



# Mass Mortality Events of Invasive Freshwater Bivalves: Current Understanding and Potential Directions for Future Research

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## OPEN ACCESS

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### Specialty section:

This article was submitted to  
Population and Evolutionary  
Dynamics,  
a section of the journal  
Frontiers in Ecology and Evolution

**Received:** 10 March 2019

**Accepted:** 19 August 2019

**Published:** 13 September 2019

### Citation:

McDowell WG and Sousa R (2019)  
Mass Mortality Events of Invasive  
Freshwater Bivalves: Current  
Understanding and Potential  
Directions for Future Research.  
*Front. Ecol. Evol.* 7:331.  
doi: 10.3389/fevo.2019.00331

Mass mortality events, the rapid, catastrophic die-off of organisms, have recently been recognized as important events in controlling population size, but are difficult to quantify given their infrequency. These events can lead to large inputs of animal carcasses into aquatic ecosystems, which can have ecosystem scale impacts. Invasive freshwater bivalves such as the Asian clam *Corbicula fluminea*, the zebra mussel *Dreissena polymorpha*, the golden mussel *Limnoperna fortunei*, and the Chinese pond mussel *Sinanodonta woodiana* can attain high densities and biomass and play important roles in aquatic ecosystems through filtration, bioturbation, and excretion. Invasive bivalve species can best be described as R-selected species and appear not to have the same tolerance to abiotic stressors as native species, causing them to be prone to mass mortality events in their invasive range. In contrast to their ecological effects while alive, the frequency and impacts of mass mortality events of invasive freshwater bivalves are not well-understood. Here we review the causes and impacts of mass mortality events, as well as identify important questions for future research. Extreme abiotic conditions, including both drought and flooding, as well as high and low temperatures were the primary drivers of mass mortality events. Short-term impacts of mass mortality events include large pulses of nitrogen and increased oxygen stress due to large amounts of soft tissue decomposition, while shells can impact habitat availability and nutrient cycling for decades. Impacts on biological communities (bacteria, fungi, and macroinvertebrates) are less studied but some examples exist concerning *C. fluminea*. Better documentation of mass mortality events, particularly their magnitude and frequency, is needed to fully understand the impacts invasive bivalve species have on ecosystems, especially as climate change may make mass mortality events more frequent and/or have a larger magnitude.

**Keywords:** boom-bust dynamics, die-off, extreme events, invasive species, non-indigenous species, *Corbicula*

## BACKGROUND

Mass mortality events, “the rapid, catastrophic die-off of organisms that punctuate background mortality rates” (Fey et al., 2015), have recently been recognized as important events in controlling population size, but it can be difficult to put the significance of these events in a broader context given their infrequency (Fey et al., 2015). A meta-analysis showed that mass mortality

events are increasing in both frequency and magnitude across several taxa, including marine invertebrates (Fey et al., 2015); however, freshwater invertebrates were not included within this study. For invasive species, research often focuses on quantifying effects as a function of their range, abundance, and per capita impact (Parker et al., 1999). In doing this, much research has focused on their impacts while alive, without capturing the impacts of possible periodic mortality events.

Within freshwater ecosystems, bivalves such as clams and mussels play a critical role in a wide range of ecosystem functions, including filtering bacteria, particulates, and primary producers from the water column, bioturbation via movement and pedal feeding, and excretion of important nutrients such as nitrogen and phosphorus (Covich et al., 1999; Vaughn and Hakenkamp, 2001; Vaughn and Hoellein, 2018). Many of these processes directly benefit humans as ecosystem services, such as removing nutrients and sediment from water (Vaughn, 2018). Globally, freshwater mussels (Bivalvia, Unionida) are among the most threatened organisms on earth (Strayer et al., 2004; Lopes-Lima et al., 2017, 2018) and many populations are experiencing large scale declines (Haag, 2012; Ferreira-Rodríguez et al., 2019). In many ecosystems, declines of native mussels have been coupled with the establishment of invasive bivalve species that evolved elsewhere in the world and now have negative economic and ecological impacts (Strayer and Malcom, 2018).

Invasive bivalves, including the zebra mussel *Dreissena polymorpha*, the golden mussel *Limnoperna fortunei*, the Asian clam *Corbicula fluminea*, and the Chinese pond mussel *Sinanodonta woodiana*, have been shown to have dramatic ecological and economic impacts on freshwater ecosystems and are among the most widespread and damaging invasive species in the world (Sousa et al., 2014). Many invasive bivalve species have large-scale impacts on ecosystem function (Caraco et al., 1997; Strayer et al., 1999; Zhu et al., 2006) and can act as ecosystem engineers (Sousa et al., 2009). They can also often times reach extremely high densities of several hundreds to thousands of individuals per square meter (Caraco et al., 1997 for *D. polymorpha*, McDowell and Byers, 2019 for *Corbicula* sp., Bódis et al., 2016 for *Sinanodonta woodiana*), and sometimes even on the order to hundreds of thousands of individuals per square meter for the golden mussel *Limnoperna fortunei* (Sylvester et al., 2007). Invasive bivalves have also been observed to die en masse (Ilarri et al., 2011), with sometimes 90–99% of individuals dying within a short period of time (Haag and Warren, 2008; McDowell et al., 2017). This leads to millions of individuals dying at once, with their bodies releasing nutrients within a few days (McDowell et al., 2017).

