PERSPECTIVES

Exploitation trajectory of a declining fauna: a century of freshwater mussel fisheries in North America

James L. Anthony and John A. Downing

Abstract: Freshwater mussels (Bivalvia: Unionidae) have been an economically valuable biological resource in North America since the mid-1800s. Although the industries based upon mussel harvest are quite distinct from one another, the trends apparent in harvest statistics are remarkably similar among each successive harvest era. Whether fished for freshwater pearls, button production, or cultured pearl production, market factors have driven commercial harvests while the life history and ecology of mussels have been largely ignored. Annual yields of freshwater mussels are declining throughout the United States and catch per unit effort (CPUE) has declined dramatically in some of the most important American mussel fisheries. Harvest statistics indicate that mussel populations are dangerously depleted due to the erosion of the latest industry based upon their harvest. It seems likely that the exhaustive harvests of both the distant and recent past, coupled with habitat loss and degradation, have left North American unionid mussel populations at levels insufficient to support the substantial harvests consistently demanded by industry. This century-long exploitation trajectory provides valuable lessons about the mechanisms of fisheries collapse that are necessary to ensure the sustainable management of aquatic resources.

Résumé : Les moules d'eau douce (Bivalvia: Unionidae) constituent une ressource biologique d'importance économique considérable en Amérique du nord depuis le milieu du 19e siècle. Bien que les diverses industries basées sur la récolte des moules soient différentes les unes des autres, les tendances dans les statistiques de récolte sont remarquablement semblables au cours des différentes périodes de récolte qui se sont succédées au cours du temps. Que les récoltes aient été faites pour la collecte de perles d'eau douce, la fabrication de boutons, ou la production de perles cultivées, les forces du marché ont contrôlé les récoltes commerciales, alors que le cycle biologique et l'écologie n'ont pas été en grande mesure pris en compte. Les rendements annuels de moules d'eau douce décroissent partout aux États-Unis et les captures par unité d'effort (CPUE) ont décliné de façon spectaculaire dans quelques-uns des plus importants sites américains de récolte de moules. Les statistiques des récoltes indiquent que les populations de moules sont dangereusement hypothéquées au moment où l'industrie la plus récente basée sur les moules est en train de s'effriter. Il semble probable que les récoltes exhaustives du passé lointain et du passé plus récent, combinées à la perte et la dégradation des habitats, ont laissé les population nord-américaines de moules unionidés à des densités qui ne permettent plus les récoltes intensives requises par l'industrie. L'histoire de cette exploitation centenaire fournit des enseignements précieux sur les mécanismes d'effondrement des pêches, renseignements qui sont indispensables pour mettre sur pied une gestion durable des ressources aquatiques.

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Introduction

North American freshwater mussels (Bivalvia: Unionidae) are valuable components of freshwater biodiversity. Through their suspension feeding, these slow-growing long-lived organisms (Anthony et al. 2001) may influence phytoplankton ecology (Daukas et al. 1981), water quality, and nutrient cycling (Nalepa et al. 1991). Mussels may also constitute a significant proportion of the freshwater macrobenthic biomass (e.g., Negus 1966) and their obligate parasitic larvae can impact fish mortality (Matteson 1948).

Historically, the importance of freshwater mussels has not been solely ecological, however. Although mussels may have provided a valuable supplemental food source to indigenous peoples for centuries prior to European settlement (Parmalee and Bogan 1998), large-scale commercial interest in these freshwater bivalves did not develop until the freshwater pearl rushes of the mid-1800s (Kunz 1893; Claassen 1994). Soon

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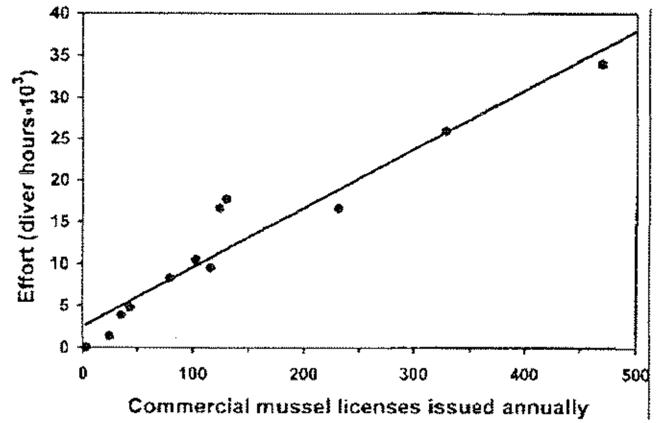
thereafter, many freshwater mussel species were extensively harvested for the production of pearl buttons, and presently, the shells of freshwater mussels, which are ground into spherical nuclei, are the foundation of the multi-million dollar Asian cultured-pearl industry (Thiel and Fritz 1993; Claassen 1994; Fassler 1994).

Despite their ecological and economic importance, the nearly 300 North American unionid mussel species are apparently one of the most rapidly declining components of freshwater biodiversity with nearly 72% of the North American species considered extinct, endangered, threatened, or species of special concern (Williams et al. 1993). The rapid decline of many unionid mussel species has been attributed to commercial exploitation, water quality degradation, impoundment, habitat destruction, exotic species introduction, and watershed alteration (Williams et al. 1993). These substantial declines in unionid mussels will likely have serious implications for both North American freshwater ecology and biodiversity, as well as for mussel fisheries.

Although several attempts to examine United States mussel fisheries have incorporated investigation of short periods of the mussel exploitation trajectory, synoptic examination of a broad time frame is necessary to adequately portray more than a century of extensive harvests. For example, Thiel and Fritz (1993) briefly summarize historic mussel harvests in the Upper Mississippi River, but consider primarily recent harvests and regulations enacted since the 1980s. Similarly, Fassler (1994) provides an extensive synopsis of the market factors that gave rise to and continue to drive the relatively recent cultured-pearl industry. Although Claassen (1994) provides a valuable comprehensive examination of historic and recent mussel industries of the U.S. Mississippi River basin as well as a colorful account of those involved, the focus is primarily upon the social implications of mussel harvest and industry trends rather than the biological ramifications of exhaustive mussel harvest. Several statewide harvest reports also have been published, but most are largely limited to recent mussel harvests or to very localized harvest sites (e.g., Anderson et al. 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998). Some historical overviews of U.S. mussel harvests also discuss harvest yields and their values without normalizing monetary estimates (e.g., Thiel and Fritz 1993; Claassen 1994), making it difficult to evaluate the market factors driving historic mussel fisheries. Most also fail to adhere to the use of the Latin nomenclature of commercially exploited mussel species (e.g., Carlander 1954; Claassen 1994), thereby increasing the difficulty of examining the species-level impacts of mussel harvests.

An understanding of the historical markets and fisheries for freshwater mussels is critical for evaluating the potential effects of future harvests in the U.S. More broadly, however, such an assessment may serve as an important model for other species. This historical perspective goes beyond previously published efforts by providing an overview spanning all phases of exploitation and integrating both catch statistics and economic forces. Furthermore, we include compilations and analyses of long-term time trends in mussel catch statistics that have not been attempted elsewhere. This assessment of historic U.S. mussel fisheries not only provides the holistic view necessary to discern the potential role of harvest on population viability in exploited species, but may also augment our understanding of mussel ecology through a more complete and accurate knowledge of the patterns of commercial harvest that have shaped the present condition of populations.

Fig. 1. Effort (diver hours), 1987–1998, is strongly positively correlated with the number of commercial licenses issued in the state of Iowa's Mississippi River freshwater mussel fishery (r^2 = 0.92). Data are from the Iowa Department of Natural Resources.[2]



Methods

We examined historic and recent commercial harvest statistics compiled by U.S. federal agencies (U.S. Bureau of Fisheries, U.S. Fish and Wildlife Service, U.S. National Marine Fisheries Service) and from various state agencies (e.g., Indiana Department of Natural Resources, Iowa Department of Natural Resources, Kentucky Department of Fish and Wildlife Resources, Missouri Department of Conservation, Wisconsin Department of Natural Resources). Annual estimates of commercial mussel yields, as well as their values, were examined in the context of market trends and regulatory legislation allowing us to attribute probable causation (i.e., market influences vs. mussel population trends) to the many rapid fluctuations evident in annual harvest levels.

Throughout this analysis, it is important to appreciate that mussel catch statistics are generally based only upon those animals actually utilized for button or pearl production and often do not reflect the significant unmarketable by-catch of the actual harvest (Anderson et al. 1993; Claassen 1994). In addition, commercial license holders in many states (e.g., Iowa, Indiana, Tennessee) have only recently been legally obligated to report their yields to state agencies (Anderson et al. 1993; Todd 1993; Gritters and Aulwes 1998). Many estimates of annual harvest are therefore based upon the report of only a limited proportion of the actual mussel harvest and are therefore substantial underestimates of that actually harvested. Where the proportion of reporting license holders is known, however, we have extrapolated harvest levels in an attempt to correct for the unreported proportion of the harvest. All historic nomenclature has been revised to reflect presently accepted unionid taxonomy following Parmalee and Bogan (1998).

Estimates of catch per unit effort (CPUE) are rare in the commercial mussel fishery statistics. Alternatively, commercial licensing numbers are more readily available. We have therefore attempted to use yield-per-license as a surrogate of CPUE where CPUE data

[2] S. Gritters, Iowa Department of Natural Resources, Guttenburg Fisheries Office, 331 S. River Park Dr., Guttenburg, IA 52052, U.S.A., unpublished data.

do not exist. In the state of Iowa, where both effort (diver hours) and license data from 1987 to 1998 have been recorded (Gritters and Aulwes 1998), we have observed that effort is strongly correlated with the number of commercial licenses issued (r^2 = 0.92) (Fig. 1). It therefore seems probable that yield per license is a valid surrogate of CPUE from the present, back through at least the mid-1980s. It is unknown to what degree the strong correlation between diver effort and license numbers may be extended to other methods of taking mussels including brailing and dredging. For this reason, where yield per license data from other states are used as a surrogate of CPUE, the results are interpreted with caution.

All monetary estimates provided here are normalized to reflect the 1998 value of the U.S. dollar. This allows us to accurately compare monetary values of industries and yields at any point during the nearly 150-year history of extensive commercial mussel harvest. Failure to do so could lead to an erroneous representation of the market factors driving commercial mussel harvest, and to underestimation of the true magnitude of the economic value of early harvests.

Results and discussion

Freshwater pearl era: 1850–1900: development and history of the industry

The freshwater pearls created by unionid mussels were esteemed by North American aboriginal cultures long before the arrival of the first Europeans to this continent (Kunz 1893; Ward 1985). Likewise, the first extensive North American mussel harvests of the 19th century were fueled by an increasing demand for these freshwater counterparts of the already popular marine pearls (Kunz 1893). Despite the existence of few statistics for these early harvests, these pearl rushes are important in both historical and ecological contexts. Although often ignored, profits from early pearl rushes, such as those in New Jersey (1857), Iowa (1860), and Arkansas (1897) (Kunz 1893), surpassed those of several important U.S. industries including mining and petroleum production (Claassen 1994).

Historical mussel harvests for freshwater pearls were governed largely by boom-and-bust trends. Large-scale migrations of pearl prospectors often followed the discovery of pearls. For example, the discovery of a 93-grain (4.65 g) freshwater pearl from Notch Brook near Patterson, N.J., and its subsequent sale for over $60 000 (1998 $U.S.), fueled the exhaustion of mussel beds in Notch Brook and other nearby streams (Kunz 1893). In the years that followed, valuable freshwater pearls from throughout the U.S. were sold in domestic and international markets (Kunz 1893; Shira 1913; Wilson and Danglade 1914).

