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Consistency and Characterization of Mussel Populations in Shallow Channel Border Areas, Mississippi River

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ABSTRACT

To determine the extent to which mussels inhabit channel border areas of the Mississippi River, 28 locations were sampled in Pools 19 through 26. Mussels were found in 17 of these 28 sites, at least one site with mussels occurred in each pool. All but three of the sites were in channel border areas not previously described as mussel beds. Three sites had been described as commercially valuable mussel beds and were located in or adjacent to the channel.

Thirty species of mussels were collected. The bed with the greatest diversity, 24 species, and density, >70 /m^2, was located at the head of Mud Island (RM362), which is just below Lock and Dam 19. The mussel fauna downstream of this bed was very low in both density and diversity at all sites examined. In Pool 19, a relatively diverse mussel fauna occurred in channel border habitats. These populations contained some species unique to the habitat but were dominated by Amblema plicata. The mussel beds in channel areas had higher diversities and densities but were also usually dominated by Amblema plicata.

Relationships between the dense, channel mussel beds and populations in the channel border habitat indicated some similarities between these communities. This was probably due to the common occurrence of Amblema plicata and the Quadrula group. When these species were evaluated genetically, differences between relative movement of the two species was found. Movement or exchange of genetic information between populations of Amblema plicata was apparently not inhibited by Lock and Dam 19 or relative location of a population. By contrast, movement between populations of Quadrula quadrula is more restricted and was greatest between adjacent populations. Lock and Dam 19 does act as a barrier to this species.

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INTRODUCTION

Interest in mussels of the Mississippi River has its origins in the 19th century, first as a source of freshwater pearls, then as a source of button-blanks for the pearl button industry (O'Hara 1980). The latter industry extended well into the 20th century and in Illinois there were still 16 button plants operating in the early 1920's. In spite of their commercial importance, the first comprehensive survey of mussel populations in the upper Mississiippi River did not occur until the Ellis survey in the early 1930's (van der Schalie and van der Schalie 1952). Several other surveys of the upper Mississippi River followed, particularly after completion of the lock and dam navigation system, including those of Perry (Rasmussen 1979), Fuller (1978), Ecological Analysis (1981), Sparks and Blodgett (1983) and Cawley (1984). Additional studies in navigation pools 19 and 26 have been underway from 1982 to present as part of a National Science Foundation (NSF) program on Long-term Ecological Research (LTER) (Bhowmik et al. in press). Other than the NSF-LTER ongoing study, only the studies of Sparks and Blodgett (1983) and Cawley (1984) were

quantitative reports, generally restricted to areas with known mussel beds of high densities.

Mussel beds are described as areas of "high" densities of mussels. However the previously mentioned surveys have indicated that both density and diversity have declined in mussel beds throughout the upper Mississippi River (Carlander 1954). Over-fishing, navigation structures, dredging activity, burial due to siltation, and chemical or organic pollutants have all been implicated in this decline. Though the pearl button industry has collapsed mussels from these mussel beds are still harvested for use in the cultured pearl industry and the number of licensed mussel fisherman has increased (Sparks and Blodgett 1983). This will place further pressure on mussel beds in spite of greater selectivity in species taken and restictions on size of shells which can be harvested. Reports from the NSF-LTER study (Anderson and Vinikour 1984, Anderson et al. submitted and Holm and Anderson submitted) indicated shallow channel border areas of navigation Pool 19 may harbor low densities of mussels. Even though only low densities of mussels occur in these areas, this type of habitat accounts for most of the area in most navigation pools of the upper Mississippi River. Consequently, larger numbers of individuals may exist in this habitat type than in the higher density mussel beds usually located in or

adjacent to channels. In addition, the population in this habitat may serve as a source of individuals for recruitment into the mussel bed. Anderson et al. (submitted) has suggested that the shallow channel border area may serve as a nursery for mussels and populations which develop in this habitat. Movement into mussel beds may be a result of scouring by the river current or directional movement of the mussels oriented by current direction. Most of the evidence for this recruitment is circumstantial, based on size frequency distribution and distribution patterns of the species of mussels found. Traditional mark and recapture techniques for evaluating mussel movement have only recently begun and require marking of extremely large number of mussels.

There were 2 purposes for this study, one was to determine if shallow channel border areas in navigation pools below Pool 19 also have low density mussel populations similar to those found in Pool 19. Secondly, through the use of electrophoretic techniques, to determine if individuals move between populations and habitats within and between navigation pools.

Starch gel electrophoresis allows an investigator to determine many things about the population structure of natural populations without resorting to expensive, labor intensive field techniques. With regard to the

mussels in this study, we were capable of determining the levels of genetic diversity within and among species. From such data, inferences about gene movements among populations can be determined since rare electromorphs (electrophoretic alleles) can be traced as markers. More sophisticated analyses utilizing inbreeding coefficients (Wright 1978) and Nei's genetic distance (Nei 1972) can even yield estimates of effective population size (N) as well as the number of migrant individuals per generation (m) moving into a population (Larson 1984, Larson et al. 1984). In this study, genetic distance values (Rogers 1972) were coupled with heterozygosity measurements in order to make assumptions about the relative degree of isolation and population densities.

SITE DESCRIPTION

Evaluation of channel border habitat occurred in all of the 7 navigation pools from Lock and Dam 18 to Lock and Dam 26. Each navigation pool is named after and defined by the down stream dam which forms the pool. At least 2 channel border sites within each pool were selected for sampling. The sites were selected based on similarity of physical conditions among all sites and proximity to the navigation channel. Twenty-eight sampling sites were evaluated (Fig.1 and 2). All sites were examined for species composition and density. Populations at O'Connell Slough, Ft. Madison, and Chaney Creek in Pool 19 and Mud Island in Pool 20 were examined electrophoretically.

Pool 26 extends 41.5 river miles (RM) from lock and dam 26 at Alton, IL to Lock and Dam 25. The upper pool has many large islands and side channels and few channel border habitats. Below the confluence of the Illinois River at Grafton, IL, there are wide channel border areas and all three sample locations were in this river reach (Fig. 1). The three sampling sites located in 32-RM long Pool 25 were also located in the lower end of the pool due to presence of similar channel border habitat in this area. Only 2 sites were sampled in the 27.89 RM of Pool 24 due to the extensive island braiding in this pool. Six sites were sampled in Pool 22 and were located throughout the 23.7 RM of