Our understanding of the importance and impacts of animal carcasses in aquatic ecosystems remains incomplete. Pulses of nutrients into systems can have major bottom-up impacts on food webs (Yang, 2004), especially in aquatic systems where nutrients can move rapidly through the food web (Nowlin et al., 2008). Although a great deal of research has focused on the importance of carcasses of anadromous salmon to aquatic ecosystems and adjacent forests (e.g., Helfield and Naiman, 2002; Hocking and Reynolds, 2011) in the Pacific Northwest region of the United States, examples on other faunal groups and

continents are less frequent (but see Subalusky et al., 2017). However, recent research has highlighted the importance of the remains of animals in freshwater ecosystems, and the impacts of the reduction of animal remains in freshwater ecosystems due to overall population declines (Wenger et al., 2019). For example, Wenger et al. (2019) estimate that dissolution of mussel shells could have provided 1% of the total phosphorus load in rivers during median flow and typical shell production rates; periodic mass mortality events that generate more shell might have played a more important role. Even less studied are the possible impacts of massive mortalities by invasive species in the invaded range.

From an ecological theory perspective, invasive bivalves may be prone to frequent, episodic mortality events due to their tendency to be “weedy” R selected species that have lower tolerance to abiotic stressors (McMahon, 2002), which may make them more prone to “boom-bust” dynamics where populations undergo large fluctuations (Strayer et al., 2017). The “boom-bust” model of invasive species has been documented in a variety of organisms, including plants (Stott et al., 2010), insects (Lester and Gruber, 2016), and molluscs (Moore et al., 2012).

In order to better understand the roles of mass mortality events of invasive bivalves in aquatic ecosystems, here we: 1. Review the known mass mortality events of invasive freshwater bivalves, including their causes, impacts, and whether or not native species were affected; and 2. Identify nine important questions for future research on mass mortality events of invasive freshwater bivalves.

## CAUSES OF MASS MORTALITY EVENTS

We identified documented mass mortality events of invasive bivalves through a literature review searching for studies examining “mass mortality,” “die-offs,” or “population declines” of invasive bivalves in freshwater ecosystems using Google Scholar over any time period. In particular, we focused on the following invasive bivalves that are abundant and widespread: the Asian clam *Corbicula* sp., the zebra mussel *Dreissena polymorpha*, the golden mussel *Limnoperna fortunei*, and the Chinese pond mussel *Sinanodonta woodiana*. All studies identified may be found in **Table 1**. It is important to note that mass mortality events are not unique to invasive bivalves, and can also occur with native bivalve species (e.g., Vaughn et al., 2015 in Oklahoma, Sousa et al., 2018 in the Iberian Peninsula). While this review focuses on mass mortality events of invasive bivalves, a critical and open research question is to what extent the responses of native and invasive bivalves may differ and or interact (DuBose et al., 2019). Generally speaking, mass mortality events of invasive bivalve species were triggered by extreme abiotic conditions, including drought, flood, extreme high temperatures, and extreme low temperatures (**Figure 1**).

### Drought and High Temperatures

Drought and high temperatures, which typically co-occurred and therefore cannot be split apart as separate stressors, were the dominant driver of mass mortality events of invasive freshwater bivalves. We found documented high temperature mortality events in the southern United States in particular

**TABLE 1** | Summary of documented mass mortality events of invasive bivalves. Studies are sorted by cause, then species.

References	Location	Habitat	Species	Cause
Golladay et al. (2004)	GA, USA	Stream/river	<i>Corbicula</i>	Drought/heat
Gagnon et al. (2004)	GA, USA	Stream/river	<i>Corbicula</i>	Drought/heat
Haag and Warren (2008)	AL and MI, USA	Stream/river	<i>Corbicula</i>	Drought/heat
Atkinson et al. (2014)	OK, USA	Stream/river	<i>Corbicula</i>	Drought/heat
McDowell et al. (2017)	GA, USA	Stream/river	<i>Corbicula</i>	Drought/heat
Mouthon and Daufresne (2006)	France	Stream/river	<i>Corbicula</i>	Drought/heat
Foekema et al. (2008)	The Netherlands	Stream/river	<i>Corbicula</i>	Drought/heat
Ilarri et al. (2011)	Portugal	Stream/river	<i>Corbicula</i>	Drought/heat
Bódis et al. (2014a)	Hungary	Stream/river	<i>Corbicula</i> , <i>S. woodiana</i>	Drought/heat
Balogh et al. (2008)	Hungary	Lake/Reservoir	Zebra mussel	Drought/heat
Churchill (2013)	TX and OK, USA	Lake/Reservoir	Zebra mussel	Drought/heat
Churchill et al. (2017)	TX and OK, USA	Lake/Reservoir	Zebra mussel	Drought/heat
White et al. (2015)	MI, USA	Lake/Reservoir	Zebra mussel	Drought/heat
Sousa et al. (2012)	Portugal	Stream/river	<i>Corbicula</i>	Flood
Castañeda et al. (2018)	Canada	Stream/river	<i>Corbicula</i>	Low temperatures
Smith et al. (2018)	WI, USA	Stream/river	<i>Corbicula</i>	Low temperatures
Werner and Rothhaupt (2008)	Switzerland	Lake/Reservoir	<i>Corbicula</i>	Low temperatures/desiccation
Leuven et al. (2014)	The Netherlands	Lake/Reservoir	<i>Corbicula</i> , Zebra mussel	Low temperatures/desiccation

(Georgia: Gagnon et al., 2004; Golladay et al., 2004; McDowell et al., 2017, **Figure 2A**; Alabama and Mississippi: Haag and Warren, 2008; Oklahoma: Atkinson et al., 2014; Vaughn et al., 2015; Texas and Oklahoma: Churchill, 2013; Churchill et al., 2017). High summer temperatures were also associated with mortality events for *C. fluminea* in both Portugal (Ilarri et al., 2011) and France (Mouthon and Daufresne, 2006), as well as a mortality event in Hungary which affected *Corbicula* sp., *S. woodiana*, and native mussels (Bódis et al., 2014a, **Figure 2B**). During drought events, small streams may be impacted more heavily, as they are more prone to dewatering; following a drought in Alabama and Mississippi, *C. fluminea* populations declined 90–98% in small streams, but significantly increased in two of the three large river sites studied (Haag and Warren, 2008).

