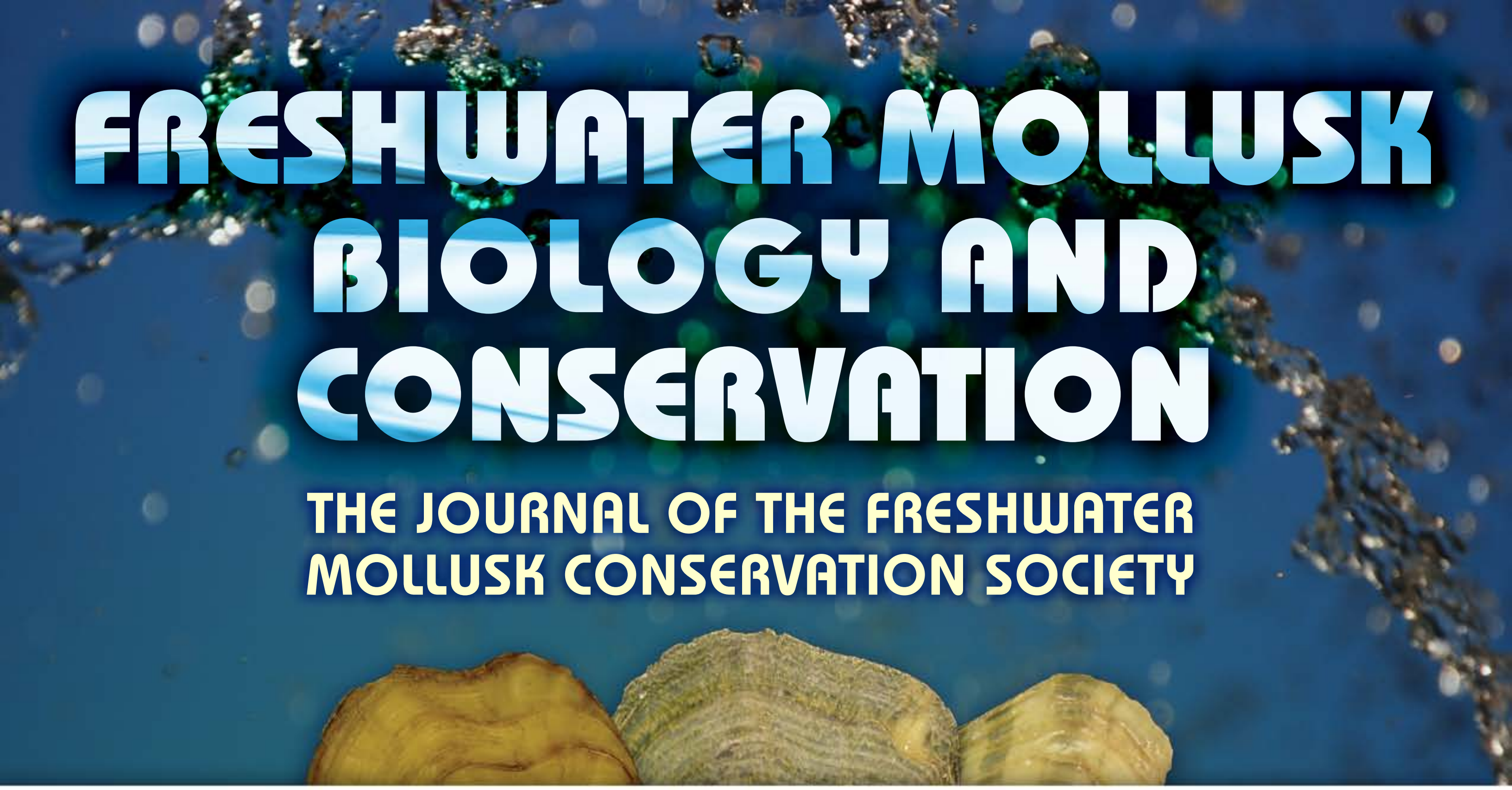

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REGULAR ARTICLE

A REVISED LIST OF THE FRESHWATER MUSSELS (MOLLUSCA: BIVALVIA: UNIONIDA) OF THE UNITED STATES AND CANADA

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ABSTRACT

We present a revised list of freshwater mussels (order Unionida, families Margaritiferidae and Unionidae) of the United States and Canada, incorporating changes in nomenclature and systematic taxonomy since publication of the most recent checklist in 1998. We recognize a total of 298 species in 55 genera in the families Margaritiferidae (one genus, five species) and Unionidae (54 genera, 293 species). We propose one change in the Margaritiferidae: the placement of the formerly monotypic genus *Cumberlandia* in the synonymy of *Margaritifera*. In the Unionidae, we recognize three new genera, elevate four genera from synonymy, and place three previously recognized genera in synonymy. We recognize for the first time two species (one native and one nonindigenous) in the Asian genus *Sinanodonta* as occurring in North America. We recognize four new species and one subspecies and elevate 21 species from synonymy. We elevate 10 subspecies to species status and no longer recognize four subspecies. We change common names for five taxa, correct spelling for eight species, and correct the date of publication of original descriptions for four species.

KEY WORDS: Unionidae, Margaritiferidae, taxonomy, systematics, nomenclature, mussel scientific names, mussel common names

INTRODUCTION

During the past 50 yr, there has been considerable interest in freshwater mussels (order Unionida) in the United States and Canada. Much of this interest was brought about by passage of the U.S. Endangered Species Acts of 1966, 1969, and 1973 and the Canadian Species at Risk Act of 2002. These legislative actions and the environmental movement that accompanied them focused conservation attention on all animals and plants, as well as their habitats. This in turn led

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to assessment of species conservation status and the development of faunal lists for many states and provinces. The task of developing species lists was difficult for most invertebrates, including mussels, because so little attention had been given to the study of their biology, ecology, and systematics. In 1970, only six U.S. states had recent lists or books covering their mussel fauna. The first modern attempt to provide a comprehensive list of freshwater mussels of North America was published by Burch (1973, 1975).

The first comprehensive list of freshwater mussels of the United States and Canada was compiled in Turgeon et al. (1988) and revised a decade later (Turgeon et al. 1998). Williams et al. (1993) was another important resource during this period; although mainly an assessment of species conservation status, this paper also provided a comprehensive and widely used species list similar to those of Turgeon et al. (1988, 1998). These lists standardized and provided taxonomic stability to mussel common and scientific names to an extent that was previously unavailable. However, systematic taxonomy of mussels was poorly known at that time, and classifications at all taxonomic levels were based largely on concepts from the early 1900s.

Since publication of Turgeon et al. (1988, 1998) and Williams et al. (1993), many studies have refined our understanding of mussel systematic taxonomy. Several major publications have addressed systematic relationships within the class Bivalvia, including the order Unionida (Bieler et al. 2010; Carter et al. 2011; Bolotov et al. 2016; Araujo et al. 2017; Combosch et al. 2017). Major studies specific to the Unionida include Graf and Ó Foighil (2000), Hoeh et al. (2001, 2002, 2009), Roe and Hoeh (2003), Campbell et al. (2005), Walker et al. (2006), Graf and Cummings (2007, 2017), Cummings and Graf (2010), and Campbell and Lydeard (2012a, 2012b). In addition, many studies have examined systematic relationships at lower taxonomic levels (e.g., Serb et al. 2003; Jones et al. 2006; Lane et al. 2016). Together, this body of work depicts a view of mussel taxonomy that differs substantially from that of previous lists of the North American fauna.

We present a revised classification and list of the freshwater mussels of the United States and Canada (Tables 1 and 2). The primary purpose of this revision is to provide in a single resource a comprehensive list and taxonomic classification that reflects recent refinement of mussel systematics.

METHODS

We used as a starting point the list of Turgeon et al. (1998). We revised this list and its taxonomic classification based on a review of peer-reviewed mussel taxonomic and nomenclatural literature produced since 1998, unpublished research by the authors, and discussions with other experts on mussel systematics. We also corrected the spelling of specific epithets and publication dates of original descriptions based on the International Code of Zoological Nomenclature (http://www.iczn.org/iczn/index.jsp). Species mentioned in the text, but not included in Table 2, have author and date of publication following the name. Author and date of publication for all other species are given in Table 2.

Mussel common names follow Turgeon et al. (1998) with minor exceptions, but they are capitalized as is now the practice for many other animal groups (e.g., birds, reptiles, amphibians, fishes). Capitalization of common names helps avoid confusion by identifying standardized common names. For example, reference to a "fragile papershell" could apply to several thin-shelled species, but the capitalized "Fragile Papershell" is unambiguously recognized as the common name for *Leptodea fragilis*. We note and explain other instances where we changed common names from those of Turgeon et al. (1998) or where recognition of previously unrecognized species necessitated creation of a new common name.

We provide a rationale for and discussion of all taxonomic changes in the following accounts for each family and genus and in Table 2. There is a degree of uncertainty and subjectivity in our revised list that is unavoidable given our still imperfect understanding of mussel systematics. We attempted to reconcile divergent views regarding mussel systematics based on our assessment of the strength of evidence for these views. In cases where evidence did not allow reconciliation, we attempted to provide a plausible conclusion based on our professional judgment and experience; these conclusions were based on consensus among the authors to the extent possible.

Subspecies is a taxonomic category applied to populations that are morphologically distinct and geographically separated but that exhibit intergradation in contact zones (Mayr et al. 1953; Gilbert 1961). We evaluated morphological and molecular evidence relating to the status of subspecies recognized by Turgeon et al. (1998) and subsequent workers (Jones and Neves 2010). In most cases, recent evidence did not support recognition of subspecies but supported either subsuming subspecies under the nominal species or elevating subspecies to species status; we discuss this evidence for each case. However, strong evidence with which to evaluate their status was lacking for several, mostly extinct, subspecies (see *Epioblasma*). The designation of subspecies versus species is arbitrary and inconsistent for many animal groups (Huang and Knowles 2016), and this has historically been the case for mussels (e.g., Ortmann 1918, 1920). For subspecies that lacked strong evidence for synonymization or elevation, we recognize all as species to provide more consistent null hypotheses regarding potential diversity in these groups.

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RESULTS

Freshwater bivalve higher classification continues to evolve as more data are generated and new techniques are developed. Fossil and modern bivalve higher classification has

Table 1. Higher classification of the Unionoidea present in the United States and Canada.

CLASS Bivalvia Linnaeus, 1758
  INFRACLASS Heteroconchia Hertwig, 1895
    COHORT Uniomorphi Gray, 1854 [=Paleoheterodonta]
      ORDER Unionida Gray, 1854
        SUPERFAMILY Unionoidea Rafinesque, 1820
MARGARITIFERIDAE Henderson, 1929
      Margaritifera Schumacher, 1816
UNIONIDAE Rafinesque, 1820
  ANODONTINAE Rafinesque, 1820
    Anodontini Rafinesque, 1820
      Alasmidonta Say, 1818
      Anodonta Lamarck, 1799
      Anodontoides Simpson in Baker, 1898
      Arcidens Simpson, 1900
      Lasmigona Rafinesque, 1831
      Pegias Simpson, 1900
      Pyganodon Crosse and Fischer, 1894
      Simpsonaias Frierson, 1914
      Strophitus Rafinesque, 1820
      Utterbackia Baker, 1927
      Utterbackiana Frierson, 1927
    Cristariini Lopes-Lima, Bogan, and Froufe, 2017
      Sinanodonta Modell, 1945
  GONIDEINAE Ortmann, 1916
    Gonideini Ortmann, 1916
      Gonidea Conrad, 1857
  AMBLEMINAE Rafinesque, 1820
    Amblemini Rafinesque, 1820
      Amblema Rafinesque, 1820
    Lampsilini Ihering, 1901
      Actinonaias Crosse and Fischer, 1894
      Cyprogenia Agassiz, 1852
      Cyrtonaias Crosse and Fischer, 1894
      Dromus Simpson, 1900
      Ellipsaria Rafinesque, 1820
      Epioblasma Rafinesque, 1831
      Glebula Conrad, 1853
      Hamiota Roe and Hartfield, 2005
      Lampsilis Rafinesque, 1820
      Lemiox Rafinesque, 1831
      Leptodea Rafinesque, 1820
      Ligumia Swainson, 1840
      Medionidus Simpson, 1900
      Obliquaria Rafinesque, 1820
      Obovaria Rafinesque, 1819
      Plectomerus Conrad, 1853
      Potamilus Rafinesque, 1818
      Ptychobranchus Simpson, 1900
      Toxolasma Rafinesque, 1831
      Truncilla Rafinesque, 1819
      Venustaconcha Frierson, 1927
      Villosa Frierson, 1927

Table 1, continued.

    Pleurobemini Hannibal, 1912
      Elliptio Rafinesque, 1819
      Elliptoideus Frierson, 1927
      Eurynia Rafinesque, 1820
      Fusconaia Simpson, 1900
      Hemistena Rafinesque, 1820
      Parvaspina Perkins, Gangloff, and Johnson, 2017
      Plethobasus Simpson, 1900
      Pleurobema Rafinesque, 1819
      Pleuronaia Frierson, 1927
    Quadrulini Ihering, 1901
      Cyclonaias Pilsbry in Ortmann and Walker, 1922
      Megalonaias Utterback, 1915
      Quadrula Rafinesque, 1820
      Theliderma Swainson, 1840
      Tritogonia Agassiz, 1852
      Uniomerus Conrad, 1853
  AMBLEMINAE (*incertae sedis*)
      Disconaias Crosse and Fischer, 1894
      Popenaias Frierson, 1927
      Reginaia Campbell and Lydeard, 2012

recently been summarized by Carter et al. (2011), with standardized endings for higher taxa within Bivalvia. Recent evidence supports the order Unionida as a monophyletic clade (Combosch et al. 2017). There have been two recent assessments of the taxonomy for Margaritiferidae (Bolotov et al. 2016; Araujo et al. 2017). Higher level relationships within the Unionidae have recently been reviewed by Lopes-Lima et al. (2017). Based on these publications, we provide our assessment of higher classification of the Unionida and its position in the class Bivalvia (Table 1).

There is general agreement on the three subfamily divisions within the Unionidae in North America and seven subfamilies worldwide, but there remains some uncertainty regarding classification at lower levels. We adopted a subfamily-, tribe-, and generic-level classification for the United States and Canada based on recent phylogenetic research (Table 1). We recognize the Anodontinae as a subfamily with two tribes in the United States and Canada. We recognize the subfamily Gonideinae, containing the genus *Gonidea*. We recognize the subfamily Ambleminae as consisting of four tribes: Amblemini, Lampsilini, Pleurobemini, and Quadrulini. The placement of many genera within tribes in the Ambleminae is well supported and consistent among studies, but the placement of others is less certain and varies among studies (e.g., *Plectomerus*, Campbell et al. 2005). The Mexican and Central American genera *Disconaias* and *Popenaias* and North American *Reginaia* lack sufficient phylogenetic information to be confidently assigned to a classification, and we placed them in Ambleminae incertae sedis (Table 1).

Our revised list includes many taxonomic changes at the

Table 2. List of Margaritiferidae and Unionidae of the United States and Canada. Currently recognized taxa are bolded. Taxa preceded by an asterisk and not bolded appeared in Turgeon et al. (1998) but are no longer recognized or reassigned to other genera.

Scientific Name	Common Name	Changes in Scientific and Common Names
MARGARITIFERIDAE Henderson, 1929		
Cumberlandia Ortmann, 1912		Synonym of *Margaritifera*
**Cumberlandia monodonta* (Say, 1829)	Spectaclecase	Reassigned to *Margaritifera*
***Margaritifera* Schumacher, 1816**		
***Margaritifera falcata* (Gould, 1850)**	Western Pearlshell	
***Margaritifera hembeli* (Conrad, 1838)**	Louisiana Pearlshell	
***Margaritifera margaritifera* (Linnaeus, 1758)**	Eastern Pearlshell	
***Margaritifera marrianae* Johnson, 1983**	Alabama Pearlshell	
***Margaritifera monodonta* (Say, 1829)**	Spectaclecase	Reassigned from *Cumberlandia*
UNIONIDAE Rafinesque, 1820		
***Actinonaias* Crosse and Fischer, 1894**		
***Actinonaias ligamentina* (Lamarck, 1819)**	Mucket	
***Actinonaias pectorosa* (Conrad, 1834)**	Pheasantshell	
***Alasmidonta* Say, 1818**		
***Alasmidonta arcula* (Lea, 1838)**	Altamaha Arcmussel	
***Alasmidonta atropurpurea* (Rafinesque, 1831)**	Cumberland Elktoe	
***Alasmidonta heterodon* (Lea, 1829)**	Dwarf Wedgemussel	Publication date corrected
***Alasmidonta marginata* Say, 1818**	Elktoe	
***Alasmidonta mccordi* Athearn, 1964**	Coosa Elktoe	
***Alasmidonta raveneliana* (Lea, 1834)**	Appalachian Elktoe	
***Alasmidonta robusta* Clarke, 1981**	Carolina Elktoe	
***Alasmidonta triangulata* (Lea, 1858)**	Southern Elktoe	
***Alasmidonta undulata* (Say, 1817)**	Triangle Floater	
***Alasmidonta varicosa* (Lamarck, 1819)**	Brook Floater	
***Alasmidonta viridis* (Rafinesque, 1820)**	Slippershell Mussel	
***Alasmidonta wrightiana* (Walker, 1901)**	Ochlockonee Arcmussel	
***Amblema* Rafinesque, 1820**		
***Amblema elliottii* (Lea, 1856)**	Coosa Fiveridge	
***Amblema neislerii* (Lea, 1858)**	Fat Threeridge	
***Amblema plicata* (Say, 1817)**	Threeridge	
***Anodonta* Lamarck, 1799**		
**Anodonta beringiana* Middendorff, 1851	Yukon Floater	Reassigned to *Sinanodonta*
***Anodonta californiensis* Lea, 1852**	California Floater	
**Anodonta couperiana* Lea, 1840	Barrel Floater	Reassigned to *Utterbackiana*
**Anodonta dejecta* Lewis, 1875	Woebegone Floater	Synonym of *Anodonta californiensis*
**Anodonta heardi* Gordon and Hoeh, 1995	Apalachicola Floater	Reassigned to *Utterbackiana*
**Anodonta implicata* Say, 1829	Alewife Floater	Reassigned to *Utterbackiana*
***Anodonta kennerlyi* Lea, 1860**	Western Floater	
***Anodonta nuttalliana* Lea, 1838**	Winged Floater	
***Anodonta oregonensis* Lea, 1838**	Oregon Floater	
**Anodonta suborbiculata* Say, 1831	Flat Floater	Reassigned to *Utterbackiana*
***Anodontoides* Simpson in Baker, 1898**		
***Anodontoides denigrata* (Lea, 1852)**	Cumberland Papershell	Elevated from synonymy
***Anodontoides ferussacianus* (Lea, 1834)**	Cylindrical Papershell	
***Anodontoides radiatus* (Conrad, 1834)**	Rayed Creekshell	
***Arcidens* Simpson, 1900**		
***Arcidens confragosus* (Say, 1829)**	Rock Pocketbook	
***Arcidens wheeleri* (Ortmann and Walker, 1912)**	Ouachita Rock Pocketbook	Reassigned from *Arkansia*
**Arkansia* Ortmann and Walker, 1912		Synonym of *Arcidens*
**Arkansia wheeleri* Ortmann and Walker, 1912	Ouachita Rock Pocketbook	Reassigned to *Arcidens*

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Cyclonaias* Pilsbry in Ortmann and Walker, 1922**		
***Cyclonaias archeri* (Frierson, 1905)**	Tallapoosa Orb	Elevated from synonymy
***Cyclonaias asperata* (Lea, 1861)**	Alabama Orb	Reassigned from *Quadrula*
***Cyclonaias aurea* (Lea, 1859)**	Golden Orb	Reassigned from *Quadrula*
***Cyclonaias houstonensis* (Lea, 1859)**	Smooth Pimpleback	Reassigned from *Quadrula*
***Cyclonaias infucata* (Conrad, 1834)**	Sculptured Pigtoe	Reassigned from *Quincuncina*
***Cyclonaias kieneriana* (Lea, 1852)**	Coosa Orb	Elevated from synonymy
***Cyclonaias kleiniana* (Lea, 1852)**	Florida Mapleleaf	Elevated from synonymy
***Cyclonaias mortoni* (Conrad, 1835)**	Western Pimpleback	Species elevated from subspecies; reassigned from *Quadrula*
***Cyclonaias nodulata* (Rafinesque, 1820)**	Wartyback	Reassigned from *Quadrula*
***Cyclonaias petrina* (Gould, 1855)**	Texas Pimpleback	Reassigned from *Quadrula*
***Cyclonaias pustulosa* (Lea, 1831)**	Pimpleback	Reassigned from *Quadrula*
***Cyclonaias refulgens* (Lea, 1868)**	Purple Pimpleback	Reassigned from *Quadrula*
***Cyclonaias succissa* (Lea, 1852)**	Purple Pigtoe	Reassigned from *Fusconaia*
***Cyclonaias tuberculata* (Rafinesque, 1820)**	Purple Wartyback	
***Cyprogenia* Agassiz, 1852**		
***Cyprogenia aberti* (Conrad, 1850)**	Western Fanshell	
***Cyprogenia stegaria* (Rafinesque, 1820)**	Fanshell	
***Cyrtonaias* Crosse and Fischer, 1894**		
***Cyrtonaias tampicoensis* (Lea, 1838)**	Tampico Pearlymussel	
***Disconaias* Crosse and Fischer, 1894**		
***Disconaias fimbriata* (Frierson, 1907)**	Fringed Mucket	Elevated from synonymy
**Disconaias salinasensis* (Simpson, 1908)	Salina Mucket	Synonym of *Disconaias fimbriata*
***Dromus* Simpson, 1900**		
***Dromus dromas* (Lea, 1834)**	Dromedary Pearlymussel	
***Ellipsaria* Rafinesque, 1820**		
***Ellipsaria lineolata* (Rafinesque, 1820)**	Butterfly	
***Elliptio* Rafinesque, 1819**		
***Elliptio ahenea* (Lea, 1843)**	Southern Lance	
***Elliptio angustata* (Lea, 1831)**	Carolina Lance	
***Elliptio arca* (Conrad, 1834)**	Alabama Spike	
***Elliptio arctata* (Conrad, 1834)**	Delicate Spike	
**Elliptio buckleyi* (Lea, 1843)	Florida Shiny Spike	Synonym of *Elliptio jayensis*
***Elliptio chipolaensis* (Walker, 1905)**	Chipola Slabshell	
***Elliptio cistellaeformis* (Lea, 1863)**	Box Spike	
***Elliptio complanata* (Lightfoot, 1786)**	Eastern Elliptio	
***Elliptio congaraea* (Lea, 1831)**	Carolina Slabshell	
***Elliptio crassidens* (Lamarck, 1819)**	Elephantear	
***Elliptio dariensis* (Lea, 1842)**	Georgia Elephantear	
**Elliptio dilatata* (Rafinesque, 1820)	Spike	Reassigned to *Eurynia*
***Elliptio downiei* (Lea, 1858)**	Satilla Elephantear	
**Elliptio errans* (Lea, 1856)	Oval Elliptio	Synonym of *Elliptio icterina*; publication date corrected
***Elliptio fisheriana* (Lea, 1838)**	Northern Lance	
***Elliptio folliculata* (Lea, 1838)**	Pod Lance	
***Elliptio fraterna* (Lea, 1852)**	Brother Spike	
***Elliptio fumata* (Lea, 1857)**	Gulf Slabshell	Elevated from synonymy
**Elliptio hepatica* (Lea, 1859)	Brown Elliptio	Synonym of *Elliptio icterina*
***Elliptio hopetonensis* (Lea, 1838)**	Altamaha Slabshell	
***Elliptio icterina* (Conrad, 1834)**	Variable Spike	

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Elliptio jayensis* (Lea, 1838)**	Florida Spike	Common name changed from Flat Spike
**Elliptio judithae* Clarke, 1986	Plicate Spike	Synonym of *Elliptio roanokensis*
***Elliptio lanceolata* (Lea, 1828)**	Yellow Lance	
**Elliptio lugubris* (Lea, 1834)	Sad Elliptio	Synonym of *Elliptio icterina*
***Elliptio marsupiobesa* Fuller, 1972**	Cape Fear Spike	
***Elliptio mcmichaeli* Clench and Turner, 1956**	Fluted Elephantear	
***Elliptio monroensis* (Lea, 1843)**	St. Johns Elephantear	
***Elliptio nigella* (Lea, 1852)**	Winged Spike	
***Elliptio occulta* (Lea, 1843)**	Hidden Spike	Elevated from synonymy
***Elliptio producta* (Conrad, 1836)**	Atlantic Spike	
***Elliptio pullata* (Lea, 1856)**	Gulf Spike	Elevated from synonymy
***Elliptio purpurella* (Lea, 1857)**	Inflated Spike	Elevated from synonymy
**Elliptio raveneli* (Conrad, 1834)	Carolina Spike	Synonym of *Elliptio icterina*
***Elliptio roanokensis* (Lea, 1838)**	Roanoke Slabshell	
***Elliptio shepardiana* (Lea, 1834)**	Altamaha Lance	
***Elliptio spinosa* (Lea, 1836)**	Altamaha Spinymussel	
**Elliptio steinstansana* Johnson and Clarke, 1983	Tar River Spinymussel	Reassigned to *Parvaspina*
**Elliptio waccamawensis* (Lea, 1863)	Waccamaw Spike	Synonym of *Elliptio congaraea*
**Elliptio waltoni* (Wright, 1888)	Florida Lance	Synonym of *Elliptio ahenea*
***Elliptoideus* Frierson, 1927**		
***Elliptoideus sloatianus* (Lea, 1840)**	Purple Bankclimber	
***Epioblasma* Rafinesque, 1831**		
***Epioblasma ahlstedti* Jones and Neves, 2010**	Duck River Dartersnapper	Described as new species
***Epioblasma arcaeformis* (Lea, 1831)**	Sugarspoon	
***Epioblasma aureola* Jones and Neves, 2010**	Golden Riffleshell	Species elevated from subspecies
***Epioblasma biemarginata* (Lea, 1857)**	Angled Riffleshell	
***Epioblasma brevidens* (Lea, 1831)**	Cumberlandian Combshell	
***Epioblasma capsaeformis* (Lea, 1834)**	Oyster Mussel	
***Epioblasma cincinnatiensis* (Lea, 1840)**	Ohio Riffleshell	Elevated from synonymy
***Epioblasma curtisii* (Frierson and Utterback, 1916)**	Curtis Pearlymussel	Species elevated from subspecies
***Epioblasma flexuosa* (Rafinesque, 1820)**	Leafshell	
***Epioblasma florentina* (Lea, 1857)**	Yellow Blossom	
**Epioblasma florentina aureola* Jones and Neves, 2010	Golden Riffleshell	Described as new subspecies; elevated to species
**Epioblasma florentina curtisii* (Frierson and Utterback, 1916)	Curtis Pearlymussel	Subspecies elevated to species
**Epioblasma florentina florentina* (Lea, 1857)	Yellow Blossom	Nominotypical subspecies not required
**Epioblasma florentina walkeri* (Wilson and Clark, 1914)	Tan Riffleshell	Subspecies elevated to species
***Epioblasma gubernaculum* (Reeve, 1865)**	Green Blossom	Species elevated from subspecies
***Epioblasma haysiana* (Lea, 1834)**	Acornshell	
***Epioblasma lenior* (Lea, 1842)**	Narrow Catspaw	
***Epioblasma lewisii* (Walker, 1910)**	Forkshell	
***Epioblasma metastriata* (Conrad, 1838)**	Upland Combshell	
***Epioblasma obliquata* (Rafinesque, 1820)**	Catspaw	
**Epioblasma obliquata obliquata* (Rafinesque, 1820)	Catspaw	Nominotypical subspecies not required
**Epioblasma obliquata perobliqua* (Conrad, 1836)	White Catspaw	Subspecies elevated to species
***Epioblasma othcaloogensis* (Lea, 1857)**	Southern Acornshell	
***Epioblasma penita* (Conrad, 1834)**	Southern Combshell	
***Epioblasma perobliqua* (Conrad, 1836)**	White Catspaw	Species elevated from subspecies
***Epioblasma personata* (Say, 1829)**	Round Combshell	
***Epioblasma propinqua* (Lea, 1857)**	Tennessee Riffleshell	
***Epioblasma rangiana* (Lea, 1838)**	Northern Riffleshell	Species elevated from subspecies

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Epioblasma sampsonii* (Lea, 1861)**	Wabash Riffleshell	
***Epioblasma stewardsonii* (Lea, 1852)**	Cumberland Leafshell	
***Epioblasma torulosa* (Rafinesque, 1820)**	Tubercled Blossom	
**Epioblasma torulosa gubernaculum* (Reeve, 1865)	Green Blossom	Subspecies elevated to species
**Epioblasma torulosa rangiana* (Lea, 1838)	Northern Riffleshell	Subspecies elevated to species
**Epioblasma torulosa torulosa* (Rafinesque, 1820)	Tubercled Blossom	Nominotypical subspecies not required
***Epioblasma triquetra* (Rafinesque, 1820)**	Snuffbox	
***Epioblasma turgidula* (Lea, 1858)**	Turgid Blossom	
***Epioblasma walkeri* (Wilson and Clark, 1914)**	Tan Riffleshell	Species elevated from subspecies
***Eurynia* Rafinesque, 1820**		Elevated from synonymy
***Eurynia dilatata* Rafinesque, 1820**	Spike	Reassigned from *Elliptio*
***Fusconaia* Simpson, 1900**		
**Fusconaia askewi* (Marsh, 1896)	Texas Pigtoe	Synonym of *Fusconaia chunii*
**Fusconaia barnesiana* (Lea, 1838)	Tennessee Pigtoe	Reassigned to *Pleuronaia*
***Fusconaia burkei* (Walker, 1922)**	Tapered Pigtoe	Reassigned from *Quincuncina*
***Fusconaia cerina* (Conrad, 1838)**	Gulf Pigtoe	Common name changed from Southern Pigtoe
***Fusconaia chunii* (Lea, 1861)**	Texas Pigtoe	Elevated from synonymy
***Fusconaia cor* (Conrad, 1834)**	Shiny Pigtoe	
***Fusconaia cuneolus* (Lea, 1840)**	Finerayed Pigtoe	
**Fusconaia ebena* (Lea, 1831)	Ebonyshell	Reassigned to *Reginaia*
***Fusconaia escambia* Clench and Turner, 1956**	Narrow Pigtoe	
***Fusconaia flava* (Rafinesque, 1820)**	Wabash Pigtoe	
**Fusconaia lananensis* (Frierson, 1901)	Triangle Pigtoe	Synonym of *Fusconaia chunii*
***Fusconaia masoni* (Conrad, 1834)**	Atlantic Pigtoe	
***Fusconaia mitchelli* (Simpson, 1895)**	False Spike	Reassigned from *Quincuncina*
***Fusconaia ozarkensis* (Call, 1887)**	Ozark Pigtoe	
***Fusconaia subrotunda* (Lea, 1831)**	Longsolid	
**Fusconaia succissa* (Lea, 1852)	Purple Pigtoe	Reassigned to *Cyclonaias*
***Glebula* Conrad, 1853**		
***Glebula rotundata* (Lamarck, 1819)**	Round Pearlshell	
***Gonidea* Conrad, 1857**		
***Gonidea angulata* (Lea, 1838)**	Western Ridged Mussel	
***Hamiota* Roe and Hartfield, 2005**		Described as new genus
***Hamiota altilis* (Conrad, 1834)**	Finelined Pocketbook	Reassigned from *Lampsilis*
***Hamiota australis* (Simpson, 1900)**	Southern Sandshell	Reassigned from *Lampsilis*
***Hamiota perovalis* (Conrad, 1834)**	Orangenacre Mucket	Reassigned from *Lampsilis*
***Hamiota subangulata* (Lea, 1840)**	Shinyrayed Pocketbook	Reassigned from *Lampsilis*
***Hemistena* Rafinesque, 1820**		
***Hemistena lata* (Rafinesque, 1820)**	Cracking Pearlymussel	
***Lampsilis* Rafinesque, 1820**		
***Lampsilis abrupta* (Say, 1831)**	Pink Mucket	
**Lampsilis altilis* (Conrad, 1834)	Finelined Pocketbook	Reassigned to *Hamiota*
**Lampsilis australis* Simpson, 1900	Southern Sandshell	Reassigned to *Hamiota*
***Lampsilis binominata* Simpson, 1900**	Lined Pocketbook	
***Lampsilis bracteata* (Gould, 1855)**	Texas Fatmucket	
***Lampsilis brittsi* Simpson, 1900**	Northern Brokenray	Species elevated from subspecies
***Lampsilis cardium* Rafinesque, 1820**	Plain Pocketbook	
***Lampsilis cariosa* (Say,1817)**	Yellow Lampmussel	
***Lampsilis dolabraeformis* (Lea, 1838)**	Altamaha Pocketbook	
***Lampsilis fasciola* Rafinesque, 1820**	Wavyrayed Lampmussel	

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Lampsilis floridensis* (Lea, 1852)**	Florida Sandshell	Elevated from synonymy
**Lampsilis fullerkati* Johnson, 1984	Waccamaw Fatmucket	Synonym of *Lampsilis radiata*
**Lampsilis haddletoni* Athearn, 1964	Haddleton Lampmussel	Reassigned to *Obovaria*
***Lampsilis higginsii* (Lea, 1857)**	Higgins Eye	
***Lampsilis hydiana* (Lea, 1838)**	Louisiana Fatmucket	
***Lampsilis ornata* (Conrad, 1835)**	Southern Pocketbook	
***Lampsilis ovata* (Say, 1817)**	Pocketbook	
**Lampsilis perovalis* (Conrad, 1834)	Orangenacre Mucket	Reassigned to *Hamiota*
***Lampsilis powellii* (Lea, 1852)**	Arkansas Fatmucket	
***Lampsilis radiata* (Gmelin, 1791)**	Eastern Lampmussel	
**Lampsilis radiata conspicua* (Lea, 1872)	Carolina Fatmucket	Subspecies no longer recognized
**Lampsilis radiata radiata* (Gmelin, 1791)	Eastern Lampmussel	Nominotypical subspecies not required
***Lampsilis rafinesqueana* Frierson, 1927**	Neosho Mucket	
***Lampsilis reeveiana* (Lea, 1852)**	Arkansas Brokenray	
**Lampsilis reeveiana brevicula* (Call, 1887)	Ozark Brokenray	Subspecies no longer recognized
**Lampsilis reeveiana brittsi* Simpson, 1900	Northern Brokenray	Subspecies elevated to species
**Lampsilis reeveiana reeviana* (Lea, 1852)	Arkansas Brokenray	Nominotypical subspecies not required
***Lampsilis satura* (Lea, 1852)**	Sandbank Pocketbook	
***Lampsilis siliquoidea* (Barnes, 1823)**	Fatmucket	
***Lampsilis splendida* (Lea, 1838)**	Rayed Pink Fatmucket	
***Lampsilis straminea* (Conrad, 1834)**	Rough Fatmucket	
**Lampsilis straminea claibornensis* (Lea, 1838)	Southern Fatmucket	Subspecies no longer recognized
**Lampsilis straminea straminea* (Conrad, 1834)	Rough Fatmucket	Nominotypical subspecies not required
***Lampsilis streckeri* Frierson, 1927**	Speckled Pocketbook	
**Lampsilis subangulata* (Lea, 1840)	Shinyrayed Pocketbook	Reassigned to *Hamiota*
***Lampsilis teres* (Rafinesque, 1820)**	Yellow Sandshell	
***Lampsilis virescens* (Lea, 1858)**	Alabama Lampmussel	
***Lasmigona* Rafinesque, 1831**		
***Lasmigona alabamensis* Clarke, 1985**	Alabama Heelsplitter	Species elevated from subspecies
***Lasmigona complanata* (Barnes, 1823)**	White Heelsplitter	
**Lasmigona complanata alabamensis* Clarke, 1985	Alabama Heelsplitter	Subspecies elevated to species
**Lasmigona complanata complanata* (Barnes, 1823)	White Heelsplitter	Nominotypical subspecies not required
***Lasmigona compressa* (Lea, 1829)**	Creek Heelsplitter	
***Lasmigona costata* (Rafinesque, 1820)**	Flutedshell	
***Lasmigona decorata* (Lea, 1852)**	Carolina Heelsplitter	
***Lasmigona etowaensis* (Conrad, 1849)**	Etowah Heelsplitter	Elevated from synonymy
***Lasmigona holstonia* (Lea, 1838)**	Tennessee Heelsplitter	
***Lasmigona subviridis* (Conrad, 1835)**	Green Floater	
***Lemiox* Rafinesque, 1831**		
***Lemiox rimosus* (Rafinesque, 1831)**	Birdwing Pearlymussel	
***Leptodea* Rafinesque, 1820**		
***Leptodea fragilis* (Rafinesque, 1820)**	Fragile Papershell	
***Leptodea leptodon* (Rafinesque, 1820)**	Scaleshell	
***Leptodea ochracea* (Say, 1817)**	Tidewater Mucket	
**Lexingtonia* Ortmann, 1914		Synonym of *Fusconaia*
**Lexingtonia dolabelloides* (Lea, 1840)	Slabside Pearlymussel	Reassigned to *Pleuronaia*
**Lexingtonia subplana* (Conrad, 1837)	Virginia Pigtoe	Synonym of *Fusconaia masoni*
***Ligumia* Swainson, 1840**		
***Ligumia nasuta* (Say, 1817)**	Eastern Pondmussel	
***Ligumia recta* (Lamarck, 1819)**	Black Sandshell	
***Ligumia subrostrata* (Say, 1831)**	Pondmussel	

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Medionidus* Simpson, 1900**		
***Medionidus acutissimus* (Lea, 1831)**	Alabama Moccasinshell	
***Medionidus conradicus* (Lea, 1834)**	Cumberland Moccasinshell	
**Medionidus mcglameriae* van der Schalie, 1939	Tombigbee Moccasinshell	Synonym of *Leptodea fragilis*
***Medionidus parvulus* (Lea, 1860)**	Coosa Moccasinshell	
***Medionidus penicillatus* (Lea, 1857)**	Gulf Moccasinshell	
***Medionidus simpsonianus* Walker, 1905**	Ochlockonee Moccasinshell	
***Medionidus walkeri* (Wright, 1897)**	Suwannee Moccasinshell	
***Megalonaias* Utterback, 1915**		
***Megalonaias nervosa* (Rafinesque, 1820)**	Washboard	
***Obliquaria* Rafinesque, 1820**		
***Obliquaria reflexa* Rafinesque, 1820**	Threehorn Wartyback	
***Obovaria* Rafinesque, 1819**		
***Obovaria arkansasensis* (Lea, 1862)**	Southern Hickorynut	Reassigned from *Villosa*
***Obovaria choctawensis* (Athearn, 1964)**	Choctaw Bean	Reassigned from *Villosa*
***Obovaria haddletoni* (Athearn, 1964)**	Haddleton Lampmussel	Reassigned from *Lampsilis*
**Obovaria jacksoniana* (Frierson, 1912)	Southern Hickorynut	Synonym of *Obovaria arkansasensis*
***Obovaria olivaria* (Rafinesque, 1820)**	Hickorynut	
***Obovaria retusa* (Lamarck, 1819)**	Ring Pink	
**Obovaria rotulata* (Wright, 1899)	Round Ebonyshell	Reassigned to *Reginaia*
***Obovaria subrotunda* (Rafinesque, 1820)**	Round Hickorynut	
***Obovaria unicolor* (Lea, 1845)**	Alabama Hickorynut	
***Parvaspina* Perkins, Gangloff, and Johnson, 2017**		Described as new genus
***Parvaspina collina* (Conrad, 1836)**	James Spinymussel	Reassigned from *Pleurobema*; publication date corrected
***Parvaspina steinstansana* (Johnson and Clarke, 1983)**	Tar River Spinymussel	Reassigned from *Elliptio*
***Pegias* Simpson, 1900**		
***Pegias fabula* (Lea, 1838)**	Littlewing Pearlymussel	
***Plectomerus* Conrad, 1853**		
***Plectomerus dombeyanus* (Valenciennes, 1827)**	Bankclimber	
***Plethobasus* Simpson, 1900**		
***Plethobasus cicatricosus* (Say, 1829)**	White Wartyback	
***Plethobasus cooperianus* (Lea, 1834)**	Orangefoot Pimpleback	
***Plethobasus cyphyus* (Rafinesque, 1820)**	Sheepnose	
***Pleurobema* Rafinesque, 1819**		
**Pleurobema altum* (Conrad, 1854)	Highnut	Considered a *nomen dubium*
***Pleurobema athearni* Gangloff, Williams, and Feminella, 2006**	Canoe Creek Clubshell	Described as new species
**Pleurobema avellanum* Simpson, 1900	Hazel Pigtoe	Synonym of *Pleurobema rubellum*
***Pleurobema beadleianum* (Lea, 1861)**	Mississippi Pigtoe	
**Pleurobema bournianum* (Lea, 1840)	Scioto Pigtoe	Synonym of *Pleurobema clava*
**Pleurobema chattanoogaense* (Lea, 1858)	Painted Clubshell	Synonym of *Pleurobema decisum*
***Pleurobema clava* (Lamarck, 1819)**	Clubshell	
**Pleurobema collina* (Conrad, 1836)	James Spinymussel	Reassigned to *Parvaspina*
***Pleurobema cordatum* (Rafinesque, 1820)**	Ohio Pigtoe	
***Pleurobema curtum* (Lea, 1859)**	Black Clubshell	
***Pleurobema decisum* (Lea, 1831)**	Southern Clubshell	
***Pleurobema fibuloides* (Lea, 1859)**	Kusha Pigtoe	Elevated from synonymy
**Pleurobema flavidulum* (Lea, 1861)	Yellow Pigtoe	Synonym of *Pleurobema perovatum*
**Pleurobema furvum* (Conrad, 1834)	Dark Pigtoe	Synonym of *Pleurobema rubellum*
***Pleurobema georgianum* (Lea, 1841)**	Southern Pigtoe	

