CHAPTER 5

Past and future patterns of freshwater mussel extinctions in North America during the Holocene

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5.1 Introduction

Humans have had profound impacts on the ecology of North America both before and since colonization by Europeans. Modern-day human impacts extend to nearly every type of habitat, but evidence for pre-Columbian human impacts is limited almost exclusively to terrestrial ecosystems. In pre-Columbian times, human activities, especially burning and agriculture, transformed significant areas of North America (Delcourt and Delcourt 2004; Mann 2005; see also Chapter 11 in this volume) and, in some cases, even short-term, small-scale agriculture resulted in persistent ecosystem changes (Briggs *et al.* 2006). The linkage between current-day land-use practices and freshwater ecosystem integrity is clear and central to some of the most pressing contemporary conservation issues (e.g. Diaz and Rosenberg 1995; Malakoff 1998), but this linkage has not been shown widely for pre-Columbian human land use. Recent studies in the Americas and Europe have shown that prehistoric Holocene human activities, including low-intensity agriculture, caused long-lasting and sometimes drastic changes in productivity, faunal composition, and water chemistry of small lakes and ponds (Douglas *et al.* 2004; Ekdahl *et al.* 2004; Miettinen *et al.* 2005). Although these studies demonstrate the potential for early human impacts to aquatic habitats, the impact of pre-Columbian humans on the diverse riverine ecosystems of North America remains virtually unknown. In rivers of the south-eastern and central USA the relative abundance of the freshwater mussel genus *Epioblasma* declined steadily over the last 5000 years prior to European colonization but most steeply after the advent of maize agriculture (Peacock *et al.* 2005), suggesting that even larger freshwater ecosystems might have experienced impacts from pre-Columbian human activities.

In the past 100 years, North American freshwater mussels (order Unionoida) have experienced one of the highest rates of extinction of any group of organisms (Neves *et al.* 1997). North America is home to the most diverse freshwater mussel fauna on Earth, including about 300 species; in contrast, there are about 85 species in Africa and 11 species in Europe (Graf and Cummings 2007). Highest mussel diversity and endemism occurs in the eastern half of the continent, especially in the large streams of the central and south-eastern USA. Mussels have a number of ecological attributes that render them especially vulnerable to changes in aquatic habitats. First, as mostly sedentary filter feeders, mussels are directly impacted by changes in the landscape that affect water and substrate quality (Brim Box and Mossa 1999; Arbuckle and Downing 2002). Second, because many species are long-lived (>50 years) and have low recruitment rates (Haag 2002), they may not be able to sustain high adult mortality and may be slow to recolonize disturbed habitats. Finally, mussels have a complex life history in which larvae (glochidia) are obligate parasites on fishes for a brief period before becoming free-living juveniles. Host use varies among mussel species from generalists that use a wide range of fish species to specialists that are able to

complete metamorphosis to the juvenile stage on only a few closely related fish species (Haag and Warren 1997). Long-term survival of mussel populations is therefore dependent not only on the presence of suitable mussel habitat but also on the distribution and abundance of host fishes.

Freshwater mussels offer an excellent opportunity to study long-term patterns of extinction and assemblage change in response to human impacts. Spurred by conservation concern about mussels, intensive field surveys over the last 30 years have made possible a detailed accounting of recent species losses and declines at multiple scales across much of North America (e.g. Metcalfe-Smith *et al.* 1998; Brim Box and Williams 2000; Warren and Haag 2005). In addition, a large body of historical and pre-Columbian material exists that allows assessment of trends prior to recent surveys. Because of the beauty and easy preservation of their shells (Fig. 5.1), mussels were a particular fascination of nineteenth- and early twentieth-century naturalists who collected extensively and solicited specimens from other collectors throughout the country. Many of these large private collections survived and ultimately formed the nuclei of most major institutional research collections. Furthermore, the economic importance of mussels for pearl harvest and shell button manufacturing, both of which peaked in the early 1900s, spurred systematic surveys of many river systems before major human impacts

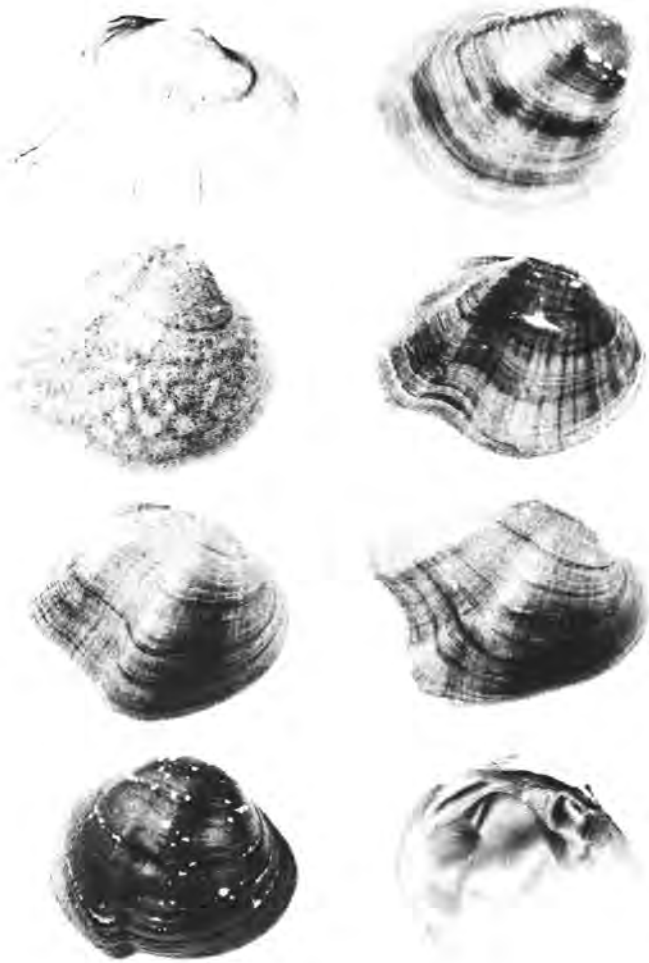

Figure 5.1 Some extinct North American mussel species. From top (left to right): *Lampsilis binominata, Pleurobema marshalli, Quadrula stapes, Epioblasma biemarginata, Epioblasma flexuosa* (male), *Epioblasma flexuosa* (female), *Epioblasma haysiana*, and *E. haysiana* (shell interior). Photographs © Richard T. Bryant.

to these streams had occurred. Finally, extensive shell middens resulting from harvest of bivalves by aboriginal peoples occur along many streams, providing a record of mussel abundance and diversity spanning a period of over 4000 years prior to European contact. Together, these sources provide an extraordinarily comprehensive record of distribution and in some cases abundance throughout the Holocene that exists for few organisms in general and is unprecedented for invertebrates.

In this chapter, I present a systematic treatment of freshwater mussel extinctions in North America throughout the Holocene. First, I evaluate how human activities from pre-Columbian times to the present day have affected the North American mussel fauna and identify the major causes and timing of mussel extinctions. Second, I examine ecological and life-history attributes that have rendered freshwater mussel species more or less vulnerable to extinction. Finally, I examine current patterns of species imperilment and make a prognosis about how additional mussel extinctions will occur in the future.

5.2 Pre-Columbian human impacts on mussel communities

Since at least 5000 years BP, humans in North America have used freshwater mussels extensively. Aboriginal peoples used mussel shells for production of jewelry and implements, and as a source of tempering material for pottery, but harvested mussels primarily for food (Parmalee and Klippel 1974). Shell middens associated with human habitation sites occur commonly along water bodies ranging in size from small streams to the Mississippi River (e.g. Klippel *et al.* 1978; Theler 1987a) but are particularly numerous and extensive along the large rivers of the central and south-eastern USA (Fig. 5.2). Hundreds of middens are found throughout the 1050 km length of the Tennessee River (e.g. Parmalee *et al.* 1982; Hughes and Parmalee 1999); along the middle portion of the river in Alabama, 'the banks of the river are lined with shell middens up to 18–20 ft. (5.5–6.1 m) in depth' (Webb and DeJarnette 1942). Similarly, at least 48 shell deposits are known within a four-county area along the Green River in Kentucky, and several of these deposits each cover nearly 1 ha (Morey and Crothers 1998). Although harvest of mussels was likely periodic and may have coincided with periods of scarcity of other resources (Lyman 1984; Theler and Boszhardt 2006), pre-Columbian people doubtlessly exerted tremendous local pressure on mussel populations.