The exact trigger for the mortality can vary from case to case. High temperatures and drought can lead to bivalves being stranded on sand bars or within disconnected pools as flows decline (Atkinson et al., 2014), or even mortality of individuals still within flowing water, due to high temperatures and low dissolved oxygen concentrations (Foekema et al., 2008 as cited in Ilarri et al., 2011; Leuven et al., 2014; McDowell et al., 2017). In estuarine areas, drought can lead to increases in salinity, which may be a contributing factor to *Corbicula* mass mortality events within the Minho River in Portugal (Ilarri et al., 2011). Within lakes, drought can lead to water level fluctuations, leaving individuals stranded, as was observed in a zebra mussel mortality event in Lake Balaton, Hungary (Balogh et al., 2008) and in Lake Texoma on the border between Texas and Oklahoma, USA (Churchill, 2013; Churchill et al., 2017). Mortality events may occur regularly during heat waves and with a large enough magnitude to control population sizes, as Ilarri et al. (2011) noted that the lowest observed population densities of *C. fluminea*

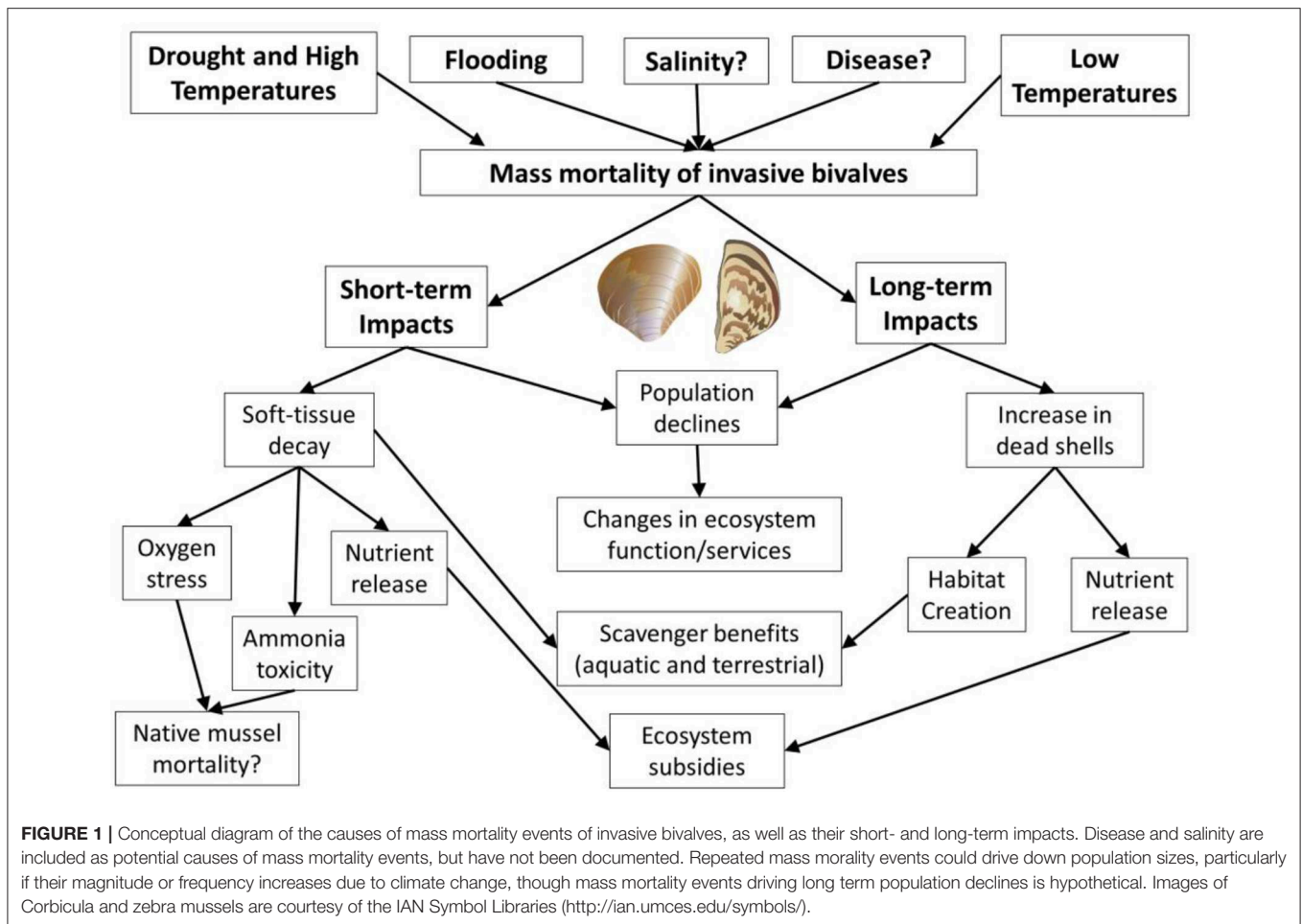
corresponded to years with summer heat waves. Mortality events can also occur at temperatures that are “sub-lethal” per laboratory experiments (White et al., 2015), emphasizing the importance of field research on these events.

