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EFFECTS OF DISTURBANCES ON LARGE-RIVER MUSSEL ASSEMBLAGES

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ABSTRACT

Data from more than 10 years of quantitative sampling from stable gravel shoals in large rivers of the central US were used to test effects of specific disturbances (passage of commercial navigation vessels, the flood of 1993, and introduction of Corbicula fluminea) on native freshwater mussels (Family: Unionidae). Although many lotic species of Unionidae have been eliminated from large rivers because of degraded water quality, poor land use practices, and large-scale navigation projects, the resulting fauna appears to tolerate many disturbances. For example, high density populations of C. fluminea had no effect on unionid density at two shoals in the lower Ohio River. The record flood of 1993 in the upper Mississippi River had no measurable effect on mussels at three locations; species richness (22–25), density (45.3–60.3), and percentage of juveniles (11–26%) varied among years but showed no temporal trend. In a barge turning basin that was dredged in 1976, density of recently recruited Amblema plicata plicata was not significantly different from density at a reference site for six of nine study years indicating that recruitment is proceeding at a similar rate regardless of current traffic levels. The mussel fauna now inhabiting large rivers, dominated by thick-shelled species tolerant of reduced water velocity and increased sedimentation, appears to be quite resilient to many natural and man-induced disturbances. © 1998 John Wiley & Sons, Ltd.

KEY WORDS: Unionidae; bivalves; Corbicula fluminea; Dreissena polymorpha; disturbance; large rivers

INTRODUCTION

Freshwater mussels (Family: Unionidae) dominate the benthic biomass of stable gravel shoals in medium-sized to large rivers in the central US. They are virtually nonmotile, most species live 20 or more years, and feed by filtering particulate organic matter from the water. Eggs are fertilized and brooded in the gills, and immature mussels, once released from the female, spend a brief period on the fins or gills of a host fish (Coker, 1919; Fuller, 1974; Russell-Hunter, 1979; McMahon, 1991). Before the widespread use of plastics, shells were used in the button industry; today they are used to culture pearls (Sweaney and Latendresse, 1982; Sitwell 1985). Most thick-shelled species are tolerant of days or weeks of desiccation, and close their valves to avoid short periods of anoxia or poor water quality. Once large-river species reach adult size, their thick shells make them invulnerable to most predators.

Despite their resilience to disturbance, many species are in danger of extinction (Neves 1993). Williams et al. (1993) recognized 297 unioinid species in the US and Canada and considered 7.1% to be possibly extinct, 14.5% to be threatened, 24.2% to be of special concern, 4.7% of undetermined status, and only 23.6% to be currently stable. Some of the many reasons for extinction and local extirpation of the mussel fauna has been the subject of much speculation and discussion by many authors and includes: introduction of nonindigenous species such as Corbicula fluminea (Parmalee, 1945; Cummings and Mayer, 1992; Williams et al., 1993) and Dreissena polymorpha (Schloesser and Kovalak, 1991; Nalepa, 1995) poor land use policies and reservoir construction (Bates, 1962; Neel, 1966; Isom, 1971; Fuller, 1974; Harman, 1974; Kessler and Miller, 1978), dredging and other waterway modifications for commercial use (Cummings and Mayer, 1992; Williams et al., 1993). Degraded water quality immediately downriver of

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large cities such as St. Paul, Chicago, and Pittsburgh was responsible for local extirpation of mussels and other clean-water species (Fremling, 1964; Starrett, 1971; Cavanaugh and Mitsch, 1989).

One of the most obvious examples of impacts to the native mussel fauna occurred early in this century when large, free-flowing rivers were converted to run-of-river reservoirs. This caused an almost complete elimination of riffle-inhabiting molluscan genera such as *Pleurobema*, *Plethobasus*, and *Epioblasma* (Neel and Allen, 1964; Stansbery and Taft, 1976; Cummings and Mayer 1992). Large, regulated rivers are now dominated by species tolerant of reduced water velocity and increased sedimentation rates such as *Amblema plicata plicata* and *Quadrula* spp. (Miller and Payne, 1988; Hornbach et al., 1992).

Since 1983 we have used divers and quantitative methods (0.25-m² total substratum samples) to collect bivalves at stable gravel shoals in large rivers of the central US (Miller et al., 1994). Analyses of these data sets provides an opportunity to assess effects of manmade and natural disturbances, as well as introduction and spread of nonindigenous species, on native mussel assemblages. In this paper we will examine effects of specific disturbances (passage of commercial navigation vessels, extreme high and low water, and introduction of nonindigenous bivalves) on density and age structure of native mussel assemblages in large rivers. We will determine if selected man-induced impacts cause disturbance as defined by Pickett and White (1985) and Resh et al. (1988).

