Extinction Risk of Western North American Freshwater Mussels: Anodonta Nuttalliana, the Anodonta Oregonensis/Kennerlyi Clade, Gonidea Angulata, and Margaritifera Falcata

Authors: Blevins, Emilie, Jepsen, Sarina, Box, Jayne Brim, Nez, Donna, Howard, Jeanette, et al.

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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*

Emilie Blevins[1]*, Sarina Jepsen[1], Jayne Brim Box[2], Donna Nez[2], Jeanette Howard[3], Alexa Maine[2], and Christine O'Brien[4]

[1] *Xerces Society for Invertebrate Conservation, 628 NE Broadway Suite 200, Portland, OR 97232 USA*
[2] *Confederated Tribes of the Umatilla Indian Reservation, Department of Natural Resources, Fisheries Program, Freshwater Mussel Project, 46411 Timine Way, Pendleton, OR 97801 USA*
[3] *The Nature Conservancy, 201 Mission Street, 4th Floor, San Francisco, CA 94105 USA*
[4] *Browns River Consultants, LLC, 130 Sesame Street, Waynesville, NC 28785 USA*

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

*Corresponding Author: emilie.blevins@xerces.org

(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.	$\geq$80%
Endangered (EN)	Risk is very high.	$\geq$50%
Vulnerable (VU)	Risk is high.	$\geq$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

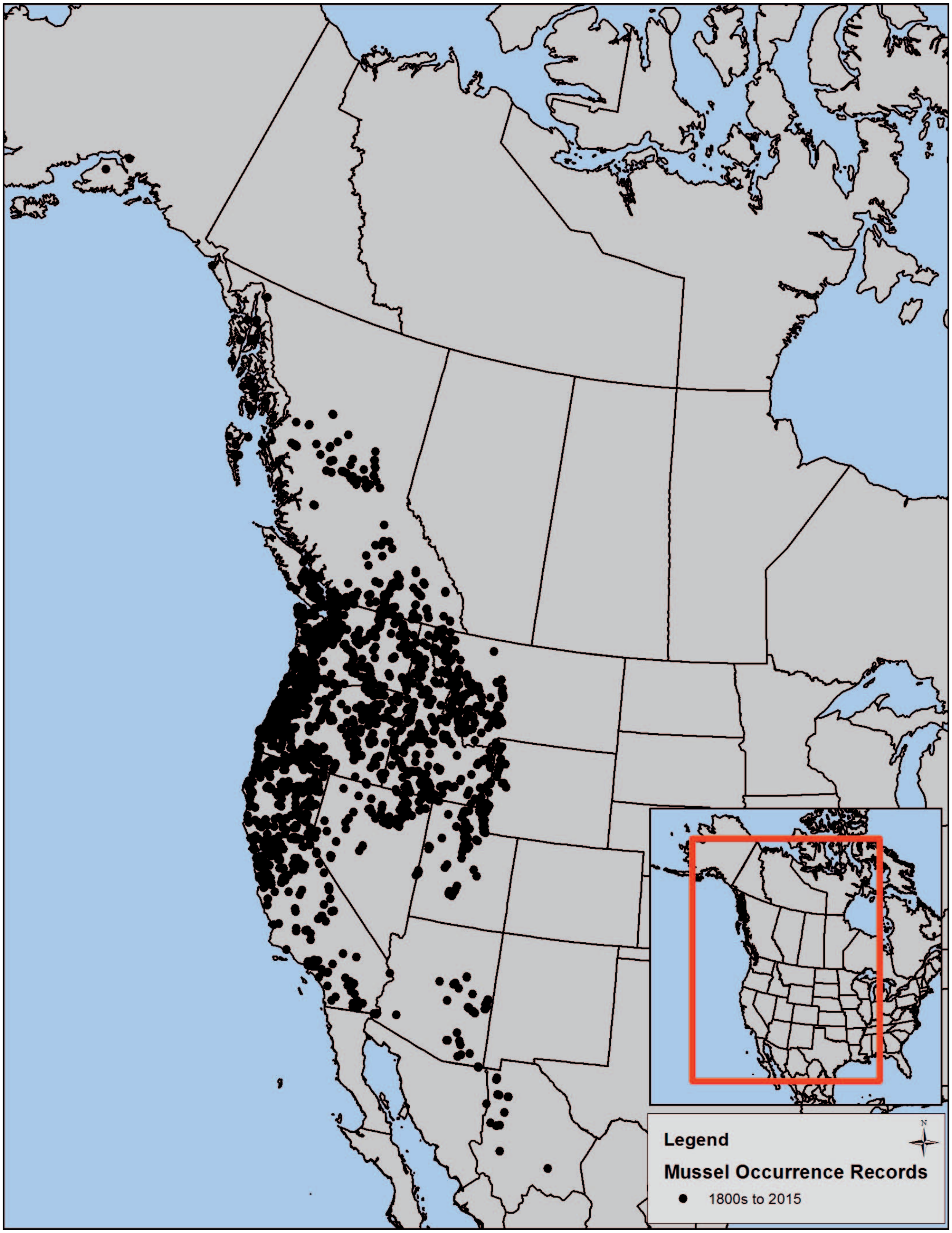

Figure 1. Occurrence records for four western North American freshwater mussel species/clades.