## Flooding

Flooding, the other hydrologic extreme, can also lead to mass mortality events. Floods typically do not directly kill the bivalves, but instead transport them to unsuitable habitats during high flows after which they are stranded when flood waters recede. High flow events can play an important role in controlling the distribution of a bivalve within a river (Strayer, 1999), and can lead to mass mortality events of invasive species (Sousa et al., 2012, **Figure 3**). Flooding during the winter months in northern Portugal led to deposition of up to 2,200 individuals m<sup>-2</sup> and 10,200 g<sup>-2</sup> wet biomass on adjacent river banks. *Corbicula fluminea* was the most common species transported during flood mortality events, both by biomass and density, despite *C. fluminea* not being the dominant bivalve at some of the study sites (Sousa et al., 2012).

## Low Temperatures

Extreme cold can also lead to mass mortality events of freshwater bivalves. Though minimum temperatures have been shown to be an important controller for the distribution of *C. fluminea* through modeling (McDowell et al., 2014) mass mortality events induced by low temperature are often associated with human manipulations of temperature or water level. In Europe, an extremely cold winter coupled with low water levels in Lake Constance led to a 99% mortality rate for *Corbicula* that were either stranded or in water up to 3 m deep (Werner and Rothhaupt, 2008). Similarly, low water levels and cold temperatures led to high mortality of zebra mussels within



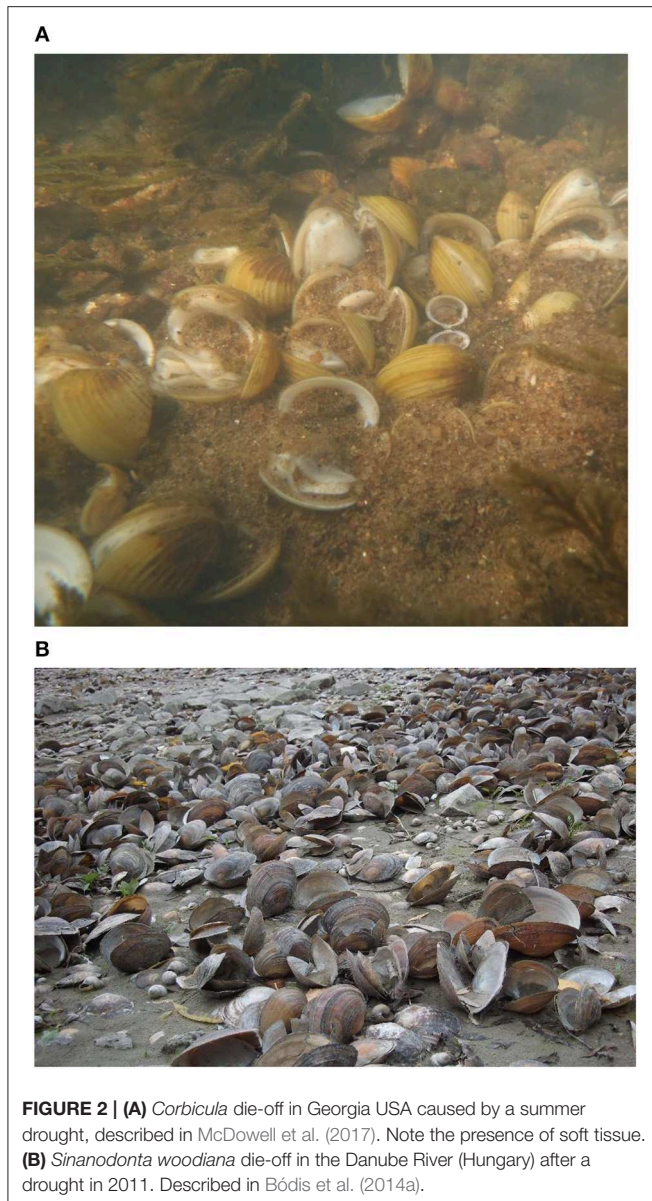
impounded sections of the Rhine and Meuse Rivers in the Netherlands (Leuven et al., 2014). The combination of water level drawdowns and low temperatures has been used as a mechanism to control zebra mussel populations (Grazio and Montz, 2002, as cited in Leuven et al., 2014). Conversely, while industrial cooling water plumes may provide thermal refuge for invasive species in areas that are otherwise climatically unsuitable, the cessation of industrial activities can lead to rapid extirpation of populations that relied on the artificial warming to persist. Both individuals and populations can thrive in thermal effluent—one study in the River Shannon, Ireland found that within thermal plumes individuals were more than twice as large by length and body mass, densities were more than 13 times higher, and biomass was nearly 50 times higher (Penk and Williams, 2019). In North America, a population of *Corbicula* was well-established within the St. Lawrence River in the cooling water plume of a power plant (Simard et al., 2012), but a rapid extirpation followed the decommissioning of the power plant (Castañeda et al., 2018). Mortality events can also occur despite thermal refuge during particularly severe winters, as was documented in the Great Lakes region of the United States with a near extirpation of *Corbicula* in the Fox River (Smith et al., 2018).