By 1860, pearlers were extensively harvesting freshwater mussels for pearls in Arkansas, Florida, Iowa, Kentucky, Nebraska, New Jersey, Ohio, Tennessee, Texas, Vermont, Washington, and Wisconsin (Kunz 1893; Claassen 1994). Just as in Notch Brook, all sizes and species of mussels in a stream were quickly harvested until both the supply of pearls and the populations of mussels were exhausted. These unsustainable harvests usually resulted in the search for previously "idle" streams in which the same exhaustive practices were repeated (Kunz 1893; Coker 1914). Although virtually all mussel species were exploited, some were especially renowned for their pearls (Table 1); consequently, they bore the brunt of these early harvests (Kunz 1893).

Table 1. During the mid- to late 1800s, 13 freshwater mussel species, listed here with their pre-1900 Latin nomenclature (Kunz 1893), were renowned for their pearls and became some of the most actively sought species of the 19th century pearl rushes. All Latin nomenclature was revised to reflect presently accepted unionid taxonomy following Parmalee and Bogan (1998).

Present nomenclature	Historic nomenclature
Amblema plicata	*Unio costatus*
Elliptio complanata	*Unio complanatus*
Fusconaia flava	*Unio globus*
Lampsilis abrupta	*Unio orbiculatus*
Lampsilis ovata	*Unio ovata*
Leptodea fragilis	*Unio fragilis*; *Unio gracilis*
Megalonaias nervosa	*Unio undulatus*
Obovaria retusa	*Unio torsus*
Quadrula metanevra	*Unio nodosus*
Quadrula pustulosa	*Unio mortoni*
Unknown	*Unio buddianus*
Unknown	*Unio ellioti*
Unknown	*Unio virginianus*

Even disregarding their exhaustive nature, harvests for freshwater pearls were hardly efficient. Often, not a single pearl in thousands of mussels was discovered. Shira (1913) reported that, of 793 392 individual mussels harvested in Texas, only 53 actually contained pearls. Even worse, relatively few pearls were of marketable quality (Kunz 1893). Owing in part to their limited numbers, however, the value of freshwater pearls surpassed that of marine pearls by 1889 and the already exhaustive harvests intensified (Kunz 1893).

Despite the widespread sentiment that mussel stocks were inexhaustible, the industry was declining and few pearlers remained in states that had previously led the nation in freshwater pearl harvests (e.g., Vermont, New Jersey, Ohio) (Kunz 1893). Marketable pearls had become relatively rare by the onset of the 20th century, although pearling was still important in some locations. As late as 1889, extensive pearling was noted on Wisconsin's Pecatonia and Apple rivers. Harvests of freshwater pearls on Illinois' Mackinaw River remained high as late as 1890 as did those on Iowa's Wolf Creek. Some remaining harvests exclusively for freshwater pearls were also noted as late as 1913 in Louisiana and Texas (Shira 1913) while others continued through 1914 in South Dakota (Coker and Southall 1915), Missouri and Arkansas (Utterback 1914), and Minnesota (Wilson and Danglade 1914).

Some of these remaining harvests were substantial. Pearls gathered in Caddo Lake and its tributaries in Louisiana and Texas were valued at over $1 600 000 (1998 $U.S.) in 1912, during what was even considered a relatively poor season (Shira 1913). By 1919, although mussels were harvested primarily for the production of buttons, freshwater pearls obtained as byproducts of the mussel catch were valued at $3 468 783 (1998 $U.S.), nearly half the value of the shells themselves (Smith 1919). As late as 1921, revenue from the sale of pearls composed up to one third of the average musseler's annual income (Roberts 1921). Substantial pearl harvests such as these became relatively rare, however, and harvests solely for freshwater pearls slowly vanished.

Conservation during the freshwater pearl era

Not long after the onset of the first extensive mussel harvests, some fishery biologists and malacologists were growing concerned. George Kunz (1893), in a presentation to the American Fisheries Society, called the inefficient, exhaustive harvests of North American mussels "the wholesale destruction" of the resource. Kunz, commenting on less intrusive and nonlethal European methods of freshwater pearl extraction, considered the exhaustive harvests of North American mussels unnecessary and irresponsible and he became one of the first to suggest that protective legislation should be enacted to preserve the mussel resource. J.W. Collins (1893), in a letter to the American Fisheries Society, echoed Kunz's concerns, adding that "no state can afford to neglect legislation on a subject more important". These regards were widely ignored, however, and nearly complete exhaustion characterized the remaining freshwater pearl harvests (Fassler 1994).

The pearl button industry: 1890–1960: development and history of the industry

Prior to the mid 1850s, Americans were reliant upon imports to satisfy their demand for mother of pearl buttons. By 1855, however, American manufacturers had begun to produce buttons from the shells of marine mollusks (Josephsson 1909), although there is published evidence of failed attempts to commercially produce buttons from the shells of freshwater mussels in 1802 in Kentucky (Coker 1919) and in the late 1880s in Tennessee and Illinois (Coker 1919; footnote 3). It was not until the arrival of Johann Frederic Böpple, a German immigrant and button manufacturer, however, that North American freshwater mussels would prove commercially viable in the button trade.

Johann Böpple brought the button industry to the banks of the Mississippi River in Muscatine, Iowa in the late 1880s. In 1886, prior to his arrival in the U.S., Böpple had examined shells from Illinois, principally *Amblema plicata* (formerly *Quadrula undulata*) and *Actinonaias ligamentina* (formerly *Lampsilis ligamentinus*), and concluded that the high-quality North American freshwater mussel shells were suitable for button production. He promptly sold his Ottensen, Germany, button manufacturing business (which generally utilized marine shells, ivory, bone, and buffalo horn) and headed for the U.S. Upon his arrival, Böpple first studied mussel shells from the Sangamon and Rock Rivers of Illinois but was dissatisfied with their quality. With subsequent experimentation on shells of *Lampsilis teres* (formerly *Lampsilis anodontoides*; *Lampsilis fallaciosus*) from the Mississippi River, near Muscatine, Iowa, and *Tritogonia verrucosa* (formerly *Tritogonia tuberculata*) from the Iowa River near Columbus Junction, Iowa, however, Böpple perfected the technology and procedures for producing buttons from freshwater shells.[3]

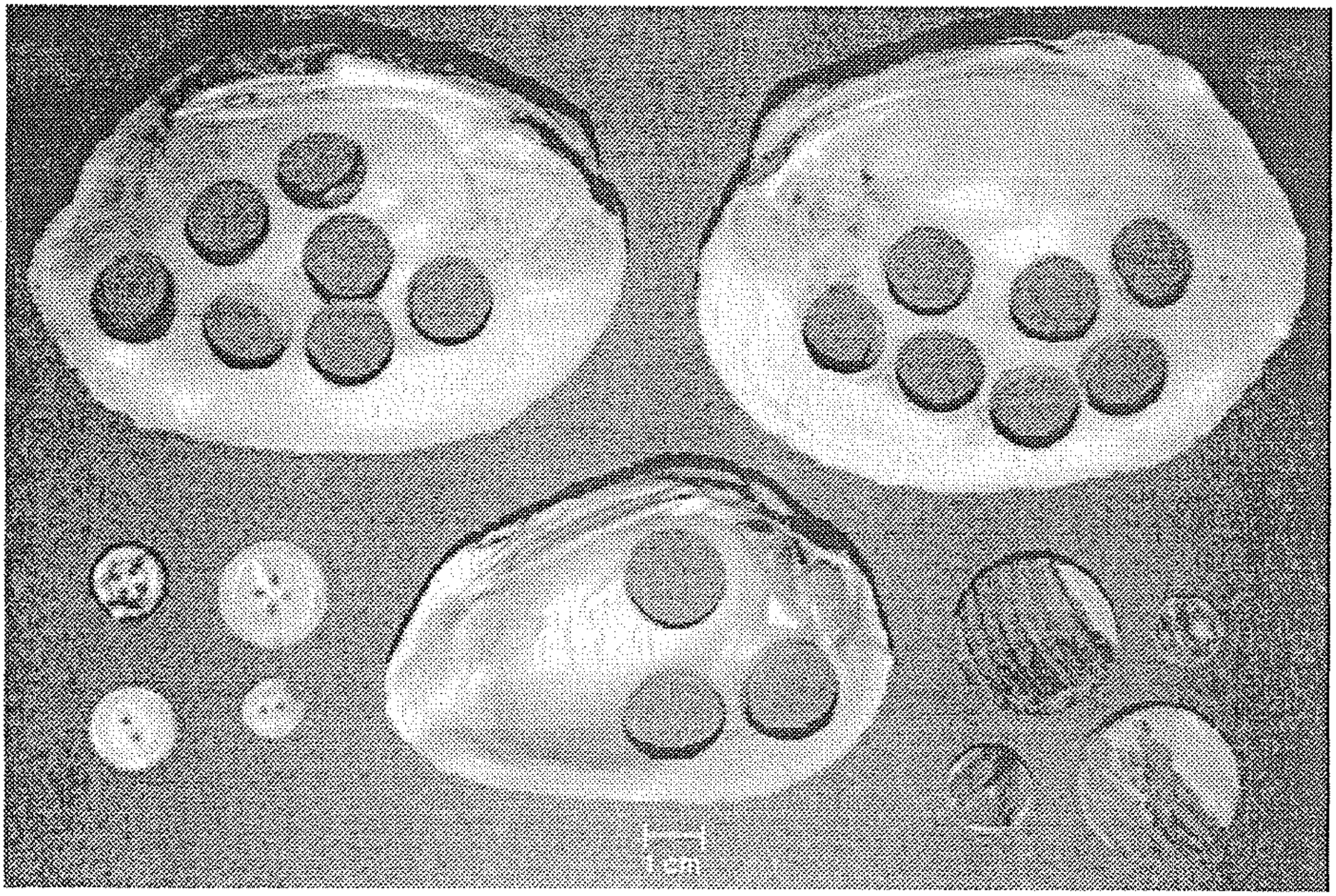
Imported buttons and marine shell material were inexpensive and available in large quantities, stifling Böpple's attempts to market his product. The McKinley Tariff of 1890, however, substantially increased the prices of these imported goods and created the opportunity necessary to establish freshwater mussel shells as the staple material source of the American button industry (Smith 1899; footnote 3). By 1892, Böpple had begun large-scale production of his freshwater pearl buttons. These buttons (Fig. 2) could be made inexpensively and in large quantities, effectively out-competing the higher priced imports (footnote 3; see also Coker 1919).

Capitalization of the button industry on the shores of the Mississippi River was rapid. By 1899, the seven-year-old industry was valued at over $23 000 000 (1998 $U.S.) (Anonymous 1902) and, 10 years later, the value of the unprocessed shell alone exceeded $7 000 000 (1998 $U.S.) (Coker 1919). Sixty button factories were located in the Mississippi River Valley by 1899, and one year later, 10 more had begun production (Anonymous 1902). Less than 10 years after its inception, the industry supported thousands of workers and played a crucial role in the economies of many river towns (Anonymous 1902). Despite some early failures of inexperienced manufacturers, the pearl button industry continued to grow.[3] Buttons produced using freshwater shells composed nearly 50% of the American button product by 1900 (Josephsson 1909), and by 1905, over two thirds of the mother of pearl buttons produced in the U.S. were made from freshwater mussels (Anonymous 1909). In the latter year, over 100 button factories specializing in freshwater mussel shells were operating in the U.S. (Anonymous 1909). In 1916, the industry's peak production year, the U.S. produced over 5.75 billion buttons valued at over $175 000 000 (1998 $U.S.) (Claassen 1994). The industry remained productive until around 1925 when it began to decline in both output and value (Fig. 3) as labor issues in years prior to the Great Depression and competition with new foreign markets began to take their toll (Claassen 1994).