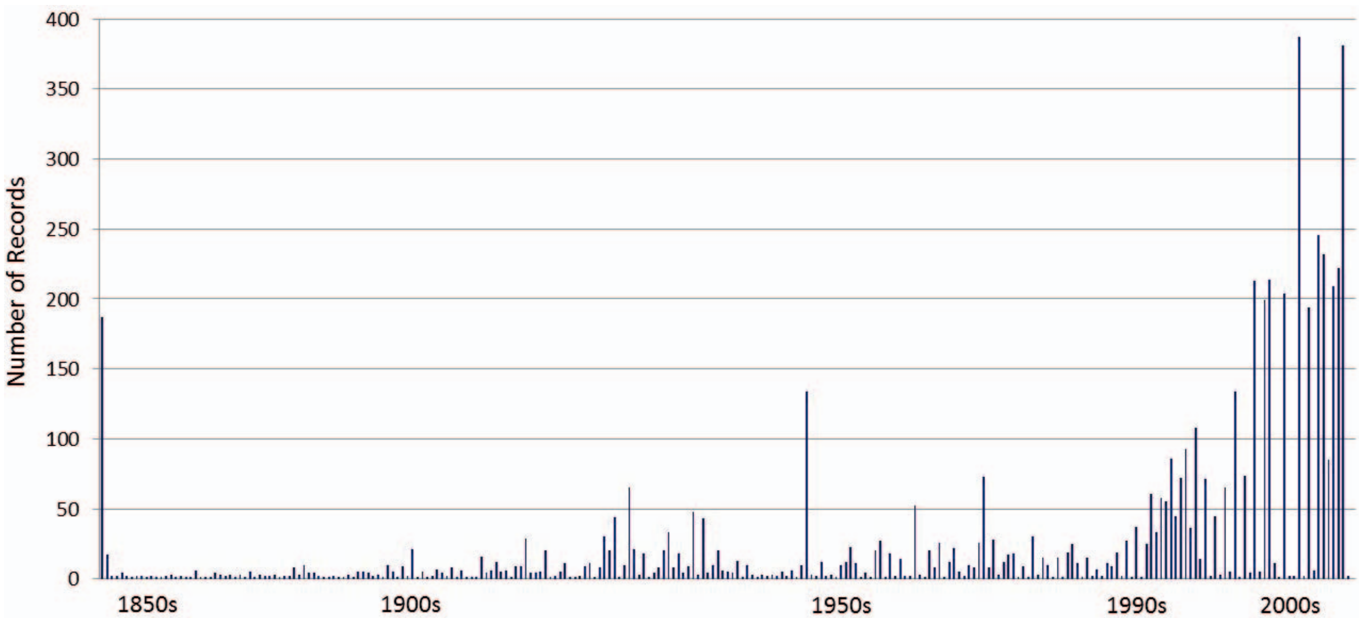

Figure 2. Number of records for freshwater mussels by year in the data set used for this analysis. Pre-1850s records are pooled across multiple years and include archeological evidence of mussel occurrences.

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.

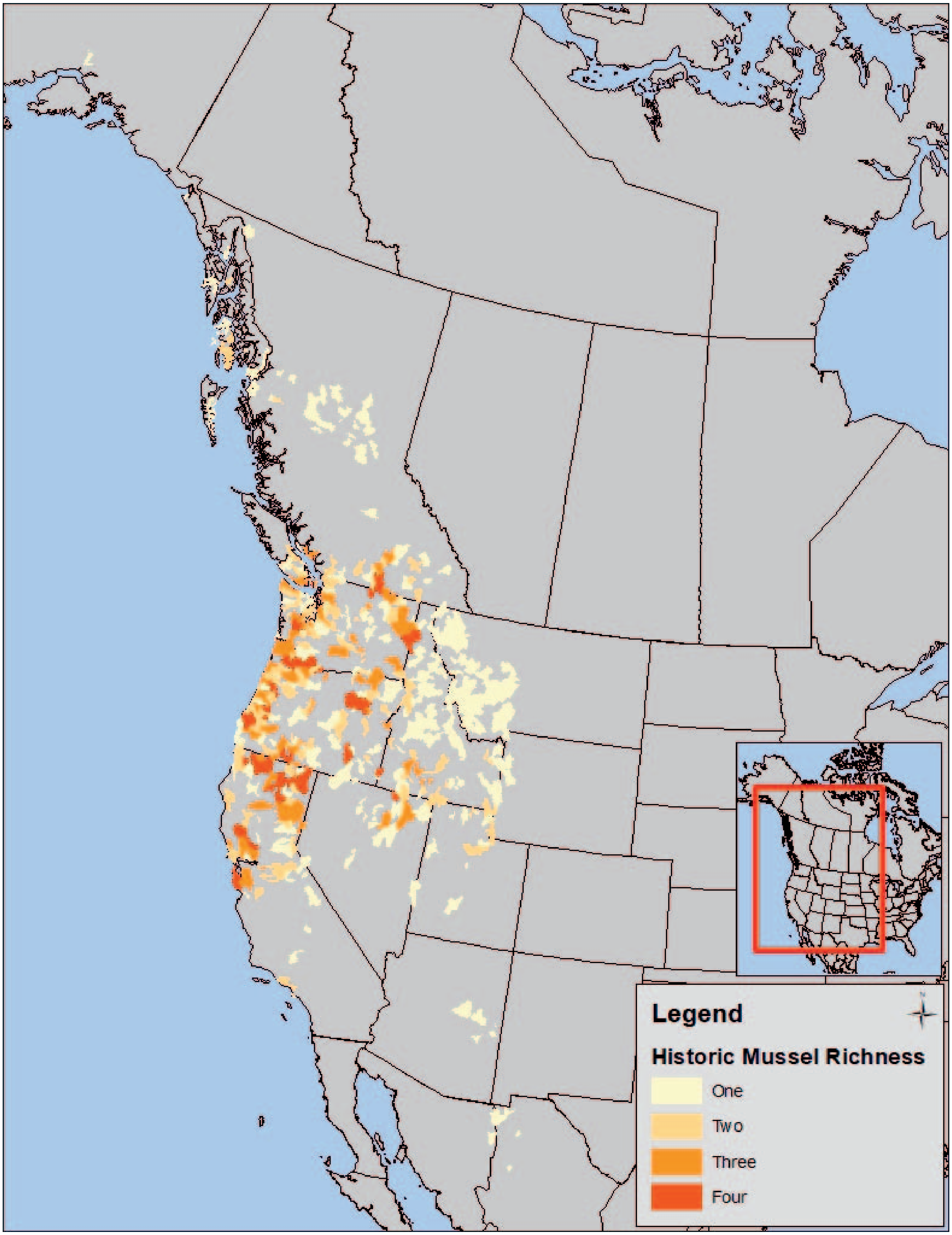

Figure 4. Historic (pre-1990) western freshwater mussel presence and richness by level 8 HydroBASIN.