To illustrate the magnitude of aboriginal harvest pressure exerted on mussel populations I estimated the number of mussels contained in three adjacent shell middens along the Green River, using data from Morey and Crothers (1998). Three large shell middens (Haynes, Carlston Annis, and DeWeese) along an 8 km reach of river each ranged from 0.6 to 1.0 ha in area, 2.2 to 2.6 m in depth, and 5300 to 5800 m^3 in volume. I assumed an average volume of 5550 m^3 for each midden and estimated that 20% of the material in the midden was shell, based on the average representation of shell reported across the stratigraphic profile of one of the excavated features (Haynes). In the laboratory, I counted the number of disarticulated shell valves contained in 0.001 m^3 (1 litre; $\bar{x}=82$ valves ± 2.9 SE, three replicate counts); shells were of small to medium-sized individuals representing a diverse array of species characteristic of dense, main-channel mussel assemblages in the region. I divided the mean number of valves/0.001 m^3 by 2 (to convert number of disarticulated valves to number of individual bivalves), then multiplied by a density of 0.2 (20% of midden material; see above) to yield an average of 8.2 individuals/0.001 m^3 of midden material. Extrapolating this shell density to the combined volume of material in the middens yields an estimate of over 135 million mussels contained in all three middens. Radiocarbon dates from one of the middens (Haynes) indicated that shells were deposited over a time period of approximately 560 years (see Morey and Crothers 1998). Applying this time frame to all three middens indicates that on average 242 000 mussels were harvested from this 8 km reach of river each year.

Apart from direct mortality due to harvest, pre-Columbian human populations could have impacted mussel resources indirectly if land-use activities altered aquatic habitats. Beginning about 5000 years BP, the growing human population of North America resulted in increased rates of land

Figure 5.2 Prehistoric Native American freshwater mussel shell middens along the Tennessee River, Colbert County, Alabama, USA (feature ct27, excavated 1936). Top: east profile of mound. Bottom: detail of interior of mound showing shell material; for scale, note trowel at bottom of photo. Photos courtesy Tennessee Valley Authority and University of Alabama Museums.

clearance and disturbance associated with agriculture, acquisition of fuel wood, and burning for game management (Delcourt 1987a; Johannessen 1993). These disturbances intensified with the adoption of large-scale maize agriculture beginning about 1000 years BP (Lopinot 1992). Fields reaching tens to hundreds of hectares in size became a common feature across the landscape (Peacock 1998), and supported large settlements organized around an agricultural surplus (Peebles 1978; Mann 2005). During this time, indicators of anthropogenic disturbance such as charcoal influx and sedimentation rates increased markedly (Chapman *et al.* 1982), showing widespread intensification of land use and soil erosion (Delcourt 1987a, 1997; Steponaitis 1986). The impact of these land-use changes on riverine ecosystems is poorly known, but even low-intensity agriculture associated with small, transient settlements was sufficient in some cases to cause dramatic and persistent changes in diatom and rotifer assemblages in small lakes (Ekdahl *et al.* 2004). The large human population of North America prior to European contact had profound impacts on the terrestrial landscape, and it is highly plausible if not probable that these impacts also resulted in changes to aquatic communities.

5.2.1 Evidence for pre-Columbian mussel extinctions

Despite high harvest pressure and the potential effects of human land-use practices on aquatic

habitats, no extinctions of mussel species have been documented in prehistory. Zooarchaeological research over nearly the past 100 years has resulted in examination of millions of shells from pre-Columbian middens across North America. To date, only a single species identified in these middens (*Fusconaia apalachicola*) was not subsequently documented by naturalists early in the historical period (Bogan 1990). *F. apalachicola* was found at sites along the Apalachicola River, Florida, ranging in age from 1500 to 650 years BP (Williams and Fradkin 1999), but the timing of its extinction is not known. This species continued to occur at multiple sites into late pre-Columbian times (at least 650 years BP). However, this region was impacted heavily by humans by the early 1800s, and little scientific collecting occurred prior to those impacts, suggesting that this species may have gone extinct during early phases of European settlement (Williams and Fradkin 1999). Other than *F. apalachicola*, all species recorded from pre-Columbian middens throughout North America survived until at least the late 1800s, supporting the conclusion that no North American species were driven to extinction by harvest pressures or human-mediated stream alterations prior to European colonization.

Similarly, there is little evidence that pre-Columbian human activities resulted in local extinctions of species. I compiled data on species presence/absence for 15 stream reaches in the central and south-eastern USA for which comprehensive pre-Columbian and historical data were available. At all sites, a high percentage of species present in the pre-Columbian fauna persisted until the historical period (Table 5.1). Further, pairwise distance matrices of sites (Euclidean distance) based on species presence/absence were highly associated between the pre-Columbian and historical periods (randomized Mantel test, 1000 permutations: Mantel $r = 0.9094$, $P < 0.001$), showing that local patterns of species composition changed little over an extended time period prior to major, modern impacts to streams.

At all stream reaches, historical surveys recorded more species than were found in pre-Columbian middens (Table 5.1). A high degree of consistency in species missing from middens suggests that the higher richness of historical surveys is due to collection and preservation bias associated with midden samples. The genera *Leptodea*, *Lampsilis*, *Lasmigona*, *Potamilus*, *Truncilla*, and *Villosa* were documented historically but were absent in middens at over half of the sites; *Leptodea fragilis* was documented at 14 sites historically, but occurred in middens at only two sites. Other species that were consistently underrepresented in middens relative to historical samples included *Alasmidonta marginata*, *Cumberlandia monodonta*, *Megalonaias nervosa*, *Pyganodon grandis*, and *Utterbackia imbecillis*. Aboriginal people concentrated harvest efforts in high-density mussel beds characteristic of main-channel river habitats (Matteson 1960; Peacock 2000a), resulting in the consistent absence in middens of species characteristic of lentic backwaters and sloughs (e.g. *L. fragilis*, *Potamilus* spp., *Pyganodon grandis*, *U. imbecillis*) or specialized habitats (e.g. *C. monodonta*). Thin-shelled species can be underrepresented in middens due to poor preservation or destruction of these specimens during archaeological recovery (Klippel *et al.* 1978; Morey and Crothers 1998). Thin-shelled species include those characteristic of lentic habitats, compounding their rarity in middens, but also riverine species (e.g. *Alasmidonta* spp., *Lampsilis* spp., *Lasmigona* spp., *Leptodea leptodon*, *Villosa* spp.). Finally, harvesters consistently avoided both very large species such as *Megalonaias nervosa* that are less palatable and occur in deeper habitats (Ortmann 1909; Parmalee 1956) and very small species that are difficult to collect (e.g. *Truncilla* spp., *Villosa fabalis*). *M. nervosa* occurs sporadically in archaeological contexts, but specimens are often modified for use as tools (Theler 1991). In contrast to aboriginal harvesters, early naturalists were interested in generating comprehensive species lists from a wide variety of habitats regardless of food value or the efficiency and ease of procurement.

Unlike the consistent absence of certain species in middens, species that were present in middens but not detected by historical surveys were not consistent across sites in Table 5.1. With the exception of *Epioblasma stewardsoni*, which was present in middens but not detected historically at two sites, there was no overlap among sites in species not detected historically. Species not detected historically but present in middens included mussels that

Table 5.1 Persistence of pre-Columbian mussel assemblages into the historical period in 15 streams in the central and south-eastern USA. The pre-Columbian fauna represents the number of species recovered from aboriginal human shell middens adjacent to the streams. The historical fauna represents the number of species documented in stream reaches before major twentieth-century human impacts to these streams. Species persisting to the historical period represents the percentage of species recorded in pre-Columbian assemblages that were also documented by historical collections.

Stream reach	Number of species		Species persisting to historical period (%)	Sources
	Pre-Columbian fauna	Historical fauna		
Big Black River, Hinds Co., MS	20	29	90	Hartfield and Rummel (1985); Peacock and James (2002)
Clinch River, Roane/Anderson/ Knox Co., TN	39	52	92	Ortmann (1918); Johnson (1978); Parmalee and Bogan (1986)
Cumberland River, Smith/ Trousdale Co., TN	37	44	89	Wilson and Clark (1914); Parmalee *et al.* (1980)
Duck River, Bedford/Marshall/ Maury Co., TN	28	43	96	Ortmann (1924); Isom and Yokley (1968); Parmalee and Klippel (1986)
Ohio River, upper river, WV/PA	30	39	90	Johnson (1978); Taylor (1989)
Illinois River, Fulton Co., IL	28	40	100	Starrett (1971); Warren (1995)
Illinois River, Pike Co., IL	30	40	90	Matteson (1959); Starrett (1971)
Mississippi River, near Prairie Du Chien, WI	28	39	100	Havlik and Stansbery (1978); Theler (1987a)
Pomme de Terre River, Hickory Co., MO	16	24	100	Klippel *et al.* (1978)
South Fork Holston River, Sullivan Co., TN	28	38	93	Ortmann (1918); Parmalee and Polhemus (2004)
Tennessee River, Loudon/Knox Co., TN	38	57	100	Ortmann (1918); Hughes and Parmalee (1999)
Tennessee River, Muscle Shoals, Colbert/Lauderdale Co., AL	62	68	94	Ortmann (1925); Stansbery (1964); Hughes and Parmalee (1999); Garner and McGregor (2001)
Tombigbee River, Lowndes/Clay Co., MS	33	35	97	van der Schalie (1981); Robison (1983)
Tombigbee River, Pickens/ Greene Co., AL	25	31	96	van der Schalie (1981); Robison (1983); Williams *et al.* (1992)
Wabash River, lower river, IL/IN	35	43	94	Parmalee (1969); Cummings *et al.* (1988)
Average (±SE)			95 (±1)	

remain widespread currently (e.g. *Elliptio dilatata, Lampsilis teres, Ptychobranchus fasciolaris, Villosa iris*) as well as those that are now extinct (e.g. *E. stewardsoni*) or imperiled (e.g. *Pegias fabula, Pleurobema clava, Quadrula intermedia*), and collectively these species include a representative cross-section of sensitivity to modern-day human impacts. Across all sites, 68% of species present in middens but not detected historically are currently of conservation concern, similar to 72% of North American species overall (Williams *et al.* 1993), showing that species absent from historical samples are not disproportionately composed of species highly sensitive to habitat alteration. In the late 1800s and early 1900s, the difficulty of travel and lack of modern sampling gear (e.g. SCUBA) and methods (e.g. Smith 2006) precluded the exhaustive sampling effort necessary to detect most or all mussel species in an assemblage. In contrast, midden samples are composed of thousands of shells collected over many years resulting in a more complete representation of species richness in main channel habitats, even

