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T E C H N I C A L R E P O R T

Turtle communities in the Upper Mississippi River System, 1992- 1995

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EXECUTIVE SUMMARY

The fisheries component of the Long-Term Resource Monitoring Program (LTRMP), which utilizes many sorts of collecting methods, began sampling in 1989. Beginning in 1992, fisheries component specialists at each of six field stations began to systematically record data on turtles collected as a by-product of fisheries monitoring. Herein we summarize data collected on turtle communities in the UMRS from 1992 to 1995. Our analysis is important because it is the first based on long-term collections that encompass a wide geographic area made in any large river. Overall, we caught 4,414 individual turtles of 10 species from all reaches and in all years. Species of chelonians collected included the common map turtle (*Graptemys geographica*), the false map turtle (*G. pseudogeographica*), the Ouachita map turtle (*G. ouachitensis*), the painted turtle (*Chrysemys picta*), the red-eared slider (*Trachemys scripta elegans*), the river cooter (*Pseudemys concinna*), the common snapping turtle (*Chelydra serpentina*), the smooth softshell (*Apalone mutica*), the spiny softshell (*A. spinifera*), and the stinkpot (*Sternotherus odoratus*). The number of species collected tended to increase from north to south. We found the southern reaches to contain more species, but with reduced diversity indices due to decreased evenness in the sample and with increased density as measured by catch per unit (CPU) effort. Apparently, increased density accrued from increased number of individuals from one or two dominant species present rather than a general increase in all species present.

Species diversity as measured by number of species collected did not vary with habitat type. We sampled tributaries, backwaters, impoundments, channel borders, side channels, and tailwater zones. Habitat was an important determinant in the sorts and proportions of turtle species collected. Backwaters and impoundments were dominated by *C. picta* and *T. s. elegans*. In contrast, species of *Graptemys* dominated main channel border and side channel borders. Tailwater habitats differed from other habitats in species

composition due to the importance of *A. spinifera*. Species composition within particular habitats was strongly affected by sampling location within the system.

Among all the gear types used by fisheries components at the LTRMP field stations, fyke nets were by far the most effective at catching turtles. This gear type accounted for 65% of all turtles collected. Temporal variation accounted for a significant amount of variation in carapace length for some species. Turtles collected earlier in the year (i.e., June, July, or August) tended to be larger than those collected later in the year (i.e., September or October). Overall our models on the influence of variables on turtle size accounted for 28 to 48% of the variance excepting the *A. spinifera* model, which accounted for 82% of the variance in carapace length.

Sexual size dimorphism was found for many of the species collected. In such cases males were smaller than females. Dimorphism was most pronounced in the two softshell species and least pronounced for the Stinkpot and common snapping turtle.

Navigation dams such as those found in the UMRS create impoundments that have different ecological features than the more natural habitat types such as backwaters, channel borders, etc. We found effects that may be attributable to impoundment. We found no effect on the number of species in impoundments as all major habitats for all reaches combined contained nine species. However, species diversity indices were greater for backwater habitats than impoundments. The difference seems to be due to greater unevenness in impoundments where one or two species dominate collections. Despite this, the number of individuals collected in impoundments was fewer than those collected in backwater habitats. This suggests that protection of backwater habitats from alteration and maintaining their riverine nature is important in maintaining species diversity and density among aquatic turtles in the UMRS.

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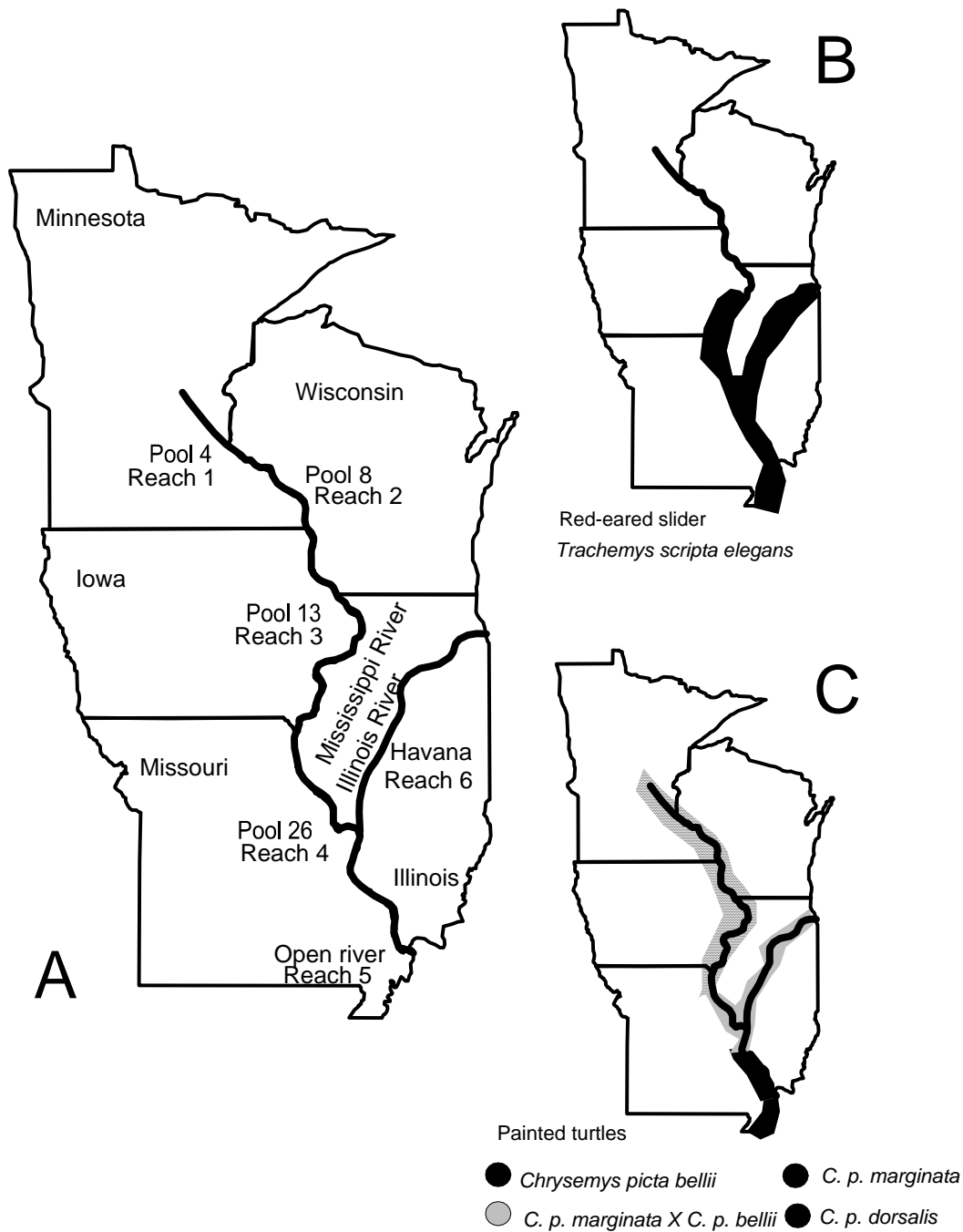
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INTRODUCTION

Studies of turtle assemblages are few (see Bury, 1979 for a review of older studies; more recent studies were reviewed by Stone et al., 1993). In general, such studies are complicated by collecting biases and species' habitat preferences. Studies of turtle communities in large rivers are even more difficult. Except for studies of some tropical communities (e.g., Moll and Legler, 1971; Moll, 1990) and studies of limited geographic areas (e.g., VanDeWalle and Christiansen, 1993; Gritters and Mauldin, 1994), no large scale and longer-term studies have been published on turtle communities in large rivers. Large rivers are difficult habitats to sample because to do so require considerable logistic outlay even when one or a few geographic localities are sampled (i.e., Gritters and Mauldin, 1994). Even so, many turtle species in North America and elsewhere typically occur in large rivers and their associated backwater and side channel habitats (Ernst and Barbour, 1989; Conant and Collins, 1991; Ernst et al., 1994).

The Long Term Resource Monitoring Program (LTRMP) was authorized by an act of Congress in 1986 (Public Law 99-662) as an element of the U. S. Army Corps of Engineers' Environmental Management Program. The LTRMP is being implemented by the Environmental Management Technical Center, an office of the National Biological Service in cooperation with natural resource agencies in the five states (Illinois, Iowa, Minnesota, Missouri, and Wisconsin) bordering the Upper Mississippi River System (UMRS). The UMRS includes the portion of the Mississippi and Illinois Rivers most influenced by navigation dams (Theiling, 1995; Theiling et al., 1996). The LTRMP, which was developed in response to environmental concerns unique to regulated rivers, monitors water quality variables as well as invertebrate and vertebrate communities in the UMRS through an organized program of collecting and data analysis by personnel at five field stations scattered throughout the UMRS (Fig. 1A).



Figures 1A-C. A: Location of the six Long Term Resource Monitoring Program field stations and the reaches that they sample; range maps for the red-eared slider (B) and painted turtle (C). Range for painted turtle subspecies follows Conant and Collins (1991), whereas the other maps are from Ernst et al. (1994).

The fisheries component of the LTRMP, which utilizes many sorts of collecting methods to reduce collecting biases inherent in fisheries sampling, began sampling in 1989. Beginning in 1992, fisheries component specialists at each field station began to systematically record data on turtles collected as a by-product of fisheries monitoring. Prior to 1992, no measurements were recorded but some field stations did record species identity of turtles caught (i.e., Gritters and Mauldin, 1994). Herein we summarize data collected on turtle communities in the UMRS from 1992 to 1995. Our analysis is important because it is the first based on long-term collections that encompass a wide geographic area made in any large river. Moreover, collecting methods and gear types are for the most part standardized over all years and all locations. Thus, we can directly compare these samples from disparate collecting locations without complications due to collecting biases because any undetected collecting biases would be similar for all field stations.