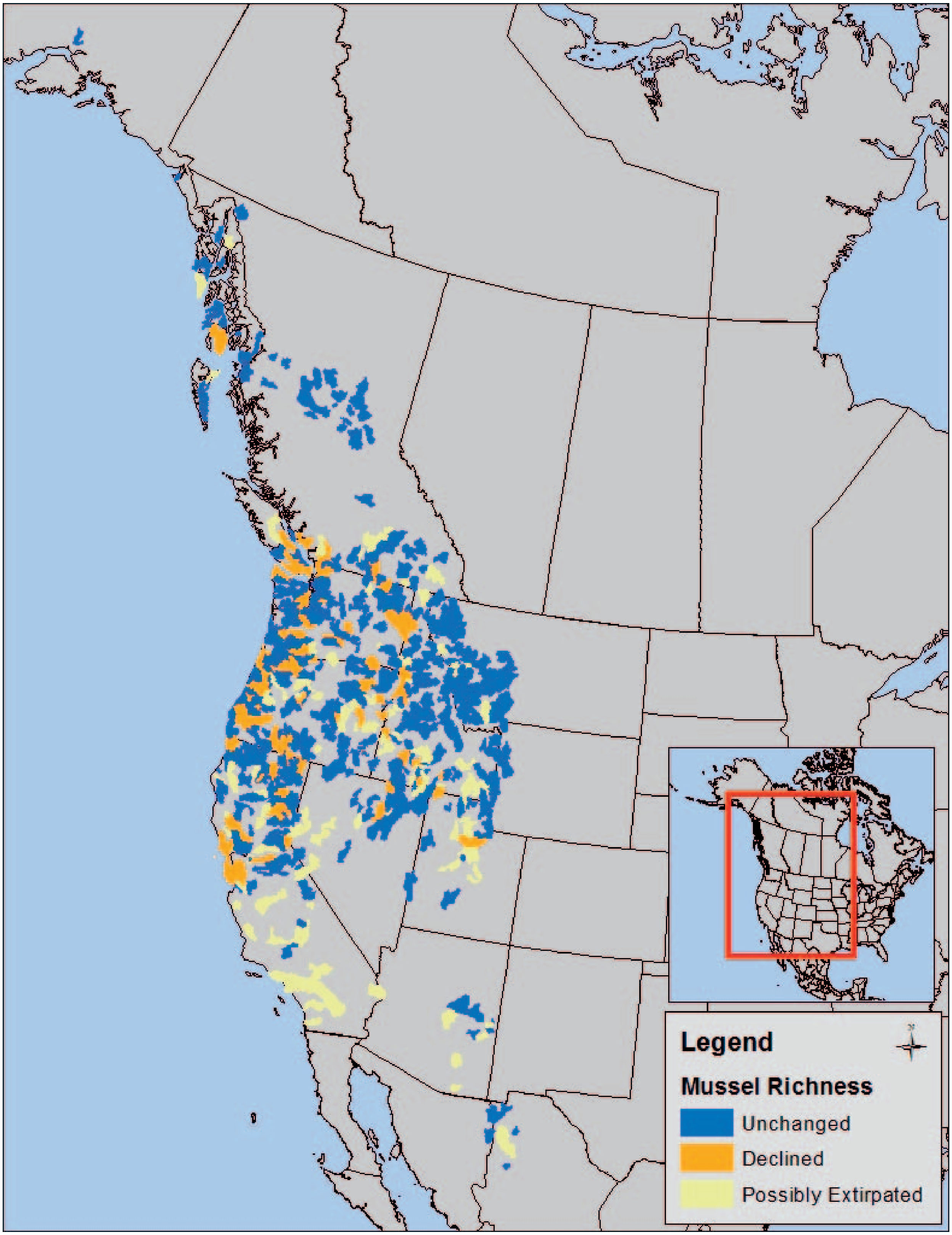

Figure 5. Change in western freshwater mussel richness by level 8 HydroBASIN between historic (pre-1990) and recent (1990–2015) time periods.

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, Washington, 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

