll 0.001$ ).



**Fig. 4.** Systematic view of drought impacts. Numbers in parentheses indicate the section number where the topic is discussed in the text. Arrows indicate an effect, e.g. nutrient cycling and biofiltration affect ecosystem services. At the individual level, impacts on mortality and physiological and behavioural responses may vary among species and species groups with different traits. Reproduction and recruitment of mussels is not only directly affected by high temperature and dewatering, but also indirectly affected by impacts on their host fish. Effects on mussel populations and communities include direct and indirect effects, including predation, invasion, and habitat conditions. Both changes in abiotic conditions and mussel communities affect ecosystem services provided by mussels.

points. The remaining 17 experimental studies addressed other effects where timing of mussel exposure did not apply [e.g. effects on other organisms like host fish or parasites, organ performance (e.g. mitochondria from dissected mussels), etc.]. The factors tested during experimental trials commonly fell under three categories: effects of temperature, effects of emersion and desiccation, or effects of hypoxia and anoxia (Table 1). These effects often interact in complex ways during drought events, with concurrent effects potentially amplifying the challenges faced by mussels during drought. More research is necessary on the synergistic effects of drought to understand how interacting stressors may intensify the negative consequences for mussels, similar to recent work in fish (Wild *et al.*, 2023).

#### (a) Thermal stress

Temperature and thermal stress represent important direct impacts of drought on mussel species, which have been chronically understudied. High temperatures can have both immediate and delayed consequences for mussels (Wagner *et al.*, 2024; Table 1). Lethal thermal tolerances have been estimated for less than 10% of North American fauna (Fogelman *et al.*, 2023), despite evidence that several species are already living at or above their lethal thermal tolerances (Pandolfo *et al.*, 2010b; Ganser, Newton & Haro, 2013; Khan *et al.*, 2020; Goldsmith *et al.*, 2022; Fogelman *et al.*, 2023; Cushway & Schwalb, 2024; Rangaswami *et al.*, 2023b;

Pandolfo *et al.*, 2024). Generally, larvae and juveniles are more sensitive to thermal stress than adult mussels (Fogelman *et al.*, 2023), with mollusc thermal tolerance increasing with age (Collas *et al.*, 2014). Traits contributing to thermal tolerance may be conserved phylogenetically across genera or taxonomic groupings (Khan *et al.*, 2020; Goldsmith *et al.*, 2022), but may also exhibit differences across life-history strategies, and at the species and population level (Goldsmith *et al.*, 2022). Density may also be important for temperature resistance, as dense mussel beds may be less susceptible to high temperatures because of increased thermal inertia from the bed acting as an aggregate and slowing collective heating (Wagner *et al.*, 2024).

The effects of high temperatures on mussels may be influenced by acclimation temperature (Galbraith, Blakeslee & Lellis, 2012; Galbraith *et al.*, 2020), although studies examining this have yielded mixed results (Nagabhushanam & Lomte, 1970; Falfushynska *et al.*, 2014; Abdelsaleheen, Kortet & Vornanen, 2022; Fogelman *et al.*, 2023) and extreme warming may negate potential increases in thermal tolerance due to acclimation (Falfushynska *et al.*, 2014). Despite this, small increases in temperature can yield considerable increases in mortality (Pandolfo *et al.*, 2010b; Khan *et al.*, 2020; Wagner *et al.*, 2024). Given that Fogelman *et al.* (2023) have already reviewed lethal thermal tolerances of North American freshwater mussels, we will focus mostly on the sublethal effects of thermal stress as they relate to drought.

Table 1. Examples of sublethal physiological effects of drought. Note that the list of physiological effects and the relevant articles may not be exhaustive.

Stressor	Response	Description	Positive effects	Negative effects	Relevant citations
Temperature	Respiration/oxygen consumption	Increases or decreases in respiration rates and oxygen consumption; respiration in some species may exhibit a bell-shaped curve with increasing temperature, with initial increases in metabolic activity up to a threshold, and inhibition occurring at the highest temperatures	May increase growth rates	Reduced availability of metabolic resources like oxygen at higher temperatures may be insufficient to support increased oxygen consumption/respiration, resulting in a switch to anaerobic metabolism; additional energy required to support respiration	Kilbus & Kautsky (1996); Myers-Kinzie (1999); Gagné <i>et al.</i> (2006); Lurman <i>et al.</i> (2013); Gausner <i>et al.</i> (2015); Ferreira-Rodriguez & Pardo (2017); Haney <i>et al.</i> (2020); Galbraith <i>et al.</i> (2020); Luck & Ackerman (2022); Van Ee <i>et al.</i> (2022)
	Excretion	Increased, decreased, or unchanged excretion rates of ammonia, nitrogen, and phosphorus; some species may exhibit a bell-shaped relationship; thermal tolerance influences excretion rate	Increased excretion can result in increased ecosystem services like nutrient cycling	Loss of thermally sensitive species can reduce population-level excretion rates; alteration of N:P excretion ratios	Spooner & Vaughn (2006, 2008, 2012); Vaughn <i>et al.</i> (2007); Atkinson <i>et al.</i> (2014); Ferreira-Rodriguez & Pardo (2017); DuBose <i>et al.</i> (2019); Van Ee <i>et al.</i> (2022)
	Body condition	Decreased body condition due to thermal stress or lack of metabolic resources	NA	Degradation of health and bodily functions	Gnatyshyna <i>et al.</i> (2014); Said & Nassar (2022)
	Filtration rate	Increased, decreased, or unchanged filtration rates; effects of temperature on filtration may vary based on acclimation temperature, geographic distribution, maximum temperature tested, species, or exposure time; increases are most common	Potential increases in short-term ecosystem services (increased filtration); increased food consumption to support growth, survival, and reproduction	Loss of ecosystem services (decreased filtration); increased energy expenditure required for filtering	Vanderploeg <i>et al.</i> (1995); Eversole <i>et al.</i> (2008); Beggel <i>et al.</i> (2017); Ferreira-Rodriguez <i>et al.</i> (2018b); Malish & Woolnough (2019); Van Ee <i>et al.</i> (2022)
	Growth rate	Increased growth rates due to heightened metabolic processes, or cessation of growth in response to physiological stress; most studies report increased growth, but there may be temperature thresholds above which growth ceases, as observed in marine bivalves (Jones & Quitmyer, 1996)	Increased body size	Smaller maximum body size as species approach thermal maxima; net-negative effects of growth at the expense of longevity or reproduction	Wagner (1976); Eversole <i>et al.</i> (2008); Schöne <i>et al.</i> (2004); Versteegh <i>et al.</i> (2009); Rodland <i>et al.</i> (2009); Black <i>et al.</i> (2010); Clarke (2010); Kendall <i>et al.</i> (2010); Gausner <i>et al.</i> (2013); Bolotov <i>et al.</i> (2018); Herath <i>et al.</i> (2019); Lundquist <i>et al.</i> (2019); DuBose <i>et al.</i> (2022); Wagner <i>et al.</i> (2024)

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Table 1. (Cont.)

Stressor	Response	Description	Positive effects	Negative effects	Relevant citations
	Heart rate	Increased, decreased, or unchanged heart rate; effects of temperature on heart rate may vary based on magnitude of increase, acclimation time, species, age, and exposure	Lowered heart rates may conserve energy during periods of stress	Decreased circulation and metabolic function at reduced heart rates; increased energy expenditures to maintain higher heart rates	Dietz & Tomkins (1980); Polhill & Dimock (1996); Pandolfo <i>et al.</i> (2009); Ganser <i>et al.</i> (2013)
	ATP production	Decreased ATP production due to inhibited function in mitochondria	Mitochondrial thermal tolerance may partially determine organism thermal tolerance because of its importance for energy production	Disruption of energy balances; inability to maintain essential life functions	Ganser <i>et al.</i> (2015); Payton <i>et al.</i> (2016); Falfushynska <i>et al.</i> (2019); Hraoui <i>et al.</i> (2020); André <i>et al.</i> (2021); Said & Nassar (2022)
	Heat shock protein synthesis	Synthesis and upregulation of heat shock proteins (HSPs) such as HSP60, HSP70, and HSP 90; long-term exposure to thermal stress can lead to down-regulation of HSPs, especially in thermally sensitive species	Stabilise protein folding (HSP70), act as chaperones in signal transduction pathways associated with cellular stress (HSP90); it has been proposed that higher temperatures may stimulate HSP expression in mussels, contributing to thermal tolerance, which has been observed in other organisms (Barua & Heckathorn, 2004)	Upregulation of HSP60 can be an indication of respiratory burdens associated with mitochondrial stress	Galbraith <i>et al.</i> (2012); Luo <i>et al.</i> (2014); Payton <i>et al.</i> (2016); Ferreira-Rodriguez <i>et al.</i> (2018b); Jeffrey <i>et al.</i> (2018)
	Increased SERCA activity	Increased activity of sarcoplasmic reticulum $\text{Ca}^{2+}$ ATPase (SERCA) in adductor and (to a lesser extent) foot muscles for regulation of calcium important for muscle contraction and movement	May aid in thermal tolerance by promoting behaviours like valve opening or closure (and hence, filtration, respiration, defence, etc.) or movement	Potentially diverts energy from other life functions	Abdelsaleheen <i>et al.</i> (2022)
	DNA damage/apoptosis	DNA fragmentation, nuclear abnormalities, or cell death	NA	Loss or alteration of cell function; decreased longevity	Kolarević <i>et al.</i> (2013); Luo <i>et al.</i> (2014); Falfushynska <i>et al.</i> (2015, 2018)

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Table 1. (Cont.)