Table 5.2 Freshwater mussel community composition at different times during prehistory in the eastern USA. Sample date was obtained either from estimates given in the source or by taking the midpoint of the reported cultural period (e.g. late Woodland; see Peacock *et al.* 2005). Within a site, sample sizes were standardized using rarefaction (1000 randomizations; Gotelli and Entsminger 2001) to interpolate estimated species richness and evenness of larger samples based on a sample size equal to the smallest sample at the site; values for the smallest samples have no 95% confidence intervals (95% CI) because they are observed values. Richness (including confidence intervals) is rounded to the nearest whole number. Evenness gives the probability that two randomly sampled individuals from the assemblage represent two different species (Gotelli and Entsminger 2001). Correlation coefficients (Pearson's) are for the association of individual species abundances between samples.

Site[1]	Sample	Date (years BP)	Species richness (±95% CI)	Evenness (Hurlbert's PIE, ±95% CI)	Correlation coefficient (r)	
					Sample 2	Sample 3
Clinch River	1	1697	35 (±32–37)	0.913 (±0.910–0.916)	0.906	–
	2	750	34	0.937	–	–
Cumberland River A	1	852	33 (±31–35)	0.905 (±0.901–0.909)	0.959	–
	2	652	40	0.925	–	–
Cumberland River B	1	3502	30	0.874	0.987	–
	2	3027	29 (±28–31)	0.874 (±0.872–0.876)	–	–
Green River	1	4850	33	0.886	0.950	–
	2	4520	31 (±30–31)	0.887 (±0.886–0.887)	–	–
Platte River	1	3407	16 (±16–16)	0.538 (±0.535–0.541)	0.992	–
	2	1407	16	0.518	–	–
Tennessee River A	1	1750	30	0.882	0.952	0.937
	2	1250	28 (±25–30)	0.808 (±0.790–0.825)	–	0.943
	3	750	22 (±20–24)	0.835 (±0.823–0.846)	–	–
Tennessee River B	1	3750	21	0.704	0.983	0.984
	2	2250	22 (±21–22)	0.744 (±0.738–0.749)	–	0.954
	3	1500	23 (±21–24)	0.75 (±0.739–0.761)	–	–
Tennessee River C	1	3750	33 (±30–36)	0.866 (±0.853–0.879)	0.958	–
	2	1500	33	0.765	–	–

[1]Sources and localities: Clinch River (Roane Co., TN; Parmalee and Bogan 1986); Cumberland River A (Davidson Co., TN; Peacock 2000b); Cumberland River B (Jackson Co., TN; Breitburg 1986); Green River (Butler Co., KY; Morey and Crothers 1998); Platte River (Grant Co., WI; Theler 1987b); Tennessee River A (Meigs/Rhea Co., TN; Parmalee *et al.* 1982); Tennessee River B (Jackson Co., AL; Warren 1975); Tennessee River C (Lauderdale Co., AL; Parmalee 1994)

though species characteristic of other habitats not sampled by aboriginal harvesters are underrepresented or absent. The lack of consistent patterns of species present during pre-Columbian times but not detected in historical surveys strongly suggests that these discrepancies are due to random sampling error and provide no evidence of systematic patterns of local extinctions in prehistory.

5.2.2 Pre-Columbian changes in mussel assemblage composition

Even if human activities did not result in range-wide or local extinctions, heavy harvest pressure or impacts to streams due to land use should be expected to cause detectable shifts in mussel assemblage composition. I compared mussel assemblage composition between pairs of temporally successive samples representing assemblages harvested by pre-Columbian people from the same stream site at different times (eight sites, 18 time periods; Table 5.2). These pairs of samples represent a range of time periods including prior, during, and after adoption of maize agriculture. Species richness differed among time periods at only three sites, but decreased at two and increased at one. Assemblage evenness differed among time periods at six sites but the magnitude of change was

small and evenness decreased at three sites and increased at three others. Further, evenness of most samples was high (>0.75), showing that throughout pre-Columbian times these were extremely diverse assemblages that were not dominated by one or a few species. Finally, individual species abundances were highly correlated between all temporally successive pairs of samples ($P>0.90$) which, along with lack of consistent trends in richness or evenness, shows that assemblage structure was remarkably similar over time.

The only evidence of significant changes in mussel assemblages during prehistory is a steady decline in relative abundance of *Epioblasma* spp. occurring over the 5000 years preceding European settlement (Fig. 5.3; Peacock *et al.* 2005). Apart from avoiding very large or very small species, aboriginal people probably harvested mussels within high-density mussel beds indiscriminate of species (Matteson 1960; Peacock 2000a). It is therefore unlikely that the disproportionate decline of *Epioblasma* was caused by preferential harvest of these species. Over the past 100 years, *Epioblasma* has suffered the most severe decline of any mussel genus (Johnson 1978), suggesting that these species are especially intolerant of human impacts to streams. It is unknown whether the decline of *Epioblasma* in prehistory is also a result of accelerating human environmental impacts or due to other long-term changes unrelated to human activities. However, the rate of decline increased after the widespread adoption of maize agriculture about 1000 years BP (Peacock *et al.* 2005), suggesting that intensification of anthropogenic disturbance associated with a rapidly expanding human population (e.g. Delcourt 1987a, 1997) began to exert substantial pressures on riverine ecosystems late in prehistory.

Because data on pre-Columbian mussel assemblages are derived almost exclusively from shell middens harvested by humans, it is impossible to determine whether assemblages changed during the early phases of pre-Columbian human settlement of North America. However, data spanning nearly 5000 years of human occupation show that mussel assemblages changed little even in the face of intense harvest and during periods of major human-induced changes on the landscape. Although humans intensively exploited mussel communities as a food resource, harvesters likely operated under an optimal foraging model in which harvest location shifted as local stocks became depleted but well before they were extirpated completely (e.g. Raab 1992). Frequent shifts in the location of harvest and the presence of large mussel populations throughout an interconnected river network would have allowed recovery of mussel numbers after local depletion. It remains unclear to what extent mussels were affected by habitat deterioration due to pre-Columbian human land-use activities, but at most these impacts resulted in only subtle changes in assemblage composition (e.g. declines of *Epioblasma*) and did not result in species extinctions or consistent, widespread

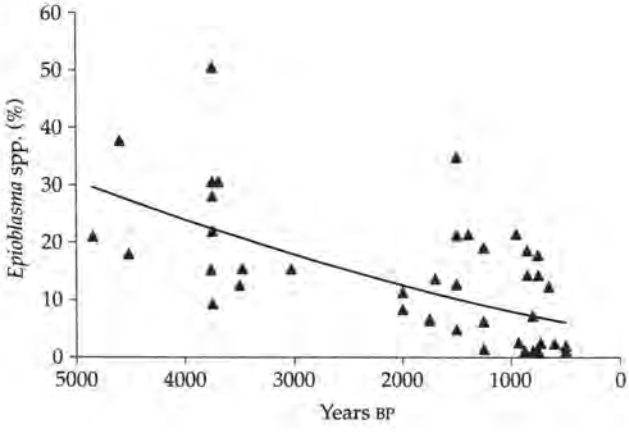

Figure 5.3 Relationship between time and relative abundance of *Epioblasma* spp. in the eastern USA (arcsine [relative abundance] = 12.119−0.0043 time, $r^2=0.369$, $P<0.0001$). From Peacock *et al.* (2005).

patterns of local extinctions. Overall, the mussel fauna of North America was intact at the time of European settlement.

