

SPECIAL REVIEW

Developing environmental flow recommendations for freshwater mussels using the biological traits of species guilds

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SUMMARY

1. North American freshwater mussels (Unionidae) are a diverse and imperilled fauna that are very sensitive to flow alterations. Previous attempts to develop environmental flows for mussels have struggled to accommodate their varied habitat requirements and complex life histories.
2. We review what is known about the habitat requirements of mussels, how they can vary among species within a community, and how this variation influences the effectiveness of different environmental flow methodologies.
3. We propose a trait-based environmental flow method that addresses the needs of mussel guilds differentiated by their thermal tolerances and reproductive strategies. Used previously for fish, plants and macroinvertebrates, the guild approach groups species by traits and identifies flow requirements of guilds as opposed to entire communities.
4. We apply the guild approach to the mussel fauna of the Kiamichi and Little Rivers in south-eastern Oklahoma, U.S.A., and illustrate how changes in the hydrograph can be made to better meet the seasonal flow needs of differing mussel guilds and their host fish.
5. The guild environmental flow method can provide flow recommendations that cater to the life history and habitat requirements represented within diverse mussel communities. In addition, the method can be adapted among regions where trait data are available or combined with rating models that estimate trait data for understudied species.

Keywords: biodiversity, conservation, e-flow, trait, Unionidae

Introduction

Freshwater mussels are especially sensitive to changes in hydraulic conditions. Their complex life cycle and sedentary adult life stage require adequate stream flows that permanently maintain wetted habitat, buffer water quality and provide adequate food. In addition, the ectoparasitic juvenile life stage of mussels requires flows that support the presence of host fish species during the appropriate season. Previous attempts to develop environmental flows for mussels have not fully accommodated their unique habitat

requirements or complex life history and have consequently not provided effective flow recommendations. We review the unique requirements of mussels and how they influence the effectiveness of different environmental flow models. We propose a method that addresses the needs of mussel guilds differentiated by their thermal tolerances and reproductive strategies. Using streams in south-eastern Oklahoma, U.S.A., as a case study, we discuss where previous models used to estimate environmental flows have not adequately protected mussels and how future efforts can be improved.

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E-flow needs of mussels

The unionids of North America are a highly diverse and imperilled fauna (Bogan, 1993; Strayer *et al.*, 2004). A complex life history makes them reliant on natural flow regimes and especially susceptible to environmental changes, including habitat fragmentation, habitat disturbance and introduction of non-native species (Vaughn & Taylor, 1999; Lydeard *et al.*, 2004; Haag, 2012). Over the past century, as the physical landscape of North America has changed, freshwater mussels have experienced significant declines in abundance and diversity (Neves *et al.*, 1997; Ricciardi, Neves & Rasmussen, 1998; Vaughn & Taylor, 1999; McMahon & Bogan, 2001; Strayer *et al.*, 2004) largely due to alterations in the natural flow regime (Watters, 1999; Poff *et al.*, 2007). Understanding how to sustain remaining populations is vital to their long-term persistence.

Freshwater mussels have a complex life cycle. Freshwater mussel larvae (glochidia) are ectoparasites, attaching to the gill or fin tissue of a host fish where they metamorphose and eventually release as juveniles into new habitat (McMahon & Bogan, 2001; Haag, 2012). The juvenile life stage is the most sensitive and least understood (Sparks & Strayer, 1998; Beck & Neves, 2003; Newton *et al.*, 2003; Fisher & Dimock, 2006; Hanlon & Neves, 2006). Once established in a new location, adult mussels are sedentary filter feeders, moving only 1–100 m (Green, Singh & Bailey, 1985; Waller, Gutreuter & Rach, 1999; Kappes & Haase, 2012). The mixed sedentary and mobile life histories are adapted to a flow regime that maintains wetted habitat for adults and host fish while also buffering water quality and providing adequate food replenishment.

Changes in flow regimes can be potentially catastrophic to population persistence because mussels are generally very slow to recover from population declines. Mussel species exhibit a range of life spans (6–60 years) but are generally long-lived compared to many aquatic organisms, and usually do not become sexually mature until 6 years of age or older (Imlay, 1982; McMahon & Bogan, 2001). Fecundity rates are very high (200 000–17 000 000), but survival from the glochidial stage to adulthood is typically low (Yeager, Cherry & Neves, 1994; Sparks & Strayer, 1998; McMahon & Bogan, 2001; Jones & Neves, 2011). Disturbances that affect larvae or juveniles may lead to the loss of entire year-classes (Payne & Miller, 1989) or populations within river systems. Mussels are patchily distributed throughout rivers in diverse species beds (Strayer *et al.*, 1994, 2004) that serve as small populations within drainage meta-populations

(Vaughn, 1993). The loss of a significant proportion of small populations can decrease the viability of a drainage metapopulation, making it more difficult for existing populations to recover (Vaughn, 2012).

Freshwater mussels are particularly sensitive to flow alterations created by impoundment releases (Vaughn & Taylor, 1999; Galbraith & Vaughn, 2011; Allen *et al.*, 2013). Such releases often produce large fluctuations in discharge that differ from those of a river's natural flow regime in their timing, magnitude, duration and rate of change (Yeager, 1993; Poff *et al.*, 1997; Richter & Richter, 2000). The success of mussel reproduction and the following larval life stage are dependent on flows that mimic the flow regime under which mussels and their host fish co-evolved (Barnhart, Haag & Roston, 2008). Increases in the magnitude of high flows may prevent juvenile mussels from settling in new habitat or dislodge newly settled juveniles (Neves & Widlak, 1987; Holland-Bartels, 1990; Layzer & Madison, 1995; Hardison & Layzer, 2001; Daraio, Weber & Newton, 2010a). Increases in flow magnitude may also create sediment scour that physiologically interferes with mussel feeding, reproduction and survival (Young & Williams, 1983; Dennis, 1984; Aldridge, Payne & Miller, 1987). In contrast, variation in the timing of high and low flows may cause mussel beds to be exposed to altered temperature regimes (Galbraith & Vaughn, 2011) or indirectly affect mussels by preventing host fish species from being present at the proper time to carry larvae (Freeman & Marcinek, 2006; Gido, Dodds & Eberle, 2010).