Stressor	Response	Description	Positive effects	Negative effects	Relevant citations
Enzyme expression	Increased expression of transaminase, aspartate aminotransferase (AST) and alanine aminotransferase (ALT) in hemolymph	Help break down proteins, carbohydrates, or lipids during stress	Indicative of tissue damage	Archambault <i>et al.</i> (2013); Fritts <i>et al.</i> , (2015a,b)	
Protein breakdown	Degradation of proteins	NA	Deterioration of muscle tissue, possibly leading to inhibition of movement or valve closure	Ganser <i>et al.</i> (2015)	
Lysosomal stability	Decreased stability of lysosomal membranes and increased cathepsin D activity, possibly signalling lysosomal damage caused by stress and high energy demands	NA	Higher susceptibility to pathogens because of loss of lysosomal functions important for preventing viral/bacterial infections	Falfushynska <i>et al.</i> (2014, 2015); Ferreira-Rodriguez <i>et al.</i> (2018b)	
Degradation of hemolymph/hemocytetes	Increased occurrence of nuclear lesions and micronuclei in hemocytes; decreased hemocyte levels and hyalinocyte mortality; elevated calcium and bicarbonate levels indicative of respiratory acidosis	NA	Degradation of immune responses and increased susceptibility to pathogens; elevated hemolymph PCO <sub>2</sub>	Xie <i>et al.</i> (2011); Falfushynska <i>et al.</i> (2014); Fritts <i>et al.</i> , (2015b); Beggel <i>et al.</i> (2017)	
Dysregulation of immune mediators	Disruption of immune mediators like tumour necrosis factor alpha (TNF-α; an innate cytokine) and receptors important for pathogen recognition (e.g. Toll-like receptor 3)	Some species (e.g. <i>Unionens tetradasmus</i> ) may up-regulate defensin peptides associated with antimicrobial activity to counteract negative effects	Increased susceptibility to pathogens	Luo <i>et al.</i> (2014)	
Mineral imbalance	Decreased magnesium concentrations	NA	Potential inhibition of ion osmoregulation	Fritts <i>et al.</i> (2015a)	
Oxidative stress	Increase in reactive oxygen species (ROS) production and oxidative damage, indicated by increased lipid peroxidation or decreased total antioxidant capacity	Production of antioxidants can help restore oxidative damage	May result in antioxidant deficit because of high levels of ROS; depletion of energy reserves; reduced growth	Gnatyshyna <i>et al.</i> (2014); Falfushynska <i>et al.</i> (2014, 2018); André <i>et al.</i> (2021); Khoma <i>et al.</i> (2021); Said & Nassar (2022)	
Altered carbohydrate/lipid/ protein availability	Depletion or increase of carbohydrate (e.g. glycogen) and lipid stores in foot/gonad tissues, hepatopancreas, gills, siphon, or mantle in response to high energy demands during physiological stress	Mussels may alter availability of carbohydrates, lipids, or proteins in different tissues to minimise energy loss	Depletion of energy reserves required for survival, reproduction, and growth	Mane & Muley (1989); Fritts <i>et al.</i> (2015a); Said & Nassar (2022)	

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Table 1. (Cont.)

Stressor	Response	Description	Positive effects	Negative effects	Relevant citations
Emersion/ desiccation	Filtration rate	Inability to filter feed	NA	Reduced energy; reduced growth; starvation	André <i>et al.</i> (2021)
	Growth rate	Decreased growth rate due to inability to filter feed and physiological stress	NA	Lower body condition, smaller sizes	Kelemen <i>et al.</i> (2017); André <i>et al.</i> (2021)
	Altered fluid osmolarity	Concentration of solutes in extracellular fluid due to evaporation of internal moisture or alkalosis of mantle fluid	Secretion of mucus in the siphonal region can help maintain internal body moisture and prevent increased osmolarity	Disruption of homeostasis; altered cell functions	Dietz (1974); Heming <i>et al.</i> (1988); Byrne & McMahon (1991)
	Oxidative stress	See above	See above	See above	André <i>et al.</i> (2021)
	Altered carbohydrate/lipid/protein availability	See above	See above	See above	Badman & Chin (1973); Greseth <i>et al.</i> (2003)
	Gas exchange/oxygen consumption	Reduced aerial gas exchange in the absence of water	Dissolution of calcium carbonate reserves in shell may help prevent alterations of hemolymph pH due to accumulation of CO <sub>2</sub> ; diffusion of CO <sub>2</sub> through aerial exposure of mantle tissue can reduce CO <sub>2</sub> levels but may result in faster desiccation	Elevated mantle fluid CO <sub>2</sub> partial pressure; decreased oxygen partial pressure, respiratory acidosis; oxygen debt	Dietz (1974); Heming <i>et al.</i> (1988); Byrne & McMahon (1991, 1994)
	Altered ion concentrations	Disruption of ion diffusion gradients due to decreased ion concentrations	Calcium concretions in gills may serve as repositories for calcium; mussels may redistribute NaCl to intracellular compartments; excretion of extra ions into suprabranchial chamber through maintenance of renal function	Interruption of cellular functions	Silverman <i>et al.</i> (1983); Byrne & McMahon (1994)

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Table 1. (Cont.)

Stressor	Response	Description	Positive effects	Negative effects	Relevant citations
	Accumulation of metabolic byproducts	Build-up of toxic byproducts of metabolism (e.g. ammonia) or anaerobiosis	Mussels may suppress amino acid catabolism to avoid ammonia accumulation in hemolymph; produce less toxic alanine or succinate salts rather than lactate	Acidification of hemolymph; ammonia toxicity	Dietz (1974); Heming <i>et al.</i> (1988); Byrne & McMahon (1994)
Hypoxia/anoxia	Oxygen consumption	Decrease in ability to regulate oxygen consumption at low dissolved oxygen (DO) concentrations; may vary across species	Some species are able to store oxygen-rich water in their mantle cavity	Inability of environmental DO concentrations to support metabolic processes	Eddy & Cunningham (1934); Haney <i>et al.</i> (2020)
	Heart rate	Reduction in heart rate	Alteration of phosphofructokinase properties may help provide energy for heart contractions even when DO concentrations are low	Metabolic depression through the conversion of pyruvate kinase and phosphofructokinase into less active forms	Michaelidis & Athanasiadou (1994)
	Altered carbohydrate, lipid, and protein availability	Reduction in carbohydrate, lipid, and protein availability; faster use of glucose and glycogen during anaerobiosis; potential Pasteur effect, where rapid decrease in glycogen occurs immediately after exposure to reduced DO concentrations	Some species may exhibit anoxic endogenous oxygenation, which allows upwards of 50% of energy from carbohydrates stored as glycogen in the tissues to meet energetic needs (has not been directly tested for freshwater mussels)	Rapidly depleted carbohydrate stores (Pasteur effect) resulting in lower energy reserves	Zs-Nagy & Borovyagin (1972); Badman & Chin 1973; Zs-Nagy (1973)

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Table 1. (Cont.)

Stressor	Response	Description	Positive effects	Negative effects	Relevant citations
ATP production		Decreased ATP production due to metabolic depression during stressful conditions	Some species (e.g. <i>Anodonta cygnea</i> ) can accumulate fatty acids, expelling CO <sub>2</sub> without depleting chemical energy from the decarboxylation of succinate to propionate, which allows them to maintain energy stores	Disruption of energy balances; inability to maintain essential life functions	Zs-Nagy (1973); Gäde <i>et al.</i> (1975); Haney <i>et al.</i> (2020); Said & Nassar (2022)
Anaerobiosis		Use of anaerobic metabolic pathways in the absence of sufficient DO concentrations	Production of energy even when metabolic resources are in short supply	Oxygen debt; accumulation of toxic byproducts such as succinate, propionate, and acetate, potential Pasteur effect	Badman & Chin (1973); Lomte & Nagabhushanam (1971); Lomte & Jadhav (1982); Holwerda & Veenhof (1984)
Altered cytosome structure		Increases in cytosomal membrane structures that are not part of the granular matrix; eventual breakdown of cytosome structures	Increases in membranous structure may increase the amount of reaction surface available for electron-transport during energy production	Breakdown of cytosomes may result in decreased energy production	Zs-Nagy & Borovyagin (1972)

Temperature increases speed up metabolic processes in poikilothermic organisms like mussels (Kiibus & Kautsky, 1996; Chen, Heath & Neves, 2001; Ganser, Newton & Haro, 2015), including oxygen consumption, respiration, and excretion (Table 1). At the same time, increasing stream temperatures result in lower dissolved oxygen concentrations in streams (Piatka *et al.*, 2021). This can be problematic during drought, given that metabolic resources like dissolved oxygen or food may be limited (Haag, 2012; Ganser *et al.*, 2015).

Mussels coping with drought often face energetic trade-offs associated with metabolic demands and resource utilisation. Thermally tolerant species may benefit from stronger adaptive responses to high temperatures, which permit continued allocation of energy to processes like growth, despite increased metabolic demands and stressful conditions (Spooner & Vaughn, 2008; Payton, Johnson & Jenny, 2016). The negative impacts of elevated temperatures tend to be compounded as exposure time increases (Ganser *et al.*, 2013). Juvenile mussels may have reduced adaptive capacity, resulting from limited prior exposure to conditions, further exacerbating these impacts (Ganser *et al.*, 2013). Examples of sublethal physiological effects of high temperature on mussels can be found in Table 1.

In addition to the direct effect of high temperatures, emerging research has examined the combined effects of elevated temperatures and pollutants (Kumar *et al.*, 2013; Beggel *et al.*, 2017; Falfushynska *et al.*, 2019; Bogatov, Prozorova & Nikulina, 2023). In many cases, elevated temperatures exacerbate the negative effects of pollutants like pesticides and herbicides (Mane & Muley, 1989; Moulton, Fleming & Purnell, 1996; Keller & Ruessler, 1997; Kumar *et al.*, 2013; Khoma *et al.*, 2021), ammonia (Pinkney *et al.*, 2015; Bogatov *et al.*, 2023), metals and metal compounds (Pandolfó, Cope & Arellano, 2010a; Gnatyshyna *et al.*, 2014; Falfushynska *et al.*, 2014, 2015, 2018), and pharmaceutical and municipal effluents (Gagné *et al.*, 2006; Khoma *et al.*, 2021). However, a few studies indicate that temperature does not always interact synergistically with pollutants (Tessier, Vaillancourt & Pazdernik, 1994; Beggel *et al.*, 2017; Kunz *et al.*, 2021), and one study found that high temperatures may actually positively influence mussel metabolic responses to sublethal levels of zinc oxide, although the mechanisms behind this are unknown (Falfushynska *et al.*, 2019). Synergistic effects of temperature and pollution may in part be dependent on the concentration of pollutants and the temperatures tested (Falfushynska *et al.*, 2015; Kunz *et al.*, 2021). Stress response pathways utilised in response to multiple stressors may be unable to compensate for synergistic stressors (Falfushynska *et al.*, 2015), and as anthropogenic impacts on streams continue to increase, more research is necessary on how drought and high temperature may impact the toxicity of pollutants.

