

Freshwater Mussels (*Bivalvia: Unionoida*) of the Umatilla and Middle Fork John Day Rivers in Eastern Oregon

Abstract

Freshwater mussels are valuable components of intact salmonid ecosystems and are culturally important to Native Americans. An inventory of the freshwater mussels in the Umatilla and Middle Fork John Day rivers in Oregon was conducted in the summer of 2003. Freshwater mussels were found at all sites surveyed in the Middle Fork John Day River, but at less than 10% of the sites sampled in the Umatilla River system. All three genera of freshwater mussels known to occur in the western United States were found in the Middle Fork John Day River, and co-occurred at almost 50% of the sites sampled. In the Umatilla River, two genera were found, *Anodonta* and *Gonidea*, but only in the lower main stem and one tributary. Live *Margaritifera* were not found in the Umatilla River, although historically they occurred in the system. Shell material collected in the current survey suggests *Margaritifera* occurred in the Umatilla River main stem until very recently. Habitat degradation, including active channel change and the decline of salmonid and other native fish populations may have contributed to the extirpation of freshwater mussels from historical locations. The data collected in this survey will be used to provide essential information for designing a recovery plan for freshwater mussels in the Umatilla River system, as part of ongoing efforts to rebuild ecosystem function and diversity.

Introduction

Freshwater mollusks are an integral component of aquatic ecosystems and are useful indicator species for assessing the health of freshwater environments. The richest freshwater mollusk fauna in the world is found in North America north of Mexico, and is represented by about 600 species of gastropods and 340 species of bivalves. Among these, freshwater mussels are considered the most endangered faunal group in North America (Master 2000), with over 70% of species either imperiled or extinct (Neves et al. 1997). Globally freshwater mollusks have suffered the highest number of documented extinctions of any major taxonomic group (Lydeard et al. 2004) and in North America, suffer much higher rates of imperilment than most terrestrial groups, including birds and mammals (Williams et al. 1993, Lydeard et al. 2004).

Although the greatest diversity of freshwater mollusks occurs in the southeastern United States, the western states contain at least eight species of freshwater mussels, six of which are endemic. At least seven species occurred in Oregon and Washington: the western pearlshell, *Margaritifera falcata* (Gould, 1850); western ridged mussel,

Gonidea angulata (I. Lea, 1838); Yukon floater, *Anodonta beringiana* Middendorff, 1851; California floater, *Anodonta californiensis* I. Lea, 1852; western floater, *Anodonta kennerlyi* I. Lea, 1860; winged floater, *Anodonta nuttalliana* I. Lea, 1838; and Oregon floater, *Anodonta oregonensis* I. Lea, 1838 (Williams et al. 1993, Frest and Johannes 1995, USDA Forest Service 2004).

Records of western freshwater mussels in Oregon date back to 1838, and additional isolated collections were made over the next 160 years (USDA Forest Service 2004). Although there are about 100 published records of freshwater mussel occurrences from Oregon, with about a third of these from the Columbia River drainage, we knew of no historical records from the rivers that were the focus of this study. There is a dearth of current information on the distribution and abundance of western freshwater mollusks, mainly because comprehensive surveys are lacking. Although it is recognized that freshwater mussel populations are declining, conservation and recovery efforts are hampered by a lack of basic information on western freshwater mussel ecology, life history, genetics, taxonomy and zoogeography. For example, we know of no systematic surveys for freshwater mussels in Oregon rivers that have encompassed the entire length of the main stem and tributaries.

¹Author to whom correspondence should be addressed
E-mail: JeanetteHoward@ctuir.com

Freshwater mussels have a highly specialized life history that includes a life stage called a glochidium that is a non-lethal obligate parasite of fish. The mussel/fish relationship is often species-specific, in that only certain fish species can serve as hosts for a particular freshwater mussel species (Brunderman and Neves 1993, Haag and Warren 1997, O'Brien and Brim Box 1999). The relationship between freshwater mussels and their fish hosts is not well understood, and only about a quarter of the fish hosts for North American freshwater mussels have been determined (Watters 1994). In addition, most western drainages also contain a number of non-indigenous fishes, and their impacts on native freshwater mussel populations are unknown.

Native freshwater mussels provide important ecosystem services and are a powerful management tool for maintaining and reclaiming water quality (McMahon and Bogan 2001, Kreeger et al. 2004). Freshwater mussels can play a significant role in local food webs by increasing the flux of organic and inorganic matter to river beds, which in turn influences macroinvertebrate assemblages (Howard and Cuffey 2006). Freshwater mussels may have significant trophic relevance in the benthic community structure by converting and redirecting food resources, and providing indirect links between trophic levels. Freshwater mussels can also be important food items for fish, mink, otters, muskrats, and raccoons (Dillon, Jr. 2000).

Freshwater mussels were an important food for tribal peoples of the Columbia River Basin and the archeological record of harvest dates back over 10,000 years (Lyman 1984). Freshwater mussels also provided a source of ornament shells (Osborne 1951). Although the use of freshwater shellfish by Native Americans has declined in recent decades due to changes in subsistence needs, the harvest of freshwater shellfish from the Umatilla and Middle Fork John Day River systems remains a reserved treaty right for members of the Confederated Tribes of the Umatilla Indian Reservation (CTUIR). Tribal and federal agencies would like to restore freshwater mussels to the Umatilla River Basin as part of their ongoing efforts to rebuild ecosystem diversity, function, and traditional cultural opportunities. However, restoration efforts are hampered by a lack of empirical data on the current status and distribution of freshwater mussels in the Umatilla and Middle Fork John Day River systems. The

objectives of this study were to determine the distribution and status of freshwater mussels in the Umatilla and Middle Fork John Day River systems. These inventories constitute the first systematic surveys for freshwater mussels in any major river drainage in Oregon.

Methods

Field Surveys

In part because it was suspected that freshwater mussels could be extirpated from the main stem of the Umatilla River, the goal of this survey was to thoroughly sample all potential freshwater mussel habitat at a particular site. In 2003 freshwater mussels were inventoried in the Umatilla River and its tributaries (Figure 1), the Middle Fork John Day River, and approximately the lower 45 kms of the North Fork John Day River (Figure 1). Sites were picked based on the following criteria: to obtain a thorough and even coverage of the target rivers; to survey sites where, based on habitat characteristics, there was the maximum chance of encountering freshwater mussels; to re-survey any sites where there was a historical record of freshwater mussel occurrence (e.g., through shell middens, museum records, published literature and reports). Collections were made at approximately 4 km intervals from the headwaters to the mouth of the main stems of the Umatilla and Middle Fork John Day rivers.

This survey was conducted using timed searches, which are effective for detecting the majority of freshwater mussel species present at a site (Miller and Payne 1993, Strayer et al. 1997, Vaughn et al. 1997, Strayer 1999, Strayer and Smith 2003). All freshwater mussels were collected by hand by snorkeling or by direct observation in shallow areas. At each site, all possible habitats where freshwater mussels could occur were checked, including root and sedge mats, rock crevices, logs, aquatic vegetation, etc. At some sites density estimates were also obtained by counting all freshwater mussels encountered within defined areas. At other sites, quadrat (0.25m²) samples were taken within defined mussel beds to obtain estimates of maximum densities.