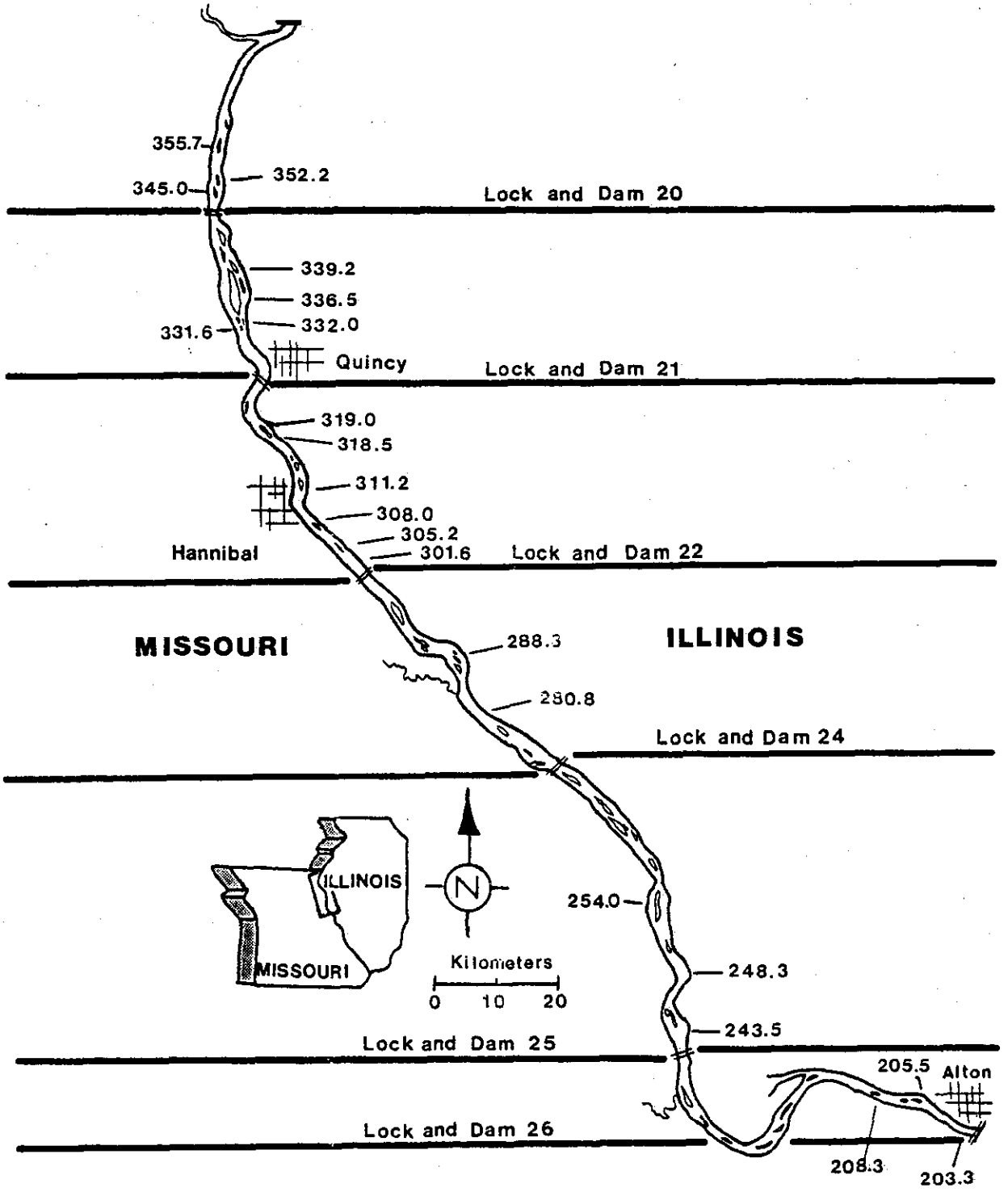

Figure 1. Location of sampling sites in Pools 20 to 26. Left or right channel border area are indicated by the side on which the River Mile is indicated.

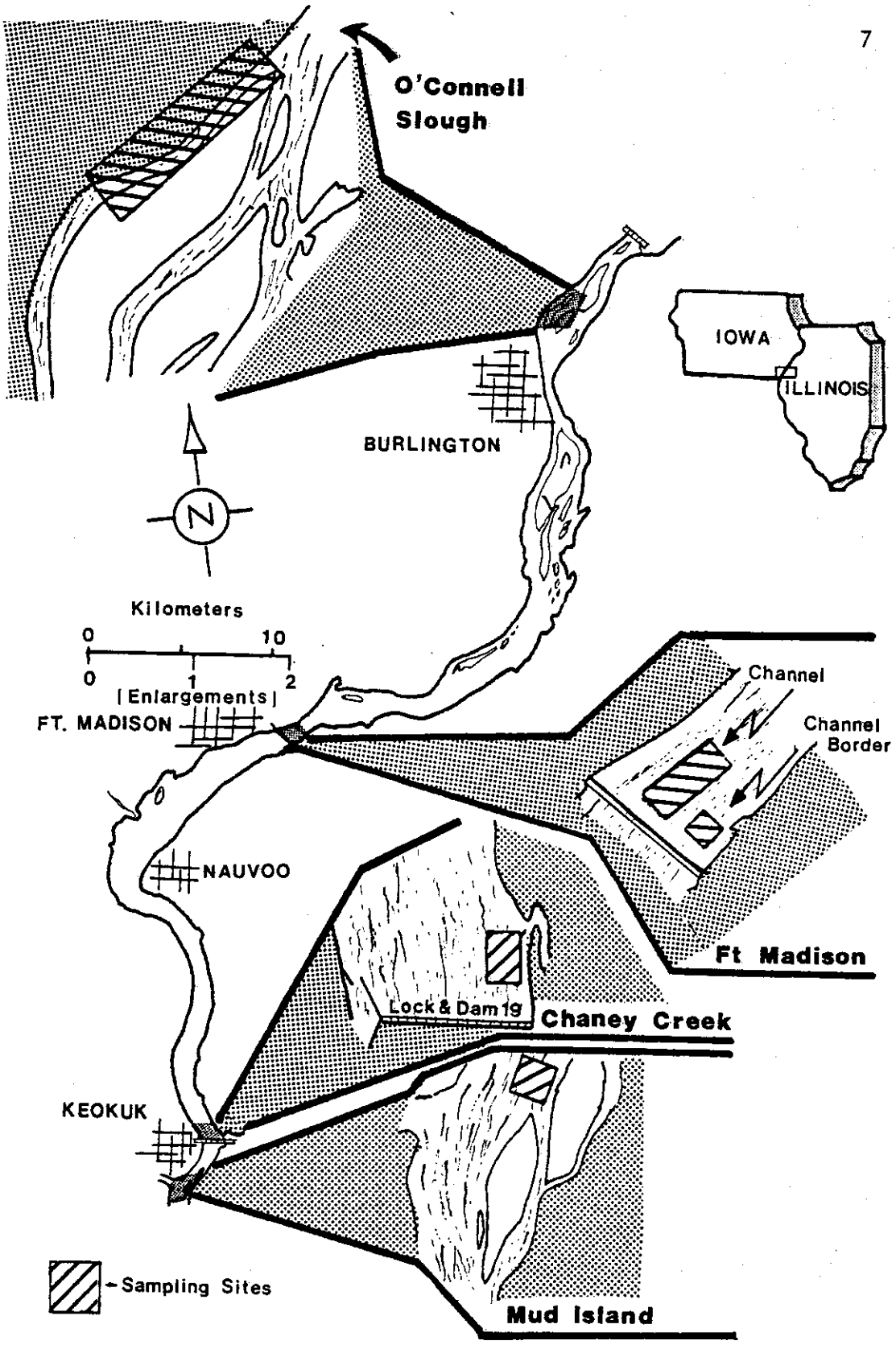

Figure 2. Location of sampling sites in Pool 20 and 19. Insets are sites from which mussels used in electrophoretic analysis were collected.

the pool. All of the sites in Pool 22 were located along the Illinois shore where a majority of the backwaters and channel border habitats are found. Four sampling sites, all above Quincy, were located in the 18.4 RM of Pool 21. Most of the sites were located in Canton Chute on the Illinois side of a large chain of islands found in the pool. Pool 20 had 4 sites in the 21 RM of the pool. Three were in the lower reach of the pool in channel border habitat. The fourth was in the upper part of the pool just above the confluence of the Des Moines River on the Illinois side of the channel between a series of wing dams. This area is known to have a dense mussel bed (Fuller 1978) and was sampled primarily for electrophoretic comparisons.