Optimum flows for mussels maintain habitat continuously for juveniles and adults, and seasonally for host fish. The maintenance of habitat must encompass the abiotic and biotic factors that determine mussel distribution as well as incorporating the relationship between flow and water quality. Unfortunately, defining the characteristics that determine mussel distribution has been very challenging (Strayer, 2008). The distribution of freshwater mussels is thought to be most strongly influenced by complex hydraulic parameters (such as Froude and Reynolds numbers, shear stress and shear velocity; Hardison & Layzer, 2001; Gangloff & Feminella, 2007; Steuer, Newton & Zigler, 2008; Zigler *et al.*, 2008; Allen & Vaughn, 2010), followed by geomorphology (Gangloff & Feminella, 2007; Atkinson, Julian & Vaughn, 2012) and substratum (Gangloff *et al.*, 2004; Steuer *et al.*, 2008; Allen & Vaughn, 2010; Bodis *et al.*, 2011). There is consensus that complex hydraulic conditions during extreme events (floods or droughts) have a stronger influence on the distribution of adult mussels than average hydraulic conditions (Gangloff & Feminella, 2007;

Zigler *et al.*, 2008; Allen & Vaughn, 2010). For example, extreme hydraulic events during juvenile settling may prevent the growth and formation of mussel beds (Neves & Widlak, 1987; Holland-Bartels, 1990; Layzer & Madison, 1995; Hardison & Layzer, 2001). Optimum flows need to be low enough to maintain hydrological bed stability for deep pools while being high enough to prevent sedimentation and exposure to lethal water quality conditions (Vannote & Minshall, 1982; Hartfield & Ebert, 1986; Strayer, 1993, 1999).

Optimum flows for mussels also create optimal seasonal temperature regimes to which mussel and host fish life cycles are adapted. Mussels are thermoconformers whose physiological processes are constrained by water temperature (Spooner & Vaughn, 2008; Pandolfo, Kwak & Cope, 2012). Flow alteration often causes changes in the thermal regime experienced by mussels. For example, decreases in water temperature below hypolimnetic release dams have been shown to reduce and even eliminate mussel populations for long distances (Ahlstedt, 1983; Miller, Rhodes & Tippit, 1984; Yeager, 1993; Lydeard & Mayden, 1995; Vaughn & Taylor, 1999). Release of cold water during the summer when water temperatures should be warm suppresses mussel metabolic rates during a time of year when growth should be high (McMahon & Bogan, 2001) and inhibits reproduction (Layzer, Gordon & Anderson, 1993). Cold-water releases also may eliminate or inhibit reproduction of some species of warm-water fishes (Layzer *et al.*, 1993; Yeager, 1993) and increase the success of introduced cold-water species such as trout. Therefore, abnormally cold discharge, particularly in summer, may act as a permanent colonisation barrier to non-generalist mussels (Vaughn & Taylor, 1999).

Because mussels are dependent on host fish, any effects of hydrological alterations on host fish also affect mussel populations. Distribution, abundance and movement patterns of host fish have been shown to be critical to the distribution and abundance of mussels (Watters, 1993; Vaughn, 1997, 2012; Haag & Warren, 1998; Vaughn & Taylor, 2000). The disappearance of mussel species from several rivers has been linked to the disappearance of the appropriate host fish (Kat & Davis, 1984), and mussels have re-colonised rivers after their host fish were re-introduced (Smith, 1985). Low-head dams have been shown to block host fish migration and lead to the extirpation of mussels in reaches above the dams (Watters, 1996). Altered flow regimes can decrease both the species richness and abundance of fish communities (Gore & Bryant, 1986; Kinsolving & Bain, 1993; Scheidegger & Bain, 1995), potentially eliminating mussel

hosts. Impacts probably vary both seasonally and with river microhabitat. For example, a high proportion of nest-building fish species, such as centrarchids, are common mussel hosts (Kat, 1984; Vaughn, 2012; Cummings & Watters, 2014). Thus, altered hydrology that reduces or eliminates populations of nesting fish species could result in mussel glochidia failing to attach to hosts, reducing mussel recruitment.

E-flows for mussels under a changing climate

Changing climate conditions are elevating the negative impacts of flow alterations on mussels. While summer months are historically lower flow months in many regions of North America, drought conditions in the past decade have exacerbated the effects of low flows during the warmest months of the year for many mussel populations (Watters, 1999; Golladay *et al.*, 2004; Galbraith, Spooner & Vaughn, 2010; Allen *et al.*, 2013). Drought conditions across the southern U.S.A. have increased the occurrence and the magnitude of low flow conditions leading to temperature extremes and mass mussel die-offs (Haag & Warren, 2008; Galbraith *et al.*, 2010; Gough, Landis & Stoeckel, 2012; Randklev *et al.*, 2013; Shea *et al.*, 2013).

Discharge that is too low, especially when combined with high temperatures, negatively affects mussels (Gagnon *et al.*, 2004; Golladay *et al.*, 2004; Haag & Warren, 2008). Decreases in river discharge can affect benthic organisms by decreasing water velocity, water depth and wetted channel width, increasing sedimentation and changing the thermal regime and water chemistry (Dewson, James & Death, 2007). Adult mussels are sedentary, precluding relocation when environmental conditions become suboptimal. What is considered suboptimal varies by species and is heavily influenced by temperature (Spooner & Vaughn, 2008, 2009; Gough *et al.*, 2012). Confounding the effects of high temperatures, mussels are thermoconformers and lack the ability to regulate their own temperature, further increasing mortality rates during extreme temperature exposures (McMahon & Bogan, 2001; Pandolfo *et al.*, 2012).