METHODS AND MATERIALS

Collecting methods. Most of the turtles caught in this study were collected with one of three basic gear types. Fyke nets were most effective at collecting turtles. These Wisconsin-type nets contained three sections, the lead, the frame, and the cab. The 15 m lead was 1.3 m high. Together the frame and cab were 6 m long when fully extended. The frame section was formed by two rectangular spring-steel frames that were 0.9 m high and 1.8 m long. Two mesh wings extended from the sides of the first frame toward the middle of the second frame. The cab was constructed of six hoops, 0.9 m in diameter. All netting material had a 1.8 cm diameter bar mesh. All nets were placed with the lead towards shore and the net set perpendicular to the shoreline. Mini-fyke nets also caught many turtles. These nets, which were smaller versions of fyke nets, were also set perpendicular to the shoreline with a 15 m lead. The nets were 0.6 m high, 1.2 m wide, and 3 m long with 3 mm mesh netting. Neither sort of fyke nets was baited. Fyke nets and mini-fyke nets

were fished for 24 h. For all reaches combined, we placed 817 fyke net sets and 1343 mini-fyke sets.

We also caught significant numbers of turtles in each reach with hoop nets. Both large and small hoop nets were used. In the analysis below, we combined samples for these sorts of hoop nets. The nets differed in size and dimensions. Large hoop nets were constructed from seven hoops and were 4.8 m long. The first hoop was 1.2 m in diameter and the diameter of successive hoops decreased incrementally by 2.5 cm toward the cod end of the net. Nets were constructed of 3.7 cm diameter bar mesh. Small hoop nets have seven hoops and were 3 m long. The first hoop was 0.6 m in diameter and successive hoops decreased incrementally in diameter by 2.5 cm. Nets were constructed of 1.8 cm diameter bar mesh. Both sorts of hoop nets were baited with 3 kg of soybean cake bait to attract fishes. Hoop nets were deployed in pairs with the open end of the net facing downstream. Each pair consisted of one large hoop net and one small hoop net. Hoop net sets were fished for 48 h. Overall, we placed 2193 hoop net sets for a total of 4386 trap days.

We also caught some turtles by electrofishing, with gill nets, with trammel nets, by trawling, and with tandem fyke nets. We included those turtles in species lists by reach and year but not in the statistical analysis because too few turtles were caught in each reach or year by those methods.

Collecting sites. Individual collecting sites on the Mississippi River were located in Pools 4, 8, 13, and 26, and in the open river near Cape Girardeau, Missouri. We also collected turtles from the Illinois River near Havana, Illinois (Fig. 1). Prior to 1993, collecting locations in each reach were fixed and had been selected subjectively in 1989. Beginning in 1993, all collecting sites in each year for each reach were randomly selected by a stratified random design. Site selection was stratified according to habitat type.

Habitat types. We sampled six basic habitat types. These included

backwaters, impoundments (*sensu* Theiling, 1995 and Theiling et al., 1996), main channel borders, side channel borders, tailwater zones near the locks and dams, and some larger tributary streams. The latter were sampled in Reach 5 only. In some instances, these basic habitat types were further subdivided by net placement (off shore or shoreline) or by navigation improvements (unstructured vs. wingdams). However, in this analysis, we examined turtles based on the basic habitat type and do not consider subdivisions of each habitat type. To do so reduced statistical power without adding materially to the results.

Data collection. Each turtle collected was identified to species. Specific identifications of turtles followed Ernst et al. (1994). We restricted our analysis to the species level because field identification of subspecific status for polytypic species was not practical given the time constraints on fisheries crews. We measured the carapace length to the nearest 1 mm for most specimens. Some larger specimens were measured to the nearest 1 cm. Consequently data for all turtles were rounded to the nearest 1 cm for analyses such as length frequency distributions. Sex for most individuals was identified in the field. However, sex of some individuals was not recorded and sex identification practices varied among field stations. We also could not determine maturity of collected turtles because all individuals were examined briefly and then released. Consequently, we do not classify turtles by sex for this analysis.

Statistical analysis. We used SAS (SAS Institute, 1988) for statistical analyses. Because the data set included many classification variables but only a single measure of turtle size, analysis of variance (ANOVA) was complicated by interaction between classification variables in instances where degrees of freedom were 0. To reduce the number of such occurrences, we limited ANOVA to the seven most common species collected in four habitat types (i.e., backwaters, impoundments, main channel borders, and side channel

borders) caught by three gear types (i.e., fyke nets, mini-fyke nets, and hoop nets). We performed two general sorts of ANOVA. First, we designed a general model that included reach, gear, and habitat type along with their interactions as main effects to explore their influence on variance in carapace length. We performed ANOVA with this model for each of the seven most common species. Secondly, we performed separate ANOVA's by reach and species to determine the importance of two temporal classification variables (i.e., month and year of collection) on variance in carapace length. These two temporal variables could not be included in the general model without sacrificing much of the statistical power for species represented by relatively few individuals (i.e., less than 500).

Because many statistical comparisons were performed by these ANOVAs, a significant risk existed in uncritical acceptance of values of P for these analyses. These tests were not independent of each other. Consequently, type I errors could be misleading because each statistical test carried a 0.05 probability of such an error. Consequently, we used the sequential Bonferroni method (Rice, 1989) to identify values of P that do not reduce the probability of type I errors to less than 0.05. In each table containing results from ANOVA we give the unadjusted values of P along with the minimum value of P required to reduce the overall possibility of type I errors to 0.05 or less.

We employed cluster analysis using the average difference method (SAS Institute, 1988) to generate trees to visualize similarities in faunal composition among reaches and among reaches and habitats. In these analyses, the proportions of each species in each reach or reach and habitat were used as continuous variables. Reach or reach and habitat were identified as the classification variable. Because the purpose of these analyses was to identify relatedness but not the degree of relatedness, we only summarize distance statistics rather than explore them in detail.

The Shannon diversity index (Brower and Zar, 1984) was used to quantify

species diversity. The form of this index used was $H' = (N \log N - \sum n_i \log n_i)/N$, where H' = the diversity index, N = total number of individual turtles of all species, and n_i = number of individuals of the i th species. In our study we use this index to quantify species diversity but do not manipulate it further.

RESULTS

Interspecific analysis. Overall, we caught 4,414 individual turtles of 10 species from all reaches and in all years (Table 1). We caught seven species per reach in Reaches 1-3 and eight or nine species per reach in Reaches 4-6. Thus, the number of species collected tended to increase from north to south. Our collections are consistent with previously reported ranges for the ten species (Figs. 1-3). The increased number of species collected in Reaches 4-6 was due to the appearance of two species (*Sternotherus odoratus* and *Trachemys scripta elegans*) in collections from Reaches 4-6. Neither of these species ranges into Reaches 1-3 (Figs. 1B and 3B). Despite collecting more species in southern reaches, species diversity actually declined from north to south (Table 1) because samples from southern reaches were dominated by one or two species.

Although species diversity indices decreased from north to south, the number of turtles collected per unit effort (= CPU) increased from north to south. Thus, not only were collections in southern reaches less even, but more turtles were collected in Reaches 4 and 5 than in any of the other reaches we sampled. This effect was most pronounced for fyke net CPU (Table 1), which was the gear that caught the bulk of the turtles that we examined (see below, and Table 1). We found these southern reaches to contain more species, but with reduced diversity indices due to decreased evenness in the sample and with increased density as measured by CPU. Apparently, increased density accrued from increased number of the one or two dominant species present rather than a general increase in all species present.

Table 1. Carapace length (in mm) for species of turtles collected from 1992 to 1995 at six LTRM field stations by all methods.

Species	Reach 1		Reach 2		Reach 3		Reach 4		Reach 5		Reach 6	
	N	Mean (SD)/ Range	N	Mean (SD)/ Range	N	Mean (SD)/ Range	N	Mean (SD)/ Range	N	Mean (SD)/ Range	N	Mean (SD)/ Range
<i>Graptemys geographica</i>	52	159(47.1)/ 90-250	72	153(46.4)/ 62-325	52	133(44.4)/ 72-256	1	106	-	-	12	129(30.9)/ 100-190
<i>Graptemys pseudogeographica</i>	190	166(53.1)/ 30-320	121	160(46.5)/ 79-300	37	120(28.4)/ 34-210	12	134(44.0)/ 87-226	764	143(37.1)/ 56-266	4	120(43.6)/ 90-170
<i>Graptemys ouachitensis</i>	4	198(40.3)/ 140-230	27	153(44.1)/ 75-241	1	108	9	112(37.5)/ 55-192	-	-	3	107(35.1)/ 70-140
<i>Chrysemys picta</i>	149	149(23.8)/ 90-190	831	150(17.0)/ 88-233	230	155(21.1)/ 60-230	92	133(22.3)/ 57-173	1	159	38	132(25.0)/ 70-170
<i>Trachemys scripta elegans</i>	-	-	-	-	-	-	509	168(44.9)/ 43-281	179	188(39.1)/ 67-268	195	187(44.1)/ 60-270
<i>Pseudemys concinna</i>	-	-	-	-	-	-	-	-	1	140	-	-
<i>Chelydra serpentina</i>	73	290(53.9)/ 130-440	100	293(69.4)/ 114-440	11	295(48.1)/ 211-360	30	285(50.6)/ 208-400	14	271(44.9)/ 185-350	15	259(50.1)/ 190-360
<i>Apalone mutica</i>	19	258(62.9)/ 140-360	20	177(15.4)/ 143-212	8	168(13.3)/ 137-179	4	168(5.4)/ 160-172	46	175(43.0)/ 40-280	4	155(7.1)/ 150-160
<i>Apalone spinifera</i>	152	239(78.7)/ 30-400	155	198(54.3)/ 39-400	9	176(11.2)/ 163-191	19	183(53.5)/ 75-312	25	207(53.5)/ 139-334	86	203(70.4)/ 70-350

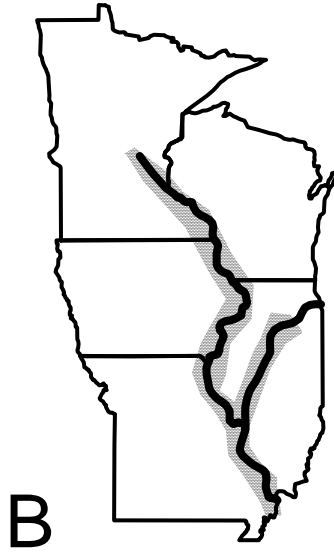
Table 1 continued.