The presence of all freshwater mussels encountered was recorded for each site. Each site was surveyed until no new species were found or all potential habitats where freshwater mussels

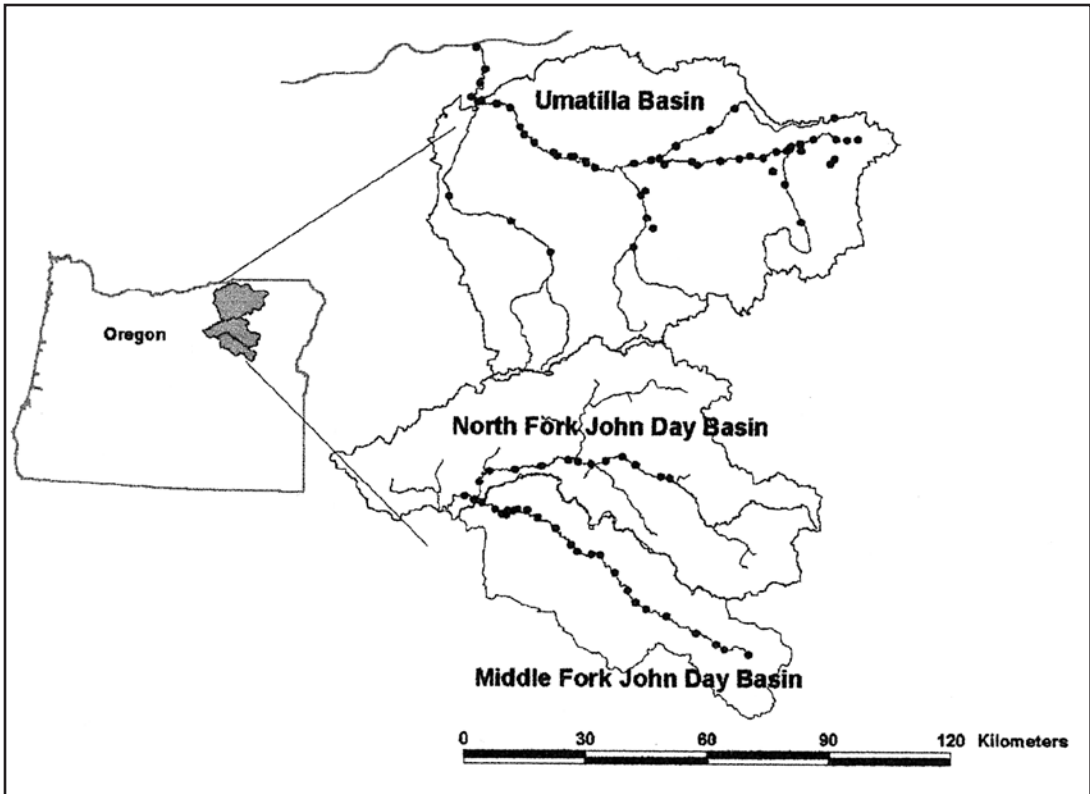


Figure 1. Map of the Umatilla, North Fork John Day and Middle Fork John Day watersheds. Gray circles represent sites sampled for freshwater mussels.

could occur were surveyed. A minimum of one-person hour was spent at each site. At most sites freshwater mussels were identified, counted and returned to the river. Voucher freshwater mussels from some sites were returned to the laboratory and live animals were relaxed using sodium pentobarbital and preserved in 95% ethanol for genetic analysis.

Historical Freshwater Mussel Occurrence

Mollusk collections at the California Academy of Sciences (CAS) in San Francisco, the United States National Museum (USNM) in Washington, D.C., and the Academy of Natural Sciences (ANSP) in Philadelphia were physically inventoried. Photo documentation of figured type specimens was obtained from the USNM to establish a template to identify freshwater mussel specimens collected in the survey described herein, to aid in the possible resurrection of species currently in synonymy and to, if necessary, describe new species.

Interviews were conducted with tribal elders and with staff members of the Cultural Resources Protection Program of the CTUIR. These interviews were conducted to obtain information on the historical occurrence and usage of freshwater mussels in the Umatilla River drainage.

Results

Field Surveys

A total of 94 collections were made from 92 sites, and over 17,000 freshwater mussels were counted during this survey, although this number reflects only a fraction of animals encountered. All three genera of freshwater mussels (*Anodonta*, *Gonidea* and *Margaritifera*) known for the western United States were found during the survey. Of the specimens counted, approximately 65% of freshwater mussels were *Margaritifera*, 27% were *Anodonta*, and 8% were *Gonidea* (Table 1). Freshwater mussels were much more common

TABLE 1. Percentage of sites where mussels were found by drainage.

	Umatilla mainstem	Umatilla tributaries	MF John Day mainstem	NF John Day mainstem
Number of Sites	31	24	24	13
% Sites w/ <i>Anodonta</i>	10	8	92	46
% Sites w/ <i>Gonidea</i>	6	0	63	15
% Sites w/ <i>Margaritifera</i>	0	0	83	85
% Sites with all species	0	0	50	15

TABLE 2. Number of mussels found in each river drainage.

	Umatilla mainstem	Umatilla tributaries	MF John Day mainstem	NF John Day mainstem
Number of collections	31	24	25	14
Number of <i>Anodonta</i>	61	10	4,396	375
Number of <i>Gonidea</i>	4	0	5,623	21
Number of <i>Margaritifera</i>	0	0	1,982	4,921
Total Mussels Counted	65	10	12,001	5,317

in the Middle Fork John Day River than in the main stem and tributaries of the Umatilla River. In addition, no live *Margaritifera* were found in the Umatilla River system.

Freshwater mussels were rare in the main stem and tributaries of the Umatilla River (Table 2) and were found at only six of the 55 sites sampled. Only two genera, *Anodonta* and *Gonidea*, were found in the basin. Although no live *M. falcata* were found, at one site approximately 115 km upstream numerous *M. falcata* shell fragments were scattered on the floodplain.

In the Middle Fork and North Fork John Day rivers, a total of 39 collections were made from 37 sites. Freshwater mussels were common in these two rivers, and at least one mussel specimen was found at every site sampled. All three genera were found at half of the sites surveyed on the Middle Fork John Day, and at 15% of the sites on the North Fork John Day (Table 1). The total number of freshwater mussels counted in the Middle Fork and North Fork exceeded 17,000 animals (Table 2). Given that these counts were obtained during timed searches, they are most likely but a small fraction of the total number of freshwater mussels in the two river systems.

The longitudinal distribution and qualitative abundance of freshwater mussels changed from

the headwaters to the confluence in each system. For example in the Umatilla River, *Anodonta* were collected from only the three most downstream sites sampled (Figure 2). *Gonidea* were found at two of the five most downstream sites sampled (Figure 2). No live freshwater mussels were found above these five downstream sites in the main stem of the Umatilla River during this survey. However, in the summer of 2004, a few live *Anodonta* were found in the main stem about 115 kms upstream (CTUIR, unpublished data) in the same river reach where *Margaritifera* shells (but not live animals) were found during the survey. Live *Anodonta* were also found during the survey at two of the four sites sampled in Wildhorse Creek, located approximately 90 kms upstream.