5.3 Recent human impacts on mussel communities

5.3.1 European settlement until 1924

European settlers began to significantly impact the aquatic communities of North America by at least the early 1800s. Harvest of mussels for pearls represented the first large-scale and widespread historical impact to freshwater mussels. Pearling was widespread over much of the continent by 1860, and several areas experienced pearl rushes during which large numbers of prospectors converged on a stream following the discovery of pearls (Anthony and Downing 2001). Because gem-quality pearls occur in a small percentage of individuals, pearling was a highly wasteful endeavour that required harvest of large numbers of mussels in order to realize even a modest return. By the early 1900s, pearling had resulted in a reduction of mussel abundance in many streams. In 1911, piles of shells discarded by pearlers, each as large as 3 tons, were present along much of the Cumberland River (≈845 km) in Kentucky and Tennessee, and larger mussels most likely to have pearls were absent from mussel beds in some areas (Wilson and Clark 1914). Pearling also resulted in impacts to stream habitats in some areas. Pearlers were known to work 'a plow drawn by a strong team' through shoals in the Clinch River, Tennessee, to expose buried mussels (Böpple and Coker 1912).

Harvest of mussels for pearls paled in comparison to harvests by the shell-button industry. Use of mussel shells for manufacture of buttons and other mother-of-pearl items began on a large scale in 1892 and soon grew into a multi-million dollar industry, peaking in 1916 but lasting until the mid-1960s (Anthony and Downing 2001). The pearl-button industry encompassed at least 20 states along the large rivers of the central and south-eastern USA and was therefore overlaid precisely on the region of highest mussel diversity. Similar to harvests for food by pre-Columbian settlements, the pearl button fishery resulted in the harvest of staggering numbers of mussels (Fig. 5.4). In 3 years, over 9000 tons of shells were taken from a single mussel bed less than 0.75 km^2 in size in the Mississippi River in Illinois; this harvest represented over 100 million animals (Smith 1898 in Anthony and Downing 2001). Harvests of similar magnitude were reported throughout the region and eventually mussel resources of many streams were seriously overexploited from a commercial fishery perspective (Anthony and Downing 2001).

In addition to intense harvest pressures, mussel populations suffered from a variety of other insults associated with a rapidly expanding human population and an increasingly industrialized society. With an absence of environmental regulation of any kind, by the early 1900s mussel populations had been reduced or eliminated completely in stream reaches throughout the USA by chronic and severe point-source pollution, dams and other stream channel modifications, and massive erosion and sedimentation (Bogan 1993; Neves *et al.* 1997). Between 1900 and 1920 mussel life was eliminated almost completely in nearly 200 km of the Illinois River due to discharge of raw sewage from Chicago and other cities (Starrett 1971). The extinction of *F. apalachicola* in the Apalachicola River system is probably attributable to discharge of industrial effluents combined with sedimentation caused by widespread hillside clearing for cotton production after the Civil War (Williams and Fradkin 1999). These impacts to the Apalachicola system demonstratively resulted in the elimination of many other mussel species from large portions of the system by the early 1900s (Brim Box and Williams 2000).

Despite intense harvest pressures and a wide variety of serious insults to streams, no extinctions of freshwater mussels were documented by contemporary observers prior to 1924. Although commercial harvest resulted in massive reduction in mussel abundance in many streams, of the 50 most important commercial species (Anthony and Downing 2001), 38% are currently of conservation concern, which is about half the rate of imperilment for the North American fauna as a whole (72%; Williams *et al.* 1993). This result can be interpreted in two non-mutually exclusive ways: (1) commercially exploited species in general are less sensitive to human impacts or (2) commercial harvest had

Figure 5.4 Commercial harvest of freshwater mussels in the early twentieth century. Top: barges loaded with shells in Arkansas (from Coker 1919). Bottom: mussel shells at a button factory on the upper Mississippi River (photo courtesy US Fish and Wildlife Service).

little effect in propelling species into a sustained downward spiral of abundance. Regardless, even intense unregulated harvest did not result in species extinctions. Similarly, although extensive stream reaches were practically defaunated by a wide array of insults to stream habitats during this period, resulting in extinction of local populations, species richness of the North American fauna as a whole remained largely unchanged.

Mussels remained remarkably abundant and diverse in many areas, with large streams supporting the highest diversity of mussel species. Species composition across much of the eastern USA remained similar to pre-Columbian assemblages (Table 5.1) and numerous authors of the time describe dense aggregations of mussels that in some cases extended for many stream kilometres (e.g. Wilson and Clark 1914; Ortmann 1924, 1926; Clench 1926). However, these same authors reported localized declines in mussel populations due to harvest, pollution, and habitat destruction. In the Green River, Kentucky, in 1925, at one site '...most of the Unionidae have been killed here by pearl-hunters', while at other sites mussels '...were extremely abundant' or were 'so thick that they touched one another' (Ortmann 1926). In the Cumberland River, Kentucky and Tennessee, in 1910–1911, 'in spite of the great number of mussels taken out [for the button industry], the river as a whole...does not show any marked depletion except in one or two restricted localities' (Wilson and Clark 1914). In the Tennessee River system in 1912–1915 with regard to mussel abundance and diversity '...conditions are fair, in some parts splendid; but there are already polluted streams, in which the fauna is gone' (Ortmann 1918).

These descriptions exemplify the state of the North American mussel fauna and the freshwater landscape in general in the early decades of the twentieth century. Stream systems at this time

were a mosaic of disturbed and relatively undisturbed reaches. Similar to pre-Columbian harvest, harvest for pearls and buttons shifted location frequently when local mussel abundance fell below commercially exploitable levels (Coker 1919; Neves *et al.* 1997; Anthony and Downing 2001). Similarly, some impacts such as sedimentation due to logging and mining were also shifting in nature. Because stream systems remained largely contiguous and were fragmented by few permanent physical barriers, the enormous reproductive potential contained within dense mussel populations in undisturbed reaches allowed repopulation of impacted areas following abatement of impacts. In at least some instances, mussel beds depleted by harvest but subsequently abandoned recovered to commercially exploitable levels in several years (Coker 1919). Despite intense harvest pressure and a variety of severe insults to stream habitats, the scattered and shifting nature of these impacts coupled with the interconnectivity of stream systems allowed the North American mussel fauna as a whole to survive intact well into the twentieth century.

5.3.2 Systematic habitat destruction 1924–1984

> The building of dams...also has a deteriorating effect upon mussel life, and...surely will increase in the future (Ortmann 1918)

Despite his prophetic words, the early mussel biologist Arnold E. Ortmann could not likely have imagined the scale and rapidity of dam construction in North America that commenced in earnest shortly after these words were written. Although many dams were built before 1924 and dam construction continues, the end points of 1924–1984 encompass the most intensive period of large dam construction in the USA and are symbolic in the context of freshwater mussel extinctions. As one of the largest dams in the world at the time of its completion in 1924, Wilson Dam on the Tennessee River in Alabama simultaneously drowned much of Muscle Shoals, the most diverse site for freshwater bivalves on the planet (≈70 species; Stansbery 1964; Garner and McGregor 2001), and ushered in the age of large dams in North America. The next 60 years witnessed a frenzy of dam building and stream channelization for the ostensible purposes of flood control, hydroelectric power generation, navigation, water storage, and recreation. The Tennessee-Tombigbee Waterway in Alabama and Mississippi was completed in 1984, and included construction of 10 locks and dams and 377 km of navigation channel (Tennessee-Tombigbee Waterway Development Authority 2007). This project effectively destroyed the Tombigbee River, which represented the last unpolluted, free-flowing large stream reach in the Mobile Basin, one of the most diverse stream systems in North America (Abell *et al.* 2000), and to date has resulted in the extinction of three endemic mussel species (*Pleurobema curtum*, *P. marshalli*, and *Quadrula stapes*). Whereas the necessity and cost-benefit ratios of earlier dam and channelization projects varied widely, the Tennessee-Tombigbee Waterway eclipsed any single previous project in terms of cost, dubious need, misrepresented justification, and environmental destruction (Stine 1993), and was the grand finale of the golden age of large dam building and stream channelization in the USA.

The result of this frenzy of dam building was to eliminate most free-flowing large rivers and many small and medium-sized rivers in the USA (Benke 1990; Dynesius and Nilsson 1994). In their natural state, even the largest rivers had extensive gravel and sand bars that created shallow shoals at times of low water. The Ohio River could be crossed seasonally by wading at Cincinnati, Ohio (Fig. 5.5), and Muscle Shoals on the Tennessee River was a shallow, 85 km complex of islands, shoals, and rocky reefs (Garner and McGregor 2001) that blocked river traffic at low water. This type of shallow, shoal habitat was lost completely from most large rivers after impoundment. Stream reaches not directly impounded but located downstream from large dams were fundamentally modified by dam releases having highly altered flow, temperature, and oxygen regimes (Miller *et al.* 1984; Layzer *et al.* 1993). During this period, four of the most diverse rivers in the world, from a freshwater mussel perspective (Tennessee, Cumberland, Ohio, and Coosa), were transformed into a series of reservoirs and regulated reaches with little or no free-flowing main-channel habitat remaining. In addition, most of the large tributaries in these systems were

Figure 5.5 The Ohio River at Cincinnati, Ohio (approximately 1888), before impoundment. Photo was taken at low water, showing presence of shallow shoals and gravel bars. Note people on gravel bars in the distance for scale. From the collections of The Public Library of Cincinnati and Hamilton County, and the Cincinnati Historical Society Library.

impounded. In the Tennessee River drainage alone there are 53 major dams (defined as impounding >40 ha): nine on the main channel and the remainder on tributaries (Etnier and Starnes 1993).