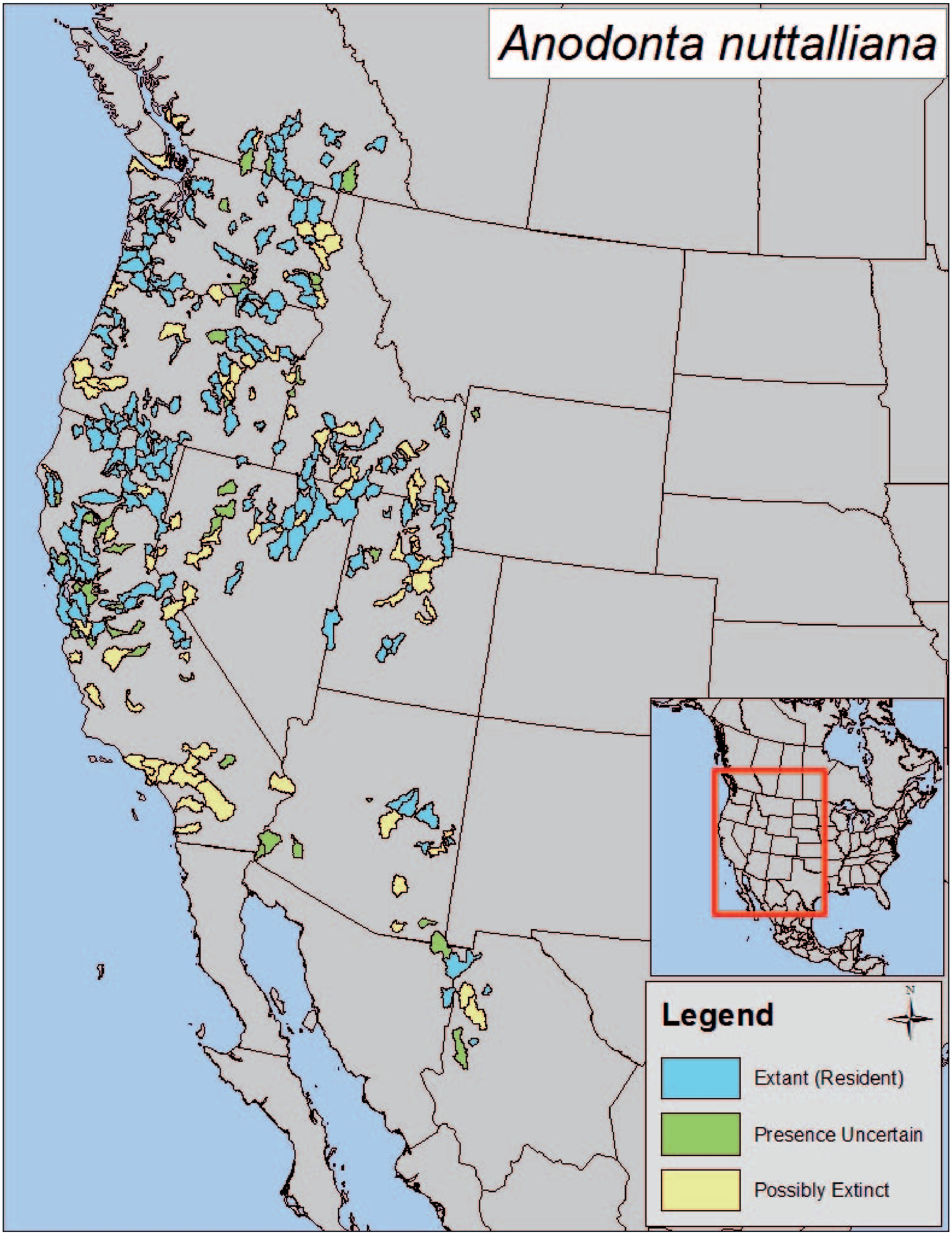

Figure 6. *Anodonta nuttalliana* status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

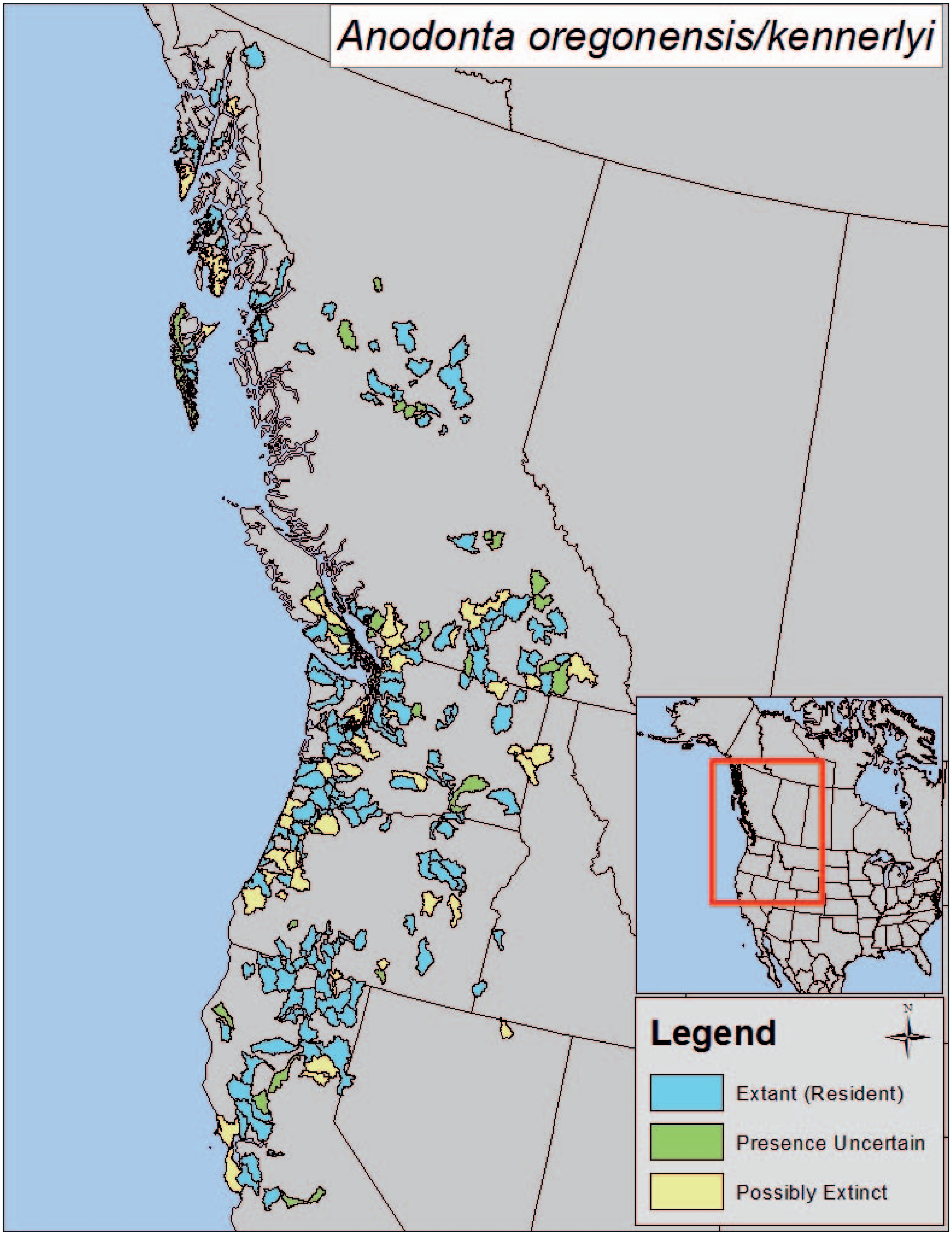

Figure 7. *Anodonta oregonensis/kennerlyi* clade status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