#### (b) Emersion and desiccation stress

Desiccation tolerance is, in part, dependent on temperature and humidity (Peredo *et al.*, 2006; Bartsch *et al.*, 2000; Gough,

Gascho Landis & Stoeckel, 2012) and physiological responses vary between short- and long-term emersion. Some studies have reported that mussels can tolerate emersion at moderate temperatures for short time periods [e.g. hours (Waller *et al.*, 1995, Greseth *et al.*, 2003, Peredo *et al.*, 2006)]. Tolerance of short-term emersion (i.e. less than 60 min) may be indicated by minimal changes in carbohydrate, lipid, and protein concentrations in the mantle tissue at different temperatures (Greseth *et al.*, 2003). However, emersion for longer periods can have various physiological consequences for individual mussels that may result in reduced growth, mortality, and reproductive output (Table 1). Some species are relatively intolerant of emersion [e.g. *Pyganodon grandis* (Say, 1829), *Lampsilis teres* (Rafinesque, 1820)], while others [e.g. *Unio merus tetralasmus* (Say, 1831)] can survive several months to over a year of emersion (Holland, 1991; Mitchell *et al.*, 2018).

Conditions that induce high oxidative stress and reduce growth and mass (related to starvation and dehydration) are related to lower emersion tolerance during extended air exposure (i.e. periods of days), and species with greater longevity tend to be more tolerant of emersion (André, Bibeault & Gagné, 2021). A single study examined the synergistic effects of acute water-borne pollution (specifically 96 h exposure to zinc oxide and nano-zinc oxide) and aerial exposure (Gagné *et al.*, 2015). Mussels exposed to pollution were more susceptible to mortality and survived for shorter periods of emersion (Gagné *et al.*, 2015). Overall, the synergistic effects of emersion and other anthropogenic or environmental factors are largely understudied.

#### (c) Hypoxia and anoxia

One of the indirect effects of high temperature and dewatering caused by drought (Fig. 4) concerns changes to water chemistry, particularly low dissolved oxygen (DO) concentrations (Piatka *et al.*, 2021). During drought, DO concentrations may decline as temperatures increase, or as reduced fluvial discharge results in remnant pools with water stratification. Siltation and colmation of interstitial spaces (Geist & Auerwald, 2007), accumulation and decomposition of rotting leaf litter, or massive blooms of aquatic plants like duckweed during drought can also create hypoxic conditions (Hoess & Geist, 2020; Bogatov *et al.*, 2023). Additionally, siltation due to reduced discharges can bury or suffocate mussels (Inoue *et al.*, 2014).

Some mussel species are able to sustain respiration during periods of low DO concentration (i.e. oxyregulators), while others require steady DO concentrations (i.e. oxyconformers; Sheldon & Walker, 1989). Oxyconformers that thrive in riffle habitats, where higher discharges support high DO concentrations, may be most vulnerable to drought because shallow riffles are most susceptible to drying (Chen *et al.*, 2001). Some species may be relatively tolerant of hypoxia but are more negatively affected during anoxia [e.g. *Pleurobema sintoxia* (Rafinesque, 1820)], during which they exhibit elevated glucose levels (Badman & Chin, 1973). Juvenile individuals may experience

lethal effects of low DO concentrations soon after exposure (Dimock & Wright, 1993). Specific physiological effects of hypoxia and anoxia on freshwater mussels are listed in Table 1.

### (3) Behavioural responses to drought

Thirty-seven articles examined behavioural responses of freshwater mussels to drought. Most articles focused on vertical or horizontal movement ( $N = 19$ ), but articles also examined gaping behaviour, valve closure, foot extension, siphoning, reproductive behaviours, righting behaviour (i.e. movement of the mussel to an upright position), surfacing, and adjusting aperture width (Table 2).

Movement behaviour during drought included vertical movement (e.g. burrowing) to seek thermal refuge, horizontal movement such as tracking receding water lines, and righting behaviour (Waller, Gutreuter & Rach, 1999; Gough *et al.*, 2012; Lymbery *et al.*, 2021). Movement behaviour was influenced by environmental conditions such as high temperatures (Waller *et al.*, 1999; Block, Gerald & Levine, 2013; Archambault, Cope & Kwak, 2013, 2014b), emersion (Samad & Stanley, 1986; Waller *et al.*, 1999; Archambault *et al.*, 2014b), and dewatering rate (Galbraith, Blakeslee & Lellis, 2015; Mitchell *et al.*, 2018), which is likely to differ between regulated and unregulated streams. High temperatures may inhibit both horizontal and vertical mussel movement (Archambault *et al.*, 2013, 2014b), but could also evoke greater movement to escape unfavourable conditions (Block *et al.*, 2013; Zapitis *et al.*, 2021). When dewatering and emersion occurs, retreating water may serve as a stimulus for horizontal movement (Curley *et al.*, 2022). However, the success of mussels in tracking receding water lines is variable, with some studies reporting some directionality of movement (Gough *et al.*, 2012; Curley *et al.*, 2022; Lymbery *et al.*, 2021), while other studies reported limited or inconsistent tracking success (Samad & Stanley, 1986; Mitchell *et al.*, 2018). Habitats that have steeper slopes may help mussels track receding water when dewatering occurs (Burlakova & Karatayev, 2007; Curley *et al.*, 2022), but faster rates of dewatering may provide insufficient time for mussels to respond with tracking (Galbraith *et al.*, 2015; Mitchell *et al.*, 2018).

Movement can be influenced by mussel size, age, and population density, although findings have not been consistent across studies. Curley *et al.* (2022) found that larger mussels exhibited more movement and had more directional movement during drawdowns. By contrast, Lymbery *et al.* (2021) found that smaller mussels may be more successful when tracking receding water. Juvenile mussels have been shown to display vertical movement towards the sediment surface when interstitial oxygen concentrations are particularly low (Sparks & Strayer, 1998). Higher native mussel density may also increase the probability of movement, although the reasons for this are unknown (Curley *et al.*, 2022).

Movement strategies in response to drought are species specific (Waller *et al.*, 1999; Galbraith *et al.*, 2015; Newton, Zigler & Gray, 2015) and may be influenced by species' traits

or life-history strategies (Gough *et al.*, 2012; Mitchell *et al.*, 2018). Drought-tolerant species may be more likely to exhibit vertical burrowing movement (Gough *et al.*, 2012), while intolerant species may exhibit higher rates of horizontal movement to escape unsuitable conditions (Gough *et al.*, 2012; Mitchell *et al.*, 2018). Some species fail to exhibit thermal compensation during behavioural responses, possibly because of a lack of evolutionary pressure in the past (Lurman, Walter & Hoppeler, 2013, 2014). These species may be inadequately equipped to cope with rising temperatures, making them more susceptible to mortality.

### (4) Effects on reproduction and recruitment

Successful reproduction and recruitment of freshwater mussels requires that several important conditions are met at each stage in the mussel life cycle, all of which may be impacted by drought (Fig. 5). Most mussel species go through a parasitic life stage (termed glochidia or lasidia, referred to here as larvae) that requires an obligate relationship with a host fish, making them especially vulnerable to drought (Modesto *et al.*, 2018). The effects of drought on reproduction comprise disruption of reproductive strategies and success of adult mussels, larval health and infestation success, and juvenile metamorphosis and survival (Fig. 5).

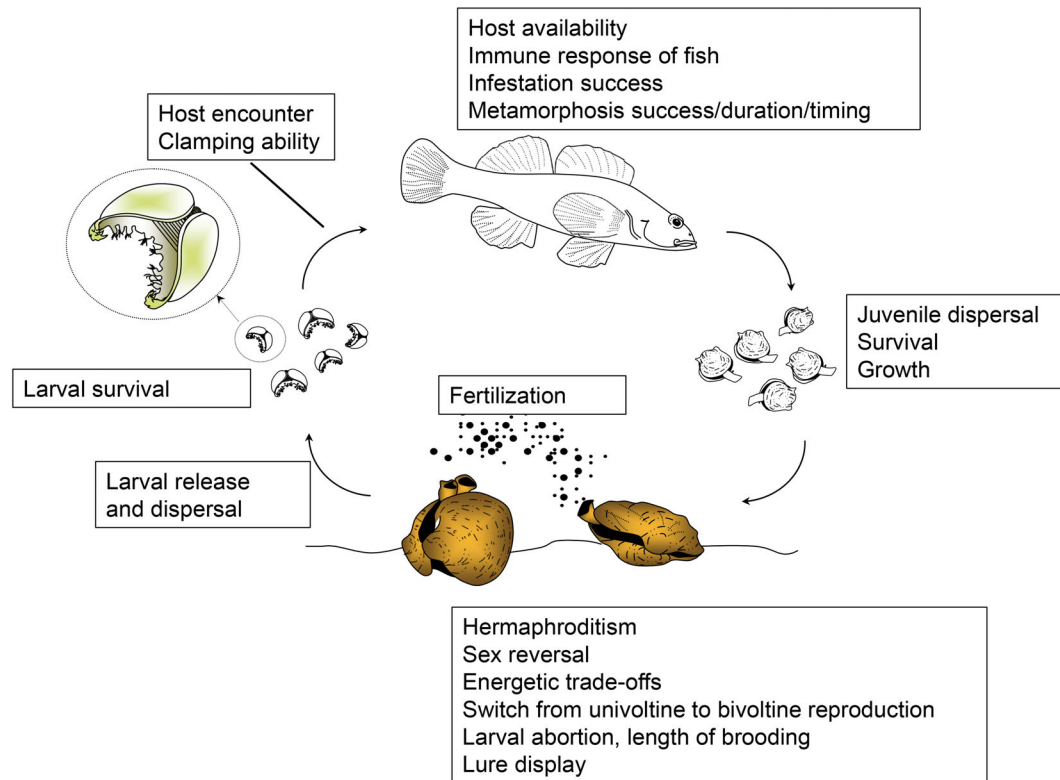
#### (a) Adult reproductive success, fertilisation, and host attraction