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
**Pleurobema gibberum* (Lea, 1838)	Cumberland Pigtoe	Reassigned to *Pleuronaia*
**Pleurobema hagleri* (Frierson, 1900)	Brown Pigtoe	Synonym of *Pleurobema rubellum*
***Pleurobema hanleyianum* (Lea, 1852)**	Georgia Pigtoe	
***Pleurobema hartmanianum* (Lea, 1860)**	Cherokee Pigtoe	Elevated from synonymy
**Pleurobema johannis* (Lea, 1859)	Alabama Pigtoe	Synonym of *Pleurobema perovatum*
***Pleurobema marshalli* Frierson, 1927**	Flat Pigtoe	
**Pleurobema murrayense* (Lea, 1868)	Coosa Pigtoe	Synonym of *Pleurobema stabile*
**Pleurobema nucleopsis* (Conrad, 1849)	Longnut	Synonym of *Pleurobema georgianum*
***Pleurobema oviforme* (Conrad, 1834)**	Tennessee Clubshell	
***Pleurobema perovatum* (Conrad, 1834)**	Ovate Clubshell	
***Pleurobema plenum* (Lea, 1840)**	Rough Pigtoe	
***Pleurobema pyriforme* (Lea, 1857)**	Oval Pigtoe	
***Pleurobema riddellii* (Lea, 1861)**	Louisiana Pigtoe	
***Pleurobema rubellum* (Conrad, 1834)**	Warrior Pigtoe	
***Pleurobema rubrum* (Rafinesque, 1820)**	Pyramid Pigtoe	
***Pleurobema sintoxia* (Rafinesque, 1820)**	Round Pigtoe	
***Pleurobema stabile* (Lea, 1861)**	Coosa Pigtoe	Elevated from synonymy
***Pleurobema strodeanum* (Wright, 1898)**	Fuzzy Pigtoe	
***Pleurobema taitianum* (Lea, 1834)**	Heavy Pigtoe	
**Pleurobema troschelianum* (Lea, 1852)	Alabama Clubshell	Synonym of *Pleurobema georgianum*
***Pleurobema verum* (Lea, 1861)**	True Pigtoe	
***Pleuronaia* Frierson, 1927**		Elevated from synonymy
***Pleuronaia barnesiana* (Lea, 1838)**	Tennessee Pigtoe	Reassigned from *Fusconaia*
***Pleuronaia dolabelloides* (Lea, 1840)**	Slabside Pearlymussel	Reassigned from *Lexingtonia*
***Pleuronaia gibber* (Lea, 1838)**	Cumberland Pigtoe	Reassigned from *Pleurobema*; spelling correction of species name
***Popenais* Frierson, 1927**		
***Popenais popeii* (Lea, 1857)**	Texas Hornshell	
***Potamilus* Rafinesque, 1818**		
***Potamilus alatus* (Say, 1817)**	Pink Heelsplitter	
***Potamilus amphichaenus* (Frierson, 1898)**	Texas Heelsplitter	
***Potamilus capax* (Green, 1832)**	Fat Pocketbook	
***Potamilus inflatus* (Lea, 1831)**	Inflated Heelsplitter	Common name changed from Alabama Heelsplitter
***Potamilus metnecktayi* Johnson, 1998**	Salina Mucket	Described as new species
***Potamilus ohiensis* (Rafinesque, 1820)**	Pink Papershell	
***Potamilus purpuratus* (Lamarck, 1819)**	Bleufer	
***Ptychobranchus* Simpson, 1900**		
***Ptychobranchus fasciolaris* (Rafinesque, 1820)**	Kidneyshell	
***Ptychobranchus foremanianus* (Lea, 1842)**	Rayed Kidneyshell	Elevated from synonymy
***Ptychobranchus greenii* (Conrad, 1834)**	Triangular Kidneyshell	
***Ptychobranchus jonesi* (van der Schalie, 1934)**	Southern Kidneyshell	
***Ptychobranchus occidentalis* (Conrad, 1836)**	Ouachita Kidneyshell	
**Ptychobranchus subtentum* (Say, 1825)	Fluted Kidneyshell	Incorrect spelling of species name
***Ptychobranchus subtentus* (Say, 1825)**	Fluted Kidneyshell	Spelling correction of species name
***Pyganodon* Crosse and Fischer, 1894**		
***Pyganodon cataracta* (Say, 1817)**	Eastern Floater	
***Pyganodon fragilis* (Lamarck, 1819)**	Newfoundland Floater	
***Pyganodon gibbosa* (Say, 1824)**	Inflated Floater	
***Pyganodon grandis* (Say, 1829)**	Giant Floater	
***Pyganodon lacustris* (Lea, 1857)**	Lake Floater	Publication date corrected

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Quadrula* Rafinesque, 1820**		
***Quadrula apiculata* (Say, 1829)**	Southern Mapleleaf	
**Quadrula asperata* (Lea, 1861)	Alabama Orb	Reassigned to *Cyclonaias*
**Quadrula aurea* (Lea, 1859)	Golden Orb	Reassigned to *Cyclonaias*
***Quadrula couchiana* (Lea, 1860)**	Rio Grande Monkeyface	
**Quadrula cylindrica cylindrica* (Say, 1817)	Rabbitsfoot	Nominotypical subspecies not required; reassigned to *Theliderma*
**Quadrula cylindrica strigillata* (Wright, 1898)	Rough Rabbitsfoot	Subspecies no longer recognized
***Quadrula fragosa* (Conrad, 1835)**	Winged Mapleleaf	
**Quadrula houstonensis* (Lea, 1859)	Smooth Pimpleback	Reassigned to *Cyclonaias*
**Quadrula intermedia* (Conrad, 1836)	Cumberland Monkeyface	Reassigned to *Theliderma*
**Quadrula kieneriana* (Lea, 1852)	Coosa Orb	Reassigned to *Cyclonaias*
**Quadrula metanevra* (Rafinesque, 1820)	Monkeyface	Reassigned to *Theliderma*
***Quadrula nobilis* (Conrad, 1854)**	Gulf Mapleleaf	Elevated from synonymy
**Quadrula nodulata* (Rafinesque, 1820)	Wartyback	Reassigned to *Cyclonaias*
**Quadrula petrina* (Gould, 1855)	Texas Pimpleback	Reassigned to *Cyclonaias*
**Quadrula pustulosa mortoni* (Conrad, 1835)	Western Pimpleback	Subspecies elevated to species; reassigned to *Cyclonaias*
**Quadrula pustulosa pustulosa* (Lea, 1831)	Pimpleback	Nominotypical subspecies not required; reassigned to *Cyclonaias*
***Quadrula quadrula* (Rafinesque, 1820)**	Mapleleaf	
**Quadrula refulgens* (Lea, 1868)	Purple Pimpleback	Reassigned to *Cyclonaias*
***Quadrula rumphiana* (Lea, 1852)**	Ridged Mapleleaf	
**Quadrula sparsa* (Lea, 1841)	Appalachian Monkeyface	Reassigned to *Theliderma*
**Quadrula stapes* (Lea, 1831)	Stirrupshell	Reassigned to *Theliderma*
**Quadrula tuberosa* (Lea, 1840)	Rough Rockshell	Synonym of *Theliderma metanevra*
**Quincuncina* Ortmann, 1922		Synonym of *Fusconaia*
**Quincuncina burkei* Walker, 1922	Tapered Pigtoe	Reassigned to *Fusconaia*
**Quincuncina infucata* (Conrad, 1834)	Sculptured Pigtoe	Reassigned to *Cyclonaias*
**Quincuncina mitchelli* (Simpson, 1895)	False Spike	Reassigned to *Fusconaia*
***Reginaia* Campbell and Lydeard, 2012**		Described as new genus
***Reginaia apalachicola* (Williams and Fradkin, 1999)**	Apalachicola Ebonyshell	Described as new species; reassigned from *Fusconaia*
***Reginaia ebenus* (Lea, 1831)**	Ebonyshell	Reassigned from *Fusconaia*; spelling correction of species name
***Reginaia rotulata* (Wright, 1899)**	Round Ebonyshell	Reassigned from *Obovaria*
***Simpsonaias* Frierson, 1914**		
***Simpsonaias ambigua* (Say, 1825)**	Salamander Mussel	
***Sinanodonta* Modell, 1945**		Not previously reported from North America
***Sinanodonta beringiana* (Middendorff, 1851)**	Yukon Floater	Reassigned from *Anodonta*
***Sinanodonta woodiana* (Lea, 1834)**	Chinese Pondmussel	Introduced and established in New Jersey
***Strophitus* Rafinesque, 1820**		
***Strophitus connasaugaensis* (Lea, 1858)**	Alabama Creekmussel	
***Strophitus subvexus* (Conrad, 1834)**	Southern Creekmussel	
***Strophitus undulatus* (Say, 1817)**	Creeper	
***Theliderma* Swainson, 1840**		Elevated from synonymy
***Theliderma cylindrica* (Say, 1817)**	Rabbitsfoot	Reassigned from *Quadrula*
***Theliderma intermedia* (Conrad, 1836)**	Cumberland Monkeyface	Reassigned from *Quadrula*
***Theliderma metanevra* (Rafinesque, 1820)**	Monkeyface	Reassigned from *Quadrula*
***Theliderma sparsa* (Lea, 1841)**	Appalachian Monkeyface	Reassigned from *Quadrula*
***Theliderma stapes* (Lea, 1831)**	Stirrupshell	Reassigned from *Quadrula*

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Toxolasma* Rafinesque, 1831**		
***Toxolasma corvunculus* (Lea, 1868)**	Southern Purple Lilliput	
***Toxolasma cylindrellus* (Lea, 1868)**	Pale Lilliput	
***Toxolasma lividum* Rafinesque, 1831**	Purple Lilliput	Spelling correction of species name; parentheses unnecessary
**Toxolasma lividus* (Rafinesque, 1831)	Purple Lilliput	Incorrect spelling of species name
**Toxolasma mearnsi* (Simpson, 1900)	Western Lilliput	Synonym of *Toxolasma texasiense*
***Toxolasma parvum* (Barnes, 1823)**	Lilliput	Spelling correction of species name
**Toxolasma parvus* (Barnes, 1823)	Lilliput	Incorrect spelling of species name
***Toxolasma paulum* (Lea, 1840)**	Iridescent Lilliput	Spelling correction of species name
**Toxolasma paulus* (Lea, 1840)	Iridescent Lilliput	Incorrect spelling of species name
***Toxolasma pullus* (Conrad, 1838)**	Savannah Lilliput	
***Toxolasma texasiense* (Lea, 1857)**	Texas Lilliput	Spelling correction of species name
**Toxolasma texasiensis* (Lea, 1857)	Texas Lilliput	Incorrect spelling of species name
***Tritogonia* Agassiz, 1852**		
***Tritogonia verrucosa* (Rafinesque, 1820)**	Pistolgrip	
***Truncilla* Rafinesque, 1819**		
***Truncilla cognata* (Lea, 1860)**	Mexican Fawnsfoot	
***Truncilla donaciformis* (Lea, 1828)**	Fawnsfoot	
***Truncilla macrodon* (Lea, 1859)**	Texas Fawnsfoot	
***Truncilla truncata* Rafinesque, 1820**	Deertoe	
***Uniomerus* Conrad, 1853**		
***Uniomerus carolinianus* (Bosc, 1801)**	Eastern Pondhorn	Common name changed from Florida Pondhorn
***Uniomerus columbensis* (Lea, 1857)**	Apalachicola Pondhorn	Elevated from synonymy
***Uniomerus declivis* (Say, 1831)**	Tapered Pondhorn	
***Uniomerus tetralasmus* (Say, 1831)**	Pondhorn	
***Utterbackia* Baker, 1927**		
***Utterbackia imbecillis* (Say, 1829)**	Paper Pondshell	
***Utterbackia peggyae* (Johnson, 1965)**	Florida Floater	
***Utterbackia peninsularis* Bogan and Hoeh, 1995**	Peninsular Floater	
***Utterbackiana* Frierson, 1927**		Elevated from synonymy
***Utterbackiana couperiana* (Lea, 1840)**	Barrel Floater	Reassigned from *Anodonta*
***Utterbackiana hartfieldorum* (Williams, Bogan, and Garner, 2009)**	Cypress Floater	Described as new species; reassigned from *Anodonta*
***Utterbackiana heardi* (Gordon and Hoeh, 1995)**	Apalachicola Floater	Reassigned from *Anodonta*
***Utterbackiana implicata* (Say, 1829)**	Alewife Floater	Reassigned from *Anodonta*
***Utterbackiana suborbiculata* (Say, 1831)**	Flat Floater	Reassigned from *Anodonta*
***Venustaconcha* Frierson, 1927**		
***Venustaconcha ellipsiformis* (Conrad, 1836)**	Ellipse	
***Venustaconcha pleasii* (Marsh, 1891)**	Bleedingtooth Mussel	
***Venustaconcha trabalis* (Conrad, 1834)**	Tennessee Bean	Reassigned from *Villosa*; common name changed from Cumberland Bean
***Venustaconcha troostensis* (Lea, 1834)**	Cumberland Bean	Elevated from synonymy
***Villosa* Frierson, 1927**		
**Villosa amygdala* (Lea, 1843)	Florida Rainbow	Incorrect spelling of species name
***Villosa amygdalum* (Lea, 1843)**	Florida Rainbow	Spelling correction of species name
**Villosa arkansasensis* (Lea, 1862)	Ouachita Creekshell	Reassigned to *Obovaria*
**Villosa choctawensis* Athearn, 1964	Choctaw Bean	Reassigned to *Obovaria*
***Villosa constricta* (Conrad, 1838)**	Notched Rainbow	
***Villosa delumbis* (Conrad, 1834)**	Eastern Creekshell	
***Villosa fabalis* (Lea, 1831)**	Rayed Bean	

Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Villosa iris* (Lea, 1829)**	Rainbow	
***Villosa lienosa* (Conrad, 1834)**	Little Spectaclecase	
***Villosa nebulosa* (Conrad, 1834)**	Alabama Rainbow	
***Villosa ortmanni* (Walker, 1925)**	Kentucky Creekshell	
**Villosa perpurpurea* (Lea, 1861)	Purple Bean	Synonym of *Venustaconcha trabalis*
***Villosa sima* (Lea, 1838)**	Caney Fork Rainbow	Elevated from synonymy
***Villosa taeniata* (Conrad, 1834)**	Painted Creekshell	
**Villosa trabalis* (Conrad, 1834)	Cumberland Bean	Reassigned to *Venustaconcha*
***Villosa umbrans* (Lea, 1857)**	Coosa Creekshell	Species elevated from subspecies
**Villosa vanuxemensis umbrans* (Lea, 1857)	Coosa Creekshell	Subspecies elevated to species
***Villosa vanuxemensis* (Lea, 1838)**	Mountain Creekshell	
**Villosa vanuxemensis vanuxemensis* (Lea, 1838)	Mountain Creekshell	Nominotypical subspecies not required
***Villosa vaughaniana* (Lea, 1838)**	Carolina Creekshell	
***Villosa vibex* (Conrad, 1834)**	Southern Rainbow	
***Villosa villosa* (Wright, 1898)**	Downy Rainbow	

genus, species, and subspecies levels relative to previous lists. We recognize in total 298 freshwater mussel species from the United States and Canada. These comprise the families Margaritiferidae with one genus and five species and Unionidae with 54 genera and 293 species (Table 2). Turgeon et al. (1998) recognized in total 304 taxa: Margaritiferidae with two genera and five species and Unionidae with 49 genera, 286 species, and 13 subspecies. We summarize our changes to Turgeon et al. (1998) as follows. We recognize eight additional genera, including three recently described (*Hamiota*, *Parvaspina*, and *Reginaia*), four elevated from synonymy (*Eurynia*, *Pleuronaia*, *Theliderma*, and *Utterbackiana*), and one newly reported from North America (*Sinanodonta*). We place in synonymy four genera, including one in the Margaritiferidae (*Cumberlandia*) and three in the Unionidae (*Arkansia*, *Lexingtonia*, and *Quincuncina*). We recognize 25 additional species (all Unionidae), including four newly described species and 21 species elevated from synonymy. We place in synonymy 29 species and consider *Pleurobema altum* a nomen dubium, and we reassigned 41 species to other genera. We corrected the specific epithet spelling for eight species, corrected the date of publication for four, and changed the common names of five. Last, we recognized no subspecies, elevating 10 subspecies to species status and subsuming four subspecies into their nominal species (see Methods).

Margaritiferidae Henderson, 1929

Turgeon et al. (1998) recognized two genera in Margaritiferidae, *Cumberlandia* (one species) and *Margaritifera* (four species). On the basis of shell morphology and soft anatomy, Smith (2001) placed *Cumberlandia* in *Margaritanopsis* and *Margaritifera* (in part) in *Pseudunio*, but this classification was not widely accepted. In a molecular phylogenetic analysis, Huff et al. (2004) considered *Cumberlandia* a junior synonym of *Margaritifera*, and this classification was followed by some subsequent authors (e.g., Graf and Cummings 2007, 2017; Cummings and Graf 2010), but others continued to recognize the genus as valid (e.g., Williams et al. 2008; Watters et al. 2009; Haag 2012). A more comprehensive phylogeny of the Margaritiferidae that included eight of 13 currently recognized species (three from North America) retained the use of *Cumberlandia* (Bolotov et al. 2015). However, based on more recent evidence (Bolotov et al. 2016; Araujo et al. 2017), we consider *Cumberlandia* a junior synonym of *Margaritifera*.

Cumberlandia *Ortmann, 1912*.—Turgeon et al. (1998) recognized one species, *Cumberlandia monodonta*. We place *Cumberlandia* in the synonymy of *Margaritifera* (see Margaritiferidae).

Margaritifera *Schumacher, 1816*.—Turgeon et al. (1998) recognized four species of *Margaritifera*. Placement of *Cumberlandia* in the synonymy of *Margaritifera* brings the number of recognized species to five (see Margaritiferidae).

Unionidae Rafinesque, 1820

Turgeon et al. (1998) recognized 49 genera, 286 species, and 13 subspecies in Unionidae. We recognize 54 genera, 293 species, and no subspecies. We provide support for and discussion of these changes in the following assessments of genera.

Actinonaias *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized two species, *Actinonaias ligamentina* and *Actinonaias pectorosa*. Molecular analyses (e.g., Campbell et al. 2005; Zanatta and Murphy 2006) found that the two species of *Actinonaias* together did not represent a monophyletic grouping, but the position of each of these lineages within the Lampsilini was unresolved. The type locality for *Actinonaias* is central Mexico, and 10 recognized species are restricted to this region (Graf and Cummings 2017), but no species attributable to *Actinonaias* occur between Mexico and the range of *ligamentina* and *pectorosa* in the central United States and southern Canada. No phylogenetic research has examined relationships among Mexican *Actinonaias* and *ligamentina* and *pectorosa*, but it is unlikely they are closely related considering the disjunct distribution and lack of precedent for such a geographical pattern in other freshwater taxa (e.g., Miller et al. 2005). *Actinonaias ligamentina* and *pectorosa* require placement in two different genera, but at this time we retain these two species in the genus *Actinonaias* pending the outcome of further phylogenetic research.

Alasmidonta *Say, 1818*.—Turgeon et al. (1998) recognized 12 species, and recent evidence supports no changes to this classification.

Amblema *Rafinesque, 1820*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification.

Anodonta *Lamarck, 1799*.—Turgeon et al. (1998) recognized 10 species. Mock et al. (2004) and Zanatta et al. (2007) found *Anodonta* to be polyphyletic, with eastern North American species forming a monophyletic clade distinct from the one that includes the type species (*Anodonta cygnea*, which occurs in Eurasia) and western North American *Anodonta*. Without discussion, Graf and Cummings (2007) and Cummings and Graf (2010) placed *Anodonta couperiana*, *A. heardi*, and *A. suborbiculata* in *Utterbackia*, and *A. implicata* in *Pyganodon*. Because no supporting evidence was provided, we do not recognize these changes. The next available genus for the eastern North American clade (*A. couperiana*, *A. heardi*, *A. suborbiculata*, and *A. implicata*) identified as distinct by Mock et al. (2004) is *Utterbackiana*. *Anodonta hartfieldorum* Williams, Bogan, and Garner, 2009, was described subsequently and also belongs to *Utterbackiana* (see *Utterbackiana*).

In a phylogenetic analysis of western North American *Anodonta*, Chong et al. (2008) found *A. beringiana* to be more closely related to the Asian species *Sinanodonta woodiana* than to North American species. Based on this evidence, we reassign *beringiana* to *Sinanodonta* (see *Sinanodonta*).

We retain the remaining four western North American species within *Anodonta* (*A. californiensis*, *A. kennerlyi*, *A. nuttalliana*, and *A. oregonensis*) based on their phylogenetic affinity to Eurasian *Anodonta* (Mock et al. 2004; Zanatta et al. 2007; Chong et al. 2008). *Anodonta dejecta* was recognized by Turgeon et al. (1998), Graf and Cummings (2007), and Cummings and Graf (2010). This species is treated as a synonym of *A. californiensis* by Bequaert and Miller (1973) and the Arizona Game and Fish Department (2017). We do not recognize *A. dejecta*, which is here placed in synonymy of *A. californiensis*.

Anodontoides *Simpson in Baker, 1898*.—Turgeon et al. (1998) recognized two species. One additional species, *Anodontoides denigrata*, was recognized without discussion by Neves et al. (1997) and Cicerello and Schuster (2003). Haag and Cicerello (2016) recognized *A. denigrata* on the basis of molecular data showing that upper Cumberland River drainage populations were distinct from *A. ferussacianus* (Bogan and Raley 2013), and we recognize this species for the same reason. Bogan and Raley (2013) referred to *A. denigrata* as *A. argenteus* (Lea, 1840), for which the type locality is Stones River, Tennessee. The Stones River is a tributary of the middle Cumberland River and well downstream of the putative distribution of *A. denigrata* and other species considered endemic to the upper Cumberland River drainage upstream of the hypothesized original location of Cumberland Falls (Haag and Cicerello 2016). Until further research delineates this species' distribution more precisely, we use *A. denigrata*, for which the type locality is in the upper Cumberland River drainage (Clear Fork, Campbell County, Tennessee; see Ortmann 1918). Ahlstedt et al. (2016) reported a possibly distinct *Anodontoides* species from the Powell River, Virginia, but further work is needed to determine its validity and taxonomy.

Arcidens *Simpson, 1900*.—Turgeon et al. (1998) recognized one species, *Arcidens confragosus*. Clarke (1981) considered *Arkansia* (see *Arkansia*) a junior synonym of *Arcidens* (see also Graf and Cummings 2007), and this classification was supported by morphological and molecular data (Inoue et al. 2014). We recognize two species of *Arcidens*.

Arkansia *Ortmann and Walker, 1912*.—*Arkansia* was described as a monotypic genus including *A. wheeleri*, which was recognized by Turgeon et al. (1998). We place *Arkansia* in the synonymy of *Arcidens* (see *Arcidens*).

Cyclonaias *Pilsbry in Ortmann and Walker, 1922*.—Turgeon et al. (1998) recognized *Cyclonaias*, which has long been considered a monotypic genus for *C. tuberculata*. *Cyclonaias tuberculata* has been aligned with the Quadrulini based on morphological (e.g., Frierson 1927; Modell 1964) and protein polymorphism data (Davis and Fuller 1981). Heard and Guckert (1971) placed *Cyclonaias* in the Pleurobemini based on its ectobranchous brooding (see also Graf and Cummings 2007). However, it appears that ectobranchy arose multiple times (Davis and Fuller 1981; Graf 2002; Roe and Hoeh 2003), meaning that this trait does not necessarily exclude *Cyclonaias* from the Quadrulini, and some female *C. tuberculata* brood glochidia in all four gills (Frierson 1927).

Recent molecular studies consistently supported inclusion of *Cyclonaias* in the Quadrulini, but they further show that it is a member of a monophyletic clade including *Q. pustulosa* and related species (Campbell et al. 2005; Campbell and Lydeard 2012b). Serb et al. (2003) did not support this relationship, but these results were later attributed to an error in sample labeling (Campbell and Lydeard 2012b). However, Serb et al. (2003) as well as Campbell et al. (2005) and Campbell and Lydeard (2012b) support the monophyly of the *Quadrula pustulosa* clade and its distinctiveness from other species of *Quadrula* (see *Quadrula* and *Theliderma*). In addition to *Cyclonaias tuberculata*, the *Quadrula pustulosa* clade identified by these studies includes the following species recognized by Turgeon et al. (1998): *Q. asperata*, *Q. aurea*, *Q. houstonensis*, *Q. nodulata*, *Q. petrina*, *Q. pustulosa*, and *Q. refulgens*, as well as *Fusconaia succissa* and *Quincuncina infucata* (see *Fusconaia* and *Quincuncina*).

The name *Quadrula* is not available for the *Q. pustulosa* clade because the type species, *Q. quadrula*, is a member of another distinct, monophyletic clade (see *Quadrula*). Graf and Cummings (2007) elevated the generic name *Amphinaias* Crosse and Fischer, 1894, for the *Q. pustulosa* clade. The type species for *Amphinaias* (by original designation) is *Unio couchianus* Lea, 1860, which has a quadrate shell and sulcus (but lacks pustules) similar to the *Q. quadrula* clade. This morphology is very different from the rounded, pustulose shells of the *Q. pustulosa* clade. *Quadrula couchiana* is considered extinct and genetic data are unavailable; however, we do not consider *Amphinaias* an available name for the *Q. pustulosa* clade because of the strongly divergent morphology of the type species. Campbell and Lydeard (2012b) proposed *Rotundaria* Rafinesque, 1820, as a name for the *Q. pustulosa* clade, presuming its availability based on statements in Valenciennes (1827). However, Valenciennes noted that Rafinesque had confused two species, one for which he kept Rafinesque's name *Unio verrucosa* and named the other *Unio tuberculosa* [sic]. As such, Valenciennes's statement cannot be accepted as a subsequent designation of *Obliquaria tuberculata* Rafinesque, 1820, as the type species of *Rotundaria* (P. Bouchet, Muséum National d'Histoire Naturelle, Paris, personal communication), and Herrmannsen (1848) later designated *Obliquaria subrotunda* Rafinesque, 1820, as the type species of *Rotundaria*. Rafinesque did not select a type species for *Rotundaria* and because more than one species was included by him in the genus, the type species cannot be fixed by monotypy. Therefore, *Rotundaria* is not available for the *Q. pustulosa* clade. Frierson (1927) erected the subgenus *Bullata* for *Q. pustulosa* but realized this was preoccupied and created the replacement name *Pustulosa* with the same type species. Thus, *Cyclonaias* becomes the oldest available name for this group.

Of the 10 species discussed above as members of *Cyclonaias*, three were not recognized by Turgeon et al. (1998) (*C. archeri*, *C. kieneriana*, and *C. kleiniana*), and one was considered a subspecies (*C. mortoni*, as *Quadrula pustulosa mortoni*). Graf and Cummings (2007) elevated *Q. archeri* from synonymy with *Q. asperata*, but they provided no justification for this change. The distinctiveness of *C. archeri* was recognized by Williams et al. (2008) based on its morphology, absence of intergrades, and isolated and restricted distribution. We recognize *C. archeri*. The distinctiveness of *C. kieneriana* was recognized by Williams et al. (2008) based on shell morphology; however, it was not supported by molecular data (Serb et al. 2003), but that study included only one specimen of this putative taxon. We recognize *C. kieneriana* until additional information becomes available (see Williams et al. 2008). *Cyclonaias kleiniana* was synonymized under *Quincuncina infucata* by Clench and Turner (1956), but molecular studies supported the distinctiveness of these species and their inclusion in *Cyclonaias* (Lydeard et al. 2000; Campbell and Lydeard 2012b). Molecular data supported the distinctiveness of *C. mortoni* from *C. pustulosa* (Serb et al. 2003). In summary, we recognize *Cyclonaias* as including 14 species: *C. tuberculata*, seven species recognized by Turgeon et al. (1998) under *Quadrula*, one subspecies recognized by Turgeon et al. (1998) but now elevated to species status (*C. mortoni*), two species recognized by Turgeon et al. (1998) in different genera (*C. infucata* and *C. succissa*), and three species elevated from synonymy (*C. archeri*, *C. kieneriana*, and *C. kleiniana*).

Cyprogenia *Agassiz, 1852*.—Turgeon et al. (1998) recognized two species. Subsequent molecular data suggested cryptic species diversity in the genus (Serb and Barnhart 2008; Grobler et al. 2011). The most recent molecular analysis of *Cyprogenia* identified three independent evolutionary lineages: *C. aberti* in the Ozark drainages of Arkansas, Missouri, and Kansas; *C. stegaria* in the Ohio River Basin; and a third lineage in the Ouachita River drainage in Arkansas (Chong et al. 2016). Confusion regarding the type locality of *Unio lamarckianus* Lea, 1852, requires resolution to determine whether that name is available for the Ouachita River drainage population. We recognize the distinctiveness of this species but defer including it in our list until a specific epithet can be designated.

Cyrtonaias *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized one species, *Cyrtonaias tampicoensis*, and recent evidence supports no changes to this classification. Five other species are recognized, all of which occur in Mexico or Central America (Graf and Cummings 2017).

Disconaias *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized one species, *Disconaias salinasensis* Simpson in Dall, 1908, which was subsequently placed in the synonymy of *Disconaias fimbriata* by Graf and Cummings (2007). Five other species are recognized, all of which occur in Mexico (Graf and Cummings 2017). We recognize *Disconaias fimbriata* as the only species of the genus occurring in the United States (Rio Grande drainage).

Dromus *Simpson, 1900*.—Turgeon et al. (1998) recognized one species, *Dromus dromas*, and recent evidence supports no changes to this classification.

Ellipsaria *Rafinesque, 1820*.—Turgeon et al. (1998) recognized one species, *Ellipsaria lineolata*, and recent evidence supports no changes to this classification.

Elliptio *Rafinesque, 1819*.—Turgeon et al. (1998) recognized 36 species, making it the largest unionid genus in the United States and Canada, but species concepts within this group remain mostly untested, and their highly variable shell morphology precludes traditional approaches for species diagnosis. Recent molecular studies have largely supported the monophyly of *Elliptio* with two exceptions (Campbell et al. 2005; Campbell and Lydeard 2012b; Perkins et al. 2017). *Elliptio dilatata*, which is morphologically and anatomically similar to many *Elliptio*, is not a member of this group; we recognize reassignment of this species to *Eurynia* (Campbell and Lydeard 2012b). We also recognize reassignment of *Elliptio steinstansana* to *Parvaspina* based on molecular data (Perkins et al. 2017). It is important to note that phylogenetic affinities remain unknown for most species that we currently recognize under *Elliptio* and some may prove to be members of other genera (e.g., *Eurynia*; Elderkin et al. 2008; Campbell and Lydeard 2012b).

Because of our poor understanding of species diversity within *Elliptio*, we largely retain the classification of Turgeon et al. (1998) with the following exceptions. We stress that this classification is provisional and meant to provide a stable, working hypothesis for diversity within the genus. We elevate from synonymy four species of *Elliptio*: *E. fumata* (from *E. complanata*), *E. occulta* and *E. pullata* (from *E. icterina*), and *E. purpurella* (from *E. arctata* and *E. strigosa*); these changes are based primarily on differences in shell morphology (Brim Box and Williams 2000; Williams et al. 2008, 2011, 2014). We place eight species into synonymy. Four Atlantic Slope species (*E. errans*, *E. hepatica*, *E. lugubris*, and *E. raveneli*) were recognized by Turgeon et al. (1998) based on Davis and Mulvey (1993). The research by Davis and Mulvey (1993) was confined almost exclusively to the Savannah River drainage and has no context within the greater Atlantic Coast region. The validity of these species has not been evaluated further. We return these species to synonymy following Johnson (1970) as follows: *E. errans* is synonymized under *E. complanata*; and *E. hepatica*, *E. lugubris*, and *E. raveneli* are synonymized under *E. icterina*. We place *Elliptio waccamawensis* into the synonymy of *E. congaraea* based on molecular data (McCartney et al. 2016). We place the following species into synonymy based on examination of shell type material by Clarke (1992) and Williams et al. (2011, 2014): *E. waltoni* (synonymized under *E. ahenea*), *E. judithae* (synonymized under *E. roanokensis*), and *E. buckleyi* (synonymized under *E. jayensis*). After these changes, we recognize 30 species of *Elliptio*, and it remains the largest unionid genus in the United States and Canada.

Turgeon et al. (1998) listed the common names Flat Spike and Florida Shiny Spike for *Elliptio jayensis* and *E. buckleyi*, respectively. We follow the recommendation of Williams et al. (2014) that the common name of *E. jayensis* be changed to Florida Spike because the species is largely endemic to that state and is neither consistently flat nor shiny.

Elliptoideus *Frierson, 1927*.—Turgeon et al. (1998) recognized one species, *Elliptoideus sloatianus*, and recent evidence supports no changes to this classification.

Epioblasma *Rafinesque, 1831*.—Turgeon et al. (1998) recognized 20 species and five subspecies. Our changes to this classification involve recognition of two newly described cryptic species, elevating one species from synonymy, and elevating subspecies to species status. We recognize *Epioblasma ahlstedti* Jones and Neves, 2010, a cryptic species formerly included within *E. capsaeformis*, and we recognize and elevate to species status *Epioblasma aureola* Jones and Neves, 2010, formerly identified as *E. florentina walkeri* but described as *E. florentina aureola* Jones and Neves, 2010.

Epioblasma cincinnatiensis was not recognized by Turgeon et al. (1998), and it has been considered a synonym (e.g., Parmalee and Bogan 1998) or a subspecies (e.g., Morrison 1942) of *Epioblasma torulosa*. Williams et al. (2008) elevated this species from synonymy based on examination of shell type material. Watters et al. (2009) also recognized this taxon but placed it in the synonymy of *Epioblasma phillipsii* (Conrad, 1835). However, *E. phillipsii* is considered a synonym of *Obliquaria reflexa* (see Williams et al. 2008). We follow Williams et al. (2008) in recognizing *E. cincinnatiensis*.

Turgeon et al. (1998) recognized eight subspecies of *Epioblasma* in three nominal species: *florentina* (three), *obliquata* (two), and *torulosa* (three). A conclusive assessment of the taxonomic status of these taxa may be impossible at this time because half are considered extinct (*E. florentina florentina*, *E. f. curtisii*, *E. torulosa torulosa*, and *E. t. gubernaculum*). Cummings and Berlocher (1990) found no evidence of intergradation between *E. t. torulosa* and *E. t. rangiana* and both taxa co-occurred at many sites; based on this evidence, we elevate these subspecies to species status. *Epioblasma aureola* and *E. walkeri* represent morphologically and genetically distinct sister taxa (Jones and Neves 2010, as *E. florentina aureola* and *E. florentina walkeri*). These taxa appear to be restricted to two different river systems (Tennessee and Cumberland, respectively); based on the low probability of exchange between these populations and their distinctiveness, we recognize and elevate to full species status *E. aureola* and *E. walkeri*. There is little information with which to assess the taxonomic status of *E. florentina florentina*, *E. florentina curtisii*, *E. obliquata obliquata*, *E. obliquata perobliqua*, and *E. torulosa gubernaculum*, but all have distinctive shell morphology or occupy distinct geographical regions and we recognize all these taxa as distinct species (see Methods).

We recognize 28 *Epioblasma* species, making it the second largest unionid genus in the United States and Canada.

Eurynia *Rafinesque, 1820*.—*Eurynia* was not recognized in Turgeon et al. (1998). *Eurynia* was elevated from synonymy by Campbell and Lydeard (2012b) to accommodate *Elliptio dilatata*, which consistently falls outside the *Elliptio* clade in molecular analyses (see also Perkins et al. 2017). We consider *Eurynia* monotypic at this time, but more inclusive molecular studies may identify other species that belong to this genus, including some now assigned to *Elliptio* (Elderkin et al. 2008; Campbell and Lydeard 2012b).

Fusconaia *Simpson, 1900*.—Turgeon et al. (1998) recognized 13 species. Several studies showed that the genus *Fusconaia* as portrayed by Turgeon et al. (1998) was polyphyletic (Lydeard et al. 2000; Serb et al. 2003; Campbell et al. 2005; Campbell and Lydeard 2012a, 2012b; Pfeiffer et al. 2016). Based on these results, we reassign three species recognized by Turgeon et al. (1998) to other genera: *F. succissa* to *Cyclonaias*, *F. barnesiana* to *Pleuronaia*, and *F. ebenus* to *Reginaia*. *Pleuronaia* was resurrected to accommodate *F. barnesiana*, along with two other species in the clade (Williams et al. 2008; Campbell and Lydeard 2012a, 2012b; see *Pleuronaia*). *Reginaia* was described to accommodate *F.*

ebenus and two other species (Campbell and Lydeard 2012a; see *Reginaia*).

These studies also showed that several species assigned to other genera belonged in *Fusconaia*. Based on these results, *Quincuncina* is a junior synonym of *Fusconaia*, and we reassign *Q. burkei* and *Q. mitchelli* to *Fusconaia* (Lydeard et al. 2000; Serb et al. 2003; Campbell et al. 2005; Pfeiffer et al. 2016; see *Cyclonaias*, *Quadrula*, and *Quincuncina*). *Lexingtonia* was placed in the synonymy of *Fusconaia* when its type species, *L. subplana*, was determined a junior synonym of *Fusconaia masoni* based on molecular data (Bogan et al. 2003).

Fusconaia chunii was not recognized by Turgeon et al. (1998), but they recognized two other *Fusconaia* from Texas: *F. askewi* and *F. lananensis*. Subsequent molecular data showed that all *Fusconaia* in Texas drainages from the Sabine River west belonged to a single species (Burlakova et al. 2012). However, *Unio chunii* Lea, 1861, has priority over *Unio askewi* Marsh, 1896, and *Quadrula lananensis* Frierson, 1901, so we place *F. askewi* and *F. lananensis* in the synonymy of *F. chunii*.

We adopt the former common name for *F. askewi*, Texas Pigtoe, for *F. chunii* because it is descriptive of the species' range. Turgeon et al. (1988) listed the common name Gulf Pigtoe for *Fusconaia cerina*, but it was changed to Southern Pigtoe in Turgeon et al. (1998) without comment. However, Turgeon et al. (1998) also used Southern Pigtoe as the common name of *Pleurobema georgianum*. We designate the common name Gulf Pigtoe for *F. cerina*.

In summary, we recognize 11 species of *Fusconaia*, including eight species recognized by Turgeon et al. (1998) under *Fusconaia*, two species recognized by Turgeon et al. (1998) in other genera, and one species elevated from synonymy.

Glebula *Conrad, 1853*.—Turgeon et al. (1998) recognized one species, *Glebula rotundata*, and recent evidence supports no changes to this classification.

Gonidea *Conrad, 1857*.—Turgeon et al. (1998) recognized one species, *Gonidea angulata*, and recent evidence supports no changes to this classification.

Hamiota *Roe and Hartfield, 2005*.—*Hamiota* was described subsequent to Turgeon et al. (1998) to accommodate a monophyletic clade of four species that produce superconglutinates (Roe et al. 2001). They were previously recognized under *Lampsilis*: *L. altilis*, *L. australis*, *L. perovalis*, and *L. subangulata* (Roe and Hartfield 2005). We recognize all four of these species under *Hamiota*.

Hemistena *Rafinesque, 1820*.—Turgeon et al. (1998) recognized one species, *Hemistena lata*, and recent evidence supports no changes to this classification.

Lampsilis *Rafinesque, 1820*.—Turgeon et al. (1998) recognized 28 species and four subspecies. Molecular data indicated that *Lampsilis*, as presented by Turgeon et al. (1998), is polyphyletic (Graf and Ó Foighil 2000; Campbell et al. 2005). There are likely unrecognized taxa in the genus *Lampsilis* (e.g., in Arkansas; Harris et al. 2009). The genus *Hamiota* was described to accommodate a monophyletic clade of four species, *Lampsilis altilis*, *L. australis*, *L. perovalis*, and *L. subangulata* (Roe and Hartfield 2005), and we recognize reassignment of these species from *Lampsilis* to *Hamiota*. We also recognize reassignment of *Lampsilis haddletoni* to *Obovaria* (Williams et al. 2008; see *Obovaria*). In addition to *Hamiota*, molecular data suggested the existence of at least two other paraphyletic clades within *Lampsilis* as recognized by Turgeon et al. (1998). *Lampsilis cardium*, *L. ornata*, and *L. ovata* formed a monophyletic clade sister to *Hamiota*, and *L. siliquoidea* and *L. teres* were members of a clade sister to the latter two groups; however, these groupings were not consistently or strongly supported, and the analyses did not include other species of putative *Lampsilis* (Campbell et al. 2005). Additional generic-level changes regarding *Lampsilis* will likely occur in the future, but we retain traditional use of this genus for all species except those reassigned to *Hamiota* and *Obovaria*.