This systematic destruction of large-stream habitat resulted in the first wave of mussel species extinctions, beginning in the 1930s (Table 5.3). The exact timing of extinction is difficult to determine for any species (e.g. Diamond 1987; Reed 1996) and can be especially difficult for freshwater mussels because relict individuals of some species can survive for more than 30 years in radically altered habitats that no longer support viable populations (Parmalee and Klippel 1982; Ahlstedt and McDonough 1993). A species can be considered functionally extinct when reports of its existence cease or when all populations are no longer viable and extinction becomes inevitable (Holdaway 1999b; DeLord 2007). Here, I define functional extinction of mussels as occurring when all suitable habitat has been destroyed or when a species becomes so rare that the chances of finding an individual, or of the species reproducing, becomes essentially zero. For the remainder of this chapter I discuss the time of functional extinction of species but refer to this as simply extinction.

The first wave of mussel extinctions was composed primarily of obligate large-river species. Unaltered main-channel habitat in the Ohio and Tennessee Rivers was completely eliminated between 1924 and 1944, and species endemic to these habitats were likely the first to become extinct (e.g. *Epioblasma flexuosa*, *E. f. florentina*, *E. personata*, *E. propinqua*; Table 5.3). Due to the difficulty of accessing and sampling large rivers, the relative dearth of mussel biologists during this period, and the rapid pace of dam construction, the temporal and spatial sequence of the disappearance of many of these species is poorly known; rather, these species were simply never seen again after impoundment of large stream habitat was complete. For example, *E. flexuosa* was last documented with certainty in 1900 from the Ohio River (Stansbery 1970), but because early twentieth-century collecting in the middle and lower reaches of this river was sporadic and restricted to only a few localities, the species probably persisted here until complete impoundment of the river. For other species the timing of extinction can be determined with more precision. By the mid-1940s, all known habitat for *E. lewisii* had been impounded or altered by dam release except

Table 5.3 Species of freshwater mussels in North America that became extinct in the twentieth century. Time of extinction is the probable time of functional extinction (see text). Several taxa of uncertain taxonomic status (e.g. *Alasmidonta robusta*, *Pleurobema* spp., *Quadrula tuberosa*; see text) are omitted from this list.

Species	Time of extinction	Cause of extinction[1]	Last known occurrence
Alasmidonta mccordi	1964	1	Coosa River, AL
Alasmidonta wrightiana	1930s	2,3	Ochlockonee River, FL
Elliptio nigella	1950s	2	Coolewahee Creek, GA
Epioblasma arcaeformis	1940s	1	Holston River, TN
Epioblasma biemarginata	1970	2	Elk River, TN
Epioblasma flexuosa	1920s–1930s	1	Ohio River, KY
Epioblasma florentina curtisi	1990s	3	Little Black River, MO
Epioblasma florentina florentina	1940s	1	Holston River, TN
Epioblasma haysiana	1970	2	Clinch River, VA
Epioblasma lenior	1967	1	Stones River, TN
Epioblasma lewisii	1950	1	Cumberland River, KY
Epioblasma metastriata	1980s	2	Conasauga River, GA
Epioblasma othcaloogensis	1970s	2	Conasauga River, GA
Epioblasma personata	1920s–1930s	1	Tennessee River, AL
Epioblasma propinqua	1936	1	Clinch River, TN
Epioblasma sampsoni	1930s–1940s	2	Wabash River, IL/IN
Epioblasma stewardsoni	1940s	1	Holston River, TN
Epioblasma torulosa gubernaculum	1980s	2	Clinch River, TN
Epioblasma torulosa torulosa	1970s	1	Kanawha River, WV
Epioblasma turgidula	1976	1	Duck River, TN
Lampsilis binominata	1970s	3	Flint River, GA
Pleurobema curtum	1990s	2	East Fork Tombigbee River, MS
Pleurobema marshalli	1984	1	Tombigbee River, AL/MS
Quadrula couchiana	Early 1900s	3	Rio Grande, TX
Quadrula stapes	1980s	2	Sipsey River, AL
Quincuncina mitchelli	1970s	3	Rivers in central Texas

[1]Causes of extinction: 1, direct loss of all habitat by stream impoundment or channelization; 2, indirect effects of fragmentation due to habitat destruction; 3, small original range and non-impoundment related habitat degradation.

for the Caney Fork River, Tennessee (Cumberland River system), and the upper Cumberland River, Kentucky. The species persisted in both of these stream reaches until 1948 and 1950 respectively (Neel and Allen 1964; Layzer *et al.* 1993), when dam construction on these streams eliminated all remaining habitat for the species. Similarly, by the 1970s, *Pleurobema marshalli* persisted only in a single free-flowing reach of the Tombigbee River in Alabama and Mississippi which was destroyed by completion of the Tennessee-Tombigbee Waterway in 1984, resulting in the extinction of the species (Haag 2004a).

Mussels were eliminated in many river reaches due to the abrupt and profound transformation of shallow, riverine habitat into deep, still, and often hypolimnetic reservoirs designed primarily for floodwater storage or hydroelectric generation, or by severely altered hydrological conditions downstream of such reservoirs. These transformations created habitats to which few or no mussel species could adapt, resulting in near total loss of the mussel fauna (Miller *et al.* 1984; Layzer *et al.* 1993). However, dams designed primarily for navigation, such as those on the Alabama, lower Cumberland, Mississippi, Ohio, and Tennessee Rivers, eliminated

shallow shoal habitats but created run-of-the-river impoundments that retain some riverine characteristics, especially in tailwater reaches downstream of dams. Relative to original river conditions, tailwater reaches below navigation dams have greatly increased depth (≈6–15 m) and altered daily hydrographs (Garner and McGregor 2001; Freeman *et al.* 2005) and can experience periods of low dissolved oxygen (<5 mg/l; Voightlander and Poppe 1989) sufficient to cause mussel mortality (Johnson 2001). However, unlike other reservoir habitats, tailwater reaches have flow sufficient to keep gravel and sand substrates silt-free, providing habitat for a variety of riverine organisms (Voightlander and Poppe 1989). In these impounded riverine habitats, only a portion of the original mussel fauna was eliminated while other species were able to maintain recruiting populations.

Navigation dams affected species selectively and the likelihood of persisting in impounded riverine habitats was not simply a function of pre-impoundment abundance. In the Tennessee River, some of the most abundant species both in pre-Columbian and historical times were eliminated by impoundment (e.g. *Epioblasma torulosa torulosa, E. biemarginata, Dromus dromas*) while other species that were rare before impoundment persisted or even increased (e.g. *Fusconaia ebena, Megalonaias nervosa*; Ortmann 1918; Morrison 1942; Garner and McGregor 2001). This selective loss of species was caused in large part by differences in fish host use among species and not by inter-species differences in habitat requirements of the mussels themselves.

Mussel species that adapted to impounded riverine habitats are either host-generalists or specialize in the use of host fishes that also could adapt to these habitats. For example, in the Tennessee River, all but one host-specialist mussel species that survived as a reproducing population after impoundment use catfishes, freshwater drum, skipjack herring, sunfishes (including black basses), gar, or sauger (Table 5.4). These fishes all thrive in the run-of-the-river reservoirs of the Tennessee River (Etnier and Starnes 1993). The single exception, *Ptychobranchus fasciolaris*, is extremely rare in the impounded Tennessee River (Garner and McGregor 2001). In contrast, 89% of mussel species that did not adapt to impoundment of the Tennessee River used darters, riverine minnows, sturgeon, or rock bass as hosts (Table 5.4). These fishes were eliminated or greatly reduced in impounded rivers, even in riverine tailwater reaches, largely as a result of the loss of shallow shoal habitat (Voightlander and Poppe 1989; Etnier and Starnes 1993; Freeman *et al.* 2005). The logperch *Percina caprodes*, a darter that serves as primary host for several mussel species, including species of *Epioblasma*, persists in some sections of the impounded Tennessee River, but likely leaves the river in spring to spawn in shoal habitat of small tributary streams (Etnier and Starnes 1993). Such a migration, coinciding with the period of glochidial release by these mussel species, would effectively render these fishes unavailable as hosts, despite their continued seasonal presence in the reservoirs. Because small stream fishes such as darters and minnows have short lifespans (<5 years), impoundment resulted in abrupt changes in the fish assemblage, eliminating hosts for a large number of mussel species.