METHODS

At each site ten samples were collected at each of three subsites separated by approximately 10 m. A diver removed all sand, gravel, shells, and live mussels from the confines of a 0.25-m² aluminum quadrat (0.5 m on a side). Substratum was transported to shore in a 20-l bucket, sieved through a nested screen series with mesh sizes of 6.4, 12.7 and 34.0 mm. All live mussels were identified and total shell length measured with digital calipers. Bivalve nomenclature was consistent with Williams et al. (1993). More detail on field sampling methods can be found in Miller and Payne (1991) and Miller et al. (1994).

Total density estimates were based upon the mean number of all sizes of all or a single species present in ten 0.25-m² quadrat samples. An index of recruitment was calculated based upon the total number of mussels of all species less than 30 mm total shell length, and the total number of species with at least one individual present less than 30 mm total shell length. Based on examination of annuli counts in our laboratory, these individuals would be no older than 2-3 years.

RESULTS

Possible effects of disturbance caused by commercial navigation vessels on the native Unionid, Amblema plicata plicata

Pulses of turbulence and elevated suspended solids following passage of commercial vessels in large waterways may negatively affect freshwater mussels and their habitat (Nielsen et al., 1986). Vessel-induced disturbances are intermittent, unlike sustained impacts such as dredging, channel modification, construction of ports, or point and nonpoint source pollution.

Configuration of the upper Mississippi River (UMR) near Prairie du Chien, WI (approximate river mile 635) provided an excellent opportunity to study effects of commercial vessel movement on freshwater mussels. The river separates into an east and west or main channel (Figure 1). Substratum in most of the east channel consists of fine-grained silt and sand less than 6.5 mm in diameter (50%), particles larger than 6.5 mm in diameter (5%), and broken shell material (45%) (Miller and Payne, unpublished information). Velocity during normal stage in the summer is typically 20 cm/s.

Virtually the entire east channel supports dense and diverse mussel populations, including an endangered species, *Lampsilis higginsi* (Havalik and Stansbery, 1977). Approximately 30 species of unionids have been collected in this reach of the UMR and the fauna is dominated by *Amblema p. plicata*, a commercially valuable species that comprises 50-70% of the assemblage (Miller and Payne, 1988;

Hornbach et al., 1992, 1996). A barge loading facility that handles shipments of grain and other products is located in a slough in the north end of the channel and a second facility is located along the east bank of the channel to the south. Single barges are shuttled from mooring sites in the main channel to loading facilities by an 596-kW (800 hp) workboat.

Approximately 300 barges are moved through the east channel each season. Barges must pass through a turning basin at the north end of the east channel to reach either of the loading facilities. The turning basin and adjacent areas were dredged in 1976 which removed most of the adult mussels (Havalik and Marking, 1981). At low water barges occasionally scrape the bottom of the turning basin and can scrape or crush shells.

Divers used quantitative sampling methods to collect mussels for 9 years starting in 1994 through 1996. The purpose was to determine whether vessels passing through the turning basin effected recruitment of A. p. plicata. Mean density of A. p. plicata greater than 30 mm total shell length ranged from 6.0 (\pm 1.6