The varying temperature sensitivities of mussel species can lead to feedback cycles that increase mortality during low flow and high temperature extremes. Extended periods of exposure to high temperatures, low dissolved oxygen and high ammonia levels are lethal for mussels (Gagnon *et al.*, 2004; Golladay *et al.*, 2004; Cherry *et al.*, 2005; Haag & Warren, 2008; Strayer & Malcom, 2012); however, there is often a range of physiological tolerances among species within a mussel bed

(Spooner & Vaughn, 2008, 2009). The least temperature tolerant species are the first to experience mortality during high temperature events and their decay can further decrease habitat suitability for the remaining mussels. For example, compared to most mussel species *Corbicula fluminea* is a widespread invasive bivalve with a relatively low anaerobic capacity that can lead to mass die-offs under suboptimal conditions (White & White, 1977; Milton & McMahon, 1999; Haag & Warren, 2008; Weitere *et al.*, 2009). Known for reaching high abundances, *Corbicula* is common in many mussel beds and is often the most sensitive species present. Low flow summer conditions combined with extreme temperatures and low dissolved oxygen levels have caused massive *Corbicula* die-offs in recent years. Die-off events have negative cascading impacts on other mussel bed inhabitants by decreasing dissolved oxygen and increasing ammonia to potentially toxic levels (Cherry *et al.*, 2005; Cooper, Bidwell & Cherry, 2005). Indirectly, ammonia released by decaying *Corbicula* can fertilise algae, leading to large algal blooms, which, following algal die-off, further decreases dissolved oxygen and habitat suitability for other mussel bed inhabitants (Sousa *et al.*, 2012).

Environmental flow recommendations for mussels need to address the biotic and abiotic feedbacks of invasive species and climate change in addition to their unique life history. Incorporating the complex requirements of mussels is vital to developing flow recommendations that increase population viability and promote persistence.

E-flows methods for mussels

There are many methods available for determining environmental flows, which have been extensively reviewed by previous authors (Jowett, 1997; Arthington & Zalucki, 1998; Gore, Layzer & Mead, 2001; Tharme, 2003; Acreman & Dunbar, 2004; Annear *et al.*, 2004; Anderson *et al.*, 2006; Caissie, El-Jabi & Hebert, 2007; Petts, 2009; Poff & Matthews, 2013; Acreman *et al.*, 2014a,b). Methods can be grouped into categories by methodology (Tharme, 2003; Acreman & Dunbar, 2004) or resource objective (Annear *et al.*, 2004, 2009) and have more recently been viewed along a series of continua relating to scale and comprehensiveness (Acreman *et al.*, 2014a). The methodology classification is generally accepted and includes the categories of hydrological, hydraulic rating, habitat rating and holistic methods (Tharme, 2003; Table 1). While there is some overlap among methods, each offers varying advantages and disadvantages (Jowett, 1997; Tharme, 2003; Acreman & Dunbar, 2004;

Table 1 Environmental flow methods by methodology (Tharme, 2003) and objective (Annear *et al.*, 2009). Methods listed represent the 14 most commonly used methods in North America (Annear *et al.*, 2009)

Method	Methodology	Objective
PHABSIM	Biological rating	Habitat
2-D hydraulic	Biological rating	Habitat
Target fish community	Biological rating	Habitat
IFIM	Biological rating	Holistic
DFA	Biological rating*	Holistic
Wetted perimeter	Hydraulic rating	Habitat
SNTMP	Hydraulic rating*	Water quality
HEC-RAS	Hydraulic rating*	Geomorphology
Tennant	Hydrological	Habitat
Flow duration curve	Hydrological	Habitat
Geomorphic stream classification	Hydrological*	Geomorphology
Channel maintenance flow	Hydrological*	Geomorphology
IHA	Hydrological	Hydrology
RVA	Hydrological	Hydrology

PHABSIM, Physical HABitat Simulation Model; IFIM, instream flow incremental methodology; DFA, demonstration flow assessment; SNTMP, stream network temperature modelling; HEC-RAS, Hydrologic Engineering Centers River Analysis System; IHA, indicators of hydrologic alteration; RVA, range of variability approach. *Model was not specifically mentioned in the publication.

Petts, 2009). For our review, we focus on the specific models and methodologies that have the potential to successfully model the unique environmental flow needs of mussels.

Hydrological environmental flow methods focus on hydraulic characteristics, making them potentially useful for defining mussel habitat; but their simplistic ecological assumptions have many drawbacks. Hydrological models assume that as the wetted area of a river is increased, biological productivity increases (Jowett, 1997; Caissie *et al.*, 2007). These models do not incorporate seasonal or life-history changes in habitat requirements, but consider biological activity as a by-product of flow. Also called 'fixed percentage' or 'look-up tables', hydrological models use historical discharge records to establish minimum and optimal flow recommendations (Tharme, 2003; Caissie *et al.*, 2007). They have often been used as a starting point for environmental flow recommendations because they are relatively easy to assemble (Tharme, 2003; Caissie *et al.*, 2007). While hydrological methods have been applied to help protect mussels indirectly (Orth & Maughan, 1982 (Tennant); Jones & Fisher, 2005 (IHA); Li *et al.*, 2009 (Tennant); Turton *et al.*, 2009 (HIT and HIP)), they cannot specifically address their varying life-history needs or the effects of climate change and invasive species.