Similar to the Umatilla River, in the Middle and North Fork John Day rivers freshwater mussel occurrences varied by genera (Figures 3 and 4). In addition, the relative abundance of each genus varied from upstream to downstream reaches. For example, although *Margaritifera* were found at multiple sites in both rivers, *Margaritifera* relative abundance per site declined from the headwaters to the confluence. At approximately river km 50 in the Middle Fork John Day River, the species composition changed from a dominance of *Margaritifera* to greater abundances of *Anodonta* and *Gonidea* (Figure 4). These latter two genera were

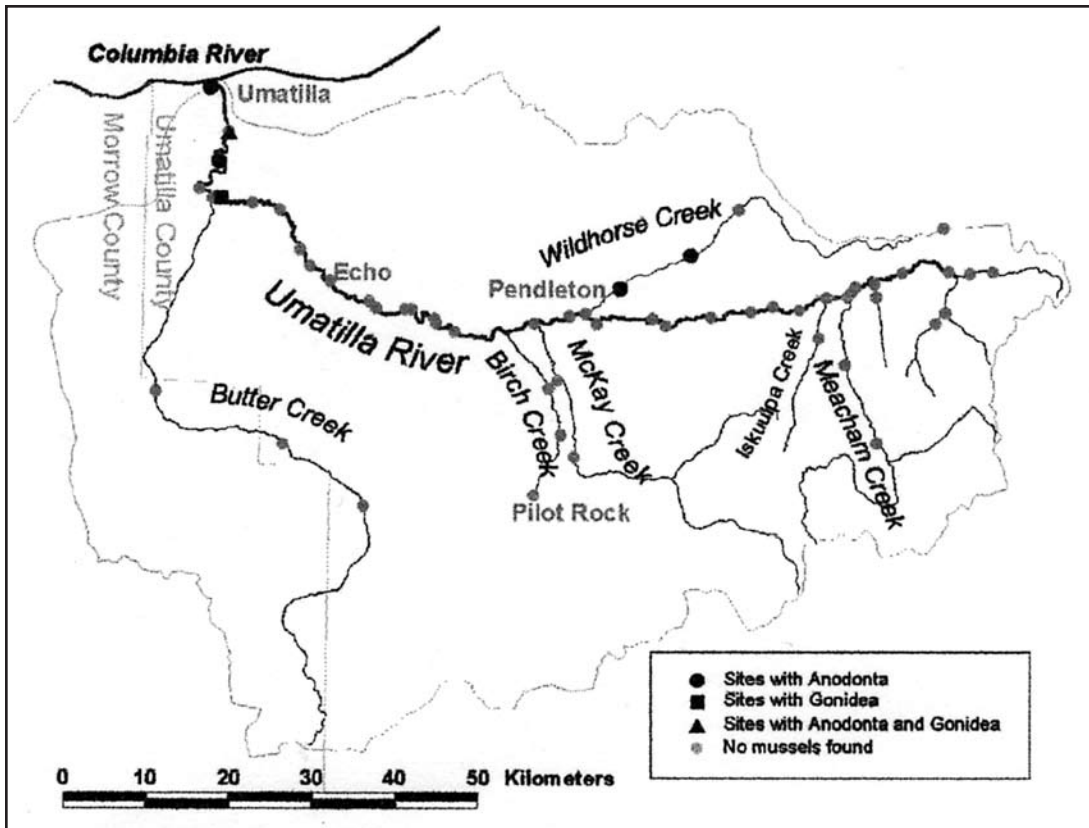


Figure 2. Sites sampled in Umatilla River. Small gray circles denote sites where no mussels were found; dark circles represent sites with *Anodonta* sp.; the dark square represents a site where one live *Gonidea angulata* specimen was found; and the triangle denotes a site where both *Anodonta* sp. and *G. angulata* were found. Note that no *Margaritifera falcata* specimens were found in the Umatilla basin.

absent from the five most upstream sites sampled. One site in the lower half of the Middle Fork John Day River, however, did not fit this distributional pattern, and more *Margaritifera* were found there than at any other site on that river.

Anodonta and *Gonidea* were more common in downstream than headwater sites, in both the Middle Fork and the North Fork John Day rivers. For example, *Gonidea* in the North Fork John Day River were only found at the two of the most downstream sites sampled (Figure 3), and in the Middle Fork John Day River, were absent from the five most upstream sites sampled.

At a few sites where freshwater mussel beds were present, quantitative estimates of maximum mussel densities were obtained. Maximal densities of *Gonidea* (~575 individuals/m²) and *Anodonta* (~275 individuals/m²) were found in the Middle

Fork John Day River, and maximal densities of *Margaritifera* (~230 individuals/m²) were found in the North Fork John Day River. At multiple sites in both rivers, freshwater mussel beds were a conspicuous component of the benthic environment. The maximum number of freshwater mussels counted in the Umatilla River at one site was 52 *Anodonta*. *Anodonta* were more abundant here than at other Umatilla River sites, but were too dispersed to sample quantitatively.

Historical Freshwater Mussel Data

Over 750 historical records (i.e., shell material repositied in museum collections) of freshwater mussels from the western United States were found at the ANSP, CAS and USNM. Many of these records were from the Columbia River Drainage. Although all eight species known from the western

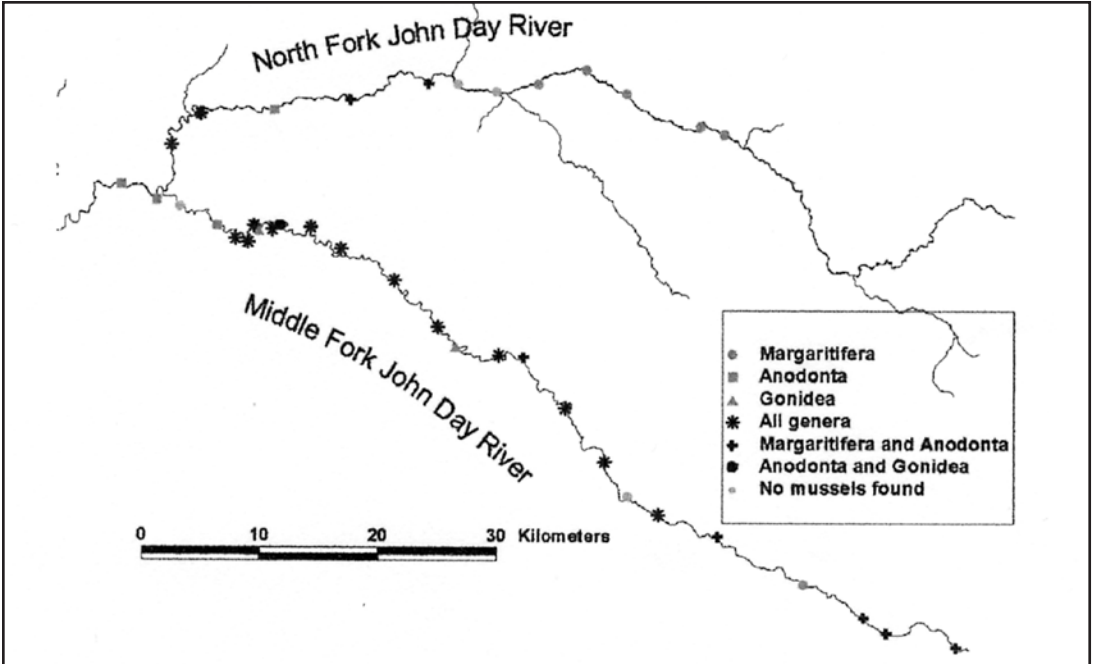


Figure 3. Sites sampled in the North and Middle Fork John Day rivers. The legend denotes the various species found at the sites.