At the adult life stage, stressful conditions induced by drought may prevent successful mussel reproduction if necessary energy reserves are diverted towards maintaining homeostasis (Ganser *et al.*, 2015). Furthermore, mussels are sperm-casters: male mussels will release sperm into the water column, which females inhale to achieve fertilisation (Haag, 2012). As a result, low discharges and isolation due to loss of stream connectivity can inhibit fertilisation (Mosley, 2012) because this process depends on the availability of water for filtration (Gough *et al.*, 2012). Some mussels, however, exhibit hermaphroditism and are able to self-fertilise (Bauer, 1987). Such strategies are more prevalent in populations that occur in standing water with minimal flow velocity (Hinzmann *et al.*, 2013). High temperatures can also initiate sex reversal and hermaphroditism through regulation of sex-related genes like *Dmrt1* (Xu *et al.*, 2022). Therefore, more frequent low-discharge or high-temperature conditions could increase the prevalence of hermaphroditism, with implications for genetic diversity, especially in isolated populations.

If fertilisation is successful, mussels brood fertilised embryos in modified gill tissue (i.e. marsupial gill) until they are fully developed and ready to infest a host fish (Graf & Foighil, 2000). At this stage, female mussels have a variety of strategies for attracting host fish including luring behaviour with a modified mantle flap, broadcasting larvae into the water column, or developing conglutinates (i.e. packages of larvae) that resemble prey items (Haag, 2012). However, hypoxic stress and high temperatures initiated by drought

Table 2. Behavioural adaptations and responses not related to vertical or horizontal movement observed for freshwater mussels in response to drought conditions such as increased temperature, desiccation, and low dissolved oxygen concentrations.

Behavioural response	Description	Positive effects	Negative effects	Number of sources	Relevant citations
Gaping	Sustained opening of the shell aperture	Increased oxygen uptake/carbon dioxide release	Increased desiccation risk	17	Dietz (1974); Heming <i>et al.</i> (1988); Byrne & McMahon (1991, 1994); Waller <i>et al.</i> (1995); Sparks & Strayer (1998); Bartsch <i>et al.</i> (2000); Peredo <i>et al.</i> (2006); Rodland <i>et al.</i> (2009); Galbraith <i>et al.</i> (2012, 2015, 2020); Block <i>et al.</i> (2013); Lurman <i>et al.</i> (2013, 2014); Güler (2020); Zapitis <i>et al.</i> (2021)
Foot extension	Extending foot outside of shell	Increased surface area for oxygen uptake	Increased desiccation risk	8	Dietz (1974); Bartsch <i>et al.</i> (2000); Block <i>et al.</i> (2013); Ferreira-Rodriguez (2019); Galbraith <i>et al.</i> (2020); Curley <i>et al.</i> (2021); Peredo <i>et al.</i> (2006); Waller <i>et al.</i> (1995)
Altered siphoning behaviour	Extending siphon outside of shell	Increased surface area for oxygen uptake	Increased desiccation risk	5	Sparks & Strayer (1998); Rodland <i>et al.</i> (2009); Archambault <i>et al.</i> (2014b); Beggel <i>et al.</i> (2017); Ferreira-Rodriguez (2019)
Valve closure	Closure and sealing of valves	Decreased evaporative water loss	Inhibited aerobic metabolism and food acquisition	11	Dietz (1974); Massabuau <i>et al.</i> (1991); Byrne & McMahon (1994); Moulton <i>et al.</i> (1996); Rodland <i>et al.</i> (2009); Kumar <i>et al.</i> (2013); Ferreira-Rodriguez (2019); Haney <i>et al.</i> (2020); Curley <i>et al.</i> (2021); Hyvärinen <i>et al.</i> (2022); Küibus & Kautsky (1996)
Increased transition frequency	Adjusting width of valve opening post-emersion	Increased oxygen uptake	Increased energetic costs	1	Curley <i>et al.</i> (2021)
Righting behaviour	Returning to upright position after disturbance	Improved functioning	Increased energetic costs	2	Waller <i>et al.</i> (1995); Bartsch <i>et al.</i> (2000)
Larval abortion	Premature release of larvae from gills	Increased gill surface area for oxygen uptake	Decreased reproduction and recruitment	2	Aldridge & McIvor (2003); Schneider <i>et al.</i> (2018)
Altered host attraction strategies	Decreased (or unaltered) luring frequency or switch from lure display to conglutinate release	Decreased energetic costs and increased gill surface area for oxygen uptake	Decreased reproduction and recruitment	2	Gascho Landis <i>et al.</i> (2012); Malish & Woolnough (2019)



**Fig. 5.** Processes that can be affected by drought during various stages of the freshwater mussel life cycle.

conditions may lead to premature larval abortion to enable female mussels to increase their gill surface area for enhanced oxygen uptake (Aldridge & McIvor, 2003; Schneider, Nilsson & Österling, 2018; Khalloufi, Aissaoui & Béjaoui, 2019; Sangsawang, Kovitvadhi & Kovitvadhi, 2019; Fluharty, Abdelrahman & Stoeckel, 2023). Tankersley & Dimock (1993) found that female mussels brooding larvae consume less oxygen and respire less than male mussels, possibly because of inhibited circulation in marsupial gills, reduced gill surface area, or competition with larval mussels for oxygen resources (Fluharty *et al.*, 2023). High temperatures may inhibit luring strategies and trigger a switch from luring to conglutinate release, alleviating the respiratory burden of housing larvae in the gills (Gascho Landis *et al.*, 2012). Extreme temperatures have also resulted in a switch from univoltine to bivoltine reproduction, which may divert females' energy away from other important life processes to support increased reproduction (Pichler-Scheder, Gumpinger & Csar, 2011).

#### (b) Larval health and host infestation

The timing of development and release of larvae may be influenced by thermal and hypoxic cues: drought or heat-wave conditions could alter the timing of reproduction, potentially decoupling mussel reproductive activity and host availability (Hastie *et al.*, 2003; Galbraith & Vaughn, 2009; Österling, 2015; Schneider *et al.*, 2018;

Melchior, Clearwater & Collier, 2023). Changes in timing or reproductive behaviours can result in decreased recruitment success if larvae are released before they are fully developed, or where female mussels fail to attract a host (Gascho Landis *et al.*, 2012).

Larval success may also be hindered by drought conditions. Low discharges can prevent larvae or conglutinates from being suspended or transported in the water column, affecting larval dispersal and reducing the probability of host fish exposure (Johnson *et al.*, 2001). Larval viability, survival, and hypoxic tolerance are also reduced at higher temperatures and lower DO concentrations (Zimmerman & Neves, 2002; Akiyama & Iwakuma, 2007; Schneider *et al.*, 2018; Sangsawang *et al.*, 2019; Benedict & Geist, 2021; Hyvärinen *et al.*, 2022; Fluharty *et al.*, 2023), with infestation success and length of the brooding and parasitic phases decreasing as temperatures increase (Widarto, 2001; Pandolfo, Kwak & Cope, 2012; Marwaha *et al.*, 2017; Schneider *et al.*, 2018). In general, colder temperatures help suppress host fish immune responses. Consequently, higher temperatures associated with drought may cause higher rates of larval rejection (Taubert, El-Nobi & Geist, 2014) or shorter encystment times (Johnson *et al.*, 2001).

Successful infestation also depends on the availability of host fish. Spooner *et al.*, (2011) projected that decreased discharge could result in fish species extirpations of 5–60% based on future climate scenarios. Furthermore, increasing temperatures could negatively impact coldwater species like



salmonids, an important host for margaritiferid mussels (Hastie *et al.*, 2003; Geist, 2010). Drought conditions may result in high mortality of drought-intolerant fish and can cause a decoupling of host and adult mussel distributional ranges as fish move to cooler water (Pandolfo *et al.*, 2012; Taeubert *et al.*, 2014; Terui *et al.*, 2014). Early life stages of fish are particularly susceptible to drought effects, which is problematic for mussels because infestation success is higher on younger fish with weaker immune responses (Sternecker, Denic & Geist, 2014; Modesto *et al.*, 2018; Wild *et al.*, 2023). In addition, drought-related loss of stream connectivity can limit fish movement (Irmscher & Vaughn, 2015), lowering the chances of larval attachment in deeper pools (Neves & Widlak, 1987).

### (c) Juvenile metamorphosis and survival

High temperatures can decrease metamorphosis and recruitment success (Taeubert *et al.*, 2014; Gosselin *et al.*, 2023) and newly transformed juveniles may be physiologically stressed by reduced flow, high temperatures, low DO concentrations, or high siltation induced by drought conditions (Clarke, 2010; Pandolfo *et al.*, 2012; Irmscher & Vaughn, 2015; Hoess & Geist, 2020). Altered timing of metamorphosis in response to increased temperature could also lead to juvenile mussels dropping off fish in the winter, when higher discharges prevent settlement and limit availability of suitable habitat (Österling, 2015). In addition, high temperature and desiccation can inhibit byssus production in juvenile mussels, potentially impacting juvenile dispersal capabilities (Archambault *et al.*, 2013, 2014b).

## (5) Population and community-wide responses to drought

In addition to individual impacts, drought can have varied but important effects on mussels at the population and community levels. This includes the effects of habitat conditions on mussel distribution and species' ranges.