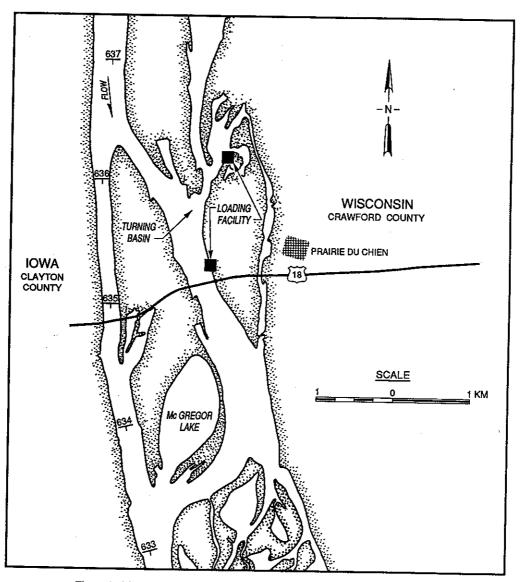


Figure 1. The study area in the East Channel of the upper Mississippi River

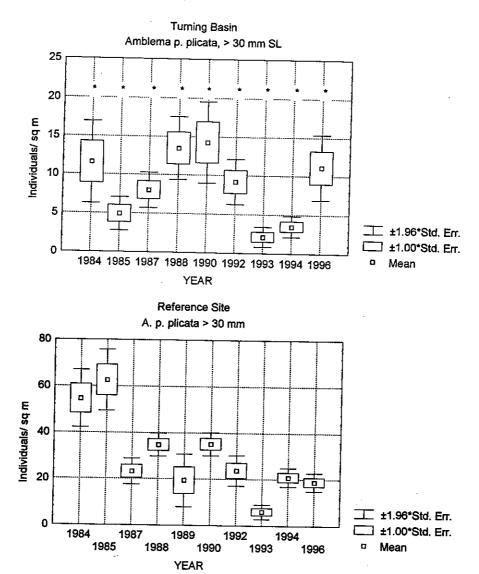


Figure 2. Density of A. p. plicata > 30 mm total SL at the turning basin and reference site in the east channel of the upper Mississippi River. The asterisk (*) denotes significant density difference (p < 0.05) between locations for that year

S.E., standard error of the mean) to $62.53~(\pm 6.5~\mathrm{S.E.})$ individuals/m² in the reference site, which was significantly greater than density of larger sized individuals in the turning basin (unpaired t-test, p < 0.05) for all study years (Figure 2). Reduced density in the turning basin is attributed to the dredging in 1976 which removed most mussels. However, comparatively poorer substratum in the turning basin, unconsolidated coarse sand, when compared with the reference site, which consists mainly of consolidated silt and shells, is a contributing factor.

Density of mussels less than 30-mm total SL, evidence of recruitment within the last 2-3 years, was not significantly different between the two sites for six of the nine study years (Figure 3). This suggests that recruitment is proceeding at a similar rate at both sites regardless of early dredging, continued use of the turning basin by vessels, and the slightly poorer physical conditions for unionids in the turning basin. Conditions in the turning basin appear to have little effect on recruitment or density of small sized A. p. plicata. However, juvenile mussels produced in the early 1980s would have ample time to grow to intermediate or adult size by the mid-late 1990s. Differences in density of the larger sized mussels at this

time could be due to movement of commercial vessels, different physical conditions at the two sites, both of which could have an effect on survivorship of all sizes of mussels. Although intersite density differences for small mussels in 1992–1994 was significant at the 0.05 level, it is unlikely that these had biological significance. For example, in 1992 the difference between four individuals/m² (one mussel in a 0.25 m² quadrat) and one individual/m² (one mussel in three or four quadrats) is minor. Recruitment was approximately the same and extremely low at both sites during these years; minor differences in density should be considered biologically insignificant.

Extreme low water in the lower Ohio River

Seasonal and annual variation in river stage is great in the free-running reach of the Ohio River near Olmsted, Illinois between Lock and Dam 53 and the Mississippi River. Inspection of daily stage records

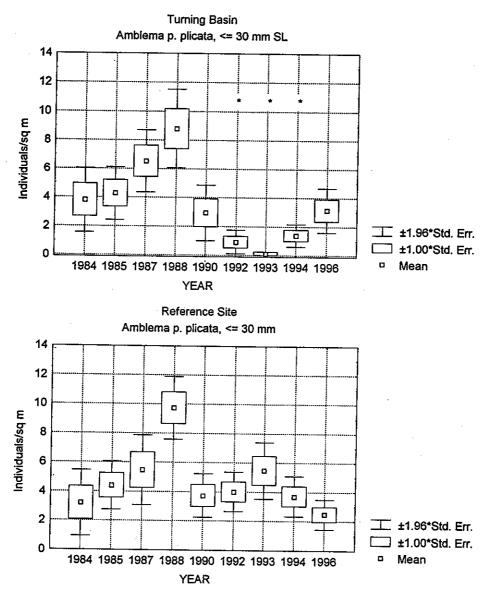


Figure 3. Density of A. p. plicata \leq 30 mm total SL at the turning basin and reference site in the east channel of the upper Mississippi River. The asterisk (*) denotes significant density difference (p < 0.05) between locations for that year

Table I. Record of low river stages 1975-1988 in the lower Ohio River (Cairo, Illinois gauge)