Hydraulic and biological rating models offer a direct connection between flow and measurable habitat parameters (Tharme, 2003). These models focus on the effect that various flows are expected to have on measures of habitat availability as a result of river morphology. Hydraulic and biological rating methods are typically employed when environmental flows are designed specifically for biota; however, many of these methods were originally developed for fish (Jowett, 1997; Tharme, 2003; Annear *et al.*, 2009), limiting their applicability to other organisms (Layzer & Madison, 1995; Gore *et al.*, 2001). Rating methods define habitat by taking cross sections of a river and measuring the change in habitat as a function of flow. The primary assumption is that habitat determines the distribution of biota within a river and that, as habitat changes, the distribution of biota will change in a predictable manner determined by habitat suitability criteria (Layzer & Madison, 1995; Jowett, 1997). Freshwater mussels challenge this assumption because many species require benthic habitat that is persistent under all flow conditions and their distribution is best predicted by complex hydraulic variables that readily change with changing flows (Gore *et al.*, 2001). Further, evidence suggests that hydraulic preferences of mussels may vary with flow conditions (Layzer & Madison, 1995; Layzer & Scott, 2006). Despite these limitations, rating models can be designed to incorporate habitat permanence for mussels (Layzer & Madison, 1995; Maloney *et al.*, 2012) and may provide better predictive results for mussel habitat than any other currently available option (Layzer & Madison, 1995; Gore *et al.*, 2001).

Perhaps the greatest challenge of using rating models for mussels is measuring the habitat variables that are most influential in determining species presence and abundance (habitat suitability criteria). Difficulty defining mussel habitat is a common theme in environmental flow modelling that creates a tendency to over-estimate the availability of habitat (Gore *et al.*, 2001). Previous researchers have advocated carefully addressing site-specific mussel bed conditions when selecting habitat suitability criteria and defining habitat for rating models (Layzer & Madison, 1995). Site-specific information is important because mussel beds tend to be in stable locations where they probably serve as centres for dispersal and subsequent recruitment of new beds (Vannote & Minshall, 1982). Mussel relocation projects have even relied on relocations into existing beds for a higher probability of success without a full grasp of the conditions that make existing beds optimal (Layzer & Scott, 2006). Layzer & Madison (1995) conducted one of the

first attempts to model the specific variables associated with individual mussels and mussel beds to develop environmental flow recommendations for mussels in Horse Lick Creek, Kentucky, U.S.A. The authors found that when complex hydraulic variables were used to develop habitat suitability curves under all flow conditions, the suitability of habitat varied with flow (Layzer & Madison, 1995). The correlation between mussel abundance and complex hydraulic parameters was much stronger at lower base flows typical of those experienced during juvenile settlement periods (Layzer & Madison, 1995). In addition, higher shear stress over mussel beds at high flow suggested that extreme conditions immediately following juvenile settlement could be a limiting factor for mussel population growth (Layzer & Madison, 1995). The authors also used a habitat-rating model (PHABSIM) to model host fish species presence at existing beds, but found no correlation between the number of known suitable host fish species and mussel abundance (Layzer & Madison, 1995). The authors stressed the need for site-specific assignment of environmental flows that are designed to maintain habitat for existing mussel beds (Layzer & Madison, 1995). The popularity of such site-specific and species-specific environmental flow recommendations has generally declined in recent years in favour of more holistic river management approaches (Tharme, 2003; Anderson *et al.*, 2006; Poff *et al.*, 2010b). Unfortunately, there is little evidence that habitat models for benthic organisms can be successfully used to make generalised predictions among locations even when rivers are similar (Jowett, 2003).

Recent regionally specific work with endangered mussel species has provided novel applications of rating models to address the unique habitat requirements of mussels. Maloney *et al.* (2012) applied a two-dimensional hydrodynamic flow model to measure habitat availability at varying flows for the endangered dwarf wedge mussel (*Alasmidonta heterodon*) in the Upper Delaware River, U.S.A. Using simple and complex hydraulic variables, the researchers controlled for permanently available mussel habitat at low and high flows (Maloney *et al.*, 2012). Results suggested that existing mussel beds were located in refuge areas of lower shear stress and velocity, but ground truthing revealed that existing mussel beds only occupied a fraction of persistently available habitat predicted by the model (Maloney *et al.*, 2012). Also working with *A. heterodon*, Castelli, Parasiewicz & Rogers (2012) applied a novel use of time series analysis to develop temperature ratings based on historical records and knowledge of temperature thresholds. By rating past extreme temperature events, they

were able to develop flow recommendations to decrease thermal stress for *A. heterodon* in the Delaware River without prior knowledge of the thermal optima for the species (Castelli *et al.*, 2012).

Rating models have also been successfully used to explore settling patterns of juvenile mussels. Daraio *et al.* (2010a,b) applied a hydrodynamic model to simulate juvenile mussel dispersal in large rivers. Model simulations indicated that dam operations probably affected juvenile settling by altering complex hydraulic parameters during periods when recently metamorphosed juveniles release from fish (Daraio *et al.*, 2010a). Similarly, Morales *et al.* (2006a) used a hydrodynamic model to simulate dispersal of juvenile mussels in the Upper Mississippi River, U.S.A. and found shear stress and substratum type, combined, could accurately predict settling into existing mussel bed locations. While only a portion of the life history of mussels, juvenile settling work is providing crucial information about how flow alterations can directly and indirectly optimise mussel bed formation and persistence (Daraio *et al.*, 2010a,b, 2012). Juvenile settling work is also being used to inform models that simulate mussel population dynamics incorporating biotic interactions and abiotic conditions (Morales *et al.*, 2006b).

Despite such recent advances, mussel environmental flow modelling has yet to be combined into a framework that can be applied to entire mussel assemblages. The community modelling approach has been used successfully to develop flow recommendations for benthic assemblages where species in a community can be assumed to require similar habitat (Dunbar *et al.*, 2010); however, this method is not well suited for mussels due to varying species requirements (Gore *et al.*, 2001; Hardison & Layzer, 2001; Jowett, 2003). Alternatively, the guild approach allows flow recommendations to be made for clusters of species based on species traits (Aadland, 1993 (fish); Baumgartner *et al.*, 2014 (fish); Merritt *et al.*, 2010 (plants); Poff *et al.*, 2010a (macroinvertebrates)) or habitat associations (Leonard & Orth, 1988 and Jowett & Richardson, 1995 (fish-habitat); Brunke, Hoffmann & Pusch, 2001 (benthic invertebrates including mussels-habitat)). The guild approach to developing environmental flows may be especially suitable for taxa with poorly defined habitat requirements (Souchon *et al.*, 2008) and has been suggested as a potentially promising approach for mussels (Gore *et al.*, 2001).