### (a) Population responses

At the population level, mass mortality events and declining populations have been documented in response to heatwaves and drought and drying events across the globe (e.g. Samad & Stanley, 1986; Mima, Tutumi & Kondo, 1996; Gagnon *et al.*, 2004; Haag & Warren, 2008; Mouthon & Daufresne, 2010; Jones & Byrne, 2010; Kakino *et al.*, 2011; Vaughn, Atkinson & Julian, 2015; Sousa *et al.*, 2018; DuBose, Ashford & Vaughn, 2020; Paschoal *et al.*, 2020; Cosgrove *et al.*, 2022; Lopez *et al.*, 2022; Bogatov *et al.*, 2023). Effects are particularly severe when habitats dry completely, and some studies have reported mortality levels exceeding 65–98% of the population, risking local extirpations (Samad & Stanley, 1986; Haag & Warren, 2008; Randklev *et al.*, 2013). Populations affected by drought tend to have long recovery times (Mouthon & Daufresne, 2015; Nogueira

*et al.*, 2021), especially if species densities fall below levels that support reproduction (Haag & Warren, 2008). However, less-severe drought conditions are unlikely to cause pronounced effects (Howells, Mather & Bergmann, 2000; Golladay *et al.*, 2004). Isolation caused by repeated drought events can lead to loss of intraspecific genetic diversity (Inoue & Berg, 2017; Gomes-dos-Santos *et al.*, 2019) or genetically distinct populations (Inoue, Lang & Berg, 2015).

In some populations, shifts in size distribution and age structure can occur (Sousa *et al.*, 2018; Nogueira *et al.*, 2021). Mussels during early life-history stages (i.e. larval and juvenile stage) are generally more sensitive to drought-related impacts than are adult mussels. Juvenile mussels and smaller individuals may have higher mortality due to greater susceptibility to external temperature increases, resulting from higher surface area to volume ratios (Bartsch *et al.*, 2000; Sousa *et al.*, 2018). However, some studies have found higher levels of mortality in large mussels, which may be driven by age-related habitat preferences (juvenile mussels in limnic habitats may differentially occupy deeper water and more stable habitats; Paschoal *et al.*, 2020). Other studies have found that drought may influence all size classes similarly (Güler, 2020; Nogueira *et al.*, 2021). More research regarding how drought differentially impacts different age and size classes of mussels is necessary to elucidate how drought-related mortality across classes may impact long-term survival outcomes for mussel populations.

### (b) Community-wide responses

Community-wide declines in response to drought have been observed in many systems (Gagnon *et al.*, 2004; Galbraith, Spooner & Vaughn, 2010; Karatayev, Miller & Burlakova, 2012; Vaughn *et al.*, 2015; Karlin, Buer & Stark, 2017; Lopez *et al.*, 2022; Sánchez González *et al.*, 2021; Tarter *et al.*, 2023). Communities often fail to recover to pre-drought levels, causing long-term declines (Mouthon & Daufresne, 2015; Vaughn *et al.*, 2015; Tarter *et al.*, 2023), and providing opportunities for colonisation by invasive species such as *Corbicula* spp. (Mouthon & Daufresne, 2010), which are more likely to outcompete native mussels under disturbed conditions (Geist *et al.*, 2023). As a result of community-wide declines, species occurrence post-drought is correlated with abundances prior to drought conditions (Haag & Warren, 2008; Mitchell *et al.*, 2021), with changes in community composition resulting from extirpation of rare species (Haag & Warren, 2008; Brown, Daniel & George, 2010; Markovic *et al.*, 2014; Collas *et al.*, 2018).

Not all freshwater mussel species or genera respond in the same way to the effects of drought (Holland, 1991; Gough *et al.*, 2012; Mitchell *et al.*, 2018). Rather, as demonstrated in Sections III.2, III.3, and III.4, there is evidence that species' traits (e.g. life-history strategy, physiology, behaviour) influence drought tolerance (Gates *et al.*, 2015; Mitchell *et al.*, 2018; Lopez *et al.*, 2022). However, only 11.6% of the studies we reviewed used a trait-based evaluation,

emphasising the need to incorporate species' traits into drought studies. Community structures will be impacted by drought-induced declines based on mussel traits (Spooner *et al.*, 2011). Host specialists will be more impacted than host generalists due to loss of sensitive fish species (Spooner *et al.*, 2011). Shifts in community composition towards more drought- or thermally tolerant species have also been observed (Galbraith *et al.*, 2010; Graeber *et al.*, 2013; Nakano *et al.*, 2017; Sánchez González *et al.*, 2021; Lopez *et al.*, 2022). Opportunistic species that are adapted to high levels of disturbance and can tolerate high temperatures and low DO concentrations (e.g. *Leunio lienosa*; Mitchell *et al.*, 2018), or reproduce and recolonize quickly after droughts [e.g. *Utterbackia imbecillis* (Haag, 2012; Lopez *et al.*, 2022)], may dominate drought-prone systems in the future.

### (c) Effects of habitat conditions on mussel distribution and range

Mussel distribution is affected by drought and climate change at local and regional scales (Gagnon *et al.*, 2004; Jones, 2007; Dascher *et al.*, 2018). At a fine scale, water depth or mesohabitat type (e.g. riffle, run, pool) may influence whether mussels are exposed to drying and desiccation, influencing their distribution within or across habitat types (Layzer & Madison, 1995; Clarke, 2010; Randklev *et al.*, 2018b). Loss of stream connectivity and increased fine bed material deposits can reduce mussel and host fish dispersal, reducing species distributional ranges (Baldan *et al.*, 2021). Refuge habitats may also influence where mussels are able to persist (Table 3). Larger, basin-wide or regional distributions may be influenced by habitat conditions during drought, in part due to the influence of stream size and stream position (Reckendorfer *et al.*, 2006). Habitat

conditions in larger streams are more buffered from drought because of larger quantities of water, so mussel assemblages are often less impacted compared to small streams (Gagnon *et al.*, 2004; Haag & Warren, 2008; Shea *et al.*, 2013). For example, Mitchell *et al.* (2021) found that smaller streams experiencing the highest temperatures and lowest discharges during a drought in Texas exhibited the greatest declines in species richness. Mussel distribution in drought-prone regions may be a legacy of past drought conditions (Gagnon *et al.*, 2004), and over time, frequent disturbances in small streams can lead to depauperate communities composed mainly of tolerant species (Gagnon *et al.*, 2004). In more temperate regions, however, smaller streams may provide more stable temperatures as temperature becomes less variable closer to springs and less likely to exceed thermal limits of mussels (Drainas *et al.*, 2023). As increased drought severity and intermittency lead to local extirpation of some species (Haag & Warren, 2008; Brown *et al.*, 2010; Markovic *et al.*, 2014; Collas *et al.*, 2018), species ranges are also likely to contract when drought-prone habitat becomes unsuitable, limiting mussel persistence, particularly in small streams (Spooner *et al.*, 2011; Shea *et al.*, 2013; da Silva *et al.*, 2022). In cases of reduced fluvial discharge, changes in water and sediment chemistry, such as increased salinity, can affect mussel distribution and habitat suitability as well, particularly in coastal areas or heavily anthropogenically impacted streams (Peterson *et al.*, 2011; Karatayev *et al.*, 2012; Pinkney *et al.*, 2015).

### (6) Biotic interactions

The documented indirect biotic effects of drought and drying on mussels were mostly associated with three main factors:

Table 3. Potential drought refuges suggested by articles examining the impact of drought on freshwater mussels (order Unionida). Thirty-four articles we reviewed included suggestions for refuge habitats, with some articles suggesting multiple habitat types.

Scale	Refuge type	Number of sources	Relevant citations
Global or regional	High-order streams	1	Shea <i>et al.</i> (2013)
	High-altitude rivers	2	Bolotov <i>et al.</i> (2018); da Silva <i>et al.</i> (2022)
	Regions with stable climate and low invasion potential	1	Gallardo & Aldridge (2013)
	Habitats where the natural flow regime is maintained	1	Araujo & Álvarez-Cobelas (2016)
Local	Habitats with hyporheic, alluvial, groundwater, or spring cool water inputs	6	Gagnon <i>et al.</i> (2004); Briggs <i>et al.</i> (2013); Dascher <i>et al.</i> (2018); Karlin <i>et al.</i> (2017); Holcomb <i>et al.</i> (2018); Rangaswami <i>et al.</i> (2023a)
	Deep pools and areas near thalweg	7	Jones (2007); Haag & Warren (2008); Randklev <i>et al.</i> (2018b); Sousa <i>et al.</i> (2018); Bogan <i>et al.</i> (2019); Hoess <i>et al.</i> (2022); Bogatov <i>et al.</i> (2023)
	Wetlands and backwater areas	2	Tarter <i>et al.</i> (2023); Bogatov <i>et al.</i> (2023)
	Irrigation ponds	1	Nakano <i>et al.</i> (2017)
	Cool, water-saturated sediment	7	Newton <i>et al.</i> (2013); Archambault <i>et al.</i> (2014a,b); Güler (2020); Lymbery <i>et al.</i> (2021); Pandolfo <i>et al.</i> (2024); Wagner <i>et al.</i> (2024)
	Habitats with woody debris	3	Gagnon <i>et al.</i> (2004); Golladay <i>et al.</i> (2004); Sousa <i>et al.</i> (2018)
	Water mill canals and anthropogenic habitats	6	Burlakova & Karatayev (2007); Kakino <i>et al.</i> (2011); Nakano (2018); Sousa <i>et al.</i> (2019); Sullivan & Littrell (2020); Cushway & Schwalb (2024)

impacts on host fish, predation, and interactions with invasive species. One additional article discussed the interaction of mussels with parasitic trematodes, which experienced increased duration of cercarial shedding in response to high temperatures, potentially leading to increased reproductive success and higher parasitic loads for mussels (Taskinen *et al.*, 2022). A thorough overview of the impacts of drought on fish populations is outside of the scope of this review [see Magoulick & Kobza (2003) or Lennox *et al.* (2019) for more information], but see Section III.4 for more details on drought impacts on host fish.