Even after loss of their fish hosts precluded recruitment, many long-lived mussel species continued to persist in impounded riverine habitats as aging, relict populations. *Pleurobema cordatum* was a dominant component of main channel mussel assemblages in the Tennessee River but has realized little recruitment subsequent to impoundment of the river. In 1957 the mean age of *P. cordatum* was 22 years, but increased to 49 years by 1993 (Scruggs 1960; Ahlstedt and McDonough 1995–1996); in both cases, these estimates show that most individuals recruited just before or just after construction of dams in this section of the river in 1940 and 1942. Diverse, relict assemblages of species intolerant of impoundment (e.g. *Cyprogenia stegaria, Dromus dromas, Epioblasma* spp., *Obovaria retusa*) persisted in the Cumberland River, Tennessee, for at least 25 years after dam construction (Parmalee *et al.* 1980; Parmalee and Klippel 1982) and in several sections of the Tennessee River, Alabama and Tennessee (Ahlstedt and McDonough 1993; Garner and McGregor 2001). Similarly, *Epioblasma torulosa torulosa* continued to be harvested by mussel fisherman in the lower Ohio River for 30 years after impoundment (Parmalee 1967). These relict populations were composed exclusively of older individuals that had

Table 5.4 Host fish use by the mussel fauna of the Tennessee River near Muscle Shoals, Alabama. Impoundment-tolerant species are defined here as those that were able to maintain reproducing populations in impounded riverine habitat remaining in dam tailwaters in this section of the river (see text). Intolerant species are those that were eliminated completely soon after impoundment, or those for which little or no recruitment occurred after impoundment even though adults may persist for many years. Species occurrence and impoundment tolerance was assessed from Garner and McGregor (2001) and Ortmann (1925). Host use was determined from a large body of published and unpublished literature (for an introduction to this literature, see Watters 1994, and Mussel/host database, The Ohio State University Museum of Biological Diversity, Division of Mollusks, www.biosci.ohio-state.edu/~molluscs/OSUM2/index.htm). For some species with unknown hosts, host use was inferred based on information for congeners. Species with no host information or information for congeners were excluded from the table, but these included both tolerant (e.g. *Obliquaria reflexa*) and intolerant (e.g. *Hemistena lata*) species.

Mussel species	Primary host fish use
Impoundment-tolerant species	
Amblema plicata	Generalist
Cyclonaias tuberculata	Catfishes (*Ictalurus, Pylodictis olivaris*)
Ellipsaria lineolata	Freshwater drum (*Aplodinotus grunniens*)
Elliptio crassidens	Skipjack herring (*Alosa chrysochloris*)
Fusconaia ebena	Skipjack herring
Lampsilis abrupta	Black basses (*Micropterus*)
Lampsilis ovata	Black basses
Lampsilis teres	Gar (Lepisosteidae)
Leptodea fragilis	Freshwater drum
Ligumia recta	Sauger (*Sander canadense*), black basses
Megalonaias nervosa	Generalist
Plethobasus cyphyus	Sauger
Potamilus alatus	Freshwater drum
Ptychobranchus fasciolaris	Darters (*Ammocrypta, Etheostoma,* or *Percina*)
Quadrula pustulosa	Catfishes
Quadrula quadrula	Catfishes
Toxolasma (2 spp.)	Sunfishes (Centrarchidae)
Tritogonia verrucosa	Catfishes
Truncilla (2 spp.)	Freshwater drum
Villosa vanuxemensis	Sculpins (*Cottus* spp.), sunfishes
Impoundment-intolerant species	
Cyprogenia stegaria	Darters
Dromus dromas	Darters
Elliptio dilatata	Darters
Epioblasma (10 spp.)	Darters
Fusconaia barnesiana	Riverine minnows (e.g. *Cyprinella, Erimystax, Nocomis,* or *Notropis*)
Fusconaia cor	Riverine minnows
Fusconaia cuneolus	Riverine minnows
Lampsilis fasciola	Black basses, rock bass (*Ambloplites rupestris*)
Lasmigona costata	Generalist
Lemiox rimosus	Darters
Leptodea leptodon	Freshwater drum
Lexingtonia dollabelloides	Riverine minnows
Medionidus conradicus	Darters
Obovaria olivaria	Sturgeon (*Scaphirhynchus*)
Obovaria retusa	Darters

Table 5.4 *Continued*

Mussel species	Primary host fish use
Pleurobema (5 spp.)	Riverine minnows
Ptychobranchus subtentum	Darters
Quadrula cylindrica	Riverine minnows
Quadrula fragosa	Catfishes
Quadrula intermedia	Riverine minnows
Strophitus undulatus	Generalist
Villosa iris	Black basses, rock bass
Villosa taeniata	Rock bass
Villosa trabalis	Darters

recruited prior to impoundment and continue to exist in some streams today. The widespread persistence of these relict faunas shows that adults of many species could survive even in highly modified riverine habitats but the lack of younger individuals shows that recruitment effectively ceased soon after impoundment.

Many species that were eliminated from large river habitats also occurred in medium-sized tributary streams and therefore survived the destruction of large rivers. However, impoundment of tributaries also resulted directly in extinction of some species with limited ranges. By the late 1960s, *Epioblasma lenior* and *Epioblasma turgidula* had both been reduced to single populations, in the Stones River, Tennessee, and the Duck River, Tennessee, respectively (Stansbery 1970, 1976), until construction of J. Percy Priest Reservoir (Stones River) in 1967 and Normandy Reservoir (Duck River) in 1976 eliminated the last habitat for these species. However, impoundment of tributary streams, although widespread, was in general less complete than the impoundment of large rivers, and many tributaries remained free-flowing and continued to support diverse mussel faunas.

Although most extinctions during this period were due directly to elimination of all suitable habitat by dams, other factors were responsible for extinctions of species with very small natural ranges (Table 5.3). *Alasmidonta wrightiana* is known only from 15 specimens collected at two sites in the Ochlockonee River, Florida, prior to 1932 (Clarke 1981; Williams and Butler 1994). The construction of Talquin Dam in 1927 inundated one of these sites but left the other intact. Reduction of the already small range of this rare species may have reduced the population size below a viable level; alternatively the dam may have eliminated an anadromous host fish required for reproduction by this species (R. Butler, personal communication). *Lampsilis binominata* occurred historically only in the upper Flint and Chattahoochee Rivers, Georgia, mostly above the Fall Line demarcating uplands from the Coastal Plain (Brim Box and Williams 2000). This species was extirpated from the Chattahoochee River by the 1940s but persisted in the upper Flint River until expansion of the Atlanta urban area in the 1970s degraded the remaining habitat (Gillies *et al.* 2003). Other species with very small historical ranges may have been relicts that went extinct naturally before significant human impacts to their habitat. *Quadrula couchiana* was endemic to the Rio Grande system in Texas and Chihuahua, Mexico. This species is frequent in the recent fossil record but only a few living individuals were ever found, the last in 1898 (Howells *et al.* 1996), suggesting that this species became extinct naturally before major human impacts to the Rio Grande in the 1900s.

Most species that went extinct during the period of systematic habitat destruction were morphologically distinctive (see Fig. 5.1), were well known to early naturalists, and are well represented in historical museum collections. However, a precise accounting of the number of extinctions during this period will never be possible because of uncertainty about the phylogenetic status of some morphologically similar or poorly known taxa. Of

the numerous species of *Pleurobema* described from main-channel habitats in the Mobile Basin, especially the Coosa River, Alabama, as many as 14 of these taxa are now considered extinct (Neves *et al.* 1997; Turgeon *et al.* 1998). However, some of these taxa likely represent expressions of clinal variation (Turgeon *et al.* 1998) within both extant and extinct species, resulting in an overestimate of extinction in this group. Other species previously considered extinct based on the existence of only one or two historical specimens (e.g. *Medionidus macglameriae*; Neves *et al.* 1997; Turgeon *et al.* 1998) were based on misidentifications of extant species (Williams *et al.* 2008). The validity of other poorly known taxa that were restricted to large rivers and now considered extinct (e.g. *Pleurobema bournianum*, *Quadrula tuberosa*) will never be known because tissues from these animals are unavailable. On the other hand, current species concepts prevalent in freshwater mussel taxonomy may underestimate diversity and past extinctions in other mussel groups due to the presence of previously unrecognized cryptic species (e.g. Jones *et al.* 2006a; Serb 2006).

By the close of the most intensive era of dam construction, the mussel fauna of North America had been changed radically. At least 12 species that occurred only in free-flowing large rivers had been rendered extinct directly by elimination of all existing habitat (Table 5.3), and a large number of other species were eliminated from these habitats and reduced to smaller populations in tributary streams. Large-stream mussel faunas were now composed of a smaller number of species that could adapt to impounded riverine habitats, and the highest mussel diversity now occurred in tributary streams not directly affected by impoundment. Although the mussel fauna of many tributaries was eliminated or greatly reduced by impoundment as well as other impacts, as a whole the small and medium-sized stream fauna of North America remained largely intact. However, this diverse fauna was now highly fragmented by dams or by long stream reaches that no longer provided suitable mussel habitat. Therefore, even though diverse and abundant mussel faunas remained in many streams, these assemblages were now composed of isolated and highly vulnerable populations.