Pool 19 formed by Lock and Dam 19 at Keokuk, Iowa, is the oldest pool in the system. The dam was completed in 1913. It is 46.3 RM long and has extensive channel border areas in the lower lacustrine area of the pool. Five of the 6 sites sampled were located in this lacustrine reach (Fig. 2). Of the sites evaluated, 2 were known mussel beds, one at O'Connell Slough the other adjacent to the channel at Ft. Madison. Samples from these beds were used to provide population comparisons for electrophoretic analysis. All samples for electrophoretic analysis were collected in June and July, 1985. Specific site or habitat evaluation was done in August, 1985.

METHODS

Mussel populations were sampled using a variety of techniques depending on water depth. Samples in deep water were collected using a 2 m long brailing bar with 50 hooks. Each brailing period was timed and the distance the brail was pulled recorded. The distance was determined by placing a marker bouy at the begining and end of the brailing run and measuring the distance between the bouys with a range finder. Data were then expressed as number per unit effort, density based on surface area sampled and corrected for the low efficiency of the brailing technique (may be as low as 0.6%, Sparks and Blodgett 1983), or frequency of occurrence. A marine benthic dredge with a fine mesh (2 cm) bag and no teeth was also used in deeper water. When this technique was used data was also expressed in the same way as for the brail. Both of these techniques are selective for larger mussels.

Whenever possible (water less than 1.5 m deep) samples were collected by wading and hand picking. A 1 m^2 frame was placed on the river bottom and all mussels within the frame were removed. A minimum of 10 frames were searched at each location sampled by this technique. Data were expressed as number per square meter and frequency. The effort required varied depending on density of mussels at a particular location.

Except for mussels used for electrophoretic analysis, collected mussels were identified, morphometric measurements taken, and a unique identifying number etched in the shell. The mussels were then returned to the habitat from which they were removed.

Four species of mussels; Amblema plicata, Quadrula nodulata, Q. pustulosa, and Q. quadrula, were selected for electrophoretic analysis. A maximum of 25 individuals of each of these species were collected from the sites previously indicated as sampled for electrophoretic analysis. All other specimens were identified, measured, marked and returned to the habitats. The species selected for analysis were chosen because of their ubiquitous occurrence in the Mississippi River system and their importance as commercially valuable species. They also have been found in both channel border habitats and in mussel beds (Anderson et al. submitted). Site selection for electrophoretic analysis was based on relative location within Pool 19 so that sites were located down the length of the pool (Fig. 2)and habitat type including channel and channel border areas. Two sites, both at Ft. Madison, were selected to compare a dense mussel bed and low-density channel border population which were next to each other. The site in Pool 20, a few kilometers below Lock and Dam 19, was selected to

compare the population in a bed located below the physical barrier of the dam a low density bed (Chaney Creek location) just above the dam.

Genetic variation was examined by means of horizontal starch gel elctrophoresis (Selander et al. 1971). Following morphological measurements, specimens were frozen at -20 C. Foot muscle tissue was homogenized in a buffer of 2% 2-phenoxyethanol - 0.25 M sucrose. We chose foot tissue to avoid any possible complications from intestinal contents. The 2-phenoxyethanol buffer dissolves lipid membranes and, along with sucrose, maintains enzyme stability (Nakanishi et al. 1969). The homogenate was then centrifuged at 12,000 g at 0 C for 40 min on a Sorvall RC 2B centrifuge with an ss34 rotor. The supernatant solution was then frozen at -20 C until the following day when it was used for electrophoresis.

Electromorphs (alleles) from 15 presumptive structural loci were analyzed in this study: two malate dehydrogenases (Mdh-1, Mdh-2), three leucine aminopeptidases (Lap-1, Lap-2, Lap-3), two phosphoglucomutases (Pgm-1, Pgm-2), two esterases (Est-1, Est-3), general protein (Gp), glutamate dehydrogenase (Gdh), glutamate oxaloacetate transaminase (Got), superoxided dismutase (Sod), sorbitol dehydrogenase (Sdh), and alcohol dehydrogenase (Adh). Proteins were separated on the following

buffer systems: Mdh-2 on an n-(3-aminopropyl)-morpholine-citrate buffer (pH 6.0) (Clayton and Tretiak 1972); Sdh on a Tris-borate-edta buffer (pH 8.7) (Markert and Faulhaber 1965); Gp, Pgm-2, Lap-1, Lap-2, Lap-3, and Sod on a Tris-citrate, sodium borate buffer (pH 8.7 gel, pH 8.2 electrode) (Selander et al. 1971); Gdh, Got, Mdh-1, Pgm-1, Pgm-2, Est-1, Est-3, and Adh on a Tris-citrate (pH 8.0) (Selander et al. 1971). Pgm-2 was examined on two buffer systems in order to elucidate cryptic variants which did not resolve using any single buffer system. All gels were 15% Sigma starch, Lot 94F-06941.

Electromorphs of an enzyme were assigned numbers corresponding to their mobilities relative to the most common electromorph in Quadrula nodulata. Although, Q. nodulata proved quite scarce, it was the least variable species in terms of number of alleles giving us a reliable organism to use as a reference on each gel. For multiple isozyme systems, the isozyme (different molecular form of a particular enzyme) with the greatest anodal migration is designated as "1" with progressively slower isozymes receiving progressively higher designations (i.e. Mdh-1, Mdh-2).

Populations from each sampling site were compared using Morisita's index of overlap and Shannon-Weaver diversity index (Zar 1985). Electromorph frequency data was analyzed by means of the BIOSYS-1 program

(Swofford and Selander 1981). Allele frequencies, the percentage of polymorphic loci, proportion of heterozygous genes per individual (mean heterozygosity or H), and genetic distance measures were calculated using this program. Roger's (1972) genetic distance was summarized for all populations using the unweighted pair group method with arithmetic averages (UPGMA) of Sneath and Sokal (1973) to produce the phenogram of species relationships.

RESULTS

A total of thirty species of mussels were found during this study (Table 1). The largest number of species (24) occurred in Pool 20 in the mussel bed at Mud Island (RM 362) (TAble 2). Twenty-four species were also found in Pool 19 but the maximum at any one site was 20 species, found in the mussel bed located near the channel at Ft. Madison, IA (RM 384.2). The maximum number of species occurring downstream of the mussel bed at Mud Island (Pool 20) was 7, found at a site (RM 280.8) in Pool 24 (Table 3). Of the thirty sites examined (Figs. 1 and 2) only 18 (Tables 2 and 3) had mussels and only those from Mud Island upstream had densities greater than 1 mussel per m^2.

Amblema plicata was the most frequently found mussel, occurring at all but 2 of the sites where mussels where found (Tables 2 and 3). It was usually the most abundant mussel found; densities ranged from 0.03 to 15.1 /m^2. Other species which were frequently collected and locally abundant included Quadrula pustulosa and Q. quadrula. Below the Mud Island site (RM 362) species other than A. plicata only occurred sporatically. Above this site 9 taxa (Tables 2 and 3) were found at all sampling sites though abundance at specific sites varied. Four species; Actinonaias ligamentina, Cyclonaias tuberculata, Plethobasus cyphyus, and Pleurobema cordatum, were found only at

Table 1. List of species collected from Pools 19 through 26, on Mississippi River.