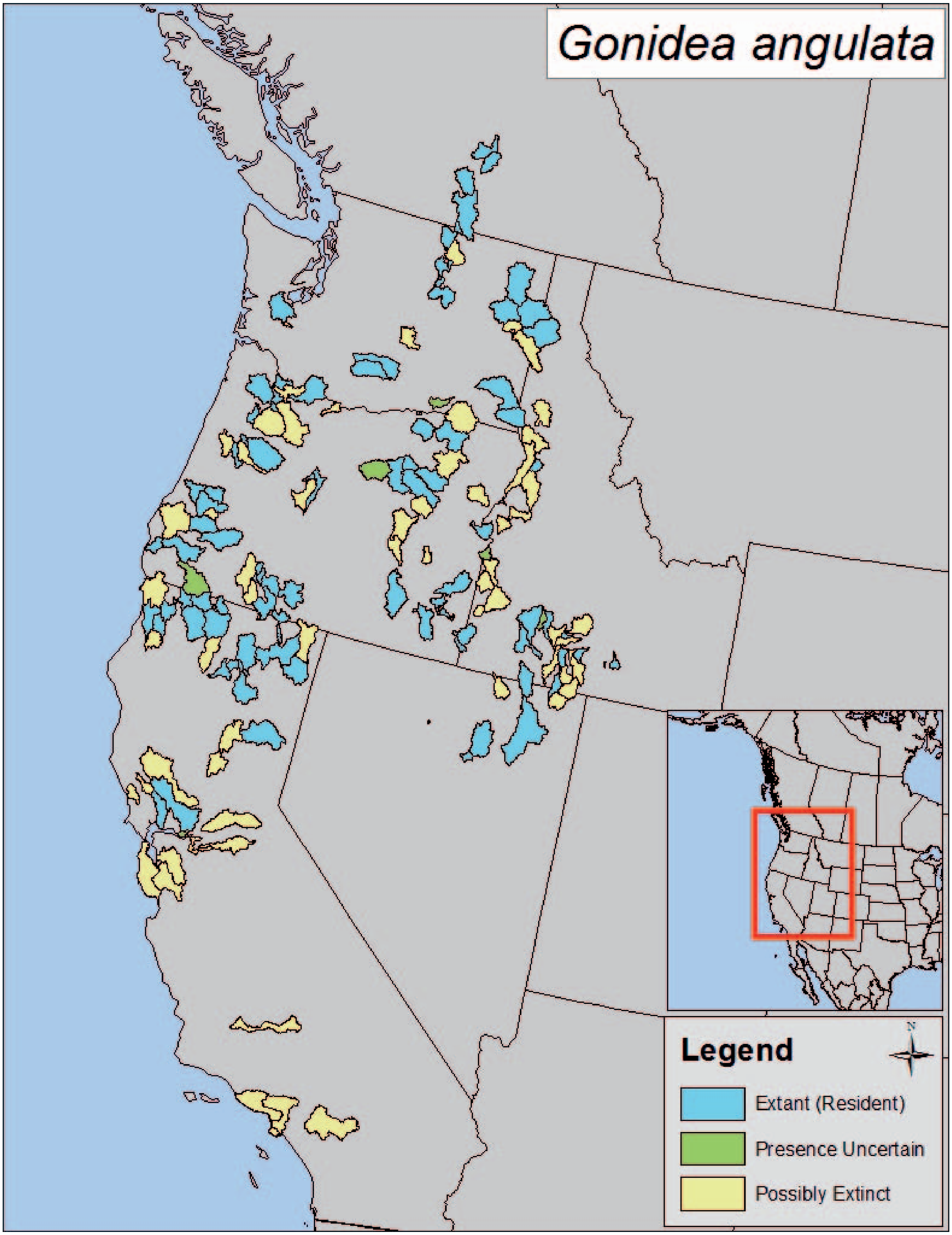

Figure 8. *Gonidea angulata* status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

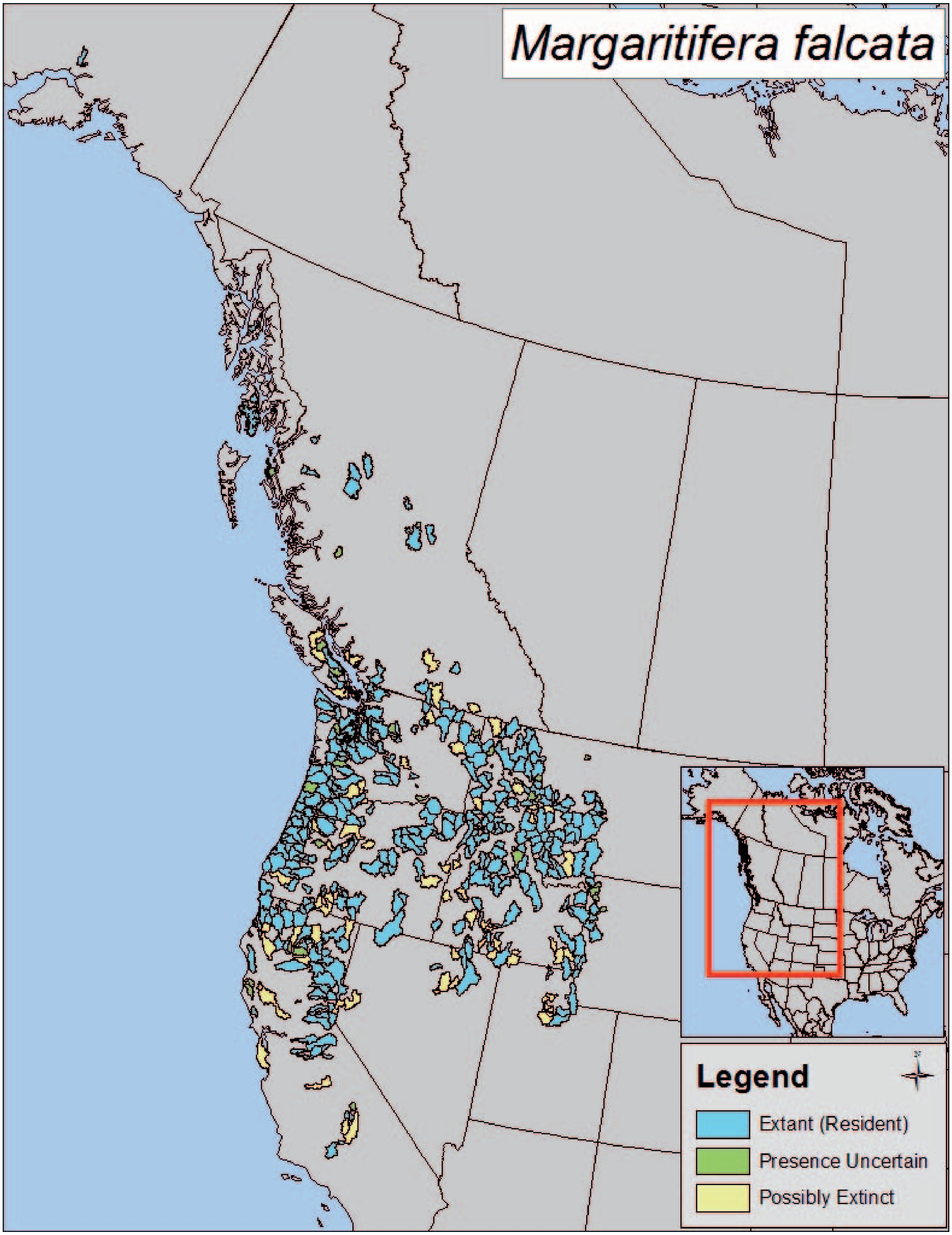

Figure 9. *Margaritifera falcata* status by level 8 HydroBASIN. Basins were used to calculate changes in extent of occurrence and watershed area between historic (pre-1990) and recent (1990–2015) time periods.