#### (a) Predation

Emersion and aerial exposure due to dewatering during drought increases predation risk for mussels (Sparks & Strayer, 1998; Karlin *et al.*, 2017). Dry seasonal conditions that expose mussels and limit terrestrial prey availability may lead to seasonal use of mussels as an opportunistic food source (Shannon & Mendyk, 2009; van Ee, Nickerson & Atkinson, 2020). Drought-induced predation on mussels has been observed for several organisms (Table 4), and in some cases predation rates may be extremely high: some studies reported 41–90% of drought-related mortality was associated with predation (Morales, Peñin & Lizana, 2011; Lymbery *et al.*, 2021) observed after several days of emersion. Size-selective predation may result in greater loss of smaller individuals because they are easier to consume (Walters & Ford, 2013; Lymbery *et al.*, 2021). Moreover, the dispersal and invasion success of non-native predators such as the North American signal crayfish [*Pacifastacus leniusculus* (Dana, 1852)], which preferentially preys upon native European freshwater mussels (Dobler & Geist, 2022), may be enhanced by increasing temperatures.

#### (b) Invasive species

Negative interactions with invasive species may be exacerbated by drought and heatwave conditions (Geist *et al.*, 2023). Geographic ranges of invaders are expected to increase in response to global warming (Collas *et al.*, 2018; Ferreira-Rodríguez *et al.*, 2018a). Native and invasive species

may differ in physiological tolerance of thermal stress, but even those invasive species that are more sensitive to increasing temperatures could retain a competitive advantage in response to heatwaves and drying events because of higher reproductive outputs (Ferreira-Rodríguez *et al.*, 2018b; Hillebrand *et al.*, 2024). Behaviours that help mussels avoid emersion can be inhibited by the presence of invasive species (Burlakova & Karatayev, 2007; Ferreira-Rodríguez, 2019). For example, high densities of invasive plants can prevent horizontal movement of mussels into deeper water because of decreased habitat suitability resulting from higher temperatures, diel oxygen depletion, and reduced fluvial discharge (Burlakova & Karatayev, 2007).

The impact of invasive *Corbicula* spp. on mussels during droughts and heatwaves has been studied more intensively in the USA and Europe (Iberian Peninsula) in recent years (e.g. Cherry *et al.*, 2005; Cooper, Bidwell & Cherry, 2005; Ferreira-Rodríguez & Pardo, 2017; Ferreira-Rodríguez *et al.*, 2018a; Ferreira-Rodríguez, 2019). Ferreira-Rodríguez (2019) found that higher densities of *Corbicula* spp. led to decreased pedal movement in native *Unio delphinus* (Spengler, 1793) in laboratory conditions, which may inhibit movement responses to climate stressors like heat waves. Furthermore, high *Corbicula* spp. densities can inhibit native mussel physiological rates (e.g. faeces production and food acquisition) through competition at high temperatures, decreasing the food resources available to native mussels to cope with higher metabolic demands (Ferreira-Rodríguez & Pardo, 2017). Mass mortality of sensitive invasive species can also degrade water quality and result in reduced DO concentrations, nitrogen pulses, and altered nutrient cycling (McDowell & Sousa, 2019). Due to their relative thermal intolerance, drought and heatwave conditions can lead to mass die-offs of *Corbicula* spp. The decomposition of invasive mussels can increase water-column and pore-water ammonia to potentially lethal levels for early life stages of native mussels (Cherry *et al.*, 2005; Cooper *et al.*, 2005; Oosterhuis, Pardo & Ferreira-Rodríguez, 2021). However, temperature, discharge, pH, and *Corbicula* density all influence ammonia concentration, and relatively high *Corbicula* densities may be needed to induce lethal levels of ammonia in overlying water ( $\geq 10,000$  individuals  $m^{-2}$ ) and porewater ( $\geq 200$  individuals  $m^{-2}$ ).

Table 4. Organisms recorded preying on freshwater mussels (order Unionida) during drought events.

Organism	Number of sources	Relevant citations
Wild boar ( <i>Sus scrofa</i> , Linnaeus, 1758)	3	Morales <i>et al.</i> (2011); Sousa <i>et al.</i> (2018); Nogueira <i>et al.</i> (2021)
Raccoon ( <i>Procyon lotor</i> , Linnaeus, 1758)	2	Burlakova & Karatayev (2007); Walters & Ford (2013)
Skunk ( <i>Mephitis mephitis</i> , Schreber, 1776)	1	Burlakova & Karatayev (2007)
Monitor lizard ( <i>Varanus panoptes panoptes</i> , Storr, 1980)	1	Shannon & Mendyk (2009)
Black rat ( <i>Rattus rattus</i> , Linnaeus, 1758)	1	Lymbery <i>et al.</i> (2021)
Crow ( <i>Corvus</i> spp.)	2	Sandaas <i>et al.</i> (2004); Cosgrove <i>et al.</i> (2022)
Oystercatcher ( <i>Haematopus ostralegus</i> , Linnaeus, 1758)	1	Sandaas <i>et al.</i> (2004)
Purple swamp hen ( <i>Porophyrus porophyrus</i> , Linnaeus, 1758)	1	Lymbery <i>et al.</i> (2021)
Australian wood duck ( <i>Chenonetta jubata</i> , Latham, 1801)	1	Lymbery <i>et al.</i> (2021)
Gull (family Laridae)	2	Sandaas <i>et al.</i> (2004); Cosgrove <i>et al.</i> (2022)

(Cherry *et al.*, 2005; Cooper *et al.*, 2005; McDowell, McDowell & Byers, 2017)].

### (7) Effects on ecosystem services

Freshwater mussels provide a variety of ecosystem services that serve essential roles in aquatic ecosystems. These include biofiltration, biodeposition, nutrient cycling and storage, food-web support, and habitat alteration and creation (Vaughn, 2018; Zieritz *et al.*, 2022; Atkinson *et al.*, 2023; Boeker *et al.*, 2016; Lummer, Auerswald & Geist, 2016). The supply of ecosystem services depends on environmental conditions (e.g. fluvial discharge and temperature) that are influenced by drought and drying (Vaughn, Spooner & Galbraith, 2007; Spooner & Vaughn, 2012; Spooner, Vaughn & Galbraith, 2012). At low discharges, materials that are excreted by mussels may accumulate in slow-moving habitats, increasing the impact of services like nutrient cycling (Spooner & Vaughn, 2006). Mussels may also subsidise aquatic food webs during drought,

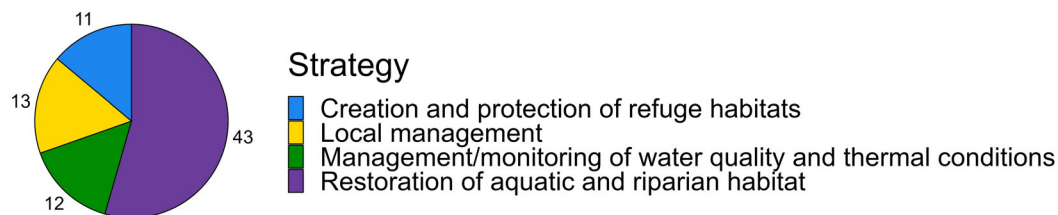
increasing macroinvertebrate density and facilitating survival of fish (DuBose *et al.*, 2020). Drought-induced mass mortality events can produce large nutrient pulses (mainly nitrogen and phosphorus), stimulating short-term ecosystem productivity in aquatic systems and the surrounding terrestrial environment (Bódis, Toth & Sousa, 2014; DuBose *et al.*, 2019; Paschoal *et al.*, 2020).

Despite some mussel-provided services being amplified during drought conditions, many ecosystem services are hindered. For instance, poor environmental conditions can lead to loss of bioturbation and nutrient cycling (Oosterhuis *et al.*, 2021). Large nutrient pulses may also result in algal blooms that create hypoxic conditions and degrade water quality (Galbraith *et al.*, 2020). Filtration rates of mussels can be affected by low discharges and high levels of total suspended solids (Dycus, Wisniewski & Peterson, 2015; Luck & Ackerman, 2022). Furthermore, mussel species that are thermally intolerant may contribute less to ecosystem services (e.g. nutrient cycling) during drought because their rates of assimilation decrease at

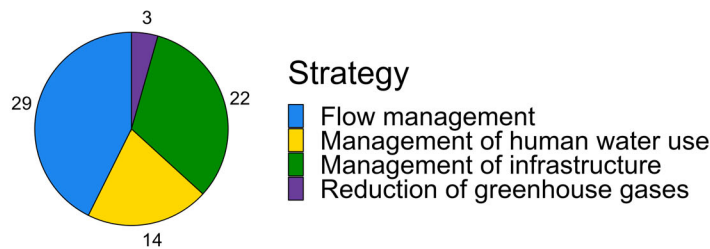
## A. Management of mussel populations



## B. Management of habitat conditions



## C. Management of anthropogenic influences



**Fig. 6.** Topics covered by papers addressing mitigation strategies, including (A) management of mussel populations, (B) management of habitat conditions, and (C) management of anthropogenic influences.

Table 5. Collated suggested drought mitigation strategies for managing mussel populations.