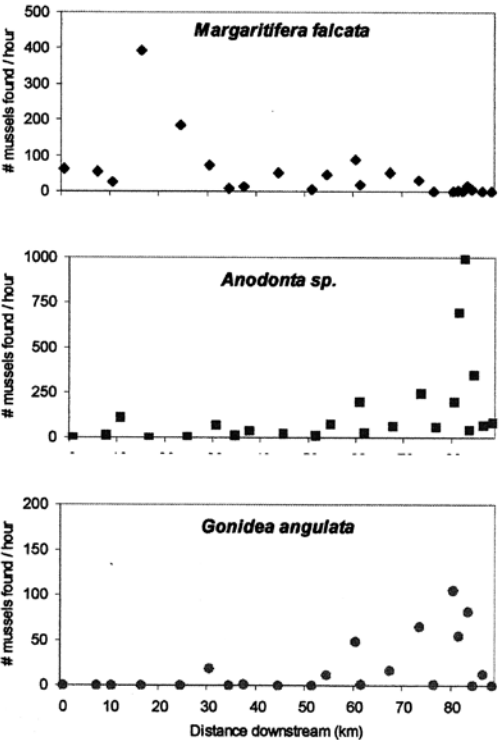


Figure 4. Changes in longitudinal abundance (number of mussels found per unit effort) for three genera of mussels found in the Middle Fork John Day River.

United States were present in the museum collections, none were from the three rivers targeted in this study. A collection of *Gonidea* shells from the main stem John Day River, collected in 1971, was found at the USNM.

Although we found no historic records for freshwater mussels in the Umatilla, Middle or North Fork John Day rivers, several tribal elders remembered gathering mollusks at the mouth of the Umatilla and Walla Walla rivers and at the mouth of Squaw Creek, a tributary of the Umatilla River. One tribal member commented, “at one time mussels were plentiful in all tributaries and bigger mussels were found in the main stem of the Umatilla River” (Armand Minthorn, CTUIR tribal member, personal communication). In the mid-1940s, freshwater mussel shells were observed scattered along the upper reaches of the banks of the Umatilla River (Bernadette Nez, CTUIR tribal member, personal communication). Tribal elders of the Umatilla, Nez Perce and Cayuse tribes also recalled eating *M. falcata* (Hunn 1990). Archaeologists reported finding shell middens at old village sites, indicating that freshwater mussels may have been an important part of the diets of tribal peoples in the Columbia Plateau (Lyman 1984). The shells of *M. falcata* have also been

found in Umatilla burial sites along the Columbia River (Osborne 1951).

Discussion

All three genera of freshwater mussels known from the western United States were found at multiple sites on the Middle and North Fork John Day rivers, suggesting that those rivers provide suitable habitat and host fishes for extant and reproducing freshwater mussel populations. In contrast, freshwater mussels were uncommon in most of the main stem of the Umatilla River and its tributaries. Shell evidence and interviews with tribal elders suggest that freshwater mussels were once found in the main stem of the Umatilla River at least 115 river km above its confluence with the Columbia River.

Possible Causal Factors of Freshwater Mussel Population Declines

Declines in freshwater mussel populations may be due to many factors, and van der Schalie (1938), Fuller (1974), Bogan (1993), Williams et al. (1993), and Lydeard et al. (2004) reviewed these factors. Some possible contributing factors of decline that pertain to the Umatilla and John Day River systems are summarized below.

Sedimentation and Sediment Characteristics

Human-induced increases in sedimentation rates in streams throughout the United States are thought to be one of the contributing factors of freshwater mussel declines (Vannote and Minshall 1982, Burkhead et al. 1997, Brim Box and Mossa 1999, Brim Box et al. 2002). Increased suspended sediments clog the gills of freshwater mussels, and have been linked to a decrease in filter time (e.g., feeding time) and overall growth rates of some freshwater mussel species (Ellis 1936, Kat 1982). The degree to which freshwater mussels are affected by increased sedimentation appears to be species dependent (Brim Box et al. 2002). Suspended sediment may also interfere with the delicate mussel/host fish relationship. For example, some freshwater mussel species visually attract their host fish by displaying elaborate lures that mimic prey items (Kreamer 1970, O'Brien and Brim Box 1999, Watters and O'Dee 1999). Increased suspended sediment can reduce water clarity, which may reduce the effectiveness of these

visual lures to attract host fish (O'Brien and Brim Box 1999) and thus hinder successful glochidial encystment on viable host fish.

Channel Modifications

Since the early part of the century, the Umatilla River has undergone intensive channel modifications. Nearly 70% of its channel has been physically modified through straightening, mining, levee construction, or repositioning. Because freshwater mussels are relatively sedentary animals these direct channel modifications may have negatively impacted suitable freshwater mussel habitat in the Umatilla River system. Although it was difficult to explore the impacts of these channel modifications, we were able to examine possible correlations between freshwater mussel occurrence and channel modifications in the upper Middle Fork John Day River. McDowell (2001) divided the upper reaches of the Middle Fork John Day River into valley segments that were associated with major channel modifications. We found *M. falcata* was less abundant in the channelized and/or mined reaches (segments C, I, J) than in reaches with no modifications (segments F, H) (Table 3). Although these findings are preliminary, they do provide a nexus to examine process-based links between freshwater mussel populations and the local physical environment, in both the Umatilla River and the Middle and North Fork John Day rivers.

Dams and Impoundments

Changes in freshwater mussel faunas (e.g., silt-intolerant to silt-tolerant species) after dam construction have been well documented (e.g., Bates 1962, Williams et al. 1992). As the habitat is altered from a lotic to a lentic one, the biota may be impacted through three pathways; 1) physical, including modified sedimentation rates through channel erosion, streambed scour, and the accumulation of fine sediments behind impoundments; 2) hydrological, including changes in flows, nutrients, temperature, and the accumulation of pollutants; 3) biological, including shifts in the composition of other taxa, especially food resources and host fishes (Ellis 1942, Baxter 1977, Williams et al. 1993, Watters 1996, Hamilton et al. 1997, Watters 2000). Changes in the water quality of impounded rivers, such as increased (or decreased) temperatures and decreased oxygen levels, can also adversely impact freshwater mussel populations by altering

TABLE 3. Associated channel modifications within stream segments of the Middle Fork John Day River and associated *Margaritifera falcata* abundances (modified from McDowell 2003).