## IMPACTS OF MASS MORTALITY EVENTS

The most immediate response to mass mortality events is the input and subsequent decomposition of dead tissue into ecosystems (Figure 1). The largest bivalve mortality event documented was caused by drought conditions in the Danube River and created an input of over  $20\text{--}30\text{ kg m}^{-2}$  of wet biomass (which includes shells) and over  $1,000\text{ g m}^{-2}$  of ash free dry mass at the sites with the highest densities of invasive bivalves (Bódis et al., 2014a). This mortality event primarily affected the Chinese pond mussel *S. woodiana*, but also included two other invasive bivalves: *Corbicula* sp. and the zebra mussel *D. polymorpha*. The decay of soft tissues can be quite rapid, on the order of days (McDowell et al., 2017), and this rapid decay, particularly during warm summer months, could exacerbate already stressful oxygen conditions (Gagnon et al., 2004; McDowell et al., 2017).

### Short-Term Effects

During the decay of soft tissues decay, large amounts of nutrients are released, creating a pulse of resources (Sousa et al., 2012). This can lead to large scale shifts on both a local and ecosystem level. McDowell et al. (2017) estimated that a mortality event of  $\sim 100$  million *Corbicula* released  $\sim 751\text{ kg}$  of carbon,  $180\text{ kg}$  of nitrogen,



and 45 kg of phosphorus as soft tissues decayed. The release of nutrients from a mass mortality event can lead to potentially toxic concentrations of unionized ammonia for unionid mussels, in both the water column (Cherry et al., 2005) and the porewater of sediment (Cooper et al., 2005). However, in a manipulative study simulating a die-off of *C. fluminea* in Minho River (Iberian Peninsula) no changes were detected in the structure of aquatic microbial and invertebrate communities nor litter breakdown rate (Novais et al., 2017).

### Long-Term Effects

The impacts of the decay of soft tissue can be quite large, but short lived, whereas the impacts of shells could extend for decades, given their slow breakdown rate (Strayer and Malcom, 2007; Ilarri et al., 2015). The time frame for the impact of additional



**FIGURE 3 |** Accumulation of *C. fluminea* after the 2001 flood in the banks of Minho River. This photo was taken in 2014, 13 years after the flooding, showing the longer-term impacts that additions of shells can have on an ecosystem.

shells can vary substantially depending on whether or not they are found in a terrestrial or aquatic ecosystem, as the decay rate for a variety of bivalve shells (including *C. fluminea*) is six to twelve times faster in aquatic systems than in terrestrial (Ilarri et al., 2015). Shells, and the trickled release of nutrients, could play an important role in the biogeochemistry of rivers and adjacent flood plains, as bivalve shells can provide significant storage of nutrients, particularly carbon and nitrogen (Vaughn et al., 2015). While shells are relatively poor in both nitrogen and phosphorus [ $\sim 1\%$  N and  $0.01\%$  P for unionid mussels Christian et al., 2008; Atkinson et al., 2010] compared to soft tissue, the sheer mass of shells can provide a significant release of nutrients over time. Wenger et al. (2019) estimated that based on historical densities, the breakdown of mussel shells once provided  $\sim 1\%$  of the total phosphorus load in rivers in the southeastern United States.

### Habitat Creation

The shells of invasive freshwater bivalves can alter the physical habitat within a river, contributing to their role as ecosystem engineers (Sousa et al., 2009). Within the Danube River, empty bivalve shells increased the abundance of a variety of macroinvertebrates. For rivers that are dominated by fine sediment, these shells can provide important habitat for benthic invertebrates and increase their abundance and biomass (Bódis et al., 2014b). Other studies have shown that shell density of *C. fluminea* is positively associated with biomass, diversity, and density of macroinvertebrates (Ilarri et al., 2012). Shells resulting from die-offs can also have significant effects on estuarine and freshwater macroinvertebrates than can use them as substrate or as refuge from predators (e.g., Ilarri et al., 2012, 2014, 2018; Bódis et al., 2014b; Novais et al., 2015).

## Foodweb Alterations

Given the importance of filter feeding bivalves in aquatic foodwebs (Vaughn and Hakenkamp, 2001; Vaughn and Hoellein, 2018), it is unsurprising that mass mortality events would alter foodwebs. We have identified two main ways these foodweb alterations can occur: direct benefits to scavenging organisms and ecosystem subsidies from aquatic to terrestrial ecosystems.

### Scavenger Benefits

The addition of soft tissue should be a benefit for scavenging species as well, though published reports of this are limited. Mouthon (2001) reported that soft tissue from *Corbicula* mortality events was consumed by silurid fishes, though to our knowledge that is the only published account documenting this behavior. Anecdotally, researchers and fishermen have reported estuarine fish moving upstream in Portuguese rivers to consume *C. fluminea* corpses (Sousa personal observation) and within Georgia rivers, flocks of crows have been observed consuming dead *Corbicula* that were stranded on a sandbar (McDowell personal observation). Any aquatic scavengers such as crayfish ought to benefit as well, but again, this has not been reported in the literature and remains an open question (see below).

### Ecosystem Subsidies

Nutrients from bivalve decay often cross ecosystem boundaries, providing important subsidies that span the terrestrial aquatic interface. Subsidies from aquatic to terrestrial systems play an important role in many ecosystems, often through anadromous fish such as salmon (Helfield and Naiman, 2002). Mass mortality of invasive freshwater bivalves, particularly through drought or flooding, can lead to ecosystem subsidies of energy and nutrients to terrestrial ecosystems (Sousa et al., 2012; Bódis et al., 2014a, **Figure 3**). Addition of carrion can impact both nutrient dynamics and communities, as two studies (Novais et al., 2015, 2017) simulating massive die-offs of *Corbicula* in terrestrial ecosystems after floods showed clear effects on soil chemistry, fungal biomass, and bacterial, fungal, and macroinvertebrate communities. Pulses of nutrients could also increase insect emergence rates in response to additions of phosphorus (Mundie et al., 1991) and both nitrogen and phosphorus (Blumenshine et al., 1997) in experimental stream mesocosms. These higher emergence rates could be an additional way that mass mortality events strengthen subsidies to terrestrial ecosystems, as these insects provide an important food source for riparian predators (Baxter et al., 2005).