Japanese button manufacturers entered the American button market by 1907 (Anonymous 1909) and intense competition with these foreign producers quickly led to declines in both production and profit for the American industry (Fig. 3). With cheap available labor, the Japanese producers remained competitive (Anonymous 1909; Roberts 1921) and American manufacturers focused increasingly on the production of only high-grade buttons. The near abandonment of low-grade button production would have forced American manufacturers to cut fewer blanks per shell to avoid the cracked or damaged blanks useful only for low-grade buttons (Claassen 1994). Furthermore, as large mussels grew scarce, fewer high-quality blanks could be produced from remaining smaller individuals. Even though output of buttons per se was declining, this implies that larger harvests were necessary simply to maintain a viable industry. For example, Coker (1914) noted that 900 kg of 10-cm *Fusconaia ebena* shells required around 3200 mussels. Alternatively, 900 kg of 5-cm shells required over 20 000 individuals. Therefore, as beds became depleted of larger mussels in the early 20th century, substantially more individual mussels were necessary to sustain the same level of button production and the rate of depletion was accelerated (Coker 1914). Although competition and overexploitation had apparently taken a heavy toll on the industry, many continue to attribute the rising prevalence of inexpen-

[3] J.F. Böpple, Fairport Biological Station (presently Fairport Fish Hatchery), Iowa Department of Natural Resources and United States Fish and Wildlife Service, United States Bureau of Fisheries, Fairport, Iowa, U.S.A., unpublished data.

Fig. 2. Round blanks cut from the shells of freshwater mussels were polished into buttons between 1891 and the mid-1960s. Photo by J.L. Anthony.



sive plastic buttons through the 1940s to the degradation and eventual demise of the pearl button industry by the mid-1960s (e.g., Claassen 1994; Fassler 1994; Neves 1999).

Mussel harvests and conservation during the pearl button era

The rapid capitalization of the button industry prompted an equally rapid expansion of the freshwater mussel fishery, which began near the first button factories at Muscatine, Iowa (Coker 1914). In 1897, soon after the onset of button production, 3180 tonnes (t) of shells were harvested from the Mississippi River in the immediate vicinity of Muscatine. The following year, 3306 t were harvested, and by 1899 harvests in the same area yielded 21 628 t of mussel shells (Anonymous 1902). These fisheries were lucrative ventures for the thousands they employed and musseler's camps lined the shores of many U.S. streams and rivers (Fig. 4). By 1922, the freshwater mussel fishery was considered one of the largest and most profitable inland fisheries in the U.S. (Rich 1927).

Harvests of freshwater mussels increased to keep pace with the demands of the rapidly growing button industry. In the Peoria Lake stretch of the Illinois River, Ill., two fishermen could expect to harvest over 1.6 t of mussels per day in 1912. In the same river, 27 t and 45 t of shells had been taken at Havana and Bath, Ill., respectively, in preceding years (Danglade 1912). In 1910, musselers at Keokuk, Iowa removed nearly 1500 t of shells from a 6–8 km stretch of the Mississippi River (Coker 1919), and Roberts (1921) noted

Fig. 3. The U.S. pearl button industry's output in billions of buttons per year (●) and value of the button output as millions of 1998 $U.S. (◇) from 1897 through 1958. The gray (output) and black (value) lines are smooth fits of the market trends of output and value, respectively. Data follow Claassen (1994).

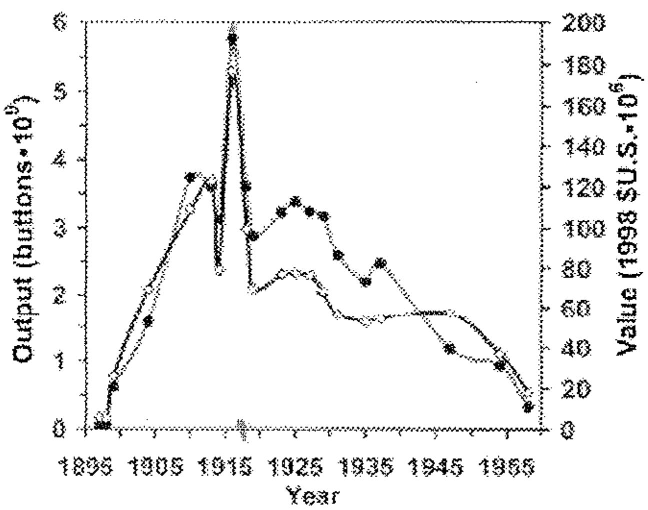
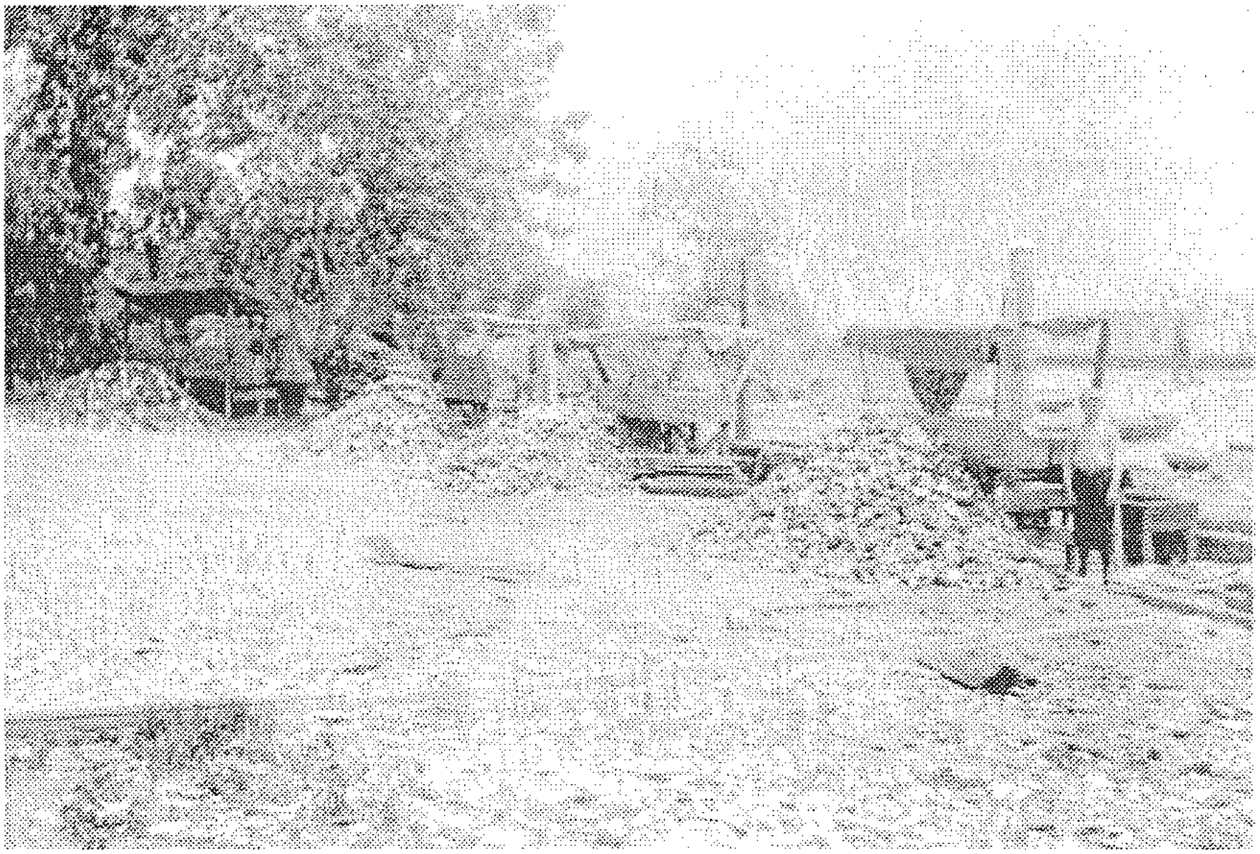


Fig. 4. Mussel camps and cookout stations lined many U.S. streams in the early 1900s. Note the piles of shell and numerous culled shells lining the banks of the river. A floating cutting station in a white houseboat is visible in the background. Photo from an unspecified location, probably the Illinois River, Ill., in the early 1900s. Photo courtesy of the Peoria Historical Society Collection, Bradley University Library, Peoria, Ill.



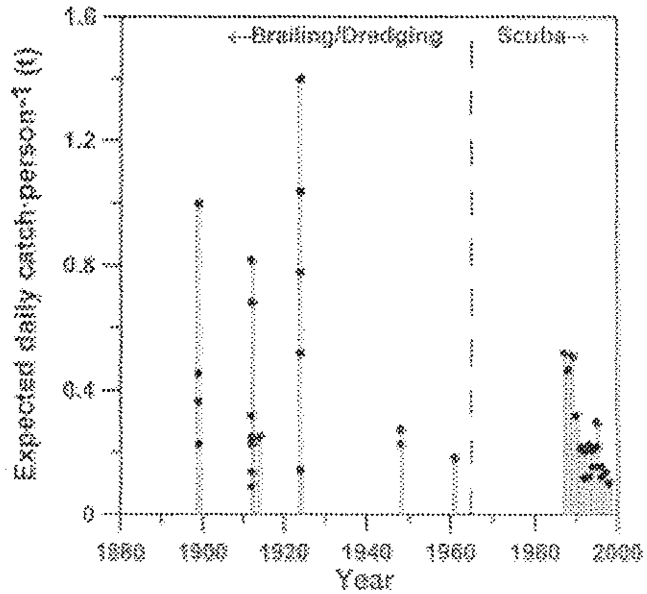
that mechanical dredges were capable of harvesting over 9 t of shells daily. Other historical anecdotes suggest that, despite their exhaustive nature, these impressive rates of harvest were not uncommon (Fig. 5).

Musselers often concentrated their exhaustive efforts on small, dense beds of mussels. For example, in 1896, Mississippi River musselers harvested over 450 t of mussels from a bed with an area of just over 1 km^2. This represents harvests of 0.45 $kg \cdot m^{-2}$. Similarly, over 9000 t (12 $kg \cdot m^{-2}$) of shells were taken between 1894 and 1897 from a single bed with an area of less than 0.75 km^2 near New Boston, Ill. (Smith 1898). Smith (1898) estimated that the New Boston catch was composed of over 100 million animals. The exhaustion of relatively small, compact beds was noted after 1900 as well. In 1914, a single harvester removed over 2.7 t of mussels from a bed only tens of meters in length at the outlet of Lake Bemidji, Minn. (Wilson and Danglade 1914). Coker and Southall (1915) noted that a four-person crew had harvested 2.7 t of shell in only three hours from the James River near Milltown, S. Dak.

It was not long before mussel populations throughout the Mississippi River Basin were showing classical signs of overexploitation. Near the onset of exploitation, only the largest and highest quality specimens of the commercial species were marketable (Coker 1914) and many undersized or noncommercial species were likely killed as by-catch (Wilson and Danglade 1914; Coker 1919). Excessive incidental catch of noncommercial or unmarketable individuals may intensify overexploitation, however (Dasgupta 1982). Gradually, economic forces rendered smaller individuals more marketable, prompting the harvest of progressively smaller mussels until beds were nearly exhausted. Even juvenile mussels (<1.25 cm) were often taken to increase the appraised harvest weight, but were simply discarded at the production line (Coker 1914), and it became common for shells <5 cm in length to compose up to 60% of the total catch (Coker 1914, 1919). This classical impact of intense harvest pressure on exploited populations, known as growth overfishing, may result in declining harvest weight and declining average sizes near to or below age at first reproduction (Gulland 1983). It is therefore of no surprise that natural recovery of these exploited beds was rare (Coker 1919). In fact, mussel populations in Iowa's inland streams, which were subject to intense harvest pressure, have never recovered from these exhaustive harvests and are presently nearly extinct (K.E. Arbuckle and J.A. Downing, Iowa State University, Ames, Iowa, U.S.A., unpublished data).