Stream segment	Segment length	Type of channel modification	<i>Margaritifera falcata</i> abundance per site
A	4.05	Road encroachment	177
B	3.05	Channel straightening	No sample in reach
C	4.4	Channel straightening, placer mining	45
D	3.24	None	No sample in reach
E	8.49	Channel straightening, rip rap	104
F	3.2	None	370
G	3.4	Channel straightening, placer mining	No sample in reach
H	8.34	None	550
I	5.69	Bank stabilization with barbs	24
J	1.5	Channel straightening	78
K	1.31	Channel straightening	No sample in reach
L	1.52	None	No sample in reach
M	4.21	None	No sample in reach
N	1.32	None	124

growth rates, gametogenesis, glochidial release, and the time required for glochidial metamorphosis (Waller et al. 1988, Allan 1995, O'Brien and Brim Box 1999, Watters 2000).

Dams act as physical and genetic barriers for many riverine species (Allan 1995, Watters 1996). A common example is the disappearance of salmon runs as dams block upstream migrations. Freshwater mussel populations that rely on migratory host fish for reproduction and dispersal are therefore likely to be negatively affected by dam construction (Watters 1996, Watters 2000).

Seven dams are currently maintained on the main stem of the Umatilla River. Although these are mainly small diversion dams for irrigation, they can potentially impact freshwater mussel populations by several of the mechanisms listed above. For example, *M. falcata* is known to occur in "running" streams (Clarke 1981, Taylor 1981). In the Pit River system in northern California, *M. falcata* were found only in the "free-flowing" habitat available between impoundments (Spring Rivers Ecological Sciences 2001). Similarly, *Gonidea* occurred in "riverine" habitats between impounded reaches of the Pit River system (Spring Rivers Ecological Sciences 2001). Impoundments are listed as a possible threat to existing populations of *Margaritifera* and *Gonidea* in California (Taylor 1981). Impounded waters are often unsuit-

able for freshwater mussels, even for species that occur in naturally-formed pools (Watters 2000). For example, 15 species of freshwater mussels were found in an impoundment segment of the Mississippi River, while in an adjacent, naturally-formed pool, 30 freshwater mussel species were found (van der Schalie 1938). *Anodonta*, however, are morphologically adapted to live in low-flow environments (e.g., they lack lateral and pseudocardinal teeth), and in some studies were commonly found in impoundments, even when other species were absent (Brim Box and Williams 2000, Mock et al. 2004). Quantitative studies of the effects of impoundments on *Anodonta* species in the western United States are lacking.

Possible Impacts from Loss of Native Fish Species

Interviews with tribal elders and shell evidence suggest that *Margaritifera* once existed in the Umatilla River system, but now appears to be extirpated. The loss of salmonid host fish has been suggested as a probable cause of *Margaritifera* extirpations in other areas (Cosgrove et al. 2000, Bauer 2001). The host fishes for *M. falcata* were reported to include Chinook (*Oncorhynchus tshawytscha*) and Coho (*O. kisutch*) salmon, rainbow (*O. mykiss*), cutthroat (*Salmo clarkii*), and steelhead trout (*S. gairdneri*), Tahoe sucker (*Catostomus tahoensis*),

speckled dace (*Rhinichthys osculus*) and Lahontan redbreast (*Richardsonius egregius*) (Murphy 1942, Meyers and Milleman 1977, Fustish and Milleman 1978, Karna and Milleman 1978).

Historically the Umatilla River supported large populations of spring Chinook and Coho salmon, as well as steelhead trout (James et al. 2001). Due to intensive agricultural development and prolonged irrigation withdrawals between 1905 and the mid-1920s, native Chinook and Coho were extirpated from the system, and steelhead abundances were greatly reduced (Phillips et al. 2000). Therefore, for over 70 years salmonid abundance in the Umatilla River was severely impacted. The long absence of several probable host fishes for *M. falcata* in the Umatilla River may have contributed to the extirpation of *M. falcata* in that river system.

The host fishes for *M. falcata* in the Middle and North Fork John Day rivers are unknown, although Chinook salmon, summer steelhead, westslope cutthroat, brook trout, and speckled dace occur in the John Day River system (Knapp et al. 2001). In addition, the John Day River system supports the largest remaining exclusively wild runs of spring Chinook and summer steelhead in northeast Oregon, although these numbers are greatly reduced from historical anadromous fish abundances in the basin (Knapp et al. 2001).

Nothing is known about the host fishes for *G. angulata*, and little is known about the host fishes for western *Anodonta*. D'Eliscu (1972) reported that *A. californiensis* glochidia successfully transformed on the gills and fins of the western mosquitofish (*Gambusia affinis*), a species not native to the western United States. Anodontinae are the least host-specific of unionid mussels, and a wide-range of host fish have been reported for many eastern *Anodonta* species (Watters 1994). Based on preliminary results obtained from a study conducted in concurrence with this survey (see Brim Box et al. 2004), it appears that *Anodonta* in the Middle Fork John Day system use speckled dace as a host fish. The percentage (74%) of speckled dace found infected with *Anodonta* glochidia is one of the highest ever reported for wild-caught fish (Zale and Neves 1982, Weiss and Layzer 1995, Weaver et al. 1991). However, additional laboratory studies should be conducted to confirm this finding.

Possible Impacts from Nonindigenous Fishes

Most western drainages contain a number of non-indigenous fishes, and their impact on native freshwater mussel populations is unknown. For example, at least 13 species of non-indigenous fishes have been reported from the John Day and Umatilla River systems. These non-indigenous fishes could potentially affect freshwater mussel populations in either a positive or negative way. If non-indigenous fishes can serve as host fish in the absence of the original host fish, their presence may allow freshwater mussels to persist. In this case, programs aimed at eradicating these non-indigenous fishes may ultimately have a negative impact on freshwater mussel populations. Alternatively, if the original host fishes are still present in the system, the non-indigenous fishes may compete for these glochidia but serve as less efficient hosts (O'Brien and Brim-Box 1999).

If non-native fishes are predators on native fishes that serve as hosts for freshwater mussels, they may decrease the number of available host fish. For example, the large number of smallmouth bass (*Micropterus dolomieu*) found in the John Day River system could affect native salmonid species, as has been reported in other parts of the Columbia River Basin (Tabor et al. 1993, Zimmerman 1999). Freshwater mussels living in streams where the host fish density is low may infest the same fishes repeatedly with their glochidia. Fish that are exposed to freshwater mussel glochidia multiple times have been known to develop glochidial immunity (Coker et al. 1921, Kirk and Layzer 1997). Fish populations with an acquired immunity to glochidia will no longer effectively serve as hosts. If a large percentage of fish present at a site are infected with glochidia, as found in this study, there is a danger that these fish may develop immunity to further encystments. However, further studies will be needed to test this assertion in the Middle Fork John Day River.