<i>Sternotherus odoratus</i>	-	-	-	-	-	-	16	99(11.9)	2	96(8.5)/	20	112(25.3)/
								77-118		90-102		90-210
Totals	639	1326	348	692	1032	377						
Diversity index	0.71	0.55	0.48	0.43	0.36	0.62						
Fyke net CPU	1.54	3.49	1.73	4.25	4.63	1.36						
Hoop net CPU	0.24	0.26	0.02	0.31	0.80	0.07						
Mini-fyke net CPU	0.56	0.41	0.15	0.30	0.86	0.26						

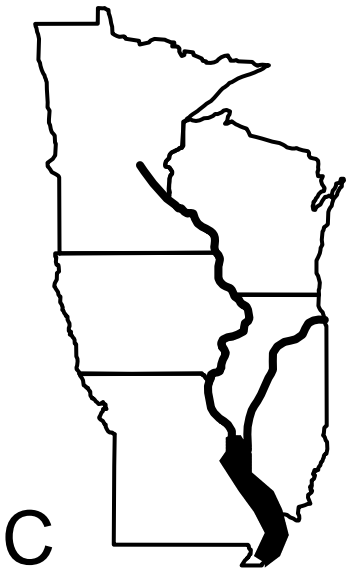
CPU = catch per unit effort with unit effort in turtles/net set; for CPU in turtles/trap day divide hoop net CPU by 2.



A
Common map turtle
Graptemys geographica



B
False map turtle
Graptemys pseudogeographica



C
River cooter
Pseudemys concinna



D
Ouachita map turtle
Graptemys ouachitensis

Figures 2A-D. Generalized range maps for four species of turtles collected by LTRMP sampling. Common map turtle range is from Conant and Collins (1991); others follow Ernst et al. (1994).



A

Common snapping turtle
Chelydra serpentina



B

Stinkpot
Sternotherus odoratus



C

Spiny softshell
Apalone spinifera



D

Smooth softshell
Apalone mutica

Figures 3A-D. Generalized range maps (after Ernst et al., 1994) for four species of turtles collected by LTRMP sampling.

Of the turtles collected, species of Emydidae dominated collections both in number of species (6 of 10 species) and number of individuals (3,586 of 4,414 turtles). Turtles of three other families (Chelydridae (1 species, 243 individuals), Kinosternidae (1 species, 38 individuals), and Trionychidae (2 species, and 547 individuals)) were also collected.

The number of turtles collected per year varied extensively among and between reaches (Table 2). In each reach, more turtles were collected in 1994 and 1995 than in 1992 and 1993 overall. In part, this reflected the effects of the 1993 flooding on the UMRS which interfered with field operations and reduced collecting effort. We calculated CPU for fyke net sets in each year to correct for differences in collecting effort among years. For all reaches combined, CPU was lowest in 1993 (1.86 turtles/net set) and highest in 1994 (4.39 turtles/net set). Results for 1992 (CPU = 2.60 turtles/net set) were lower than those for 1995 (CPU = 3.02 turtles/net set). Consequently, the relatively fewer turtles collected in 1992 and 1993 were not due solely to differences in collecting effort.

In general species diversity as measured by number of species collected did not vary with habitat type (Table 3). Nine of ten species were collected in all of the major habitat divisions sampled in the UMRS, when all reaches were combined (Table 3). Fewer species (seven of ten) were collected in tributaries but tributaries were sampled only in Reach 5 and the results were not directly comparable to samples from the UMRS habitats. It was noteworthy that the dominance of emydids in our collections also held for each of the five main habitat types (i.e., backwater, impoundment, channel border, side channel, and tailwater) in the UMRS. We collected roughly six times more emydid specimens in these five habitats than we did turtles from the other three subfamilies combined (Table 3).

Table 2. Number of specimens of each species collected during four years of study at six LTRM field stations including data from all gear types.

	Reach 1				Reach 2				Reach 3				Reach 4				Reach 5				Reach 6			
	92	93	94	95	92	93	94	95	92	93	94	95	92	93	94	95	92	93	94	95	92	93	94	95
<i>Graptemys geographica</i>	8	8	21	15	16	11	26	19	27	2	10	13	0	0	0	1	0	0	0	0	5	0	5	2
<i>Graptemys pseudogeographica</i>	19	51	72	48	32	38	28	23	10	3	19	5	7	0	3	2	233	42	316	173	2	0	2	0
<i>Graptemys ouachitensis</i>	0	0	2	2	9	8	7	3	0	1	0	0	6	0	0	3	0	0	0	0	0	0	2	1
<i>Chrysemys picta</i>	5	20	76	48	48	232	262	289	20	66	51	93	19	2	43	28	1	0	0	0	14	0	8	16
<i>Trachemys scripta elegans</i>	0	0	0	0	0	0	0	0	0	0	0	0	129	33	192	155	77	1	75	26	54	0	82	59
<i>Pseudemys concinna</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Chelydra serpentina</i>	8	20	34	11	8	18	24	50	1	0	4	6	7	1	13	9	4	0	8	2	3	1	6	5
<i>Apalone mutica</i>	5	4	10	0	6	12	1	1	2	3	1	2	2	1	0	1	7	0	17	22	2	0	0	2
<i>Apalone spinifera</i>	8	17	63	64	18	33	51	53	7	2	0	0	4	1	6	8	14	0	11	0	17	2	40	27
<i>Sternotherus odoratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	8	7	0	0	1	1	3	0	3	14
Totals	53	120	278	188	137	352	399	438	67	77	85	119	175	38	265	214	336	44	428	224	100	3	148	126

Although we collected more turtles in backwaters than in any other habitat, correction for collecting effort suggested that turtles were as common in side channel habitats as they were in backwater habitats when CPU for fyke nets were compared (Table 3). Fyke nets should be examined in this instance because they caught most of the turtles that we studied. In contrast, CPU was lowest in impoundments and tailwaters, two highly disturbed habitats (Table 3).

The dominance of emydid turtles in backwater, main and channel border, and tributary habitats resulted in lower species diversity indices for those habitats than for impoundment and tailwater habitats (Table 3). Thus, few turtles were caught in impoundments and tailwater habitats but those that were caught were more evenly distributed among the species making up the sample compared to the other habitat classifications.

However, species diversity by habitat was more variable when habitats were considered on a reach by reach basis. To illustrate this, we examined species diversity in Reaches 2-4 where collections were made in all five of the main habitat types (i.e., backwaters, impoundments, main channel borders, side channel borders, and tailwaters) in each reach. In all of these reaches, turtles collected in backwaters accounted for most of the turtles collected overall in each reach. The number of species collected ranged from six (Reach 3) to nine (Reach 4) but species diversity indices were similar among all three reaches and varied from 0.48 (Reach 2) to 0.40 (Reaches 3 and 4).

In contrast, the number of species collected in the other habitat types never exceeded the number of species collected in backwaters in each reach. For instance, we collected between 5 and 7 species in impoundments, between 3 and 6 species in main channel borders, between 2 and 7 species in side channel borders, and between 3 and 7 species in tailwaters for these reaches.

Despite collecting fewer species in nonbackwater habitats in these reaches, species diversity indices for nonbackwater habitats exceeded those of

backwater habitats for Reach 2. In this reach, diversity indices ranged from

Table 3. Distribution of all turtles caught between 1992-1995 at six LTRM field stations by species and habitat type.

Species	Total turtles	Backwater	Impoundment	Channel Border	Side channel	Tailwater	Tributary
<i>Graptemys geographica</i>	189	136	19	4	8	22	-
<i>Graptemys pseudogeographica</i>	1128	210	15	217	570	48	68
<i>Graptemys ouachitensis</i>	44	27	4	5	4	4	-
<i>Chrysemys picta</i>	1341	1203	88	11	25	14	-
<i>Trachemys scripta elegans</i>	883	607	47	11	160	23	35
<i>Pseudemys concinna</i>	1	-	-	-	-	-	1
<i>Chelydra serpentina</i>	243	174	20	5	35	6	3
<i>Apalone mutica</i>	101	31	11	19	32	3	5
<i>Apalone spinifera</i>	446	255	21	35	68	54	13
<i>Sternotherus odoratus</i>	38	19	4	1	8	4	2
Total	4414	2662	229	308	910	178	127
Diversity index		0.69	0.78	0.48	0.54	0.78	0.54
Fyke net CPU		4.05	1.57	2.45	4.87	1.45	3.71
Hoop net CPU		0.45	0.11	0.06	0.37	0.12	0.94
Mini-fyke net CPU		0.56	0.22	0.28	0.47	0.48	0.29

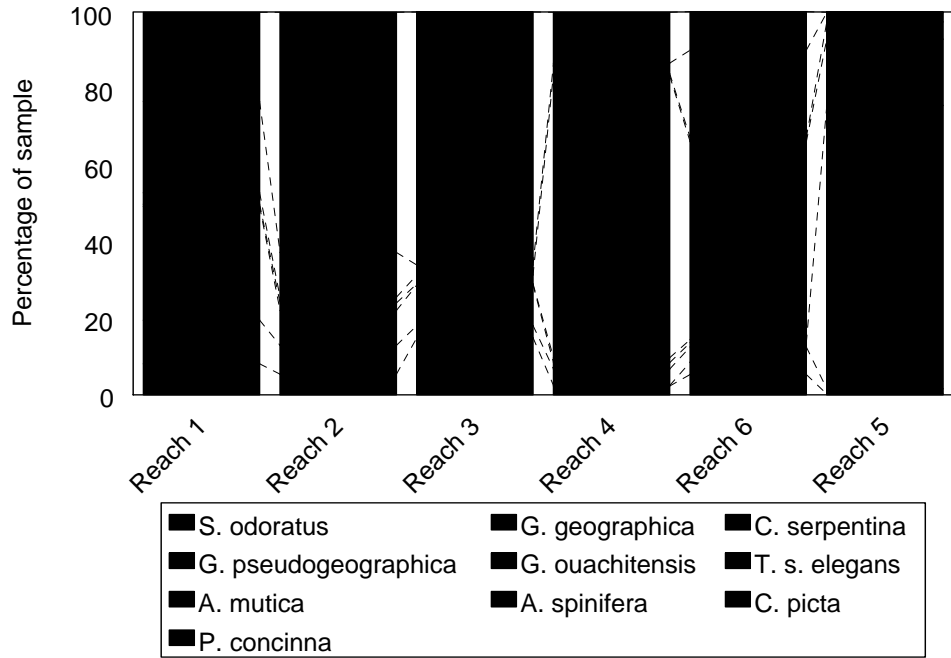
CPU = catch per unit effort with unit effort in turtles/net set; for CPU in turtles/trap day divide hoop net CPU by 2.