Species Name	Common Name
Actinonaias ligamentina	mucket
Anodonta grandis corpulenta	stout floater
A. grandis grandis	common floater
A. imbecillis	paper pondshell
Amblema plicata plicata	three-ridge
Arcidens confragosus	rock pocketbook
Carunculina parva	lilliput
Cumberlandia monodonta	spectacle case
Cyclonaias tuberculata	purple wartyback
Ellipsaria lineolata	butterfly
Elliptio dilatata	spike
Fusconia flava	Wabash pigtoe
Lampsilis ovata	pocketbook
L. teres	yellow sandshell
Leptodea fragilis	fragile papershell
Ligumia recta	black sandshell
Megalonaias gigantea	washboard
Obliquaria reflexa	three-horned wartyback
Obovaria olivaria	hickorynut
Plethobasus cyphyus	bullhead
Pleurobema cordatum	Ohio River pigtoe
Potamilus alatus	pink heelsplitter
P. laevissima	pink papershell
Quadrula metanevra	monkeyface
Q. nodulata	wartyback
Q. pustulosa pustulosa	pimpleback
Q. quadrula	mapleleaf
Strophitus undulatus	squawfoot
Tuncilla donaciformis	fawnsfoot
T. truncata	deertoe

Table 2. Density of mussels at sites described as mussel beds in Pools 19 and 20.

	Pool 20	Pool 19	
	Mud Is. RM 362	Ft. Madison* RM 384.2	O'Connell Slough RM 407.0
Actinonaias ligamentina	0.04	—	—
Anodonta grandis corpulenta	1.14	0.18	0.08
A. grandis grandis	—	—	—
A. imbecillis	—	4.02	—
Amblema plicata plicata	15.10	1.86	1.24
Arcidens confragosus	0.04	—	—
Carunculina parva	—	—	—
Cumberlandia monodonta	—	—	—
Cyclonaias tuberculata	0.01	—	—
Ellipsaria lineolata	3.25	0.07	—
Elliptio dilatata	0.34	—	—
Fusconaia flava	1.08	0.09	0.48
Lampsilis ovata	2.83	0.32	—
L. teres	—	—	—
Leptodea fragilis	1.62	2.23	0.56

Table 2. (continued)

	Pool 20	Pool 19	
	Mud Is.	Ft. Madison*	O'Connell Slough
Ligumia recta	0.72	0.02	—
Megalonaias gigantea	2.45	0.82	—
Obliquaria reflexa	5.11	1.59	0.24
Obovaria olivaria	2.84	0.41	0.88
Plethobasus cyphyus	0.01	—	—
Pleurobema cordatum	0.01	—	—
Potamilus alatus	2.66	0.75	—
P. laevissima	1.74	0.30	0.08
Quadrula metanerva	1.56	0.02	—
Quadrula nodulata	2.68	3.82	0.13
Quadrula pustulosa pustolosa	10.96	2.82	1.91
Quadrula quadrula	12.84	5.48	1.53
Strophitus undulatus	—	0.70	—
Truncilla donaciformis	0.84	4.02	0.16
T. truncata	0.90	1.55	0.24
Total	70.77	31.07	7.53
No. Species	24	20	12

* Sparks and Blodgett, unpublished data

Table 3. Density of mussels in channel border areas of Pools 26 through 19, Mississippi River. Densities are in Number per meter squared.

	Pool	26	25			24	22		21		20	19			
SPECIES	River Mile	203.3	243.5	248.3	254.0	280.8	301.6	311.2	332.0	336.5	345.0	364.8	374.4	378.0	384.2
Actinonaias ligamentina															
Anodonta grandis corpulenta						0.02						0.61	0.20	0.25	1.07
A. grandis grandis															
A. imbecillis												0.43			0.67
Amblema plicata plicata		0.07	0.10	0.06		0.14	0.09	0.03	0.03	0.10		0.86	0.56	0.75	1.67
Arcidens confragosus												0.01			0.07
Carunculina parva												0.01			
Cumberlandia monodonta												0.01	0.01		
Cyclonaias tuberculata															
Ellipsaria lineolata															
Elliptio dilatata															
Fusconia flava						0.02						0.12	0.01	0.06	0.04
Lampsilis ovata										0.05					
L. teres												0.12	0.08	0.25	0.37
Leptodea fragilis						0.01						0.18	2.16	0.12	0.22
Ligumia recta															
Megalonaias gigantea												0.06	0.01	0.06	
Obliquaria reflexa						0.01	0.01					0.24	0.16	0.02	0.22
Obovaria olivaria								0.06					0.04		
Plethobasus cyphyus															
Pleurobema cordatum															
Potamilus alatus												0.24	0.16	0.12	0.63
P. laevissima					0.02		0.02					0.06	0.04		0.67
Quadrula metanevra															
Q. nodulata						0.01						0.01	0.04	0.02	
Q. pustulosa pustulosa											0.03	0.06	0.08	0.25	0.01
Q. quadrula				0.03		0.01						0.24	0.76	0.37	0.33
Strophitus undulatus															
Tuncilla donaciformis												0.12	0.12	0.37	0.11
T. truncata												0.01	0.04	0.02	0.01
TOTAL		0.07	0.10	0.09	0.02	0.22	0.12	0.09	0.03	0.15	0.03	3.39	4.47	2.66	6.07
Total number of species		1	1	2	1	7	3	2	1	2	1	18	16	13	14

the Mud Island site but in very low densities (<0.04 /m^2 (Table 2). Anodonta imbecillis, Carunculina parva, Cumberlandia monodonta, and Strophitus undulatus were found only in Pool 19.

Sites identified as mussel beds (Peterson 1984) included Mud Island in Pool 20 (RM 362) and Ft. Madison channel (RM 384.2) and O'Connell Island Slough (RM 407) in Pool 19 (Table 2). The highest mussel density occurred in these sites and ranged from 7.53 (RM 407) to 70.77 (RM 362) /m^2. The Ft Madison and Mud Island sites also had the highest diversity, 3.55 and 3.56 respectively (Table 4). Diversity was also high, approximately 3, in channel border habitats in Pool 19 but was always quite low, < 2, in border habitats in the lower pools (Table 4). This reflects the low density and number of species found in the lower pools. By contrast, densities in the channel border sites in Pool 19 ranged from 0.66 to 6.07 /m^2 and the number of species found ranged from 13 to 18 (Table 4). Distribution of individuals among taxa was relatively even (Table 4) except at the Nauvoo site (RM 374.4) and Pool 24 site (RM 280.8) where dominance approached 40% as a result of high densities of Leptodea fragilis and Amblema plicata repectively.

Comparing composition of the mussel communities evaluated showed the greatest similarity between the communities in the channel border habitat of Pool 19

Table 4. Summary of density and number of speecies in sampled mussel populations with 7 or more species. Shannon-Weaver diversity index (log 2) and evenness are listed for these populations.

	Total Density No./M^2	Number of Species	Diversity Index	Evenness
Pool 19				
O'Connell (Channel)	7.53	12	2.97	0.83
Ft. Madison (Channel)	31.07	20	3.55	0.82
Ft. Madison (Border)	6.07	14	3.04	0.85
Devil's Is. (Border)	2.66	13	3.08	0.83
Nauvoo (Border)	4.47	16	2.51	0.63
Keokuk (Border)	3.39	18	3.33	0.80
Pool 20				
Mud Island (Channel)	70.77	24	3.56	0.78
Pool 24				
RM 280.8 (Border)	0.22	7	1.85	0.66

Channel- Mussel Bed
Border- Low density channel border population

and between the mussel beds of the Mud Island and Ft. Madison channel sites (Table 5). Community similarity rarely exceeded 0.7 (a value of 1.0 identical communities in terms of species composition and distribution of individuals within species) at other sites. The similarity between the O'Connell Island site and other sites was the most variable and ranged from a low of 0.63 for Mud Island to a high of 0.86 when compared to the community at the Nauvoo site. The communities evaluated genetically showed similarities dependent on habitat. Thus the Ft. Madison border site was similar to the Keokuk site (similarity value of 0.88) and the Ft. Madison channel site was similar to the Mud Island site (similarity value of 0.82).