We propose developing environmental flow recommendations for mussels with a site-specific method that classifies mussel species into guilds based on species traits. Using mussels in the Kiamichi and Little Rivers of

south-eastern Oklahoma as a model, we discuss how impoundment releases have affected mussels in different ways, and how life-history traits and temperature sensitivities can be aligned with hydrograph and temperature data to prioritise seasonal environmental flows that reduce mortality and optimise recruitment. We discuss where previous environmental flow recommendations have fallen short in this region and how they can be improved.

A guild approach for mussel e-flows: using species traits to identify and alleviate flow regime bottlenecks

Mussel traits and guilds

Most North American mussels belong to the family Unionidae, a large diverse group of five tribes, 50 genera and *c.* 300 species (Haag, 2012). While species-specific flow criteria have been developed for some federally listed species (Maloney *et al.*, 2012), it is not feasible to do this for all species. A more workable approach is to group species based on traits that are sensitive to flows, and then set environmental flow standards that protect the most sensitive group.

Mussel species vary in multiple traits, ranging from size and morphology (Parmalee & Bogan, 1998; Haag, 2012), to the spacing of cilia on the gills (Galbraith *et al.*, 2009), to activity and burrowing behaviour (Allen & Vaughn, 2009; Daniel & Brown, 2014). However, there are two sets of traits that are likely to be most important for survival and reproduction in the face of flow bottlenecks, physiological tolerance and reproductive traits.

As stated above, mussels are thermoconformers whose metabolic rates and physiological processes vary seasonally with water temperature (McMahon & Bogan, 2001). Thermal tolerance varies with developmental stage and juveniles are more sensitive to temperature extremes than adults (Archambault, Cope & Kwak, 2013). Thermal tolerance is also influenced by other environmental factors. For example, because metabolic activity increases and oxygen solubility decreases with temperature, increased temperatures are accompanied by higher biological oxygen demand (Galbraith, Blakeslee & Lellis, 2012). Spooner & Vaughn (2008) classified mussels from an assemblage in south-eastern Oklahoma into two guilds based on their physiological performance at warm-water temperatures (35 °C): *thermally sensitive* species displayed various levels of stress at this temperature including decreased condition, anaerobic respiration and tissue catabolism, whereas *thermally tolerant* species

increased physiological process rates and maintained good condition. For species studied to date, tolerance can be generally predicted from phylogeny. For example, the lamsilines *Actinonaias ligamentina*, *Lampsilis cardium*, *Lampsilis teres* and *Truncilla truncata* are all thermally sensitive (Spooner & Vaughn, 2008; C. Vaughn, unpubl. data) (Table 2). A fourth lamsiline, *Obliquaria reflexa*, is tolerant but is also the least derived of the lamsilines that have been tested (Spooner & Vaughn, 2008; C. Vaughn, unpubl. data).

As would be expected in such a diverse group, freshwater mussel life histories are quite variable (Barnhart *et al.*, 2008; Haag, 2012). Most species are dioecious, although facultative hermaphroditism is common under stressful conditions. Gamete maturation and spawning occur from spring to late summer in most species, and water temperature is a primary cue for spawning. Mussels are sperm-casters: males release sperm into the water and females release eggs into the suprabranchial chambers of the gills where fertilisation takes place. Fertilised eggs are then brooded by the females while they develop into larvae (glochidia). Glochidia are released by the female and infect (usually) a host fish, where they mature into juveniles that fall to the sediment and grow into an adult. Within these broad strategies, species vary at every stage, from the type and number of host fish used, to the mechanism employed in infecting the host, to the timing of glochidial development and release (McMahon & Bogan, 2001; Barnhart *et al.*, 2008; Vaughn, 2012). However, there are some broad similarities in spawning, brooding periodicity, host attraction and larval release, and host use, which can be used to group species into guilds.

While the timing and duration of glochidial brooding is variable, it can be classified into two broad groups.

In short-term brooders, eggs are fertilised in the spring or summer, and brooded for a short time (2–6 weeks), after which glochidia are released. In long-term brooders, eggs are fertilised in late summer or autumn and the developed glochidia are brooded by the female overwinter and released in spring or summer, sometimes over a protracted period of time (Graf & O'Foighil, 2000; Haag, 2012). These strategies often follow phylogenetic lines: Amblemini and Quadrulini are short-term brooders, and Anodontini and most Lampsilini are long-term brooders (Haag, 2012). Thus, even if the brooding strategy of a particular species is unknown, it can probably be inferred based on phylogeny.

The glochidia of almost all mussel species require a period of time as ectoparasites on fish (or sometimes amphibians; Haag, 2012). Mussel species vary greatly in their host use, from species that can only use a single species of fish to those that can use almost any species of fish. However, host use can be classified into broad categories of generalists and specialists. Generalists are species with broad immunological compatibility with hosts and whose glochidia can metamorphose on a taxonomically wide group of host fish, usually including multiple fish families. In contrast, specialists can metamorphose on only a few species of fish, usually within one family and sometimes on only a single species (Haag, 2012).