As early as 1899, only seven years after commercial harvests began, many of the formerly dense mussel beds near the button factories at Muscatine, Iowa were depleted (Anonymous 1902). As the quantity of high-quality mussels declined, harvesters actively sought out new beds in streams in surrounding states. This stream-to-stream depletion bears striking similarities to the exhaustive harvests of the pearl rushes

Fig. 5. Anecdotal estimates of daily mussel catch·person^{-1} illustrate a variable but generally declining trend through time. Estimates are from 1899 on the Mississippi River near Muscatine, Iowa (Smith 1899); ~1900 on the Black River near Madison, Ark. (Coker 1914); 1910 on the Black River near Black Rock, Ark. (Coker 1914); 1912 from the Illinois River near Meredosia, Kampsville, Grafton, and Peoria, Ill. (Danglade 1912); 1913 on the Black River near Madison, Ark. (Coker 1914); 1913 on Cross Lake near Pine City, Minn. (Wilson and Danglade 1914); 1914 on Rice Lake, Minn. (Wilson and Danglade 1914); 1924 on Lake Pepin in Minnesota and Wisconsin; 1948 on the Grand River, Mich. (van der Schalie 1948); and 1962 on the Tennessee River, Tenn. (Claassen 1994). Data from 1987–1998 were derived from estimates of CPUE (Hubbs and Jones 1996; Gritters and Aulwes 1998) assuming a 10-h workday. While brailing and dredging were the most common harvest method during early harvests, more efficient methods of harvest (e.g., SCUBA) became dominant after the mid-1960s (Claassen 1994).



and continued until most of the Mississippi River Drainage Basin and many streams of the Great Lakes Drainage Basin were subject to intense commercial harvest pressure (Coker 1914, 1919; Smith 1919).

An escalation of mussel shell prices, due in part to the relative scarcity of high-quality material following the exhaustive harvests of the late 1890s and early 1900s (Claassen 1994), continued even as the overall value of the button industry steeply declined after 1925 (Fig. 3). Further indicative of overexploitation, this allowed musselers to return to beds previously considered depleted and made possible the harvest of others once thought to be uneconomical (Claassen 1994; Neves 1999). The declines in some commercial species led the button industry to accept species that had previously been considered of insufficient quality for button production (Claassen 1994). At least 50 mussel species, 20 of which are presently considered endangered, threatened, or species of special concern (Williams et al. 1993), came to be exploited commercially by the end of the pearl button era (Table 2). It was this shift in the diversity of exploited species that probably allowed the mussel fishery to prolong its support of the industry's demand for shells.

Despite efforts to locate new mussel stocks (e.g., Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915) and to supplement catch with previously unmarketable species, the degradation of mussel fisheries continued. In 1898, Smith noted that the formerly productive mussel beds near New Boston, Ill. (see above) had been depleted and nearly abandoned (Smith 1898). Rapid and dramatic declines in mussel yields were evident even in the most productive mussel streams. Most of the Illinois River, the most productive mussel fishery in the U.S. between 1907 and 1911, was essentially abandoned by 1912 (Coker 1914). The Wabash River was depleted and nearly abandoned by 1914 (Coker 1914). Similarly, in 1920 musselers largely abandoned mussel beds in Lake Pepin, Minn., which had yielded over 90 t of shells between 1914 and 1919 (Grier 1922). In Arkansas' Black River, individual musselers could expect to harvest over 550 kg·day^{-1} in the late 1800s. By 1914, yields of 45–90 kg·day^{-1} were more typical (Coker 1914). These dramatic declines and the apparent depletion of mussel stocks are not surprising given the low rates of recruitment and slow growth of mussels (Anthony et al. 2001) relative to the high rates of exploitation. Natural stock replacement under these intense harvests was probably negligible relative to fishing mortality.

Extinctions of some mussel species were, by 1908, considered probable in the absence of conservation efforts. Josephsson (1909) stated that "… unless something is done to protect the mussels it will not be long before the raw material for this industry will be exhausted." Biologists and fisheries managers, however, knew little about mussel life histories and growth rates (Lefevre and Curtis 1908). The Fairport Biological Station of the U.S. Bureau of Fisheries was established in Fairport, Iowa in 1909 to answer concerns about depleted mussel stocks and to fill the void in the knowledge of mussel biology (Smith 1919). This was essentially the beginning of mussel conservation in the U.S., but began years after precipitous declines in mussels had been observed (Carlander 1954).

After the establishment of the Fairport Biological Station, and in the face of continued mussel declines, calls for fishery regulations including size restrictions, limited harvest seasons, harvest closures, and rotational harvests became more frequent (e.g., Coker 1914, 1919; Smith 1919). Hugh Smith (1919), then the Commissioner of the U.S. Bureau of Fisheries, stated, "Delay in protecting such a valuable resource is unnecessary and, in the end, fatal." Some were more optimistic, however. Despite widespread stock depletion, Roberts (1921) commented, "There is no reason to fear that our manufacturers of buttons from fresh-water shells will ever lack a supply of the basic raw material."

In response to notable declines in mussel stocks throughout the U.S., Minnesota and Illinois adopted what were apparently the first protective regulations in 1914. The states of Wisconsin and Iowa adopted similar legislation including restrictions on size, means of capture, and licensing fees by 1919 (Smith 1919), while the state of Kentucky enacted its first size restrictions in 1926 (Crowell and Kinman 1993). Unfortunately, these restrictions came only after widespread stock depletion had been noted and were created without accurate knowledge of mussel life history and ecology. Techniques then used to estimate mussel age and growth rates also had no empirical basis and have recently been shown to

Table 2. At least 50 freshwater mussel species were heavily exploited during the first half of the 20th century for the production of mother of pearl buttons. Historical citations of each species' harvest, and their corresponding nomenclature, are included to unify taxonomic references from some of the most valuable documentation of historical mussel harvests.

Present nomenclature	Historical nomenclature	Source
Actinonaias ligamentina	*Lampsilis ligamentina*	Danglade 1912; Wilson and Danglade 1914; Utterback 1914; Coker 1919; Grier 1926
	Actinonaias carinata	Grier 1926
Alasmidonta marginata	*Alasmidonta marginata*	Grier 1926
Amblema plicata	*Quadrula plicata*	Danglade 1912; Wilson and Danglade 1914; Utterback 1914; Coker 1915; Coker 1919; Grier 1926
	Quadrula perplicata	Coker 1919
	Quadrula undulata	Danglade 1912; Coker and Southall 1915; Coker 1919, Grier 1926
	Amblema costata	Grier 1926
	Amblema peruviana	Grier 1926
Arcidens confragosus	*Arcidens confragosus*	Shira 1913; Coker and Southall 1915; Coker 1919; Grier 1926
Cyclonaias tuberculata	*Quadrula tuberculata*	Coker 1919; Grier 1926
	Quadrula granifera	Coker 1919
	Rotundaria granifera	Grier 1926
Cyprogenia stegaria	*Cyprogenia irrorata*	Coker 1919
Dromus dromus	*Dromus dromus*	Coker 1919
Ellipsaria lineolata	*Plagiola securis*	Utterback 1914; Coker 1919; Grier 1926
	Plagiola lineolata	Grier 1926
Elliptio crassidens	*Unio crassidens*	Coker 1919; Grier 1926
	Elliptio niger	Grier 1926
Elliptio dilatata	*Unio gibbosus*	Danglade 1912; Utterback 1914; Coker 1919; Grier 1926
	Elliptio dilatatus	Grier 1926
Fusconaia ebena	*Quadrula ebena*	Danglade 1912; Utterback 1914
	Quadrula ebenus	Coker 1915; Coker 1919; Grier 1926
	Fusconaia ebena	Grier 1926
Fusconaia flava	*Quadrula rubiginosa*	Wilson and Danglade 1914; Utterback 1914; Coker 1919
	Quadrula subrotunda	Coker 1919
	Quadrula undata	Wilson and Danglade 1914; Coker 1919; Grier 1926
	Fusconaia undata	Grier 1926
Lampsilis abrupta	*Lampsilis orbiculata*	Coker 1919
Lampsilis capax	*Lampsilis capax*	Coker 1919
Lampsilis cardium	*Lampsilis ventricosa*	Wilson and Danglade 1914; Coker and Southall 1915; Utterback 1914; Coker 1919; Grier 1926
Lampsilis fasciola	*Lampsilis multiradiata*	Coker 1919
Lampsilis higginsii	*Lampsilis higginsii*	Coker 1919; Grier 1926
Lampsilis ovata	*Lampsilis ovata*	Coker 1919
Lampsilis siliquoidea	*Lampsilis hydiana*	Coker 1915; Coker 1919
	Lampsilis luteola	Danglade 1912; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Lampsilis luteolus	Shira 1913
	Lampsilis siliquoidea	Grier 1926
Lampsilis teres	*Lampsilis anodontoides*	Danglade 1912; Shira 1913; Utterback 1914; Coker 1919; Grier 1926
	Lampsilis fallaciosa	Danglade 1912; Shira 1913; Coker and Southall 1915; Coker 1919; Grier 1926
Lasmigona complanata	*Symphynota complanata*	Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Lasmigona complanata	Grier 1926
Lasmigona costata	*Symphynota costata*	Wilson and Danglade 1914; Coker 1919; Grier 1926
	Lasmigona costata	Grier 1926
Ligumia recta	*Lampsilis recta*	Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Eurynia recta	Grier 1926
Ligumia subrostrata	*Lampsilis subrostrata*	Coker 1919; Grier 1926
	Eurynia subrostrata	Grier 1926

Table 2 (*concluded*).

Present nomenclature	Historical nomenclature	Source
Megalonaias nervosa	*Quadrula boykiniana*	Coker 1919
	Quadrula heros	Danglade 1912; Isley 1914; Utterback 1914; Coker 1919; Grier 1926
	Megalonaias heros	Coker 1915; Grier 1926
Obliquaria reflexa	*Obliquaria reflexa*	Shira 1913; Coker 1919; Grier 1926
Obovaria olivaria	*Obovaria ellipsis*	Utterback 1914; Coker 1919; Grier 1926
	Obovaria olivaria	Grier 1926
Obovaria retusa	*Obovaria retusa*	Coker 1919
Obovaria subrotunda	*Obovaria circulus*	Coker 1919
Plectomerus dombeyanus	*Quadrula trapezoides*	Coker 1919
Plethobasus cooperianus	*Quadrula cooperiana*	Coker 1919
Plethobasus cyphyus	*Pleurobema aesopus*	Grier 1926
	Pleurobema aesopus	Coker 1919
	Plethobasus cyphyus	Grier 1926
Pleurobema cordatum	*Quadrula plena*	Coker 1919
Pleurobema plenum	*Quadrula obliqua*	Coker 1919
Pleurobema rubrum	*Quadrula pyramidata*	Coker 1919
	Pleurobema pyramidatum	Grier 1926
Pleurobema sintoxia	*Quadrula coccinea*	Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919
Potamilus alatus	*Lampsilis alata*	Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Proptera alata	Grier 1926
Potamilus purpuratus	*Lampsilis purpurata*	Coker 1919
Ptychobranchus fasciolaris	*Ptychobranchus phaseolus*	Coker 1919
Quadrula cylindrica	*Quadrula cylindrica*	Coker 1919
Quadrula fragosa	*Quadrula fragosa*	Shira 1913; Coker 1919
Quadrula metanevra	*Quadrula metanevra*	Utterback 1914; Coker 1919; Grier 1926
Quadrula nodulata	*Quadrula pustulata*	Shira 1913; Coker 1919
Quadrula pustulosa	*Quadrula pustulosa*	Danglade 1912; Shira 1913; Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1915; Coker 1919; Grier 1926
Quadrula quadrula	*Quadrula nobilis*	Coker 1915
	Quadrula lachrymosa	Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Quadrula quadrula	Grier 1926
Strophitus undulatus	*Strophitus edentulus*	Wilson and Danglade 1914
Truncilla donaciformis	*Plagiola donaciformis*	Grier 1926
	Amygdalonaias donaciformis	Grier 1926
Truncilla truncata	*Plagiola elegans*	Shira 1913; Coker 1919; Grier 1926
	Amygdalonais truncata	Grier 1926
Tritogonia verrucosa	*Tritogonia tuberculata*	Shira 1913Utterback 1914; Coker 1915; Coker and Southall 1915; Coker 1919; Grier 1926
	Quadrula verrucosa	Grier 1926
Villosa iris	*Lampsilis iris*	Coker 1919