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 (~20,000 individuals in a 0.8-km stretch in 1941 down to ~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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LITERATURE CITED

Allard, D. J., T. A. Whitesel, S. Lohr, and M. L. Koski. 2015. Western pearlshell mussel life history in Merrill Creek, Oregon: Reproductive timing, growth, and movement, 2010–2014 project completion report. U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, Washington.

BCCDC (British Columbia Conservation Data Centre). 2015. Conservation status report: *Gonidea angulata*. Available at http://a100.gov.bc.ca/pub/eswp/.

Bequaert, J. C., and W. B. Miller. 1973. The Mollusks of the Arid Southwest with an Arizona Check List. The University of Arizona Press, Tucson.

Black, B. A., J. B. Dunham, B. W. Blundon, J. Brim Box, and A. J. Tepley. 2015. Long-term growth-increment chronologies reveal diverse influences of climate forcing on freshwater and forest biota in the Pacific Northwest. Global Change Biology 21:594–604.

Blevins, E., S. Jepsen, J. Brim Box, and D. Nez. 2016a. *Anodonta nuttalliana*. The IUCN Red List of Threatened Species 2016: e.T91149898A91149903. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T91149898A91149903.en.

Blevins, E., S. Jepsen, J. Brim Box, and D. Nez. 2016b. *Anodonta oregonensis*. The IUCN Red List of Threatened Species 2016: e.T189487A69491650. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T189487A69491650.en.

Blevins, E., S. Jepsen, J. Brim Box, and D. Nez. 2016c. *Gonidea angulata*. The IUCN Red List of Threatened Species 2016: e.T173073A62905403. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T173073A62905403.en.

Blevins, E., S. Jepsen, J. Brim Box, and D. Nez. 2016d. *Margaritifera falcata*. The IUCN Red List of Threatened Species 2016: e.T91109639A91109660. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T91109639A91109660.en.

Bogan, A. E. 1993. Freshwater bivalve extinctions (Mollusca: Unionoida): A search for causes. American Zoologist 33:599–609.

Brim Box, J. C., J. K. Howard, D. Wolf, C. O'Brien, D. Nez, and D. Close. 2006. Freshwater mussels (Bivalvia: Unionoida) of the Umatilla and Middle Fork John Day rivers in eastern Oregon. Northwest Science 80:95–107.

Call, R. E. 1884. On the Quaternary and Recent Mollusca of the Great Basin, with descriptions of new forms. Bulletin of the United States Geological Survey 11:66 pp.

Chong, J. P., J. Brim Box, J. K. Howard, D. Wolf, T. Myers, and K. E. Mock. 2008. Three deeply divided lineages of the freshwater mussel genus *Anodonta* in western North America. Conservation Genetics 9:1303–1309.

Claeys, R. R., R. S. Caldwell, N. H. Cutshall, and R. Holton. 1975. Chlorinated pesticides and polychlorinated biphenyls in marine species, Oregon/Washington coast 1972. Pesticides Monitoring Journal 9:2–10.

Coney, C. C. 1993. Freshwater Mollusca of the Los Angeles River: Past and present status and distribution. Pages C1–C22 *in* K. L. Garrett, editor. The Biota of the Los Angeles River: An Overview of the Historical and Present Plant and Animal Life of the Los Angeles River Drainage. Natural History Museum of Los Angeles County Foundation, Los Angeles.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2003. COSEWIC assessment and update status report on the Rocky Mountain Ridged Mussel, *Gonidea angulata*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2010. COSEWIC assessment and update status report on the Rocky Mountain Ridged Mussel, *Gonidea angulata*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

CTUIR (Confederated Tribes of the Umatilla Indian Reservation). 2015. River Mussels through Time. Color Press Publishing, Walla Walla, Washington for the Confederated Tribes of the Umatilla Indian Reservation.

Davis, E. A., A. T. David, K. M. Norgaard, T. H. Parker, K. McKay, C. Tennant, T. Soto, K. Rowe, and R. Reed. 2013. Distribution and abundance of freshwater mussels in the mid Klamath subbasin, California. Northwest Science 87:189–206.

Downing, J. A., P. Van Meter, and D. A. Woolnough. 2010. Suspects and evidence: A review of the causes of extirpation and decline in freshwater mussels. Animal Biodiversity and Conservation 33.2:151–185.

Dudgeon, D., and B. Morton. 1983. The population dynamics and sexual strategy of *Anodonta woodiana* (Bivalvia: Unionacea) in Plover Cove Reservoir, Hong Kong. Journal of Zoology 201:161–183.

FMCS (Freshwater Mollusk Conservation Society). 2016. A national strategy for the conservation of native freshwater mollusks. Freshwater Mollusk Biology and Conservation 19:1–21.

Frest, T. J., and E. J. Johannes. 1995. Interior Columbia basin mollusk species of special concern: Final report. Prepared for Interior Columbia Basin Ecosystem Management Project. Deixis Consultants, Seattle, Washington.

Furnish, J. 2010. Biological evaluation template for *Margaritifera falcata* (Gould, 1850) the western pearlshell freshwater mussel. Pages 74–91 *in* J. Furnish, editor. Regional Forester Sensitive Species: Biological Evaluation Templates for PSW Regional Sensitive Mollusk Species. U.S. Forest Service, Pacific Southwest Region.

Gould, A. A. 1850. Descriptions of new species of shells. Proceedings of the Boston Society of Natural History 3:292–296.

Graf, D. L., and K. S. Cummings. 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). Journal of Molluscan Studies 73:291–314.

Haag, W. R. 2012. North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, Cambridge, England. 505 pp.

Haag, W. R., and J. D. Williams. 2014. Biodiversity on the brink: An assessment of conservation strategies for North American freshwater mussels. Hydrobiologia 735:45–60.