Lampsilis floridensis was not recognized by Turgeon et al. (1998), and formerly it was recognized as a subspecies (Clench and Turner 1956) or synonym (Burch 1975) of *Lampsilis teres*. We recognize *L. floridensis* as a full species based on shell morphology, unpublished molecular data, and its allopatric distribution (Williams et al. 2008).

Turgeon et al. (1998) recognized nominal *Lampsilis reeveiana* along with two subspecies, *L. r. brevicula* and *L. r. brittsi*. Molecular data showed that *brittsi* populations from the Missouri River drainage formed a well-supported monophyletic clade separate from nominal *reeveiana*, but there was no morphological or genetic distinction between nominal *L. reeveiana* and *L. r. brevicula* (Harris et al. 2004). Based on these data, we follow McMurray et al. (2012) in recognizing *L. brittsi* and *L. reeveiana* as species and placing *L. reeveiana brevicula* into the synonymy of *L. reeveiana*.

Turgeon et al. (1998) recognized nominal *Lampsilis radiata* and one subspecies, *L. r. conspicua*. However, molecular and shell morphology data did not support the distinctiveness of *L. r. conspicua* (Stiven and Alderman 1992), and we place this taxon into the synonymy of *Lampsilis radiata*. Turgeon et al. (1998) also recognized *Lampsilis fullerkati*, but we recognize placement of that species into the synonymy of *L. radiata* based on molecular data (McCartney et al. 2016).

Turgeon et al. (1998) recognized nominal *Lampsilis straminea* and one subspecies, *L. s. claibornensis*. *Lampsilis straminea straminea* is restricted to the Black Belt Prairie region of Alabama and Mississippi and is characterized by a profusion of fine, concentric ridges on the shell, which are absent in *L. s. claibornensis*. However, concentric ridges are present in some other mussels inhabiting streams in the Black Belt Prairie region and are most likely environmentally induced and not due to genetic differences (Williams et al. 2008). We do not recognize the taxonomic validity of these shell forms and place *L. s. claibornensis* in the synonymy of *Lampsilis straminea*. The common name of *Lampsilis s. straminea*, Rough Fatmucket (Turgeon et al. 1998), is descriptive of individuals in only a small portion of its range (i.e., the Black Belt Prairie). Therefore, we retain the common name for *L. straminea claibornensis*, Southern Fatmucket, for *L. straminea*.

In summary, we recognize 24 species of *Lampsilis* including one species elevated from synonymy and two species elevated from subspecies. *Lampsilis* is the third largest genus in the family Unionidae following *Elliptio* (30) and *Epioblasma* (28).

Lasmigona *Rafinesque, 1831*.—Turgeon et al. (1998) recognized six species and one subspecies. Williams et al. (2008) elevated *Lasmigona complanata alabamensis* to species status based on examination of museum shell material, and molecular data supported the distinctiveness of this taxon (King et al. 1999). Williams et al. (2008) also recognized Mobile Basin populations of *Lasmigona holstonia* as a distinct species based on unpublished molecular data and the occurrence of these populations in two different river systems. They resurrected from synonymy *Lasmigona etowaensis* to refer to Mobile Basin populations and retained *L. holstonia* to refer to Tennessee and Ohio River drainage populations. We recognize all three of these species.

Molecular studies showed that *Lasmigona* is polyphyletic: *L. alabamensis*, *L. complanata*, and *L. costata* formed a monophyletic clade, and *L. compressa* and *L. subviridis* represented another monophyletic clade more closely related to *Alasmidonta* (King et al. 1999). However, this study did not include all species of *Lasmigona*, and a broader study within the context of the tribe Anodontini is needed to clarify these relationships. Populations of *Lasmigona costata* in the Ozark Highlands represented a monophyletic clade strongly differentiated from populations east of the Mississippi River, suggesting the presence of at least one cryptic species within this taxon; additional investigation across the range of *L. costata* is needed to better understand these patterns (Hewitt et al. 2016). An endemic form of *Lasmigona* in the Barrens region of the upper Caney Fork drainage in Tennessee was recognized by Layzer et al. (1993), but the status of this putative taxon has not been evaluated further.

Lemiox *Rafinesque, 1831*.—Turgeon et al. (1998) recognized one species, *Lemiox rimosus*, and recent evidence supports no changes to this classification.

Leptodea *Rafinesque, 1820*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification. Smith (2000) proposed moving *Leptodea ochracea* into the genus *Ligumia* based on mantle margin pigment and size of glochidia. We do not accept this proposal due to the limited number of taxa (four species in two genera) in that analysis, and we retain *ochracea* in *Leptodea*.

Lexingtonia *Ortmann, 1914*.—Turgeon et al. (1998) recognized two species. However, the type species, *Lexingtonia subplana*, was subsequently relegated to the synonymy of *Fusconaia masoni* based on Johnson (1970) and Bogan et al. (2003). As such, *Lexingtonia* is a junior synonym of *Fusconaia*. The other species recognized by Turgeon et al. (1998), *Lexingtonia dolabelloides*, did not group with *Fusconaia* in molecular analyses but formed a monophyletic clade with two other species (Campbell et al. 2005; Campbell and Lydeard 2012a, 2012b). *Pleuronaia* was resurrected by Williams et al. (2008) to accommodate this clade (see *Pleuronaia*).

Ligumia *Swainson, 1840*.—Turgeon et al. (1998) recognized three species. Subsequent molecular studies indicated the genus is not monophyletic, but further research is needed to fully elucidate these patterns (Campbell et al. 2005; Kuehnl 2009). We retain the classification of Turgeon et al. (1998), but as additional information becomes available taxa assigned to this genus will likely change (see Raley et al. 2007). Gangloff et al. (2013) identified a genetically divergent clade of *Ligumia recta* from the Mobile Basin that may warrant recognition as a distinct taxon.

Medionidus *Simpson, 1900*.—Turgeon et al. (1998) recognized seven species. We no longer recognize *Medionidus mcglameriae*, which was placed in the synonymy of *Leptodea fragilis* based on examination of the type specimen (Williams et al. 2008). Campbell et al. (2005) found some evidence for polyphyly of *Medionidus*, but this evidence was not conclusive and we make no other changes to this genus.

Megalonaias *Utterback, 1915*.—Turgeon et al. (1998) recognized one species, *Megalonaias nervosa*, and recent evidence supports no changes to this classification.

Obliquaria *Rafinesque, 1820*.—Turgeon et al. (1998) recognized one species, *Obliquaria reflexa*, and recent evidence supports no changes to this classification.

Obovaria *Rafinesque, 1819*.—Turgeon et al. (1998) recognized six species. Molecular data showed that *Obovaria* as depicted by Turgeon et al. (1998) is polyphyletic (Campbell et al. 2005). Notably, *Obovaria rotulata* was not a member of this group, and it was later reassigned to *Reginaia* (Campbell and Lydeard 2012b); we recognize this reassignment. In an analysis by Campbell et al. (2005), *O. olivaria* fell outside the clade containing other *Obovaria* and *Epioblasma*, but this conclusion was not consistently supported. We retain *olivaria* within *Obovaria*, but further work on this species is needed to resolve its generic assignment.

Evidence also supports reassignment to *Obovaria* of species recognized by Turgeon et al. (1998) under other genera. We reassign *Villosa arkansasensis* and *V. choctawensis* to *Obovaria* based on molecular data (Kuehnl 2009; Inoue et al. 2013) and marsupial morphology (Williams et al. 2011, for *choctawensis*). We also recognize reassignment of *Lampsilis haddletoni* to *Obovaria* based on shell morphology of the type lot (Williams et al. 2008, 2011), but this species is considered extinct and there are no available soft parts for anatomical or molecular study. *Obovaria jacksoniana* was recognized in Turgeon et al. (1998) but is synonymous with *Villosa arkansasensis* (Inoue et al. 2013). *Unio jacksoniana* Frierson, 1912, is a junior synonym of *Unio arkansasensis* Lea, 1862, and we place *O. jacksoniana* in the synonymy of *Obovaria arkansasensis*. There is also potential for unrecognized taxa within *O. arkansasensis* in central Gulf Slope drainages (Inoue et al. 2013).

In summary, we recognize seven species of *Obovaria*, including four species recognized by Turgeon et al. (1998) and three species reassigned from other genera, one from *Lampsilis* and two from *Villosa*.

Parvaspina *Perkins, Gangloff, and Johnson, 2017*.—*Parvaspina* was described subsequent to Turgeon et al. (1998) to accommodate a monophyletic clade of two species previously recognized as *Elliptio steinstansana* and *Pleurobema collina* (Perkins et al. 2017). We recognize these species as *Parvaspina steinstansana* and *Parvaspina collina*.

Pegias *Simpson, 1900*.—Turgeon et al. (1998) recognized one species, *Pegias fabula*, and recent evidence supports no changes to this classification.

Plectomerus *Conrad, 1853*.—Turgeon et al. (1998) recognized one species, *Plectomerus dombeyanus*, and recent evidence supports no changes to this classification.

Plethobasus *Simpson, 1900*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification.

Pleurobema *Rafinesque, 1819*.—Turgeon et al. (1998) recognized 32 species, making it one of the largest unionid genera. Molecular data largely support the monophyly of *Pleurobema* as depicted by Turgeon et al. (1998) with two exceptions (Campbell et al. 2005, 2008; Campbell and Lydeard 2012b). These studies support reassignment of *P. collina* to *Parvaspina* and *P. gibberum* to *Pleuronaia* (Campbell et al. 2005, 2008; Campbell and Lydeard 2012b; see *Parvaspina* and *Pleuronaia*). However, Campbell et al. (2008) and Campbell and Lydeard (2012b) provided evidence that *Pleurobema* includes two distinct lineages, one including *P. sintoxia*, *P. cordatum*, *P. plenum*, *P. riddellii*, and *P. rubrum* and the other including all other species. Further research is needed to elucidate these relationships; we retain traditional use of *Pleurobema*.

Pleurobema rivals *Elliptio* in its large number of described species and the intractability of many species concepts, particularly in the Mobile Basin, but these problems are compounded for *Pleurobema* because many putative taxa are considered extinct. Based on a comprehensive comparison of shell type specimens and other available material, Williams et al. (2008) placed into synonymy nine species of Mobile Basin *Pleurobema* recognized by Turgeon et al. (1998): *P. chattanoogaense* (into *P. decisum*); *P. murrayense* (into *P. stabile*); *P. nucleopsis* and *P. troschelianum* (into *P. georgianum*); *P. flavidulum* and *P. johannis* (into *P. perovatum*); and *P. avellanum*, *P. furvum*, and *P. hagleri* (into *P. rubellum*). Some of these synonyms are further supported by molecular data (e.g., *P. chattanoogaense*, *P. furvum*; Campbell et al. 2008), and we recognize all of these changes. We do not recognize *Pleurobema altum* since it was deemed a nomen dubium because it is not identifiable due to incomplete description, vague type locality, and lack of type material (Williams et al. 2008). One Ohio River drainage species, *Pleurobema bournianum*, was placed into the synonymy of *Pleurobema clava* based on shell morphology (Watters et al. 2009), and we recognize this change.

We recognize four additional Mobile Basin species of *Pleurobema* not recognized by Turgeon et al. (1998). Williams et al. (2008) recognized three species based on examination of shell type specimens: *P. fibuloides*, *P. hartmanianum*, and *P. stabile*. We correct the spelling of *P. stabilis* as used by Williams et al. (2008) to *stabile* based on Lee (2008). *Pleurobema athearni* Gangloff, Williams, and Feminella, 2006, was described subsequent to Turgeon et al. (1998) based on morphological data (Gangloff et al. 2006). In addition, preliminary findings identified an undescribed species in the upper Tennessee River drainage (Schilling 2015).

In summary, we recognize 23 species of *Pleurobema*, including 19 species recognized by Turgeon et al. (1998), three species elevated from synonymy, and one newly described species.

Pleuronaia *Frierson, 1927*.—*Pleuronaia* was not included in Turgeon et al. (1998). This was the senior available name for a monophyletic clade of three species—*Fusconaia barnesiana*, *Lexingtonia dolabelloides*, and *Pleurobema gibberum*—identified in a molecular study by Campbell et al. (2005). We recognize resurrection of *Pleuronaia* to accommodate this group and reassignment of these three species to *Pleuronaia* as proposed previously (Williams et al. 2008; Campbell and Lydeard 2012a, 2012b). There are likely cryptic taxa of *Pleuronaia* in the upper Tennessee River drainage (Schilling 2015). We correct the gender agreement of the specific name of *Pleuronaia gibberum* to *gibber* (H. Lee, Jacksonville, Florida, personal communication).

Popenais *Frierson, 1927*.—Turgeon et al. (1998) recognized one species, *Popenais popeii*, and recent evidence supports no changes to this classification.

Potamilus *Rafinesque, 1818*.—Turgeon et al. (1998) recognized six species. One additional species, *Potamilus metnecktayi* Johnson, 1998, was described subsequently, and we recognize this species. *Potamilus inflatus* was referred to as the Inflated Heelsplitter by Turgeon et al. (1988) but was changed to Alabama Heelsplitter by Turgeon et al. (1998) without comment. Alabama Heelsplitter is the established common name for *Lasmigona alabamensis*, and we adopt the original common name Inflated Heelsplitter for *P. inflatus*. Roe and Lydeard (1998) found the Amite River population of *P. inflatus* to be genetically divergent, and it may warrant recognition as a distinct taxon.

Ptychobranchus *Simpson, 1900*.—Turgeon et al. (1998) recognized five species. *Ptychobranchus foremanianus* was elevated from the synonymy of *Ptychobranchus greenii* (in part) by Williams et al. (2008) based on shell morphology and periostracum color. A molecular analysis of this genus included insufficient material to resolve the relationship between these two taxa (Roe 2013), but we recognize both species. We correct the gender agreement of *Ptychobranchus subtentum* to *P. subtentus* following Lee (2008).

Pyganodon *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized five species. Graf and Cummings (2007) without comment moved *Anodonta implicata* to *Pyganodon* and omitted *P. fragilis* and *P. lacustris*. However, molecular data demonstrated the validity of *P. fragilis* and *P. lacustris* (Doucet-Beaupré et al. 2012). Based on these results and the lack of justification for movement of *A. implicata* to *Pyganodon*, we retain the classification of Turgeon et al. (1998) for *Pyganodon*.

Quadrula *Rafinesque, 1820*.—Turgeon et al. (1998) recognized 18 species and two subspecies. Molecular studies generally supported the monophyly of *Quadrula* as depicted by Turgeon et al. (1998), but they also showed that it is composed of three deeply divergent monophyletic clades plus *Tritogonia verrucosa*, each of which warranted generic recognition (Serb et al. 2003; Campbell et al. 2005; Campbell and Lydeard 2012b). The type species for *Quadrula* is *Q. quadrula*, and the clade containing this species also includes *Q. apiculata*, *Q. fragosa*, *Q. nobilis*, and *Q. rumphiana*. *Quadrula nobilis* was elevated from synonymy based on shell morphology and unspecified genetic data (Howells et al. 1996) but not recognized by Turgeon et al. (1998). Relationships among species in the *Q. quadrula* group were not clearly resolved by Serb et al. (2003), but we recognize all five species. We also recognize within this group *Q. couchiana* on the basis of its shell morphology, which is similar to that of *Q. quadrula* (see *Cyclonaias*).

Based on molecular data, we reassign to *Cyclonaias* 10 taxa recognized by Turgeon et al. (1998) under *Quadrula*, and we reassign 5 species to *Theliderma* (Serb et al. 2003; Campbell et al. 2005; Campbell and Lydeard 2012b; see also Graf and Cummings 2007). We also synonymize two taxa recognized by Turgeon et al. (1998) under *Quadrula* (see *Theliderma*). In summary, we recognize six species of *Quadrula*, including five recognized under this genus by Turgeon et al. (1998) and one elevated from synonymy (*Q. nobilis*).

Quincuncina *Ortmann, 1922*.—Turgeon et al. (1998) recognized three species. Molecular data showed that the type species, *Quincuncina burkei*, belongs in *Fusconaia* (Lydeard et al. 2000; Serb et al. 2003; Campbell et al. 2005). As such, *Quincuncina* is a junior synonym of *Fusconaia*, and we reassign to this genus *Q. burkei* and *Q. mitchelli* (see also Pfeiffer et al. 2016). Based on these findings, we also reassign *Q. infucata* to *Cyclonaias* (see *Cyclonaias*).

Reginaia *Campbell and Lydeard, 2012*.—*Reginaia* was described subsequent to Turgeon et al. (1998) to accommodate a monophyletic clade of two species identified in a phylogenetic analysis of Ambleminae (Campbell and Lydeard 2012b). The two *Reginaia* species were included in Turgeon et al. (1998) as *Fusconaia ebena* and *Obovaria rotulata* (Campbell and Lydeard 2012b); we recognize assignment of these species to *Reginaia*. We follow Watters et al. (2009) in correcting the spelling of the species name *ebena* to *ebenus*. A third species, *Fusconaia apalachicola* Williams and Fradkin, 1999, was described subsequent to Turgeon et al. (1998) from archaeological material; we reassign this species to *Reginaia* based on its shell characters, which are similar to those of *R. ebenus* and *R. rotulata*.

Simpsonaias *Frierson, 1914*.—Turgeon et al. (1998) recognized one species, *Simpsonaias ambigua*, and recent evidence supports no changes to this classification.

Sinanodonta *Modell, 1945*.—*Sinanodonta* was not included in Turgeon et al. (1998). This genus was previously considered to be confined to Asia and not part of the North America fauna. Molecular data showed that *A. beringiana* is more closely related to the Asian species *Sinanodonta woodiana* than to other western North American *Anodonta* (Chong et al. 2008; see *Anodonta*). Based on this evidence, we reassign *beringiana* to *Sinanodonta*. In 2010 *S. woodiana*, Chinese Pondmussel, was found in Wickecheoke Creek, a tributary of the Delaware River, New Jersey (Bogan et al. 2011a). Several known glochidial host fishes, native and introduced species, occur in the watershed (Bogan et al. 2011b). The species appears to have become established in that stream despite eradication efforts (J. Bowers-Altman, New Jersey Division of Fish and Wildlife, personal communication). We recognize *S. woodiana* as established in New Jersey (Table 2). This is the only nonindigenous unionid mussel known to have become established in the United States or Canada.

Strophitus *Rafinesque, 1820*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification. *Strophitus undulatus*, one of the most wide-ranging species in the United States and Canada, likely contains unrecognized cryptic taxa (Watters et al. 2009).

Theliderma *Swainson, 1840*.—*Theliderma* was not recognized by Turgeon et al. (1998). This genus was resurrected from synonymy by Graf and Cummings (2007) to accommodate a monophyletic clade of five species recognized by Turgeon et al. (1998) under *Quadrula* (*Q. cylindrica*, *Q. intermedia*, *Q. metanevra*, *Q. sparsa*, and *Q. stapes*; see Serb et al. 2003). *Theliderma* is the oldest available name for this clade and has *T. metanevra* as its type species. We recognize placement of all five of these species in *Theliderma*. No molecular data are available for *Theliderma stapes*, but its shell morphology is very similar to that of other *Theliderma*, and we include it in this genus following Graf and Cummings (2007).

Turgeon et al. (1998) recognized *Quadrula tuberosa*, but we place this taxon in the synonymy of *Theliderma metanevra* following Parmalee and Bogan (1998, as *Q. metanevra*). However, the relationship of *tuberosa* to other species is uncertain, and if it represents a valid species, it is considered extinct (see Haag and Cicerello 2016). *Quadrula cylindrica* was recognized in Turgeon et al. (1998) as containing two subspecies, *Theliderma cylindrica cylindrica* and *T. cylindrica strigillata*. These subspecies traditionally were distinguished from each other based on shell morphology and distribution, with *strigillata* being confined mainly to the upper Tennessee River system in Tennessee and Virginia (Parmalee and Bogan 1998). However, the distributional limits of *strigillata* have never been clearly defined as it grades into typical *T. c. cylindrica* in larger streams, suggesting that the shell forms represent ecophenotypic variation (Ortmann 1920), and molecular data provide no support for recognition of *T. c. strigillata* (Serb et al. 2003; Sproules et al. 2006). Based on this evidence, we do not recognize subspecies within *T. cylindrica*. Both *T. c. cylindrica* (threatened) and *T. c. strigillata* (endangered) are federally protected taxa. Synonymizing *strigillata* under *T. cylindrica* will not remove the protection provided by the Endangered Species Act but may impact the status of populations formerly recognized as *strigillata*.

Toxolasma *Rafinesque, 1831*.—Turgeon et al. (1998) recognized eight species. Recent evidence supports no changes at the genus level, but species boundaries within *Toxolasma* remain uncertain. Howells et al. (1996) placed *Toxolasma mearnsi* in the synonymy of *Toxolasma texasiense* based on electrophoretic analysis, a change overlooked by Turgeon et al. (1998); we recognize placement of *T. mearnsi* in the synonymy of *T. texasiense*. Undescribed species of *Toxolasma* have been recognized (e.g., Gulf Lilliput) but have yet to be formerly described (Williams et al. 2008, 2014).

Lee (2006) concluded that *Toxolasma* has a neuter gender, which necessitates correction of spellings from *lividus* to *lividum*, *parvus* to *parvum*, and *paulus* to *paulum*, without change to *corvunculus*, *cylindrellus*, or *pullus*; we recognize these spelling changes. Lee (2006) provided an incorrect spelling of *Toxolasma texasiense* (as *texasense*), but we correct it based on the spelling presented in the original description.

Tritogonia *Agassiz, 1852*.—Turgeon et al. (1998) recognized one species, *Tritogonia verrucosa*. Molecular data clearly supported inclusion of *T. verrucosa* within the tribe Quadrulini, but its placement within that group was unresolved, and Serb et al. (2003) recommended its placement within *Quadrula* (*sensu lato*) until relationships were better understood (e.g., see Williams et al. 2008; Haag and Cicerello 2016). Regardless of its relationship to other clades within the Quadrulini, *Tritogonia* represents a deeply divergent lineage (Serb et al. 2003; Campbell et al. 2012b), and our recognition of three other genera within this tribe (*Cyclonaias*, *Theliderma*, and *Quadrula* sensu stricto) warrants retention of *Tritogonia* as a monotypic genus (e.g., see Watters et al. 2009; Sietman et al. 2012).

Truncilla *Rafinesque, 1819*.—Turgeon et al. (1998) recognized four species, and recent evidence supports no changes to this classification.

Uniomerus *Conrad, 1853*.—Turgeon et al. (1998) recognized three species. Recent evidence supports no changes at the genus level, but species concepts within *Uniomerus* are uncertain (see Williams et al. 2008). *Uniomerus columbensis* was not recognized by Turgeon et al. (1998) but was elevated from synonymy by Williams et al. (2008) based on unpublished molecular data and shell morphology; we recognize this change. Species boundaries for other taxa (e.g., *Uniomerus declivis*) remain unresolved.

The inappropriate and misleading common name for *Uniomerus carolinianus*, Florida Pondhorn, was changed to Eastern Pondhorn by Williams et al. (2014) because the species occurs not only in Florida but northward along the Atlantic Coast; we recognize this change.

Utterbackia *Baker, 1927*.—Turgeon et al. (1998) recognized three species and recent evidence supports no changes to this classification.

Utterbackiana *Frierson, 1927*.—*Utterbackiana* was not recognized by Turgeon et al. (1998). We resurrect this genus as the senior available name for a monophyletic clade of four eastern North American species included in Turgeon et al. (1998) under *Anodonta* (*A. couperiana*, *A. heardi*, *A. implicata*, and *A. suborbiculata*; Mock et al. 2004; Zanatta et al. 2007; see *Anodonta*). The type species for the genus is *Anodonta suborbiculata* Say, 1831. In addition to the four taxa mentioned above, a new species was described subsequent to Turgeon et al. (1998), *Anodonta hartfieldorum* (Williams et al. 2009). We also place this species in *Utterbackiana* because it appears closely related to *U. suborbiculata* and was formerly associated with that species.

Venustaconcha *Frierson, 1927*.—Turgeon et al. (1998) recognized two species. Molecular data showed that *Villosa perpurpurea* and *Villosa trabalis* also are members of *Venustaconcha* (Kuehnl 2009; Lane et al. 2016). Molecular data further showed that *Venustaconcha perpurpurea* is a junior synonym of *Venustaconcha trabalis*, and populations of this species in the Tennessee River drainage are genetically and morphologically distinct from those in the Cumberland River drainage (Lane et al. 2016). Based on the type locality of *trabalis*, Flint River, Alabama, this name is applicable to the Tennessee River drainage species. *Unio troostensis* Lea, 1834, is the oldest available name for the Cumberland drainage species (type locality is Stones River, Tennessee), and we recognize this species as *Venustaconcha troostensis* (see Haag and Cicerello 2016; Lane et al. 2016). Cumberland Bean was the common name used for *V. trabalis* by Turgeon et al. (1998), but Lane et al. (2016) proposed Tennessee Bean for *Venustaconcha trabalis* and Cumberland Bean for *Venustaconcha troostensis*; we follow this use. *Venustaconcha sima* was not included in Turgeon et al. (1998) but was elevated from synonymy by Gordon (1995) based on shell coloration and conchological characters, and its distinctiveness is supported by molecular data (Kuehnl 2009). This species was synonymized under *Villosa iris* by Parmalee and Bogan (1998), and molecular data support its relationship to *Villosa* (Kuehnl 2009). We recognize *sima* as a species of *Villosa*.

Villosa *Frierson, 1927*.—Turgeon et al. (1998) recognized 17 species and one subspecies. Molecular data show that *Villosa*, as depicted by Turgeon et al. (1998), is wildly polyphyletic, with species occurring in as many as seven different clades within the Lampsilini (Kuehnl 2009). These and other data support reassignment of *Villosa trabalis* to *Venustaconcha*, synonymization of *Villosa perpurpurea* under *Venustachoncha trabalis* (see *Venustaconcha*), and reassignment of *Villosa choctawensis* and *V. arkansasensis* to *Obovaria* (see *Obovaria*). Most other species will require reassignment to existing genera (e.g., *V. vaughniana* to *Ligumia*; Raley et al. 2007; Kuehnl 2009) or resurrected or newly described genera, potentially with only *Villosa amygdala* and *V. villosa* remaining in *Villosa* (Kuehnl 2009). However, these relationships are not fully understood, and currently synonymized or newly described generic names have not been proposed. With the exception of *Villosa trabalis*, *V. perpurpurea*, *V. choctawensis*, and *V. arkansasensis*, we retain all other species recognized by Turgeon et al. (1998) in *Villosa*.

Villosa vanuxemensis umbrans was elevated to species status by Williams et al. (2008) based on shell characters and preliminary molecular data, and subsequent molecular data support this change (Kuehnl 2009); based on this evidence, we recognize *V. umbrans*. There are several undescribed taxa within *Villosa* (Kuehnl 2009; Harris et al. 2009). We recognize correction of gender agreement for *Villosa amygdala*, as given by Turgeon et al. (1998), to *Villosa amygdalum* following Williams et al. (2011, 2014). We recognize fifteen species of *Villosa*.

DISCUSSION

Changes in mussel taxonomy compared to Turgeon et al. (1998) reflect our better understanding of mussel phylogenetic relationships obtained mainly from molecular genetic data (e.g., Serb et al. 2003; Campbell and Lydeard 2012a, 2012b; Inoue et al. 2013, 2014; Pfeiffer et al. 2016). Molecular genetics continues to be one of the most important tools for understanding unionoid relationships and taxonomy, but other data sets (e.g., life history, host use, soft anatomy, shell morphology, zoogeography) are informative and should not be overlooked when constructing phylogenies and conducting taxonomic studies (e.g., Roe et al. 2001; Jones and Neves 2010; Lane et al. 2016).

We recognize a larger number of genera than Turgeon et al. (1998; 56 vs. 49), but the number of currently recognized species is similar. However, recent studies show that considerable cryptic biodiversity exists in the Unionidae (e.g., *Cyprogenia*, *Lampsilis*, *Villosa*). Most of this biodiversity remains to be discovered, and its future recognition may result in increased numbers of species in the United States and Canada (see Haag 2012). Currently unrecognized species may be narrowly distributed (e.g., one river system) and in need of conservation measures. Development of additional molecular markers, more inclusive taxon sampling, advancements in phylogenetic analyses, and other techniques for species delineation are facilitating taxonomic recognition of species. More thorough understanding of life histories with improved husbandry techniques should also help facilitate species recognition.

Future research will most likely reveal unrecognized taxa. Conversely, additional synonymy may be warranted for some currently recognized species. Much more research is needed to delineate true diversity of the mussels of the United States and Canada.

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REGULAR ARTICLE

MUSSEL SPECIES RICHNESS ESTIMATION AND RAREFACTION IN CHOCTAWHATCHEE RIVER WATERSHED STREAMS

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ABSTRACT

We determined the number of samples necessary to accurately estimate species richness at three sites in the Choctawhatchee River watershed in Alabama and Florida. We sampled each site eight times using 5 person-hr timed searches with a combination of visual and tactile searching from June to October 2012. We estimated total species richness at each site using the Chao 2 estimator to construct rarefaction curves. We used these relationships to determine sampling effort necessary to detect 80%, 90%, 95%, and 99% of the estimated total species richness and the percentage of species detected with successive samples. We conducted the same analyses using a subset of the data including only federally threatened or endangered (TE) species. Species detection and effort requirements differed among streams and were primarily influenced by mussel abundance. We detected 62–88% of estimated total species richness with one sample, and detection of 90–99% of species required 2.1–8.0 samples. At two sites with high mussel abundance, detection of $\geq$90% of estimated total species richness required 1.3–2.2 samples, but five samples were required to detect a similar percentage of species at a site with lower mussel abundance. A single sample was sufficient to detect all TE species present at two sites where these species were abundant, but a single sample in a stream with lower mussel abundance detected only 45% of TE species, and eight samples were required to detect 90% of TE species.

Key Words: number of samples, species richness, freshwater mussels, endangered mussels, mussel assemblages

INTRODUCTION

Substantial declines in freshwater mussel populations in North America have occurred over the past several decades (Strayer et al. 2004; Shea et al. 2013; Haag and Williams 2014). Species richness estimation is an important component of biodiversity studies and conservation, especially when considering at-risk fauna (Boulinier et al. 1998; Kéry et al. 2009). Observations of trends in species richness can focus conservation efforts in areas where diversity is declining, since few studies show significant correlations between specific habitat variables and mussel assemblages (Strayer and Ralley 1993; Niraula et al. 2015a, 2015b). Determining true species richness at a site is seldom possible (Colwell and Coddington 1994); rather, richness typically is estimated from sample data, resulting in an underestimation of species richness, the extent of which is dependent on sampling effort (Hellman and Fowler 1999). The effort required to detect a reasonable percentage of species at a site is important to know when designing sampling programs.

Due to their clustered distribution and benthic nature, mussels are difficult to sample adequately, and species richness often is underestimated due to incomplete detection (false absences) (Strayer and Smith 2003; Shea et al. 2013; Wisniewski et al. 2013). Qualitative protocols have not been well tested with regard to species detection within a given reach (Huang et al. 2011). Recent studies have used occupancy

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modeling to explicitly quantify probability of nondetection (e.g., Meador et al. 2011; Wisniewski et al. 2013). This approach provides more accurate information on species richness and other community and population variables than can be obtained from most standard sampling methods, but occupancy modeling can be labor intensive and requires specific study designs.

Rarefaction and species accumulation curves provide an alternative to occupancy modeling that can be applied more easily and quickly to standard qualitative sampling methods. A species accumulation curve is constructed by plotting the cumulative number of species found at a site versus a measure of sampling effort (e.g., number of samples, person-hours) (Colwell et al. 2004). Sampling variability (e.g., environmental factors and human bias) affects the shape of a species accumulation curve such that different sampling events provide different curves (Colwell and Coddington 1994; Moreno and Halffter 2000). The solution to this problem is a form of interpolation known as rarefaction. Rarefaction curves are constructed by repeatedly randomizing the order in which samples are added to the species accumulation curve and taking the mean values of cumulative species richness until a smooth curve is obtained (Longino and Colwell 1997). The rarefaction curve demonstrates the number of species that one would expect to find, on average, after x number of samples (Gotelli and Colwell 2001).

The Choctawhatchee River watershed in Alabama and Florida historically contained at least 21 native mussel species, of which one is now presumed extinct and five are federally threatened or endangered (TE) (Williams et al. 2008; USFWS 2012). We sampled mussels at three sites in the Choctawhatchee River watershed eight times each over 4 mo ($N = 24$). Two sites were in close proximity on the same stream (Eightmile Creek) to compare results at two similar locations. Our objectives were to (1) determine the number of samples needed to detect 80%, 90%, 95%, and 99% of the estimated total species richness at each site, and (2) determine what percentage of the estimated total species richness was detected after one to eight samples. The same analysis was performed on a subset of the community using only TE species due to their specific and limited habitat preferences (see Niraula et al. 2015a, 2015b, 2016). We also assessed species richness estimates as a function of the number of individuals encountered to allow application and comparison of our conclusions to other streams.

METHODS

Study Area

The Choctawhatchee River watershed is located in the Southeastern Plains Level III ecoregion of southeast Alabama and northwest Florida (USEPA 2013). The watershed covers approximately 12,297 km^2 and drains into Choctawhatchee Bay in Florida (Heath et al. 2010). We sampled three wadeable sites in the Choctawhatchee River watershed. All sites had predominantly sandy substrates typical of Gulf Coastal Plain streams, low to moderate amounts of woody debris, and depths generally less than 0.75 m. One site was located on the West Fork Choctawhatchee River at Blue Springs State Park, Barbour County, Alabama (BS, 31°39′49.6″N, 85°30′18.8″W), beginning about 10 m upstream of the bridge and extending 100 m upstream. This site was a fourth-order stream with an average width of 11.8 m. The second and third sites were located on a third-order stream, Eightmile Creek, Walton County, Florida. The second site (8M1, 30°58′50.3″'N, 86°10′45.5″W) began at the County Road 181 bridge and extended 68 m upstream with an average width of 6.3 m. The third site (8M2, 30°58′46.7″N, 86°10′45.4″W) was located about 75 m upstream of 8M1 (~150 m upstream of the County Road 181 bridge) and extended 40 m upstream with an average width of 6.3 m. Both streams had densely vegetated riparian zones and canopy cover.

We chose these sites because they supported diverse and abundant mussel assemblages including three federally threatened mussel species. Two additional endangered species were also documented historically at the West Fork Choctawhatchee River site (Pilarcyzk et al. 2006; Reátegui-Zirena et al. 2013). A total of eight species were reported at Eightmile Creek and 12 species were reported at BS (Pilarczyk et al. 2006).

Field Methods

We sampled each site using 5 person-hr timed searches for the initial sample. The area sampled on the initial visit was marked and mussels were sampled within the same reach at each subsequent visit, with each subsequent sampling occasion being approximately 5 person-hr. Sampling was conducted by searching all available habitat within the reach using a combination of visual searching and tactile probing at least 5 cm deep into the substrate (Carlson et al. 2008). Each site was sampled on two consecutive days at 1-mo intervals from June to October 2012 (for a total of eight sampling occasions), following Pollock's robust capture–recapture design (Pollock 1982). The Pollock design was used for a concurrent mark–recapture study at the same sites (Hyde et al. 2016), but the structure of the sampling design was not incorporated into this analysis. Mussels were identified and returned to the vicinity from which they were collected.

Data Analysis

We used the Chao 2 estimator to compute S_{est}, the estimated total species richness for each site (Chao 1987); this is a nonparametric estimator that makes no assumptions about the underlying population distribution and is commonly used to estimate species richness (Wei et al. 2010). We used the classic form of the Chao 2 estimator:

$$S_{est} = S_{obs} + \frac{q_1^2}{2q_2},$$

Table 1. Number of individuals needed to detect various percentages of estimated total mussel species richness at three sites in the Choctawhatchee River watershed, Alabama/Florida. N is the mean number of mussels/sample.

		% Estimated Total Species Richness			
Site	N	80	90	95	99
BS	121	310	550	732	921
8M1	509	—	1124	2780	4104
8M2	273	66	362	845	1665

where S_{est} is estimated total species richness, S_{obs} is detected species richness, and q_1 and q_2 are the number of uniques and duplicates, respectively. Uniques are species that were found in only one sample, and duplicates are species that were found in exactly two samples. We used this estimate to extrapolate a rarefaction curve past the reference sample (actual sampling effort, $N = 8$) using the formulas in the next paragraph. Thus, the curve to the left of the reference sample is the rarefaction curve (interpolation), while the curve to the right is the extrapolated curve.

The computer program EstimateS 9.0 (Colwell 2013) was used to calculate sample-based rarefaction curves using the following equation (equation 17 of Colwell et al. 2012):

$$\tilde{S}_{\mathrm{sample}}(t) = S_{\mathrm{obs}} - \sum_{Y_i>0}\left[\binom{T-Y_i}{t}\Big/\binom{T}{t}\right],$$

where $\tilde{S}_{\mathrm{sample}}$ (t) is the mean number of species expected in t subsamples from all T collected samples. The number of times each species was detected (i.e., incidence frequencies) is represented by Y_i, and S_{obs} is the total detected species richness. Curves were calculated for all three sites using number of samples ($N = 8$) and number of individuals as a measure of sampling effort. The following equation was used to extrapolate each rarefaction curve to 32 samples (equation 18 of Colwell et al. 2012):

$$\tilde{S}_{\mathrm{sample}}(T+t^*) = S_{\mathrm{obs}} + \hat{Q}_0\left[1-\left(1-\frac{Q_1}{Q_1+T\hat{Q}_0}\right)^{t^*}\right],$$

where $\tilde{S}_{\mathrm{sample}}$ $(T + t^*)$ represents the number of species expected after $T + t^*$ samples, T is the total number of samples actually collected, and t^* is the number of additional samples to which one wishes to extrapolate. The number of species found in only one sample is represented by Q_1. The estimated number of species not found in any of the samples is represented by $\hat{Q}_0$. The Chao 2 estimator was used to estimate $\hat{Q}_0$ (equal to the second term from the Chao 2 estimator formula above), and the value computed from the above formula was used as the asymptote that each extrapolated curve approached.

Table 2. Number of 5 person-hr samples needed to detect various percentages of estimated total mussel species richness at three sites in the Choctawhatchee River watershed, Alabama/Florida. Percentages were calculated from the line of best fit in Figure 1. S_{obs} is the cumulative number of species detected; S_{est} is the estimated total species richness.

	% Estimated Total Species Richness					
Site	80	90	95	99	S_{obs}	S_{est}
BS	2.6	4.5	6.0	7.6	11	11.2
8M1	—	2.2	5.4	8.0	8	8.1
8M2	0.2	1.3	3.1	6.4	8	8.1

Table 3. Observed percentage of estimated total mussel species richness (Chao 2) detected after successive samples at three sites in the Choctawhatchee River watershed, Alabama/Florida. Percentages ≥90 are bolded. Small discrepancies between this table and Table 2 are a result of differences between observed percentages and predictions from fitted equations.

	Sample							
Site	1	2	3	4	5	6	7	8
BS	62	76	84	89	**93**	**95**	**97**	**98**
8M1	88	**90**	**91**	**93**	**94**	**96**	**97**	**99**
8M2	87	**93**	**96**	**98**	**99**	**99**	**99**	**99**

Rarefaction curves were used to determine the percentage of S_{est} sampled during each visit by dividing the cumulative number of expected species in t subsamples by the estimated total species richness of each site (S_{est}). We also fit a line to our rarefaction curves in Excel and used the resulting equation to calculate the expected number of samples needed to detect 80%, 90%, 95%, and 99% of S_{est}. The same analysis was done using only TE species to determine the sampling effort needed to detect 80%, 90%, 95%, and 99% of these species at BS. This calculation was not done for 8M1 and 8M2 because all three TE species were encountered on all eight sampling occasions at those sites.

RESULTS

A total of 7,222 mussels representing 11 species were collected over eight samples at all three sites. The cumulative number of mussel species detected after eight samples was eight at both 8M1 and 8M2, which is supported by historical findings of the same eight species at that location (Pilarczyk et al. 2006). The mean number of individuals in each sample was 509 at 8M1 and 273 at 8M2 (Table 1). The cumulative number of mussel species detected after eight samples was 11 at BS, where historical records show the same 11 species in addition to one federally endangered species, *Ptychobranchus jonesi* (Southern Kidneyshell), which we did not detect (Pilarczyk et al. 2006). The mean number of individuals in each sample at BS was 121.