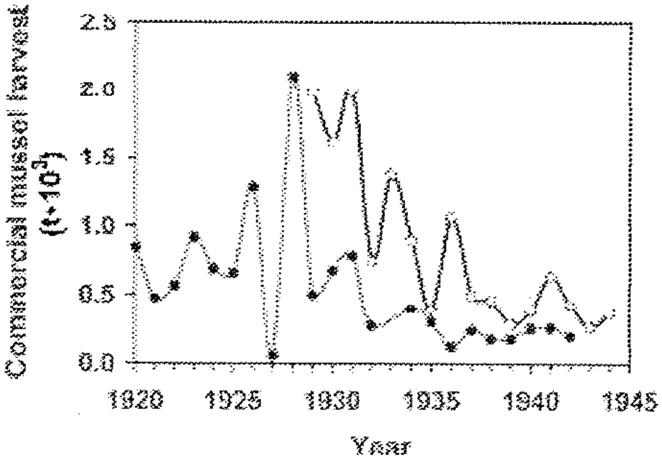
Note: Historic nomenclature was revised to reflect presently accepted unionid taxonomy following Parmalee and Bogan (1998).

provide marked underestimates of mussel age (Anthony et al. 2001). Additionally, in many states, no species-specific size restrictions were enacted for several decades. Mussel species, both large and small, were therefore considered equally productive by the early attempts at protective legislation although it is unlikely that a uniform size restriction across all harvested species would protect all species' pre-reproductive individuals.

In addition to regulatory legislation, efforts to artificially propagate and reintroduce mussels were mounted by the biologists at the Fairport Biological Station to supplement low natural recruitment (Smith 1919). Mussel sanctuaries were established where propagated juvenile mussels were introduced. Although by 1925 some recovery was noted in populations in these sanctuaries (Southall 1925; Grier 1926), it was short-lived as intensive harvests devastated the populations in the years following the end of harvest moratoria (Southall 1925).

Paradoxically, following a report in 1931 that documented commercial harvest as a primary factor involved in mussel declines (Ellis 1931), many restrictions on mussel harvests were lifted (Carlander 1954). Other factors, including the

Fig. 6. The trends in freshwater mussel yields (t) of Iowa's Mississippi River fishery (●; gray line) are shown for 1920 to 1942. The trends evident for Iowa's total freshwater mussel catch (○; black line) from 1929 to 1944) show the majority of Iowa's freshwater mussel harvests originated in the Mississippi River fishery. Data are from the Iowa Department of Natural Resources.[2]



construction of the system of navigation locks and dams now present on the Mississippi River, were expected to cause further declines in freshwater mussel populations (Ellis 1931). The U.S. Bureau of Fisheries felt it was of greater value to use up the resource before it was "inevitably" destroyed through environmental degradation (Carlander 1954). Although the removal of restrictions and the rising value of shell should have led to increased harvests, Mississippi River catch statistics from the state of Iowa show that overall, mussels remained in decline (Fig. 6). These decreased harvests even after a relaxation of harvest regulations suggest that commercial mussel stocks were so severely depleted by the early 1930s that lifting harvest restrictions could not augment yields.

Budget constraints at the U.S. Bureau of Fisheries prevented comprehensive surveys of catch statistics from the Mississippi River between 1931 and 1950 (Anderson and Peterson 1953), but statistics for states where data are relatively complete (e.g., Alabama, Arkansas, Illinois, Indiana, Iowa, Kentucky, Tennessee) allow an examination of the patterns and magnitudes of harvests within the Mississippi River Drainage Basin during this period. Although yields in all states exhibit an overall decline through time, the substantial magnitudes and variable nature of harvests are apparent (Fig. 7*a*, 7*b*). Most available catch data are, however, for years following the most extensive mussel harvests and are, in fact, from the period of the button industry's slow demise (Fig. 3).

Although it seems likely, given anecdotal evidence, that mussel stocks were being rapidly depleted throughout the U.S., the correspondence of trends in mussel yields among states suggests that market factors associated with fluctuations in the button production industry's demand for shells, rather than population limitations, were important stimuli to the patterns and magnitudes of annual harvests during 1930–1959 (Fig. 7*a*, 7*b*). The ability of mussel populations to support short-term high commercial harvests despite widespread stock depletion illustrates that these historic beds must have been more extensive and densely populated than today's remnant populations.

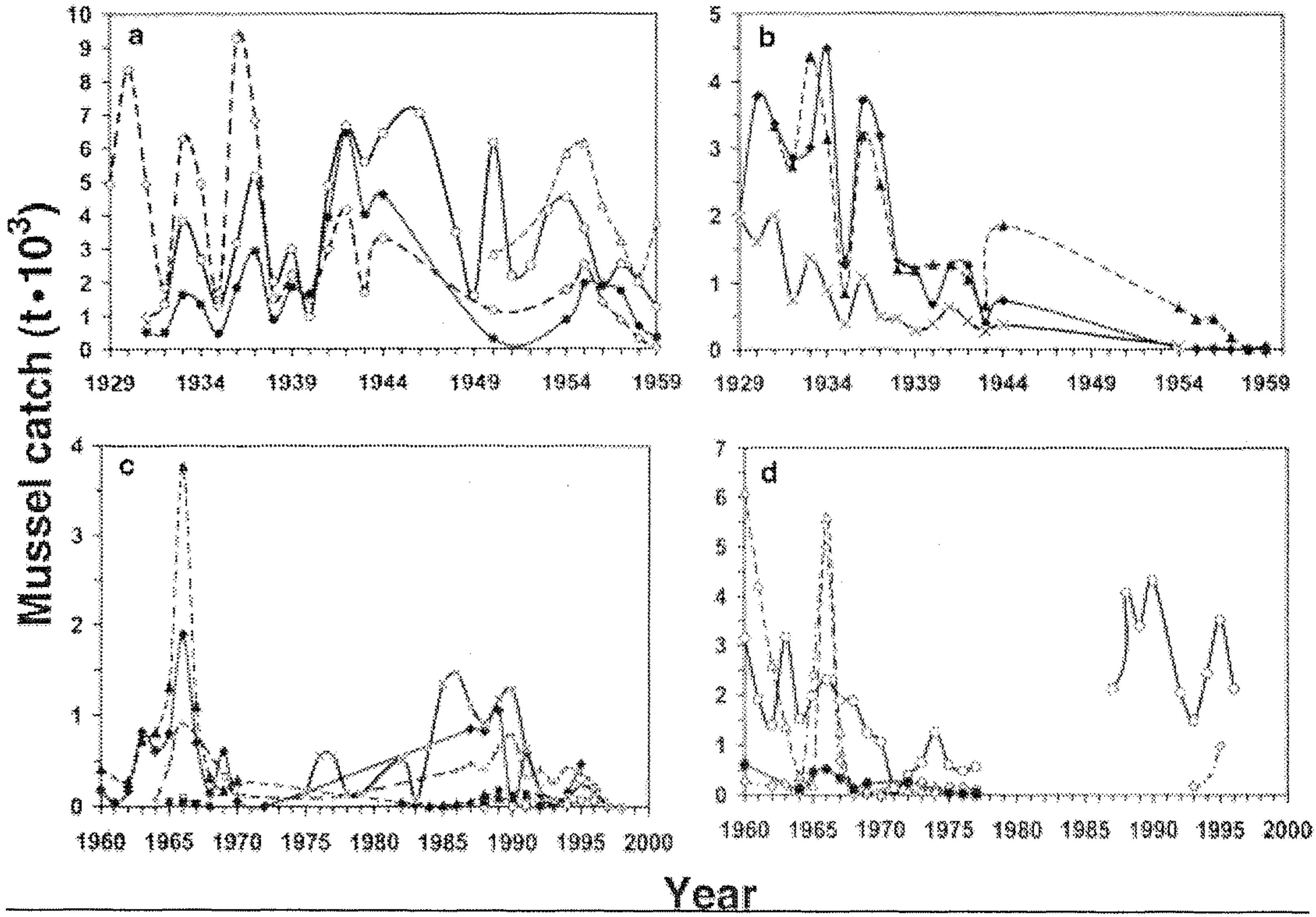
The relatively complete catch statistics from the state of Iowa for mussel harvests on the Mississippi River and other smaller Iowa rivers, as well as those of the fisheries of the Great Lakes Drainage Basin, provide further insight into the role of mussel stock depletion in the decline of the button industry. Although harvests in the Mississippi River were important to the Iowa mussel fishery, the significant proportion of harvests from Iowa's inland streams is apparent (Fig. 6). Catch statistics from these smaller inland streams.[2] show that yields peaked near the onset of the button industry's economic decline and exhibited dramatic declines thereafter (Fig. 8). Although the Iowa harvests on the Mississippi River show a similar pattern of decline (Fig. 6), it is notable that the harvests of smaller inland populations fell to near zero decades before those of the Mississippi River. That these declines were occurring despite the fact that increased value of shell probably increased demand for shell indicates overexploitation in these fisheries. Recent surveys of many of the same inland streams corroborate this suggestion because mussel populations have shown no signs of recovery in the five decades following closure of the pearl button industry (K.E. Arbuckle and J.A. Downing, Iowa State University, Ames, Iowa, U.S.A., unpublished data).

Some of the trends of peaks and declines in commercial mussel yields from Iowa's smaller interior streams correspond to those seen in the state-wide harvest statistics and indicate an influence of overall market factors (Fig. 8). The patterns of mussel harvest in Iowa's inland fisheries may not, however, only reflect economic oscillations of a dying button industry. Rather, the alternating patterns of increasing and decreasing yields among some of these inland streams probably indicate patterns of rapid exploitation and depletion of rich mussel beds and their subsequent abandonment for newly discovered or more economical beds on nearby streams (e.g., Fig. 8*a*). This stream-to-stream depletion of mussel stocks is often described in documentation of historical mussel harvests (e.g., Coker 1914, 1919; Smith 1919).

Mussel catch data for the fisheries of the U.S. Great Lakes Drainage Basin also implicate local stock depletion as a major factor influencing the decline of U.S. mussel fisheries (Fig. 9). Even as the value per unit mass of mussels exploited in these fisheries more than doubled, declining mussel harvests made only a weak recovery in 1936 before declining rapidly to near zero in 1940 (Fig. 9). These years of minimal yield preceded the rapid decline in shell value in this fishery that became apparent by the late 1930s (Fig. 9).