0.75 (tailwaters) to 0.63 (side channel borders). Species diversity indices for nonbackwater habitats in the other two reaches varied compared to those for backwater habitats. Species diversity indices for Reach 3 varied from 0.16 (side channel borders) to 0.64 (tailwaters) compared to 0.36 (tailwaters) to 0.51 (side channel borders) for Reach 4.

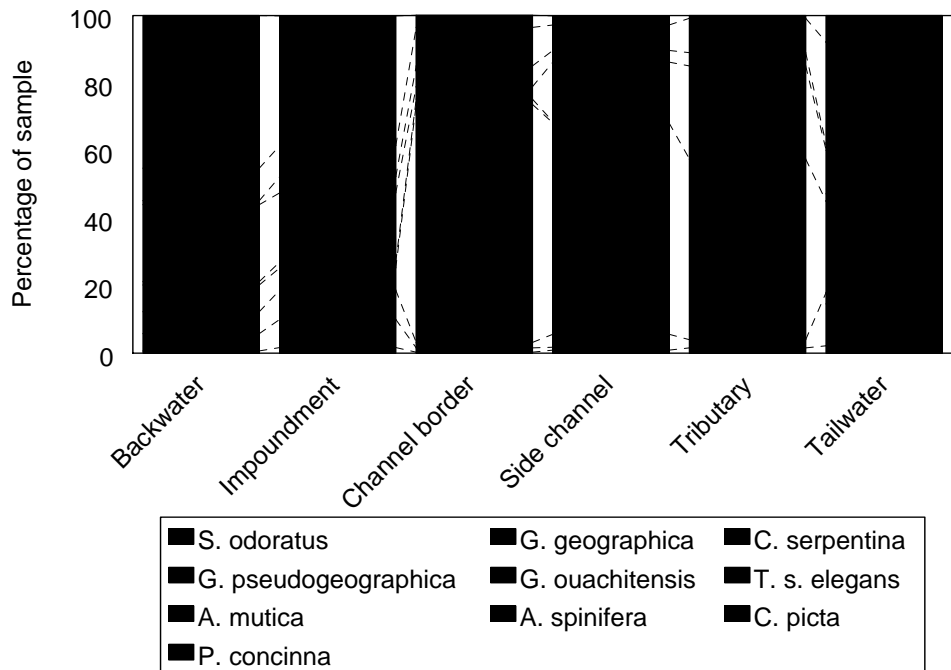
Note that the most and least diverse nonbackwater habitats for Reaches 3 and 4 were reversed. This sort of more or less random variation in the number and diversity of species collected in nonbackwater habitats suggested to us that too few turtles were collected in most of these habitats in most reaches to yield a valid comparison among habitats and reaches. Thus, the results for the comparison of species numbers and diversity for all reaches combined or for backwaters only appeared to be the most reliable comparative measure of species diversity. Excepting Reach 5 where collections were limited to main channel borders, side channel borders, or tributaries, we collected between 125 (Reach 2 impoundment) and 6 (Reach 3 main channel border) turtles from all other nonbackwater habitats in the other five reaches.

Although emydid turtles made up the bulk of the turtles caught, the particular species of emydid most important in our collections varied among reaches (Fig. 4A) and habitats (Fig. 4B). Reach 1 collections were dominated by *C. picta* and *G. pseudogeographica* along with *A. spinifera*, a trionychid turtle (Fig. 4A, Table 1). Further south, *C. picta* made up the bulk of all turtles collected in Reaches 2 and 3. However, faunal composition shifted in Reaches 4-6 where either *T. s. elegans* (Reaches 4 and 6) or *G. pseudogeographica* (Reach 5) more or less replaced *C. picta* as the dominant emydid turtle collected (Fig. 4A). Excepting *A. spinifera* in Reaches 1 and 6, no nonemydid turtle made up more than 10% of the collections from any of the reaches sampled.

A



B



Figures 4A-B. Faunal composition for turtles collected at six LTRMP field stations by reach (A) and by habitat (B).

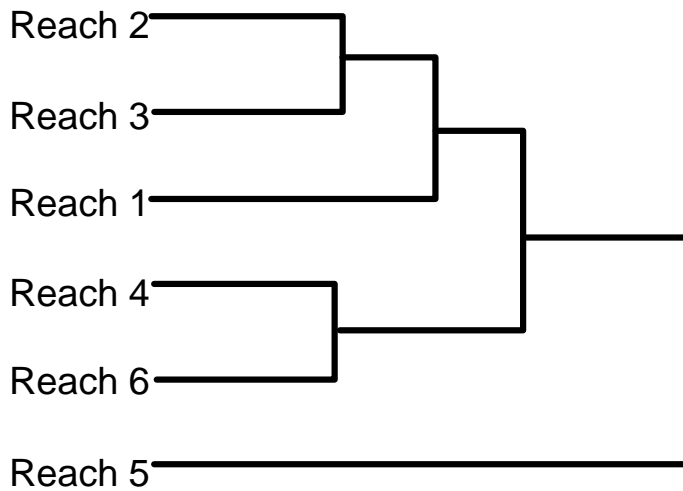


Figure 5. Tree generated by cluster analysis using proportions of species collected from each reach as variables with reach as the classification variable. Branch lengths are not shown but average 0.74 units (range = 0.20-1.16 units, sample standard deviation = 0.17 units).

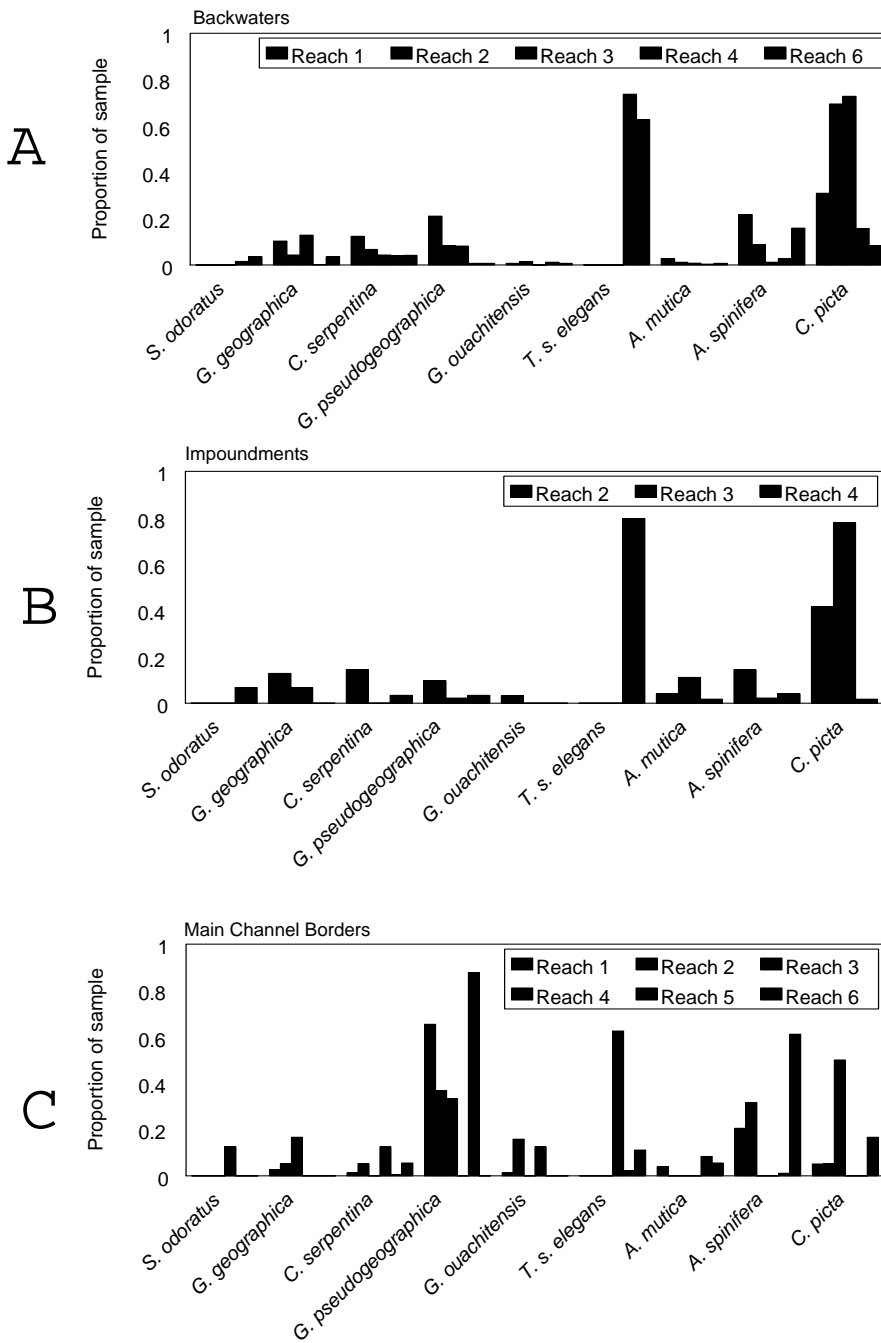
We used cluster analysis to examine the effect of species composition on faunal similarity among the reaches surveyed. The importance of *C. picta* caused the three northern reaches to cluster together (Fig. 5), whereas the appearance of large numbers of *T. s. elegans* resulted in clustering of Reaches 4 and 6. Note that drainage patterns were not differentiated by this analysis. Reach 4 located on Pool 26 of the Mississippi River clustered with Reach 6, which was located on the Illinois River. Reach 5 did not cluster with the other two groups but was more similar to the Reach 4 and 6 cluster. Despite the lack of congruence with drainage basins, the cluster analysis was consistent with latitudinal variation in dominant emydid present in each reach (i.e., Fig. 4A).