Date	Consecutive days exposing elevation of (m)			
	84.4	85.0	85.6	
September 1976	25			
December 1980-January 1981	35	14	0	
June 1988-July 1988	44	37	24	
July 1988-September1988	59	16	24 4	
October 1988-November 1988	35	6	ñ	

of the Ohio River (Cairo gauge) for the last 25 years shows that, on average, stage varies from approximately 11 m in spring to 5 m in late summer and early autumn. However, in any 1 year, deviation from these average highs and lows can be impressive. Since 1983, we have monitored and studied a mussel bed at a gravelly shoal approximately 7 km downriver of the lock and dam. Extensive collecting, including transect sampling in 1985, 1993, and 1994, allowed us to map the near and farshore limits of the bed. The farshore limit occurs where substratum becomes erosional; near mid-channel the gravel shoal is replaced by shifting sand and scoured bedrock. Suitably stable gravel extends several hundred feet more toward shore than dense populations of mussels. Although not obvious during most years, occasional brief periods of extreme low water prohibit the bed from extending toward the shore as far as substratum allows.

The nearshore limit of the bed occurs, within 0.3-0.6 m, along the 85-m elevation contour—closely corresponding to the limit of aerial exposure caused by the lowest of low-water conditions (Table I). River stage was sufficiently low to expose the river bottom at this elevation for a single day in September 1976, 14 days in January 1981, and 59 days during an extreme drought in 1988. In that year, river stage fell low enough to expose the 85.6-m elevation contour for 24 consecutive days. In the laboratory, Fusconaia ebena, the heavily dominant species, had a mean survival time of 24.6 days (S.D. = 8.6 days) during aerial exposure at 24°C and 95% relative humidity (Payne and Miller, unpublished data). In the autumn of 1976, the winter of 1980-1981 and the summer and autumn of 1988, consecutive days of aerial exposure exceeded this mean survival time at the 84.4-m elevation contour. Thus, the nearshore limit of the bed occurs approximately at that elevation which, every few years, is exposed to air long enough to cause mortality.

In summary, this mussel bed in the lower Ohio River is limited in the farshore direction by substrate instability and in the nearshore direction by historic patterns of low river stage.

Extreme high-water in the upper Mississippi River

The flood of 1993, which affected the central portion of the US, was caused by heavy snow cover and rainfall, and saturated soil conditions throughout the watershed in 1992–1993 (Scott, 1994). The peak discharge on 1 August 1993 at St. Louis, MO, was 30302 m³/s, which was estimated to be a 175-year recurrence interval event. The flood was unusual in that it occurred in July and August when river stages normally are falling. The record stage in August 1993 was almost 6 m above the previous highest stage recorded for that month. The flood was also of an extremely long duration; at most gauging stations in the UMR it lasted more than 150 days (McConkey, 1994).

Data from quantitative collections (1988–1994) at three locations between RM 299.6 and 635.2 in the main channel of the UMR were examined to determine if the high water in 1993 affected total mean density of three species of mussels, A. p. plicata, Quadrula pustulosa pustulosa, and Truncilla truncata. Unlike A. p. plicata, and Q. p. pustulosa, which reach a maximum SL of 178 and 102 mm, respectively, T. truncata reaches a maximum SL of 51 mm (Cummings and Mayer, 1992). Based upon annuli of specimens collected in the UMR, T. truncata lives approximately 3 or 4 years. Mean density was variable

among years for A. p. plicata and Q. p. pustulosa and showed no specific trends (Figure 4). High density of the former species in 1989 was the result of unusually high recruitment, first observed during that year. Mean density of T. truncata, showed no specific trends with respect to the high water of 1993.

Results of quantitative collections from a near and farshore site on the main channel of the UMR were used to calculate the percentage of all mussels less than 30 mm total SL and percentage of species with at least one individual less than 30 mm total SL (Table II). Differences in recruitment were similar at the near and farshore site but showed no specific trend through time. There is no evidence that greater than usual water velocities associated with the high water in 1993 had any effect on percentage of small

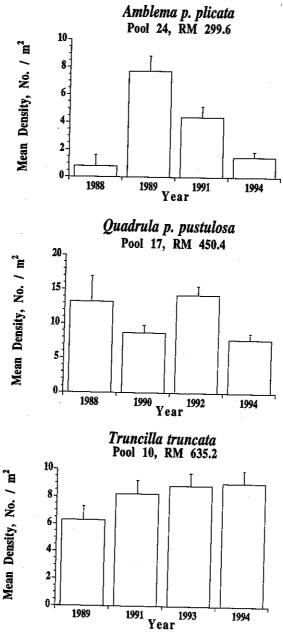


Figure 4. Mean density (\pm standard error) of three species of freshwater mussels at three locations in the upper Mississippi River, 1988-1994