Category	Strategy	Description	Challenges	Number of sources	Relevant citations
Translocation	Translocation	Relocate stranded or emersed mussels to areas with deeper water, different locations or sites, or <i>ex-situ</i> facilities; consider multi-species translocation to ensure access to host fish	Risks spread of pathogens in mussel translocations; higher mortality at relocation sites; ignores location-specific host adaptations	19	Archambault <i>et al.</i> (2018); Bódis <i>et al.</i> (2014); Cosgrove <i>et al.</i> (2022); Curley <i>et al.</i> (2022); Gallardo & Aldridge (2013); Gough <i>et al.</i> (2012); Hastie <i>et al.</i> (2003); Jones & Neves (2011); Morales <i>et al.</i> (2011); Nogueira <i>et al.</i> (2021); Pandolfo <i>et al.</i> (2010b); Paschoal <i>et al.</i> (2020); Sousa <i>et al.</i> (2018); da Silva <i>et al.</i> (2022); Fogelman <i>et al.</i> (2023); Schneider <i>et al.</i> (2018); Osterling (2015); Hassall <i>et al.</i> (2017); Sullivan & Lirtrell (2020)
Stocking and propagation	Stocking and propagation	Support existing mussel populations with individuals from hatcheries and propagation facilities or larger tributary streams; establish new mussel populations in drought refuge habitats	Limited systematic testing; may act as a sink for stocked populations if habitat conditions remain unfavourable; possible genetic concerns	12	Archambault <i>et al.</i> (2018); Haag & Warren (2008); Hastie <i>et al.</i> (2003); Inoue <i>et al.</i> (2014); Nogueira <i>et al.</i> (2021); Pandolfo <i>et al.</i> (2010b); Paschoal <i>et al.</i> (2020); Sousa <i>et al.</i> (2018); da Silva <i>et al.</i> (2022); Schneider <i>et al.</i> (2018); Hassall <i>et al.</i> (2017); Wagner <i>et al.</i> (2024)
Long-term monitoring	Long-term monitoring	Establish long-term monitoring sites to understand temporal responses to drought events better	Time consuming; mussels are long-lived; requires consistent methodology	13	Cosgrove <i>et al.</i> (2022); Hastie <i>et al.</i> (2003); Inoue & Berg (2017); Inoue <i>et al.</i> (2014); Jones (2007); Karlin <i>et al.</i> (2017); Khan <i>et al.</i> (2020); Lopez <i>et al.</i> (2022); Mitchell <i>et al.</i> (2021); Nogueira <i>et al.</i> (2021); Payton <i>et al.</i> (2016); Randklev <i>et al.</i> (2018a); Verbrugge <i>et al.</i> (2012)
Maintenance and protection of biodiversity	Protect biodiversity hotspots	Protect and conserve hotspots of biodiversity to sustain rare and diverse communities	Protection of isolated hotspots may not ensure persistence and survival of species in a river	2	Dascher <i>et al.</i> (2018); Sánchez González <i>et al.</i> (2021)
	Protect host fish	Protect and manage host fish populations and account for host fish requirements when managing mussel populations	Specific host fish may be unknown; fish may disperse away from managed habitats	2	Schneider <i>et al.</i> (2018); da Silva <i>et al.</i> (2022)

Table 6. Collated suggested drought mitigation strategies for managing habitat conditions.

Category	Strategy	Description	Challenges	Number of sources	Relevant citations
Management and monitoring of water quality and thermal conditions	Thermal management	Management of cold-water releases or effluent temperatures	May have unintended consequences (e.g. growth or reproduction impacts)	8	Archambault <i>et al.</i> (2014a); Castelli <i>et al.</i> (2012); Cole <i>et al.</i> (2018); Galbraith <i>et al.</i> (2020); Gates <i>et al.</i> (2015); Taubert <i>et al.</i> (2014); Vaughn <i>et al.</i> (2015); Hoess <i>et al.</i> (2022)
	Monitor water quality	Monitor and maintain adequate water quality during and prior to drought conditions	May be difficult to implement; recognises but does not address poor water quality	4	Chen <i>et al.</i> (2001); Inoue <i>et al.</i> (2014); Beggel <i>et al.</i> (2017); Kunz <i>et al.</i> (2021)
	Holistic restoration	Restoration of physicochemical and biological conditions with consideration of all or many aspects of aquatic ecosystems	May be expensive and time consuming; may be difficult to implement	5	Hoess & Geist (2020); Khan <i>et al.</i> (2019); Paschoal <i>et al.</i> (2020); Reckendorfer <i>et al.</i> (2006); Bogatov <i>et al.</i> (2023)
Restoration and management of aquatic and riparian habitat	Restoration	Restoration of aquatic habitat conditions	May be expensive and time consuming	16	Allen <i>et al.</i> (2013); Collas <i>et al.</i> (2018); Galbraith <i>et al.</i> (2015); Gomes-dos-Santos <i>et al.</i> (2019); Jones & Byrne (2010); Kuemmerlen <i>et al.</i> (2022); Nogueira <i>et al.</i> (2021); Pandolfo <i>et al.</i> (2010b); Paschoal <i>et al.</i> (2020); Pérez-Quintero (2011); Randklev <i>et al.</i> (2018b); Reckendorfer <i>et al.</i> (2006); Baldan <i>et al.</i> (2021); Hoess <i>et al.</i> (2022); Graeber <i>et al.</i> (2013); Wagner <i>et al.</i> (2024)
	Riparian vegetation restoration	Restoration of riparian vegetation to provide shade and reduce instream temperatures	May be expensive and time consuming	17	Atkinson <i>et al.</i> (2014); Cosgrove <i>et al.</i> (2022); Ferreira-Rodriguez <i>et al.</i> (2018b); Hastie <i>et al.</i> (2003); Lymbery <i>et al.</i> (2021); Oosterhuis <i>et al.</i> (2021); Pandolfo <i>et al.</i> (2010b); Santos <i>et al.</i> (2015); Taubert <i>et al.</i> (2014); Baldan <i>et al.</i> (2021); da Silva <i>et al.</i> (2022); Hoess <i>et al.</i> (2022); Osterling (2015); Said & Nassar (2022); Hassall <i>et al.</i> (2017); Newton <i>et al.</i> (2013); Wagner <i>et al.</i> (2024)
Restoration and management of aquatic and riparian habitat	Sediment management and restoration	Establish methods for preventing excessive fine sediment accumulation (e.g. sediment-retention ponds, vegetated filter strips)	May be expensive and time consuming	2	Baldan <i>et al.</i> (2021); Hyvärinen <i>et al.</i> (2022)
	Preserve habitat connectivity	Maintain sections of flowing water to provide adequate habitat conditions	Difficult to control; may require e-flows and management of anthropogenic water use	2	Baldan <i>et al.</i> (2021); Clarke (2010)
	Remove forestry plantations	Restore natural vegetation and end logging operations	May be expensive and time consuming; possible stakeholder pushback	1	Kuemmerlen <i>et al.</i> (2022)

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Table 6. (Cont.)

Category	Strategy	Description	Challenges	Number of sources	Relevant citations
Creation and protection of refuge habitats	Refuge creation	Create refuge habitats such as deeper pools to help mussels persist	May not ensure persistence, some species may experience high mortality in refuge habitats	5	Cosgrove <i>et al.</i> (2022); Kakino <i>et al.</i> (2011); Markovic <i>et al.</i> (2014); Nakano (2018); Hoess <i>et al.</i> (2022)
	Wetland protection	Protect wetlands that provide refuge habitat and help regulate water availability	Economic or social conflicts regarding water protection or use	3	Cosgrove <i>et al.</i> (2022); Kuemmerlen <i>et al.</i> (2022); Tarter <i>et al.</i> (2023)
Local management	Protect natural parks and establish protected areas	Protect mussel populations in natural parks and establish areas where mussels are protected	Economic or social conflicts regarding water protection or use	2	Pérez-Quintero (2011); da Silva <i>et al.</i> (2022)
	Remnant stream protection	Protect remnant streams that maintain adequate habitat conditions	Economic or social conflicts regarding water protection or use	1	Bogan <i>et al.</i> (2019)
	Local management	Manage habitat conditions and mussel populations on a site-by-site basis	Requires knowledge of local populations and habitat requirements	13	Curley <i>et al.</i> (2022); Galbraith <i>et al.</i> (2012); Haney <i>et al.</i> (2020); Hoess & Geist (2020); Jones & Byrne (2010); Khan <i>et al.</i> (2019); Kuemmerlen <i>et al.</i> (2022); Layzer & Madison (1995); Newton <i>et al.</i> (2015); Peterson <i>et al.</i> (2011); Shea <i>et al.</i> (2013); da Silva <i>et al.</i> (2022); Cushway & Schwalb (2024)

Table 7. Potential drought mitigation strategies suggested by articles for mitigating drought impacts by managing anthropogenic influences.

Category	Strategy	Description	Challenges	Number of sources	Relevant citations
Flow management	Environmental flows	Establish minimum discharges or emulate natural flow regime	Minimum discharge standards may not protect small to mid-sized populations; may have unintended impacts if entire ecosystem is not considered	27	Allen <i>et al.</i> (2013); Cole <i>et al.</i> (2018); Cosgrove <i>et al.</i> (2022); Ferreira-Rodriguez <i>et al.</i> (2018b); Gates <i>et al.</i> (2015); Goldsmith <i>et al.</i> (2022); Haney <i>et al.</i> (2020); Hoess & Geist (2020); Khan <i>et al.</i> (2019); Khan <i>et al.</i> (2020); Layzer & Madison (1995); Mallen-Cooper & Zampatti (2020); Oosterhuis <i>et al.</i> (2021); Pandolfo <i>et al.</i> (2010b); Peterson <i>et al.</i> (2011); Randklev <i>et al.</i> (2018a,b); Rypel <i>et al.</i> (2009); Santos <i>et al.</i> (2015); Tacubert <i>et al.</i> (2014); Vaughn <i>et al.</i> (2015); Wolaver <i>et al.</i> (2014); Cushway & Schwalb (2024); Graeber <i>et al.</i> (2013); Rangaswami <i>et al.</i> (2023a,b); Newton <i>et al.</i> (2013) Wisniewski <i>et al.</i> (2016); Duda <i>et al.</i> (2023)
Management of infrastructure	Flow augmentation Manage dams and drawdowns	Supplement discharge conditions by transporting water from other locations or water sources Manage dam releases, drawdown timing and rate and discharges associated with dams and infrastructure; maintain and preserve stretches of unregulated streams	May be expensive and time consuming; can deplete groundwater resources; limited systematic testing; potential issues with unintended spread of pathogens and invasive species Difficult to balance human water needs with ecosystem needs; possible public/private opposition	2 19	Allen <i>et al.</i> (2013); Atkinson <i>et al.</i> (2014); Castelli <i>et al.</i> (2012); Curley <i>et al.</i> (2022); Ford <i>et al.</i> (2016); Galbraith <i>et al.</i> (2010, 2020); Gates <i>et al.</i> (2015); Howells <i>et al.</i> (2000); Layzer <i>et al.</i> (1993); Mallen-Cooper & Zampatti (2020); Nakano (2018); Newton <i>et al.</i> (2015); Nogueira <i>et al.</i> (2021); Randklev <i>et al.</i> (2013); Sethi <i>et al.</i> (2004); Tacubert <i>et al.</i> (2014); Vaughn <i>et al.</i> (2015); Cushway & Schwalb (2024)
Reduction of greenhouse gases	Dismantle old infrastructure Reduce greenhouse gases	Dismantle and remove old or unused infrastructure Reduce global greenhouse gas emissions to reduce global warming	Expensive and time consuming; can result in ecosystem effects like siltation or dewatering Requires united global effort	3 3	Hoess & Geist (2020); Mallen-Cooper & Zampatti (2020); Santos <i>et al.</i> (2015) Hastie <i>et al.</i> (2003); Inoue & Berg (2017); Markovic <i>et al.</i> (2014)

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Table 7. (Cont.)