Spatial Distribution of Freshwater Mussels

The longitudinal distribution of freshwater mussel species composition changed from the headwaters to the confluence in each system. *M. falcata* were relatively more common in the upper reaches of the Middle and North Fork John Day rivers, and *Anodonta* and *Gonidea* were relatively more common in lower reaches (Figure 4). These results were

not surprising, in that a similar spatial distribution for *Margaritifera* and *Anodonta* was recently documented in a river system in California (Howard and Cuffey 2003). Differences in the spatial distribution of the superfamilies Margaritiferidae and Unionidae may be linked to food supply (Bauer 1991). In Europe, *M. margaritifera* grew in rivers with low primary production, possibly because this species had a lower metabolic rate than other species of freshwater mussels, including *Anodonta* (Bauer 1991). *Anodonta* and *Gonidea* may require a richer food supply if their metabolic rates are higher than *Margaritifera*. These differences in food requirements could be correlated with the longitudinal food availability in a stream system. Energy inputs increase as streams widen in a downstream direction, due primarily to an increase in algal primary production (Vannote et al. 1980). The spatial occurrence of *Anodonta* and *Gonidea* in the Middle and North Fork John Day rivers may be explained, in part, by their higher metabolic rates (relative to *Margaritifera*) and the differences in food availability in various stream reaches. This assertion should be tested with field trials and laboratory experiments (e.g., metabolic rates for *Gonidea* have not been reported).

Cultural Significance

Historically freshwater mussels were an important food for tribal peoples of the Columbia River Basin. Native Americans in the interior Columbia River Basin harvested freshwater mussels for at least 10,000 years (Lyman 1984). Ethnographic surveys of Columbia Basin tribes reported that Native Americans collected freshwater mussels in late summer and in late winter through early spring during salmon fishing (Spinden 1908, Ray 1933, Post 1938). A few tribal elders from the Columbia and Snake River basins recalled that freshwater mussels were collected whenever conditions of the rivers were favorable (Hunn 1990, Chatters 1995). Tribal harvesters collected freshwater mussels by hand. When wading was not possible they used forked sticks (Post 1938). They prepared freshwater mussels for consumption by baking, broiling, steaming, and drying (Spinden 1908, Post 1938). The Umatilla preferred to boil freshwater mussels for consumption (Ray 1942).

Native American use of freshwater mussels decreased during the last 200 years, probably due to declines in Native American populations and

assimilation following Euro-American settlement (Chatters 1987). A Umatilla tribal elder, however, remembered his parents trading fish for dried mussels as late as the 1930s (Eli Quaempts, CTUIR tribal member, personal communication). In addition, shell middens found at village sites near the mouth of the Umatilla River (Lyman 1984), as well as the presence of mussels at burial sites in the same area (Osborne 1951) suggest that historically freshwater mussels were important to Native Americans of the mid-Columbia Plateau for multiple reasons.

Conclusions

Freshwater mussels have been extirpated from most of the main stem of the Umatilla River and its tributaries. Shell evidence and historical records via interviews with tribal elders suggest that freshwater mussels were once found in the main stem of the Umatilla River at least as far as 115 km upstream, but now are confined to a few, mainly downstream sites. Although *M. falcata* probably until recently was extant in the Umatilla River system, it is now extirpated. The reasons for the extirpation are not known, although dams, channel modifications, and the subsequent loss of salmonid species may have negatively affected freshwater mussel populations in that system. In contrast, all three genera of freshwater mussels known from the western United States were found at multiple sites on the Middle and North Fork John Day rivers, suggesting that those rivers provide suitable habitat and host fishes for extant and reproducing freshwater mussel populations.

Tribal and federal agencies would like to restore freshwater mussels to the Umatilla River Basin as part of their ongoing efforts to rebuild ecosystem diversity, function, and traditional cultural opportunities in the basin. In order to do so, additional work on freshwater mussels in the basin should include a quantitative assessment of freshwater mussel densities and macro- and microhabitat variables in selected freshwater mussel beds in the Middle Fork John Day River, and possibly the lower Umatilla River where limited, remnant freshwater mussel populations remain. In addition, changes in channel morphology in the Middle Fork John Day and Umatilla rivers should be assessed to ascertain impacts on freshwater mussel populations. Research on freshwater mussel population genetics and host

fish relationships should be conducted, as these components will be crucial for future efforts to reintroduce freshwater mussels, especially *M. falcata*, into the Umatilla River system.

Acknowledgements

We thank the following individuals for their valuable assistance in the field and laboratory: Justine Bronson, Pat Luke, Byron Morris, Derek Muniz, John C. Sampson, Shane Shippentower, Jacob

Welch, Andrew Wildbill, and Melissa Van Pelt. We thank Ken P. Currens, Gary James, and Jeff Kershner for their technical help and guidance. We thank Suzanne Schwab, Bruce Z. Lang, and an anonymous reviewer for their helpful comments on an earlier draft of this manuscript. This study was supported by the Bonneville Power Administration (Project number 200203700) and the USDA Forest Service, Rocky Mountain Research Station, Logan, Utah.