5.3.3 The post-dam construction era: fragmentation, isolation, and the extinction debt

Widespread recognition of the extinction of mussel species and the endangered status of others occurred by 1970 (Stansbery 1970, 1971) and conservation efforts to protect mussel diversity began in earnest with passage of the US Endangered Species Act in 1973. Although the vulnerability of isolated populations of rare species was recognized, the long-term effects of habitat fragmentation have not become clear until recently. In isolated populations, declines in population size due to stochastic events, whether natural or human-caused, cannot be offset by colonization from other populations; therefore, a single major impact or a series of lesser impacts can cast a population into a slow, downward spiral of abundance from which it may never recover (Gilpin and Soulé 1986). Unlike direct, immediate effects of habitat destruction, extinctions due to habitat fragmentation have a time lag during which the isolated community bears an extinction debt to be repaid in the future (Tilman *et al.* 1994; Hanski and Ovaskainen 2002). Although extinction of an isolated population may ultimately be caused by a single factor unrelated to fragmentation, the true cause is an accumulation of impacts over time, beginning with the initial fragmentation of the species' habitat. Because connectivity can be as important as the size of the population in determining vulnerability to extinction (Paquet *et al.* 2004), the complete isolation of many remnant mussel populations following dam construction predicted a large number of delayed extinctions.

In some cases, payment of the extinction debt created by habitat fragmentation is already underway. Due mostly to widespread impoundment of their habitat, by the 1960s, *Epioblasma haysiana* and *Epioblasma torulosa gubernaculum* both survived only in a single free-flowing section of the Clinch River in Tennessee and Virginia, upstream of Norris Reservoir. In 1967 and 1970, industrial chemical spills occurred within this section of river, eliminating all molluscs for over 18 river kilometres, reducing mussel abundance for at least 124 km (US Fish and Wildlife Service 1983), and killing nearly all fishes for over 100 km (Jenkins and Burkhead

1993). Other mussel species that were distributed more widely within the river or had larger population sizes before the spill survived, but *E. haysiana* was never seen again after the spill, and *E. t. gubernaculum* was evidently reduced to a population size too small for recovery. Only two individuals of *E. t. gubernaculum* were found after the spill, with the last individual seen in 1982 (US Fish and Wildlife Service 1983).

In the Tombigbee River system, elimination of main channel habitat by the Tennessee-Tombigbee Waterway reduced two obligate large-river species, *Pleurobema curtum* and *Quadrula stapes*, to single, small populations, each of which occurred in the lower reaches of two tributaries, the East Fork Tombigbee River (Mississippi) and the Sipsey River (Alabama) respectively (McCullagh *et al.* 2002; Haag 2004b). These populations each persisted for at least 10 years after destruction of the Tombigbee River, but recent intensive surveys in these and other unimpounded tributaries have failed to find the species and they are now considered extinct. The East Fork Tombigbee and Sipsey Rivers both continue to support diverse mussel assemblages composed of species not restricted to main-channel habitats (McCullagh *et al.* 2002). However, tributary populations of *P. curtum* and *Q. stapes* were probably sinks that were sustained solely by immigration from source populations in the main river. After the loss of the source populations, tributary populations were too small to be reproductively viable and disappeared as remnant adults reached the end of their lifespan.

Epioblasma metastriata became extinct when populations were reduced and fragmented by reservoirs, followed by gradual deterioration of habitat for the few remaining populations. Most habitat for *E. metastriata* was destroyed by impoundment of the Black Warrior and Coosa Rivers. By the 1960s, the species survived in three tributary streams in the Cahaba and Upper Coosa River basin, but these populations declined steadily and living animals have not been found since 1973 (Cahaba) and the 1980s (Coosa) (US Fish and Wildlife Service 2000, Williams *et al.* 2008). The decline of these remnant populations is attributable to a combination of sub-acute stressors (e.g. sedimentation and other non-point-source contaminants) within the watersheds that occurred at different times over the last 40 years. In a large, interconnected watershed such as existed before dams, these populations could have been sustained or rescued by immigrants from other populations, allowing them to recover from periodic, localized stress. However, without the potential for immigration, the steady erosion of these populations over time ultimately resulted in the extinction of the species.

With the exception of these and a handful of other recently extinct species (Table 5.3), most of the fauna that remained after the era of dam building survives to the present day. However, the major portion of the principal on the extinction debt held by this fauna remains unpaid. The combination of indirect effects of fragmentation and isolation coupled with an array of acute and chronic stressors, similar to that which led to the extinction of *E. metastriata*, has set the stage for a second wave of mussel extinctions that will likely surpass the first extinction wave caused by direct habitat destruction. Currently, at least 31 species survive only as one or two populations (Table 5.5); in the remainder of this chapter I refer to these species as critically imperiled. For many of these species, only short reaches of habitat remain, and populations are extremely small for all. For example, *Lampsilis streckeri* is known to inhabit only about 10 km of stream in Arkansas (US Fish and Wildlife Service 1991). Only five living individuals of *Medionidus simpsonianus* have been seen in the last 35 years, including two in 1974, one in 1993, and two in 2007 (US Fish and Wildlife Service 2003, J. Williams personal communication). All of these critically imperiled species are in imminent danger of extinction due to stochastic events. For some, it is likely that abundance has already fallen below a threshold necessary for successful reproduction, and those species can be considered functionally extinct.

In addition to these critically imperiled species, a large number of other mussel species persist as a handful of isolated populations, only one or two of which are large and robust. In these cases, natural or human-caused stochastic events can quickly degrade a species' status to critically imperiled. Prior to 1990, the Little South Fork Cumberland River and Horse Lick Creek, both in Kentucky, supported two of the most important remnants of the diverse and highly endangered mussel fauna

Table 5.5 Critically imperiled mussel species in North America. A population is defined here as a collection of occurrences within a contiguous stream system that can conceivably exchange immigrants. For most species on this table, populations do not extend for more than approximately 80 stream kilometres. Species that occur only in one large population but covering much more than 80 km of contiguous habitat (e.g. several endemic mussel species in Altamaha River, GA) are not included in this table. Host use was determined as described for Table 5.4, with the exception that host use of many of these species is not known; for these species host use was inferred based on information for congeners (see Haag and Warren 2003). Species for which no host-use information was available for congeners or closely related species are listed as unknown. Region of occurrence gives the general biogeographic affinity of each species: Gulf of Mexico refers to Gulf drainages not including the Mississippi and Mobile basins; Ohio River encompasses all tributaries of this river including the Cumberland and Tennessee River drainages.

Species	Number of extant populations	Primary hosts	Region of occurrence
Alasmidonta triangulata	2	Generalist	Gulf of Mexico
Amblema neislerii	2	Generalist	Gulf of Mexico
Arkansia wheeleri	2	Generalist	Lower Mississippi Basin
Dromus dromas	2	Darters[1]	Ohio River
Elliptio chipolaensis	1	Generalist	Gulf of Mexico
Elliptio spinosa	1	Generalist	Atlantic coast drainages
Epioblasma obliquata obliquata	1	Darters[1]	Ohio River
Epioblasma obliquata perobliqua	1	Darters[1]	Great Lakes Basin
Epioblasma penita	1	Darters[1]	Mobile Basin
Epioblasma florentina walkeri	2	Darters[1]	Ohio River
Fusconaia rotulata	1	Unknown	Gulf of Mexico
Hemistena lata	2	Unknown	Ohio River
Lampsilis streckeri	1	Black basses[3]	Lower Mississippi Basin
Lampsilis virescens	1	Black basses[3]	Ohio River
Margaritifera marrianae	2	Madtom catfishes[4]	Gulf of Mexico/Mobile Basin
Medionidus parvulus	2	Darters[1]	Mobile Basin
Medionidus simpsonianus	1	Darters[1]	Gulf of Mexico
Medionidus walkeri	1	Darters[1]	Gulf of Mexico
Obovaria retusa	1	Darters[1]	Ohio River
Plethobasus cicatricosus	1	Sauger[5]	Ohio River
Plethobasus cooperianus	2	Sauger[5]	Ohio River
Pleurobema furvum	2	Riverine minnows[2]	Mobile Basin
Pleurobema gibberum	2	Riverine minnows[2]	Ohio River
Pleurobema taitianum	1	Riverine minnows[2]	Mobile Basin
Ptychobranchus jonesi	1	Darters[1]	Gulf of Mexico
Quadrula intermedia	2	Riverine minnows[2]	Ohio River
Quadrula petrina	2	Catfishes[6]	Gulf of Mexico
Quadrula sparsa	2	Riverine minnows[2]	Ohio River
Quincuncina burkei	2	Unknown	Gulf of Mexico
Toxolasma cylindrellus	1	Sunfishes[7]	Ohio River
Truncilla cognatus	1	Freshwater drum[8]	Gulf of Mexico