## Alterations to Ecosystem Function

Given the importance of filter feeding bivalves in aquatic ecosystems (Vaughn and Hakenkamp, 2001; Vaughn, 2018), including filtration, bioturbation, and nutrient storage, a mortality event can also dramatically alter ecosystem function. For example, within a Georgia River, overall filtration rates by *Corbicula* dropped 99.6% following a mass mortality event (McDowell et al., 2017). Filtration is a particularly important function of freshwater bivalves, as it removes particles from the water column and connects the water column and benthic food webs (Vaughn and Hakenkamp, 2001). Few studies have focused

on shifts in ecosystem function following mortality of invasive freshwater bivalves, but Vaughn et al. (2015) showed that multiple severe droughts over 20 years caused native mussel mortality that substantially reduced the ecosystem function they provided. Losses were disproportionately felt by thermally sensitive species, which had higher percentages of both nitrogen and phosphorus in their tissues (Atkinson et al., 2014). These impacts are driven by the massive decline in population size, and therefore the overall role of the species in the ecosystem, and can be short-term and transient if the populations recover, or long-term if the population size remains low or is unable to fully recover due to repeated mortality events. It is unclear if these changes at the ecosystem level will return systems to function closer to their pre-invasion status thanks to the diminished role of invasive species, or if the dramatic decline in filter feeding bivalves will push these systems farther from historical function, even though the dominant bivalves are invasive. Although we are not aware of quantitative studies, similar effects are possible in response to massive declines in density and biomass of dominant invasive freshwater bivalves after massive die-offs.

## OPEN QUESTIONS

In attempting to understand the overall causes and impacts of mass mortality events of invasive freshwater bivalves, we identified several important open questions which researchers should/may address in future studies.

### How Frequent Are Mass Mortality Events of Invasive Bivalves?

To date, most research has focused on quantifying the magnitude and impacts of mass mortality events, rather than their frequency. In addition to the impacts described above, if ecosystems are experiencing regular mortality events, this could also lead to depressed population sizes, and therefore reduce the impacts of invasive species on ecosystem function. Harri et al. (2011) found some indication that mass mortality events temporarily depressed population sizes, as *C. fluminea* densities were the lowest in years following notable heat waves. Overall, it is not clear if mass mortality events are unusual, and best described as a “solitary boom-bust” model in which the population of an invasive expands rapidly, only to decline (Strayer et al., 2017), or if mass mortality events are regular occurrences, best fitting either the “recurrent” or “cyclic” models of boom-bust dynamics where population declines are occurring at least twice, and may occur at regular intervals (Strayer et al., 2017).

The responses of the invasive bivalves to mortality events may vary due to different life spans, with *S. woodiana* having a much longer life span [~12 years Dudgeon and Morton, 1983], than *Limnoperna fortunei* [2–3 years Ricciardi, 1998] or *Corbicula* and zebra mussels [~3–5 years McMahon and Bogan, 2001; Strayer and Malcom, 2006], so it would be expected that the recovery trajectories differ as well. For several of these species, we do not have a long enough period of monitoring to determine long term responses to mass mortality events. In addition to possible differences in responses and recovery from mortality

events at the species level, populations from different latitudes or subjected to different abiotic conditions (e.g., food resources, altitude; Crespo et al., 2015) may respond differently following a mortality event. Assuming that invasive populations are able to recover, the frequency of mass mortality events fundamentally alters the balance of the impacts invasive bivalves have while alive (filtration, storage and excretion of nutrients, bioturbation) and the impacts they have during mass mortality events (nutrient release, availability of empty shells, loss of filtration). A critical component to answering this question will be better monitoring of mass mortality events; for *Corbicula* sp., for example, anecdotal evidence indicates that mortality events are relatively common, although they are not well-described in the literature (McDowell et al., 2017). In some cases, mortality of invasive species is only briefly described as part of a study more heavily focused on native species (e.g., Vaughn et al., 2015). In order to better assess the impact and novelty of mass mortality events as part of our overall understanding of the impact of invasive species, better quantitative documentation is needed, and in particular we must know:

### Are Native Species Affected Similarly to Invasive Bivalves?

Invasive species are often considered “weedy,” with high reproduction rates but poorer tolerance to stressful abiotic conditions than native species, so therefore ought to experience more frequent mortality events (McMahon, 2002). It is important to note, however, that native species do not represent a homogenous group. Within the United States, the native unionid mussels vary substantially in their ability to tolerate a wide variety of stressors such as desiccation, high temperatures, or low dissolved oxygen (Haag, 2012). Differences in abiotic tolerances should lead to differences in the frequency and magnitude of mortality events in communities dominated by invasive species compared to those with an intact mussel community, especially as an intact native community ought to have a more heterogeneous response to abiotic stressors. Using a trait based framework for the bivalve community as a whole could be an illuminating way to compare the differing roles in and impacts on ecosystems that native and invasive bivalves have in the face of extreme events (de Bello et al., 2010). This approach could lead to broader, more generalizable results than explicit pairwise comparisons of native and invasive species (McGill et al., 2006). Few studies have quantified the mortality of both native and invasive bivalves, but those have generally shown a higher mortality rate for the invasive species induced by both drought (Haag and Warren, 2008; Bódis et al., 2014a) and flood (Sousa et al., 2012). In contrast to the “missing dead”—a decline in the number of animal carcasses in aquatic ecosystems due to widespread population declines—described by Wenger et al. (2019), if mass mortality events of invasive species are occurring more frequently or to a larger magnitude than we would expect in an uninvaded community, mortality events could represent a source of “found dead” instead, increasing overall inputs of shell and soft tissue into aquatic ecosystems. While baseline mortality would be contributing shell and soft tissue, repeated massive

mortality followed by rapid population growth could increase the overall amount of inputs of tissue and shell into the system.