Literature Cited

- Allan, J. D. 1995. Stream ecology. Chapman and Hall, London, UK.
- Bauer, G. 2001. Factors affecting naiad occurrence and abundance. Pages 155-162 in G. Bauer and K. Wächtler (editors). Ecology and evolution of the freshwater mussels Unionoida. Ecological Studies Vol. 145. Springer-Verlag, Berlin.
- Bates, J. M. 1962. The impact of impoundment on the mussel fauna of Kentucky Reservoir, Tennessee River. American Midland Naturalist 68:232-236.
- Bauer, G., S. Hochwald, and W. Silkenat. 1991. Spatial distribution of freshwater mussels: the role of host fish and metabolic rate. Freshwater Biology 26:377-386.
- Baxter, R.M. 1977. Environmental effects of dams and impoundments. Annual Review of Ecology and Systematics 8:255-283.
- Bogan, A. E. 1993. Freshwater bivalve extinctions (Mollusca: Unionoida): A search for causes. American Zoologist 33:599-609.
- Brim Box, J. 2002. A survey of the aquatic mollusk species of the Lassen National Forest, California. Final Report submitted to the USDA/FS, June 21, 2002. Contract FSA 01-IA-11050660-020, Susanville, California.
- Brim Box, J., and J. Mossa. 1999. Sediment, land use, and freshwater mussels: prospects and problems. Journal of the North American Benthological Society 18(1):99-117.
- Brim Box, J. and J. D. Williams. 2000. Unionid mussels of the Apalachicola Basin in Alabama, Florida, and Georgia. Bulletin of the Alabama Museum of Natural History 21:1-143.
- Brim Box, J., R. M. Dorazio, and W. D. Liddell. 2002. Relationships between streambed substrate characteristics and freshwater mussels (Bivalvia:Unionidae) in Coastal Plain streams. Journal of the North American Benthological Society 21(2):253-260.
- Brim Box, J., D. Wolf, J. Howard, C. O'Brien, D. Nez, and D. Close. 2004. Distribution and status of freshwater mussels in the Umatilla River System. 2002-2003 Annual Report, Project No. 200203700, 74 electronic pages, (PPA Report DOE/BP-00011402-1).
- Bruenderman, S. A., and R. J. Neves. 1993. Life history of the endangered finereyed pigtoe *Fusconaia cuneolus* (Bivalvia: Unionidae) in the Clinch River, Virginia. American Malacological Bulletin 10:83-91.
- Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled southern Appalachian ecosystem. Pages 375-444 in G. W. Benz and D. E. Collins (editors). Aquatic fauna in peril: the southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute. Lenz Design and Communications, Decatur, Georgia.
- Chatters, J. C. 1987. Shell of *Margaritifera margaritifera falcata* as a source of paleoenvironmental and cultural data. in M. S. Kelly, E. Nilsson, and J. H. Cleland, (editors). Archaeological Investigations at Lake Britton, California, Pacific Gas and Electric Company, San Francisco, California, Appendix F.
- Chatters, J. C. 1995. Population growth, climatic cooling, and the development of collector strategies on the Southern Plateau, Western North America. Journal of World Prehistory 9:341-400.
- Clarke, A. H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada.
- Coker, R.E., A. F. Shira, H. W. Clark, and A. D. Howard. 1921. Natural history and propagation of freshwater mussels. Bulletin of the U.S. Bureau of Fisheries 37:75- 181.
- Cosgrove, P. J., M. R. Young, L. C. Hastie, M. Gaywood, and P. J. Boon. 2000. The status of the freshwater pearl mussel *Margaritifera margaritifera* Linn. in Scotland. Aquatic Conservation: Marine and Freshwater Ecosystems 10:197-208.
- D'Eliscu, P. N. 1972. Observation of the glochidium, metamorphosis, and juvenile of *Anodonta californiensis* Lea, 1857. The Veliger 15: 57-59.
- Dillon, R.T., Jr. 2000. The ecology of freshwater molluscs. Cambridge University Press, United Kingdom.
- Ellis, M. M. 1936. Erosion silt as a factor in aquatic environments. Ecology 17:29-42.
- Ellis, M. M. 1942. Fresh-water impoundments. Transactions of the American Fisheries Society, 71st Annual Meeting, 80-93.
- Frest, T. J., and E. J. Johannes. 1995. Freshwater mollusks of the upper Sacramento system, California, with particular reference to the Cantara spill. 1995 final report to the California Department of Fish and Game. Deixis Consultants, Seattle, Washington.
- Fuller, S. L. H. 1974. Clams and mussels (Mollusca: Bivalvia). Pages 215-273 in C. W. Hart, Jr. and S. L. H. Fuller (editors). Pollution ecology of freshwater invertebrates. Academic Press, New York, New York.
- Fustish, C.A., and R.E. Millemann. 1978. Glochidiosis of salmonid fishes. II. Comparison of tissue response of coho and Chinook salmon to experimental infection

- with *Margaritifera margaritifera* (L.) (Pelecypoda: Margaritanidae). *Journal of Parasitology* 64(1):155-157.
- Gould, A.A. 1850. Shells from the United States Exploring Expedition. *Proceedings of the Boston Society of Natural History* 3(19): 292-296.
- Haag, W. R. and M. L. Warren. 1997. Host fish and reproductive biology of 6 freshwater mussel species from the Mobile Basin, USA. *Journal of North American Benthological Society* 16:576-585.
- Hamilton, H., J. B. Box, and R. M. Dorazio. 1997. Effects of habitat suitability on the survival of relocated freshwater mussels. *Regulated Rivers: Research and Management* 13:537-541.
- Howard, J. K. and K. M. Cuffey. 2003. Freshwater mussels in a California North Coast Range river: occurrence, distribution, and controls. *Journal of the North American Benthological Society* 22:63-77.
- Howard, J. K. and K. M. Cuffey. 2006. Functional role of freshwater mussels in the benthic environment. *Freshwater Biology* 51:460-475.
- Hunn, E. S. 1990. Nch'i-Wana "The Big River" Mid-Columbia Indians and Their Land. University of Washington Press, Seattle, Washington.
- James, G., and 28 other contributors. 2001. Umatilla and Willow Creek Subbasin Summary (Draft). Fisheries Program, Department of Natural Resources, Confederated Tribes of the Umatilla Indian Reservation, Pendleton, Oregon. Umatilla Basin plan for fish, wildlife and habitat submitted to the Northwest Power Planning Council, Portland, Oregon.
- Karna, D. W. and R. E. Millemann. 1978. Glochidiosis of salmonid fishes. III. Comparative susceptibility to natural infection with *Margaritifera margaritifera* (L.) (Pelecypoda: Margaritanidae) and associated histopathology. *Journal of Parasitology* 64(3):528-537.
- Kat, P. W. 1982. Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia: Unionidae). *Malacological Review* 15:119-127.
- Kirk, S. G. and J. B. Layzer. 1997. Induced metamorphosis of freshwater mussel glochidia on nonhost fish. *The Nautilus* 110(3):102-106.
- Knapp, S., and 22 other contributors. 2001. John Day Subbasin Summary (Draft). Oregon Department of Fish and Wildlife, submitted to the Northwest Power Planning Council, Portland, Oregon.
- Kraemer L.R. 1970. The mantle flap in three species of *Lampsilis* (Pelecypoda: Unionidae). *Malacologia* 10:225-282.
- Kreeger, D., C. Gatenby, and D. Raksany. 2004. Beyond biodiversity: the conservation and propagation of native mussel biomass for ecosystem services. Abstract from paper presented at the 2nd Annual Meeting of the Pacific Northwest Native Freshwater Mussel Working Group, April 20, 2004, Vancouver, Washington.
- Lea, I. 1838. Description of new freshwater and land shells. *Transactions of the American Philosophical Society* 6(N.S.):1-154 + plates i-xxiv.
- Lea, I. 1852. Descriptions of new species of the family Unionidae. *Transactions of the American Philosophical Society* 10(N.S.):253-294 + plates 12-19.
- Lea, I. 1860. Descriptions of seven new species of Unionidae from the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 12(1860):306-307.
- Lydeard, C., and fifteen other contributors. 2004. The global decline of nonmarine mollusks. *BioScience* 54(4): 321-330.
- Lyman, R. L. 1984. A model of large freshwater clam exploitation in the prehistoric southern Columbia Plateau culture area. *Northwest Anthropological Research Notes* 18:97-107.
- Master, L. L., B. A. Stein, L. S. Kutner, and G. A. Hammerson. 2000. Vanishing assets: Conservation status of U.S. species. Pages 93-118 in B. A. Stein, L. S. Kutner, and J. S. Adams (editors). *Precious heritage: the status of biodiversity in the United States*. Oxford University Press, New York.
- McDowell, P. F. 2001. Spatial variations in channel morphology at segment and reach scales, Middle Fork John Day River, Northeastern Oregon. *Geomorphic Processes and Riverine Habitat Water Science and Applications* 4:159-172.
- McMahon, R.F., and A.E. Bogan. 2001. Mollusca: Bivalvia. Pages 331-429 in J. H. Thorp and A. P. Covich (editors). *Ecology and classification of North American freshwater invertebrates*. Second Edition. Academic Press, Inc, New York.
- Meyers, T. R., and R. E. Millemann. 1977. Glochidiosis of salmonid fishes. I. Comparative susceptibility to experimental infection with *Margaritifera margaritifera* (L.) (Pelecypoda: Margaritanidae). *Journal of Parasitology* 63:728-733.
- Middendorff, A.T. von 1851. Beschreibung einiger neuer Mollusken-Arten, nebst einem Blicke auf den geographischen Charakter der Land- und Süßwasser-Mollusken Nord-Asiens. *Bulletin de la Classe Physico-Mathématique de l'Académie Impériale des Sciences de saint-Petersbourg* 9:108-112.
- Miller, A. C., and B. S. Payne. 1993. Qualitative versus quantitative sampling to evaluate population and community characteristics at a large-river mussel bed. *American Midland Naturalist* 130:133-145.
- 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* 13:1085-1098.
- Murphy, G. 1942. Relationship of the fresh-water mussel to trout in the Truckee River. *California Fish and Game* 28(2):89-102.
- Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity. Pages 44-86 in G. W. Benz and D. E. Collins (editors). *Aquatic fauna in peril: the southeastern perspective*. Special Publication 1, Southeast Aquatic Research Institute. Lenz Design and Communications, Decatur, GA.
- O'Brien, C. A. and J. Brim Box. 1999. Reproductive biology and juvenile recruitment of the shinyrayed pocketbook, *Lampsilis subangulata* (Bivalvia: Unionidae) in the Gulf Coastal Plain. *American Midland Naturalist* 142:129-140.