Mussels have different mechanisms for infecting host fish with their glochidia, ranging from broadcasting free larvae to elaborate mantle lures. As with brooding periodicity, these strategies often follow phylogenetic lines. In many species, glochidia are bound by mucus into packets called conglomerates (Watters, 2008). These can

Table 2 Thermal and reproductive traits for some common mussel species in the Kiamichi River. Thermally sensitive species decrease ecological process rates and deplete energetic stores via anaerobic mechanisms at temperatures of 35 °C or above while thermally tolerant species continue to function normally at this temperature (Spooner & Vaughn, 2008). Short-term brooders spawn, brood and release glochidia over a relatively short time period in spring/summer (2–6 weeks), while long-term brooders spawn in late summer/autumn, brood eggs over the winter and release glochidia in the spring and summer, sometimes over a protracted period. Data on reproductive traits are from Vaughn (2012), Haag (2012), Barnhart *et al.* (2008), Zanatta & Murphy (2006), Graf (1997) and Cummings & Watters (2014)

Species	Tribe	Thermal guild	Brooding length	Primary host group	Primary host infection mode
<i>Actinonaias ligamentina</i>	Lampsilini	Sensitive	Long	Centrarchids	Conglomerate
<i>Amblema plicata</i>	Amblemini	Tolerant	Short	Generalist	Release free glochidia
<i>Fusconaia flava</i>	Pleurobemini	Tolerant	Short	Minnnows	Conglomerate
<i>Lampsilis cardium</i>	Lampsilini	Sensitive	Long	Centrarchids	Mantle lure
<i>Lampsilis teres</i>	Lampsilini	Sensitive	Long	Gar	Mantle lure
<i>Obliquaria reflexa</i>	Lampsilini	Tolerant	Short	Minnnows	Conglomerate
<i>Megaloniaias nervosa</i>	Quadrulini	Tolerant	Short	Generalist	Conglomerate
<i>Quadrula pustulosa</i>	Quadrulini	Sensitive	Short	Catfishes	Conglomerate
<i>Quadrula verrucosa</i>	Quadrulini	Sensitive	Short	Catfishes	Conglomerate
<i>Truncilla truncata</i>	Lampsilini	Sensitive	Long	Drum	Unknown

be loose structures that fall to the stream bottom or elaborate structures that mimic the structure and colour patterns of the intended host fish's prey (Barnhart *et al.*, 2008). Glochidia are released when the host fish bites the conglutinate and are carried onto the gills by respiratory currents. Many members of the tribe Lampsilini have pigmented modifications of the mantle (mantle lures) that surround the swollen gills (marsupia) where the female broods the glochidia. Gravid females move the lures and they resemble the prey items (i.e. minnows, crayfish) of predacious fish. When a host fish attacks the mantle flaps, the gills are ruptured and glochidia are released and carried onto the gills by respiratory currents (Barnhart *et al.*, 2008).

Applying the guild approach: Kiamichi River and Little River case studies

The Kiamichi and Little Rivers are adjacent, major tributaries of the Red River in south-eastern Oklahoma. The Kiamichi River is 5th order with a catchment area of 4650 km², and the Little River is 6th order with a catchment area of 10 720 km². Both rivers are known for their high aquatic biodiversity (Kiamichi River 86 fish species, 31 mussel species; Little River 110 fish species, 35 mussel species) with four federally listed mussels and one listed fish (Master, Flack & Stein, 1998; Matthews *et al.*, 2005; Galbraith, Spooner & Vaughn, 2008). Mussel assemblages in the two rivers are very similar, sharing 29 species in common (Allen *et al.*, 2013). These assemblages have been affected by altered flow regimes in recent decades, but in different ways due to different water management strategies (Allen *et al.*, 2013).

Prior environmental flow models have been used to draft flow recommendations for mussels in the region, but they have not addressed the distinct threats to mussels in these rivers. Many of the flow recommendations have been made for fish and do not meet the habitat needs of mussels for reasons described previously (Orth & Maughan, 1981 (Tennant); Orth & Maughan, 1982 (IFIM, PHABSIM); Layher & Brinkman, 2004 (PAM)). A Hydroecological Integrity assessment Process (HIP) was recently designed for Oklahoma to identify hydrological indices that are ecologically relevant for maintenance of the natural flow regime and protection of aquatic species of conservation concern (Turton *et al.*, 2009; HIP/HIT). While this effort can provide flow recommendations based on historic discharge and thermal regimes, designation of only hydrological indices will not address the habitat needs of mussel juveniles, mussel adults or host fish species. An Instream Flow Incremental Methodology

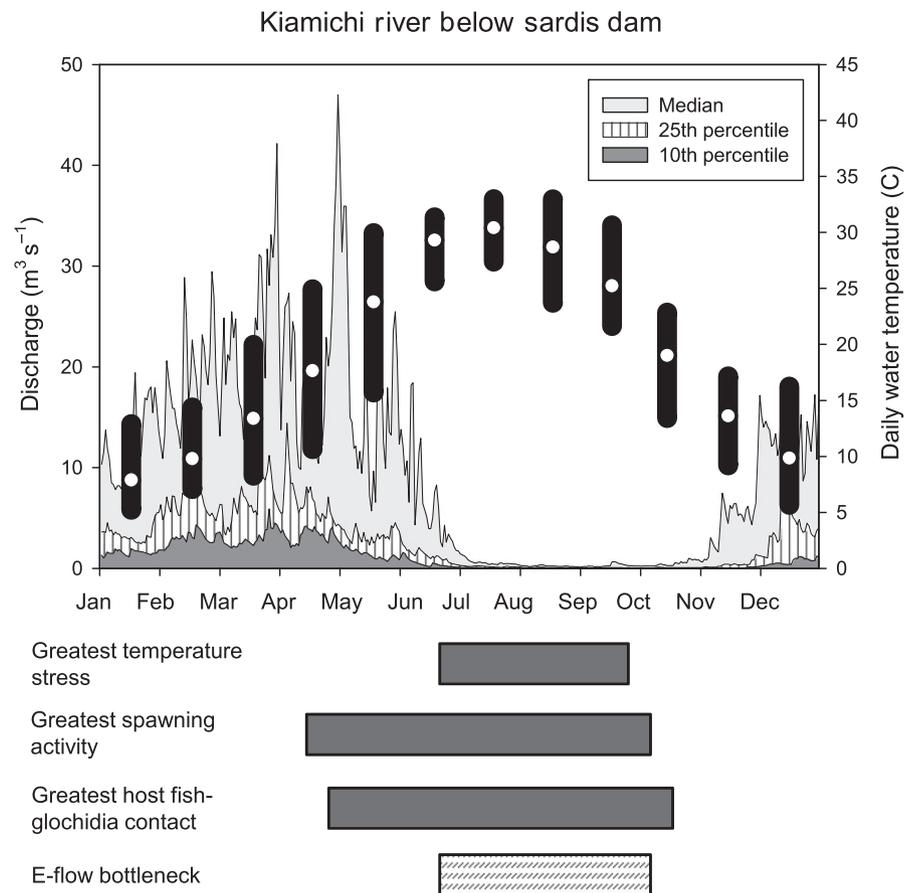
(IFIM) and a Physical Habitat Simulation Model (PHABSIM) have also been used to model habitat permanence at existing mussel beds in the Kiamichi River, providing flow specific depths for mussel bed maintenance (Jones & Fisher, 2005). This model provided valuable information about flow and depth relationships for existing beds, but did not incorporate temperature thresholds, water management practices, the presence of temperature sensitive invasive species (*Corbicula*, discussed above) or the seasonal habitat requirements of host fish.