Rarefaction curves indicated that 310 and 550 individuals were needed to detect 80% and 90%, respectively, of the estimated total species richness at BS (Table 1); given our sampling method and mussel abundance at this site, this translated to 2.6 and 4.5 samples, respectively (Table 2). Detection of 95% of estimated total species richness at BS

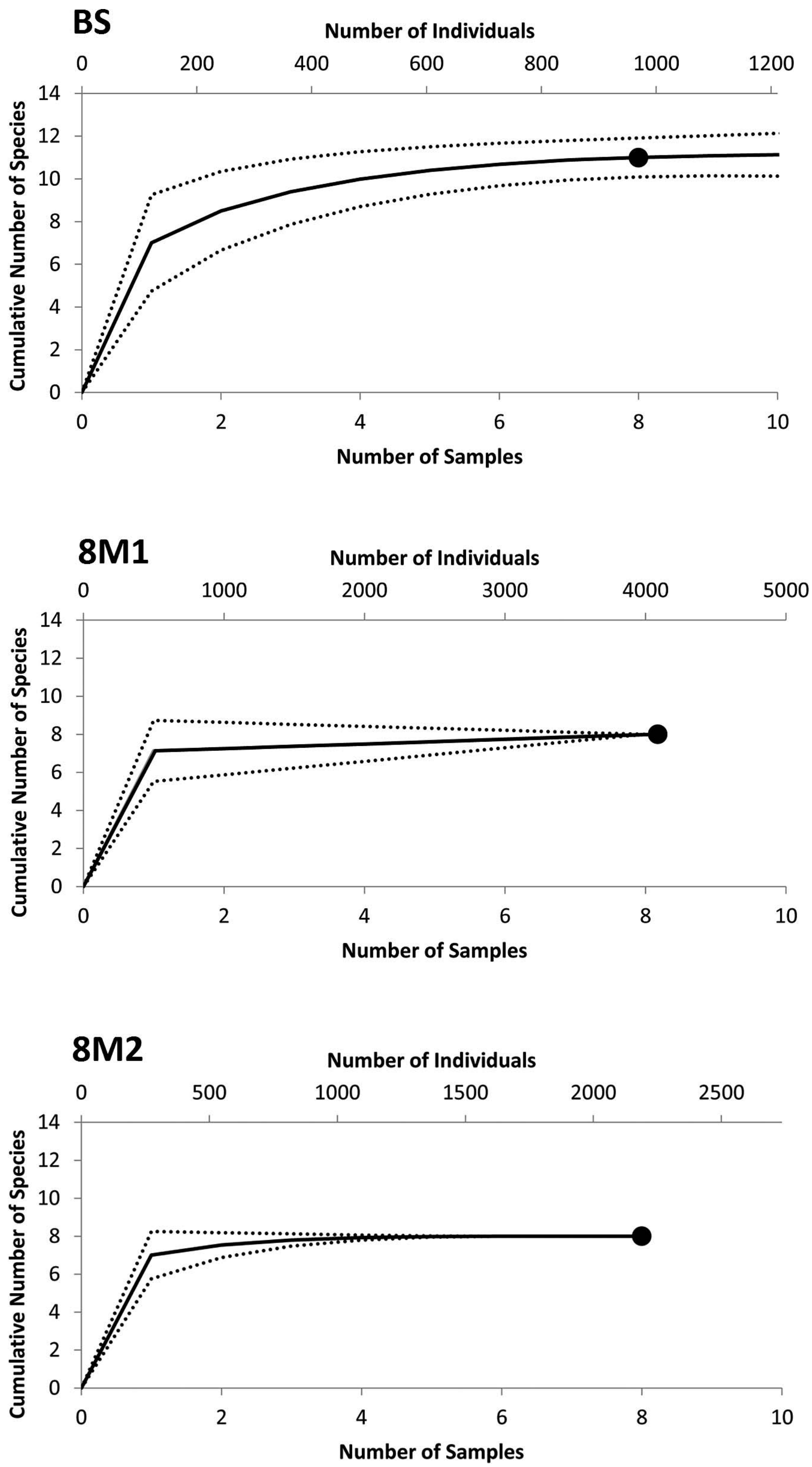

Figure 1. Rarefaction curves showing the cumulative number of species detected as a function of the number of samples and individuals collected at three sites in the Choctawhatchee River watershed, Alabama/Florida. Dotted lines are 95% confidence intervals.

required 732 individuals (6.0 samples). A single sample was sufficient to detect 80% of the estimated total species richness at both 8M1 (<510 individuals) and 8M2 (<273 individuals). Detection of 95% of the estimated total species richness at Eightmile Creek required a larger number of individuals but a smaller number of samples than at BS (8M1: 2,780 individuals, 5.4 samples; 8M2: 845 individuals, 3.1 samples).

Site BS had a much more gradual species accumulation curve than sites 8M1 and 8M2 (Table 3 and Fig. 1). With one sample, the percentage of estimated total species richness detected was much lower at BS (62%) than at 8M1 and 8M2 (88% and 87%, respectively), but percentage of detection converged for all three sites at around five samples. Percentage of detection reached only 98% at BS after all eight samples were taken. Both 8M sites had similar, steep species accumulation curves, but site 8M2 reached an asymptote after five samples, while 99% detection was not reached at 8M1 until eight samples were taken (Table 3 and Fig. 1).

All three TE species at 8M1 and 8M2 were found on all eight sampling occasions, indicating that one sample was sufficient to detect all the TE species at these sites. In contrast, only one TE species was found on all sampling occasions at BS (*Pleurobema strodeanum*, Fuzzy Pigtoe), and five samples were needed to detect *Fusconaia burkei* (Tapered Pigtoe). Only 45% of the estimated number of TE species (about two out of five of the historically recorded species) were detected at BS after one sample and only 90% (about four out of five species) were detected after all eight samples. An estimated 15.1 samples were needed to detect 99% of the federally listed species present at BS.

DISCUSSION

Local abundance is one of the primary influences on the number of samples needed to adequately estimate species richness. Blue Springs had lower abundance and higher diversity of mussels than the Eightmile Creek sites, with a correspondingly lower number of mussels per sample. A rarefaction study of fish in the Little Choctawhatchee River watershed found that very low abundance usually resulted in a lower percentage of species being detected for a given number of samples when compared with sites with higher abundance (Hyde et al. 2014). That study, along with our observations, suggests that higher abundance should result in higher species detectability. At least nine samples (electrofishing 35 times stream width) were needed to detect 90% of the estimated fish species richness based on a study of 12 sites, suggesting that mussel assemblages may require fewer repeat sampling events than fish to detect a similar percentage of species (Hyde et al. 2014). This difference likely is a result of fishes having greater mobility, decreased capture probability, and generally higher species richness.

A study in wadeable Illinois streams found means of 60.5%, 79.0%, and 87.4% of the estimated mussel species across 18 sites after 4, 10, and 14 person-hr, respectively (27–942 individuals and 5–18 species per site; Huang et al. 2011). These results are similar to our species richness estimates at BS after one, two, and three samples (62%, 76%, and 84%, respectively, 5 person-hr each), despite the fact that the Illinois study encompassed greater environmental variability and used an estimator based on abundance (Chao 1) rather than incidence data. Huang et al. (2011) also found that sampling adequacy decreased as stream size increased. This phenomenon may partially explain the lower number of samples needed to estimate species richness in Eightmile Creek, while the higher number of individuals needed at Eightmile Creek is likely a result of higher mean abundance per sample and the consequent lack of small sample sizes at those sites.

One sample (5 person-hr) was sufficient to find all TE species at both 8M1 and 8M2 because these species are locally abundant at the sites (Pilarcyzk et al. 2006; Reátegui-Zirena et al. 2013). At BS, TE species were much less common and greater effort was necessary to detect them. The Chao 2 estimator predicted 4.4 TE species at BS and five TE species were reported historically from this site, but we found only four TE species. The only TE species we did not find was the federally endangered *Ptychobranchus jonesi*; this species is on the verge of extinction and only a few individuals have been found in the last 20 yr with the exception of Gangloff and Hartfield (2009) who found 13 individuals in Pea River (Blalock-Herod et al. 2005; Pilarcyzk et al. 2006; Williams et al. 2008). In another study, increasing sampling effort from 1.5 to 4.5 person-hr at a site dramatically increased detection of rare mussel species, but even this increased effort was not sufficient to consistently detect extremely rare species (Metcalfe-Smith et al. 2000). Our model predicted that 15 samples were necessary to detect all species at BS, but for extremely rare species such as *P. jonesi*, detection is largely a matter of chance.

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NOTE

VERIFICATION OF TWO CYPRINID HOST FISHES FOR THE TEXAS PIGTOE, *FUSCONAIA ASKEWI*

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ABSTRACT

We evaluated the suitability of three cyprinid fishes previously proposed as hosts for the state threatened Texas Pigtoe (*Fusconaia askewi*). We collected naturally infested fishes from the wild, held them in captivity until glochidial development and juvenile excystment occurred, and identified a subsample of juveniles to species using the mitochondrial gene ND1. The Red Shiner (*Cyprinella lutrensis*), Blacktail Shiner (*Cyprinella venusta*), and Bullhead Minnow (*Pimephales vigilax*) all carried glochidial infestations from May to August. Red Shiners and Blacktail Shiners produced large numbers of juvenile mussels (metamorphosis success = 29.4% and 46.3%, respectively), and all sequenced individuals ($N = 15$) were identified as *F. askewi*, confirming that these species serve as hosts in the wild. Bullhead Minnows carried the highest glochidial infestation but produced only two juveniles (metamorphosis success = 0.3%), neither of which could be positively identified to species.

KEY WORDS: unionid, glochidia, genotyping, freshwater mussel, conservation

INTRODUCTION

The life cycle of most freshwater mussels (family Unionidae) involves an obligate ectoparasitic stage during which the larvae (glochidia) attach to and encyst on the gills or fins of fishes where they develop into juveniles and excyst to begin a free-living existence. Many unionids are specialists whose glochidia can develop only on certain, usually closely related, fish species. Host use is known reasonably well for about one-third of North American unionids, but host information for many other species is based on unconfirmed relationships (O'Dee and Watters 2000; Haag 2012). Host information exists for only about half of the 51 unionid species reported from Texas (Howells et al. 1996; Winemiller et al. 2010; Marshall 2014).

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Two methods used to determine host fishes of unionids are laboratory-based artificial infestations and morphological or molecular identification of glochidia on the gills of wild-caught fish (e.g., Zale and Neves 1982; O'Dee and Watters 2000; Martel and Lauzon-Guay 2005; Kneeland and Rhymer 2007). Artificial infestations in the laboratory can confirm the ability of glochidia to develop on a particular fish species, but they do not incorporate all of the biotic and abiotic variables that could influence larval development in a natural setting (Neves et al. 1985; Bauer and Wächtler 2001; Gillis 2011). Identification of glochidia naturally infested on wild fishes can provide information from a more natural context, but these observations do not provide conclusive evidence of host suitability because glochidia may attach briefly to nonsuitable hosts before they are rejected by the host's immune system (Watters and O'Dee 1996; Haag 2012).

Marshall (2014) determined 17 potential host fishes for the state threatened Texas Pigtoe (*Fusconaia askewi*), with the Red Shiner (*Cyprinella lutrensis*), Blacktail Shiner (*Cyprinella venusta*), and Bullhead Minnow (*Pimephales vigilax*) showing the greatest infestations. These proposed relationships were based on observations of *F. askewi* glochidia naturally infested on wild fishes and identified by molecular markers, but production of juvenile mussels on these fish species was not confirmed. We evaluated the suitability of *C. lutrensis*, *C. venusta*, and *P. vigilax* as hosts for *F. askewi*. We collected wild individuals of the three target fish species that carried natural infestations of mussel glochidia from three eastern Texas streams, housed them in the laboratory until juvenile mussels were released, then identified the juvenile mussels with molecular methods. We also report differences in juvenile mussel production among fish species as another way to evaluate their relative suitability as hosts.

METHODS

Field Sites and Sampling

Cyprinella lutrensis, *C. venusta*, and *P. vigilax* were collected from three streams in eastern Texas that support

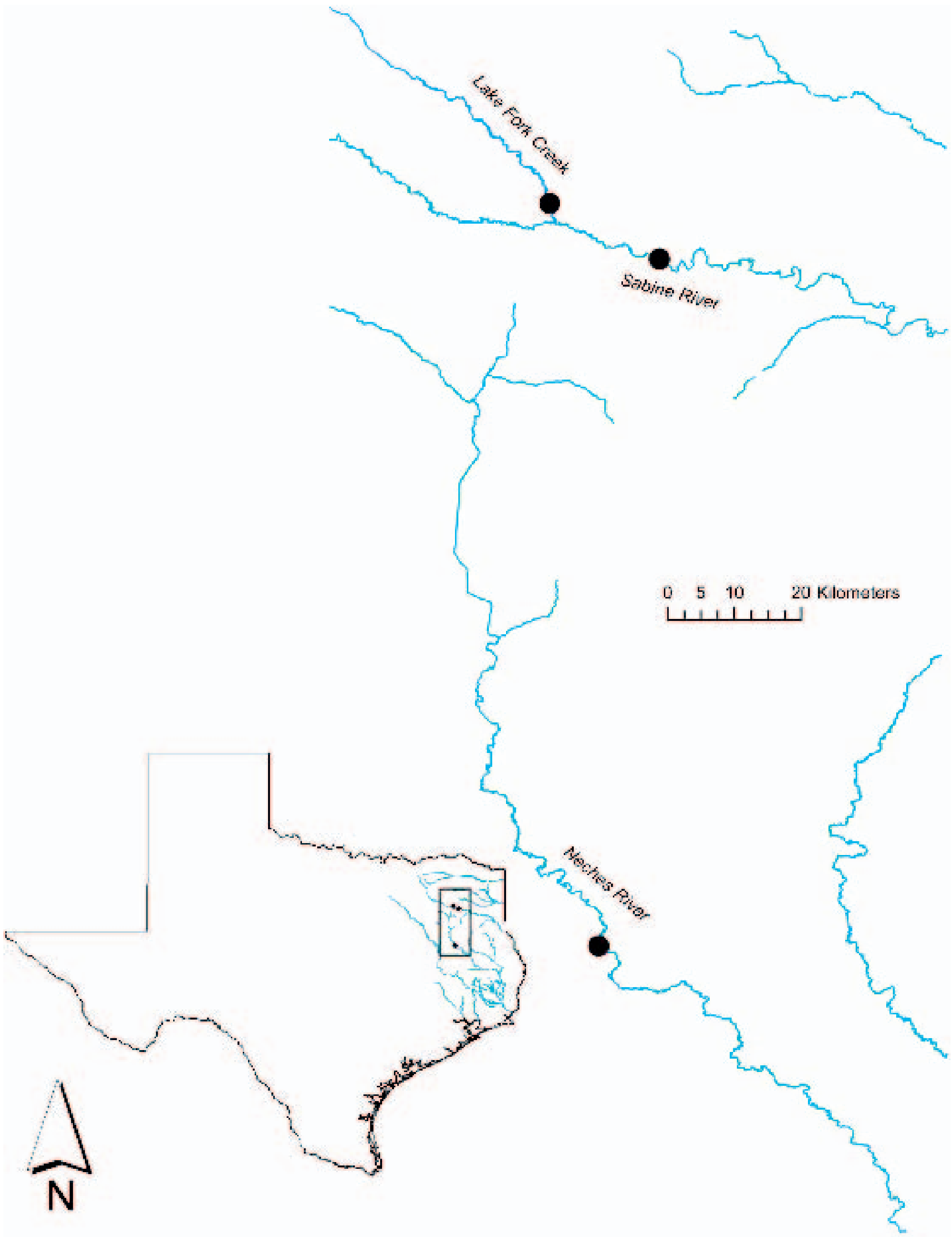

Figure 1. Texas collection locations for Red Shiners (*Cyprinella lutrensis*), Blacktail Shiners (*Cyprinella venusta*), and Bullhead Minnows (*Pimephales vigilax*).

populations of *F. askewi*: Sabine River near Highway 14, Smith County; Neches River near Highway 294, Anderson County; and Lake Fork Creek near Highway 80, Wood County (Fig. 1). We collected fishes from the Sabine and Neches rivers on eight different days between May and October of 2014 (Table 1) based on times of maximum glochidial infestation in these rivers reported by Marshall (2014). We collected fishes from Lake Fork Creek on a single date (August 4, 2014) to increase sample sizes of target fishes when high flow prevented sampling on the Sabine and Neches rivers. Fishes were collected from each site over a 150-m reach near mussel beds using a 7.5-m bag seine. Electrofishing was not used to avoid mortality or stress to fish that may cause release of encysted glochidia. We attempted to collect fishes of varying sizes (3–7 cm length) for each species. Water temperature, pH, and conductivity were measured using a YSI multi-probe meter (YSI Incorporated, Yellow Springs, OH, USA) for each sampling event.

Laboratory Housing of Fishes

Fishes collected from the field were brought back to the Department of Biology Aquatic Ecology Laboratory at the University of Texas at Tyler. Fish were then placed in 3-L

Table 1. Infestation of Red Shiners (*Cyprinella lutrensis*), Blacktail Shiners (*Cyprinella venusta*), and Bullhead Minnows (*Pimephales vigilax*) by mussel glochidia at three eastern Texas collection sites (Sabine = SBN, Neches = NCHS, Lake Fork Creek = LKFRC). (*n*) refers to the number of fishes examined on each date. Number of glochidia is divided into those that excysted as juveniles (Juv.), those that were sloughed prior to metamorphosis into juveniles (Gloch.), and those that remained encysted at the end of the experiment (Encysted).

	(*n*)	Date	Site	Juv.	Gloch.	Encysted	Total
Cyprinella lutrensis	46	May 29, 2014	SBN	111	205	3	319
	26	July 10, 2014	SBN	45	75	17	137
	10	July 11, 2014	NCHS	7	87	15	109
	11	August 4, 2014	LKFRC	13	172	33	218
	15	August 7, 2014	NCHS	67	45	5	117
	3	October 23, 2014	SBN	0	0	0	0
	3	October 24, 2014	NCHS	0	0	0	0
Total	114			243	584	73	900
Cyprinella venusta	14	June 3, 2014	SBN	16	0	1	17
	6	July 10, 2014	SBN	0	0	2	2
	7	July 11, 2014	NCHS	9	14	0	23
	23	August 4, 2014	LKFRC	18	57	60	135
	22	August 7, 2014	NCHS	25	8	4	37
	15	October 24, 2014	NCHS	0	0	0	0
Total	87			68	79	67	214
Pimephales vigilax	1	May 29, 2014	SBN	0	0	0	0
	2	June 3, 2014	SBN	2	251	0	253
	3	July 10, 2014	SBN	0	405	0	405
	14	October 23, 2014	SBN	0	0	0	0
	26	October 24, 2014	NCHS	0	0	0	0
Total	46			2	656	0	658

tanks in an AHAB unit (Pentair Aquatic Eco-Systems, Inc., Apopka, FL, USA) in groups of up to seven smaller individuals or two to three larger individuals and separated by species, collection date, and collection site. Multiple individuals of the same species and origin were housed together to decrease stress in these shoaling species and because our system was limited to 20 tanks. We monitored water temperature, pH, and conductivity every other day with a multi-probe YSI meter, and we adjusted these conditions to be similar to river sites where the fish were collected.

Juvenile Collection

Juvenile collection devices consisting of 3.5-cm-long polyvinyl chloride pipe segments with 118-μm mesh netting on one end were placed on each tank; these permitted water exiting the tanks to flow through while retaining glochidia and juvenile mussels (Barnhart 2006). This mesh size is smaller than the minimum size of *F. askewi* glochidia (128 μm; Howells et al. 1996). We removed and inspected juvenile collectors every other day for the first 2 wk of the trial and sporadically until termination of the trial. We examined material retained on the netting under an Olympus SZ dissection microscope (Olympus Corporation of the Americas, Center Valley, PA, USA) and counted all glochidia and juveniles. Juvenile mussels were distinguished from glochidia based on the presence of internal tissue development and movement, such as protrusion of the foot from the shell (Howells et al. 1996). We calculated overall infestation intensity ([number of juveniles + number of sloughed or encysted glochidia]/number of fish), juvenile production (number of juveniles produced/number of fish), and metamorphosis success (number of juveniles/[number of juveniles + number of sloughed glochidia]) for each potential host species across all trials. We collected subsamples of at least 10 juveniles for genetic identification from each tank on each day that tanks were inspected. Each individual was placed in a separate 1.5-mL centrifuge tube with 95% ethanol and stored at –20°C.

Duration of each trial ranged from 3 to 6 wk. If juvenile production ceased or if fishes did not produce any glochidia or juveniles for 3 wk, we terminated the trial and euthanized all fishes in that tank. This 3-wk termination criterion was based on past observations of the authors, as well as observations that unionid glochidia tend to excyst between a few days and several weeks following encystment (e.g., Haag and Warren 1997), with this process expedited in warmer regions (Watters and O'Dee 2000). Euthanized fish were then examined for glochidial encystment on their gills and fins.

DNA Sequencing and Identification

Genomic DNA was extracted from individual juveniles using a Chelex double-stranded DNA extraction protocol

(Casquet et al. 2011). We modified the protocol of Casquet et al. (2011) by adding 50 μL of a 1:15 solution of proteinase K and 10% Chelex 100 resin instead of the recommended 150 μL; this was done to avoid diluting the small amounts of genomic DNA extracted from juvenile mussel tissue. Extracted DNA was stored at –20°C until use in PCRs. The primers Leu-uurF and LoGlyR were used to amplify mitochondrial (mtDNA) NADH dehydrogenase (ND1) gene (Serb et al. 2003). PCR reactions used for amplification of the ND1 gene consisted of 20 μL: 6.7 μL purified H_2O, 0.1 μL TopTaq, 2.0 μL PCR buffer (Qiagen Sciences Inc, Germantown, MD, USA), 0.4 μL dNTPs, 2.0 μL 10X Coral Load (Qiagen), 4.0 μL Q-Solution, 1.0 μL of each primer, 0.4 μL bovine serum albumin, and 2.4 μL of DNA (~150 ng/μL). An extra 10% of the PCR reaction was created to provide a negative control with each PCR. An Eppendorf Mastercycler gradient thermal cycler (Eppendorf, Hamburg, Germany) with a heated lid was used to amplify the reactions. The reaction settings for amplification of double-stranded DNA were as follows: 94°C for 5 min; 30 cycles of 94°C for 45 s, 54°C for 60 s, and 72°C for 60 s; followed by a final extension of 72°C for 5 min. Gel electrophoresis was used to test the quality of amplification. The successfully amplified PCR products were purified using and E.Z.N.A. cycle pure kit (Omega Bio-tek, Norcross, GA, USA) following the protocol with an additional 30 μL of purified water for resuspension. Purified DNA was concentrated at 17–20 ng/μL with a 260/280 ratio around 1.8 to 2.0 as recommended by Eurofins MWG Operon where reactions were shipped to for sequencing using BigDye Terminator v 3.1 Cycle Sequencing kits (Applied Biosystems, Foster City, CA, USA). Sequences were edited with the Sequencher 5.2.4 program (Gene Codes Corporation, Ann Arbor, MI, USA) and then initially compared with unionid sequences available on the National Center for Biotechnology Information database (http://www.ncbi.nlm.nih.gov). The edited sequences were also cross-referenced with an adult molecular key that provides sequences for all the 37 unionid species that occur in eastern Texas (Marshall 2014). The tissue samples from mussels used to create the molecular key included adult mussels collected from the same sampling sites we used on the Sabine River and Neches River. ClustalX2.0.11 (Conway Institute UCD, Dublin, Ireland) was used to generate an alignment file of the juvenile sequences with the adult sequences of the molecular key. The alignment file from ClustalX2.0.11 was then uploaded into Mesquite (version 2.75, Mesquite Project Team, http://mesquiteproject.org) to provide ocular observation of the alignment with the sequences of the molecular key.

RESULTS

Infestation on Wild-caught Fish

A total of 114 *C. lutrensis*, 87 *C. venusta*, and 46 *P. vigilax* were collected during the study (Table 1). *Pimephales vigilax* had the highest glochidial infestation intensity (average = 14.3/fish), but only two juveniles were produced in a single trial from the Sabine River (overall juvenile production = 0.04 juveniles/fish; metamorphosis success = 0.3%). No glochidia were found encysted on the gills of deceased *P. vigilax* at the end of our trials. *Cyprinella lutrensis* had a lower glochidial infestation intensity (7.9/fish), but it had the highest rate of juvenile production (2.1/fish) and moderate metamorphosis success (29.4%). In addition, 73 glochidia were encysted on the gills of deceased fish at the end of our trials. *Cyprinella venusta* had the lowest infestation intensity (2.5/fish) and the second highest juvenile production (0.8/fish), but it had the highest metamorphosis success (46.3%). Sixty-seven glochidia were found encysted on deceased fish at the end of our trials. For all three fish species, glochidial infestation was observed from late May to early June until July or early August, and no fishes were infested in October.

Molecular Identification of Glochidia and Juvenile Mussels

DNA was extracted from a total of 127 juveniles, which consisted of 86 juveniles from *C. lutrensis*, 39 juveniles from *C. venusta*, and the two juveniles from *P. vigilax*. Of these, DNA from eight juveniles from *C. lutrensis* and seven juveniles from *C. venusta* was succesfully amplified, sequenced, and identified. These juveniles included at least one individual from each fish species from all three sampling sites. We were unsuccessful in amplyfing and sequencing DNA from juveniles collected from *P. vigilax*.

Fourteen of our 15 sequences represented a single haplotype (GenBank accession number KY442832) that was 100% identical to both a National Center for Biotechnology Information sequence from *F. askewi* and one generated by Marshall (2014) for Triangle Pigtoes (*Fusconaia lananensis*) and *F. askewi*. Only one sequence represented a haplotype (GenBank accession number KY442833) not previously detected in eastern Texas, but this sequence was consistent with *F. lananensis* and *F. askewi*, and it differed from the other haplotype we detected by only a single base pair difference and was over 99% identical to that haplotype.

DISCUSSION

Our results confirm Marshall's (2014) identification of *C. lutrensis* and *C. venusta* as hosts for *F. askewi*. We show that these fishes routinely become infested by mussel glochidia in the wild, and these infestations result in production of juveniles with moderate metamophosis success (30–46%). We cannot assess the overall robustness of these host relationships because we successfully sequenced only 15 individuals, and the identity of the majority of juveniles produced by these fishes is unknown. However, we also examined the morphology of juveniles we collected and all were consistent with the distinctive shell morphology observed in *Fusconaia* from eastern Texas (Marshall 2014).

In addition to *F. askewi*, our juvenile sequences were identical to *F. lananensis*, which also is reported from Texas (Howells et al. 1996). However, *F. lananensis* is not genetically distinguishable from *F. askewi*, and the two species are considered synonymous (Burlakova et al. 2012). Marshall (2014) also found large numbers of glochidia of the Louisiana Pigtoe (*Pleurobema riddelli*) encysted on *C. lutrensis* and *C. venusta*. However, none of the sequences we generated corresponded to this species, and shell morphology of juveniles we harvested was inconsistent with *P. riddelli* as described by Marshall (2014).

All other *Fusconaia* for which host data exist appear to be specialist on minnows, but the extent of specialization varies among species. *Fusconaia cerina*, *Fusconaia cor*, and *Fusconaia cuneolos* used a wide variety of minnow species in several genera, but *Fusconaia burkei* used only *C. venusta* (Bruenderman and Neves 1993; Haag and Warren 2003; White et al. 2008). Marshall (2014) found glochidia of *F. askewi* on a wide variety of minnow species, but we can confirm the suitability only of *C. lutrensis* and *C. venusta*. Additional laboratory studies are needed to confirm the degree of specialization in *F. askewi*.

Another potential host for *F. askewi* identified by Marshall (2014) was *P. vigilax*, but this species did not appear to be a suitable host in our study despite having the highest infestation intensity. We were unable to sequence and identify the two juveniles produced from *P. vigilax*, but their shell morphology was inconsistent with *F. askewi* juveniles identified from *C. lutrensis* and *C. venusta* (see Marshall 2014). *Pimephales vigilax* was an unsuitable host for *Fusconaia cerina*, and *Pimephales notatus* was a marginal host that produced inconsistent and low numbers of juveniles (Haag and Warren 2003). Mussel host infection strategies are thought to be highly evolved mechanisms to reduce glochidial mortality from encystment on unsuitable fishes (Haag 2012). The few studies that identified naturally encysted glochidia on fishes or juveniles produced from natural infestations generally show a low incidence of glochidial encystment on unsuitable fish species (Neves and Widlak 1988; Boyer et al. 2011; Hove et al. 2012). The high incidence of glochidial parasitism but low metamorphosis success on *P. vigilax* is unusual and seems maladaptive. Glochidia can be rejected from otherwise suitable hosts prior to metamorphosis due to stress of the fish, acquired immune responses, or the presence of scar tissue from multiple prior encystments (Meyers et al. 1980; Neves et al. 1985). We do not know if our unusual results for *P. vigilax* are due to one of these or other factors or if they simply show that host attraction strategies for some mussel species are relatively inefficient and nonspecific.

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REGULAR ARTICLE

EXTINCTION RISK OF WESTERN NORTH AMERICAN FRESHWATER MUSSELS: *ANODONTA NUTTALLIANA*, THE *ANODONTA OREGONENSIS/KENNERLYI* CLADE, *GONIDEA ANGULATA*, AND *MARGARITIFERA FALCATA*

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ABSTRACT

The recent declines in eastern North American species of freshwater mussels have been well documented, but the status of western species has been comparatively understudied. However, various local and regional studies and anecdotal observations indicate that western mussels are also declining, suggesting the need for range-wide assessments of extinction risk and changes in freshwater mussel distributions. Using historic (pre-1990) and recent (1990–2015) occurrence data from across western states and incorporating observations of recent population dynamics, we assessed the extinction risk of western freshwater mussels according to the categories and criteria of the International Union for Conservation of Nature (IUCN) Red List. Percent change in occupied watersheds (by area) between historic and recent time periods was evaluated against IUCN-established thresholds. Additionally, we considered whether evidence of declines was also supported by reported observations of changes in abundance or occurrence in studied water bodies, watersheds, or regions. We also assessed the proportion of watersheds that have reduced species richness as compared with historic levels. We evaluated four western freshwater mussel taxonomic entities: three currently recognized species and one clade consisting of two currently recognized species. Of the four entities assessed, two are Vulnerable (*Anodonta nuttalliana* and *Gonidea angulata*), one is Near Threatened (*Margaritifera falcata*), and one is Least Concern (*Anodonta oregonensis/kennerlyi* clade). Freshwater mussel richness declined 35% across western watersheds by area, and among the most historically diverse watersheds, nearly half now support fewer species/clades. Future research and conservation efforts should prioritize identifying the proximate causes for these declines and preserving existing habitat and populations.

KEY WORDS: extinction risk, freshwater mussel, IUCN Red List, *Anodonta, Gonidea angulata, Margaritifera falcata*

INTRODUCTION

Freshwater mussels (Bivalvia: Unionoida) are a diverse, important component of freshwater ecosystems in North America and globally, and only recently has their ecological importance been well documented (Vaughn and Hakenkamp 2001; Howard and Cuffey 2006; Vaughn et al. 2008; Haag 2012; Lopes-Lima et al. 2014; Vaughn 2017). Their cultural importance in North America dates back more than 10,000 yr

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(reviewed in Haag 2012), including in the Pacific Northwest (Osborne 1951; Lyman 1984), where they remain culturally significant today (Brim Box et al. 2006; Norgaard et al. 2013; CTUIR 2015). Despite their ecological and cultural significance, freshwater mussels are among the most imperiled faunal groups worldwide (Bogan 1993; Williams et al. 1993; Lydeard et al. 2004).

North America has the greatest freshwater mussel diversity in the world, with more than 300 species currently recognized (Haag and Williams 2014). Much of this diversity is concentrated in the eastern (i.e., east of the Continental Divide), and specifically southeastern, USA (Graf and Cummings 2007; Haag 2012). The western freshwater mussel fauna from the Pacific region, which includes drainages flowing into the Pacific Ocean, Arctic Ocean, and the endorheic Great Basin, is composed of three genera (*Anodonta*, *Gonidea*, and *Margaritifera*). *Gonidea angulata* (Lea, 1838) is monotypic among North American freshwater mussels, being the only extant member of the genus. Both *G. angulata* and *Margaritifera falcata* (Gould, 1850) are easily identified and have well-defined distributions across western states in comparison with species comprising the genus *Anodonta*, for which the number and identity of species is a continuing source of confusion. Diagnostic shell characters are lacking in *Anodonta*. As a result, identification of specimens can be challenging, and misidentification is common, further complicating the interpretation of ranges of western *Anodonta*. Misidentification is also common, which further complicates the interpretation of ranges in western *Anodonta*.

Western species of *Anodonta* recognized by Turgeon et al. (1998) include *Anodonta beringiana* Middendorff, 1851; *Anodonta dejecta* Lewis, 1875; *Anodonta nuttalliana* I. Lea, 1838; *Anodonta oregonensis* I. Lea, 1838; *Anodonta californiensis* Lea, 1852; and *Anodonta kennerlyi* Lea, 1860. Recent genetic research by Chong et al. (2008; mitochondrial markers) and Mock et al. (2010; nuclear and mitochondrial markers) suggested that western *Anodonta* are composed of three distinct clades: *A. nuttalliana*/*A. californiensis*, *A. oregonensis*/*A. kennerlyi*, and *A. beringiana*. Furthermore, Lopes-Lima et al. (2017) advocate for reassigning *A. beringiana* to the genus *Sinanodonta*. Within the *A. nuttalliana*/*californiensis* clade, Chong et al. (2008) and Mock et al. (2010) found that shell morphology (including degree of inflation and wing prominence, characteristics historically used to identity individual species) was incongruous with genetic identity and relationships. In combination with the evident relatedness of populations and lack of interspecific differentiation, these findings indicate that there is only one species in that clade (properly named *A. nuttalliana* according to the rules of the ICZN Code [1999]). Because the geographic sampling was not very extensive for the *oregonensis*/*kennerlyi* clade, and because nuclear markers were not included in the study by Chong et al. (2008), the number of species within that clade remains unresolved.

The validity of an additional western *Anodonta* species, *A. dejecta*, also remains unresolved. Its validity was questioned by Bequaert and Miller (1973), although the Turgeon et al. (1998) and Graf and Cummings (2007) checklists include this species. Genetic analysis of *Anodonta* sampled from multiple basins in the southwest, within what has historically been considered the range (Simpson 1897, 1914), has only confirmed the presence of *A. nuttalliana* sensu lato (Mock et al. 2010; Culver et al. 2012, Arizona Game and Fish Department, unpublished report). Lewis' (1875) original type locality has long been considered in error, and Simpson redefined the type locality of *A. dejecta* on the basis of limited evidence (1897, 1914). Given the failure to confirm the presence of any *Anodonta* species distinct from *A. nuttalliana* in the region, we consider *A. dejecta* a nomen dubium.

Declines of North American freshwater mussels over the past century have been well documented, with 74% of species considered imperiled (FMCS 2016). However, compared with their eastern counterparts, less is known about western freshwater mussels, and detailed information on life history, conservation status, and management priorities remains incomplete. Although local or regional status assessments have been developed for western freshwater mussels in the past few decades (e.g., Bequaert and Miller 1973; Taylor 1981; Frest and Johannes 1995; COSEWIC 2003; Hovingh 2004; Howard et al. 2015), range-wide assessments based on detailed occurrence data have not been completed (but see reviews by Jepsen and LaBar 2012; Jepsen et al. 2012a, 2012b). Such occurrence data have now been compiled for western freshwater mussels (Xerces/CTUIR 2015), with the exception of *Sinanodonta beringiana*, for which fewer historic and recent records exist. With this new database, it has become possible to assess the extinction risk of western freshwater mussels using the categories and criteria of the International Union for the Conservation of Nature (IUCN) Red List. In this study we conducted assessments of the extinction risk for *G. angulata*, *M. falcata, A. nuttalliana*, and the *A. oregonensis*/*kennerlyi* clade, and reviewed relevant threats and conservation considerations for western freshwater mussels.

METHODS

The IUCN Red List (http://www.iucnredlist.org/) ranks organisms according to seven categories of extinction risk, ranging from Extinct to Least Concern (Table 1). We assessed extinction risk for the Winged Floater (*A. nuttalliana*), the Western Ridged Mussel (*G. angulata*), the Western Pearlshell (*M. falcata*), and the *A. oregonensis*/*kennerlyi* clade by assigning them to one of the seven categories based on the IUCN criterion A, which assesses population size reduction. Specifically, we used subcriterion A2, and assessed population size reductions for each species or clade on the basis of a decline in extent of occurrence (EOO) (IUCN 2012). Our analysis relied on occurrence data, and our estimates of population trends were informed only by the presence of individuals or populations, which in turn may be based on evidence of live animals or empty shells. This method of

Table 1. International Union for Conservation of Nature (IUCN) Red List categories and criteria based on subcriterion A2c: “An observed, estimated, inferred or suspected population size reduction . . . over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on... a decline in area of occupancy, extent of occurrence and/or quality of habitat” (IUCN 2012).

Category	Risk of Extinction in the Wild	Threshold
Extinct (EX)	There is “no reasonable doubt that the last individual has died."	
Extinct in the Wild (EW)	The species is extinct in its natural habitat.	
Critically Endangered (CR)	Risk is extremely high.	≥80%
Endangered (EN)	Risk is very high.	≥50%
Vulnerable (VU)	Risk is high.	≥30%
Near Threatened (NT)	The species “is close to qualifying for or is likely to qualify for a threatened category in the near future."	
Least Concern (LC)	The species does not qualify for other extinction risk categories.	

analysis has the potential to under- or overestimate population size trends if existing populations differ in abundance from historic populations or if abundance varies among populations. Because such information is not generally available, we also incorporated relevant research or anecdotal observations to inform and support the extinction risk assessments (IUCN 2017).

We used a data set composed of nearly 7,300 occurrence records (observations or collections of shells or live animals) from 10 western U.S. states, three Canadian provinces, and two Mexican states (Figs. 1, 2; Xerces/CTUIR 2015). Data sources included state and federal wildlife agencies, tribes, university and nongovernmental organization biologists, and mussel enthusiasts. Data were also sourced through museum databases, published literature, unpublished reports, and incidental observations (Xerces/CTUIR 2015). More than 850 specimens from historical museum collections were also physically inventoried, measured, or photographed between 2003 and 2015 from the Smithsonian Institution (USNM), Natural History Museum of Los Angeles County (LACM), California Academy of Sciences (CAS), the Academy of Natural Sciences of Drexel University (ANSP), the Utah Museum of Natural History (UMNH), the Carnegie Museum of Natural History (CMNH), the Field Museum (FMNH), the Museum of Comparative Zoology–Harvard University (MCZ), the North Carolina Museum of Natural Sciences (NCMNS), the Illinois Natural History Museum (INHS), and the University of Michigan Museum of Zoology (UMMZ).

Only records with sufficient locality (at least county-level accuracy) and temporal (confident assignment to either the “historic” or “recent” time period) information were included. We sought to evaluate recent search effort across each species’ or clades’ entire range, and to reduce the number of false negatives (i.e., a freshwater mussel is not currently detected but is present at a site where it also historically occurred). Therefore, we combined our data set with an additional ∼4,200 records from recent aquatic invertebrate surveys (targeting other faunal groups in addition to freshwater mussels) to document search effort. All records used in this analysis are depicted in Figure 3.