Allele frequency data for polymorphic loci are given in Tables 6 to 8. The following six loci were fixed for a single allele in all populations surveyed: Gp-1, Gdh, Got, Sod, Mdh2, and Est-1. One other locus, Est-3, was monomorphic in all populations but Quadrula quadrula from Chaney Creek and the channel population from Ft. Madison.

A wide range of variability was demonstrated among the four species surveyed. The least variable species was Quadrula nodulata. The highest proportion of average heterozygosity (H) determined by a direct count of heterozygotes for Q. nodulata was at the Chaney Creek site. The O'Connell Island population cannot

Table 5. Community similarity using Morisita's index of overlap between all sampled populations with 7 or more species from Pools 24, 20 and 19. A value of 1.0 indicates identical communities in terms species and distribution of individuals.

	1	2	3	4	5	6	7	8
1. O'Connell (Channel)	1.0							
2. Ft. Madison (Channel)	0.75	1.0						
3. Ft. Madison (Border)	0.77	0.62	1.0					
4. Devil's Is. (Border)	0.67	0.55	0.81	1.0				
5. Nauvoo (Border)	0.86	0.64	0.87	0.90	1.0			
6. Keokuk (Border)	0.73	0.74	0.88	0.84	0.89	1.0		
7. Mud Island (Channel P. 20	0.63	0.82	0.62	0.65	0.69	0.67	1.0	
8. Pool 24 RM. 280.8 (Border)	0.76	0.57	0.57	0.69	0.64	0.56	0.44	1.0

Table 6. Allelic Frequencies at the nine loci, polymorphic in all Amblema plicata (AP) from this study.

Locus and Allele	AP-1	AP-2	AP-3	AP-4	AP-5
MDH-1					
100	—	—	—	—	—
86	—	—	—	—	—
82	1.000	1.000	1.000	1.000	1.000
71	—	—	—	—	—
LAP-1					
100	0.019	0.500	0.167	—	—
96	0.944	0.500	0.250	0.950	0.900
92	0.037	—	0.583	0.050	0.100
88	—	—	—	—	—
71	—	—	—	—	—
LAP-2					
106	—	—	—	—	—
103	—	—	—	—	—
100	—	—	—	—	—
97	0.964	1.000	0.917	1.000	1.000
95	0.036	—	—	—	—
94	—	—	0.830	—	—
89	—	—	—	—	—
LAP-3					
100	—	—	—	—	—
90	1.000	1.000	1.000	1.000	1.000
89	—	—	—	—	—
PGM-1					
130	—	—	0.083	0.100	0.050
126	1.000	1.000	0.917	0.900	0.950
113	—	—	—	—	—
100	—	—	—	—	—
95	—	—	—	—	—
110	—	—	—	—	—

1- Chaney Creek
2- O'Connell Slough
3- Mud Island
4- Ft. Madison Channel Border
5- Ft. Madison Channel

Table 6. (continued)

Locus and Allele	AP-1	AP-2	AP-3	AP-4	AP-5
PGM-2					
120	—	—	—	—	—
110	—	—	—	—	—
102	0.575	—	0.333	0.550	0.500
100	—	—	—	—	—
94	—	—	—	—	—
86	0.425	1.000	0.667	0.450	0.500
EST-3					
100	1.000	1.000	1.000	1.000	1.000
42	—	—	—	—	—
SDH					
100	—	—	—	—	—
91	—	—	—	—	—
72	1.000	1.000	1.000	1.000	1.000
ADH					
121	0.857	0.250	0.833	0.950	0.950
100	—	—	—	—	—
81	0.143	0.750	0.167	0.050	—

1- Chaney Creek
2- O'Connell Slough
3- Mud Island
4- Ft. Madison Channel Border
5- Ft. Madison Channel

Table 7. Allelic frequencies at the nine loci polymorphic in all *Quadrula quadrula* (QQ) from this study.

Locus and allele	QQ-1	QQ-2	QQ-3	QQ-4	QQ-5
MDH-1					
100	0.316	0.450	0.250	0.350	0.308
86	0.684	0.550	0.750	0.600	0.692
82	—	—	—	—	—
71	—	—	—	0.050	—
LAP-1					
100	—	0.063	—	—	—
96	—	—	—	—	0.038
92	—	—	—	—	—
88	0.833	0.938	0.800	0.800	0.846
71	0.167	—	0.200	0.200	0.115
LAP-2					
106	—	—	—	—	0.038
103	—	—	—	—	—
100	—	—	0.100	—	—
97	0.625	0.900	0.800	0.850	0.923
95	—	—	—	—	—
94	0.375	0.100	0.100	0.150	0.038
89	—	—	—	—	—
LAP-3					
100	1.000	1.000	1.000	1.000	1.000
90	—	—	—	—	—
89	—	—	—	—	—
PGM-1					
130	—	—	—	—	—
126	—	—	—	—	—
113	0.667	1.000	0.250	0.438	0.438
110	—	—	—	—	0.188
100	0.333	—	0.750	—	0.630
95	—	—	—	0.563	0.313

1- Chaney Creek
2- O'Connell Slough
3- Mud Island
4- Ft. Madison Channel Border
5- Ft. Madison Channel

Table 7. (continued)

Locus and allele	QQ-1	QQ-2	QQ-3	QQ-4	QQ-5
PGM-2					
120	0.176	0.100	0.200	0.300	0.077
110	0.824	0.900	0.800	0.700	0.923
102	—	—	—	—	—
100	—	—	—	—	—
94	—	—	—	—	—
86	—	—	—	—	—
EST-3					
100	0.900	1.000	1.000	1.000	0.923
42	0.100	—	—	—	0.077
SDH					
100	0.536	0.700	0.750	0.917	0.727
91	0.071	—	—	—	—
72	0.393	0.300	0.250	0.083	0.273
ADH					
121	—	0.300	—	—	—
100	1.000	0.700	1.000	1.000	1.000
81	—	—	—	—	—
73	—	—	—	—	—

1- Chaney Creek
2- O'Connell Slough
3- Mud Island
4- Ft. Madison ChannelBorder
5- Ft. Madison Channel

Table 8. Allelic frequencies at the nine loci polymorphic in all *Quadrula nodulata* (QN) and *Quadrula pustulosa* (QP) from this study.