We think that environmental flow recommendations for mussels in these rivers will better address population viability if they are based on the thermal and life-history traits of species in each river using the temperature and reproductive strategy guilds described above. These data are available for the most common species in the two rivers (Table 2). Overlaying these trait data with hydrographs and temperature profiles can help identify flow bottlenecks, or periods during the year where it is critical to maintain flows and appropriate water temperatures (Fig. 1).

The Kiamichi is predominately rain fed with groundwater inputs that create a hydrograph of flashy flow events in early spring, low flows in summer and lower magnitude flashy flows in autumn and winter. Flows in the lower river are influenced by releases from Sardis Dam (completed in 1983), which impounds a major tributary, Jackfork Creek, and accounts for about 24% of the run-off into the river (Vaughn & Julian, 2013). During summer droughts, water releases from this dam are the only source of flow. In recent drought years, water releases from Sardis Dam during hot summer months have been minimal or non-existent, contributing to patchy drying of the lower river and extremely high water temperatures (sometimes exceeding 40 °C). The long-term effects of combined drought and low summer flows have been lower mussel species richness, lower densities and an assemblage dominated by temperature-tolerant species (Galbraith *et al.*, 2010; Allen *et al.*, 2013; Atkinson, Julian & Vaughn, 2014). Persistence of the Kiamichi River mussel assemblage requires summer water temperatures to be kept at levels below which they experience significant physiological stress including the thermally sensitive invasive *Corbicula* that has the potential to compound water quality stress.

For example, for the 10 species for which we have robust data, six can be classified as thermally sensitive (Table 2). For these species, it is essential to have enough flow in the river during hot summer months to keep water temperatures under 35 °C (Vaughn & Julian, 2013). In addition, several species in the assemblage rely

Fig. 1 Illustration of the guild approach for determining environmental flow bottlenecks and subsequent environmental flow needs for an assemblage of mussels in the Kiamichi River. Flow data are from the USGS gage near Clayton, Oklahoma (Gage 07335790) for the period 1982–2012. The temperature plot illustrates the mean (white circle), maximum and minimum daily temperatures (black error bars). Temperature data were combined from two hobo loggers collecting data during 2011 (Clayton and Antlers). In the lower panel, dark horizontal bars represent time periods of greatest temperature stress, maximum potential spawning activity and maximum potential contact between host fish and glochidia. These data are summarised from species trait data in Table 2. The lighter shaded bar represents the E-flow bottleneck, the most critical period to maintain flows in the river based on the information above.



on contact with summer-nesting centrarchids and/or use mantle lures to infest their hosts, both of which also require adequate summer flows (Fig. 1). The overlap between periods of greatest temperature stress, greatest spawning activity and critical periods for mussel-fish host contact, all point to a bottleneck period from late June to September when it is essential to maintain flows and critical water temperatures in the Kiamichi (Fig. 1). Unfortunately, this is a high water demand period when the river has been dewatered in recent years to accommodate upstream water storage.

Mussels in the larger, adjacent Little River face a different set of challenges. This river is influenced by two reservoirs. The middle reaches of the river are influenced by a mainstem reservoir (Pine Creek Lake) that is used for flood control, municipal water supply and recreation. Flows below this reservoir mimic inflows, but never drop below $1.4 \text{ m}^3 \text{ s}^{-1}$, because flows are maintained to meet water quality criteria due to effluent from a paper mill (Galbraith & Vaughn, 2011). Unlike in the Kiamichi River, in recent drought years mussels in the middle reaches of the Little River have not declined, probably because of these sustained flows (Allen *et al.*,

2013). In contrast, lower reaches of the Little River are influenced by a tributary reservoir (Broken Bow Lake on the Mountain Fork River), from which hypolimnetic releases are used for hydropower and to maintain a stocked, non-native brown trout fishery. Mussels in this section of the river are affected by flows that are higher in magnitude and colder than those of the natural flow regime (Fig. 2; Galbraith & Vaughn, 2011). Mussel populations in this section of the river have declined dramatically from historical levels (Vaughn & Taylor, 1999) and have lower densities, lower body condition and higher parasite loads than upstream populations (Galbraith & Vaughn, 2011). The likely mechanism underlying the decline in mussel density is reduced reproduction because of high discharge and abnormally cold water during summer spawning periods. Supporting this assertion, Galbraith & Vaughn (2009, 2011) found evidence for reduced gametogenesis in species of *Quadrula* in the lower river. Applying the guild approach to the lower Little River illustrates that while the mussel species are the same as that in the Kiamichi, the hydrograph and temperature profile of the river alter the bottleneck experienced by mussels (Table 2; Fig. 2). The