Habitat was an important determinant in the sorts and proportions of turtle species collected (Fig. 4B). Backwaters (Fig. 6A) and impoundments (Fig. 6B) were dominated by *C. picta* and *T. s. elegans*. In contrast, species of *Graptemys* dominated main channel border (Fig. 6C) and side channel borders

(Fig. 7A). Tailwater habitats (Fig. 8B) differed from other habitats in species composition due to the importance of *A. spinifera*. In part, importance of various species in each habitat was related to reach. For instance, the relatively high percentage of *T. s. elegans* in samples from impoundments was due to the large number of *T. s. elegans* collected in Reach 4 impoundment but not due to the general occurrence of *T. s. elegans* in impoundments (Fig. 6B). Similarly, the dominance of side channel borders by *Graptemys* resulted from the large numbers of *G. pseudogeographica* collected in Reaches 3 and 5 (Fig. 7A).

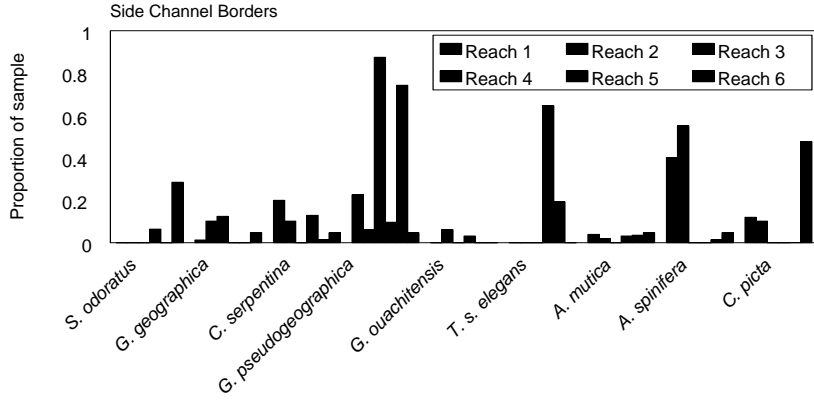
Species composition within particular habitats was strongly affected by sampling location within the system. To confirm this observation, we performed cluster analysis on the proportion of turtles making up the samples for each habitat in each reach (Fig. 8). If reach determined faunal makeup, then all habitats from each reach should cluster together. Conversely, if habitat determined faunal makeup, then all similar habitat types should cluster together regardless of reach. Clearly, neither hypothesis was supported by this analysis because clusters contained disparate reaches and habitat types.

Faunal makeup was related to the interaction between reach (i.e., geographic location within the system) and habitat type. For instance, many of the Reach 1-3 habitats clustered together (Fig. 8, painted turtle cluster) due to the large proportion of the sample made up by *C. picta*. However, Reach 6 side channel border samples also clustered here due to the relatively large number of *C. picta* collected in this habitat in Reach 6. Similarly, most Reach 5 habitats clustered together due to the high proportion of *G. pseudogeographica* collected there (Fig. 8, false map turtle cluster). Nonetheless, certain Reach 1 and 3 habitats clustered with Reach 5 habitats because *G. pseudogeographica* was also abundant in main channel and side channel habitats in those reaches.

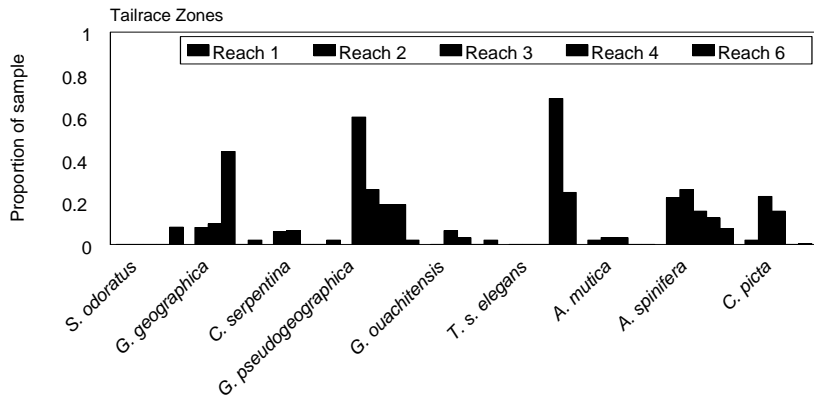


Figures 6A-C. Proportion of turtle species from each reach collected in backwater habitats (A), impoundments (B), and main channel borders (C).

A



B



Figures 7A-B. Proportion of turtle species from each reach collected in side channel borders (A) and tailrace zones (B).

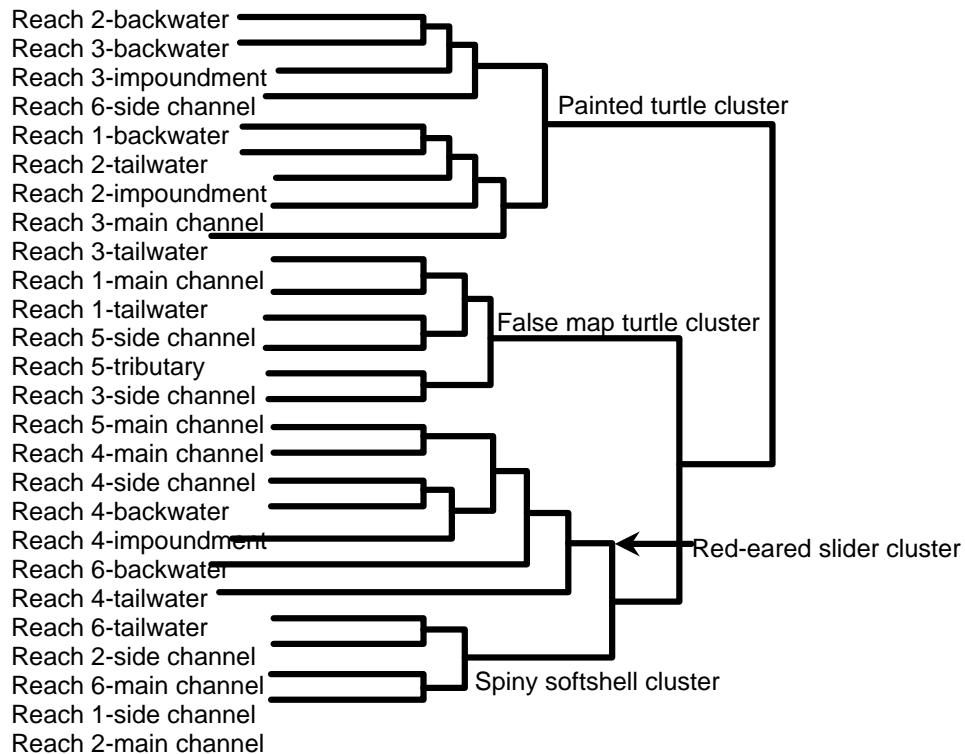


Figure 8. Tree generated by cluster analysis using proportions of species collected from each habitat type in each reach as variables with reach-habitat as the classification variable. Branch lengths are not shown but averaged 0.74 unites (range = 0.13-1.17 units, sample standard deviation = 0.16 units).

Among all the gear types used by fisheries components at the LTRMP field stations, fyke nets were by far the most effective at catching turtles (Table 4). This gear type accounted for 65% of all turtles collected. In contrast, mini-fyke nets, which were the next most productive gear type, accounted for only 15% of the turtles caught. However, effectiveness of fyke nets varied from reach to reach (Table 4) with only 40% of Reach 1 turtles being caught with fyke nets compared to 84% for Reach 3 (Table 4).

Table 4. Turtles caught in three gear types.

Gear	All	Reach 1	Reach 2	Reach 3	Reach 4	Reach 5	Reach 6
Fyke nets	2857(65%)	255(40%)	997(75%)	291(84%)	528(76%)	581(56%)	205(54%)
Mini-Fyke nets	655(15%)	106(17%)	118(9%)	43(12%)	57(8%)	254(25%)	77(20%)
Hoop nets	453(10%)	91(15%)	105(8%)	4(1%)	56(8%)	176(17%)	21(6%)
Other gear types*	449(10%)	187(28%)	106(8%)	10(3%)	51(8%)	21(2%)	74(20%)
Totals	4414	639	1326	348	692	1032	377

*For Reach 1, 37 turtles (6% of total) were caught with trammel nets and 84 turtles (13% of total) were caught with tandem fyke net sets; for Reach 2, 71 turtles (5% of total) were caught with tandem fyke net sets; for Reach 4, 41 turtles (6% of total) were caught with tandem fyke net sets; for Reach 6, 69 turtles (18% of total) were caught by trammel nets.

Table 5. Results for ANOVA for two temporal variables by reach and species.