Table II. Percentage individuals and species with at least one individual less than 30 mm SL collected in quantitative samples at RM 635.2 in the UMR. Totals for the year (columns 2 and 3) are based upon 60 quantitative samples each year with near and farshore (30 samples at each) sites combined

Year	Total		Evidence of recent recruitment			
	Density	Species	Species		Individuals	
			Nearshore	Farshore	Nearshore	Farshore
1989	58.2	22	9	9	17	16
1991	57.4	25	32	46	20	26
1993	60.3	26	51	53	16	11
1994	45.3	25	44	45	14	13

mussels. Overall species richness and density for each year show no specific trends which illustrates that changes in the percentage of new recruits cannot be the result of extirpation of sensitive species or extensive mortality of older aged individuals. Intervear variation in density and richness of these long lived organisms can only be the result of sampling slightly different sections of the bed each year.

Effects of substratum stability on bivalve population structure

Payne et al. (1989) analyzed 14 populations of C. fluminea in Mississippi streams in the spring of 1984. Individuals greater than 20 mm SL and greater than 1 year old comprised a substantial fraction (13–64%) of six of the 14 populations. These populations had distinct multiple cohorts. Four of the six populations occurred among longer lived unionids, suggesting that streambed stability was crucial to establishment of lotic populations of C. fluminea with complex size and age structure. The other eight populations of C. fluminea were characterized by a heavily dominant single cohort of small clams. Unusually high stream discharge in May and December for 2 years prior to the survey exaggerated ordinarily high winter flows. The eight populations with few large individuals probably are comprised almost exclusively of small individuals transported downstream from stable upstream sites. Seasonal high discharge and unstable substratum prevents many individuals from becoming old and large in these eight populations. Unionids were not found at these sites, a further indication of a substratum too unstable to support long-lived individuals.

Similar relationships between complexity of age structures of lotic populations and substratum stability have been reported by other authors. Sickel (1979) reported differences in size demography of *C. fluminea* in samples taken less than 2250 m apart in the Altamaha River, Georgia. Diamond (1982) reported that the complexity of age structure of lotic populations of the pleurocerid snail, *Juga plicifera*, was inversely related to the likelihood of scour by flood flows. In summary, the size structure of short-lived organisms such as *C. fluminea*, and the presence of long-lived unionids at a particular location, can be affected by episodic hydrologic disturbances in small streams.

Effects of nonindigenous bivalves on native unionids

The nonindigenous Asian clam, Corbicula fluminea, has no requirement for a fish host, buries into the substratum like unionids, but lives only 3 or 4 years (McMahon, 1983). Various authors (Keup et al., 1963; Van der Schalie, 1973) suggested that C. fluminea would ultimately displace the longer-lived unionids. Kraemer (1979) and Fuller and Imlay (1976) indicated that Corbicula could eliminate native mussels in highly disturbed areas.

Miller and Payne (1994) reported on 3 years of quantitative sampling from a stable bed in the middle Ohio River near Cincinnati, and 7 years of quantitative sampling from a stable bed in the lower Ohio River near Olmsted, Illinois. *Corbicula fluminea* density (776.8 in the middle Ohio River and 625.2

individuals/m² in the lower Ohio River) was considerably greater than for native unionids (34.8 in the middle Ohio River and 54.8 individuals/m² in the lower Ohio River). Based upon analysis of over 400 samples, 15 of 20 possible correlations between native and nonnative bivalves were weakly positive. Of the three relationships significant at either the 0.01 or 0.05 level, two were positive and one was negative. It was concluded that in stable shoals in large rivers, native mussels are not affected by high density populations of Asian clams (Miller and Payne, 1994). Because of their short life span Asian clams are often a more notable component of the benthic community immediately following disturbances, but it does not necessarily follow that this species has any competitive advantage over the long lived unionids.