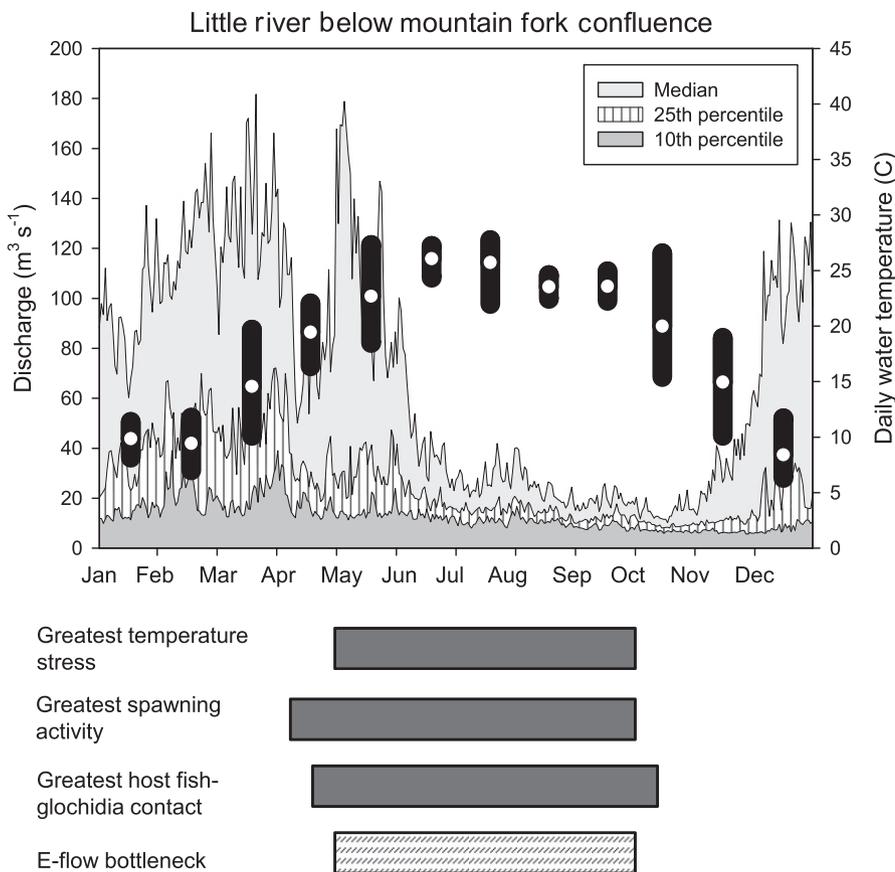


Fig. 2 Illustration of the guild approach for determining environmental flow bottlenecks and subsequent environmental flow needs for an assemblage of mussels in the lower Little River. Flow data are from the USGS gage near Horatio, Arkansas (Gage 073340000) for the period 1982–2012. The temperature plot illustrates the mean (white circle), maximum and minimum daily temperatures (black error bars). Temperature data were obtained from a hobo logger just below the confluence of the Mountain Fork River with the Little River and collected intermittently between 2003 and 2005. In the lower panel, dark horizontal bars represent time periods of greatest temperature stress, maximum potential spawning activity and maximum potential contact between host fish and glochidia. These data are summarised from species trait data in Table 2. The lighter shaded bar represents the E-flow bottleneck, the most critical period to maintain flows in the river based on the information above.

greatest temperature stress is now from colder than historic water temperatures from May to October. The bottleneck period is shifted slightly earlier in the year and lasts longer. Persistence of the lower Little River mussel assemblage will require decreasing hypolimnetic releases from May to September to encompass temperature-dependent spawning needs of both short-term and long-term brooders (Galbraith & Vaughn, 2009).

Adapting the guild approach for use in other rivers

The guild approach can be adapted for use in other rivers as long as there is an understanding of mussel species traits and how they are influenced by a set of particular stressors. As described above, mussels can be separated into reproductive guilds to assess temporal flow needs that encourage successful reproduction and recruitment. New methodologies for estimating the thermal optima of unstudied species can be used to assess physiological tolerances of lesser known species (Castelli *et al.*, 2012) or traits can be inferred from phylogeny as discussed above. Ideally, this approach can be combined with environmental flow models and used to develop flow recommendations. We suggest that environmental

flow models used in combination with the guild approach should include habitat permanence for existing mussel beds (Layzer & Madison, 1995; Maloney *et al.*, 2012), optimal shear stress (Maloney *et al.*, 2012) and water quality (temperature, dissolved oxygen and ammonia; Orth, 1987; Jowett, 1997; Spooner & Vaughn, 2008; Olden & Naiman, 2010; Spooner & Vaughn, 2012; Spooner, Vaughn & Galbraith, 2012). They also need to promote overlap with host fish during appropriate seasons and ensure connectivity between mussel beds (Vaughn, 2012). Hydraulic optima and existing mussel bed locations can be derived from previous mussel bed surveys in the region. Biological rating methods should also be used for host fish species to encourage their presence near mussel beds during the appropriate time of the year (Layzer & Madison, 1995).

We further recommend the monitoring of existing mussel beds while environmental flow criteria are being developed. Monitoring existing beds will reduce uncertainties about how mussels respond to changing flow conditions and will also allow for an adaptive management approach for managing the federally listed species (Runge, 2011). The effectiveness of environmental flows can be gauged by comparing new mussel recruitment

with historic mussel recruitment and flow data (Gore *et al.*, 2001). There is much effort required for this type of modelling. However, we feel this approach will provide flow recommendations that holistically support the complex life history of mussels while addressing regionally specific threats.

In grouping mussel species by traits, the guild approach to environmental flows can accommodate the poorly understood habitat requirements of many freshwater mussels. This approach can be easily adapted among drainage systems where mussel trait data are known and can be strengthened over time with the addition of new trait data that is measured or estimated with a rating model. Together with regional hydrological data, guild traits can provide straightforward visual representation of how current water management practices are affecting mussel guilds and how future flows can be managed to support mussel diversity. This approach can provide valuable information to design dam re-operations that meet ecological, social and economic water needs (Konrad, Warner & Higgins, 2012; Acreman *et al.*, 2014a,b).

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