	Reach 1			Reach 2			Reach 3			Reach 4			Reach 5			Reach 6		
	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P
Year																		
<i>Graptemys geographica</i>	3, 48	0.22	0.8828	3, 68	3.76	0.0147	3, 48	3.56	0.0209	0, 0	-	-	-	-	-	2, 5	0.64	0.5644
<i>Graptemys pseudogeographica</i>	3,189	3.96	0.0091	3,117	6.04	0.0007	3, 33	3.02	0.0433	2, 8	3.72	0.0644	3,760	17.12	0.0001	1, 1	0.19	0.7399
<i>Graptemys ouachitensis</i>	1, 2	3.27	0.2123	3, 23	0.77	0.5205	0, 0	-	-	1, 7	4.59	0.0693	-	-	-	1, 1	4.48	0.2809
<i>Chrysemys picta</i>	3,145	2.11	0.1017	3,827	2.13	0.0952	3,226	4.46	0.0046	3, 88	3.21	0.0269	0, 0	-	-	2, 26	2.35	0.1151
<i>Trachemys scripta elegans</i>	-	-	-	-	-	-	-	-	-	3,505	33.53	0.0001	3,178	1.67	0.1744	2,160	1.52	0.2221
<i>Pseudemys concinna</i>	-	-	-	-	-	-	-	-	-	-	-	-	0, 0	-	-	-	-	-
<i>Chelydra serpentina</i>	3, 69	1.91	0.1357	3, 96	0.39	0.7610	2, 7	2.44	0.1484	3, 26	2.06	0.1298	2, 11	0.19	0.8273	3, 9	6.33	0.0135
<i>Apalone mutica</i>	2, 16	4.29	0.0323	3, 19	1.29	0.3134	3, 4	20.96	0.0066	2, 1	0.38	0.7538	2, 43	0.40	0.6698	0, 0	-	-
<i>Apalone spinifera</i>	3,148	5.77	0.0009	3,151	1.91	0.1300	1, 7	7.75	0.0271	3, 15	5.86	0.0074	1, 23	1.07	0.3107	3, 82	4.76	0.0041
<i>Sternotherus odoratus</i>	-	-	-	-	-	-	-	-	-	2, 13	1.27	0.3136	1, 0	-	-	2, 17	1.31	0.2959

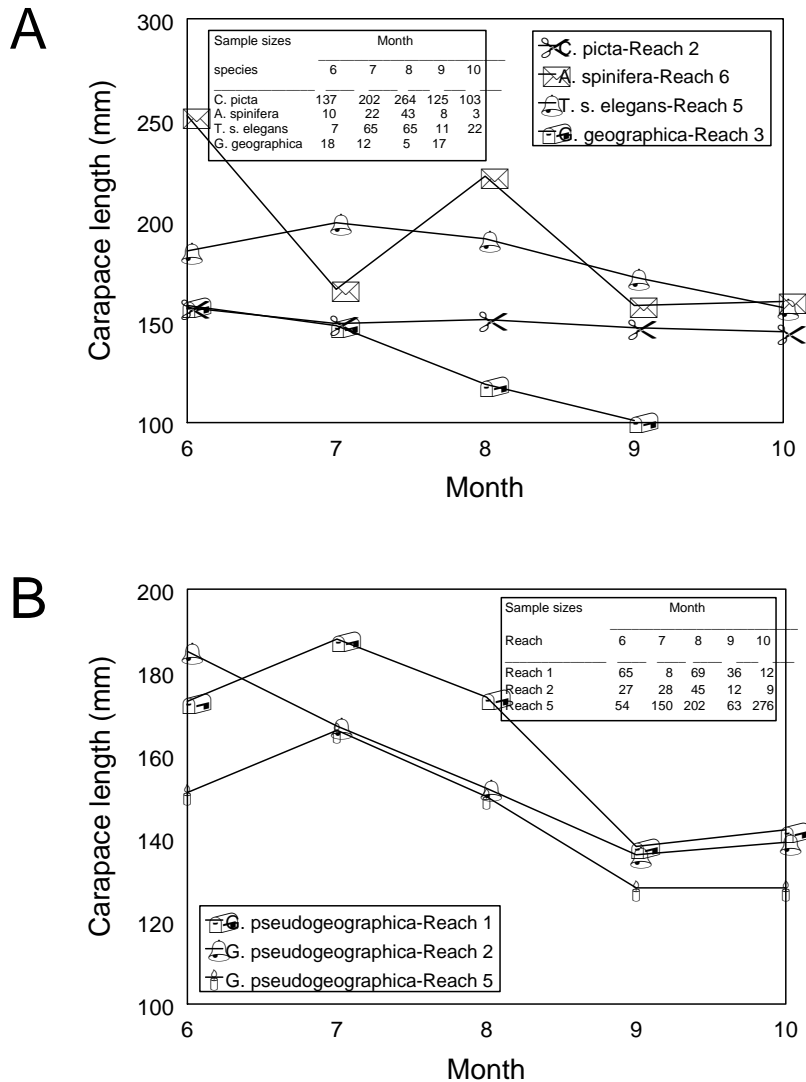
Table 5 continued

Month

<i>Graptemys geographica</i>	4, 47	1.50	0.2173	4, 68	0.26	0.9026	3, 48	7.43	0.0003	0, 0	-	-	-	-	-	3, 4	4.82	0.0815
<i>Graptemys pseudogeographica</i>	4,185	4.41	0.0020	4,116	4.07	0.0040	4, 32	0.63	0.6424	4, 7	0.98	0.4748	6,757	23.55	0.0001	2, 0	-	-
<i>Graptemys ouachitensis</i>	2, 1	48.25	0.1013	3, 23	2.40	0.0938	0, 0	-	-	2, 6	0.82	0.4838	-	-	-	1, 1	0.01	0.9476
<i>Chrysemys picta</i>	4,144	0.61	0.6587	4,826	9.39	0.0001	3,226	1.45	0.2300	4, 83	1.31	0.2734	0, 0	-	-	4, 24	0.82	0.5261
<i>Trachemys scripta elegans</i>	-	-	-	-	-	-	-	-	-	4,500	0.37	0.8332	6,172	4.15	0.0006	4,156	5.86	0.0002
<i>Pseudemys concinna</i>	-	-	-	-	-	-	-	-	-	-	-	-	0, 0	-	-	-	-	-
<i>Chelydra serpentina</i>	4, 68	0.75	0.5592	4, 95	2.30	0.0646	1, 9	0.16	0.6944	2, 27	1.93	0.1649	3, 10	2.03	0.1734	2, 10	3.02	0.0939
<i>Apalone mutica</i>	2, 16	1.96	0.1727	3, 16	1.33	0.2994	1, 6	0.40	0.5482	0, 3	-	-	5, 45	1.42	0.2396	1, 0	-	-
<i>Apalone spinifera</i>	3,148	3.03	0.0315	3,151	3.26	0.0234	2, 6	1.40	0.3179	3, 15	0.90	0.4630	4, 20	0.29	0.8819	4, 81	5.56	0.0005
<i>Sternotherus odoratus</i>	-	-	-	-	-	-	-	-	-	3, 12	1.23	0.3427	1, 0	-	-	4, 15	0.40	0.8022

Maximum degrees of freedom for year (1992-1995) = 3; for month (June-October) = 4 with the exception of Reach 5 where some turtles were also collected in April and May. Values of $P > 0.0015$ should be viewed with caution due to large number of comparisons in the ANOVAs.

Intraspecific analysis. Temporal variation accounted for a significant amount of variation in carapace length for some species in some reaches. Month of collection (Table 5; Figs. 9A and 9B) had a significant effect on variance in carapace length of *C. picta* (Reach 2), *G. geographica* (Reach 3), *G. pseudogeographica* (Reach 5, and marginally for Reach 1 and 2), *T. s. elegans* (Reaches 5 and 6), and *Apalone spinifera* (Reach 6). In each case, turtles



Figures 9A-B. A: Four species showing decrease in mean carapace length from June to October for reaches where month of collection was important in accounting for variance in carapace length; B: Three reaches where month of

collection accounted for an important portion of the variance in carapace length in *Graptemys pseudogeographica* suggesting that average size decreased from June to October.

collected earlier in the year (i.e., June, July, or August) tended to be larger than those collected later in the year (i.e., September or October). Because collecting methods did not vary in specific months, these results suggest that larger turtles tended to be more likely to be caught during the first three months of the sampling season than in the last two months.

Year of collection also contributed significantly to variation in carapace length in four instances (Table 5; Fig. 10). For *Apalone spinifera* collected in Reach 1, *T. s. elegans* collected in Reach 4, and *G. pseudogeographica* collected in Reach 5, turtles collected in 1994 and 1995 tended to be larger than those collected in 1992 and 1993. In some instances, pair wise comparisons were statistically significant among years. In one other instance, *G. pseudogeographica* collected in Reach 2 also varied significantly in carapace length by year. These turtles were largest in 1995 but those collected in 1994 were similar statistically to those collected in 1992 and 1993. ANOVA results that were marginally significant (i.e., $P > 0.004$ but < 0.01) were consistent with those that were certainly statistically significant. In all cases except for *C. picta* from Reach 3, either turtles collected in 1994 or 1995 were largest in carapace length among the four years of collections. The *C. picta* from Reach 3 were largest in 1992. Apparently, our sampling tended to catch larger turtles in 1995 and 1994 than during the first two years of the study.

Similarly, non-temporal variables and their interactions accounted for significant amounts of variation in carapace length among our samples (Table 6). However, overall our models accounted for only between 28 to 48% of the variance excepting the model for *A. spinifera*, which accounted for 82% of the

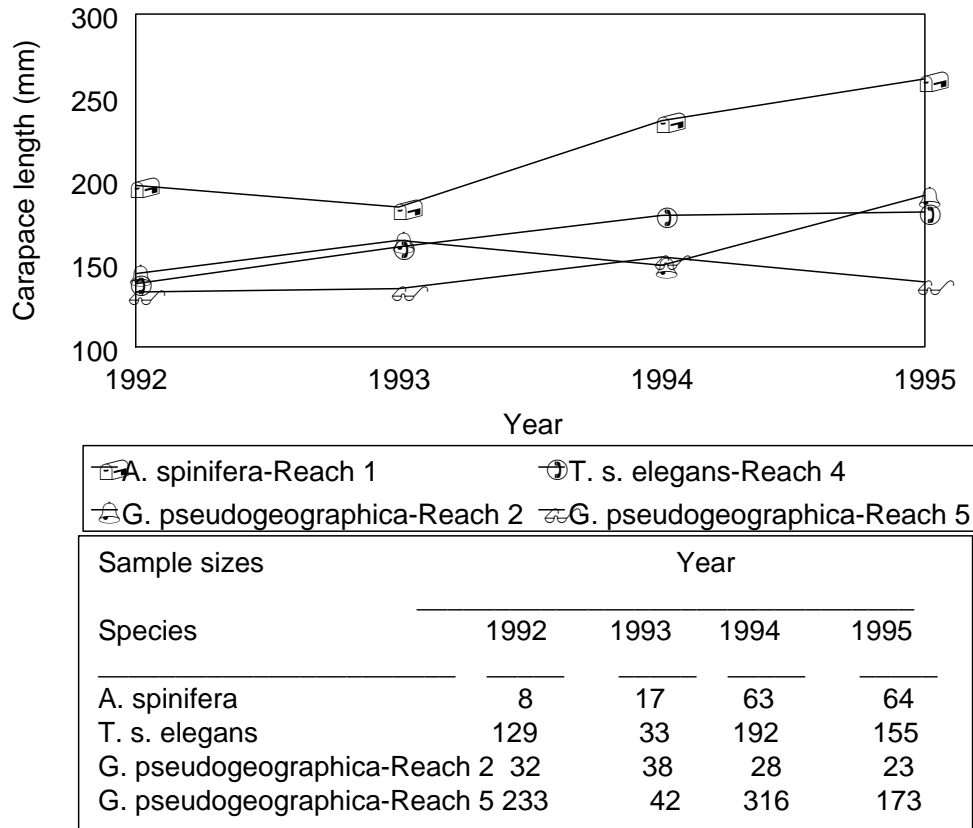


Figure 10. Four examples where year accounted for an important portion of the variance in carapace length for three species of turtles collected by LTRMP field stations. In each case, turtles collected in 1994 and/or 1995 averaged larger than those collected in 1992 and 1993.

variance in carapace length of that species. For that species, habitat, gear, and interaction between habitat and gear all accounted for significant portions of the variation in carapace length. No other species had more than two model effects that were statistically significant.