Although several have attributed the decline of the American button industry prior to the advent of plastics to the presence of foreign competition and the failure of the U.S. to implement protective tariffs (e.g., Thiel 1981; Claassen 1994; Fassler 1994), it is likely that overexploitation and the reduction in maximal size of marketable shells (Coker 1914, 1919) played a more important role than previously perceived. The lack of large, high-quality shells would have undermined the U.S. industry's ability to suppress competition, allowing the rise of foreign competitors. In fact, foreign competition did not become economically viable until the domestic mussel resource had become depleted. If mussel stocks had not been so dramatically overexploited during the

Fig. 7. Mussel harvest trends from freshwater button mussel fisheries in the U.S. states of (*a*) Alabama (△), Arkansas (◇), Tennessee (○), and Kentucky (●). (*b*) Indiana (▲), Illinois (◆), and Iowa (×) show substantial fluctuations between 1929 and 1959. Harvest trends from freshwater mussel fisheries in (*c*), the midwestern U.S. states of Illinois (◆), Indiana (▲), Minnesota (□), Missouri (■), Wisconsin (+), and Iowa (×) show substantial fluctuations between 1960 and 1998 as do trends from (*d*) Alabama (△), Arkansas (◇), Tennessee (○), and Kentucky (●) for harvests between 1960 and 1996. Data are from Fiedler (1931, 1932, 1936*a*, 1936*b*), Fiedler et al. (1936), Fiedler (1938, 1940*a*, 1940*b*, 1941), Brann (1947), Anderson and Peterson (1953), Anderson and Power (1956, 1957), Power (1958, 1959, 1960, 1961, 1962, 1963), Power and Lyles (1964), Lyles (1965, 1966, 1967, 1968, 1969), Stans (1971), Wheeland (1972, 1973), Thompson (1974), Wheeland (1975), Pileggi and Thompson (1976), Wise and Thompson (1977), Pileggi and Thompson (1978, 1980), Thompson (1984), Koch (1991, 1992, 1993), Todd (1993), the Iowa Department of Natural Resources,[2] and the Wisconsin Department of Natural Resources (K. Welke, Mississippi River Fisheries Management Office, unpublished data).



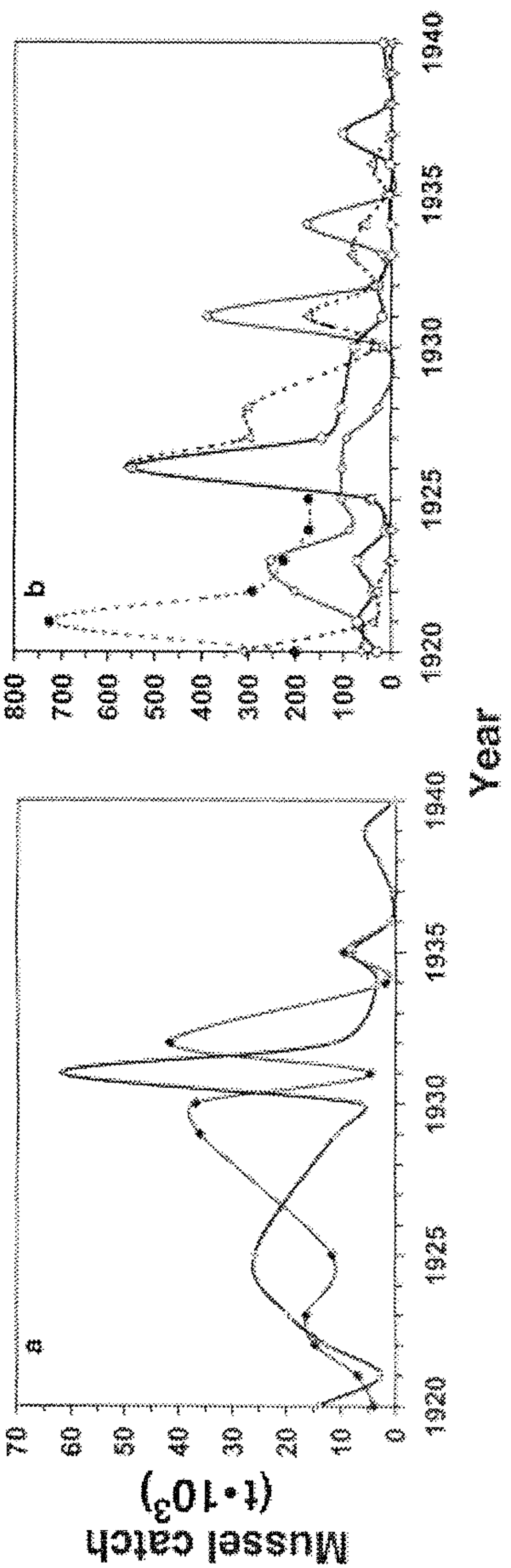


Fig. 8. The trends in freshwater mussel yields (t) for (*a*) Iowa's Skunk River (+; black line) and Iowa River (◆; gray line); (*b*) the Des Moines River (◇; solid gray line), the Wapsipinicon River (○; solid black line), the Shell Rock River (●; broken gray line), and the Cedar River (△; broken black line) fluctuated dramatically between 1920 and 1940. Data are from the Iowa Department of Natural Resources.[2]

freshwater pearl rushes and early after the button industry's onset, a larger standing supply of cheap available domestic shell material would have allowed the U.S. freshwater button industry to stifle foreign competitors and maintain a dominant economic presence until the advent of inexpensive plastics or the depletion of these large standing stocks.

Cultured-pearl industry: 1950–present: history and development of the industry

The third and most recent bout of intensive freshwater mussel exploitation in the U.S. has provided the raw material for the Asian cultured-pearl industry. A veil of secrecy surrounds this multi-billion-dollar (1998 $U.S.) industry to preserve monopolistic controls. This generally precludes an extensive synopsis of the industry, however, and literature is consequently quite limited (Fassler 1991).

As early as 1904, the Japanese were experimenting with the production of cultured pearls using artificial nuclei (Fassler 1994). It was soon discovered that when spherical beads created from the shells of freshwater mussels (Fig. 10) were placed into an incision in the tissue of a marine pearl oyster (a process called grafting), they served as exceptional nuclei as the oyster surrounded the beads with nacreous secretions (Fassler 1991). Information regarding the grafting process and the technology involved has, until recently, been closely guarded to ensure Japan's place as the world's sole producer of high-quality cultured pearls (Ward 1985; Fassler 1991, 1994).

The world's rapid acceptance of the new cultured pearls accelerated the development of the industry. By 1934, Japanese pearl farmers had nucleated over 15 million oysters (Fassler 1994), and in 1938, they produced over 11 million pearls (Claassen 1994). Although cultured-pearl farms gradually spread throughout many of the South Pacific atolls, Japan remained in control of the labor, technology, and a majority of the exports even outside of its own borders (Fassler 1991). In 1985, some individual pearls from these South Sea nations were valued at between $6000 and $60 000 (1998 $U.S.) (Ward 1985). By 1990, the expansive industry produced pearls worth over $1.1 billion (1998 $U.S.) (Fassler 1991), and presently the cultured-pearl industry employs hundreds of thousands worldwide and boasts retail sales exceeding $3 billion (1998 $U.S.) annually (Hubbs and Jones 1996).

Although Chinese shell material was the mainstay of the Japanese industry in the early days of the cultured-pearl industry, U.S. shell became the sole source of nuclei by the 1950s (Neves 1999). Japan's monopolistic control over the industry began to deteriorate with the depletion of freshwater mussel stocks in the U.S. and pollution-related mortality of the pearl oysters in Japan (Claassen 1994; Fassler 1994; Neves 1999). As American mussel stocks are dwindling, the economic viability of the cultured-pearl industry and the U.S. mussel fisheries are waning. The search for artificial nuclei to substitute for American shell has begun (Fassler 1994), prompting many to suggest that the most recent commercial market for U.S. freshwater shell has begun to dissolve (e.g., Claassen 1994; Fassler 1994). Others are optimistic (Neves 1999), and markets outside of Japan are expanding (Fassler 1994). Just as in the freshwater pearl and button industries, however, foreign competitors and alternative resources became economically viable only after substantial depletion of the American mussel resource.

Mussel harvests and conservation during the cultured-pearl era

As mussel harvests for the production of pearl buttons dwindled, U.S. freshwater mussel fisheries were revived by the cultured-pearl industry. As early as the 1920s, U.S. shell exports to Japan, composed primarily of *Fusconaia* and *Pleurobema* species, had grown large. Because it requires up to 30 kg of shells to produce a single kilogram of nuclei, the growing cultured-pearl industry demanded a substantial supply of North American shells (Claassen 1994; Fassler 1994). Exports that near the industry's onset consisted solely of raw shell saw the gradual inclusion of nuclei manufactured in the U.S. In 1968, U.S. shell exports exceeded 22 000 t annually (Claassen 1994), and by the early 1990s, shell exporting was a 70-million-dollar per year industry (Ahlstedt and McDonough 1993). Despite its substantial magnitude, the value of the U.S. shell export industry remains far below that of the pearl button industry at its peak (cf. Fig. 3).

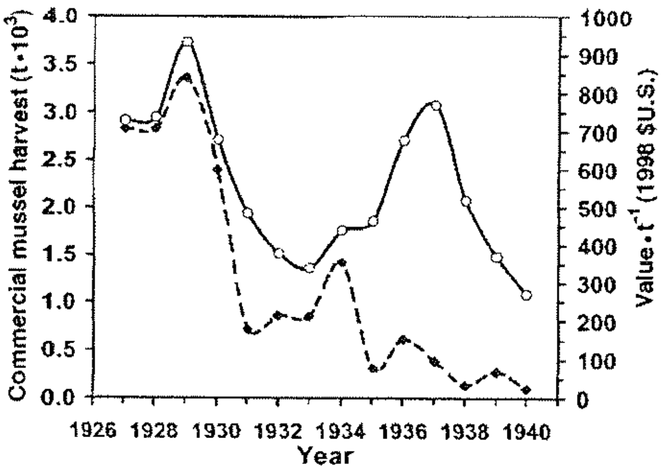
A majority of the early mussel harvests for the cultured-pearl industry consisted of *Fusconaia* and *Pleurobema* species from the Tennessee River, which pearl producers had deemed of the highest quality for nucleus production. In 1960, the nearly 900 Tennessee River musselers netted over $1 250 000 (1998 $U.S.) and, by 1962, musselers on the same stream could expect daily catches of 180 kg·person^{-1} (Claassen 1994). In spite of technologically advanced harvest methods (e.g., SCUBA, etc.), these daily takes, although substantial, were far below many historical daily catches obtained with more primitive methods (cf. Fig. 5) and the mussel resources of the Tennessee River soon became exhausted (Ahlstedt and McDonough 1993). Consequently, pearl producers began to accept increasingly larger harvests from a growing number of streams. In 1965, for example, harvests on the Wabash River peaked at over 900 t (Anderson et al. 1993) and this stream became one of the most important mussel fisheries in the U.S. (Fig. 11).

The pursuit of new fishing grounds could not stave off declining yields for long, however. Mussel resources in some of the most productive U.S. streams, including the Tennessee and Wabash Rivers, were showing signs of exhaustion (Fig. 11). Mussel densities had been declining since 1965 in the Upper Mississippi River (Thiel 1981). Mass die-offs were also becoming more common in some streams (Todd 1993; Claassen 1994) including one event that impacted mussel populations throughout an extensive stretch of the Mississippi River north of Keokuk, Iowa (Thiel and Fritz 1993).

Faced with the exhaustion of marketable shell stocks, pearl producers, just as the button manufacturers before them, began to accept more species to ensure that the desired supply of shells and nuclei could be satisfied. The washboard, *Megalonaias nervosa*, became the most valuable commercial species (Fassler 1994). Presently, at least 21 unionid mussel species, five of which are considered species of special concern (Williams et al. 1993), have some commercial value (Table 3). Nevertheless, marketable mussel stocks continued to decline as demand for shell increased.