The zebra mussel (Dreissena polymorpha) was introduced into Lake St. Clair in the late 1980s (Hebert et al., 1989) and releases eggs and sperm to the water where fertilization takes place without the requirement for host species. Zebra mussels are not infaunal but attach to virtually any firm substratum, including shells of other molluscs (Lewandowski, 1976). High unionid mortalities were reported in the Great Lakes in the late 1980s and early 1990s (Schloesser and Kovalak, 1991; Hunter and Bailey, 1992; Nalepa, 1995) and in the Illinois River in 1993 and 1994 (S.D. Whitney, Illinois Natural History Survey, unpublished information). At a mussel bed in the lower Ohio River, approximate numbers of D. polymorpha were: less than ten (1992), approximately 200/m² (1993), and up to 250000/m² (July 1994-1995). In late 1994 and early 1995, virtually all native mussels were infected to some degree, and the valves of most heavily infested individuals were actually sealed shut by byssal threads. However, virtually no unionid mortality was noted. Because of the ability to tolerate extreme crowding and attach to shells of native mussels, it would seem logical that D. polymorpha is much more likely to negatively affect unionids that C. fluminea. However, Whitney (unpublished information) reported that the majority of the unionids survived heavy infestations of D. polymorpha at RM 5.1 in the Illinois River. Results of long-term monitoring of large river mussel beds will determine if this nonindigenous species has an affect on density or recruitment of native mussels.

DISCUSSION

Pickett and White (1985) defined disturbance as a relatively discrete occurrence, either an environmental fluctuation or a destructive event. Resh et al. (1988) modified their definition slightly to include events of a frequency and intensity that 'are outside a predictable range'. Both Pickett and White (1985) and Resh et al. (1988) define a disturbance as an event that disrupts population, community, or ecosystem structure, and change resources, availability of the substratum, or the physical environment. The ability to discern change in the biota is key to the definition. With respect to freshwater mussels, it is important to distinguish between the effects of the past, large-scale waterway modification for commercial use, from relatively recent discrete natural or man-induced disturbances such as passage of commercial vessels, dredging, introduction of nonindigenous species, or periods of extreme high or low water.

The flood in 1993 in the upper Mississippi River had little measurable effect on freshwater mussel populations. Hydrologic data indicated that the flood was an event with a frequency and intensity that was outside the predictable range and which met the first part of the disturbance definition of Pickett and White (1985) and Resh et al. (1988). However, data on unionid density and recruitment indicate that the flood did not meet the second part of the definition, i.e. unionid populations were unaffected. High water did not create velocities of a magnitude to erode existing shoals and cause mortalities.

Although early information on effects of *D. polymorpha* in the Great Lakes indicated that lacustrine unionids would be severely effected, data from large rivers has been ambiguous. Whitney (unpublished information) reported that *D. polymorpha* densities declined in 1993 by 99% in the Illinois River and many unionids survived. The same appears to be happening in the lower Ohio River (Miller and Payne, unpublished information). When they expressed concern over competition between unionids and *C. fluminea*, Parmalee (1945) and Keup *et al.* (1963) probably did not view the introduction and spread of this species as a short-term, discrete event. However, results of quantitative sampling in the lower Ohio River since the early 1990s indicated that *C. fluminea* densities are now less than 10% what they were more

than 10 years ago (Miller and Payne, unpublished information). Even when densities of *C. fluminea* were more than 1000 individuals/m², native mussels were unaffected (Miller and Payne, 1994).

Although Williams et al. (1993) reported that many mussel species are imperiled, his list included species affected by past waterway modifications. Our studies in large rivers indicate that existing mussels tolerate discrete disturbances such as passage of commercial vessels, dredging, introduction and spread of C. fluminea, and extreme high water. Conversely, extended periods of extreme low water can define the inner extent of a mussel bed (lower Ohio River) and structure C. fluminea populations (small streams in Mississippi). However, we have found that not all man-induced disturbances (see Neves, 1993 and Williams et al., 1993) negatively affect recruitment, species richness, and density of large-river unionids.

As Weatherhead (1986) noted, so-called unusual events are often considered less important in long rather than short investigations. Our interpretation of effects of manmade and natural disturbances on native mussels would not have been possible with only 1 or 2 years quantitative data. Regardless, even a data set that spans 10–15 years is a comparatively short time for a molluscs that live 15 or more years. The importance of long-term field studies, designed to regularly monitor key attributes of biotic populations and communities, cannot be ignored (Likens et al., 1983; Strayer et al., 1986; Franklin, 1987; Likens, 1987). Field studies are still the best means of understanding effects of physical disturbances on naturally occurring populations and should not be discounted as 'mere monitoring' (Taylor, 1987). Long-term studies of mussels provides an opportunity to investigate effects of man-induced and natural disturbances on a resource with ecological, economic, and cultural value.

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