Haley, L., M. Ellis, and J. Cook. 2007. Reproductive timing of freshwater mussels and potential impacts of pulsed flows on reproductive success. California Energy Commission, PIER Energy Related Environmental Research Program.

Hastie, L. C., and K. A. Toy. 2008. Changes in density, age structure and age-specific mortality in two Western Pearlshell (*Margaritifera falcata*) populations in Washington (1995–2006). Aquatic Conservation: Marine and Freshwater Ecosystems 18:671–678.

Heard, W. H. 1975. Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). Malacologia 15:81–103.

Hovingh, P. 2004. Intermountain freshwater mollusks, USA (*Margaritifera, Anodonta, Gonidea, Valvata, Ferrissia*): Geography, conservation and fish management implications. Monographs of the Western North American Naturalist 2:109–135.

Howard, J. K. 2008. Strategic inventory of freshwater mussels in the northern Sierra Nevada province. Report to the US Forest Service, Pacific Southwest Region.

Howard, J. K. 2010. Sensitive freshwater mussel surveys in the Pacific Southwest Region: Assessment of conservation status. Prepared for US Forest Service, Pacific Southwest Region.

Howard, J. K., and K. M. Cuffey. 2006. The functional role of native freshwater mussels in the fluvial benthic environment. Freshwater Biology 51:460–474.

Howard, J. K., J. L. Furnish, J. Brim Box, and S. Jepsen. 2015. The decline of native freshwater mussels (Bivalvia: Unionoida) in California as determined from historical and current surveys. California Fish and Game 101:8–23.

ICZN (International Commission on Zoological Nomenclature). 1999. International Code of Zoological Nomenclature, 4th ed. [incorporating Declaration 44, amendments of Article 74.7.3, with effect from 31 December 1999 and the Amendment on e-publication, amendments to Articles 8, 9, 10, 21 and 78, with effect from 1 January 2012]. Available at: http://www.nhm.ac.uk/hosted-sites/iczn/code/

Inoue, K., T. D. Levine, B. K. Lang, and D. J. Berg. 2014. Long-term mark-and-recapture study of a freshwater mussel reveals patterns of habitat use and an association between survival and river discharge. Freshwater Biology 59:1872–1883.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. Climatic Change 113:499–524.

IUCN (International Union for Conservation of Nature). 2012. IUCN Red List Categories and Criteria: Version 3.1, 2nd ed. Gland, Switzerland and Cambridge, UK: IUCN. 32 pp.

IUCN (International Union for Conservation of Nature). 2014. METADATA: Digital Distribution Maps on The IUCN Red List of Threatened Species. Version 4. Available at http://www.iucnredlist.org/technical-documents/spatial-data.

IUCN (International Union for Conservation of Nature) Standards and Petitions Subcommittee. 2017. Guidelines for Using the IUCN Red List Categories and Criteria. Version 13. Available at http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Jepsen, S., and C. LaBar. 2012. *Gonidea angulata* (Lea, 1838) Western Ridged Mussel Bivalvia: Unionidae. The Xerces Society for Invertebrate Conservation, Portland, Oregon.

Jepsen, S. C. LaBar, and J. Zarnoch. 2012a. *Anodonta californiensis* (Lea, 1852)/*Anodonta nuttalliana* (Lea, 1838) California Floater/Winged Floater Bivalvia: Unionidae. The Xerces Society for Invertebrate Conservation, Portland, Oregon.

Jepsen, S., C. LaBar, and J. Zarnoch. 2012b. *Margaritifera falcata* (Gould, 1850) Western Pearlshell Bivalvia: Margaritiferidae. Xerces Society for Invertebrate Conservation, Portland, Oregon.

Keyghobadi, N. 2007. The genetic implications of habitat fragmentation for animals. Canadian Journal of Zoology 85:1049–1064.

Krueger, K., P. Chapman, M. Hallock, and T. Quinn. 2007. Some effects of suction dredge placer mining on the short-term survival of freshwater mussels in Washington. Northwest Science 81:323–332.

Lea, I. 1838. Description of new freshwater and land snails. Transactions of the American Philosophical Society 6:154 pp.

Lea, I. 1852. Descriptions of new species of the family Unionidæ [new fresh water and land shells]. Transactions of the American Philosophical Society 10:253–294.

Lea, I. 1860. Descriptions of seven new species of Unionidæ from the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 12:306–307.

Lehner, B., and G. Grill. 2013. Global river hydrography and network routing: Baseline data and new approaches to study the world's large river systems. Hydrological Processes 27:2171–2186.

Lewis, J. 1875. Description of a new species of *Anodonta*. Field and Forest 1:26–27.

Limm, M. P., and M. E. Power. 2011. Effect of the Western Pearlshell mussel *Margaritifera falcata* on Pacific lamprey *Lampetra tridentata* and ecosystem processes. Oikos 120:1076–1082.

Lopes-Lima, M., E. Froufe, V. T. Do, M. Ghamizi, K. E. Mock, Ü. Kebapçı, O. Klishko, S. Kovitvadhi, U. Kovitvadhi, O. S. Paulo, J. M. Pfeiffer III, M. Raley, N. Riccardi, H. Şereflişan, R. Sousa, A. Teixeira, S. Varandas, X. Wu, D. T. Zanatta, A. Zieritz, and A. E. Bogan. 2017. Phylogeny of the most species-rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): Defining modern subfamilies and tribes. Molecular Phylogenetics and Evolution 106:174–191.

Lopes-Lima, M., A. Teixeira, E. Froufe, A. Lopes, S. Varandas, and R. Sousa. 2014. Biology and conservation of freshwater bivalves: Past, present and future perspectives. Hydrobiologia 735:1–13.

Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Hershler, K. E. Perez, B. Roth; M. Seddon; E. E. Strong, and F. G. Thompson. 2004. The global decline of nonmarine mollusks. Bioscience 54:321–330.

Lyman, R. L. 1984. Model of large freshwater clam exploitation in the prehistoric Southern Columbia Plateau culture area. Northwest Anthropological Research Notes 18:97–107.

Lysne, S. J., and B. R. Krouse. 2011. *Margaritifera falcata* in Idaho: Using museum collections and GIS to demonstrate a declining trend in regional distribution. Journal of the Idaho Academy of Science 47:33–39.