Overall, reach was statistically significant as a source of variation for *C. picta* and *T. s. elegans*. For the former, turtles from Reaches 4 and 6 were smaller than those from the three northern reaches (Reaches 1-3, see Table 1). For the latter, turtles from Reach 4 were smaller on average than were those from Reaches 5 and 6, which did not differ from each other (Table 1). In

contrast, habitat type was only significant for *A. spinifera* where turtles from backwater habitats were significantly longer than those from other habitats.

Although gear type had a significant effect on variance only for *A. spinifera* where turtles caught by hoop nests were larger than those caught by either sort of fyke net, gear was marginally significant (i.e., $P < 0.009$) in three other instances and approached significance ($P < 0.05$) in two other instances. In each case, hoop nets tended to catch larger turtles than did fyke nets. Clearly, gear type had an influence on the sizes of turtles caught mostly regardless of species despite the relative difficulty in unequivocally establishing this statistically. In part, larger size of turtles caught by hoop nets may reflect the relatively large mesh size used for hoop nets. Thus, these nets may not catch more large turtles but instead allow escape of small turtles because they can squeeze through the mesh in hoop nets but not in fyke nets. Moreover, hoop nets were generally set at greater depths and further from shore than fyke nets. Consequently, smaller turtles may have been missed if they tended to avoid these deeper water sites. Regardless, gear type can bias results. Because so few turtles were caught by hoop nets (Table 4), the effect on our study was probably minimal (but see below).

Sex was also an important variable (Tables 5 and 6) but only statistically significant for *G. pseudogeographica* (Fig. 11A) and *C. picta* (Fig. 11B). In both instances, males were significantly smaller in carapace length than females (Table 6). We did not find significant differences in size among sexes for other species where it might be expected such as *A. spinifera* (Fig. 11C) and *A. mutica* (Fig. 12A). In part this reflects the difficulty in field identification of sex (see Appendix). Because inclusion of sex in the ANOVA meant that individuals of unknown sex must also be included, variance attributable to sex (i.e., male vs. female) tended to be submerged by other variables including the large number of turtles of unknown

Table 6. Results of ANOVA for four non-temporal variables and their interactions for seven most commonly collected turtle species collected by six LTRM field stations.

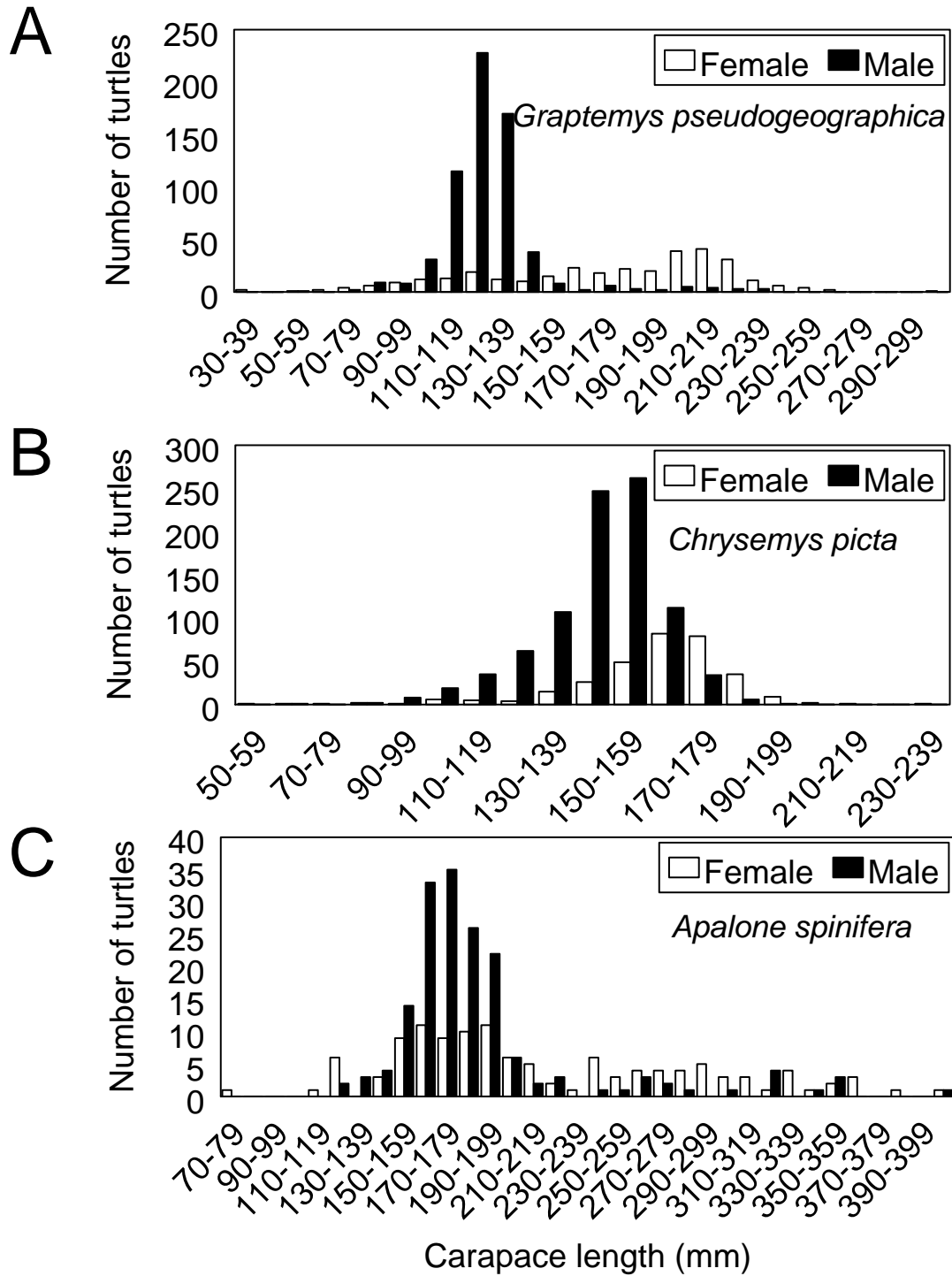
	<i>G. geographica</i>			<i>G. pseudogeographica</i>			<i>T. s. elegans</i>			<i>C. picta</i>			<i>C. serpentina</i>			<i>A. mutica</i>			<i>A. spinifera</i>		
	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P
Reach	3	2.88	0.0391	5	4.24	0.0008	2	2.68	0.0694	4	9.17	0.0001	5	1.61	0.1604	5	12.27	0.0001	5	0.94	0.4587
Habitat	3	1.24	0.2992	3	2.70	0.0445	3	4.23	0.0057	3	0.91	0.4372	3	2.40	0.0691	3	5.00	0.0037	3	1.60	0.1898
Gear	2	3.99	0.0211	2	6.23	0.0021	2	4.75	0.0089	2	1.97	0.1398	2	0.38	0.6827	2	5.01	0.0097	2	7.35	0.0008
Reach*Habitat	3	1.03	0.3839	7	0.96	0.4587	2	0.11	0.8966	6	1.96	0.0679	8	1.32	0.2367	4	4.24	0.0044	6	0.65	0.6878
Reach*Gear	3	0.76	0.5184	6	2.53	0.8196	4	2.28	0.8590	6	0.99	0.4297	7	0.77	0.6157	1	0.64	0.4262	5	1.34	0.2492
Habitat*Gear	1	0.40	0.5271	6	2.07	0.0546	5	1.86	0.0994	3	1.41	0.2397	3	1.89	0.1328	2	0.49	0.6165	8	0.13	0.9981
Reach*Habitat*Gear	0	.	.	1	0.00	0.9444	0	.	.	2	0.92	0.3974	1	0.20	0.6591	0	.	.	0	.	.
Model	16	1.49	0.1137	32	5.68	0.0001	18	8.34	0.0001	28	5.44	0.0001	29	1.56	0.0435	21	7.26	0.0001	31	2.79	0.0001
Error	118			914			679			1195			181			60			241		
R ²		0.17			0.17			0.18			0.11			0.20			0.72			0.26	

sex. Nonetheless, sexual size dimorphism was apparent among specimens of *G. geographica* (Fig. 12B) and *G. ouachitensis* (Fig. 12C), and to some extent among specimens of *T. s. elegans* (Fig. 13A), when only turtles identified at the time of collection as males or females were compared (Table 6). In all of these instances, males were statistically smaller (i.e., $P < 0.01$) than females if all other variables were ignored and specimens of unknown sex were ignored and specimens of unknown sex were not included. For *S. odoratus* (Fig. 13B), males were slightly larger than females but the comparison, which was based on few specimens, was not statistically significant ($P > 0/05$). Sexual dimorphism in size was not present in the sample of *C. serpentina* that we studied (Fig. 13C).