For the *A. nuttalliana* data set, we included records for *A. nuttalliana*, *A. wahlamatensis* (synonymized under *A. nuttalliana* by Call 1884), and *A. californiensis*. For the *A. oregonensis/kennerlyi* clade, we included records for *A. oregonensis* and *A. kennerlyi*. Given the confusion regarding identification of *Anodonta* species, many recent *Anodonta* records in our database (more than 450 in total) were only identified to genus, and in multiple instances, these were the only records for a watershed from the recent time period, providing important information regarding the recent distribution of this genus. Western *Anodonta* largely overlap in range, so when recent *Anodonta* sp. records fell within overlapping historic ranges, those records were included in each of the two *Anodonta* assessments. When recent records identified as *Anodonta* sp. fell within the historic range of only one species or clade, those records were assumed to correspond to that species or clade. Although there are several historic records of *A. oregonensis* from Utah, Nevada and southern California, previous studies (Mock et al. 2010; Culver et al. 2012, Arizona Game and Fish Department, unpublished report) and a re-examination of historical shells in museum collections (E. Blevins et al., 2016, unpublished data) suggest that only *A. nuttalliana* is known from the arid western states of Utah, Nevada, and Arizona, and from southern California

Records were divided into historic (1842–1989, but also including archeological records) and recent (1990–2015) time periods. The demarcation of historic and recent time periods was based on IUCN (2017) guidelines, which indicate that organisms should be categorized on the basis of an assessment of “the last 10 years or three generations (whichever is longer)”. Three generations would correspond to 24, 27, and 45 years for *Anodonta*, *Margaritifera*, and *Gonidea* respectively (Heard 1975; Dudgeon and Morton 1983; Toy 1998; COSEWIC 2010; Allard et al. 2015; CTUIR, 2016, unpublished data). However, we tried to reach a balance between the limitations of our data set and the necessity of conducting the analysis over an adequate time span. For example, if we had considered all records dating to 1970 or later as “recent,” which would correspond to ∼3 generations for *G. angulata*, only 30% of the records would be considered historic. The spatial distribution of these records also excludes known

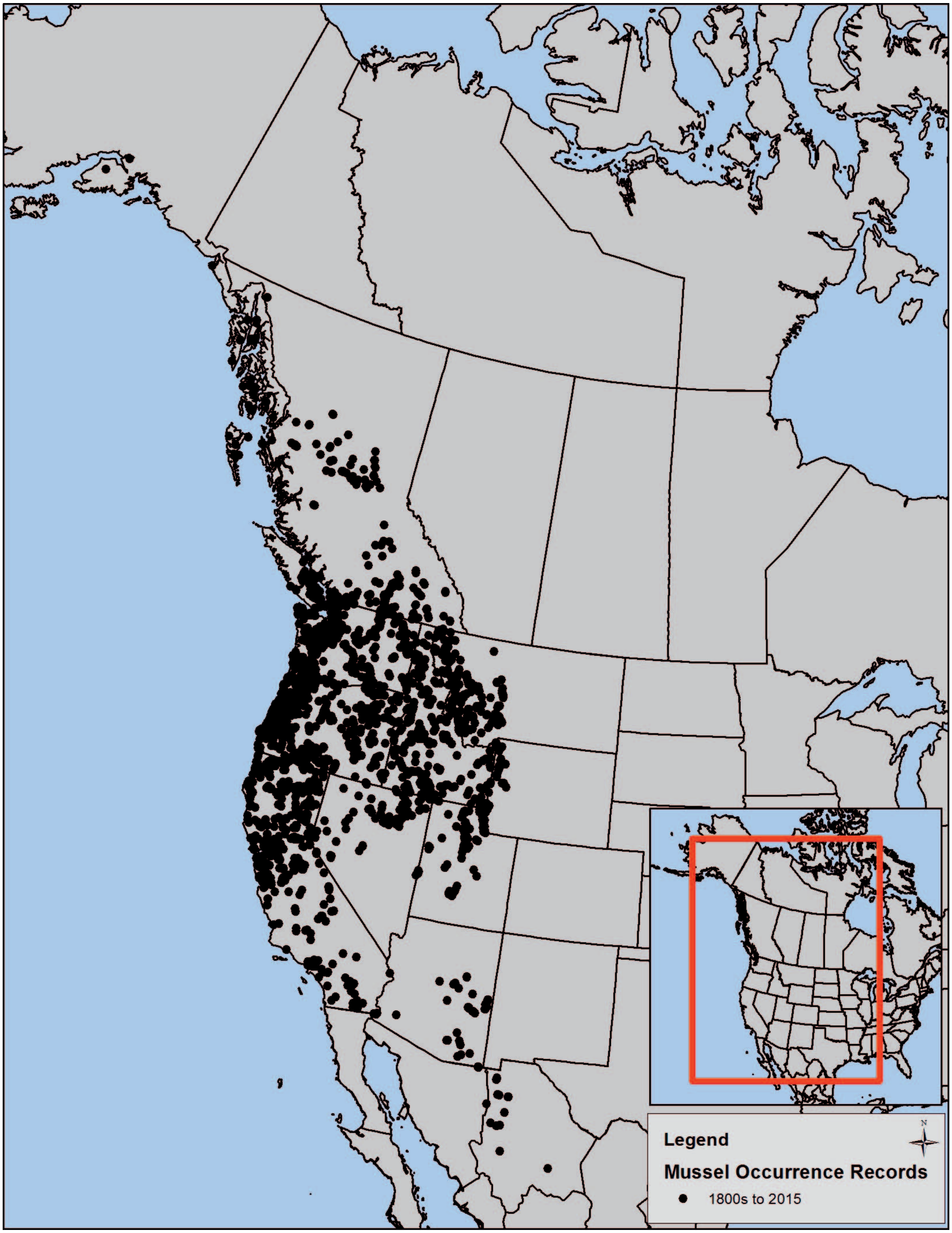

Figure 1. Occurrence records for four western North American freshwater mussel species/clades.

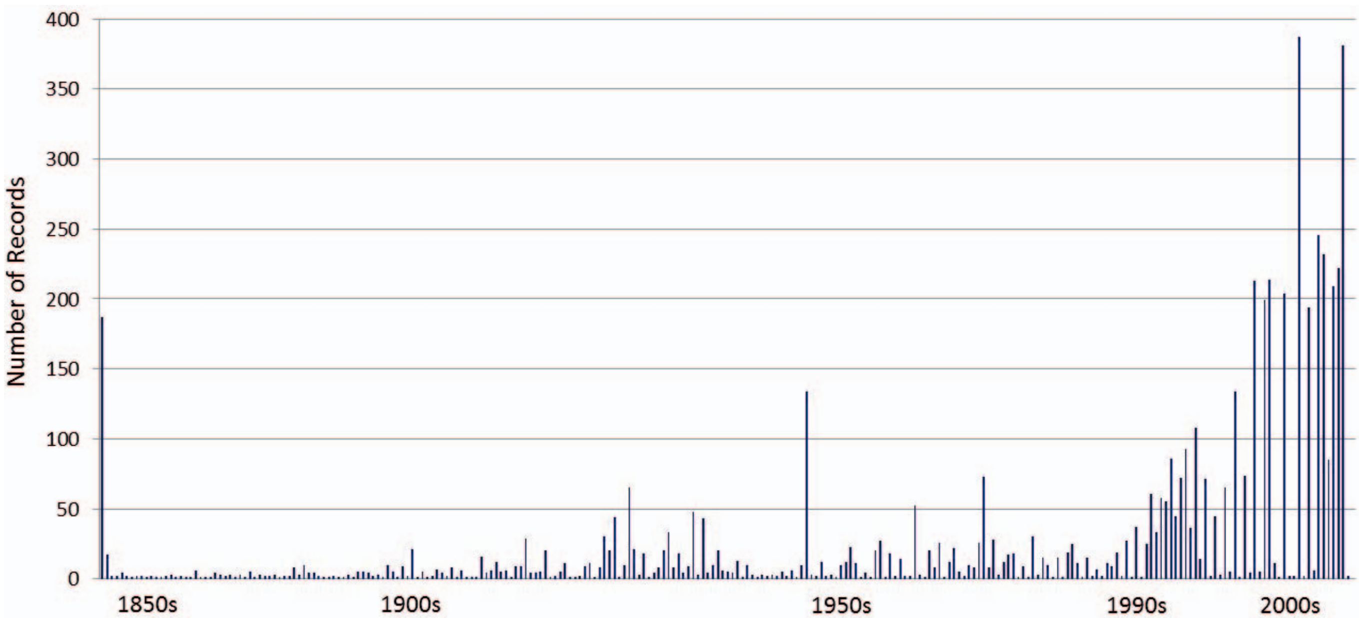

Figure 2. Number of records for freshwater mussels by year in the data set used for this analysis. Pre-1850s records are pooled across multiple years and include archeological evidence of mussel occurrences.

occurrences at range boundaries, including far-eastern Idaho and southwestern Oregon. For all western freshwater mussels, the number of records and the spatial distribution of records since 1990 provide a more complete picture of recent freshwater mussel occurrences and enable consideration of concurrent changes in mussel richness.

We compared historic and recent occurrences on the basis of occupancy of standard level 8 HydroBASINS (Lehner and Grill 2013) in the IUCN's Fresh Water Mapping Application tool, which creates convex hull polygons around selected watersheds. We selected basins on the basis of historic and recent occurrence records within watershed networks and assigned an occupancy status according to IUCN guidelines (2014). Watersheds were classified as Extant (occurrence record in recent time period) or Possibly Extinct (occurrence record in historic but not recent time period although recently searched). We calculated the EOO for each species or clade in each time period and determined percent change in area. To better depict the historical ranges of species, we also mapped watersheds that have historical records but have not been revisited as Presence Uncertain. These records were not otherwise included in our analysis based on IUCN guidelines (2014).

We also calculated a second measure: percent change in watershed area for each species or clade in each time period. This approach was based on a revised definition of EOO that incorporates hydrologic boundaries more relevant to aquatic organisms, accounting for the spatial distribution of aquatic organisms through networks of catchments (watersheds; Simaika and Samways 2010). The same measure of watershed decline was calculated using a combined data set of all records to assess general changes in freshwater mussel richness across the West.

RESULTS

The historic range of western mussels as a whole (watersheds having at least one species or clade) totaled 708 watersheds, whereas only 580 watersheds were found to be recently occupied, equaling an 18% decrease. Additionally, mussel richness has declined by 35% (Figs. 4, 5). When watersheds with higher past mussel richness (containing three or four species or clades) were considered independently, 48% of these historic "hot spots" have declined in richness in the recent time period.

Anodonta nuttalliana has declined in both EOO and watershed area (9% and 33% respectively; Table 2; Fig. 6) across Arizona, Southern California, western Nevada, and elsewhere (Blevins et al. 2016a). According to the IUCN subcriterion A2c for extinction risk (Table 1), the decline in watershed area qualifies *A. nuttalliana* for Vulnerable status. This status is also supported by recent research and observations (see Discussion). In contrast, although mussels of the *A. oregonensis/kennerlyi* clade have declined in both EOO and watershed area (9% and 26% respectively; Table 2; Fig. 7; Blevins et al. 2016b), they are still present in watersheds across the historic range, from Northern California to Alaska and east to Idaho. According to the IUCN subcriterion A2c for extinction risk (Table 1), mussels of this clade qualify as Least Concern.

In comparison, *G. angulata* has declined in both EOO and watershed area (28% and 43% respectively; Table 2; Fig. 8; Blevins et al. 2016c). According to the IUCN subcriterion A2c

Figure 3. Extent of recent (1990–2015) "search effort" in western states.

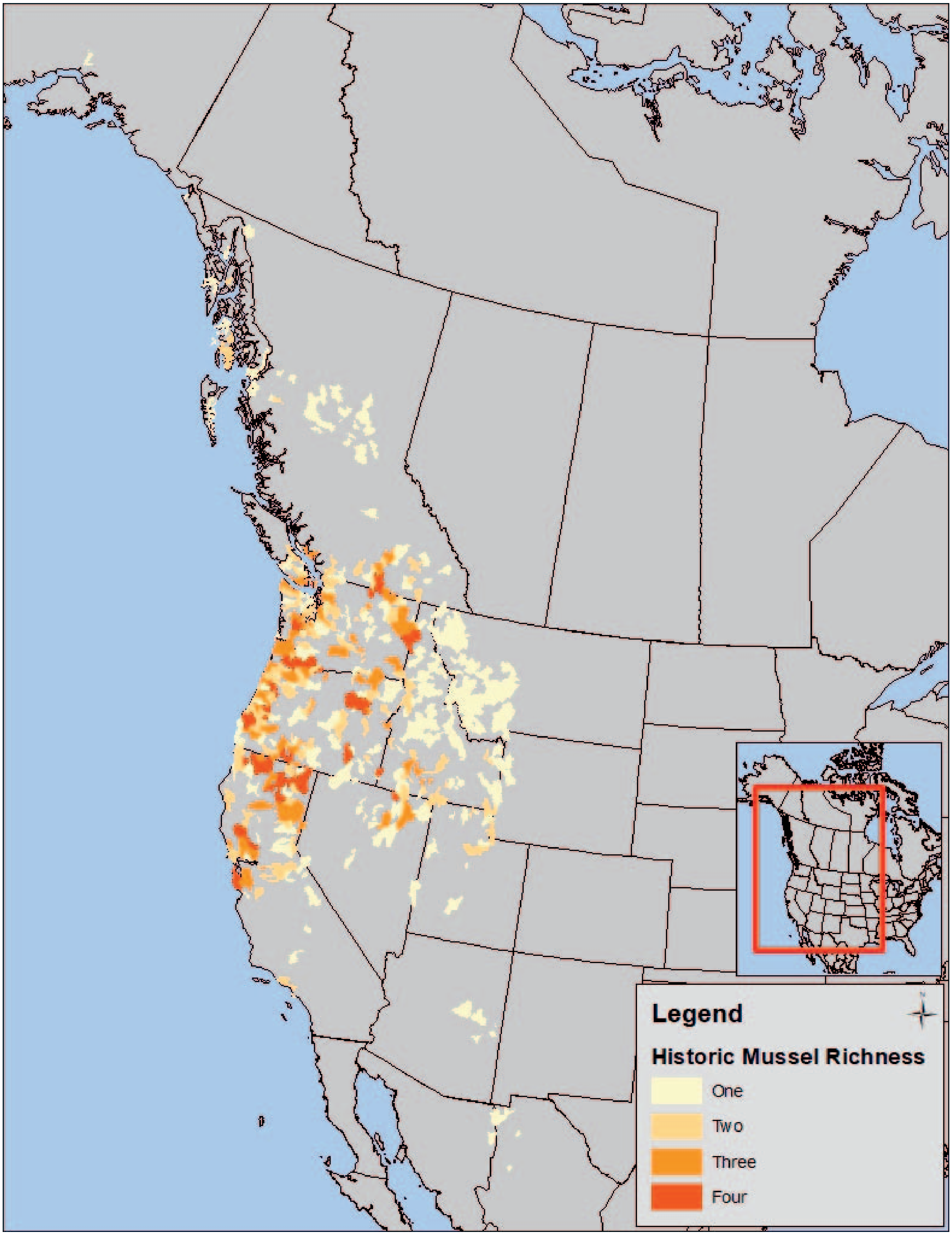

Figure 4. Historic (pre-1990) western freshwater mussel presence and richness by level 8 HydroBASIN.

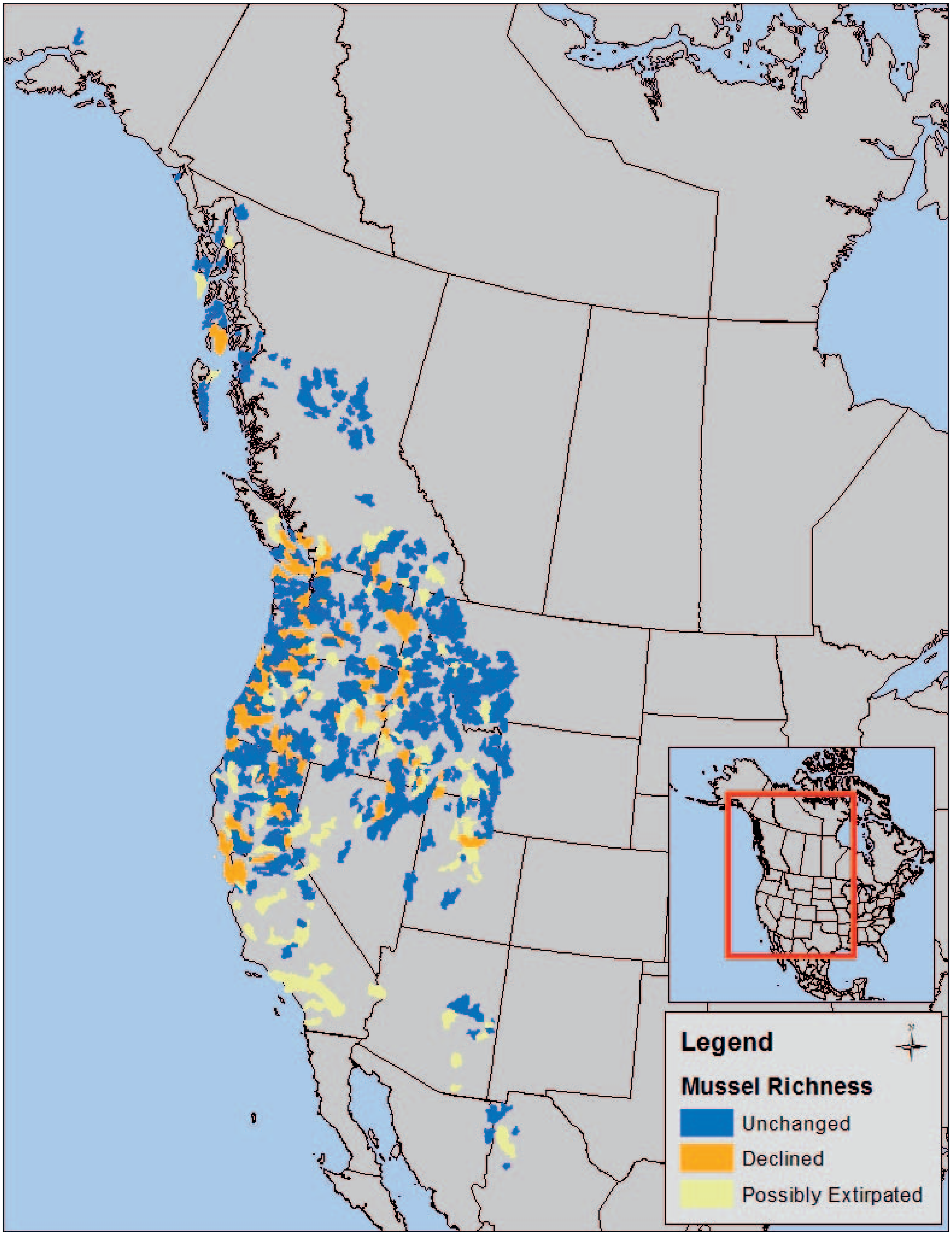

Figure 5. Change in western freshwater mussel richness by level 8 HydroBASIN between historic (pre-1990) and recent (1990–2015) time periods.

Table 2. Extinction risk assessment results for four western North American freshwater mussels.

Parameter	*Anodonta nuttalliana*	*Anodonta oregonensis/ kennerlyi* clade	*Gonidea angulata*	*Margaritifera falcata*
Generation length (yr)	8	8	15	9–45
Geographic distribution	British Columbia, Canada; Arizona, California, Idaho, Nevada, Oregon, Utah, Washington, Wyoming, USA; Chihuahua, Sonora, Mexico	British Columbia, Canada; Alaska, California, Idaho, Oregon, Washington, USA	British Columbia, Canada; California, Idaho, Nevada, Oregon, Washingon, USA	British Columbia, Canada; Alaska, California, Idaho, Montana, Nevada, Oregon, Utah, Washington, Wyoming, USA
Count of extant watersheds	223	186	99	371
Extant extent of occurrence (EOO) (km^2)	2,086,110	2,406,376	855,618	2,643,316[1]
Historic EOO (km^2)	2,294,140	2,638,209	1,195,358	2,660,131
Δ EOO (%)	−9	−9	−28	−1
Area of extant watersheds (km^2)	242,370	194,086	103,096	409,966
Area of historic watersheds (km^2)	362,797	263,560	180,743	496,005
Δ watershed area (%)	−33	−26	−43	−17
Post-1990 declines reported	Yes	No	Yes	Yes
Red List category	Vulnerable	Least Concern	Vulnerable	Near Threatened
Red List criteria	A2c		A2c	

[1]The extant EOO excludes one outlier Alaska record, as it would have resulted in a large area of the Pacific Ocean being included.

for extinction risk (Table 1), *G. angulata* qualifies as Vulnerable on the basis of decline in watershed area, a conclusion also supported by recent research and observations (see Discussion).

Margaritifera falcata has declined in watershed area by 17% but just 1% in EOO (Table 2; Fig. 9; Blevins et al. 2016d). According to the IUCN subcriterion A2c for extinction risk (Table 1), the species does not qualify for Vulnerable on the basis of quantitative criteria. However, because declines in occupancy are thought to underestimate declines in abundance of this species, and because population extirpations have been reported since 1990 (see Discussion), this species meets qualitative criteria for extinction risk equaling Near Threatened according to the IUCN Red List criteria (IUCN 2012).

DISCUSSION

Extinction Risk

We applied IUCN categories and criteria to assess extinction risk in four freshwater mussel species or clades on the basis of multiple lines of evidence, including changes in historic and recent spatial EOO, changes in watershed area occupied, research by others, and anecdotal observations across western North America. We found that although these species or clades remain relatively widespread across the West as measured by EOO (ranging from 855,618 to 2,643,316 km^2), range as measured by watershed area is considerably smaller (ranging from 103,096 to 409,966 km^2). Additionally, freshwater mussel distribution maps also depict some level of range thinning (sensu Strayer 2008). Western mussels are found in multiple types of western freshwater ecoregions, including coastal, glaciated, unglaciated, and endorheic. Given the diverse hydrology and history of western watersheds, populations in specific watershed networks may be affected by threats independently of those at the range edges. For example, *G. angulata* has not recently been reported from watersheds in several Oregon basins in the interior of its range, though the species has been documented from watersheds at the edge of its range, like the Okanagan Basin in British Columbia. Freshwater mussel richness across watersheds has also declined by 35%, and 48% of watersheds that historically had higher mussel richness (three or four species) have since lost one or more species or clades. These declines were evident despite having twice as many recent observations as historic (Figure 2).

Our analysis found that *A. nuttalliana* has declined in occurrence by as much as 33%. Historically the species occurred from Southern California north to British Columbia and east to Wyoming, but recent surveys of historic sites by Howard et al. (2015) indicated that Southern California populations are extirpated (though the species was found as far south as the Bishop Creek Canal in Inyo County, California). Observations in Arizona in the 1990s and again in the 2000s indicate that the species is probably now extant only in the Black River drainage, where populations continue to decline (Myers 2009). Thus, "recent" occupancy as

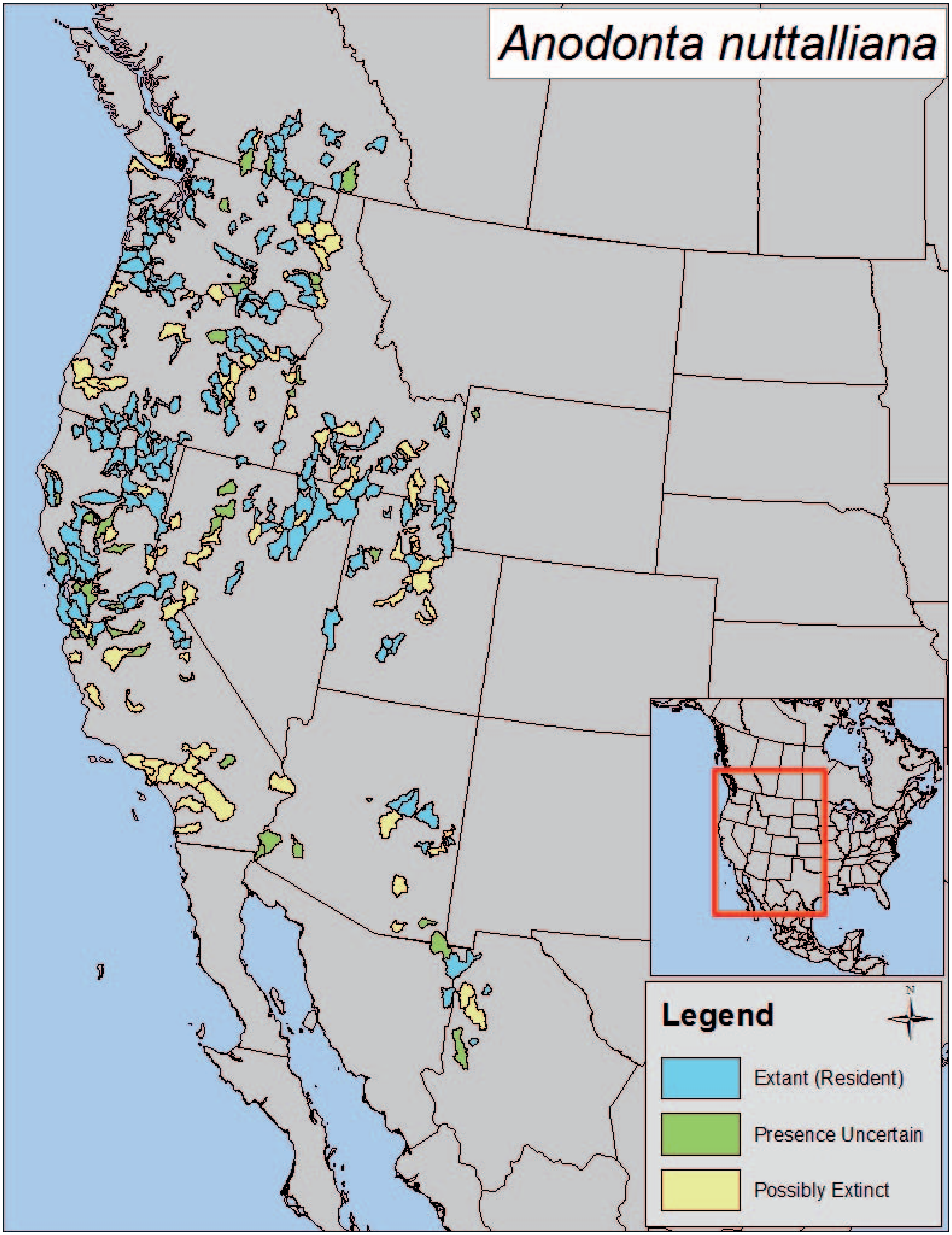

Figure 6. *Anodonta nuttalliana* status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

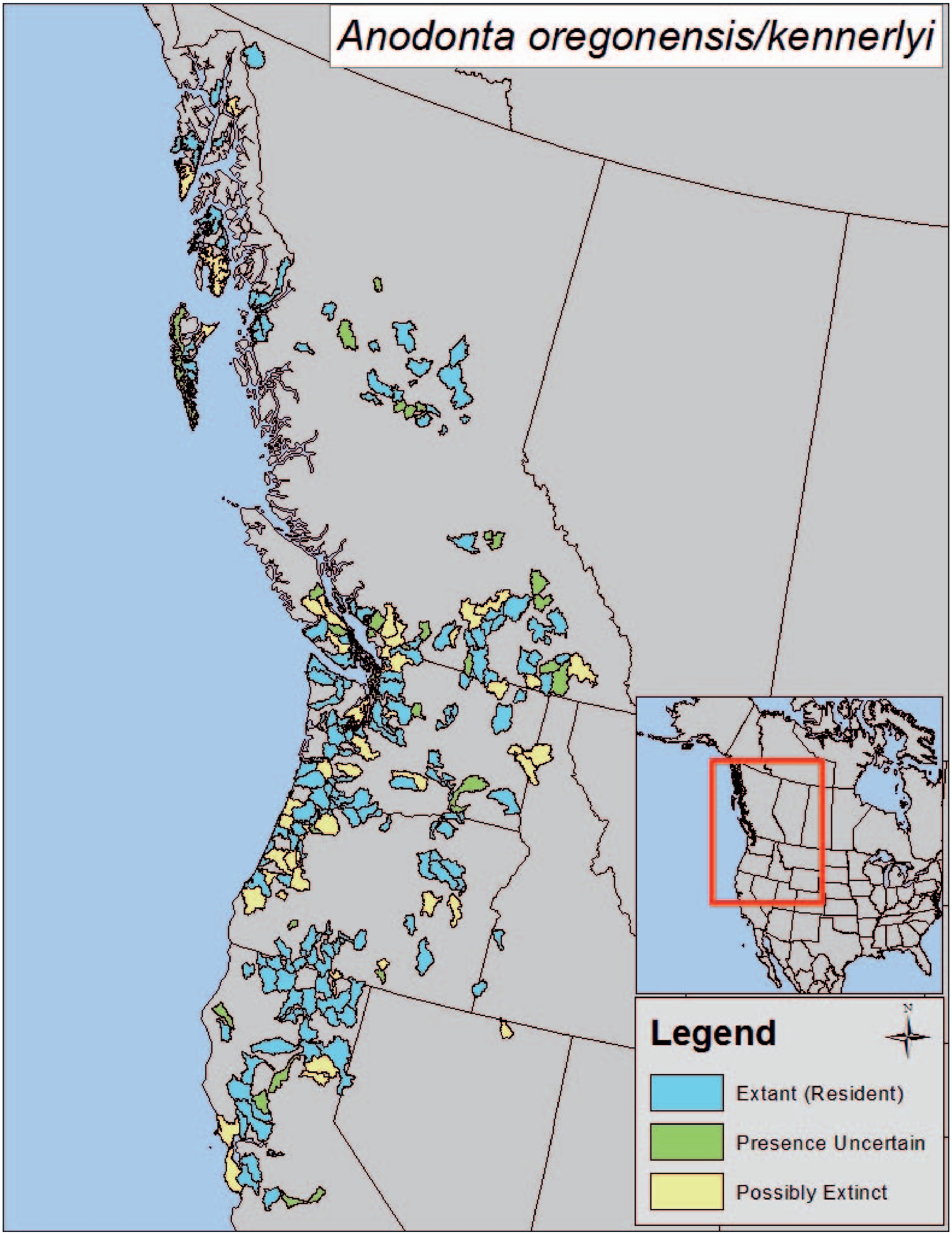

Figure 7. *Anodonta oregonensis/kennerlyi* clade status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

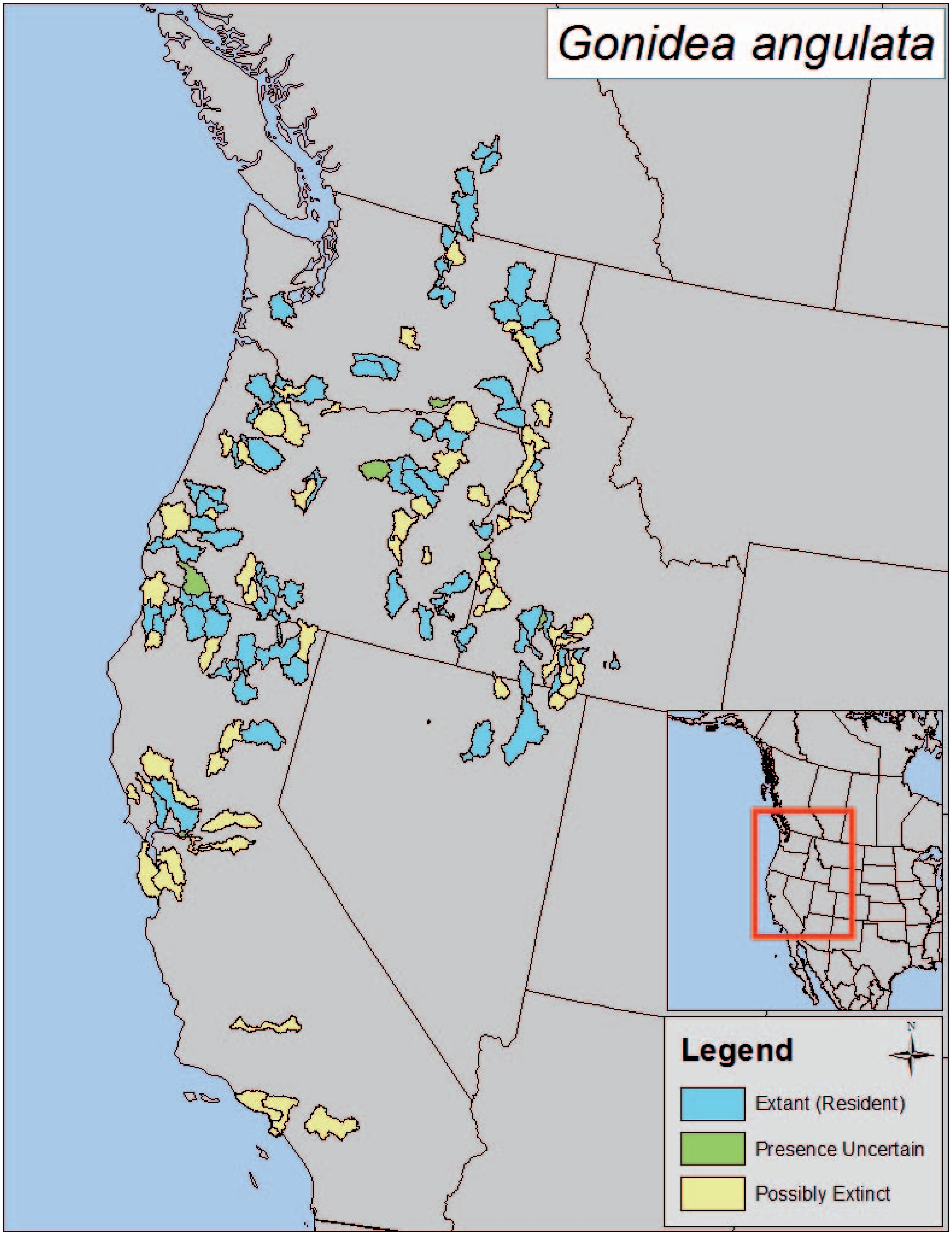

Figure 8. *Gonidea angulata* status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

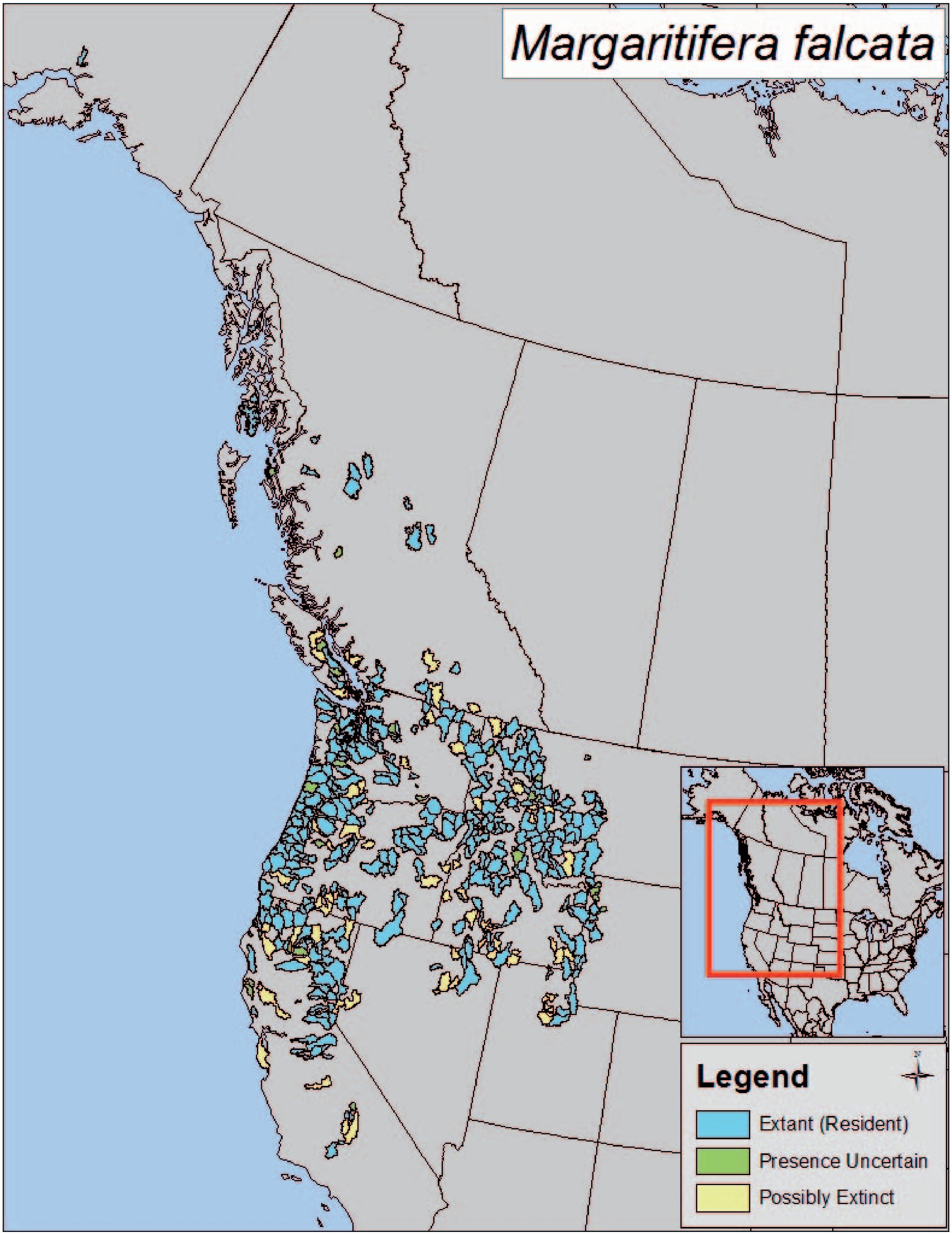

Figure 9. *Margaritifera falcata* status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

measured by this analysis may overestimate the species' current distribution, with some records now more than 25 yr old. Recent surveys in western states have also indicated that, even where the species has not been extirpated from a watershed, both the number and size of populations have declined (California: Howard et al. 2015; Wyoming: Mathias and Edwards 2014; Arizona: T. Myers, unpublished data, 2008; Myers 2009; Oregon and Washington: reviewed in Jepsen et al. 2012a; Mexico: T. Myers, unpublished data, 2008). For example, research by Brim Box et al. (2006) documented sites occupied by *Anodonta* in the Middle Fork John Day River of Oregon. In 2015, only 7 of 10 sites previously inhabited were still occupied. Among occupied sites, fewer mussels were observed overall (Maine et al. 2017). Recent research has also suggested that some populations may be at greater risk of local extinctions on the basis of low genetic diversity and isolation (Mock et al. 2004, 2010). Genetic structuring was also evident among populations spanning major drainage basins of the West and are considered evolutionarily significant units, many of which are also distinct management units (sensu Moritz 1994; Mock et al. 2010).

Decline in occurrence by watershed was only marginally less for members of the *A. oregonensis/kennerlyi* clade. However, the more dramatic declines reported for *A. nuttalliana* have not been observed in this group, and a decline of 26% only corresponds to an IUCN ranking of Least Concern. Still, taxonomic and identification issues in *Anodonta* species complicate the analysis of extinction risk.

Gonidea angulata has declined in occurrence by as much as 43%, and though the species historically occurred from Southern California north to Canada and east to Nevada and Idaho, populations were reported as extirpated from Southern California and much of the Central Valley by Taylor (1981) and Coney (1993). Recent surveys have not located the species in any historic Southern California sites and few California sites in general (Howard 2008; Howard 2010; Howard et al. 2015), although the species does still occur in large beds in some Northern California sites (Howard 2010; Davis et al. 2013). Declines in Oregon, Washington, and Idaho have also been reported (Brim Box et al. 2006; Frest and Johannes 1995; reviewed in Jepsen and LaBar, 2012). A study by Brim Box et al. (2006) documented sites occupied by *G. angulata* in the Middle Fork John Day River of Oregon (as with *Anodonta*; see above). Several of these sites were revisited in 2015, by which time one of the eight sites was extirpated and observed abundance of mussels in occupied sites had decreased (Maine et al. 2017). The species has been reported in the Humboldt Basin of Nevada since 1990, but its status should be evaluated given that more recent surveys did not identify any extant populations (A. Smith, unpublished data, 2009). COSEWIC (2010) ranked the species as endangered in Canada, citing observations of declines, limited distribution, and historic habitat alteration, as well as concerns regarding the likelihood of future introduction of zebra mussels (COSEWIC 2010; BCCDC 2015).

In comparison, *M. falcata* has declined in occurrence by as much as 17%, but populations in some parts of the range are considered stable (British Columbia: NatureServe 2015; Wyoming: Mathias and Edwards 2014) or are not well understood (Alaska and Nevada: Smith et al. 2005; Jepsen et al. 2012b). However, recent continuing declines have been observed in Montana, where less than a quarter of surveyed populations have been classified as viable, and another quarter of nonviable populations surveyed in 2010 were extirpated just 4 yr later (Stagliano 2015). Maine et al. (2017) similarly found that 2 of 13 previously surveyed occupied sites in the Middle Fork John Day River (Brim Box et al. 2006) were extirpated just 9 yr later. Though the species still occurs from California to Alaska and east to Montana and Wyoming, surveys in other states also reported recent extirpations, declining populations, and populations that appeared to lack recruitment (Utah: Hovingh 2004; Richards 2015; California: Furnish 2010; Southern California Edison Company 2010, unpublished report; Howard et al. 2015; May and Pryor 2016; Idaho: Lysne and Krouse 2011; Oregon: Brim Box et al. 2006; Nevada: Hovingh 2004; Washington: Hastie and Toy 2008; Wyoming and other states: reviewed in Jepsen et al. 2012b).

In this analysis, decline in *M. falcata* is underestimated where population abundance has decreased but the population is still extant, as with the Truckee River in California ($\sim$20,000 individuals in a 0.8-km stretch in 1941 down to $\sim$120 individuals in a 2-km stretch in 2006: Murphy 1942; Howard 2008; Howard et al. 2015) and Battle Creek in Washington (1,372 individuals in 17 m^2 in 1995 down to 334 individuals in 25 m^2 in 2006: Hastie and Toy 2008). Population genetic research has also revealed "extreme inbreeding" in multiple populations, which may result from hermaphroditism and selfing (Mock et al. 2013) and could reduce fitness in already fragmented populations (Keyghobadi 2007).

Because our data set was composed of occurrence records, we were not able to more generally quantify trends in population abundance. However, at sites where abundance has been assessed over time for western mussels, a decreasing trend has typically been reported (Hastie and Toy 2008; Howard 2008; Jepsen and LaBar 2012; Jepsen et al. 2012a, 2012b; Stagliano 2015; Maine et al. 2017). The loss of equilibrium species (i.e., those typically long lived and reaching sexual maturity at older ages, such as *G. angulata* and *M. falcata*) may go unnoticed after habitat alteration or destruction. In eastern North America, equilibrium species persisted in reservoirs for as long as 40 yr before disappearing (Haag 2012). Additionally, our study was restricted to declines between historic and recent time periods and was unable to quantitatively incorporate more recent extirpations (i.e., if a watershed was occupied in 1995 but populations were extirpated by 2014, the watershed would still be classified as "Extant"), yet our analysis demonstrated that multiple western species still qualified as Near Threatened or Vulnerable. It is therefore important to note that these estimates of decline may underestimate true species declines and extinction risk.

Threats and Conservation Considerations

Freshwater mussels serve an important role in aquatic ecosystems, improving water quality and clarity, providing nutrients and habitat for aquatic invertebrates at the core of the food web, and serving as food for aquatic and terrestrial wildlife (Vaughn et al. 2008; Vaughn 2010; Vaughn 2017), yet they have been largely ignored in western aquatic conservation efforts. Mussels filter large quantities of water and make organic material available to other aquatic organisms through biodeposition. When mussels occur in larger beds, as observed in western species and clades (Brim Box et al. 2006; Howard 2010), much of the water column may be filtered as it flows over beds, especially during lower flows and at higher densities (Vaughn et al. 2004). Other native species, such as larval Pacific Lamprey, are also known to benefit from mussel presence (Limm and Power 2011). Freshwater mussels also have significant cultural importance to many Native American tribes in the Pacific Northwest as a traditional food resource (Lyman 1984; Norgaard et al. 2013; CTUIR 2015).