Despite the decline in availability of marketable shell stocks, the rising value of shell allowed increases in fishing

Fig. 9. Trends in commercial mussel yields (t) (◆) for the Great Lakes Drainage Basin show wide fluctuations between 1927 and 1940. While yields declined dramatically beginning in 1929, value·t^{-1} (1998 $U.S.) (○) began to increase in 1933 before again declining in 1937. Data are from Radcliffe (1927), Fiedler (1931, 1932, 1936*a*, 1936*b*), Fiedler et al. (1936), and Fiedler (1938, 1940*a*, 1940*b*, 1941).



effort through the 1980s and into the 1990s in many states (Crowell and Kinman 1993). In 1991, the state of Tennessee alone supported over 2300 musselers (Todd 1993). The classical signs of overexploitation noted previously during harvests for pearl button production have again become evident in many U.S. mussel fisheries. For example, Thiel (1981) noted that previously valuable mussel beds in the Upper Mississippi River could not support musseling by the late 1970s. Mussel populations in Kansas have experienced a nearly 10-fold reduction in density since the 1960s (Busby and Horak 1993). Consequently, increasing shell value has allowed musselers to turn to previously uneconomical or unexploited beds to support annual harvests (Anderson et al. 1993). Recent accounts of commercial exploitation also note increased occurrences of illegal harvesting activity (e.g., Anderson et al. 1993; Hubbs and Jones 1996; Whitney et al. 1997).

A further indication of substantial overexploitation is that large, valuable individual mussels are absent from many fisheries despite a lucrative economic incentive for their harvest (Hubbs and Jones 1996; Neves 1999). Quantitative surveys of exploited populations also suggest that few individuals of commercially valuable species larger than the minimum legal size exist in many fisheries (e.g., Whitney et al. 1997). Even when animals do reach minimum legal size, they are quickly harvested. The decline in abundance and size of the most valuable mussel species has often prompted musselers to shift their effort to smaller individuals of less valuable species to supplement their harvests (Hubbs and Jones 1996; Neves 1999). Just as in mussel fisheries for button production, the trend toward growth overfishing is apparent.

As evident in catch statistics for the button industry, the similarities in the trends in more recent catch statistics of U.S. midwestern mussel fisheries (Fig. 7*c*), and to a lesser degree, those of southern U.S. states (Fig. 7*d*) may be indicative of market trends driving commercial harvests. Closer

Fig. 10. Round beads, or nuclei, are presently created from the shells of U.S. freshwater mussels and exported for use in the cultured-pearl industry. Nuclei are shown here below one of the currently most commercially valuable freshwater mussel species, the washboard, *Megalonaias nervosa*. Nuclei were provided by C. Lawson, Empire Shell Products, Garnavillo, Iowa. Photo by J.L. Anthony.

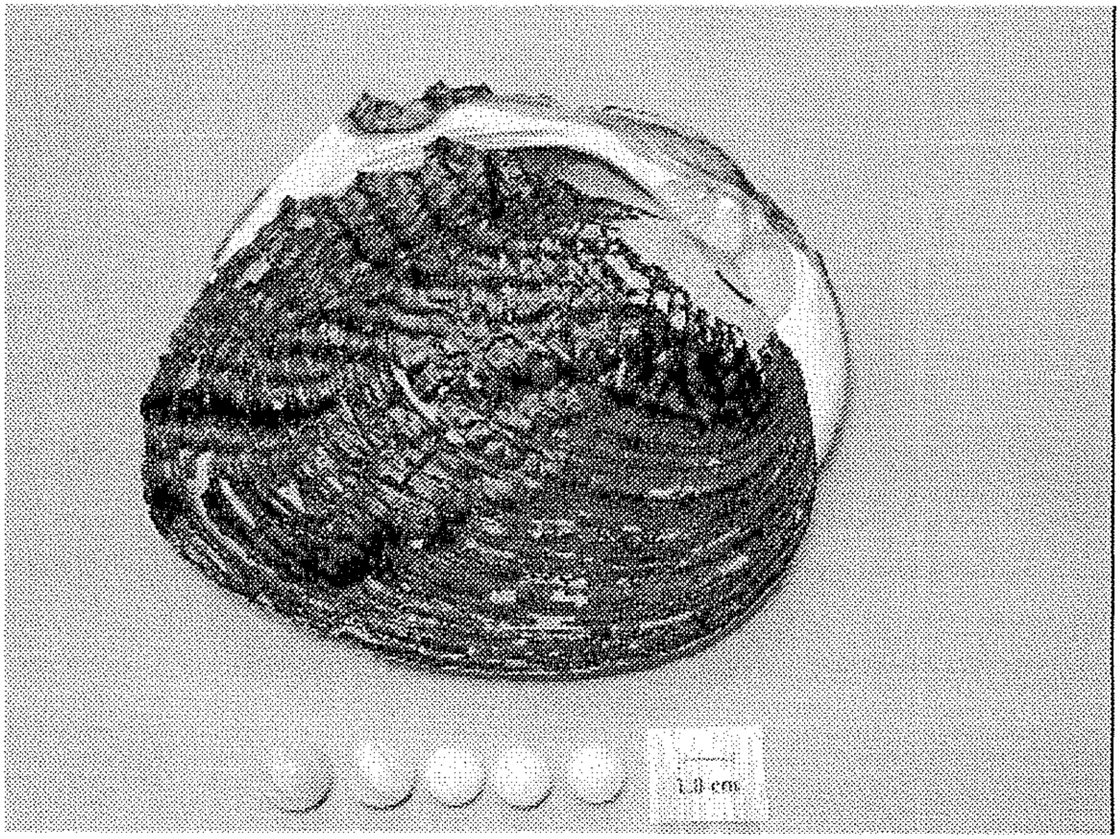
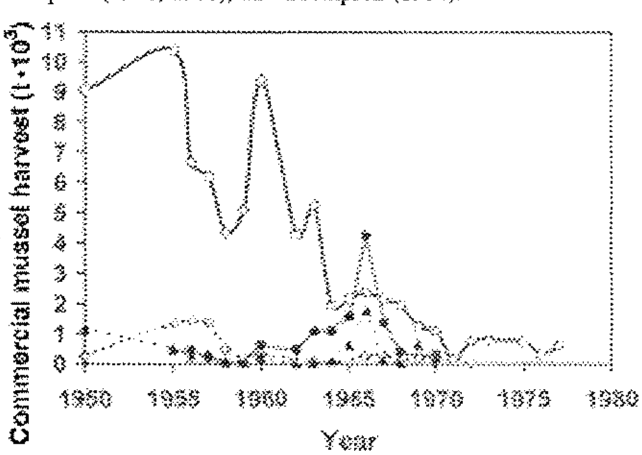


Fig. 11. Commercial harvest trends for major U.S. mussel fisheries on the Tennessee (○), Wabash (●), Ohio (◇), and Mississippi (▲) rivers show overall declines through time. Data are from Anderson and Peterson (1953), Anderson and Power (1956, 1957), Power (1958, 1959, 1960, 1961, 1962, 1963), Power and Lyles (1964), Lyles (1965, 1966, 1967, 1968, 1969), Stans (1971), Wheeland (1972, 1973), Thompson (1974), Wheeland (1975), Pileggi and Thompson (1976), Wise and Thompson (1977), Pileggi and Thompson (1978, 1980), and Thompson (1984).



examination of Iowa's Mississippi River mussel fishery with its relatively complete data, however, also seems to implicate overexploitation in recent declines in mussel yields. Following a peak year in 1986 (1464 t), commercial mussel yields in Iowa's Mississippi River have declined precipitously to less than 0.5 t in 1998 (Gritters and Aulwes 1998).

Data from the Iowa Department of Natural Resources[2] show that the value·t^{-1} of shells increased from just over \$1000 (1998 \$U.S.) in 1987 to over \$3500 (1998 \$U.S.) by 1994 (Fig. 12*a*). Meanwhile, the yields of the fishery were declining (Fig. 7*c*). Had mussel populations been healthy and capable of sustained exploitation, increases in harvests should have been observed given the high value of the shells and the high demand for shell exports. Even while shell values were rapidly increasing, however, effort was generally decreasing (Gritters and Aulwes 1998). Catch per unit effort (CPUE) also decreased substantially from 52 kg·diver $hour^{-1}$ in 1987 to 10 kg·diver $hour^{-1}$ in 1998 (Fig. 12*a*). Thus, if density is proportional to CPUE, mussel abundance within dwindling mussel beds probably declined more than fivefold in a decade. An additional consideration is that, in Iowa, Illinois, and Wisconsin, dead shells (possibly remnants of a mid-1980s die-off in the Upper Mississippi River) composed a significant proportion, and in some years, the majority of the total yield of the most highly sought mussel species, *M. nervosa* (Thiel and Fritz 1993).

Iowa's mussel fishery was not the only fishery in significant decline by the late 1990s. Even the extensive mussel fisheries in the state of Tennessee, which often yield up to 50% of the total U.S. catch (Hubbs and Jones 1996), are characterized by declining indices of CPUE since the early

Table 3. At least 21 North American freshwater mussel species presently have some commercial value for the production of nuclei for cultured pearls.

Species	Source
Actinonaias ligamentina	Anderson et al. 1993
Amblema plicata	Koch 1992; Ahlstedt and McDonough 1993; Anderson et al. 1993; Busby and Horak 1993; Crowell and Kinman 1993; Todd 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998
Cyclonaias tuberculata	Ahlstedt and McDonough 1993; Anderson et al. 1993; Todd 1993
Ellipsaria lineolata	Ahlstedt and McDonough 1993
Elliptio crassidens	Ahlstedt and McDonough 1993; Anderson et al. 1993; Todd 1993
Fusconaia ebena	Todd 1993; Hubbs and Jones 1996
Fusconaia flava	Anderson et al. 1993; Busby and Horak 1993; Todd 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998
Lampsilis cardium	Busby and Horak 1993
Obovaria olivaria	Anderson et al. 1993; Gritters and Aulwes 1998
Megalonaias nervosa	Koch 1992; Ahlstedt and McDonough 1993; Anderson et al. 1993 Crowell and Kinman 1993; Todd 1993; Hubbs and Jones 1996
Obliquaria reflexa	Ahlstedt and McDonough 1993
Pleurobema coccineum	Busby and Horak 1993
Pleurobema cordatum	Ahlstedt and McDonough 1993; Todd 1993
Potamilus alatus	Ahlstedt and McDonough 1993; Gritters and Aulwes 1998
Potamilus purpuratus	Busby and Horak 1993
Quadrula asperata	Hubbs and Jones 1996
Quadrula metanevra	Anderson et al. 1993; Busby and Horak 1993; Todd 1993; Gritters and Aulwes 1998
Quadrula nodulata	Todd 1993
Quadrula pustulosa	Ahlstedt and McDonough 1993; Anderson et al. 1993; Busby and Horak 1993; Gritters and Aulwes 1998
Quadrula quadrula	Koch 1992; Ahlstedt and McDonough 1993; Anderson et al. 1993; Busby and Horak 1993; Crowell and Kinman 1993; Todd 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998
Tritogonia verrucosa	Ahlstedt and McDonough 1993; Anderson et al. 1993

1970s (Fig. 12*b*). Likewise, indices of CPUE declined in Wisconsin's mussel fisheries beginning in the late 1980s (Fig. 12*c*).[4] These fisheries all indicate a consistent near-fivefold decline over the periods plotted. Mussel stocks may be dangerously depleted in these and other U.S. fisheries.

Many reasons have been suggested to explain these most recent mussel declines. The harmful effects of the invasion of the exotic zebra mussel are often considered one of the primary factors leading to the decline of U.S. mussel fisheries (Thiel and Fritz 1993; Fassler 1994). It is interesting to note, however, that zebra mussels became well established in the Mississippi River Basin between 1991 and 1993 (Fassler 1994). Many fisheries in the Mississippi River watershed were, at this point, already in significant decline (Fig. 7*c*, 7*d*) and characterized by declining CPUE (Fig. 12). Although zebra mussels are certainly impacting unionid mussels, it appears that unionid mussel populations were already declining in the midwestern U.S. when they arrived.