- Osborne, H. D. 1951. Excavations near Umatilla, Oregon: The archaeology of the Columbia Intermontane Province. Ph.D. dissertation, University of California, Berkeley, California.
- Phillips, J. L., J. Ory, and A. Talbot. 2000. Anadromous salmonid recovery in the Umatilla River Basin, Oregon: A case study. *Journal of the American Water Resources Association* 36(6):1287-1308.
- Post, R. H. 1938. The subsistence quest. *In* L. Spier (editor). *The Sinkaietk or Southern Okanogan of Washington*. General Series in Anthropology 6: 9-34.
- Ray, V. F. 1933. The Sanpoil and Nespelem: Salishan Peoples of Northeastern Washington. University of Washington Publications in Anthropology, Volume 5.
- Ray, V. F. 1942. Cultural element distributions: XXII Plateau Anthropological Records 8:2. University of California Press, Berkeley, California.
- Spinden, H. J. 1908. The Nez Perce Indians. *Memoirs of the American Anthropological Association* 2(3):167-274.
- Strayer, D. L. 1999. Statistical power of presence-absence data to detect population declines. *Conservation Biology* 13:1034-1038.
- Strayer, D. L., S. Claypool, and S. J. Sprague. 1997. Assessing unionid population with quadrats and timed searches. Pages 163-169 *in* K. S. Cummings, A. C. Buchanan, C. A. Mayer, and T. J. Naimo (editors). *Conservation and management of freshwater mussels II: initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois.
- Strayer, D. L., and D. R. Smith. 2003. A guide to sampling freshwater mussel populations. American Fisheries Society, Monograph 8, Bethesda, Maryland.
- Spring Rivers Ecological Sciences. 2001. River corridor habitat mapping and biota surveys, with emphasis on special-status species, for Pacific Gas and Electric Company's Pit 3, 4, and 5 hydroelectric project (FERC No. 233). Draft report prepared for the Pacific Gas and Electric Company. Spring Rivers Ecological Sciences, Cassel, California.
- Tabor, R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. *North American Journal of Fisheries Management* 13:831-838.
- Taylor, D. W. 1981. Freshwater mollusks of California: A distributional checklist. *California Fish and Game* 67:140-163.
- USDA Forest Service. 2004. Database of the Freshwater Mollusks of the Western United States. Rocky Mountain Research Station, Logan, Utah.
- van der Schalie, H. 1938. Contributing factors in the depletion of naiades in eastern United States. *Bacteria* 3:51-57.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- 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 Science* 79:4103-4107.
- Vaughn, C. C., Taylor, C. M., and K. J. Eberhard. 1997. A comparison of the effectiveness of timed searches vs. quadrat samples in mussel surveys. Pages 157- 162 *in* K. S. Cummings, A. C. Buchanan, C. A. Mayer, and T. J. Naimo (editors). *Conservation and management of freshwater mussels II: initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois.
- Waller, D. L., L. E. Holland-Bartels, and L. G. Mitchell. 1988. Morphology of glochidia of *Lampsilis higginsi* (Bivalvia: Unionidae) compared with three related species. *American Malacological Bulletin* 6:39-43.
- Watters, G. T. 1994. An annotated bibliography of the reproduction and propagation of the Unionioidea (primarily of North America). Ohio Biological Survey Miscellaneous Contributions No. 1.
- Watters, G. T. 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoida) and their hosts. *Biological Conservation* 75:79-85.
- Watters, G. T., and S. H. O'Dee. 1999. Glochidia of the freshwater mussel *Lampsilis* overwintering on fish hosts. *Journal of Molluscan Studies* 65(4):453-459.
- Watters, G. T. 2000. Freshwater mussels and water quality: A review of the effects of hydrologic and instream habitat alterations. Pages 261-274 *in* R.A. Tankersley, D. I. Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson, and R. S. Butler (editors). *Freshwater mollusk symposia proceedings. Part II. Proceedings of the first freshwater mollusk conservation society symposium*. Ohio Biological Survey Special Publication, Columbus, Ohio.
- Weaver, L. R., G. B. Pardue, and R. J. Neves. 1991. Reproductive biology and fish hosts of the Tennessee clubshell *Pleurobema oviforme* (Mollusca: Unionidae) in Virginia. *American Midland Naturalist* 126:82-89.
- Weiss, J. L. and J. B. Layzer. 1995. Infections of glochidia on fishes in the Barren River, Kentucky. *American Malacological Bulletin* 11:153-159.
- Williams, J. D., S. L. H. Fuller, and R. Grace. 1992. Effects of impoundments on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee Rivers in western Alabama. *Bulletin Alabama Museum of Natural History* 13: 1-10.
- Williams, J. D., M. Warren, K. Cummings, J. Harris, and R. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18:6-22.
- Zale, A. V., and R. J. Neves. 1982. Fish hosts for four species of lampisline mussels (Mollusca: Unionidae) in Big Moccasin Creek, Virginia. *Canadian Journal of Zoology* 60:2535-2542.
- Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River Basin during outmigration of juvenile anadromous salmonids. *Transactions of the American Fisheries Society* 128:1036-1054.

Received 13 May, 2005

Accepted for publication 7 March, 2006