### Is *Corbicula* sp. Less Tolerant to Abiotic Stressors Than Other Invasive Bivalves?

Most of the documented mass mortality events of invasive bivalves are for *Corbicula* sp., and include populations in Europe and North America. A key question that remains to be answered is if *Corbicula* is particularly vulnerable to mass mortality events or whether *Corbicula* dominates studies of mass mortality of invasive bivalves because it has been a research focus for multiple groups in Portugal, Georgia, and Oklahoma. Many of the documented mass mortality events occurred in the southern United States or in southern Europe—is the frequency of mass mortality events a product simply of the extreme heat during the summers in these regions? Mortality events for *Corbicula* were also primarily in lotic systems, so it is possible that populations in lotic systems are more vulnerable due to fluctuations in water levels and possibly food resources, which will decrease the physiological capacity to deal with a stressful event such as heatwaves. In some instances, mortality events were associated with cessation of flow, creating disconnected pools which often led to mortality of native mussels as well (Atkinson et al., 2014). This could lead to both high temperature and low oxygen, though *Corbicula* sp. is more tolerant of hypoxia than the zebra mussel at temperatures up to 25°C (Matthews and McMahon, 1999). Using laboratory experiments to better define the tolerance of *Corbicula* to stressful abiotic conditions, particularly high temperatures and low dissolved oxygen, is particularly important to help protect and conserve native bivalves, as the mortality of *Corbicula* could exacerbate the negative impacts of mass mortality events on native species via increased oxygen stress (Gagnon et al., 2004 in south Georgia) and toxic concentrations of ammonia (Cherry et al., 2005; Cooper et al., 2005).

In contrast, we did not find any documented mass mortality events of *L. fortunei* and a small number impacting *D. polymorpha*. Further research is needed in order to determine if *L. fortunei* and *D. polymorpha* follow similar patterns to *Corbicula* or *S. woodiana*, which have large-scale mortality events. The golden mussel in particular appears to be very tolerant of a wide range of abiotic conditions, including high temperatures, low dissolved oxygen, and acidic water (Boltovskoy et al., 2006; Karatayev et al., 2007), when compared to other invasive bivalves, including *D. polymorpha*. Given their robust tolerance to abiotic stressors, *L. fortunei* may be particularly unlikely to experience mass mortality events. The zebra mussel *D. polymorpha*, on the other hand, has experienced large population declines in recent years, though without clear cut mass mortality events.

### Do Salinity Fluctuations Trigger Mass Mortality Events?

For freshwater species expanding into estuarine environments, salinity is an important controller of distributions. It is also highly dynamic, with both regular fluctuations due to tides, as well as human alterations and extreme events. Salinity appears

to be particularly important in controlling the distribution of the golden mussel *Limnoperna fortunei* in estuaries (Angonesi et al., 2008). *Corbicula* sp., on the other hand, appear to be tolerant to a wide range of salinities in estuaries, with a higher tolerance of 20 ppt during cooler winter months than during summertime conditions (~15 ppt) (Ferreira-Rodríguez and Pardo, 2016), though salinity fluctuations in the lower portion of the Minho estuary were hypothesized as a potential contributor to a mortality event during an extreme heat wave and drought in Portugal (Ilarri et al., 2011). Given that salinity can control the distribution of freshwater invasive bivalves, and can vary greatly due to storms, alterations to land use, and even seasonal shifts in river discharge, salinity should be a potential trigger of mass mortality events. However, to date, none have been documented. This topic requires additional study, and our understanding of the role of salinity in controlling the distribution of invasive bivalves lags behind other abiotic factors such as temperature (Feng and Papeš, 2017).

### What Role, If Any, Do Disease Outbreaks Play in Mass Mortality Events of Invasive Freshwater Bivalves?

Our understanding of disease induced mass mortality of freshwater bivalves in general is limited, although mass mortality events driven by disease outbreaks have been shown in native unionid mussels (Carella et al., 2016) and marine bivalves such as oysters (Burreson and Ragone, 1996; Lacoste et al., 2001). Invasive species often leave behind their parasites (e.g., Blakeslee et al., 2008, 2012), so parasitic species that act as controls in the native range may simply not be found in the new invasive range. However, genetic diversity of invasive species is often lower than in their native range due to founder effects (Sakai et al., 2001), and this lack of genetic diversity should make them more vulnerable to disease outbreaks. *Corbicula*, as a species that is entirely androgenetic clones in the invasive range in both North America (Lee et al., 2005) and in Europe (Sousa et al., 2007; Gomes et al., 2016), ought to be extremely vulnerable to disease outbreaks, but to our knowledge, none have been demonstrated. There is also the possibility for the transmission of diseases between native and invasive bivalves, though this has not been documented; the transmission of new diseases by invasive species can have substantial negative impacts on native species, however (e.g., Andreou et al., 2012).