[1]Percidae: *Ammocrypta, Etheostoma, Percina*; [2]Cyprinidae: e.g. *Cyprinella, Erimystax, Nocomis, Notropis*; [3]Centrachidae: *Micropterus*; [4]Ictaluridae: *Noturus*; [5]Percidae: *Sander canadensis*; [6]Ictaluridae: *Ictalurus, Pylodictis olivaris*; [7]Centrachidae: *Lepomis, Micropterus*; [8]Sciaenidae: *Aplodinotus grunniens*.

endemic to the Cumberland and Tennessee River systems. In less than 15 years, a series of temporally successive impacts to these streams from coal mining and oil extraction resulted in the near total loss of the mussel fauna from both streams, including some of the largest remaining populations of *Pegias fabula, Pleurobema oviforme, Ptychobranchus subtentum*, and *Villosa trabalis* (Warren and Haag

2005). Because these streams are isolated by impoundments downstream, precluding recolonization from other populations, these vital free-flowing habitats are now lost as conservation refugia. Similarly, in the 1990s, free-flowing streams in Bankhead National Forest, Alabama, supported the largest and most intact example of an upland mussel fauna endemic to the Mobile Basin, including the largest remaining populations of *Hamiota perovalis*, *Pleurobema furvum*, and *Ptychobranchus greeni*. In 2000 a record drought resulted in a reduction of mussel abundance in these streams by as much as 80% (Haag and Warren 2008). Although all species survived the drought, these populations are isolated by a large reservoir downstream, and the post-drought abundance of some may now be too low for natural recovery.

Even for species considered relatively common today, their current distribution may create an illusion of future security. *Elliptio arca* remains widely distributed in the Mobile Basin, but only one large population exists, in the Sipsey River, Alabama (Haag 2004c). Loss of the Sipsey River population from either a natural or human-caused event would suddenly leave this species represented by only by a handful of small, widely scattered populations and thus highly vulnerable to extinction. Similarly, after the decline of *Ptychobranchus subtentum* in the Little South Fork of the Cumberland River (see above), this species now remains abundant only in the Clinch River, Tennessee and Virginia, even though a number of other, small populations persist. This type of distribution is now characteristic of a large number of North American species, portending that the list of critically imperiled species will increase in the future.

Unlike the first wave of extinctions, the second extinction wave will not be limited to obligate large-river species or species with specific life-history traits, such as host-fish use, but will encompass a wide range of mussel diversity. Less than half of critically imperiled species are obligate large-river species; critically imperiled mussels include species restricted to headwater streams as well as species formerly widespread in a range of stream sizes and habitats. Collectively, these critically imperiled species use a wide range of host fishes and, unlike species extirpated from large rivers by impoundment, only about half of these species use darters or riverine minnows as hosts (Table 5.5). Extinction risk in isolated tributary streams will mostly be a function of initial post-fragmentation population size and the extent and connectivity of remaining habitat that is occupied by a particular species (e.g. Loehle and Li 1996; Hanski and Ovoskainen 2002). In tributary streams that experienced mussel declines due to either natural or human-caused impacts, all species were affected non-selectively and the probability of persistence was primarily a function of predisturbance population size rather than interspecific differences in tolerance to disturbance (Warren and Haag 2005; Haag and Warren 2008). Isolated tributary streams can therefore be viewed as having a temporary excess of rare species which will be lost as the communities pay their extinction debt and reach a new equilibrium corresponding to the extent of habitat remaining after fragmentation.

With the exception of a small group of species that thrive in disturbed habitats (e.g. *Anodonta suborbiculata*, *Ligumia subrostrata*, *Pyganodon grandis*, *Toxolasma parvus*, *Utterbackia imbecillis*), mussel species that now have the greatest chance of long-term survival are large-river species that have adapted to run-of-the-river conditions present in some impounded streams. Because of the high volume and large catchments of these rivers, large-river habitats are less sensitive to single point-source impacts or natural disturbances than smaller streams (Petts 1994). Further, widespread construction of navigation dams on large rivers in the central and south-eastern USA created thousands of kilometres of contiguous habitat for impoundment-tolerant species. Unlike populations in isolated tributary streams, populations in impounded riverine habitats can recover from periodic local extinctions or declines due to the potential for recolonization from other populations.

In today's landscape, long-term survival of species in isolated streams is probable only for those having populations large enough, both in size and geographic extent, to allow them to weather periodic natural disturbances and an ever-increasing array of human impacts. The establishment of additional populations of a species in parts of its historical range that have recovered from past

insults can greatly reduce the risk of extinction. Short-term survival of some species can potentially be prolonged by intensive captive propagation and stocking programmes. However, in addition to the risks of artificial selection and other genetic hazards (e.g. Jones *et al.* 2006b) the major disadvantage of stocking as a method of sustaining small, isolated populations is the necessity of continuing these programmes in perpetuity given the continued isolation of these populations. In the long run, the extinction debt for North American freshwater mussels can be reduced while minimizing additional species losses only by increasing the extent and connectivity of suitable habitat.

Summary

The world's most diverse freshwater mussel fauna is currently experiencing a massive extinction event. In the last 100 years, at least 26 but potentially more than 40 taxa have gone extinct. An exact accounting of extinctions is impossible due to irresolvable taxonomic problems with several described species that are morphologically similar or were known historically by only a small number of specimens; most of these problematic taxa have not been seen in over 50 years. An accounting of extinctions is also hampered by the difficulty of concluding with certainty that rare species have slipped into extinction. Within the last 15 years, at least one taxon previously considered extinct (*Epioblasma obliquata obliquata*; see Neves *et al.* 1997; Turgeon *et al.* 1998) has been rediscovered, albeit in a small, isolated population (Hoggarth *et al.* 1995). Despite these uncertainties, the severity of this extinction event is clear. Most extinct species were morphologically distinctive (see Fig. 5.1) and specimens are well represented in historical collections as well as in prehistoric middens. Furthermore, mussel research efforts have increased nearly 10-fold since the 1970s (Strayer *et al.* 2004) and in the vast majority of cases intensive survey efforts have corroborated the apparent extinction of species. At least 31 surviving species are in imminent danger of extinction, and a large number of others are highly vulnerable to extinction in the long term. In total, it is likely that 25% or more of the North American mussel fauna will be extinct within a human generation.

Most recent extinctions have occurred in the region of highest mussel diversity, especially the Ohio (including the Cumberland and Tennessee systems) and Mobile River basins (Table 5.3). Similarly, critically imperiled species (i.e. species surviving as only one or two populations) are concentrated in these systems but also occur predominantly in other Gulf of Mexico drainages (e.g. Apalachicola, Escambia, Rio Grande; Table 5.5). There are currently no known species extinctions or critically imperiled species (as defined here) in the Pacific Northwest or the upper Mississippi River basin and few in the lower Mississippi River basin, Great Lakes, or Atlantic coast drainages, even though all of these areas have experienced extensive habitat loss and fragmentation, and widespread declines in mussel abundance. The low rate of extinction in these areas can be explained by three factors: (1) lower initial diversity (e.g. Pacific Northwest, northern Atlantic coast drainages), (2) no species restricted to a single habitat type (e.g. large rivers) that has been systematically destroyed, and (3) few species with highly restricted ranges (e.g. upper Mississippi River basin). However, estimates of rates of extinction or imperilment may be artificially low for some regions due to the presence of unrecognized cryptic diversity, especially within the genus *Elliptio* in southern Atlantic coast drainages. In all regions, imperilment can be expected to increase as human impacts continue to accelerate, exacerbating effects of habitat fragmentation and population isolation.

Although a small number of species may have gone extinct naturally, most mussel extinctions are a result of human impacts. Humans have exerted substantial pressures on mussel populations for over 5000 years. However, human impacts from pre-Columbian times until the early twentieth century, including intense harvest and degradation of stream habitat, resulted in no documented species extinctions despite a remarkably complete record of mussel distribution and abundance throughout this lengthy time period. The first wave of mussel extinctions occurred rapidly in the mid-twentieth century in response to large-scale, systematic destruction of large river habitat by the construction of dams and was composed mostly of species that were

restricted to this specialized habitat. In the late twentieth century a second, as yet smaller wave of extinctions followed due to a variety of proximal causes but ultimately related to indirect effects of habitat fragmentation caused by habitat destruction earlier in the century. As a result of the time lag associated with the manifestation of these indirect effects, habitat fragmentation has created a large extinction debt, the payment of which has only begun. Over time, this second extinction wave due to indirect effects of fragmentation can be expected to eclipse the first wave due to direct habitat destruction. In contrast to the first extinction wave, the second wave will not be limited to species with specific ecological attributes; rather, probability of extinction will be primarily a function of each species' initial post-fragmentation population size and the extent and connectivity of its remaining habitat, ultimately resulting in extinction of a broad cross-section of freshwater mussel diversity. Although the wide variety of impacts associated with an increasing human population would have probably caused at least some extinctions even if stream systems had retained connectivity, the legacy of fragmentation due to stream impoundment has underpinned and magnified all other insults to streams and has greatly intensified the current freshwater mussel extinction crisis in North America.

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