Locus and allele	QN-1	QN-2	QN-3	QP-1	QP-2	QP-3
MDH-1						
100	1.000	1.000	1.000	1.000	0.750	1.000
86	—	—	—	—	—	—
82	—	—	—	—	—	—
71	—	—	—	—	0.250	—
LAP-1						
100	0.917	—	1.000	0.667	0.750	1.000
96	0.83	—	—	0.333	0.250	—
92	—	1.000	—	—	—	—
88	—	—	—	—	—	—
71	—	—	—	—	—	—
LAP-2						
106	—	—	—	0.313	0.250	0.375
103	—	—	—	—	0.500	0.250
100	0.417	1.000	1.000	0.625	0.250	0.375
97	0.500	—	—	—	—	—
95	—	—	—	—	—	—
94	—	—	—	0.063	—	—
89	0.083	—	—	—	—	—
LAP-3						
100	1.000	1.000	0.917	1.000	1.000	1.000
90	—	—	—	—	—	—
89	—	—	0.083	—	—	—
PGM-1						
130	1.000	1.000	—	—	—	—
126	—	—	—	—	—	—
113	—	—	—	—	—	—
110	—	—	—	—	—	—
100	—	—	1.000	0.500	—	—
95	—	—	—	0.500	1.000	1.000
PGM-2						
120	0.800	1.000	—	—	—	—
110	—	—	—	—	0.250	0.250
102	—	—	—	—	—	—
100	0.200	—	1.000	0.500	—	—
94	—	—	—	0.500	0.750	0.750
86	—	—	—	—	—	—

Table 8. (continued)

Locus and allele	QN-1	QN-2	QN-3	QP-1	QP-2	QP-3
EST-3						
100	1.000	1.000	1.000	1.000	1.000	1.000
42	—	—	—	—	—	—
SDH						
100	1.000	1.000	1.000	0.750	0.750	0.875
91	—	—	—	0.250	0.250	0.125
72	—	—	—	—	—	—
ADH						
121	—	—	—	—	—	—
100	1.000	1.000	1.000	0.167	—	—
81	—	—	—	—	—	—
73	—	—	—	0.833	1.000	1.000

1- Channey Creek
2- O'Connell Slough
3- Mud Island
4- Ft. Madison Channel-Border
5- Ft. Madison Channel

really be considered since only one specimen was sampled. Nevertheless, in samples of five or greater, Q. nodulata demonstrated considerably lower levels of heterozygosity than any other species (Table 9). Quadrula nodulata demonstrated the lowest population densities of any of the species sampled here; consequently, it is not surprising to find low levels of genetic variability which are often associated with low population density (Lewontin 1974).

Amblema plicata also showed relatively low levels of variability with H ranging between 0.047 (border site at Ft. Madison) and 0.068 (Chaney Creek) (Table 9). Amblema plicata exhibited the lowest range of mean alleles per locus (1.1 - 1.4) along with Q. nodulata (1.1 and 1.3). Unlike Q. nodulata, however, low densities are not associated with A. plicata which shows relatively high densities at all localities (Table 10).

Quadrula quadrula and Q. pustulosa were the most genetically diverse species examined in this study (Tables 7, 8, 9). Average heterozygosity values for Q. quadrula were comparable to those of Q. pustulosa with a range of 0.095 to 0.153. The mean number of alleles for Q. quadrula was higher than that found in Q. pustulosa with a range of 1.4 to 1.7 versus 1.3 to 1.5. However, the values for Q. pustulosa may change when sample sizes are comparable to those of Q. quadrula.

Table 9. Percentage of polymorphic loci and mean heterozygosity values summarized over all populations.

Population	Mean Sample Size per locus	Mean No. of alleles per locus	Percentage of loci * Polymorphic	Mean Heterozygosity Direct Count	Mean Heterozygosity HDYWBG** Expected
1. AP-CHA	24.2 (1.1)	1.3 (0.2)	26.7	0.068 (0.040)	0.062 (0.036)
2. AP-O'C	2.0 (0.0)	1.1 (0.1)	13.3	0.033 (0.033)	0.078 (0.054)
3. AP-MUD	6.0 (0.0)	1.4 (0.2)	33.3	0.100 (0.048)	0.116 (0.052)
4. AP-FTB	10.0 (0.0)	1.3 (0.1)	26.7	0.047 (0.024)	0.061 (0.036)
5. AP-FT	10.0 (0.0)	1.3 (0.1)	26.7	0.067 (0.053)	0.061 (0.036)
6. QN-CHA	5.2 (0.4)	1.3 (0.2)	20.0	0.033 (0.024)	0.076 (0.046)
7. QN-O'C	1.0 (0.0)	1.0 (0.0)	0.0	0.000 (0.000)	0.000 (0.000)
8. QN-FT	5.9 (0.1)	1.1 (0.1)	6.7	0.011 (0.011)	0.011 (0.011)
9. QP-O'C	6.3 (0.7)	1.5 (0.2)	40.0	0.147 (0.077)	0.230 (0.084)
10. QP-MUD	1.9 (0.1)	1.4 (0.2)	33.3	0.167 (0.063)	0.189 (0.074)
11. QP-FT	3.8 (0.1)	1.3 (0.2)	20.0	0.100 (0.059)	0.095 (0.057)

AP- Amblema plicata
QN- Quadrula nodulata
QP- Quadrula pustulosa
QQ- Quadrula quadrula

CHA- Chaney Creek
FT- Ft. Madison Channel
FTB- Ft. Madison Channel Border
MUD- Mud Island
O'C- O'Connell Slough

Table 9. (continued)

Population	Mean Sample Size per locus	Mean No. of alleles per locus	Percentage of loci * Polymorphic	Mean Heterozygosity Direct Count	Mean Heterozygosity HDYWBG** Expected
12. QQ-CHA	16.7 (1.1)	1.5 (0.2)	46.7	0.113 (0.039)	0.187 (0.059)
13. QQ-O'C	7.3 (0.8)	1.4 (0.8)	40.0	0.095 (0.044)	0.130 (0.050)
14. QQ-MUD	4.2 (0.3)	1.5 (0.2)	40.0	0.153 (0.058)	0.168 (0.056)
15. QQ-FTB	9.6 (0.3)	1.5 (0.2)	40.0	0.123 (0.051)	0.152 (0.055)
16. QQ-FT	12.5 (0.4)	1.7 (0.2)	46.7	0.099 (0.032)	0.153 (0.057)

* A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99.

** Unbiased estimate (See Nei, 1978)

AP- Amblema plicata
QN- Quadrula nodulata
QP- Quadrula pustulosa
QQ- Quadrula quadrula

CHA- Chaney Creek
FT- Ft. Madison Channel
FTB- Ft. Madison Channel Border
MUD- Mud Island
O'C- O'Connell Slough

Nevertheless, both species are substantially more variable than that of A. plicata.

Inbreeding coefficients, F, (Wright 1943, 1965, 1978) for all populations were calculated for all loci and all populations (see Appendix). Unfortunately, the sample sizes for many of the populations sampled were relatively low (less than 20). Fst, the fraction of total genetic variance partitioned among populations, was calculated for all populations of A. plicata except the O'Connell Island Slough where only two specimens were taken. All populations of Q. quadrula sampled electrophoretically were utilized for the calculation of Fst. Amblema plicata exhibited an Fst of 0.14 while Q. quadrula demonstrated an Fst of 0.129. Wright (1943) suggests that the formula Fst = 1/(4Nm + 1) gives a satisfactory estimate of the gene flow parameter, Nm (the product of the effective population size, N, and the rate of migration, m), if m is small. Since Nei et al. (1977) warn that the accuracy of this formula is questional be when the number of subdivided populations examined is small, we did not calculate the gene flow parameter for Q. pustulosa or Q. nodulata. Our data suggest that gene flow is marginally higher among all populations of Q. quadrula (Nm = 1.54) than A. plicata (Nm = 1.69).

Table 10. Density of target species of mussels from genetically evaluated populations.