Unfortunately, the proximate causes for the declines we measured are unknown. Western mussels inhabit perennial lotic and lentic habitats, and rely on host fish to complete their life cycle and to populate or colonize available habitat. The specific causes of local extirpations or declines in mussel populations are not always evident (Downing et al. 2010; Haag 2012), although several threats have been identified for western freshwater mussels ranging from impacts to water quantity, quality, connectivity, or flow, degradation of streambeds or banks, restoration activities, declines in host fish, and nonnative invasive species (reviewed in Jepsen et al. 2012a, 2012b). For example, salmonids (hosts for *M. falcata*) and several other host fish species are themselves of conservation concern, and freshwater mussels may not be able to readily adapt to using nonnative fish species, which are widespread in western North America, as hosts (Tremblay et al. 2016). Acute declines in response to sudden dewatering (as can occur at aquatic restoration projects) have been observed, but enigmatic declines have also been reported (reviewed in Jepsen et al. 2012a, 2012b; Xerces/CTUIR 2015).

Several studies have specifically looked at factors that may affect western mussels and could be contributors to range-wide declines. For example, Haley et al. (2007) studied how changes to water flows, levels, and temperatures affected reproduction in a Northern California basin. Rodland et al. (2009) also observed responses of one species to thermal stress. Other researchers have examined how habitat alteration, including sedimentation and burial from changes in land use or in-stream mining, can affect western species (Vannote and Minshall 1982; Krueger et al. 2007). Bioaccumulation of contaminants (Claeys et al. 1975; Norgaard et al. 2013) and potential consequences of nonnative invasive species introductions (Sada and Vinyard 2002; COSEWIC 2010) have also received some attention.

Yet, western freshwater mussels are understudied and future western aquatic conservation efforts must be adapted to incorporate freshwater mussels and address existing and emerging threats. Many conservation and research priorities identified in the Freshwater Mollusk Conservation Society's national strategy (2016) would benefit western freshwater mussels. These strategies include improving understanding and increasing accessibility of taxonomy and distribution information, addressing past, ongoing, and emerging stressors and their impacts, improving understanding of habitat and conserving habitat, improving understanding of mussel population ecology, and restoring abundant mussel populations (FMCS 2016).

Abatement of known threats is crucial to western mussel conservation, but mussels would also benefit from additional research, including surveys to provide a more accurate understanding of freshwater mussel distributions and long-term monitoring across mussel ranges to understand population trends. For example, estimating the viability of extant populations of *M. falcata* in additional states (as done in Montana; Stagliano 2015) would improve estimates of the species' extinction risk, as it would for all western freshwater mussels. Many watersheds (32–38%) had only a single historic or recent observation for each species or clade, suggesting that even watersheds with freshwater mussel records are understudied and would benefit from further surveys. Range edges, as in Alaska, Arizona, California, and Nevada, should also be prioritized for future surveys, as these areas can greatly influence some measures of extinction risk and would improve overall understanding of current distributions. Because species of western *Anodonta* are easily confused, methods to improve accurate identification of specimens to the species level should also be prioritized. Conservation of all *Anodonta* populations, and indeed populations of all western species of mussels, is critical under existing and future threats to these freshwater mussels and their habitat. Better understanding of how certain activities, such as water management, can affect western freshwater mussels is especially important, as negative impacts will likely be further exacerbated by climate change (Isaak et al. 2012; Inoue et al. 2014; Black et al. 2015; Vaughn et al. 2015).

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REGULAR ARTICLE

SURVIVAL OF TRANSLOCATED CLUBSHELL AND NORTHERN RIFFLESHELL IN ILLINOIS

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ABSTRACT

Translocation of freshwater mussels is a conservation tool used to reintroduce extirpated populations or augment small populations. Few studies have evaluated the effectiveness of translocations, mainly because estimating survival is challenging and time-consuming. We used a mark-recapture approach to estimate survival of nearly 4,000 individually marked Clubshell (*Pleurobema clava*) and Northern Riffleshell (*Epioblasma rangiana*) translocated to eight sites over a five-year period into the Salt Fork and Middle Fork Vermilion rivers in central Illinois. Survival differed among sites and between species; Clubshell were approximately five times more likely to survive than Northern Riffleshell. Survival also increased in the fourth year following a release and decreased following high-flow events. Translocating numerous individuals into multiple sites over a period of years could spread the risk of catastrophic high-flow events and maximize the likelihood for establishing self-sustaining populations.

KEY WORDS: reintroduction, freshwater mussel, high flow, PIT tag, unionids

INTRODUCTION

North American freshwater mussels have undergone drastic population declines during the past century and are one of the most imperiled groups of animals in the world (Williams et al. 1993; Lydeard et al. 2004; Strayer et al. 2004). Translocation has been used for decades to augment populations or reintroduce mussels into regions where species have declined or are extirpated (Coker 1916; Ahlstedt 1979; Sheehan et al. 1989). Much time and effort is placed on collecting, marking, and transporting mussels for translocation, but few studies have evaluated the effectiveness of mussel reintroductions. More than a quarter of all translocation projects conducted prior to 1995 failed to report on the efficacy of those efforts (Cope and Waller 1995).

Obtaining precise and unbiased estimates of mussel survival is challenging, even for translocated individuals. Mussels often burrow beneath the substrate surface when not actively feeding or reproducing, making them difficult to detect (Amyot and Downing 1998; Watters et al. 2001; Strayer and Smith 2003). Furthermore, an unequal proportion of the population is often sampled, such as larger individuals, those found in easy-to-sample areas, or those at or near the surface (Strayer and Smith 2003; Meador et al. 2011). Reliable estimates of survival can be obtained using capture-mark-recapture techniques (Hart et al. 2001; Meador et al. 2011). Capture-mark-recapture methods are often time-intensive due to the effort needed to capture and mark a large number of individuals, but marking individuals already captured for translocation can be easily incorporated.

The federally endangered Clubshell (*Pleurobema clava*) and Northern Riffleshell (*Epioblasma rangiana*) were formerly widespread in the Ohio River and Great Lakes basins but have experienced significant range reductions during the last century. The recovery plan for the Clubshell and Northern Riffleshell set objectives of reestablishing viable populations in 10 separate river drainages across the species' historical range via augmentation and reintroduction (USFWS 1994). Bridge construction on the Allegheny River, Pennsylvania, which supports large populations of both species, prompted a salvage operation to remove thousands of individuals from the impacted area. In an attempt to meet recovery plan objectives, these individuals were translocated to multiple streams within seven states where the species had declined or had been extirpated.

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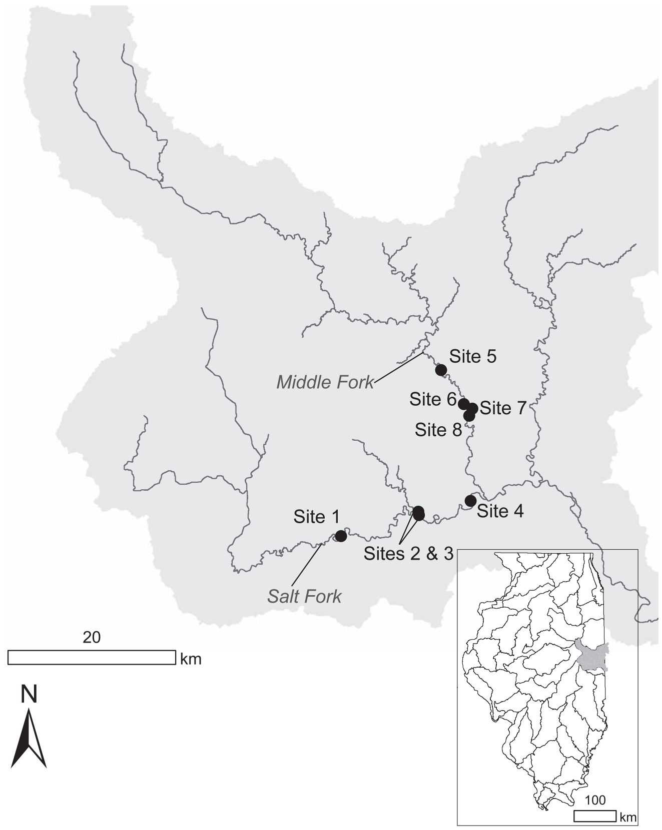

Figure 1. The Clubshell and Northern Riffleshell release sites in the Vermilion River basin (Wabash River drainage), Illinois.

Beginning in 2006, the Illinois Department of Natural Resources and the Illinois Natural History Survey partnered with the U.S. Fish and Wildlife Service and state agencies in Ohio, Pennsylvania, and West Virginia to translocate Clubshell and Northern Riffleshell from the Allegheny River to the Vermilion River system (Wabash River basin) in Illinois, where both species occurred historically (Cummings and Mayer 1997; Tiemann et al. 2007). Pilot translocations ($n <$ 75 individuals) first occurred in 2010 at one site each in the Salt Fork and Middle Fork Vermilion rivers, and more widespread translocations occurred at eight sites in 2012, 2013, and 2014. We conducted a five-year capture-mark-recapture study focusing on those individuals released in 2012, 2013, and 2014 to estimate survival of translocated mussels. Specifically, our goals were to evaluate (1) how survival differed according to species, sex, and mussel size, (2) how survival varied spatially (among sites and between rivers), and (3) how survival varied temporally after release.

METHODS

Mussel Collection and Transportation

Mussels were collected from the Allegheny River at the U.S. Highway 62 Bridge, Forest County, Pennsylvania. The Allegheny River at this site is approximately 200 m wide and drains an area of approximately 10,000 km^2. Mean daily discharge is approximately 56 m^3/s at the end of August and nearly 425 m^3/s at the beginning of April (average of 71 yr; USGS gage 03016000). We collected 197, 758, and 807 Clubshell and 957, 249, and 777 Northern Riffleshell in 2012, 2013, and 2014, respectively. We measured total length of each individual as the greatest distance from the anterior to posterior shell margin (nearest 1 mm), and affixed a 12.5 mm, 134.2 kHz PIT tag (BioMark, Inc., Boise, Idaho) to the right valve and a uniquely numbered HallPrint Shellfish tag (HallPrint, Hindmarsh Valley, South Australia) to the left valve. Northern Riffleshell averaged 45.6 mm long (range 15–70 mm) and Clubshell averaged 52.2 mm long (range 18–84 mm). We also determined the sex of each Northern Riffleshell based on shell morphology, although a few smaller individuals were classified as "unknown" (male:female ratio = 1.34:1); Clubshell sexes cannot be differentiated by external shell morphology and were all classified as "unknown." Clubshell and Northern Riffleshell were placed in coolers between damp towels and transported in climate-controlled vehicles to Illinois.

Mussel Translocation and Release

We selected release sites based on the presence of presumably suitable habitat for Northern Riffleshell and Clubshell, which consisted of clean, stable sand, gravel, and cobble riffles (Watters et al. 2009), abundant and diverse mussel populations (INHS 2017), and presence of suitable host fishes (i.e., darters and minnows) for both mussel species (Cummings and Mayer 1992; Tiemann 2008a, 2008b; Watters et al. 2009). Based on these criteria, we selected four sites each in the Salt Fork and Middle Fork Vermilion rivers in east-central Illinois (Fig. 1). These streams are an order of magnitude smaller than the Allegheny River, each 30–40 m wide and draining approximately 1,100 km^2. Mean daily discharge in the Salt Fork is 0.4 m^3/s at the end of August and 4.3 m^3/s at the beginning of April (average of 45 yr; USGS gage 03336900); mean daily discharge in the Middle Fork is 0.9 m^3/s at the end of August and 8.5 m^3/s at the beginning of April (average of 38 yr; USGS gage 03336645).

We released 3,745 mussels (both species combined) among all eight sites from 2012 to 2014 (Table 1). Mussels were released in the late summer, following a quarantine and acclimatization period (14 d for 2012 mussels and 4–5 d for 2013–2014 mussels, differences between years due to logistics). We hand-placed mussels into the substrate at each site within an area demarcated by site-specific landmarks (such as trees, boulders, water willow beds, or other discernible feature) to facilitate recapture surveys. The size of marked release areas varied with site and were between 3–10 m wide and 20–100 m long. Sites with greater suitable area received more mussels, but all sites were stocked at less than 50% of the density observed at the collection site on the Allegheny River, which is 5.5/m^2 for Northern Riffleshell and 7.5/m^2 for

Table 1. Number of Clubshell and Northern Riffleshell released into the Salt Fork and Middle Fork Vermilion rivers in 2012, 2013, and 2014.

	2012		2013		2014	
Site	Clubshell	Riffleshell	Clubshell	Riffleshell	Clubshell	Riffleshell
Salt Fork						
1	-	291	-	-	-	-
2	106	196	258	-	-	-
3	91	470	250	-	-	-
4	-	-	50	50	277	290
Middle Fork						
5	-	-	50	50	-	-
6	-	-	50	50	175	180
7	-	-	50	50	181	174
8	-	-	50	49	174	133
Totals	197	957	758	249	807	777

Clubshell (Enviroscience, Inc., personal communication); these densities are similar to those seen for these species at other locations (Crabtree and Smith 2009). We stocked Clubshell at greater densities than Northern Riffleshell due to presumed historical presence based on historical shell collection records (INHS 2017). Logistical constraints (e.g. land access, previous stocking, mussel availability) largely dictated which sites received mussels in multiple years.

Field Surveys

We surveyed for PIT-tagged Clubshell and Northern Riffleshell during 12 sampling periods from 2012 to 2016 (Appendix 1). We used a robust design sampling protocol that included primary and secondary samples (Fig. 2; Kendall and Nichols 1995; Kendall et al. 1997). We attempted to conduct primary samples every 3–4 mo to represent each season (spring, summer, autumn, winter), but environmental conditions prevented us from collecting all samples during every year. We used two to three observers during each primary sample. Each observer was considered an independent sample and represented a secondary sample in the robust design framework. We detected PIT-tagged mussels using BioMark FS2001F-ISO or BioMark HPR Plus receivers with portable BP antennas (BioMark). Each observer independently traversed the stream in a systematic manner from a unique starting point while slowly sweeping the streambed with an antenna. Surveys continued until the release site was covered

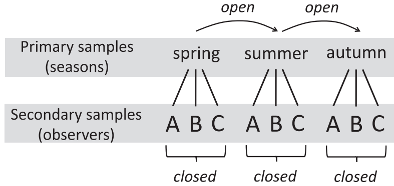

Figure 2. Robust design as employed in this study, with primary samples (seasons) and secondary samples (observers).

completely and extended 5–10 m downstream after detections ceased. Each sample typically required 2–3 h/site.

Statistical Analyses

We used the Huggins Robust Design model (Huggins 1989, 1991) to estimate apparent survival while accounting for imperfect detection and to estimate of the numbers of individuals remaining after each sampling period. Population estimates from the Huggins Robust Design model (Huggins 1989, 1991) are derived using the actual number of individuals observed during a primary sample and detection probability. We were interested in the influence of individual traits (sex, length, and species), environmental factors (site within river and whether or not flood events had occurred between primary sampling periods), and number of years following release on survival. We fit a single model that included all covariates instead of fitting a suite of models and comparing model fit (Burnham and Anderson 2002). Consequently, we attained estimates for each species released at each site during each year by estimating a species effect, site effect, and an effect of years following release, along with the individual covariates of sex and length and the environmental covariate of the presence of a flood. We did not include group (site or species) by sampling period interactions because we had no reason to believe that survival would vary along that spatio-temporal scale (Anderson and Burnham 2002). We constrained our model so there was no immigration or emigration between primary samples, which we believed was biologically reasonable given the limited vagility of freshwater mussels (Amyot and Downing 1998; Schwalb and Pusch 2007). We fit detection as a function of sampling period and site to encompass differences in sampling efficiency due to variation in flow, temperature, and depth among dates and variation in habitat conditions among sites. We did not account for species-specific differences in detection because we used PIT tags and hand-held readers for both species and did not believe detection would differ by species when using this method.

Table 2. Parameter estimates (β coefficients), standard errors (SE), log-odds (e^{β}), and log-odds lower and upper 95% confidence limits (CL) of monthly survival of translocated Clubshell and Northern Riffleshell relative to site, years following release, species, sex, mussel length, and presence of flood between primary samples. Parameter estimates should be interpreted in relation to the baseline, which was Northern Riffleshell of average length and unknown sex at Site 1, four years postrelease, and during a period with no flooding, as indicated.

Parameter	Estimate	SE	Log-odds	Lower CL log-odds	Upper CL log-odds
Intercept	4.760	0.891			
Individual traits					
Clubshell versus Riffleshell	1.670	0.623	5.312	1.567	18.011
Male versus unknown	0.207	0.620	1.230	0.365	4.150
Female versus unknown	−0.117	0.621	0.890	0.263	3.004
Length	0.009	0.004	1.009	1.003	1.016
Environmental factors					
Site 2 versus Site 1	−0.853	0.085	0.426	0.361	0.504
Site 3 versus Site 1	−1.402	0.079	0.246	0.211	0.287
Site 4 versus Site 1	−0.007	0.165	0.993	0.718	1.374
Site 5 versus Site 1	−0.999	0.130	0.368	0.286	0.475
Site 6 versus Site 1	−1.063	0.132	0.345	0.267	0.448
Site 7 versus Site 1	−1.757	0.128	0.173	0.134	0.222
Site 8 versus Site 1	−0.958	0.142	0.384	0.290	0.507
Flood versus No Flood	−0.530	0.077	0.589	0.506	0.685
Years following release					
Year 1 versus Year 4	−1.260	0.658	0.284	0.078	1.030
Year 2 versus Year 4	−1.666	0.661	0.189	0.052	0.691
Year 3 versus Year 4	−1.228	0.660	0.293	0.080	1.066

Post hoc analyses indicated that inclusion of species-specific detection had very little influence on survival probabilities (i.e., estimates were within 0.01%). We determined if a flood occurred between primary samples using the Indicators of Hydrologic Alteration software package (IHA; Richter et al. 1996) and discharge data for both streams from the U.S. Geological Survey National Water Information System (https://waterdata.usgs.gov/il/nwis/rt; gages 03336900 and 03336645). We did not differentiate between small floods and large floods as identified by IHA, and anything equivalent to or greater than a 2-yr flood event was considered a flood. We used the Huggins' p and c extension in Program MARK (White and Burnham 1999) with initial capture probability (p, probability of detecting an individual at least once during a primary sample) equal to recapture probability (c, probability of detecting an individual during a primary sample given it is detected) because secondary samples occurred via the same method on the same day. We interpreted the strength and biological meaning of each model covariate using the beta coefficients (β) and their 95% confidence intervals and log-odds ratios, which approximate how much more likely it is for an event (survival) to occur based on the beta coefficient (log-odds ratio = e^{β}, Gerard et al. 1998; Hosmer and Lemeshow 2010).

RESULTS

Detection rate averaged 0.78 across both species (range of averages = 0.66–0.90; Appendix 1). Detection was generally greatest in autumn. Average detection in autumn samples was about 1.25 times greater than for spring and summer samples; we had only one winter sample because of high flows and frozen conditions. However, detection probabilities were highly variable among sites and sampling periods (Appendix 1).

Monthly survival varied among species, sites, and sampling periods. Average monthly survival was 0.981 for Clubshell and 0.905 for Northern Riffleshell; these values translate to an approximate annual survival of 0.79 for Clubshell and 0.30 for Northern Riffleshell, irrespective of site, individual traits, and years following release. The β coefficient and log-odds ratio showed that, overall, Clubshell was approximately 5 times more likely to survive than Northern Riffleshell, but the precision of this estimate was low (95% confidence interval = 1.57–18.00×; Table 2). There was no difference in survival among males, females, and mussels of unknown sex; confidence intervals included zero for all coefficients (Table 2). There was no appreciable effect of size on survival. The log-odds ratio indicated that individuals were 1.009 times more likely to survive (95% confidence interval = 1.003–1.016) for every mm increase in length (Table 2).

Survival was greatest at Sites 1 and 4 on the Salt Fork and lowest at Site 7 on the Middle Fork (Figs. 3–6). Log-odds ratios showed that mussels were nearly 6 times less likely to survive at Site 7 than Site 1, and mussels were 2–4 times less likely to survive at Sites 2, 3, 5, and 6 (Table 2). Survival was reduced following floods. The log-odds ratio showed that

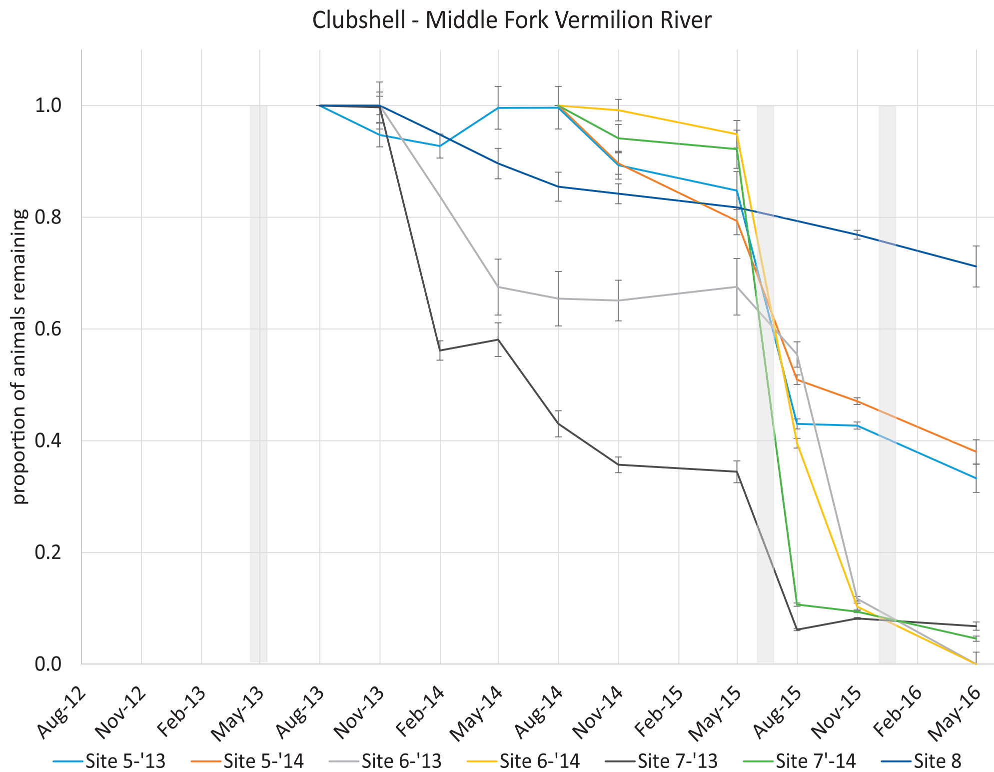

Figure 3. Derived estimates of proportion of Clubshell remaining at each release site in the Middle Fork from 2012 to 2016. Gray boxes indicate when a flood occurred. Numbers of individuals released per year per site can be viewed in Table 1.

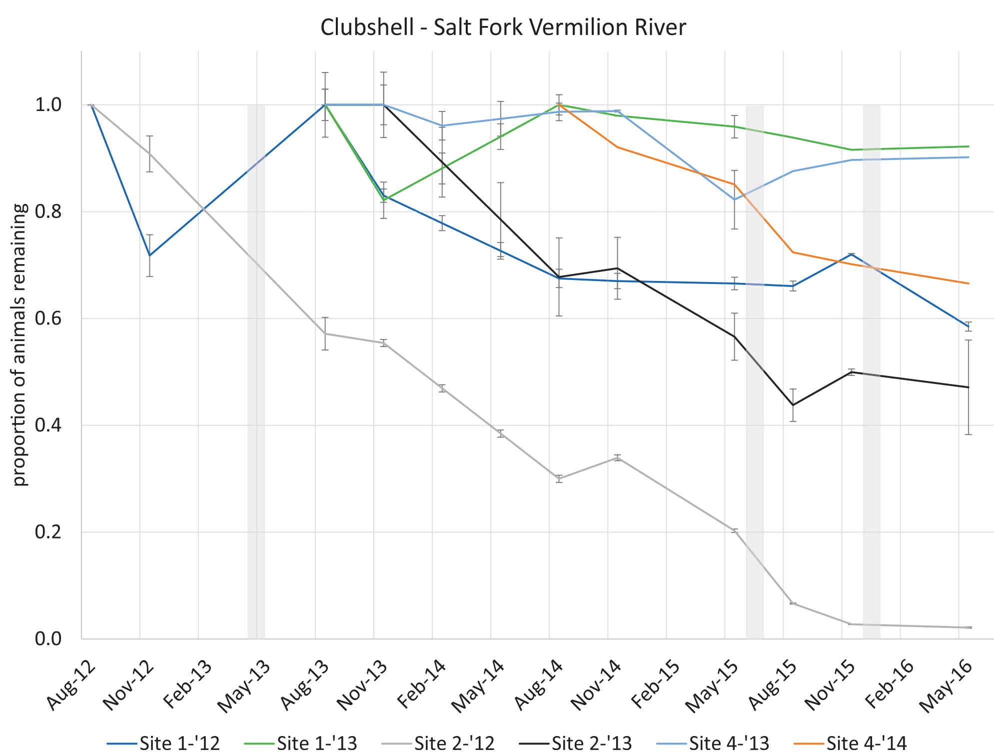

Figure 4. Derived estimates of proportion of Clubshell remaining at each release site in the Salt Fork from 2012 to 2016. Gray boxes indicate when a flood occurred. Numbers of individuals released per year per site can be viewed in Table 1.

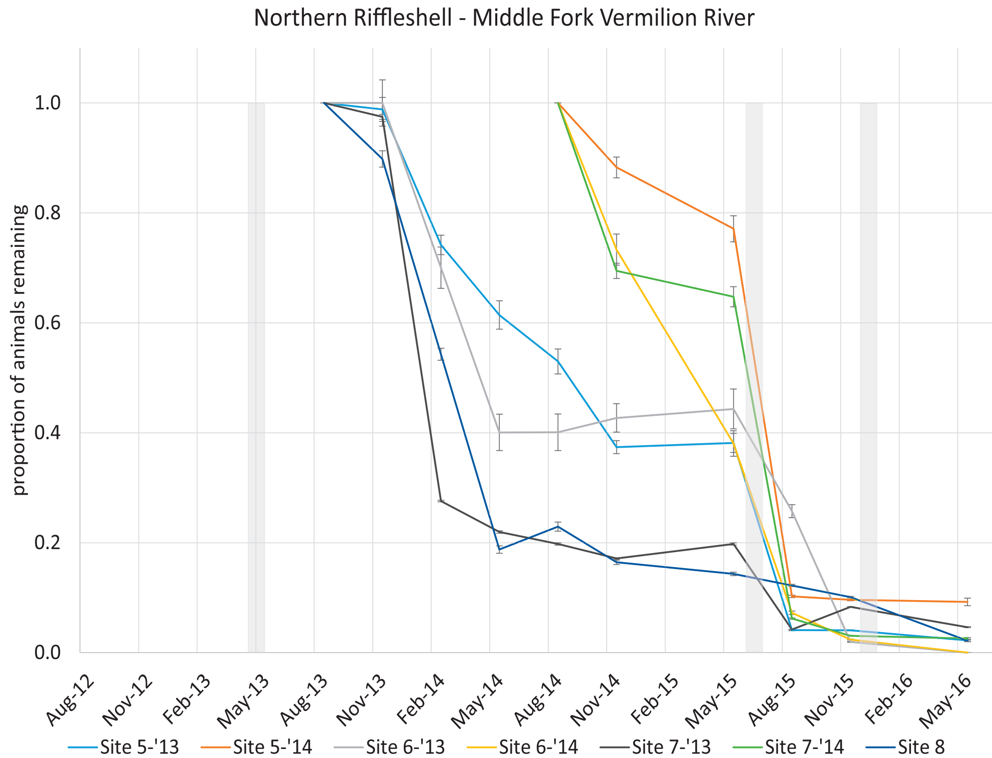

Figure 5. Derived estimates of proportion of Northern Riffleshell remaining at each release site in the Middle Fork from 2012 to 2016. Gray boxes indicate when a flood occurred. Numbers of individuals released per year per site can be viewed in Table 1.

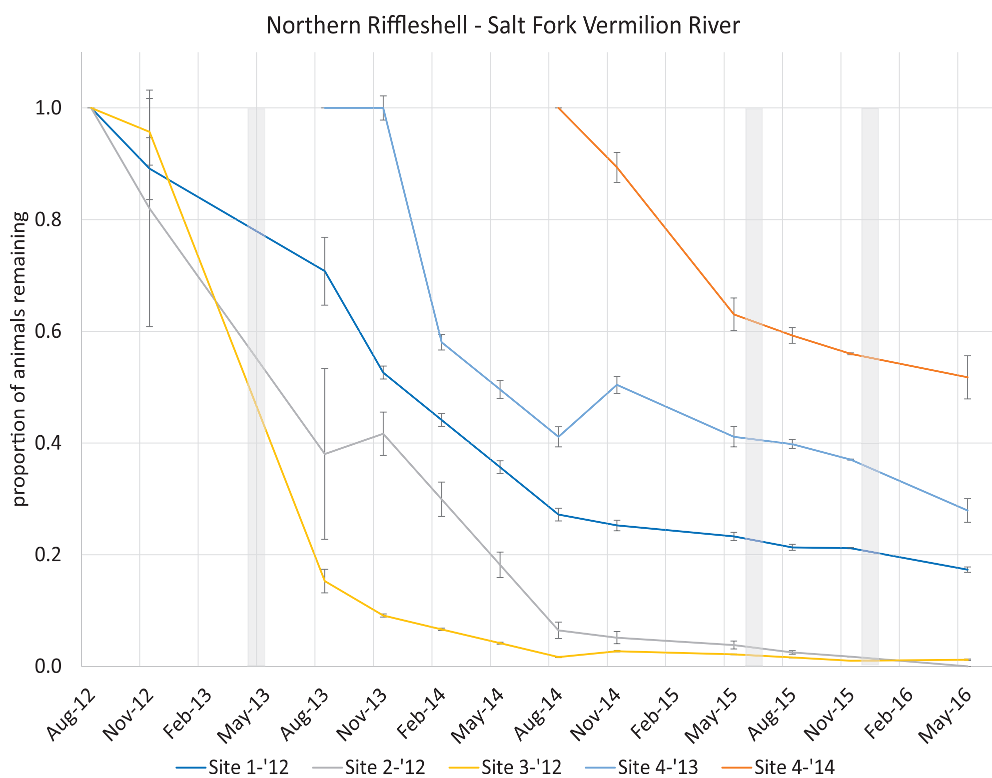

Figure 6. Derived estimates of proportion of Northern Riffleshell remaining at each release site in the Salt Fork from 2012 to 2016. Gray boxes indicate when a flood occurred. Numbers of individuals released per year per site can be viewed in Table 1.

mussels were 1.70 times less likely to survive after floods (95% confidence interval: 1.46–1.98) than after periods with no floods; this is equivalent to a reduction of monthly survival from 0.950 to 0.917 (average of all species and sites). The occurrence of a flood on the Middle Fork during June–July 2015 was associated with a sharp decline in population size for both species (Figs. 3, 5), but the influence of other flood events was not associated with similar declines. We did not model river as a separate factor (see Methods), but survival appeared to be greater in the Salt Fork than in the Middle Fork. An average of 62% of Clubshell and 19% of Northern Riffleshell were alive in the Salt Fork in 2016 compared with only 21% of Clubshell and 4% of Northern Riffleshell in the Middle Fork in 2016 (Figs. 3–6). This difference was apparent despite the fact that most mussels were translocated to the Salt Fork 1–2 yr earlier than in the Middle Fork (Table 1).

Number of years following release was an important determinant of survival. Survival was greatest in the fourth year following a release; individuals were 3.52 times more likely to survive in the fourth year following release (95% confidence interval: 0.97–12.80) compared to the first year following release (Table 2). Survival was lowest in the second year following release; individuals were 1.50 times less likely to survive (95% confidence interval: 1.30–1.70) compared to the first year (Table 2).

DISCUSSION

The long-term efficacy of a reintroduction program depends on the establishment of a self-sustaining population, which requires translocated individuals to survive until they reproduce and replace themselves. It is too early to tell if the Clubshell and Northern Riffleshell reintroduction program into Illinois has been a success because no recruitment has been documented. Reintroduction of the Clubshell appears to have been more successful initially than reintroduction of Northern Riffleshell. Reintroduced Clubshell survived at a much greater rate and represented the majority of individuals remaining after five years of monitoring. Annual survival for Clubshell (0.79) is within the estimated range for other mussel species in the wild, (0.50–0.99, Hart et al. 2001; Villella et al. 2004) and near the estimates of the closely related Southern Clubshell (*Pleurobema decisum*) (0.91, Haag 2012). However, annual survival for Northern Riffleshell (0.30) was well below those values, those reported from French Creek, Pennsylvania, which averaged 0.60 (Crabtree and Smith 2009), and those of the closely related Oystermussel (*Epioblasma capsaeformis*) (0.73, Jones and Neves 2011; Haag 2012).

Some species may be inherently more difficult to translocate. There is high variability in the success of translocation projects, ranging from nearly all individuals remaining after a few years to very few if any (e.g., Ahlstedt 1979; Sheehan et al. 1989; Cope et al. 2003). Some of this variation may be explained by inherent life history differences among species, and Clubshell probably lives longer than Northern Riffleshell. For instance, the Southern Clubshell, a congener of Clubshell, can reach 45 yr of age (Haag and Rypel 2011), while Northern Riffleshell is a relatively short-lived species with a maximum age reported in French Creek, Pennsylvania, of 11 yr (Crabtree and Smith 2009). Based on these differences, Northern Riffleshell is expected to have lower survival than Clubshell even in wild populations, and our data show that translocated populations may have even lower survival. Consequently, translocation of short-lived species such as Northern Riffleshell may require larger numbers of individuals and repeated translocations to overcome high mortality and ensure that translocated individuals experience conditions favorable for recruitment.

Differences in hydrology, either between rivers or even within the same river, may play an important role in determining the suitability of sites for freshwater mussel reintroduction (Cope et al. 2003; Carey et al. 2015). The hydrology, land use, and watershed size of the Vermilion River basin differ from the source location of the Allegheny River (Larimore and Smith 1963; Smith 1968; Larimore and Bayley 1996; White et al. 2005), thus some discrepancy in survival between the source and recipient basins may be expected. However, the Salt Fork Vermilion and Middle Fork Vermilion rivers are comparable in size and have similar land use and hydrology, yet we found that survival varied even among sites within a river. Local-scale differences among sites, such as substrate or gradient, can lead to biologically significant differences that influence survival (McRae et al. 2004). We selected release sites based on the best available habitat and species assemblage data, yet unmeasured habitat differences and stochastic events appeared to have a large effect on survival. Similar results have been observed in other translocations, such as siltation due to bank failure following flow diversion (Bolden and Brown 2002), possible washout due to earthen causeway removal (Tiemann et al. 2016), or diminished recovery of relocated individuals in sites with high current velocity in the two years following relocation (Dunn et al. 2000).

High-discharge events present an ongoing threat to the reintroduction of Clubshell, Northern Riffleshell, and similar translocation projects. High-flow events have been problematic in other translocation projects (e.g., Sheehan et al. 1989; Carey et al. 2015) and were clearly detrimental for translocated Clubshell and Northern Riffleshell. Following the flood in June–July 2015, we examined the nearest downstream gravel bar at a few sites and found numerous stranded and dead individuals. Existing native mussel communities in the Salt and Middle Fork Vermilion rivers have persisted throughout similar high-flow events, but translocated mussels may be at a disadvantage. PIT tags can decrease the burrowing rate of individuals (Wilson et al. 2011), and translocated mussels may have lower energetic status (Patterson et al. 1997), which could reduce their ability to anchor themselves in the substrate or rebury after a flood event (Killeen and Moorkens 2016). Additionally, the native mussel community represents individuals that have found optimal locations to withstand scouring and dislodging. The

Clubshell and Northern Riffleshell we translocated may not have had enough time to find optimal locations, which may have made them more vulnerable to dislodgement and may partly explain why individuals survived at a greater rate 4 yr following release.

We provide the following recommendations for conducting and monitoring reintroduction efforts. The best time to monitor Clubshell and Northern Riffleshell was during autumn, when stream flows were low and we observed the greatest probability of detection. Sampling was difficult or impossible during the spring because of high stream flows, which resulted in reduced detectability using handheld readers; sampling also was difficult in winter because of high flows and occasional ice cover. Spreading reintroduction efforts over several geographically separate river systems could lessen risk of failure due to stochastic events such as floods, chemical spills, and biological invasion (e.g., Griffith et al. 1989; Trdan and Hoeh 1993). Translocating individuals over a period of several years might also reduce the overall risk of failure due to isolated events occurring in a particular year. For instance, many Clubshell and Northern Riffleshell, especially in the Middle Fork, were lost during a late spring/early summer high-flow event in 2015. Finally, stocking greater numbers of individuals in multiple translocations for species with naturally low annual survival, such as Northern Riffleshell, may be necessary to maximize chances for natural recruitment.

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Appendix 1. Estimates of detection for each site and during each period; 95% confidence intervals are provided in parentheses.

	Middle Fork				Salt Fork			
Sample Period	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Summer 2012	-	-	-	-	-	-	-	-
Autumn 2012	0.71 (0.68–0.74)	0.67 (0.64–0.71)	0.68 (0.64–0.72)	-	-	-	-	-
Summer 2013	0.72 (0.68–0.75)	0.68 (0.63–0.73)	0.69 (0.63–0.74)	-	-	-	-	-
Autumn 2013	0.79 (0.77–0.81)	0.76 (0.74–0.70)	0.76 (0.72–0.80)	0.87 (0.85–0.89)	0.83 (0.80–0.85)	0.77 (0.73–0.80)	0.81 (0.77–0.85)	0.85 (0.82–0.88)
Winter 2014	-	-	-	0.80 (0.76–0.84)	0.84 (0.80–0.88)	-	0.83 (0.78–0.87)	-
Spring 2014	-	-	-	-	0.76 (0.72–0.80)	0.69 (0.63–0.74)	0.71 (0.66–0.76)	0.79 (0.75–0.84)
Summer 2014	0.70 (0.67–0.72)	0.66 (0.63–0.69)	0.67 (0.64–0.71)	0.81 (0.77–0.84)	0.75 (0.71–0.78)	0.67 (0.63–0.72)	0.73 (0.68–0.78)	0.78 (0.74–0.82)
Autumn 2014	-	0.75 (0.72–0.78)	-	0.85 (0.81–0.87)	0.80 (0.76–0.83)	0.73 (0.68–0.77)	0.78 (0.73–0.82)	0.82 (0.78–0.86)
Spring 2015	-	-	-	0.72 (0.67–0.77)	0.77 (0.73–0.82)	0.70 (0.64–0.75)	0.75 (0.69–0.81)	-
Summer 2015	0.80 (0.78–0.82)	0.78 (0.75–0.80)	0.78 (0.74–0.82)	0.88 (0.86–0.90)	0.84 (0.81–0.87)	0.78 (0.74–0.82)	0.83 (0.78–0.86)	-
Autumn 2015	0.86 (0.84–0.87)	0.83 (0.81–0.85)	0.84 (0.80–0.87)	0.92 (0.90–0.93)	0.88 (0.86–0.91)	0.84 (0.80–0.87)	0.87 (0.84–0.90)	0.90 (0.88–0.92)
Spring 2016	0.78 (0.74–0.81)	0.75 (0.71–0.79)	-	0.87 (0.83–0.89)	0.82 (0.78–0.86)	-	0.81 (0.75–0.85)	0.85 (0.81–0.88)

Appendix 2. Monthly apparent survival estimates for Clubshell. Years (2012–2014) represent the year animals were released. Numbers in parentheses beside primary sample indicate the number of months since the preceding sample; 95% confidence intervals are provided in parentheses beside survival estimates. Bold rows indicate a flood occurred during that period (e.g., between Su 2013 and Au 2013). Sp = spring, Su = summer, Au = autumn, Wi = winter.