### How Will Climate Change Alter the Frequency and Magnitude of Mass Mortality Events?

Climate change is predicted to have a wide variety of impacts on invasive species (Hellmann et al., 2008), including altered distributions of existing invasive species. For some invasive bivalves, warming temperatures have opened additional habitats that had previously been unsuitable climatically due to minimum temperatures (McDowell et al., 2014). Expanding into newly suitable habitats may make invasive bivalves vulnerable to occasional extreme cold, leading to mortality events, similar

to those documented in the Great Lakes region of the United States (Smith et al., 2018). Within existing populations, higher temperatures could lead to more frequent mortality events during the summer, such as those observed by McDowell et al. (2017). Finally, both drought and flooding were important causes of mortality events for both native and invasive bivalves. Given that climate change is forecasted to increase the intensity of rain events but reduce their frequency (Trenberth, 2011), both drought- and flood-induced mass mortality events are likely to become more common.

### Will the Occurrence of Die-Offs and Ecological Impacts be Similar in the Native and Invaded Range?

To our knowledge, no research has documented mass mortality events of invasive bivalve species within their native range, let alone compared the frequency and magnitude of mass mortality events between the native and invaded range. Comparisons of mass mortality events between the two ranges would allow us to determine if massive die-offs are more common in the invaded range than in the native range. In theory, invasive species would be less adapted to the abiotic conditions in their invasive range as they did not evolve there. Because invasive species can undergo rapid evolution, however, invasives may be as well-adapted to a local environment as native species (Oduor et al., 2016). If differences exist between the native and invasive ranges, the impact of invasive bivalve species on communities and ecosystem function may vary dramatically in the invasive range compared to the native. It should be noted, however, that this is currently speculative for invasive freshwater bivalves, but deserves future attention.

### Which Organisms Benefit From Mass Mortality Events?

Scavengers ought to exploit the availability of fresh carrion during mortality events, though this has not been established in the literature aside from one report (Mouthon, 2001), perhaps due to the difficulty in capturing transient effects caused by mortality events. For many other taxa the impacts have not been tested or have had inconclusive results. Within terrestrial systems, invertebrates clearly responded to a simulated mortality event, with higher diversity and density that scaled with higher inputs of carrion (Novais et al., 2015). However, a manipulative experiment in a flowing river found no difference in fungi, invertebrates and in decomposition rates (Novais et al., 2017). The responses to mortality events may be highly context dependent, with impacts in lotic systems being less pronounced than those in lentic or terrestrial environments. With inputs into terrestrial systems, there is evidence that mortality events can alter the abundance and biomass of aboveground consumers (Novais et al., 2015), but impacts on belowground communities have yet to be addressed. Further manipulative experiments are needed to fully explore the impacts mortality events have on other communities, in



particular to quantify what other organisms are benefitting from carrion inputs.

In addition to trophic benefits, the mass mortality of invasive bivalves may provide competitive release for native species if they are able to survive the trigger of the mortality event, as invasive species often compete with natives. *Corbicula* may compete with native mussels for seston food resource (Leff et al., 1990), and have been shown to lead to lower survival and growth rates of native mussels (Ferreira-Rodríguez et al., 2018) and high densities may reduce the survival of mussel glochidia (Modesto et al., 2019). Zebra mussels compete with native species for both food resources (Baker and Levinton, 2003) and space (Lauer and Spacie, 2004). A mass mortality event of invasive bivalves could lead to higher survival, growth, and reproduction of native bivalves.

## How Long Do Effects Remain in the Ecosystem?

Soft tissue from bivalves will be rapidly consumed or decompose but on the other hand, the shells can persist for several decades (see above). Additionally, the shells of *Corbicula* sp. are thicker, and more resistant to decay than those of some native species (Iarri et al., 2019). For both soft tissue and shells the decay rates are highly context dependent—for example, if shells are deposited in areas with high current velocity the decomposition rate will be very different than if shells are deposited on river banks during floods. Similarly, decomposition rates may also be very distinct in different climatic regimes—in areas with more precipitation, decomposition ought to be much faster than in more arid ecosystems. We need quantitative studies to assess the persistence of the impacts associated with mass mortality events of invasive bivalves. In addition, effects may vary from species to species. For example, bivalves with thicker or harder shells, will in theory, take more time to erode and so persist for more time in the system. Longer term monitoring of locations affected by mass mortality events may be needed to understand longer term impacts, especially within terrestrial systems.

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## CONCLUSION

Our understanding of the causes and impacts of mass mortality events of invasive freshwater bivalves is developing, though several key questions remain. It remains unclear whether these are “black swan events” (sensu Anderson et al., 2017)—rare events that can have profound impacts on populations and ecosystems—or a regular feature of a community dominated by invasive species. Our ability to answer these questions will be important in creating a better understanding of how mass mortality events of invasive bivalve currently affect aquatic ecosystems, and how they will do so in the face of continued biotic homogenization and climate change. Because invasive bivalves are well-suited for manipulative studies, this faunal group can be used to further understand the trophic and non-trophic consequences of massive mortalities in aquatic ecosystems.

## AUTHOR CONTRIBUTIONS

WM conceived of this study. WM and RS contributed to all other components of this study.

## FUNDING

This work was supported by funding from the School of Science and Engineering at Merrimack College.

## ACKNOWLEDGMENTS

Many colleagues provided comments on the early stages of this study following a presentation at the Society for Freshwater Science 2018 annual meeting. WH McDowell and KMS McDowell provided valuable feedback on drafts of this manuscript. Three reviewers also provided helpful feedback on this study. Finally, the establishment of this collaboration was aided by mentorship from JE Byers and a Research Coordination Network grant from the National Science Foundation.

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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