Category	Strategy	Description	Challenges	Number of sources	Relevant citations
Management of human water use	Manage water abstraction	Regulate surface water and groundwater use during drought conditions; including establishment of water master (administers water rights)	May be difficult to monitor; possible public opposition	10	Curley <i>et al.</i> (2022); Holcomb <i>et al.</i> (2018); Inoue <i>et al.</i> (2014); Karatayev <i>et al.</i> (2012); Khan <i>et al.</i> (2019); Mitchell <i>et al.</i> (2021); Randsklev <i>et al.</i> (2018a,b); Wolaver <i>et al.</i> (2014); Cushway & Schwalb (2024); Wolaver <i>et al.</i> (2014)
	Water markets, interbasin transfers	Transfer of water from elsewhere	Creates surface or groundwater deficit elsewhere; potential issues with unintended spread of pathogens and invasive species	1	Wolaver <i>et al.</i> (2014)
	Aquifer storage and recovery and off-stream storage	Store surplus water during floods or rain events for use in drier periods	Competition with other human water demands	2	Wolaver <i>et al.</i> (2014); Mallen-Cooper & Zampatti (2020)
	Reduce human water consumption	e.g. use of treated wastewater for industrial or irrigation uses	Lacking infrastructure	1	Wolaver <i>et al.</i> (2014)

higher temperatures (Spooner & Vaughn, 2008; van Ee, Johnson & Atkinson, 2022). Contribution to different ecosystem services depends partly on the functional traits of species (Spooner & Vaughn, 2012; van Ee *et al.*, 2022). Thus, shifts in the dominance of certain species or changes in community composition in response to drought conditions can decrease areal nitrogen and phosphorus excretion (Atkinson, Julian & Vaughn, 2014). Drought-related mass mortality events can result in declines in mussel biomass and loss of sensitive species that lead to considerable losses of ecosystem services and ecosystem function (Atkinson *et al.*, 2014; Vaughn *et al.*, 2015; DuBose *et al.*, 2019). The Kiamichi River in Oklahoma exhibited massive declines (i.e. 60% population loss) in freshwater mussels after two drought events over two decades (1991–2011), leading to reductions in estimated biofiltration (~60–80% estimated reduction), nitrogen recycling (~50–70% estimated reduction), and phosphorus recycling (~50–80% estimated reduction) at 35 °C (Vaughn *et al.*, 2015). Long-term declines in biofiltration, nutrient capacitance and storage, and decreased habitat heterogeneity from mussels and shells are also expected with drought-induced mussel losses (DuBose *et al.*, 2019). In systems where native mussels have largely been replaced by more thermally sensitive invaders like *Corbicula* spp., drought-related mass mortality may result in an almost complete loss of biofiltration services (McDowell *et al.*, 2017). While shells that remain after these mass die-offs can release nutrients slowly over time, overall ecosystem services like nutrient storage and habitat are lost (DuBose *et al.*, 2019).

### (8) Mitigation strategies

Less than half (~39%) of the articles we reviewed provided suggestions for managing and mitigating drought risk. Few articles offered specific recommendations (i.e. quantified or testable information) for mitigation strategies [but see Layzer & Madison (1995), Castelli, Parasiewicz & Rogers (2012), Wolaver *et al.* (2014), Gates *et al.* (2015), Goldsmith *et al.* (2022), and Khan *et al.* (2020) for examples], and even fewer actually tested or modelled the effectiveness of mitigation strategies (see Peterson *et al.*, 2011; Wisniewski, Abbott & Gascho Landis, 2016; Gates *et al.*, 2015; Cosgrove *et al.*, 2022). Without knowledge of the effectiveness of different mitigation strategies, it can be difficult for managers to evaluate the limitations and costs that inherently influence management decisions. Suggestions for mitigation ranged from broad and large scale to specific and small scale and fell into three general categories (Fig. 6): management of mussel populations (Table 5), management of habitat conditions (Table 6), and management of anthropogenic influences (Table 7).

A consistent theme across several articles was the need for site-specific management considerations when mitigating drought-related risks and managing mussel species (Table 5). Given the heterogeneity in habitat characteristics

and the variation in species traits, a ‘one-size-fits-all’ approach for management does not sufficiently recognise the range of approaches that may be necessary to mitigate drought-related risks.

To better guide management decisions related to drought, there is a need for (i) increased long-term monitoring of mussels and their host fish (Table 5), (ii) identification of biodiversity hotspots to protect diverse and abundant communities that may facilitate rare species (Table 5; Perez Rocha *et al.*, 2023), (iii) trait-based approaches (e.g. Gates *et al.*, 2015, Mitchell *et al.*, 2018) to provide useful frameworks for effective management plans (Gates *et al.*, 2015), and (iv) more comprehensive and evidence-based studies evaluating sublethal drought-related stress and tolerance for mussel species with non-lethal means. This is especially important for rare or endangered species. For example, stress hemolymph and tissue biomarkers have been shown to respond to thermal stress and variation in fluvial discharge (Fritts *et al.*, 2015a,b). In addition, to identify thresholds that should be avoided to protect mussels during high temperatures and reduced fluvial discharge, Uniform Continuous Above Threshold (UCAT) analysis can be applied (Castelli *et al.*, 2012; Goldsmith *et al.*, 2022; Rangaswami *et al.*, 2023b). Multi-stressor and weight-of-evidence approaches can help provide a more holistic view of how environmental factors associated with drought affect mussels, incorporating multiple approaches that consider physiological, cellular, and molecular responses (Ferreira-Rodríguez *et al.*, 2018b; Galbraith *et al.*, 2020; Luck & Ackerman, 2022). Strategies that go beyond monitoring mussel growth and condition alone are required to capture the full range of consequences that mussels face during drought (Clarke, 2010). Additional strategies exist for managing mussel populations (Table 5), managing habitat conditions (Table 6), and managing anthropogenic influences (Table 7).

#### IV. CONCLUSIONS

(1) Our review indicates that the effects of drought on freshwater mussels are far-reaching and comprehensive. Drought affects all levels of mussel biological organization, starting from individual mussel physiology, mortality, behaviour, and reproductive success, scaling up to population and community responses, and finally, interspecific interactions and ecosystem services. While our knowledge of how drought can directly and indirectly impact mussels is growing, there is an urgent need to identify specific, actionable research topics that will help scientists and managers predict and respond to challenges facing freshwater mussels in a future where droughts are likely to increase in frequency and magnitude for much of the world.

(2) Increasingly, research has indicated that species’ traits play an important role in governing drought tolerance in freshwater mussels. However, few (<15%) of the articles we reviewed incorporated trait-based evaluations, emphasising

the need to account for mussel traits in future research. Trait-based approaches will shed light on how responses to droughts may be generalizable to species with similar traits, perhaps alleviating some of the cost and time required to evaluate individual species’ responses.

(3) While there is extensive research on many of the individual effects of thermal, desiccation, and hypoxic stress for freshwater mussels, a greater understanding of the synergistic effects of multiple stressors will be an important aspect of future research. Understanding how different stressors interact to affect mussels exposed to drought will be especially important in systems that are increasingly plagued by both climate change and anthropogenic impacts.

(4) Studies on the impacts of drought and dewatering on mussels have largely focused on North American unionids, one of the most diverse assemblages worldwide. However, recent research has indicated that portions of Asia also harbour extremely diverse mussel communities that may be especially threatened by high drought risk and baseline water stress now and in the future. There is an urgent need to explore the impacts of drought in regions like this that support high diversity and endemism, as well as in less-diverse but chronically understudied Unionida families (e.g. Hyriidae, Iridinidae, Mycetopodidae, Etheriidae).

(5) While many studies we reviewed suggested potential mitigation strategies to help protect and conserve mussels in drought-prone or anthropogenically impacted systems, there is a lack of systematic testing to inform mussel conservation and management. Long-term monitoring, site- or species-specific management plans, and non-lethal monitoring methods will be important aspects of successful mitigation actions. More testing of mitigation strategies is urgently required to arm managers and scientists with the knowledge required to ensure that freshwater mussels and the ecosystem services they provide will continue to persist in the future.

#### V. ACKNOWLEDGEMENTS

This work was supported in part by the US Army Corps of Engineers’ Aquatic Nuisance Species Program’s focus on Next Generation Ecological Modeling (W912HZ2020047). The drawing of the freshwater mussel life cycle was provided by Tammy Rodela. Thanks to Hunter York for assistance with proofreading, and two anonymous reviewers for suggestions regarding improving the manuscript.

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## VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Scientific, peer-reviewed articles obtained from *Web of Science* searches or from the reference sections of selected *Web of Science* articles.

**Fig. S1.** Compiled estimate of overall risk based on drought risk, baseline water stress, and Unionida species richness.

**Table S2.** Total number of studies addressing drought effects on families in the order Unionida.

**Table S3.** Species in the order Unionida studied with respect to drought conditions, including high temperatures, desiccation, and low dissolved oxygen.

**Table S4.** Total number of studies addressing drought effects on each life stage of freshwater mussels in the order Unionida.

**Table S5.** Total number of studies using different scientific approaches to investigate the effects of drought on mussels in the order Unionida.

(Received 14 November 2023; revised 23 August 2024; accepted 29 August 2024)