	Salt Fork Vermilion River						
	Site 1		Site 2		Site 3	Site 4	
Primary Samples (mo)	2012	2013	2012	2013	2012	2013	2014
Su 2012–Au 2012 (2)	0.994 (0.993–0.995)	-	0.977 (0.974–0.981)	-	0.987 (0.984–0.989)	-	-
Au 2012–Su 2013 (9)	0.990 (0.989–0.992)	-	0.962 (0.956–0.967)	-	0.978 (0.973–0.982)	-	-
Su 2013–Au 2013 (2)	**0.992 (0.990–0.993)**	**0.994 (0.993–0.995)**	**0.966 (0.962–0.971)**	**0.977 (0.974–0.981)**	**0.980 (0.976–0.984)**	**0.994 (0.992–0.996)**	**-**
Au 2013–Wi 2014 (4)	0.992 (0.990–0.993)	0.994 (0.993–0.995)	0.966 (0.962–0.971)	0.977 (0.974–0.981)	0.980 (0.976–0.984)	0.994 (0.992–0.996)	-
Wi 2014–Sp 2014 (2)	0.992 (0.990–0.993)	0.994 (0.993–0.995)	0.966 (0.962–0.971)	0.977 (0.974–0.981)	0.980 (0.976–0.984)	0.994 (0.992–0.996)	-
Sp 2014–Su 2014 (2)	0.992 (0.990–0.993)	0.994 (0.993–0.995)	0.966 (0.962–0.971)	0.977 (0.974–0.981)	0.980 (0.976–0.984)	0.994 (0.992–0.996)	-
Su 2014–Au 2014 (4)	0.995 (0.993–0.996)	0.992 (0.990–0.993)	0.978 (0.973–0.982)	0.966 (0.962–0.971)	0.987 (0.983–0.990)	0.991 (0.988–0.994)	-
Au 2014–Sp 2015 (5)	0.995 (0.993–0.996)	0.992 (0.990–0.993)	0.978 (0.973–0.982)	0.966 (0.962–0.971)	0.987 (0.983–0.990)	0.991 (0.988–0.994)	0.994 (0.992–0.996)
Sp 2015–Su 2015 (3)	**0.991 (0.988–0.993)**	**0.986 (0.983–0.988)**	**0.963 (0.955–0.97)**	**0.944 (0.934–0.953)**	**0.979 (0.972–0.983)**	**0.986 (0.980–0.990)**	**0.990 (0.986–0.993)**
Su 2015–Au 2015 (3)	0.995 (0.993–0.996)	0.992 (0.990–0.993)	0.978 (0.973–0.982)	0.966 (0.962–0.971)	0.987 (0.983–0.990)	0.991 (0.988–0.994)	0.994 (0.992–0.996)
Au 2015–Sp 2016 (6)	**0.997 (0.990–0.999)**	**0.991 (0.988–0.993)**	**0.989 (0.961–0.997)**	**0.963 (0.955–0.970)**	**0.994 (0.977–0.998)**	**0.991 (0.986–0.994)**	**0.986 (0.98–0.990)**

Appendix 2, extended.

Middle Fork Vermilion River						
Site 5		Site 6		Site 7		Site 8
2013	2014	2013	2014	2013	2014	2013
-	-	-	-	-	-	-
-	-	-	-	-	-	-
0.985 (0.980–0.988)	**-**	**0.984 (0.979–0.988)**	**-**	**0.968 (0.959–0.975)**	**-**	**0.985 (0.981–0.989)**
0.985 (0.980–0.988)	-	0.984 (0.979–0.988)	-	0.968 (0.959–0.975)	-	0.985 (0.981–0.989)
0.985 (0.980–0.988)	-	0.984 (0.979–0.988)	-	0.968 (0.959–0.975)	-	0.985 (0.981–0.989)
0.985 (0.980–0.988)	-	0.984 (0.979–0.988)	-	0.968 (0.959–0.975)	-	0.985 (0.981–0.989)
0.977 (0.971–0.982)	-	0.976 (0.969–0.981)	-	0.953 (0.940–0.963)	-	0.978 (0.972–0.983)
0.977 (0.971–0.982)	0.985 (0.980–0.988)	0.976 (0.969–0.981)	0.984 (0.979–0.988)	0.953 (0.940–0.963)	0.968 (0.959–0.975)	0.978 (0.972–0.983)
0.962 (0.950–0.971)	**0.974 (0.966–0.981)**	**0.960 (0.946–0.97)**	**0.973 (0.964–0.980)**	**0.922 (0.898–0.941)**	**0.947 (0.931–0.959)**	**0.964 (0.951–0.973)**
0.977 (0.971–0.982)	0.985 (0.980–0.988)	0.976 (0.969–0.981)	0.984 (0.979–0.988)	0.953 (0.940–0.963)	0.968 (0.959–0.975)	0.978 (0.972–0.983)
0.975 (0.966–0.982)	**0.962 (0.950–0.971)**	**0.974 (0.963–0.981)**	**0.960 (0.946–0.97)**	**0.953 (0.940–0.963)**	**0.922 (0.898–0.941)**	**0.976 (0.967–0.983)**

Appendix 3. Monthly apparent survival estimates for Northern Riffleshell. Years (2012–2014) represent the year animals were released. Numbers in parentheses beside primary sample indicate the number of months since the preceding sample; 95% confidence intervals are provided in parentheses beside survival estimates. Bold rows indicate a flood occurred during that period (e.g., between Su 2013 and Au 2013). Sp = spring, Su = summer, Au = autumn, Wi = winter.

	Salt Fork						
	Site 1		Site 2		Site 3	Site 4	
Primary Samples (months)	2012	2013	2012	2013	2012	2013	2014
Su 2012–Au 2012 (2)	0.971 (0.907–0.991)	-	0.891 (0.706–0.965)	-	0.934 (0.806–0.98)	-	-
Au 2012–Su 2013 (9)	**0.951 (0.852–0.985)**	**-**	**0.828 (0.586–0.942)**	**-**	**0.893 (0.711–0.966)**	**-**	**-**
Su 2013–Au 2013 (2)	0.957 (0.867–0.987)	0.971 (0.907–0.991)	0.844 (0.614–0.949)	0.891 (0.706–0.965)	0.904 (0.735–0.97)	0.970 (0.904–0.991)	-
Au 2013–Wi 2014 (4)	0.957 (0.867–0.987)	0.971 (0.907–0.991)	0.844 (0.614–0.949)	0.891 (0.706–0.965)	0.904 (0.735–0.97)	0.970 (0.904–0.991)	-
Wi 2014–Sp 2014 (2)	0.957 (0.867–0.987)	0.971 (0.907–0.991)	0.844 (0.614–0.949)	0.891 (0.706–0.965)	0.904 (0.735–0.97)	0.970 (0.904–0.991)	-
Sp 2014–Su 2014 (2)	0.957 (0.867–0.987)	0.971 (0.907–0.991)	0.844 (0.614–0.949)	0.891 (0.706–0.965)	0.904 (0.735–0.97)	0.970 (0.904–0.991)	-
Su 2014–Au 2014 (4)	0.972 (0.909–0.991)	0.957 (0.867–0.987)	0.894 (0.71–0.967)	0.844 (0.614–0.949)	0.936 (0.809–0.98)	0.956 (0.862–0.987)	-
Au 2014–Sp 2015 (5)	0.972 (0.909–0.991)	0.957 (0.867–0.987)	0.894 (0.71–0.967)	0.844 (0.614–0.949)	0.936 (0.809–0.98)	0.956 (0.862–0.987)	0.970 (0.904–0.991)
Sp 2015–Su 2015 (3)	**0.953 (0.855–0.986)**	**0.928 (0.793–0.978)**	**0.832 (0.59–0.944)**	**0.762 (0.483–0.916)**	**0.896 (0.715–0.967)**	**0.928 (0.785–0.979)**	**0.951 (0.846–0.986)**
Su 2015–Au 2015 (3)	0.972 (0.909–0.991)	0.957 (0.867–0.987)	0.894 (0.71–0.967)	0.844 (0.614–0.949)	0.936 (0.809–0.98)	0.956 (0.862–0.987)	0.97 (0.904–0.991)
Au 2015–Sp 2016 (6)	**0.986 (0.923–0.997)**	**0.953 (0.855–0.986)**	**0.944 (0.746–0.99)**	**0.832 (0.59–0.944)**	**0.967 (0.836–0.994)**	**0.952 (0.849–0.986)**	**0.928 (0.785–0.979)**

Appendix 3, extended.

Middle Fork						
Site 5		Site 6		Site 7		Site 8
2013	2014	2013	2014	2013	2014	2013
-	-	-	-	-	-	-
-	**-**	**-**	**-**	**-**	**-**	**-**
0.924 (0.78–0.977)	-	0.920 (0.768–0.975)	-	0.851 (0.624–0.952)	-	0.927 (0.785–0.978)
0.924 (0.78–0.977)	-	0.920 (0.768–0.975)	-	0.851 (0.624–0.952)	-	0.927 (0.785–0.978)
0.924 (0.78–0.977)	-	0.920 (0.768–0.975)	-	0.851 (0.624–0.952)	-	0.927 (0.785–0.978)
0.924 (0.78–0.977)	-	0.920 (0.768–0.975)	-	0.851 (0.624–0.952)	-	0.927 (0.785–0.978)
0.890 (0.702–0.966)	-	0.884 (0.688–0.963)	-	0.792 (0.525–0.929)	-	0.894 (0.709–0.967)
0.890 (0.702–0.966)	0.924 (0.78–0.977)	0.884 (0.688–0.963)	0.920 (0.768–0.975)	0.792 (0.525–0.929)	0.851 (0.624–0.952)	0.894 (0.709–0.967)
0.827 (0.578–0.943)	**0.878 (0.675–0.961)**	**0.818 (0.563–0.94)**	**0.871 (0.66–0.959)**	**0.691 (0.391–0.887)**	**0.771 (0.493–0.921)**	**0.833 (0.587–0.946)**
0.890 (0.702–0.966)	0.924 (0.78–0.977)	0.884 (0.688–0.963)	0.920 (0.768–0.975)	0.792 (0.525–0.929)	0.851 (0.624–0.952)	0.894 (0.709–0.967)
0.881 (0.679–0.963)	**0.827 (0.578–0.943)**	**0.874 (0.665–0.961)**	**0.818 (0.563–0.940)**	**0.776 (0.498–0.924)**	**0.691 (0.391–0.887)**	**0.885 (0.687–0.964)**

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REGULAR ARTICLE

WHAT ARE FRESHWATER MUSSELS WORTH?

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ABSTRACT

Historically, little thought was given to the value of freshwater mussels when making decisions that affected these animals and their habitats, even though these values may be considerable, and may be greatly changed by environmental alterations. Here, I review several kinds of values provided by freshwater mussels. Direct-use (market) values of mussels were substantial when the mussels were harvested to provide buttons and pearls, amounting to about $10 billion (2017 dollars) in the USA alone. Current harvests are much smaller but still valuable. Mussels also provide indirect-use value through the ecosystem functions that they provide (water clarification, nutrient cycling, pathogen suppression, etc.). The monetary value of these functions may be substantial, but has not yet been estimated. As interesting, rare creatures, freshwater mussels may also have existence value to society. This value probably is small at present, but could be increased greatly through outreach and education, as could their option and bequest values (the value of saving them for the future). The total value of a freshwater mussel community would be the sum of direct use, indirect use, existence, option, and bequest values, and has not yet been estimated for any real mussel community. Alternatively, one could calculate the replacement value of freshwater mussels (the cost of replacing a mussel community that was damaged or destroyed); procedures for estimating replacement costs have been published. Despite uncertainty about the precise value of freshwater mussels, it is clear that they have substantial value to humans, possibly many millions of dollars in individual ecosystems, which should be taken into account in environmental decision making. Mussel ecologists and biologists can play important roles in helping society better value freshwater mussels.

KEY WORDS: bequest value, ecosystem services, market value, option value, Unionoida, use value, valuation

INTRODUCTION

"What are they worth?" must rank with "What good are they?" and "Are they good to eat?" as the most common questions that mussel ecologists and biologists hear from the general public. Although "Are they good to eat?" has a clear answer (Haag 2012), the other two interrelated questions are surprisingly complicated to answer, ranging far from biology and ecology into matters of philosophy and economics. Nevertheless, these are important questions for mussel biologists and ecologists to be able to answer, because they determine how people—including decision makers—view mussels, and how they protect and manage mussels and the habitats that they live in.

In this essay, I briefly review some of the ways in which the question of what mussels are worth might be answered, and offer suggestions about how mussel biologists and ecologists might help society reach better answers. My intent is to stimulate discussion of, not provide definitive answers to, the important problem of valuing freshwater mussels. Unless I specify otherwise, I use "freshwater mussels" (or just "mussels") to refer to members of the order Unionoida.

What is "Value"?

"Value" has many meanings in both common and technical language. In particular, economists and philosophers have discussed the idea of value extensively (e.g., Goulder and Kennedy 1997; Millennium Ecosystem Assessment 2003, 2005; Daly and Farley 2010), and have offered several definitions. I will restrict myself here to the idea of "exchange value": an object has value in terms of what other objects you'd exchange it for (Goulder and Kennedy 1997). Exchange values are subjective and individual. Thus, although almost everyone would set a higher value on a new luxury car than a used cigarette butt (i.e., they would trade away the cigarette butt to get the car), the relative value of other items is less clear. Which has higher value: a cold beer or a hot chocolate? The answer differs across people, some of whom don't like beer or are allergic to chocolate, and even within a single person over time, depending on whether they've just mowed the lawn on a hot summer day or come in from the ski slope. Thus, people don't hold set, universally accepted values for mussels or anything else.

Furthermore, value is not the same as price. Economists recognize that price is the minimum value that a buyer would place on an item (i.e., you'd buy the item at any price at or below the value you place on it) (Goulder and Kennedy 1997; Daly and Farley 2010). For instance, a thirsty person in a desert might be willing to pay $1,000 for a cold bottle of water, even though the actual price is just $1.95. In addition, we value many things (a beautiful sunrise, a baby's smile) that are not for sale on the market, and thus have no price.

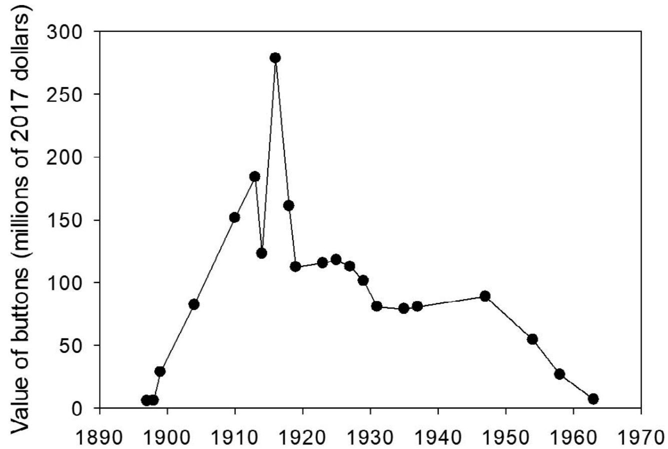

Figure 1. Value of finished buttons from the freshwater mussel fishery in the USA, 1897–1963, from data of Claassen (1994), converted to 2017 dollars using consumer price index (CPI) inflation calculator (https://data.bls.gov/cgi-bin/cpicalc.pl). The CPI inflation calculator goes back only to 1913; older data were corrected using 1913 figures and so are likely to be underestimates.

Why Might We Want to Set a Value on Freshwater Mussels?

I can think of at least two reasons why we might want to estimate the value of freshwater mussels. First, mussel biologists and ecologists could use such a value to justify research and management of freshwater mussels (FMCS 2016). For example, someone who studies a sport fish might note that expenditures on recreational fisheries in the USA in 2011 were $42 billion, with an estimated economic impact of $115 billion (Hughes 2015), as a way to convince people that sport fisheries are worth protecting, and that research on sport fish is worth doing. It could be helpful to be able to quote a figure on the value of freshwater mussels to justify spending money and time on our research and management activities.

Perhaps more important, placing a value on freshwater mussels could help us make better decisions among alternative activities that might affect freshwater mussels. Many human activities (e.g., dam construction or removal, changes in dam release schedules, habitat restoration, climate or land use change) affect freshwater mussels. When we decide whether a proposed activity is a good idea or not, it seems reasonable to try to estimate the total values resulting from the various alternative actions, which would include the values of changes to freshwater mussel populations. The more complete and accurate our valuation, the more possible it is to make a good decision about alternative actions.

Approaches to Valuing Freshwater Mussels

Below, I briefly describe several ways by which the value of freshwater mussels might be calculated, describing the approach, illustrating it with real data (if they exist), and discussing its shortcomings. I will begin with the most obvious approaches, and will roughly follow the categories of values of Goulder and Kennedy (1997) from economics.

Market values and other direct-use values.—Probably the first thing that most people think of when they think of value is market value—how much can I sell freshwater mussels for? Unlike most other freshwater invertebrates, mussels sometimes have substantial direct market value, as a source of nacre and pearls (Kunz 1898; Claassen 1994; Anthony and Downing 2001; Haag 2012). These fisheries have been very valuable in various parts of the world, but I have been able to find good data only on the fishery in the USA. Between 1897 and 1963, when there was an active fishery in many rivers for nacre for buttons, the total value of buttons was about $6 billion (2017 dollars) (Fig. 1). I have not seen good figures on the value of the freshwater pearl fisheries in the USA, but according to Claassen (1994), they were about half as valuable as buttons during the years of the button fishery. However, the commercial pearl fishery extended over a longer time span than the button fishery, beginning in 1857 or earlier (Kunz 1898). It therefore seems reasonable to estimate that the total value of the fishery (buttons plus pearls) from 1857 to 1963 was in the neighborhood of $10 billion in today's dollars.

Modern fisheries are much smaller but still valuable. In Tennessee, which accounts for about 75% of the value of modern mussel fisheries in the USA (Olson 2007), the wholesale value of mussel fisheries has been in the range of a few million dollars per year, although highly variable depending on prices that year (Fig. 2). Estimated export value of the shell is three to five times higher than the wholesale price (Hubbs 2009). Most of this harvest comes from a single reservoir (Kentucky Lake).

One particular aspect of market pricing that can work against preservation of natural resources is the common use of discount rates to estimate the net present value of a resource in deciding whether to consume it or preserve it. The idea behind using a discount rate is that, in a growing economy, a dollar today is worth more than a dollar tomorrow. In practice, planners have often used discount rates of 3–7%/yr (Arrow et

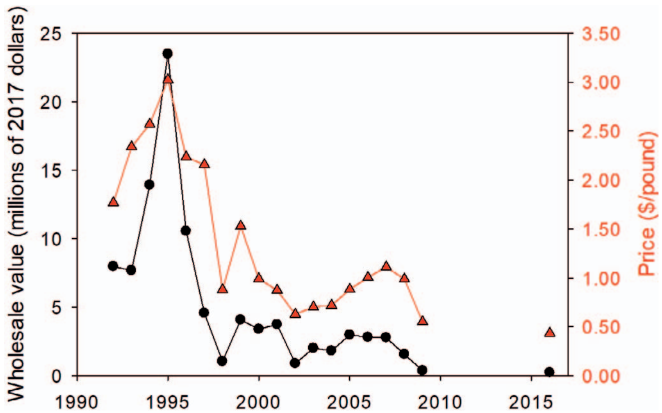

Figure 2. Wholesale value and price of mussel shells taken in the commercial fishery in Tennessee, 1992–2016, from data of Hubbs (2009) and Ganus (2016), converted to 2017 dollars using consumer price index inflation calculator (https://data.bls.gov/cgi-bin/cpicalc.pl).

al. 2013), which gives low value to benefits or costs that occur in the future, and almost no value to the distant future. In this worldview, it could have been economically sensible to harvest all of the mussels in the early 20th century, leaving none for the future. However, Arrow et al. (2013) made a compelling argument that uncertainty about future discount rates, declining population growth, and other factors should compel us to use declining discount rates, or at least use constant rates far lower than 3–7%, especially if we are considering long time horizons ($>$ 10 yr). Either of these solutions would give much higher value to future benefits and costs, and tend to favor the preservation of natural resources rather than their immediate consumption or destruction.

At least one kind of direct-use value of mussels is not reflected in a market value, and that is their use as environmental indicators. Both the soft tissues and shells of mussels have been used as monitors of environmental conditions (e.g., water temperatures, concentrations of contaminants) in contemporary or past ecosystems (e.g., Schöne et al. 2004; Newton and Cope 2007), a use that has value to people. I don't know of any attempts to place a dollar value on this use.

Although the market values of freshwater mussels are straightforward to understand, and have been substantial in particular times and places, it is unlikely that they represent the total value of these animals. To see this, apply the exchange test to mussel communities that contain no commercially valuable species, are too sparse to harvest, or occur in places where mussel harvesting is illegal, or to a rare species that is of no commercial value. These mussels have zero market value. If market value is the same as the total value of these mussels, you would gladly exchange them for a dollar, for example if a factory were proposed whose effluent would kill every mussel in the river. I doubt that many mussel ecologists or even ordinary people would make this exchange. Thus, however important market values of mussels may be, they do not represent the total value of these animals.

Indirect-use values of mussels: ecosystem services.— Mussels may also be valuable because they interact with other parts of the ecosystem that humans value, and thus indirectly increase human well-being. This could be through connections to consumptive uses, such as clean drinking water or commercially harvested fish, or nonconsumptive uses, such as clear water that is appreciated for its aesthetic or recreational value. Indirect-use values are related to the idea of ecosystem services. Recognizing the value of ecosystem services to human well-being has been a major recent advance in valuation of natural resources. The Millennium Ecosystem Assessment (2003, 2005) identified four broad classes of ecosystem services: provisioning services (where an ecosystem provides food, fresh water, wood, fuel, etc. directly to humans), regulating services (where an ecosystem regulates climate, flooding, diseases, water quality, etc.), cultural services (where an ecosystem provides aesthetic, spiritual, recreational, or educational opportunities to people), and supporting services (where an ecosystem provides structures or functions that support any of the other three classes of services; examples include soil formation and nutrient cycling). The direct-use value of mussels in providing nacre and pearls falls under provisioning services, and I will discuss cultural services in a later section on existence value, so this section corresponds roughly to supporting and regulating services.

One important contrast between direct-use value and indirect-use values is that the latter often are harder to estimate, because we cannot rely on markets to show their value. This is especially true if the direct use that is being supported is a nonconsumptive use such as water clarity, which does not have a market value. Nevertheless, the fact that indirect-use values can be hard to estimate does not mean that they are small and can be ignored, as was nicely illustrated in recent study (Walsh et al. 2016) of the costs of the invasion of Lake Mendota, Wisconsin by the nonnative cladoceran *Bythotrephes longimanus*. This predatory zooplankter substantially reduced populations of the grazer *Daphnia* in the lake, which allowed phytoplankton to proliferate, reducing water clarity by nearly 1 m. Surveys of the willingness to pay by local residents had shown that a change in water clarity of 1 m had a value of $140 million, which was almost exactly the same amount as the cost ($86–163 million) of phosphorus-reduction programs that would be needed to restore the invaded lake to its former clarity. This study showed that the indirect-use cost of this single species in a single lake was about $100 million, far from trivial.

Studies of the indirect-use values (regulating and supporting services) of freshwater mussels are relatively recent, so our knowledge of these services is still actively evolving. Vaughn (2017) provided an excellent review of this topic, so the following summary will be brief. Figure 3 summarizes what we know so far about the ecosystem services that freshwater mussels provide to humans. As suspension feeders, mussels remove particles from the water. This can increase water clarity, which can increase the recreational and aesthetic value

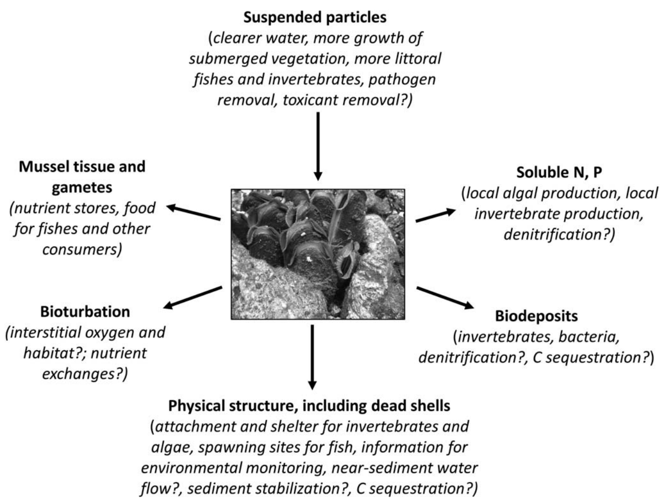

Figure 3. Summary of ecosystem services that might be provided by freshwater mussels, on the basis of the ideas of Vaughn and Hakenkamp (2001) and Vaughn (2010, 2017). Functions marked with a question mark probably occur but have not yet been definitively demonstrated. See text for further explanation. Photograph by Joel Berglund, from Wikimedia.

of a body of water and reduce treatment costs for drinking water. Increased water clarity can also lead to a whole range of subsequent effects in the ecosystem, including higher productivity of submersed plants and benthic algae, and higher productivity and diversity of littoral and benthic invertebrates, fishes, and waterfowl (Scheffer 2004), many of which may be valued by people.

In addition, freshwater mussels may improve the quality of drinking water by removing pathogens or contaminants, though this function is not yet well understood. We do know that they can remove a wide range of problematic particles and chemical compounds from the water column, including coliform bacteria, pharmaceuticals, personal care products, and algal toxins (Downing et al. 2014; Ismail et al. 2014, 2015, 2016). Freshwater mussels can capture a broad range of particle types (Vaughn et al. 2008), and we can expect from work on other bivalves (Roditi et al. 2000; Baines et al. 2005) that they may be able to remove many kinds of dissolved organic matter as well, including complexed materials such as heavy metals, so this function may be broad and important. However, for this function to be a useful service to humans, the materials removed from the water column by mussels must be quantitatively significant, and must stay out of the water column (i.e., be buried in the sediments, removed by harvesting the bivalves, or transformed into a harmless form) and not just returned to the water column upon the mussel's death.

The materials captured when mussels feed are routed to several fates, each having potential value to humans. Some of these materials are used to build mussel tissues, shells, and gametes, which can provide food to consumers and physical structure in the ecosystem. Some of the predators of juvenile and adult mussels (e.g., fishes, mammals, birds; Haag 2012) are of value to people, and little is known about the consumers of mussel sperm, glochidia, or dead mussels, even though large amounts of materials may be routed to these fates. It sometimes has been suggested that living mussels and spent shells can affect ecosystem function by serving as nutrient stores, but this will be important to the ecosystem only when the size of these stores is changing, resulting in net uptake from the ecosystem when stores are increasing and net release to the ecosystem when the stores are decreasing. The caveat also applies to the possible role of mussel shells in sequestering carbon or generating carbon dioxide (cf. Chauvaud et al. 2003). As long as spent shells are dissolving at the same rate as new shells are being formed, there will be no net effect on carbon sequestration or carbon dioxide generation; instead, spent shells must be permanently buried (which seems most likely to occur in fine-grained sediments or hard waters—Strayer and Malcom 2007), or the mass of live and dead shells must increase.

A large fraction of the material that mussels ingest ends up as wastes, either through excretion of dissolved materials (e.g., inorganic nitrogen or phosphorus) or egestion of biodeposits (feces and pseudofeces) (e.g., Christian et al. 2008; Atkinson and Vaughn 2015). The dissolved nutrients that mussels release can affect local production of algae (Atkinson et al. 2013), and this local algal production, together with the food provided by biodeposits and the shelter provided by the mussels, can likewise stimulate local production or diversity of animals (Howard and Cuffey 2006; Spooner and Vaughn 2006; Limm and Power 2011; Chowdhury et al. 2016). This local increase in productivity can extend far into the food web (Allen et al. 2012), presumably including fish. In addition, mussel beds may be sites where denitrification (the microbial conversion of nitrate to dinitrogen gas) occurs, which is an important ecosystem service in a time when many of our waters are polluted by inorganic nitrogen (e.g., Carpenter et al. 1998; Galloway et al. 2008). Denitrification requires ample nitrate and labile organic matter in a hypoxic or anoxic environment. All of these conditions could occur in dense mussel beds, and indeed denitrification occurs in beds of freshwater bivalves other than unionids (Bruesewitz et al. 2008, 2009; Turek and Hoellein 2015).

It has been suggested that unionids may stabilize sediments, but the few studies that have been done (Zimmerman and de Szalay 2007; Allen and Vaughn 2011) have provided mixed results. On the basis of work on other organisms in streams (Statzner 2012; Albertson and Allen 2015), it seems likely that mussels may either stabilize or destabilize sediments, depending on the species and densities of mussels, and the hydraulic and geomorphic setting.

The physical structures that mussels produce may have other value as well. In addition to sheltering invertebrates, mussels and their shells provide spawning sites and shelter for some fishes (Chatelain and Chabot 1983; Etnier and Starnes 1993; Aldridge 1999; Wisniewski et al. 2013). They presumably could alter near-bed and interstitial water flows as well, which could affect local habitat structure and

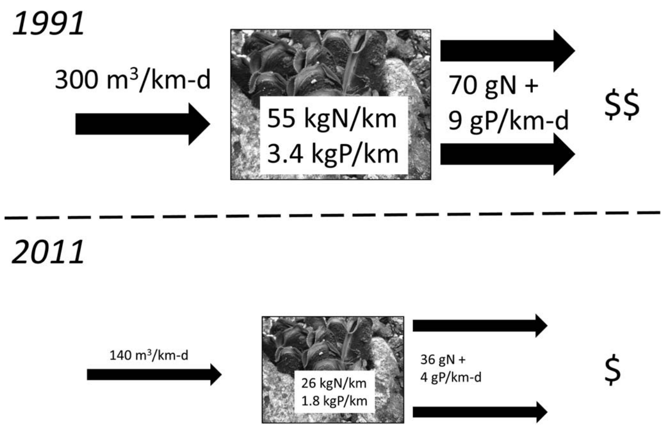

Figure 4. Changes in ecosystem functions provided by freshwater mussels in the Kiamichi River, Oklahoma after droughts between 1991 and 2011, on the basis of data of Vaughn et al. (2015). The width of arrows and the area of boxes are roughly proportional to the size of stores and flows (from left: volume of water filtered, size of stores of nitrogen and phosphorus in mussels and their shells, and excretion of inorganic nitrogen and phosphorus).

biogeochemical cycling, although this seems not to have been studied.

Sediment mixing (bioturbation) by freshwater mussels may also affect the structure of the interstitial habitat and sediment biogeochemistry, including sediment–water exchanges. This topic has received little attention (but see McCall et al. 1995).

It is therefore clear that freshwater mussels could have large and varied indirect-use values. However, several issues will make it challenging to place a dollar value on these indirect-use values (but see EPA Science Advisory Board [2009] for a good overview on estimation methods). First, we do not yet know all of the pathways that link freshwater mussels to the things that humans value about freshwater ecosystems, although great progress has been made recently. Second, the strength of these pathways depends on the environmental context, in ways that are just beginning to be appreciated (Spooner and Vaughn 2006; Vaughn 2010, 2017; Spooner et al. 2013). Third, linkages between mussels and the rest of the ecosystem also depend on the species of mussel (Spooner and Vaughn 2008; Vaughn 2010, 2017; Atkinson et al. 2013; Atkinson and Vaughn 2015). Fourth, the value to humans of the ecosystem functions provided by freshwater mussels will also be strongly context-dependent. The value of increased water clarity, for instance, will depend on whether the body of water is used for recreation, drinking water, or neither, and whether increased growth of submerged plants is viewed as a boon or as a nuisance. These complications will make it challenging to estimate the indirect-use value of freshwater mussels for even a single ecosystem, and even more difficult to make regional or global estimates.

However, as the example of Walsh et al. (2016) on zooplankton invasions shows, it would be a mistake to assume that the indirect values of mussels are unimportant just because they are hard to estimate precisely. Furthermore, we can use indirect-use values in evaluating the attractiveness of environmental alternatives, even if we do not place a dollar value on the underlying functions. The analysis of Vaughn et al. (2015) of the effects of drought on freshwater mussels in the Kiamichi River, Oklahoma provides a good example (Fig. 4). Vaughn's group sampled mussel communities along the Kiamichi both before and after serious droughts that were exacerbated by water allocation programs. By combining these data with detailed laboratory measurements of the activities of mussels, they were able to quantify the ecosystem services provided by mussels before and after the drought. Although they did not try to put a dollar value on these services, it is clear that the indirect-use value provided by mussels was substantially reduced by the drought. That is, going back to the idea of exchange value, we would gladly trade away the mussel community of 2011 to get the mussel community of 1991 on the basis of their indirect-use values. Vaughn's analysis clearly could be useful in discussing alternative water allocation schemes for the future, even without being converted into dollars.

However, another example (Fig. 5) shows a potential limitation of relying solely on direct-use and indirect-use values in assessing the total value of freshwater mussels. In the Hudson River, New York, large populations of unionid mussels (1.1 billion animals, but without commercial value) were supplanted in the early 1990s by even larger populations of dreissenids (Strayer et al. 1994; Strayer and Malcom 2014). We were able to use published studies from other ecosystems to roughly estimate ecosystem functions provided by bivalves before and after the dreissenid invasion. Although approximate, these estimates clearly show that every ecosystem function that we could estimate increased, usually very substantially, after dreissenids invaded. Again without trying to place a dollar value on these direct- and indirect-use values, we would conclude that the value of the bivalve community increased considerably after the driessenid invasion. Yet I doubt that many mussel biologists and ecologists, and perhaps many members of the general public, would happily trade away the the unionid-filled Hudson to get the dreissenid-filled Hudson. Furthermore, there are many communities of freshwater mussels so sparse that they have negligible market value and negligible indirect-use value. This again could suggest that they have nearly zero value and that we would happily exchange them for a trivial amount of money, which does not feel right. These mismatches between our intuition and calculated values suggest that the total value of freshwater mussels is not adequately represented by direct-use values plus indirect-use values.

Existence value.—Existence value is the value that people place on an item merely to know that it exists, even if they do not use (or ever intend to use) that item (Goulder and Kennedy 1997; Millennium Ecosystem Assessment 2003). As an example, it is very unlikely that I will ever travel to Asia to see snow leopards in the wild, but I like to know that these beautiful animals are still around, stalking their prey through the mountains, and so would pay some amount of money to

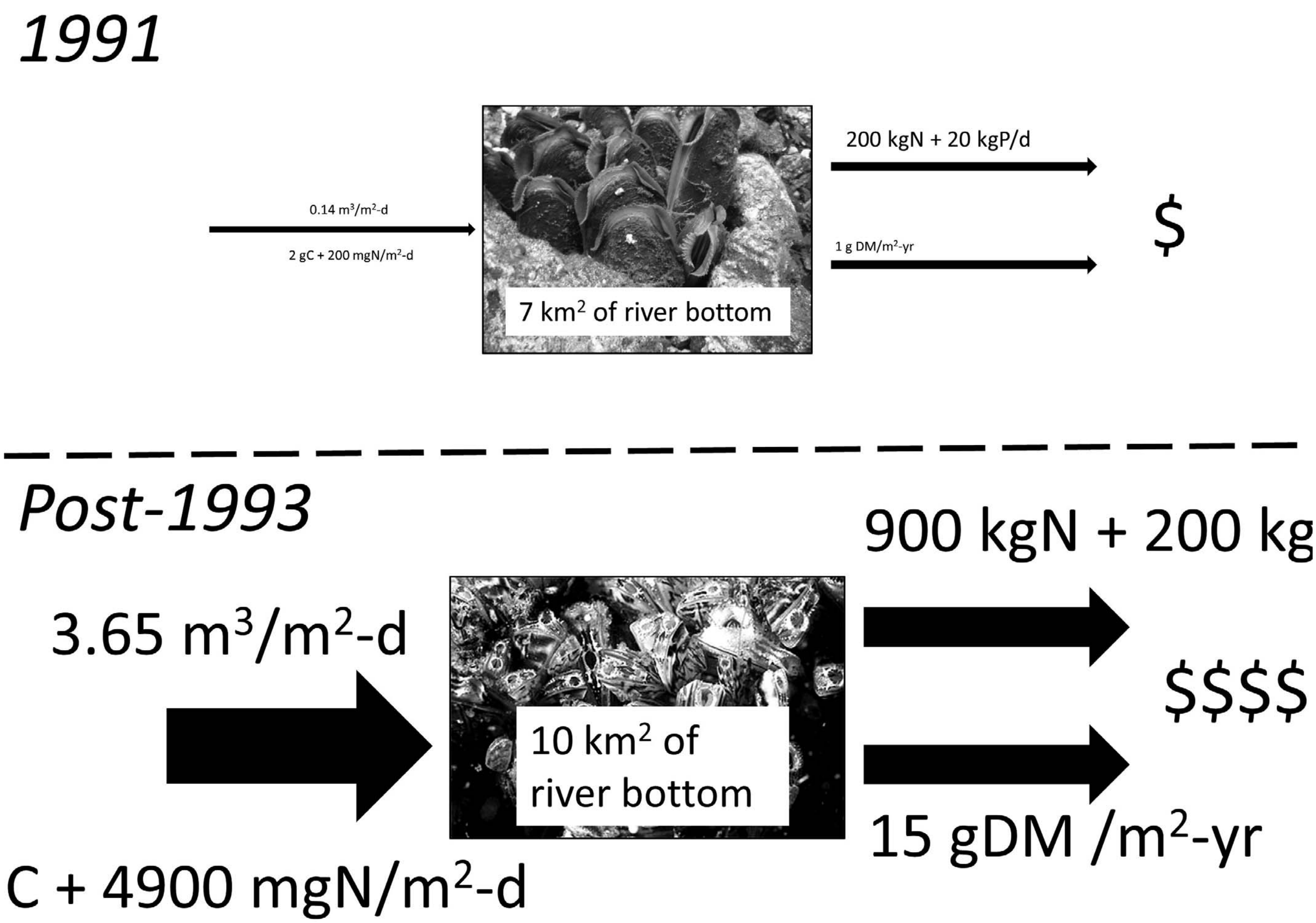

Figure 5. Changes in ecosystem functions provided by freshwater bivalves in the freshwater tidal Hudson River, New York after the invasion of the zebra mussel in the early 1990s, on the basis of the compilation of Strayer (2014) from multiple sources. The width of arrows and the area of boxes are roughly proportional to the size of stores and flows (from left: volume of water filtered [top], biodeposition of organic carbon and nitrogen in mussel beds [bottom], the spatial extent of mussel beds in the river, excretion of inorganic nitrogen and phosphorus [top], and production of bivalve tissue [bottom]).

help to preserve them. Existence value may have aesthetic, religious, or ethical foundations, and underlies many programs to conserve biodiversity or sites that are beautiful or culturally important. The large sums that people contribute to such programs show that existence value is real and can be large. People tend to assign higher existence value to things that are rare, unique, charismatic, or interesting (Goulder and Kennedy 1997), although some people have religious or ethical beliefs that assign value to the existence of all organisms or species. Surveys typically are used to estimate existence value, but it is difficult to measure accurately, and the resulting estimates tend to be controversial.

I know of no attempts to estimate the existence value of freshwater mussels. It seems likely that most people would give mussels an existence value near zero, because they don't know that freshwater mussels even exist, and know nothing about their rarity or interesting attributes. On the other hand, I suspect that many freshwater malacologists would assign a high existence value to unionids, because we know very well that they are rare and fascinating (e.g., Barnhart et al. 2008; Haag 2012; Lopes-Lima et al. 2017). Indeed, I suspect that it is a high existence value that would make many freshwater malacologists prefer a river full of unionids to the same river with a functionally similar (i.e., similar aggregate filtration rate) population of zebra mussels or *Corbicula*.

It also seems very likely that education and outreach about freshwater mussels could substantially increase their existence value outside the small community of freshwater malacologists. Kellert (1993) showed that people who knew little about invertebrates were likely to view them as unattractive and creepy, whereas people who knew a lot about invertebrates were more likely to see them as attractive and ecologically valuable. The more that people know that many freshwater mussels are rare, that some are unique or very unusual (e.g., *Epioblasma*), that many have fascinating life cycles, and that they may have direct economic or ecological utility, the higher the existence value that they are likely to give to them. Thus, websites such as the Unio Gallery (http://unionid.missouristate.edu/) and the many others that mussel biologists and their friends maintain (see http://molluskconservation.org/

Links.html for a partial list), and zoo exhibits about freshwater mussels (e.g., http://mnzoo.org/conservation/minnesota/freshwater-mussels/) may be critically important in increasing the existence value of freshwater mussels. They may even spur some additional element of nonconsumptive use value if people watch mussels in zoos or nature.

Option and bequest values.—Finally, two other kinds of values may be important but are hard to estimate. Option value is the value placed on something that you're not using today, but which you might want to use in the future (Goulder and Kennedy 1997; Gascon et al. 2015): that extra rocking chair in the attic or the can of nuts and bolts in the basement. Bequest value is similar, except that you're retaining something to give to your descendants—your grandmother's table that you are never going to use yourself, but which you'd like to pass along to a child or grandchild as a family heirloom.

We might assign option or bequest values to freshwater mussels for several reasons. We might recognize that our understanding of the practical uses or indirect-use values of mussels is incomplete, and so give them value higher than the direct- and indirect-use values that we know about today. This often is given as a reason for preserving species, whose uses in medicines or other commercial products, or roles in ecosystems, remain to be discovered (e.g., Gascon et al. 2015). We might also recognize that tomorrow's world will be different from today's as a result of climate change, species invasions, and so on, and that mussels may thus have different uses and values than they have today. In any case, it may be valuable to us to preserve mussels so that we and our descendants can use them in the future.

Option and bequest values can be estimated through surveys of people's willingness to pay to keep mussels for the future, but the resulting estimates often are uncertain and controversial. These values are also easily underestimated, especially by those who haven't thought much about them, and could be increased by education about the current and possible future utility of mussels. I am not aware of any attempts to estimate the option and bequest values of freshwater mussels.

Replacement value.—An alternative approach to valuing freshwater mussels is based on their replacement cost (Southwick and Loftus 2003). The approach, intended to restore mussel populations after an accidental kill, estimates the costs associated with propagating (or translocating) enough mussels to replace the animals that were killed, allowing for mortality between the time that the new mussels are stocked and the time they reach the size or age of the mussels that were killed. These costs can be substantial: the estimated cost of replacing a population of 15,000 *Lasmigona complanata* (a species of average propagation difficulty) was \$122,312–150,312 (2003 dollars; Southwick and Loftus 2003). This is not an especially large mussel population nor an expensive species to handle, so it is apparent that replacement value of freshwater mussels could easily reach into the millions of dollars or more. Furthermore, updated estimates of replacement costs will soon appear, resulting in values that generally are substantially higher than the 2003 estimates (R. Hoch, North Carolina Wildlife Resources Commission, personal communication).