	Amblema plicata	*Quadrula quadrula*	*Quadrula pustulosa*	*Quadrula nodulata*	Total
Mud Island RM 362	15.10	12.84	10.96	2.68	70.77
Chaney Creek RM 364.8	0.86	0.76	0.08	0.04	4.47
Ft. Madison Channel RM 384.2	1.86	5.48	2.82	3.82	31.07
Ft. Madison Border RM 384.2	1.67	0.33	0.01	0.0	6.07
O'Connell Island RM 407.0	1.24	1.53	1.91	0.13	7.58

DISCUSSION

The marked reduction in mussel densities in border-type habitat downstream of Lock and Dam 19 is consistent with the poor bed quality in pools below Pool 19 by Fuller (1978). Only 69 mussels were collected below RM 362 in the lower 6 pools compared to 1832 taken from channel border habitats in Pool 19. An additional 1350 were collected by brail from mussel bed sites at Mud Island, Ft. Madison Channel, and O'Connell Slough. The sites sampled in the lower pools were selected based on similar river morphometry to those channel border sites in Pool 19. However, substrates were much different in many of the sites, being composed of sand rather than silt or silt/sand as were the sites in Pool 19. This difference in substrate may in part account for the lower mussel density or absence of mussels at sites in the lower pools. Where mussels were found in slightly higher densities, RM 280.8 (Pool 24) and RM 301.6 (Pool 22), the site was associated with a backwater area and the substrate was not as sandy. Other factors have been suggested as contributing to the smaller mussel populations in lower pools. Below the confluence with the Des Moines River, burial and various types of pollutants from tributaries may have reduced density and diversity of mussels (Ellis 1931, Fuller 1978). Another possible reason for the lower densities in channel border areas

is the lack of aquatic macrophytes in the lower pools. The populations found in channel border habitats in Pool 19 were all located adjacent to or just downstream of, macrophyte beds. These beds could provide an abundant source of particulate organic matter and plankton for filter feeding mussels.

While diversity and density were low at sites in Pools 26 through lower Pool 20, they were relatively high at the upper sites. Historical records indicated a maximum of 21 species in this area (Ellis 1930-31 survey as reported in van der Schalie and van der Schalie 1952). Perry in 1975 found 18 and 11 species in Pools 19 and 20 respectively (Rasmussen 1979) and a survey in 1979-80 found 20 and 14 in Pools 19 and 20 respectively (Ecological Analysts Inc. 1981). Our record of 30 species in Pools 19 and 20 represent the largest number of species found since around the turn of the century. In addition, Cawley (1984) reported Lampsilis higginsi and Tritogonia verrucosa in Pool 19 in the O'Connell Island and Burlington area. Thus 32 species of mussels have been found from Mud Island (RM 362, Pool 20) to O'Connell Island Slough (RM 407, Pool 19). Again this may reflect optimum habitats for mussels in this river reach.

In terms of density and species composition, the relationship between mussels found in channel border habitats and those in mussel beds in or adjacent to the

channel show only average similarity (Table 5). Diversity in the channel border areas is not as great nor are populations as dense, and only one species, Lampsilis teres, was unique to this habitat. Cumberlandia monodonta, which was collected at 2 border sites, usually inhabits areas with rocky substrates and thus may only have been washed into this area during high flows. Similarly, Carunculina parva usually occurs in lakes or pools and may have been washed into the river during spring floods. Some species such as the rare Cyclonaias tuberculata and Plethobasus cyphyus as well as the more abundant Ellipsaria lineolata, Lampsilis ovata, and Obovaria olivaria were restricted to mussel beds where current velocities are higher and substrates coarser. However, Amblema plicata and the Quadrula group, except for metanevra, were found in both habitat types, A. plicata usually being the most abundant mussel encountered.

Davis (1984) has suggested that low genetic diversity appears to be associated with declining species diversity, ancient lineages, and low shell phenotypic diversity. Our data from populations of A. plicata and Q. nodulata are consistent with the findings of Davis that species within the subfamily Ambleminae exhibit decreased levels of polymorphism and heterozygosity with respect to those he reports for the Pleurobemini and the non-lanceolate Elliptio. Davis

also suggested that within some lineages, certain species may exhibit high levels of genic variability. The closely related species Q. pustulosa exhibited the highest H ranging from 0.100 (channel at Ft. Madison) to 0.167 (Mud Island). Likewise, Q. quadrula showed higher heterozygosities ranging between 0.095 (O'Connell Island Slough) and 0.153 (Mud Island).

Nevertheless, characteristics of demic structure such as levels of inbreeding and gene flow may also play an equally significant role. The low levels of H in Q. nodulata are likely due to bottlenecks associated with low densities at the sampled sites. Q. nodulata exhibited the lowest levels of genetic diversity with H levels of 0.011 at the channel bed at Ft. Madison and 0.033 at Chaney Creek (Table 9). Q. nodulata showed the lowest densities of all species surveyed with a high density of 3.82 individuals/m^2 at the Ft. Madison channel and 0.04 inidividuals/m^2 at Chaney Creek.

Although the population with the lowest density gives the highest apparent H, this may be a misleading statistic since Chaney Creek may represent a sparse population of migrants from different founders. This is evident from the fact that there is a substantial drop in actual heterozygosity versus expected heterozygosity (Table 9). Hornbach et al. (1980) investigated electrophoretic variation in 13 populations of Sphaerium striatinum and one population

each of S. simile, S. fabale, and S. occidentale. Mean heterozygosity per population was 0.0038 for all four species. They concluded that self-fertilization in these hermaphroditic species was responsible for the low levels of H. The Chaney Creek sample also contained a higher mean number of alleles per locus despite a very low density of individuals capable of supporting that variation. On the other hand the Ft. Madison population demonstrates an actual H equal to the expected H which shows that the population is in Hardy-Weinberg equilibrium. This coupled with the fact that population densities are high suggests a self-sustaining, reproductive population. Low population densities and bottlenecks have been shown to be responsible for low electrophoretic variability in natural populations of other species (Lewontin 1974, Kimura 1983).

A comparison of the two remaining species, A.plicata and Q. quadrula in the electrophoretic analysis are more insightful since sample sizes as ell as the number of sites sampled are more representative. Heterozygosity levels for A. plicata from Chaney Creek, the channel site at Ft. Madison, and the channel border site at Ft. Madison are similar for direct count measurements and nearly equivalent for expected H from Hardy-Weinberg calculations. In addition to this, a Nei's (1972) identity (I) value of 0.999 (Appendix B)

lower than that reported for A. plicata (Table 11). Low levels of gene flow among populations of Q. quadrula within Pool 19 have resulted in higher levels of inbreeding than that found in A. plicata.

Reasons for the differences in gene flow among populations of A. plicata and Q. quadrula are speculative, but are probably a result of differences in glochidial movements on host fish. Glochidia from Q. quadrula utilize flathead catfish as a host species. A. plicata utilize 15 different host fish for their glochidia including such wide ranging species as white bass and largemouth bass. Evidence in support of this contention may be found by contrasting migration rates between popualtions of both species in Pool 19 with that found at Mud Island in Pool 20. Since the dam separating Pools 19 and 20 should act as an effective barrier to fish movement, one would expect migration rate for A. plicata between populations in Pool 19 and the Mud Island population in Pool 20 to have a substantially lower m among populations in Pool 19. The migration rates summarized in Table substantiate this. In fact migration rates across the dam between Pool 19 and 20 for both A. plicata and Q. quadrula are roughly equivalent. This is graphically demonstrated in phenogram of Roger's (1972) distance relationships in Figure 3, where the branch distance between Mud Island and the populations clustered from Pool 19 are

was observed in all three pairwise comparisons among these populations. Nei (1975) suggests that there is a relationship between I and migration rate between populations; such that,

$$I = \underline{m}/\underline{m} + \underline{v}$$

where m= the migration rate and v = the mutation rate. Since the mutation rate is unknown, a rough estimate of 2×10^{-6} has been considered reasonable in previous studies (Larson et al. 1984) and furnishes a means of comparison in this study. Based upon this formula migration rate is relatively high among those populations, 2×10^{-3}. All of these data suggest that gene flow among these populations is relatively high.