Maine, A., D. Nez, and C. O'Brien. 2017. Freshwater mussel decline in the Middle Fork John Day River, Oregon. Poster presented at: Freshwater Mollusk Conservation Society Symposium. Cleveland, Ohio.

Mathias, P., and G. Edwards. 2014. Study increases the understanding of mussel diversity within Wyoming. Wyoming State Wildlife Action Plan Newsletter August: 36.

May, C. L., and B. S. Pryor. 2016. Explaining spatial patterns of mussel beds in a Northern California river: The role of flood disturbance and spawning salmon. River Research and Applications 32:776–785.

Middendorff, A.Th.v. 1851. Wirbellose Thiere: Annulaten. Echinodermen. Insecten. Krebse. Mollusken. Parasiten. Reise in den Äussersten Norden und Osten Sibiriens, Zoologie 2:163–508.

Mock, K. E., J. C. Brim Box, J. P. Chong, J. Furnish, and J. K. Howard. 2013. Comparison of population genetic patterns in two widespread freshwater mussels with contrasting life histories in western North America. Molecular Ecology 22:6060–6073.

Mock, K. E., J. C. Brim Box, J. P. Chong, J. K. Howard, D. A. Nez, D. Wolf, and R. S. Gardner. 2010. Genetic structuring in the freshwater mussel *Anodonta* corresponds with major hydrologic basins in the western United States. Molecular Ecology 19:569–591.

Mock, K. E., J. C. Brim Box, M. P. Miller, M. E. Downing, and W. R. Hoeh. 2004. Genetic diversity and divergence among freshwater mussel (*Anodonta*) populations in the Bonneville Basin of Utah. Molecular Ecology 7:1085–1098.

Moritz, C. 1994. Defining evolutionarily significant units for conservation. Trends in Ecology and Evolution 9:373–375.

Murphy, G. 1942. Relationship of the fresh water mussel to trout in the Truckee River. California Fish and Game 28:89–102.

Myers, T. 2009. Prehistorical, historical, and recent distribution of freshwater mussels (Unionidae: Anodonta) in the Colorado River and Río Yaqui basins (with notes on Guzmán Basin, Río Sonoyta, Río Asunción/Magdalena, and Rio Grande). Arizona Game and Fish Department.

NatureServe. 2015. NatureServe Explorer: An online encyclopedia of life. [web application] Version 7.1. Arlington, Virginia. Available at http://www.natureserve.org.

Norgaard, K. M., S. Meeks, B. Crayne, and F. Dunnivant. 2013. Trace metal analysis of Karuk traditional foods in the Klamath River. Journal of Environmental Protection 4:319–328.

Osborne, H. D. 1951. Excavations near Umatilla, Oregon: The archaeology of the Columbia Intermontane Province. Ph.D. dissertation, University of California, Berkeley.

Richards, D. 2015. Unionoida mussel and nonpulmonate snail survey and status in the Jordan River. Version 2.2. Prepared for: Central Valley Water Reclamation Facility, Salt Lake City, UT and Central Davis Sewer District, Kaysville, UT.

Rodland, D. L., B. R. Schöne, S. Baier, Z. Zhang, W. Dreyer, and N. A. Page. 2009. Changes in gape frequency, siphon activity and thermal response in the freshwater bivalves *Anodonta cygnea* and *Margaritifera falcata*. Journal of Molluscan Studies 75:51–57.

Sada, D. W., and G. L. Vinyard. 2002. Anthropogenic changes in biogeography of Great Basin aquatic biota. Pages 75–234 *in* R. Hershler and D. Madsen, editors. Great Basin Aquatic Systems History. Smithsonian Contributions to the Earth Sciences, 33.

Simaika, J. P., and M. J. Samways. 2010. Large-scale estimators of threatened freshwater catchment species relative to practical conservation management. Biological Conservation 143:311–320.

Simpson, C.T. 1914. A descriptive catalogue of the Naiades, or pearly freshwater mussels, Part I Unionidae Truncilla–Margaritana. Proceedings of the United States National Museum 22:501–1044.

Simpson, C. T. In Dall, W. H. 1897. Report on mollusks collected by the International Boundary Commission of the United States and Mexico, 1892–1894. Proceedings of the United States National Museum 19:333–378.

Smith, S. C., N. Foster, and T. Gotthardt. 2005. The distribution of the freshwater mussels *Anodonta* spp. and *Margaritifera falcata* in Alaska final report. Alaska Natural Heritage Program.

Stagliano, D. 2015. Reevaluation and trend analysis of western pearlshell mussel (SWG tier 1) populations across watersheds of western Montana. Report of State Wildlife Grant (SWG) FY2015 Activities to Montana Fish, Wildlife and Parks. Montana Natural Heritage Program.

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

Taylor, D. W. 1981. Freshwater mollusks of California: A distributional checklist. California Fish and Game 67:140–163.

Toy, K. A. 1998. Growth, reproduction, and habitat preference of the freshwater mussel *Margaritifera falcata* in western Washington. Master's thesis, University of Washington, Seattle.

Tremblay, M. E. M., T. J. Morris, and J. D. Ackerman. 2016. Loss of reproductive output caused by an invasive species. Royal Society Open Science 3:150–481.

Turgeon, D. D., J. F. Quinn, Jr., A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks, 2nd ed. American Fisheries Society, Bethesda, Maryland.

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

Vaughn, C. C. 2010. Biodiversity losses and ecosystem function in freshwaters: Emerging conclusions and research directions. Bioscience 60:25–35.

Vaughn, C. C. 2017. Ecosystem services provided by freshwater mussels. Hydrobiologia DOI 10.1007/s10750-017-3139-x.

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

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

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

Vaughn, C. C., S. J. Nichols, and D. E. Spooner. 2008. Community and foodweb ecology of freshwater mussels. Journal of the North American Benthological Society 27:409–423.

Williams, J. D., M. L. Warren, K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18:6–22.

Xerces/CTUIR (Xerces Society for Invertebrate Conservation and the Confederated Tribes of the Umatilla Indian Reservation Mussel Project). 2015. Western Freshwater Mussel Database. Available at http://www.xerces.org/western-freshwater-mussels/. List of contributors available at: http://xerces.org/western-freshwater-mussel-database-contributors/.