Replacement value is not easily related to the other kinds of values that have been discussed: it could be very much larger than the sum of other values if the species is of little economic or ecological significance but is hard to propagate, or it could be far smaller than the sum of other values if these are substantial and the species is easy to propagate.

What is the total value of mussels?—Depending on the purpose of the estimate, the total value of freshwater mussels could be estimated either as the sum of direct-use value, indirect-use value, existence value, option value, and bequest value across all stakeholders, or as replacement value. I am not aware of any attempts to estimate the total value of real mussel communities using either approach. Nevertheless, it should be obvious that the total value of mussel communities could be large (easily millions of dollars or more for an individual body of water), because we know from the examples I've presented that the values of the individual components that contribute to total value can be in the millions of dollars or more.

If total values are estimated correctly, they should match our intuition about what we would be willing to exchange a community of mussels for, whether in terms of dollars or in terms of other benefits to be produced by the ecosystem (e.g., electric power production, recreational angling, irrigation water, etc.). This is, after all, the definition of exchange value. Furthermore, even though we have not yet been able to estimate the total value of mussels in monetary terms, I suggest that even a narrative discussion about the total value of mussels, extending beyond their obvious market values to indirect-use, existence, option, and bequest values, may help us make better decisions about management actions that concern freshwater mussels.

Complications and Caveats

Several complications or caveats concerning valuation of freshwater mussels are worth discussing. The following is not intended to be comprehensive, but includes a few important considerations.

Whose values matter?—When we talk about adding up values of freshwater mussels across all stakeholders to estimate the total value of mussels to society, we gloss over the question of who the stakeholders are. We rarely would mean every human being on the planet, but there are several logical answers as to whom to include, and whom we include in the calculation can critically influence the calculation of societal value. For instance, do we include only those with legal standing (e.g., the property owners, the voting-age citizens of the political unit that claims authority over the decision), even if they are not geographically close to or directly involved with the target ecosystem (cf. Braumann et al. 2014)? Or might we recognize that natural resources belong to a broader constituency? Who should have a voice in determining the value of the last wild *Epioblasma obliquata* on the planet?

Second, does everybody's value carry the same weight, or do we give the values of some people greater weight? For example, if we are considering building a dam for hydropower, should the opinions of people who live right along the river or who benefit directly from the electricity get extra weight? What about experts? Should the opinion of economists or mussel biologists or ecologists be given special weight?

Because different groups of people often hold very different values (e.g., Hostmann et al. 2005; Castro et al. 2016), the choice of whose values are counted (and how they are counted) can be critically important in determining the value of alternative actions, and therefore the choice of the "best" alternative.

What aspect of value should we optimize?—What parameter do we attempt to optimize in a society whose members disagree on values? It is perhaps most natural to simply calculate the total value of each alternative, then choose the one with the highest value; that is, to maximize societal value. However, other alternatives may be equally reasonable. For instance, instead of maximizing value to society as a whole, one might choose to minimize the number of people who hold very negative values of each alternative (i.e., minimize total unhappiness). Hostmann et al. (2005) described such a situation, in which different groups of stakeholders were asked to rate different alternatives for the purpose of finding an alternative that provided reasonably acceptable outcomes for all stakeholder groups. On the other hand, knowing that the outcomes of many management actions are highly uncertain, and that estimates of values often are also imprecise, we may choose to minimize the chance of a catastrophic outcome. Again, the choice of the metric to be optimized may strongly affect which alternative is chosen as best.

How should we recognize the rights of future generations?—It seems reasonable to acknowledge that future generations have some rights, and that we should not leave them a useless planet. Bequest values deal partly with this problem, but are inevitably based on our values (what we think is valuable enough to leave to our descendants) rather than the values of our descendants, which are unknowable. We do know that values can change greatly from generation to generation, so it seems safe to assume that our grandchildren's values will be different from ours. For example, just a few generations ago, wetlands were largely regarded as wasteland, not as habitats that are valuable for supporting plants and animals, recharging aquifers, preventing floods, and protecting water quality. It is therefore unlikely that your great-grandparents would have thought to leave a wetland for you. Consequently, about half of the area of wetlands in the lower 48 states (and 90% of wetlands in places like Ohio and California) were destroyed (Mitsch and Gosselink 2015).

Since the values of future generations are unknowable, this problem is to some extent unsolvable. However, recognizing that future generations may value things that we do not, we might want to be very careful about making any decisions with consequences that are irreversible or even very difficult to reverse (e.g., extinction, habitat destruction). The recent emphasis on sustainability (leaving as many options open for the future as possible—e.g., United Nations 1987) seems like a step in the right direction to protect the rights of future generations.

Which alternatives should be taken off the table?—It is widely recognized that some management options may be unacceptable, regardless of their calculated value to society, because they violate an absolute right or taboo. The most familiar example probably is human life. An option that kills people usually is not chosen (or even seriously considered), regardless of its value to society, so we instead choose a highly valued option that does not kill people. Societies often recognize other taboos (e.g., desecration of sacred sites), and individuals often recognize absolute rights that are not universally recognized by the society as a whole (e.g., avoidance of animal suffering or species extinction). Which of these taboos should we recognize when evaluating possible management actions? When we are comparing the values of multiple management alternatives, which do we take off the table because they violate some absolute right?

How should we deal with uncertainty?—Some kinds of values (direct-use market values) can be estimated precisely, whereas others (e.g., indirect-use, existence, option, and bequest values) can be estimated only very approximately, and the estimates are likely to be controversial. This differential uncertainty has at least two important consequences. First, we may tend to ignore the values that are difficult to estimate, and pretend that they are not real. However, it is clear that these values can be substantial, so ignoring them could greatly underestimate the value of freshwater mussels and other items that play important roles in ecosystems, have high existence value, etc. Further, avoiding the hard-to-measure values will bias actions away from those with public benefits, because these often are harder to measure precisely than private benefits (Goulder and Kennedy 1997).

Second, large uncertainty means that highly negative and highly positive outcomes are possible, even if the expected outcome is close to neutral. People often are risk averse and choose to avoid the possibility of very negative outcomes. Thus, we may want to explicitly include the uncertainty of our value estimates when choosing among options. Specifically, we may wish to choose the option that minimizes the probability of disaster (e.g., if there is a small possibility that losing freshwater mussels would lead to toxic algae in a drinking water supply, we may want to keep the mussels).

It will not always be easy to include all classes of values when evaluating management alternatives, but simply excluding those that are hard to estimate will lead to bad choices, especially for public interests. All classes of values can at least be included at the conceptual level, even if they cannot be precisely valued in monetary terms. Further, it may be easier to estimate the difference in value between two management options than the total value of either state of the ecosystem.

How can Mussel Biologists and Ecologists Help Society Better Value Freshwater Mussels?

Freshwater mussels are valuable, even if only occasionally bought and sold these days, and their value should be taken into account in environmental decision making. Even though methods to estimate all the values provided by freshwater mussels are still in development, and it probably isn't yet possible to assign a firm monetary value to mussel populations, there are nevertheless several ways by which mussel biologists and ecologists can help society better value freshwater mussels (a point that was also made in the recent National Strategy for the Conservation of Native Freshwater Mollusks—FMCS 2016).

To begin with, we can increase people's awareness, understanding, and appreciation of freshwater mussels. Most of the people I meet, including many of the anglers and boaters I meet out on the water, don't even know that freshwater mussels exist, and they certainly don't know about their peril, fascinating biology, commercial value, or potential roles in freshwater ecosystems. Outreach and education of all kinds can help people understand why freshwater mussels might reasonably be included in decision making about environmental management. In addition, a better appreciation of freshwater mussels will almost certainly substantially increase their existence, option, and bequest values among the public.

Even if we cannot yet provide an accurate monetary value for freshwater mussel communities, we certainly can provide a narrative account of the multiple values that they provide to society. Clear and compelling narratives or diagrams of some or all of these values could increase the frequency and effectiveness with which mussels are included in environmental decision making.

As I noted earlier, our understanding of the roles of freshwater mussels in ecosystems (and their indirect-use value) still is developing. We still need research that identifies and quantifies these roles, and how they vary across different kinds of ecosystems. Although this is an obvious point, estimation of the values of freshwater mussels will require mussel ecologists (who can estimate ecosystem functions) to collaborate with social scientists (who can estimate the values of those functions) and educators (who can help us increase the existence value of mussels, as well as transmit the existence and values of mussels to the public).

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REGULAR ARTICLE

EVALUATION OF COSTS ASSOCIATED WITH EXTERNALLY AFFIXING PIT TAGS TO FRESHWATER MUSSELS USING THREE COMMONLY EMPLOYED ADHESIVES

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ABSTRACT

Despite the increasing use of passive integrated transponder (PIT) tags in freshwater mussel research and conservation, there has been no evaluation of the trade-offs in cost and effort between commonly used adhesive types. These factors could be important to consider if tag retention rates do not vary by adhesive, the effects of handling are large, or resources are limited. We modeled and evaluated how material costs and effort function over a range of sample sizes by using field data from the relocation of 3,749 PIT-tagged Clubshell (*Pleurobema clava*) and Northern Riffleshell (*Epioblasma rangiana*) in Illinois, 261 Eastern Elliptio (*Elliptio complanata*) in Maryland, and the release of 99 Cumberland Combshell (*Epioblasma brevidens*) in Virginia. Each study used externally affixed 12.5-mm, 134.2-kHz PIT tags, but used a different adhesive to encapsulate tags (Illinois, underwater epoxy resin; Maryland, surface-insensitive gel cyanoacrylate; and Virginia, dental cement). We determined the total cost-per-tag-effort (CPTE) after parameterizing cost, quantity required, application time, and time for each adhesive. After accounting for standardized costs of staff time and adhesive, cyanoacrylate was the least costly adhesive to affix, encapsulate, and cure PIT tags on a per mussel basis. Differences in CPTE were small when the number of mussels tagged was low, but they increased by US\$2–6 mussel^{-1}. A primary goal in mussel projects is reduced stress from aerial exposure. Using underwater epoxy, which requires time above water to cure, can negate this goal and increase costs as it requires more handling effort than cyanoacrylate or dental cement. Nevertheless, more resource-intensive adhesives may still be an appropriate choice when the number of study animals is low. Further study is warranted to understand how our model may vary by adhesive brand, application rate, staffing level, and environmental factors.

KEY WORDS: relocation, translocation, tagging, mark–recapture, monitoring, sensors

INTRODUCTION

Relocation and reintroduction is a common conservation strategy to address the national decline in populations of freshwater mussels (Haag and Williams 2014; FMCS 2016). Understanding survival and demographic rates of mussel populations is imperative to assess conservation and management actions, which necessitates tracking a sufficient number of individual animals or cohorts over time. Studies that seek to monitor and assess the success of freshwater mussel conservation actions (e.g., translocation, relocation, and reintroduction) typically use sampling designs that require individually marked animals (e.g., capture–recapture, Villela

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et al. 2004). The resulting models of demographics and vital rates are based on the probability of detecting a marked animal in subsequent surveys (Burnham et al. 1987). Although mostly sessile, mussels exhibit imperfect detection that can vary by species, size, environmental factors, sampling design, survey method, and observer (Metcalfe-Smith et al. 2000; Meador et al. 2011; Stodola et al. 2017). Consequently, evaluating mussel conservation actions has been hampered by low rates of recapture (Cope and Waller 1995; Cope et al. 2003), leaving the fate of many mussels unknown. An inability to recapture a sufficient number of marked animals may cause data to be deficient, imprecise, or possibly even biased and has implications for conservation (Wisniewski et al. 2013; Hua et al. 2015).

Passive integrated transponder (PIT) tags are relatively inexpensive means of uniquely marking animals that has been widely used to track populations of large and small terrestrial vertebrates (Gibbons and Andrews 2004). As PIT tag technology has advanced, the reduced size of microchips and waterproof tag readers have allowed them to be used with small-bodied aquatic vertebrates and invertebrates, including fishes (Roussel et al. 2000; Cooke et al. 2011; Pennock et al. 2016), crayfishes (Black et al. 2010), and bivalve mollusks (Kurth et al. 2007; Hamilton and Connel 2009; Hale et al. 2012). More recently, this technology has been used to study freshwater mussel movement and behavior (Peck et al. 2007; Gough et al. 2012; Newton et al. 2015) and the survival of released endangered species (wild, Fernandez 2013; hatchery produced, Hua et al. 2015). In the first evaluation of PIT tag use for mussel translocation monitoring, Kurth et al. (2007) observed recapture rates were twice as high as rates observed using visual surveys. Hua et al. (2015) found near complete detection of hatchery-stocked mussels during seven monitoring events over a 2-yr period. Tiemann et al. (2016) recovered 83% of PIT-tagged mussels during 17 monitoring events over 3 yr following a short-distance relocation.

The PIT tags are located subcutaneously in vertebrates and larger invertebrates because their body mass is large relative to the tag size. Internal insertion is generally avoided for freshwater mussels in favor of external affixation because it can result in premature tag rejection or animal mortality (Kurth et al. 2007). Although mussels have been tagged internally (e.g., Layzer and Heinricher 2004), external placement of shellfish tags is the predominant method used to mark mussels in capture–recapture studies (Lemarie et al. 2000; Villela et al. 2004), especially when using PIT tags (Kurth et al. 2007; Peck et al. 2007) and sensors (Hauser 2015; Hartman et al. 2016a, 2016b). Cyanoacrylate and epoxy resin adhesives have been primarily used to externally affix PIT tags to mussel shells, and they have variable curing times, costs, and chemical compositions, in addition to bond strength and longevity. These types of adhesives have shown low rates of mortality and high rates of PIT tag retention in laboratory and in situ settings (Young and Isley 2008). A third, less commonly used adhesive (dental cement) has shown similar performance (Kurth et al. 2007; Hua et al. 2015).

Despite their rapidly increasing use in mussel research and conservation, there has been just a few studies on the effects of external adhesion on mussel behavior, movement, growth, and survival (e.g., Wilson et al. 2011; Peck et al. 2014; Hartmann et al. 2016a; Hua et al. 2016). Furthermore, there has been no evaluation of the trade-offs in material cost and effort (i.e., application and curing time) between the three most widely implemented adhesive types. These could be important factors to consider when developing a conservation plan or ecological study that incorporates PIT tags if the effects of handling or transportation may already be large or if resources are limited. Our objective was to model and evaluate how these factors function over a range of tagging sample sizes for epoxy resin, cyanoacrylate, and dental cement adhesives.

METHODS

We used data from three case studies that represent field applications of externally affixed PIT tags by using three adhesive types with four freshwater mussel species that have been monitored for $\geq$2 yr.

Illinois Case Study

Natural resource agencies in Illinois PIT tagged 1,766 Clubshell (*Pleurobema clava*) and 1,983 Northern Riffleshell (*Epioblasma rangiana*) translocated from the Allegheny River beneath the existing U.S. Highway 62 Bridge, Forest County, Pennsylvania, between 2012 and 2014. Clubshell ranged in length from 23 to 62 mm ($\mu = 45.2$ mm), whereas Northern Riffleshell varied from 26 to 78 mm ($\mu = 53.1$ mm). Mussels were shipped in coolers from Pennsylvania to Illinois ($\sim$10 h out of water) and then placed in quarantine holding tanks at the Illinois Natural History Survey Aquatic Research Facility in Champaign-Urbana, Illinois. Each tank provided continuous ground water (temperature ranged from 20 to 22°C), lacked substrate, and was aerated using air pumps. The 2012 cohort was held in quarantine for 14 d, whereas the 2013 and 2014 classes were quarantined for 4–5 d before being released.

While in quarantine, individual mussels were externally affixed with 12.5-mm, 134.2-kHz PIT tags (BioMark, Inc., Boise, ID) by using Devcon 11800 marine grade epoxy resin (Devcon, Danvers, MA). Batches of up to 50 individuals were scrubbed to removed debris (e.g., algae and caddisfly cases), towel dried, and affixed with a PIT tag on the right valve and a uniquely numbered, vinyl shellfish tag (Hallprint, Hindmarsh Valley, South Australia) on the left valve. To affix both PIT and shellfish tags, technicians placed a small bead of cyanoacrylate to hold a tag in place; the brand of cyanoacrylate varied and no accelerant was applied to the glue (Fig. 1a). Once dried, PIT tags were completely encased in epoxy, whereas shellfish tags were encased in cyanoacrylate (Fig. 1b). Individuals were then databased (i.e., recorded species, sex, length, tag numbers, and other information) before being returned to the holding tanks. Out-of-water time averaged 30 min mussel^{-1}. Animals were held at least 24 h for the epoxy to fully cure before being hand planted at eight sites in the Vermilion River basin (Wabash River drainage).

Figure 1. Marking of Northern Riffleshell (*Epioblasma rangiana*) and Clubshell (*Pleurobema clava*) by (a) attaching passive integrated transponder (PIT) tags to shells with cyanoacrylate and (b) encapsulating PIT tags in epoxy resin; Eastern Elliptio (*Elliptio complanata*) by using cyanoacrylate by (c) attaching PIT tags to shell and (d) encapsulating the PIT tag in cyanoacrylate; and Cumberland Combshell (*Epioblasma brevidens*) by (e) attaching a PIT tag to the shell with cyanoacrylate and (f) encapsulating the PIT tag in dental cement.

Animals have since been monitored to estimate the survival and gauge the success of the project (Stodola et al. in review). Of the 3,749 animals tagged and relocated, 3,371 (90%) have been encountered at least once during subsequent recapture monitoring by using a portable submersible PIT tag antennae.

Maryland Case Study

Maryland Department of Natural Resource biologists relocated 2,345 Eastern Elliptio (*Elliptio complanata*) in 2014 from the direct and indirect impact zones of a stream bank stabilization project along Route 24 in Deer Creek, Harford County, Maryland. Particular attention was paid to the effort required to remove, process, and relocate mussels because this was the first large relocation in the state. As a result, an additional 541 mussels were collected in preremoval surveys to assess the potential effects of relocation via capture–recapture monitoring (Ashton et al. 2016). In total, 427 of the 2,866 mussels collected in the removal and preremoval surveys were externally PIT tagged. These mussels have been monitored at five relocation sites and three control sites that received no relocated mussels annually since 2014. This has resulted in an additional 149 (2015) and 112 (2016) naive (i.e., unmarked) mussels being PIT tagged. The Eastern Elliptio PIT tagged ranged in length from 19 to 86 mm ($\mu = 57.3$ mm).

Mussels collected in preremoval, removal, and monitoring surveys were held on site in flowthrough containers or aerated coolers that received frequent changes of river water before processing. After being cleaned of debris, the shell length (millimeters) of each mussel was measured, and each valve was marked with a Hallprint tag adhered using a surface-insensitive, cyanoacrylate gel. Eastern Elliptio <50 mm in shell length and every fifth naive mussel were externally affixed with a 12.5-mm, 134.2-kHz PIT tag. PIT tags were held in place on the shell in a small bead of cyanoacrylate gel (Fig. 1c). Using a separate tube of cyanoacrylate without an application tip, PIT tags were then encapsulated on all sides with additional adhesive (Fig. 1d). In 2014, PIT tags were affixed and encapsulated with LOCTITE gel control (Henkel Corp., Rocky Hill, CT). In 2015 and 2016, Turbo Fuse gel (Palm Labs Adhesives, DeBary, FL) was used to attach tags. Total time to measure and tag was maintained at 2 min mussel^{-1} to minimize aerial exposure by using one or two sprays of a cyanoacrylate curing accelerant (Turbo Set I, Palm Labs Adhesives) in all years. After processing was complete, mussels were kept in flowthrough or aerated holding containers of river water before being hand planted into the substrate. Of the 576 animals PIT tagged in 2014 and 2015, approximately 25% have been relocated through visual survey methods at least once in subsequent monitoring (M.J. Ashton et al., unpublished data).

Virginia Case Study

Ninety-nine Cumberland Combshell (*Epioblasma brevidens*) were propagated at the Freshwater Mollusk Conservation

Table 1. Comparison of adhesives to attach and encapsulate passive integrated transponder tags to freshwater mussels.

Study	Adhesive	Adhesive Type	Approximate Time to Apply (min)	Cure Time (min)	Cost (US$ g^{-1})	Adhesive (g·mussel^{-1})
Illinois	Devcon 11800	Epoxy resin	5	1,440[a]	0.14	0.72
Maryland	Palm Labs 440 Turbo Fuse Gel	Cyanoacrylate	1	1	0.35	0.54
Virginia	Fuji Glass Ionomer Luting Cement	Dental cement	1	1	2.54	0.94

[a] We estimated that 2% of the total cure time (30 min) involved costs associated with effort (e.g., transfer of mussels to holding tanks, arrangement within tank, collection for transport).

Center, Department of Fish and Wildlife Conservation, Virginia Tech in Blacksburg, Virginia. Over a 2-yr period, mussels were released from hatchery or in situ culture systems after they reached a minimum length of 20 mm into the Powell River, Claiborne County, Tennessee. Tagged Cumberland Combshell ranged in length from 17.8 to 22.9 mm ($\mu = 19.3$ mm).

While in culture, subadult Cumberland Combshell were marked with a bee tag (The Bee Works, Ontario, Canada) or vinyl shellfish tag by using cyanoacrylate. A three-step process was used to externally affix PIT tags in the field. After being cleaned and dried, PIT tags were held with LOCTITE gel control cyanoacrylate (Fig. 1e). Tags were then completely encapsulated in Fuji Glass Ionomer Luting Cement (Fig. 1f; GC Fuji Luting, Tokyo, Japan). A hypodermic needle was used to mix the dental cement powder and liquid on a manufacturer's supplied application pad and apply the mixed cement onto the PIT tag via syringe. To reduce negative effects of exposure, the PIT tagging process was conducted in the field under shade and took 2 min mussel^{-1}. Mussels were hand planted into the substrate at the monitoring site after tagging was complete. The released mussels were monitored using a portable submersible PIT tag antennae to assess individual heterogeneity of demographic rates (Hua et al. 2015). Of the 99 animals tagged and released, 97 (98%) have been encountered at least once during subsequent recapture monitoring (Hua et al. 2015).

Evaluation

We evaluated the total cost to externally affix PIT tags to freshwater mussels by parameterizing the cost (US$ g^{-1}) of each primary adhesive (A), quantity of adhesive (qA) used in each case study (g mussel^{-1}), time (min mussel^{-1}) needed to apply the adhesive and PIT tag (tA), and time (min mussel^{-1}) actively engaged with tagged mussels during the adhesive curing process (cA) (Table 1). Costs of adhesives per unit were calculated from purchase records kept in each case study. We did not include the cost of PIT tags and adhesive used to attach the tag as they were similar among studies. We also did not include adhesive use and tag application data from the 2014 portion of the Maryland case study because it was discovered that a relatively large amount of adhesive remained inside the applicator even after it appeared exhausted.

The quantity of adhesive used per mussel was determined by dividing the number of mussels tagged in each study by the quantity of adhesive consumed. We used the average hourly salary rate published by the General Services Administration's Contract-Awarded Labor Category for project scientists in the environmental services schedule with a Bachelor's or higher education level to determine a constant cost in staff time (US\$96.00 h^{-1}) to affix PIT tags (GSA 2016). Cost in time spent to cure adhesive type was calculated in the same manor, but for epoxy the time was estimated at 30 min for batches of 50 mussels instead of for an individual mussel. The parameters of cost were then totaled and extrapolated on a per mussel tagged basis (cost-per-tag-effort; CPTE in \$US) for cyanoacrylate and dental cement as follows:

$$\begin{aligned}\mathrm{CPTE} = {} & [(A \times \mathrm{q}A) \times \mathrm{N_{mussels}}] \\ & + \left[\left(\$96.00\cdot\mathrm{h}^{-1} \times (\mathrm{t}A \times \mathrm{N_{mussels}})\right]/60\,\mathrm{min} \\ & + \left(\$96.00\cdot\mathrm{h}^{-1} \times (\mathrm{c}A \times \mathrm{N_{mussels}})\right]/60\,\mathrm{min}. \end{aligned} \tag{1}$$

For epoxy, CPTE was calculated as follows:

$$\begin{aligned}\mathrm{CPTE} = {} & [(A \times \mathrm{q}A \times \mathrm{N_{mussels}})] \\ & + \left[(\$96.00\cdot\mathrm{h}^{-1} \times (\mathrm{t}A \times \mathrm{N_{mussels}}\right]/60\,\mathrm{min} \\ & + \left(\$96.00\cdot\mathrm{h}^{-1} \times (\mathrm{c}A \times \mathrm{N_{mussels}}/50)\right]/60\,\mathrm{min}. \end{aligned} \tag{2}$$

To generate a predictive equation for the relationship between CPTE and number of mussels tagged, we constructed ordinary least squares regression models for each adhesive type by using the lmList function in R package nlme (Pinheiro et al. 2016). A linear method was chosen as opposed to fitting the extrapolated parameter values against other distributions because parameters of CPTE increase at a constant rate mussel per mussel (equation 1) or batch per batch (equation 2). We used the lm method of the geom_smooth function in R package ggplot 2 (Wickham 2009) to visualize these relationships.

RESULTS

The PIT tagging of 3,749 Clubshell and Northern Riffleshell consumed approximately six 454-g epoxy adhesives over the 3-yr period. Tagging of 149 Eastern Elliptio in 2015 and 112 individuals in 2016 consumed four and three 20-g cyanoacrylate adhesives, respectively. Three 35-g dental cement adhesives were used to tag 99 Cumberlandian Combshell in 2009 and 2010. The quantity of adhesive used

Table 2. Costs of materials and effort incurred during the adhesion and curing of passive integrated transponder (PIT) tags to freshwater mussels per mussel and extrapolated per 100 individuals by adhesive type.[a]

No. Mussels Tagged	Dental cement (US$) Adhesive (q*A*)	Application (t*A*)	Cure (c*A*)	Cost (CPTE)	Cyanoacrylate (US$) Adhesive (q*A*)	Application (t*A*)	Cure (c*A*)	Cost (CPTE)	Epoxy (US$) Adhesive (q*A*)	Application (t*A*)	Cure (c*A*)	Cost (CPTE)
1	2.40	1.60	1.60	5.60	0.22	1.60	1.60	3.42	0.10	8.00	48.00	56.10
100	239.76	160.00	160.00	559.76	22.46	160.00	160.00	342.46	10.30	800.00	96.00	906.30
200	479.51	320.00	320.00	1,119.51	44.92	320.00	320.00	684.92	20.60	1,600.00	192.00	1,812.60
300	719.27	480.00	480.00	1,679.27	67.38	480.00	480.00	1,027.38	30.90	2,400.00	288.00	2,718.90
400	959.02	640.00	640.00	2,239.02	89.84	640.00	640.00	1,369.94	41.19	3,200.00	384.00	3,625.19
500	1,198.78	800.00	800.00	2,798.78	112.31	800.00	800.00	1,712.31	51.49	4,000.00	480.00	4,531.49
600	1,438.53	960.00	960.00	3,358.53	134.77	960.00	960.00	2,054.77	61.79	4,800.00	576.00	5,437.79
700	1,678.29	1,120.00	1,120.00	3,918.29	157.23	1,120.00	1,120.00	2,397.23	72.09	5,600.00	672.00	6,344.09
800	1,918.04	1,280.00	1,280.00	4,478.04	179.69	1,280.00	1,280.00	2,739.69	82.39	6,400.00	768.00	7,250.39
900	2,157.80	1,440.00	1,440.00	5,037.80	202.15	1,440.00	1,440.00	3,082.15	92.69	7,200.00	864.00	8,156.69
1,000	2,397.55	1,600.00	1,600.00	5,597.55	224.61	1,600.00	1,600.00	3,424.61	102.99	8,000.00	960.00	9,062.99

[a] q*A*, quantity of adhesive used in each case study (g mussel^{-1}); t*A*, time (min mussel^{-1}) needed to apply the adhesive and PIT tag; c*A*, time (min mussel^{-1}) actively engaged with tagged mussels during the adhesive curing process; CPTE, cost-per-tag-effort.

to PIT tag these mussels was similar across years by adhesive type.

Parameters of adhesive consumption, application, and curing effort varied by adhesive type (Table 1). Cyanoacrylate required 24% less adhesive to affix a PIT tag to an individual mussel than the epoxy and 43% less than dental cement. In contrast, epoxy was 2.5 times less costly per gram than cyanoacrylate and 18 times less costly than dental cement. Epoxy required 5 times more effort to apply and encapsulate a PIT tag than both dental cement and cyanoacrylate. Total cure time for epoxy was considerably greater than other adhesives, yet little of this time was spent handling mussels. Consequently, less effort associated with the process of adhesive curing accumulated as more mussels were tagged with epoxy than with cyanoacrylate and dental cement by handling mussels in batches of 50 (e.g., 100 mussels cured in 60 min vs. 60 mussels in 60 min).

Linear models of total cost (US$) per PIT-tagged mussel based on our cost and consumption parameters illustrated that cyanoacrylate ($\mathrm{CPTE} = \$3.42 \times N_{\mathrm{mussels}} - 1.23^{-10}$) was less costly than dental cement ($\mathrm{CPTE} = \$5.60 \times N_{\mathrm{mussels}} - 2.52^{-13}$) or epoxy ($\mathrm{CPTE} = \$9.04 \times N_{\mathrm{mussels}} + \$14.96$) (Table 2 and Fig. 2a). Costs associated with adhesive consumption increased at a greater rate for dental cement and cyanoacrylate than epoxy (Fig. 2b). The rate at which CPTE increased as the number of mussels tagged increased was higher for epoxy than cyanoacrylate and dental cement due to higher costs associated with adhesive application effort (Fig. 2c). An initial investment of effort to cure the first batch of 50 mussels led to higher upfront costs (i.e., larger y-intercept) for epoxy, but ultimately resulted in lower costs in comparison with cyanoacrylate and dental cement as the number of mussels tagged increased (Fig. 2d).

DISCUSSION

External attachment of PIT tags is a marking technique that can increase detection rates of freshwater mussels (Kurth et al. 2007) and improve the accuracy of survival and demographic rates (Hua et al. 2015; Tiemann et al. 2016). For this reason, PIT tags seem especially suited for use in mussel relocation and conservation monitoring due to historically low recapture rates (Cope et al. 1995, 2003). A primary goal in studies that employ recapture sampling is reduced stress from handling, especially out of water time (Dunn et al. 2000). Aerial exposure to apply and adhere tags to freshwater mussels by using cyanoacrylate was generally <15 min mussel^{-1} (Lemarie et al. 2000; Villella et al. 2004), yet this can be reduced to 2 min mussel^{-1} by using a curing accelerant. Dental cement has a similar curing time. Using underwater epoxy to affix PIT tags can negate the reduced handling time goal as it requires more handling and total curing time than cyanoacrylate (Table 1 and Fig. 2c).

In this evaluation of the materials and staff time needed to affix and encapsulate PIT tags to freshwater mussels from three studies, cyanoacrylate was overall less costly than dental cement and epoxy on a per mussel basis. Absolute differences in total cost compared to cyanoacrylate are relatively small when the number of mussels tagged is low, but they increased by more than $2 mussel^{-1} for dental cement and almost $6 mussel^{-1} for epoxy. We suggest that dental cement and waterproof epoxy resin may be an appropriate choice of adhesive for transmitters when the number of study animals is low. In this scenario, differences in costs among adhesive types will be negligible, and dental cement or epoxy may be better suited to protect PIT tags from damage should even minimal tag loss affect the statistical power to detect a change in population size or condition. A quicker, more controlled method of applying epoxy warrants investigation as the effort

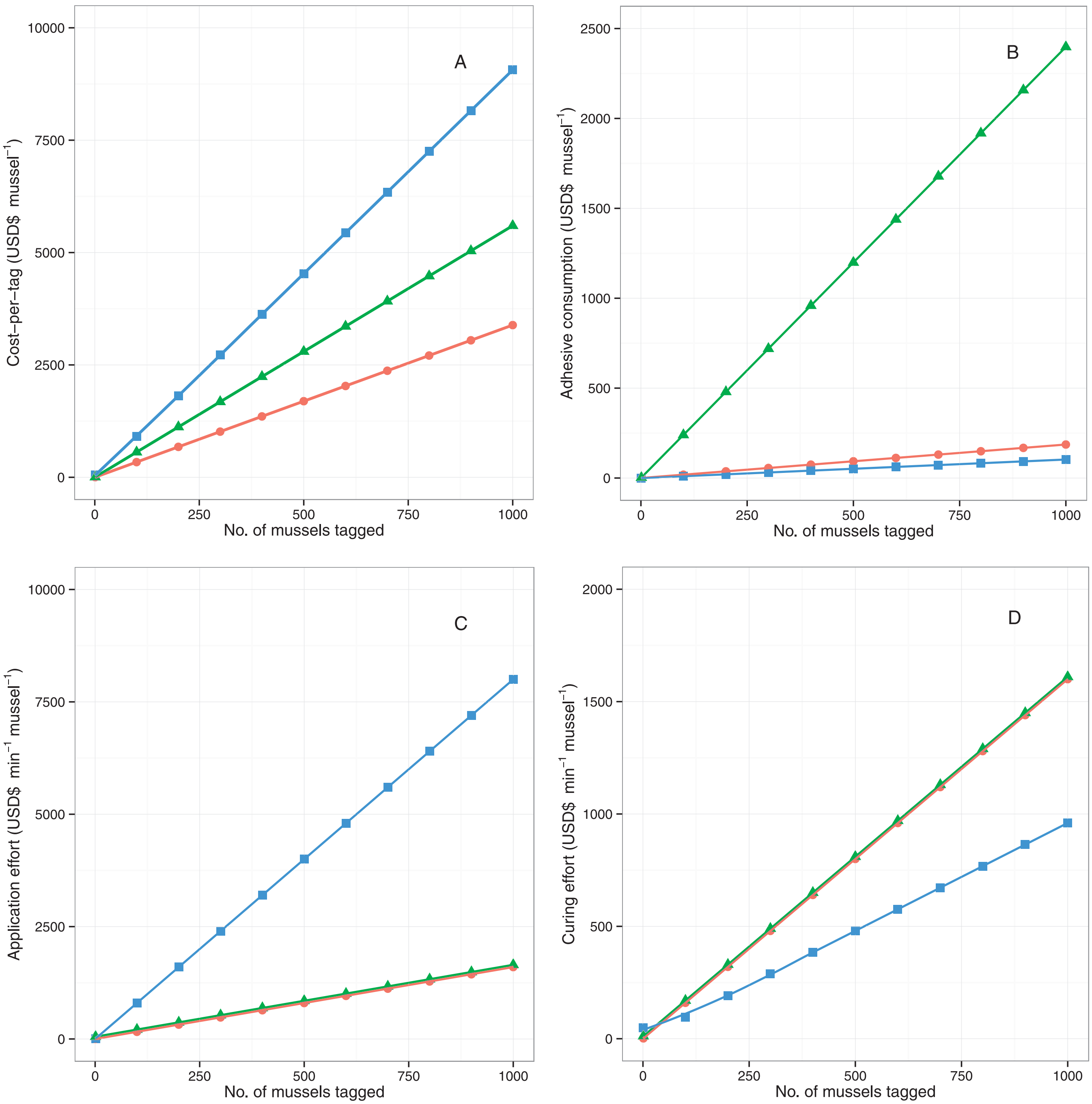

Figure 2. Linear models for epoxy resin (blue squares), cyanoacrylate (red circles), and dental cement (green triangles). Relationships between (a) cost-per-tagged mussel versus number of mussels with externally affixed PIT tags and individual cost-per-tag-effort (CPTE) parameters of (b) adhesive consumption, (c) application time, and (d) curing time versus number of mussels tagged.

associated with its application evaluated in this study was 5 times more than that of cyanoacrylate or dental cement. This difference in effort drove CPTE higher for epoxy (Fig. 2a, c), even though the cost of adhesive consumption per tag was less and curing in batches may reduce and even reverse any cost advantage achieved from using a faster curing adhesive (Fig. 2b, d). A more controlled applicator could also reduce the quantity of epoxy consumed per tag, thus realizing additional savings in materials. Because application and curing times were similar for cyanoacrylate and dental cement, differences in CPTE could be mitigated by more conservative cement application or a less costly formula.

Prices of adhesives can vary widely, especially when considering the advent of online shopping, buying in bulk, or discounts some groups receive (e.g., governmental agencies). The difference in adhesive cost per unit may in part be because the epoxy evaluated in this study is sold in a greater quantity per standard package than both dental cement and cyanoacrylate. On average, 600 individuals could be affixed with PIT tags by using a 454-g package of epoxy. In contrast, about 30 individuals could be tagged using a 35-g package of dental cement. Other factors to consider are the ability to rapidly procure adhesive, surcharges when not ordering in bulk, or unintended curing of unused product. For example, acquiring dental cement can be challenging because its intended use is in a regulated industry. Also, unexpected demand for additional adhesive (e.g., tagging more mussels than expected or more liberal adhesive application) requires the need for impromptu purchasing. We have observed prices varying by 10–30% among major retailers for the same cyanoacrylate adhesive. Cyanoacrylate adhesives and accelerants are often sold in cases of 10 or 12 and have a suggested shelf life of a year. There are often surcharges to purchase units less than a case, which would increase cost per unit parameters if a relatively small number of mussels are to be tagged. With adequate planning time, comparison shopping should help keep actual costs comparable to our studies; however, we noted a 30% increase in the price of epoxy since the last purchase from the same vendor.

Although we focused our effort on resources required to affix PIT tags, the cost of tags can also vary depending on the quantity, size, and manufacturer. For the data evaluated in our models, tag cost would have been constant because large quantities were procured from the same vendor at or about the same time. However, over the course of these studies tag price has fluctuated year to year and vendor to vendor by (+) 150 to (–) 250% (e.g., prices have ranged from $2 to $5 per tag). Other costs we did not measure and account for in our evaluation should also be considered when choosing an adhesive type for PIT tagging of freshwater mussels. For example, the curing time associated with underwater epoxies could reduce the number of mussels that can be tagged and returned to a stream in a day or require travel between study sites and laboratory facilities thus extending the number of field days. Specialized facilities and equipment may also be necessary to hold mussels in captivity during the curing time, whereas mussels can be immediately returned to the stream after cyanoacrylate and dental cures. Tiemann et al. (2016) speculated that prolonged handling and exposure may have contributed to the initial mortality observed following relocation. Factors other than cost may also warrant consideration, including the presence of potentially harmful compounds, adhesive durability, and ability to reapply in the field. For example, Hartmann et al. (2016a) chose not to adhere sensors to Duck Mussel (*Anodonta anatina*) with epoxy resin due to its complex application and presence of bisphenol-A. Environmental factors (e.g., air temperature and relative humidity) can also affect adhesive viscosity and curing time.

We propose that PIT tag retention is generally not an important factor in choosing an adhesive as previous studies have shown that retention rates do not seem to vary substantially by adhesive type (e.g., Young and Isley 2008). However, PIT tag attachment may fail regardless of adhesive type if debris causes the bond between shell and adhesive or adhesive and tag to break. Insufficient PIT tag encapsulation could cause them to be damaged if mussels become dislodged or struck with coarse particles during high flow events. Still, externally affixed PIT tag loss appears to be low over 1–2-yr periods and comparable to retention rates of vinyl shellfish tags (e.g., Lemarie et al. 2000). For example, Ashton et al. (2016) observed the loss or failure of eight (2%) cyanoacrylate-affixed PIT tags 12 mo after relocation on Eastern Elliptio that were recovered 650 to 1,500 m downstream of the point of their relocation in a coarse substrate stream. Similar levels of tag damage due to cyanoacrylate erosion were observed after 18 mo by Young and Isely (2008), but they observed no tag damage due to adhesive loss for underwater epoxy. Tiemann et al. (2016) reported one (1%) tag failure during their assessment of short-distance mussel relocation with epoxy encapsulated PIT tags. Hua et al. (2016) observed no failure of tags embedded in dental cement. We are unaware of any published studies that have evaluated PIT tag retention beyond 3 yr so we cannot speculate whether a particular type is more suited for long-term (>10-yr) study.

The findings of our evaluation are likely limited in their scope to the adhesives we evaluated (gel cyanoacrylate, dental cement, and 24-h curing waterproof epoxy resin); however, the assumptions used to parameterize our model are flexible to other costs and adhesive properties. Accordingly, the costs incurred from applying and handling with the epoxy used in this study would have been likely similar if a quicker curing formula was used based on observations of others (e.g., Young and Isley 2008). For this reason, we expect that epoxy resin would sustain higher total costs per mussel tagged without reductions in application time while also maintaining a minimal level of effort during the curing process. Further limitations in our findings may arise from a lack of quantified variation within each case study and by adhesive type. Variation when applying model parameters could arise from fluctuations in adhesive costs, level of adhesive applicator experience, and staffing. For example, actual staff costs incurred in the Illinois and Maryland case studies may have been lower than our model because some tag applicators were volunteers. However, a relocation or reintroduction involving a federally listed, cryptic species may necessitate primary investigators with specialized experience, which could lead to higher salary rates. Added variation could result from adhesive brand and environmental factors, including air temperature and relative humidity. We believe a more thorough comparison of commercially available adhesives used to externally PIT tag mussels is warranted.

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