Some of the declines in harvests and CPUE may also be the result of a tightening of restrictions, including higher licensing fees and larger minimum legal size limits, on the mussel fisheries in 1979, 1987, and during the 1990s (Thiel and Fritz 1993; Todd 1993; Gritters and Aulwes 1998). Increases in minimum legal size have generally been small, however, and as noted by Neves (1999), the value of even considerably more expensive licenses may be recovered in as little as one day of harvest. Furthermore, these recently imposed regulations may be too little, too late. For example, many of the states along the Upper Mississippi River had no species restrictions enacted before 1979, over 80 years after the first extensive mussel harvests began (Thiel and Fritz 1993). Restrictions in maximum size limits have also remained insufficiently small (Thiel and Fritz 1993) and static for decades (Busby and Horak 1993; Crowell and Kinman 1993; footnote 4) despite widespread stock depletion. Daily catch limits are also nonexistent in most states (e.g., Busby and Horak 1993; Thiel and Fritz 1993; footnote 4). Although declining yields may also be partly due to a recent decline in Japanese demand for shell (Neves 1999), there is evidence that after over a century of overexploitation and decline American freshwater mussel stocks are simply not able to support extensive exploitation.

Conclusion

Although quantitative analyses of freshwater mussel populations prior to 1900 are rare and few continuous data sets of mussel fishery statistics exist, our analysis points to substantial overexploitation as a primary contributor to the decline of mussel fisheries in the U.S. Declines in CPUE and likely harvestable mussel stocks, demonstrate a serious level of resource degradation. Furthermore, declining maximum sizes and the fact that few mussels over the minimum legal size exist suggest an overly intense level of exploitation. Both historic and recent trends in mussel fisheries have implied that unionid mussels do not support a sustainable intensive fishery even under favorable market conditions. In fact, declining indices of CPUE and yields imply that mussel populations are now incapable of supporting a sustainable fishery at levels of harvest far below those historically extracted. Knowledge of the ecology of these declining mussel

[4] K. Welke, Wisconsin Department of Natural Resources, Mississippi River Fisheries Management Office, 315 East Cedar, Prairie du Chien, WI 53821, U.S.A., unpublished data.

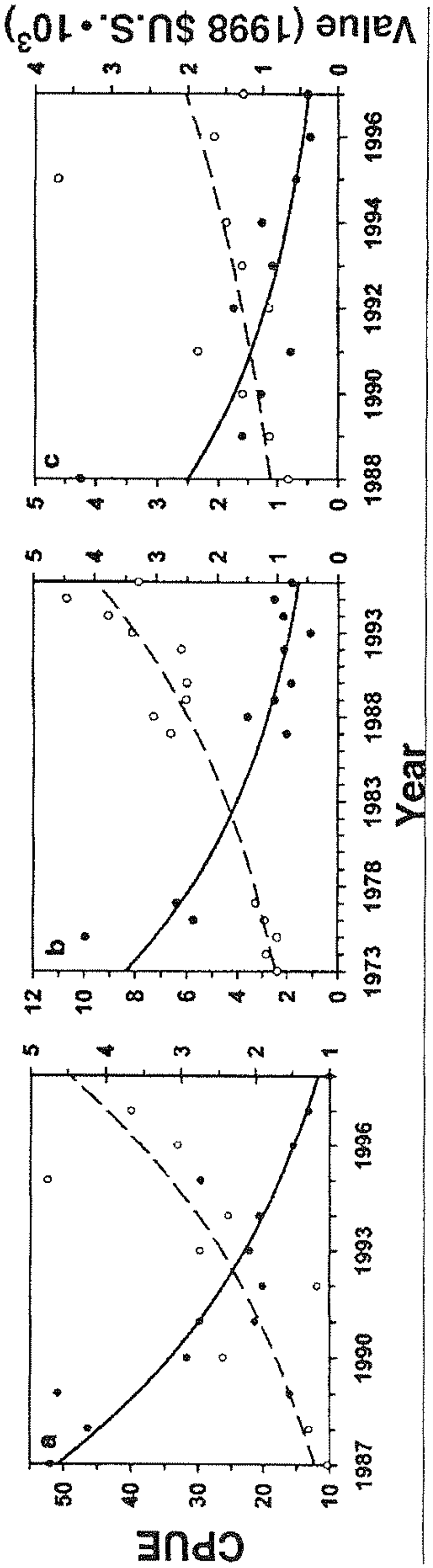


Fig. 12. CPUE (diver hours) for (*a*) Iowa's Mississippi River freshwater mussel fishery (kg·diver hour^{-1}) (●; solid black line) show dramatic declines through the mid-1980s to 1998 as shell values (1998 \$U.S.·10^3·t^{-1}) (○; broken gray line) increase. Indices of CPUE (t·license^{-1}) (●; solid black line) and shell values (1998 \$U.S.·10^3·t^{-1}) (○; broken gray line) for (*b*) Tennessee (1973–1996) and (*c*) Wisconsin (1985–1998) generally decline through time. Data are from Wise and Thompson (1977), Pileggi and Thompson (1978, 1980), and Thompson (1984), Todd (1993), and Hubbs and Jones (1996), Gritters and Aulwes (1998), and the Wisconsin Department of Natural Resources.[4]

species must be improved before mussel conservation and fishery management can be based upon adequate knowledge of these sparse and jeopardized populations.

This analysis of American mussel fisheries offers more than a means of understanding the present state of U.S. mussel populations, however. This resource trajectory is especially interesting to managers of other resources since it has been played out in almost a complete regulatory vacuum, therefore illustrating the long-term impacts of "regulation" by nearly pure market forces. It is rare that we are offered the chance to examine more than a century of the history of a group of biological resource organisms. Analysis of the history of freshwater mussel fisheries can therefore help us to contemplate the future of this and other exploited organisms. Several general conclusions emerge when the long record is assembled from these many disparate sources. Although these general lessons are not all new, they emerge clearly from this long record, and are of likely relevance to resources with shorter or less developed historical data.

Nine general lessons learned from the mussel fisheries

1. Short-term economic decisions can impede long-term resource sustainability

Exploitation regulated principally by short-term economic decisions by free entrants to the harvest arena can engender long-term resource impacts. This is because long-term sustainability has no economic relevance to those drawn to a resource by the potential for short-term monetary gain. This is most profoundly illustrated by the exhaustive harvests during the pearl rushes but is also illustrated by substantial declines in CPUE during the button and cultured-pearl nucleus eras, as well as current extensive poaching of endangered populations. Overexploitation at each stage decreased profitability of the subsequent industry.

2. Basic biology and ecology sets the upper limits for harvest intensity

Knowledge of the basics of growth, reproduction, density dependence and population dynamics must be known to estimate biological production and model renewal under exploitation scenarios. Despite over a century of commercial interest in freshwater mussels, however, even basic aspects of their growth, longevity, and population ecology are poorly known (e.g., Anthony et al. 2001; Strayer and Ralley 1993). The apparent inability of contemporary yields to approach historic magnitudes illustrates that intensive harvest in the absence of this knowledge has led to decline and near extinction of the mussel resource base. It is also possible that some classes of organisms may not reproduce or grow in the way predicted by classical fisheries management theory and may be incapable of sustained exploitation. This is not new to management theory, but the mussel industry offers yet another profound example of the impact of violating this rule.

3. Loss of exploited populations depends on the rate of harvest relative to the rate of production

Seemingly inexhaustible resources can disappear in a short time if their production intervals are long relative to the rate of harvest. This is especially clear in freshwater mussels because they were observed at near legendary densities early in the 20th century, but long lives and slow growth (e.g., Anthony et al. 2001) mean that they renew themselves very slowly. During the button and cultured-pearl industries, long-lived declines in yields after short-term high magnitude harvests illustrate the rapid exhaustion of large standing stocks, followed by negligible recovery.

4. Delays in resource management and regulation may be dangerous to resource viability

The danger signs of overexploitation should be followed rapidly with regulations to sustain the resource. In mussel fisheries, calls for regulation were ignored until decades after the onset of harvests. Even short time lags in enforcement of regulations due to short-term funding shortfalls can have long-term consequences, however. An example of this is the U.S. Bureau of Fisheries funding shortfall from the 1930s–1950s. These financial problems precluded the collection of data that would have shown extreme depletion of the mussel fauna during this period. In any case, decade-scale declines in resources should be taken as an immediate indication of a need for stringent and decisive regulation of biological resources. If management has been delayed too long, post hoc regulation (e.g., the current mussel regulation scenario) can be inadequate to restore a resource, perhaps only managing the speed of its decline to extinction.

5. Declining economic viability does not predict future resource uses

The need for conservation of a resource or its restoration cannot be denied because a resource shows current low economic viability. First, the low economic viability itself can result from overexploitation and low yields. Second, future exploitation opportunities and uses are intrinsically unpredictable. For example, pearlers could not foresee the button industry, and button manufacturers could not foresee the demand for cultured-pearl nuclei. Each successive industry would have been more lucrative and had longer-term viability if the preceding industry had managed the resource more carefully.

6. Poor resource management favors competitors

Overexploitation and poor management of domestic supplies of a resource can render foreign competitors and other substitute supplies viable. Declining mussel populations, coupled with labor disputes, probably intensified Japanese competition in the U.S. button market by undermining the American industry's competitive advantage in low-grade button production. As mussel populations continued to decline, the increasing price of pearl buttons probably fueled the switch to synthetic production. Likewise, the low rate of supply of pearl nuclei is favoring Chinese nuclei and research to find synthetic substitutes. At first sight, though, it may appear that declining economic yields are due to competing products when the competing products might not have been viable had the resource been sustained at healthier levels.

7. Overexploited resource yields show unpredictable behaviors

In an unregulated resource arena, the final stages of exploitation may show wild oscillations in yields owing to the discovery and intensive harvest of vestigial patches of declining resource populations or communities. Overexploited resources offer low profitability especially where substantial industrial investment implies high fixed costs (i.e., the rapid capitalization of the pearl button and cultured-pearl industries). In the pearl button arena, rapidly declining yields of traditional beds led to short-term exhaustive removal of mussels from some newly discovered patches, especially in smaller rivers and remote locations. Further, industries tend to press for relaxed regulations when yields are low to help them survive until higher yields return. In the mussel fisheries, rapid alterations of regulations may have caused large variations in overall yields.

8. Intensive harvest of overexploited resources degrades population renewal potential

Unless a substitute product is found early in the exploitation trajectory, economic forces tend to automatically push stocks to extreme low levels with restricted species composition and weak renewal potential. In mussel fisheries, harvest of overexploited populations led to progressive decreases in density, size, and biodiversity as prices rose due to resource rarity. Rising resource value stimulates exploitation, which intensifies degradation. In fact, little recovery of overexploited mussel populations has been documented and it is no surprise that yields during the recent cultured-pearl industry have not matched those noted historically.

9. Intensive harvest can lead to progressive reductions in biodiversity

The sequential depletion and abandonment of rich populations or substocks, noted through the duration of the American mussel fisheries, may mask the true magnitude of metapopulation decline. This leads to abrupt declines of fisheries yields only after many substocks have been driven to commercial extinction. Additionally, when managing a multispecific fishery, failing to track specific population trends may lead to the gradual extermination of less productive species (Clark 1990). This is apparent in the current imperiled status of many formerly exploited mussel species as well as in the continuous shifts of fishing effort among species that were necessary to maintain harvests at the magnitude demanded by industry.

The collapse of the American freshwater mussel fishery mirrors those of many pelagic and demersal fisheries in both fresh and marine waters. The lessons learned from this century-long exploitation trajectory of the declining American mussel fauna must be applied to fisheries management if sustainable fisheries are to persist into the future. As global demand for fisheries products continues to increase, it will be imperative that fisheries be closely monitored and sensibly managed. Failure to act quickly and decisively to protect declining stocks will increase the likelihood of fisheries collapses, limit the potential for long-term fisheries sustainability, and degrade the future value of our aquatic resources.

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