Quadrula quadrula exhibited higher H values than those found in A. plicata at all populations including the Chaney Creek, Ft. Madison channel, and Ft. Madison border sites (Table 9). However, there are striking differences between the two species at these sites. Mean heterozygosity values from direct counts of heterozygotes were consistently lower than those calculated from allele frequencies fit to the assumptions of random mating (Hardy-Weinberg equilibrium). This situation is a clear indication of inbreeding (Gardner and Snustad 1984), since inbreeding results in a drop in heterozygosity although the allelic frequencies will remain unchanged. Migration rates among these three populations were substantially

Table 11. Relative migration rates, m, between selected conspecific populations of Amblema plicata and Quadrula quadrula on Pools 19 and 20. Migration rates were calculated from Nei's (1972) I.

Amblema plicata

	Channel	Ft. Madison Channel	Ft. Madison Channel Border
Mud Island	5.7×10^{-5}	6.9×10^{-5}	5.7×10^{-5}
Channel		2.0×10^{-3}	2.0×10^{-3}
Ft. Madison Channel			2.0×10^{-3}

Quadrula quadrula

	Channel	Ft. Madison Channel	Ft. Madison Border	O'Connell Island
Mud Island	8.9×10^{-5}	6.9×10^{-5}	4.8×10^{-5}	3.3×10^{-5}
Channel		9.3×10^{-5}	5.5×10^{-5}	7.2×10^{-5}
Ft. Madison Channel			1.5×10^{-4}	6.9×10^{-5}
Ft. Madison Border				4.6×10^{-5}

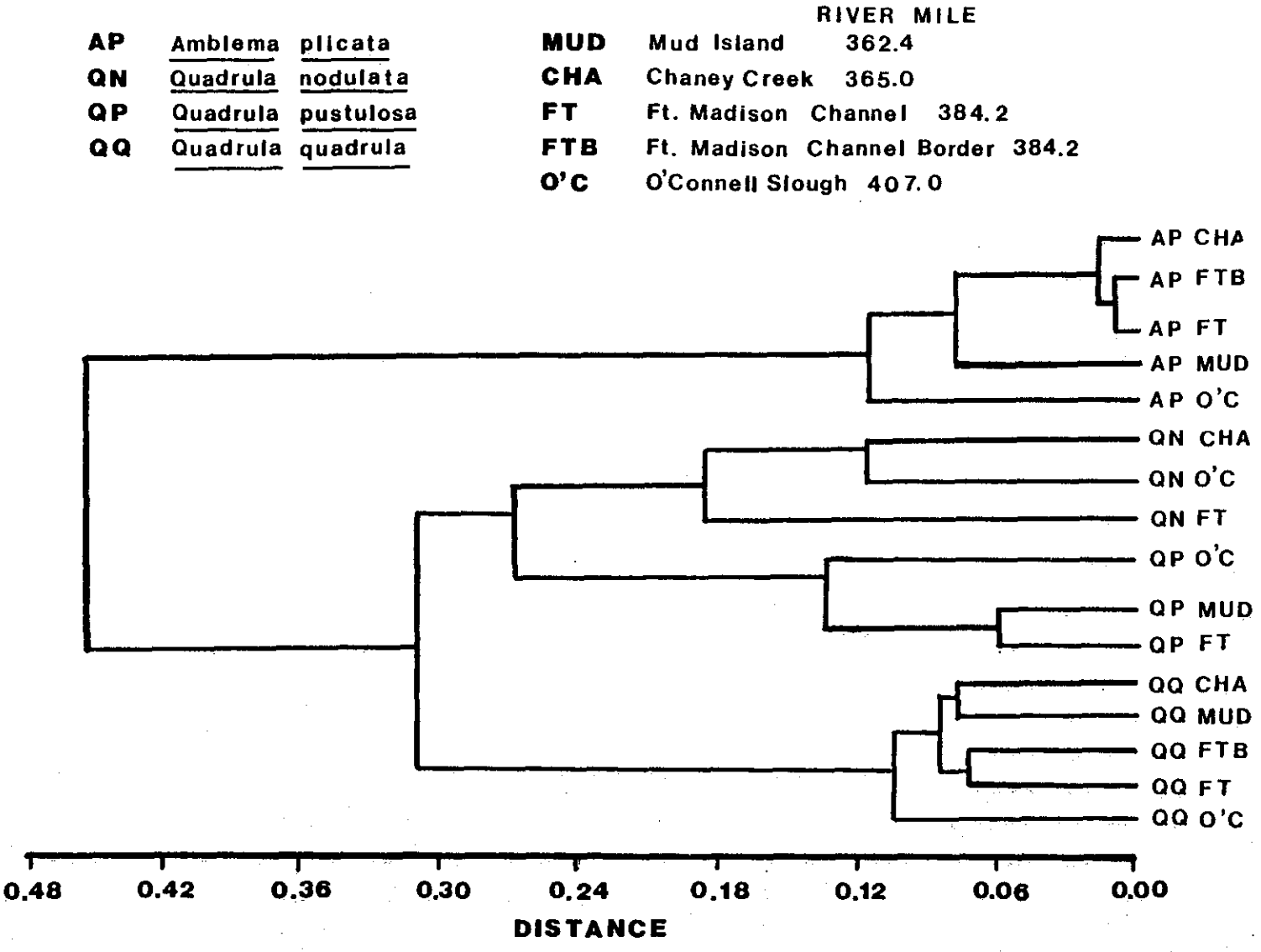

Figure 3. A dendiogram generated by UPGMA summarizing Nei's (1972) distance and relationships among populations of mussels analyzed electrophoretically.

equivalent for both species. However, the relative levels of clustering demonstrate a greater level of divergence among populations of Q. quadrula within Pool 19 than the degree of divergence within populations of A. plicata. Again this is consistent with the notion that levels of gene flow are higher among populations of A. plicata within Pool 19 than among populations of Q. quadrula. Although these data are based upon preliminary surveys, further investigation is likely to show similar patterns in other species as well as other pools within the Mississippi River.

Conclusion:

1. Low density mussel beds occur in may channel border areas. However, the density and diversity may be dependent on substrate type and association with a potential food source, such as aquatic macrophyte beds, rather than proximity to a high density mussel bed.

2. Both species diversity and density are much higher in mussel beds of Pool 19 than down stream pools with the exception of the mussel bed below Lock and Dam 19 which had the highest diversity and density of any bed.

3. Mussel populations found in channel border areas of Pool 19 are more similar to each other than to high density beds in the channel. This indicates some species occur which are unique to each habitat type.

4. In spite of Lock and Dam 19, there is movement between popultions of Amblema plicata as indicated by high heterozygosity in this species. However, movement between populations of Quadrula quadrula on occurs when populations are in close proximity to each other. Lock and Dam 19 does seem to act as a barrier to this species.

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