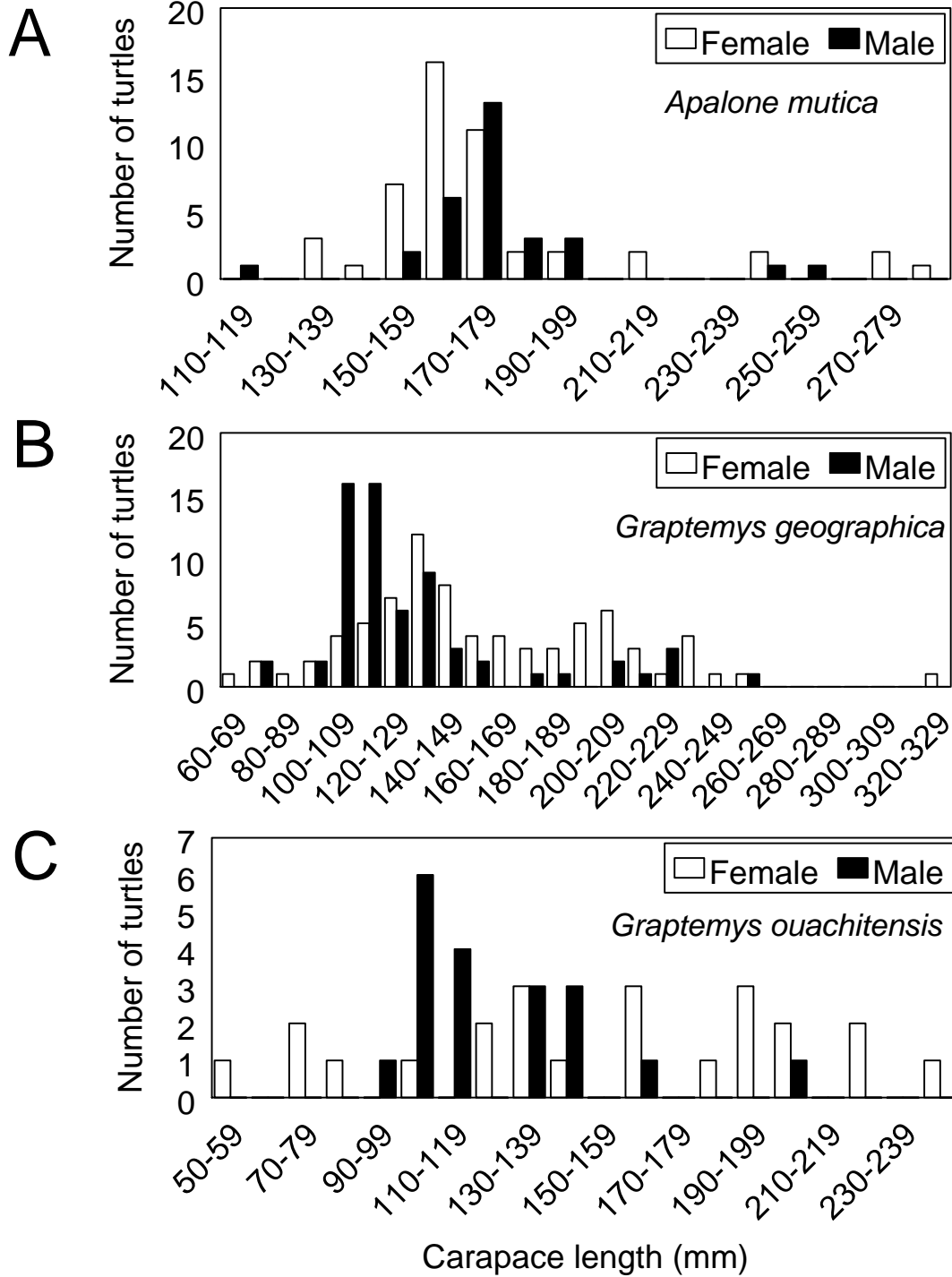
DISCUSSION

The effect of stream modification is a primary concern in conservation and restoration of UMRS habitats. Previously VanDeWalle and Christiansen (1993) suggested that their collections from impoundments in Iowa supported the hypothesis that stream modification reduced diversity of riverine turtles by eliminating intolerant species. They suggested that two turtles among those we collected (*G. pseudogeographica* and *A. mutica*) were particularly affected by impoundment.

We found no effect on the number of species in impoundments as all major habitats for all reaches combined contained nine species (Table 3; Fig. 6B). For the three reaches (Reaches 2-4) that have habitats that we identified as impounded, the number of species in impoundment habitats were either the same as backwater habitats (i.e., 7 species in both for Reach 2) or reduced (5 species in impoundment vs. 6 species in backwaters for Reach 3 and 7 species in impoundment vs. 9 species in backwaters for Reach 4). Species diversity indices were greater for backwater habitats than impoundments in Reaches 3 and 4 (0.40 vs. 0.34 or 0.37, respectively) but greater for the impoundment than for backwaters in Reach 2 (0.72 vs. 0.48, respectively). However, UMRS



Figures 11A-C. A. Size frequency distribution by sex for (A) 949 specimens of *Graptemys pseudogeographica*, for (B) 1143 specimens of *Chrysemys picta*, and for (C) 248 specimens of *Apalone spinifera*.



Figures 12A-C. Size frequency distribution by sex for (A) 77 specimens of *Apalone mutica*, for (B) 131 specimens of *Graptemys geographica*, and for (C) 34 specimens of *Graptemys ouachitensis*.

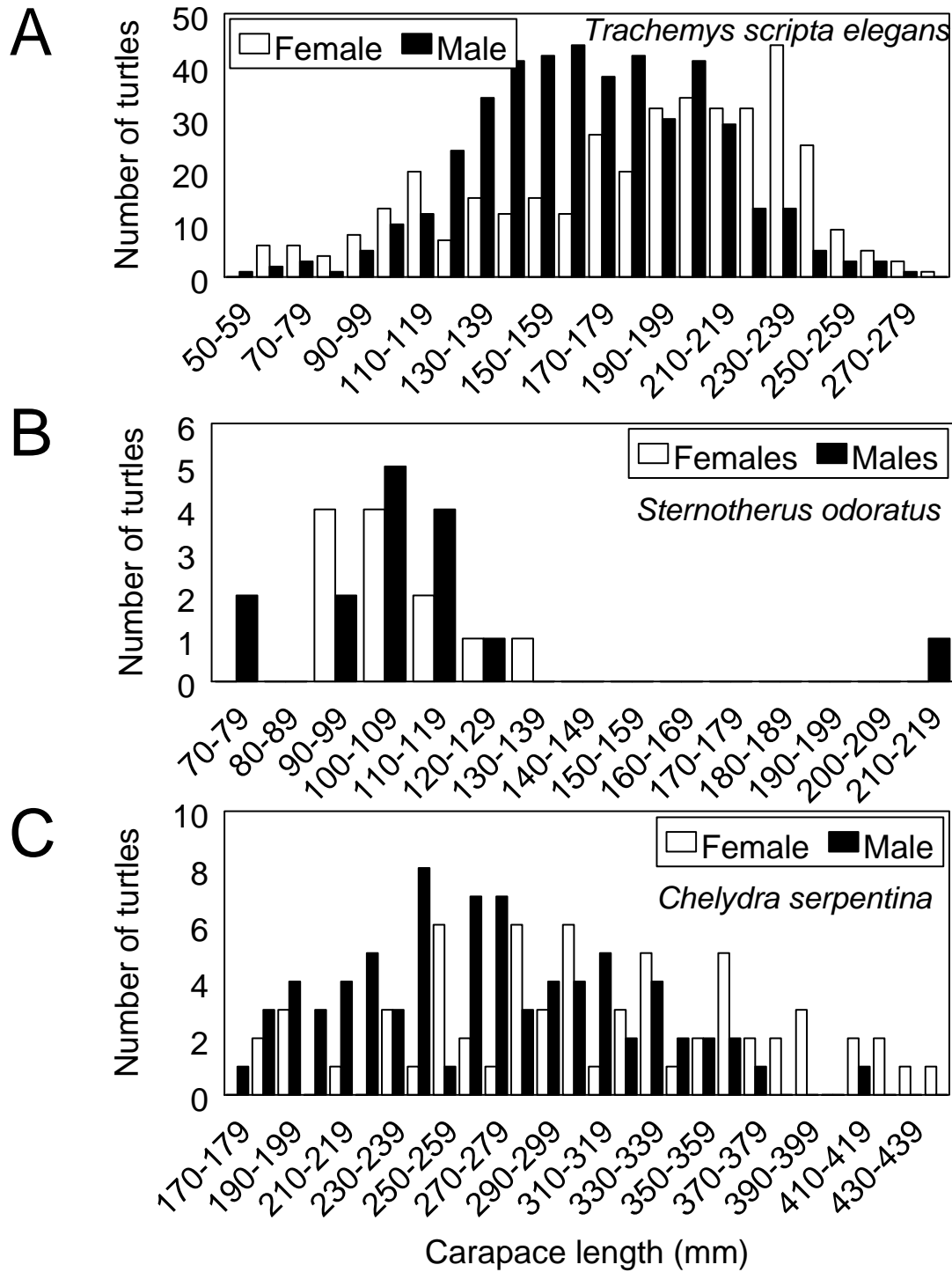


Figure 13A-C. Size frequency distribution by sex for (A) 729 specimens of *Trachemys scripta elegans*, for (B) 26 specimens of *Sternotherus odoratus*, and for (C) 133 specimens of *Chelydra serpentina*.

impoundments differ from those studied by VanDeWalle and Christiansen (1993) in that currents are always present in the former. Navigation dams control flow to regulate river depth but do not completely stop flow (i.e., Theiling, 1995).

Despite the persistence of species in impoundments in the UMRS, the number of individuals collected in impoundments was fewer than those collected in backwater habitats (Table 3). In contrast, the tailwater zone, which is more or less the mirror image of impoundments, is also highly affected by human modification. We collected even fewer specimens in tailwater zones than we did in impoundments. The reduced number of turtles in these two highly disturbed habitats is not due to differences in collecting effort because CPU for impoundments and tailwaters were about 67% less than for backwaters or side channels both of which are less disturbed. Main channel borders were roughly intermediate in CPU (Table 3).

Regardless, species diversity was highest in impoundments and tailwater zones when all reaches were combined because the small number of turtles was divided relatively evenly among all the species collected (Table 3). In other habitat types, one or two species tended to dominate the samples from those habitats.

The relatively small number of specimens collected in impoundments does not seem to be due to reduced current, per se. Collections from backwater habitats, which are also regions of little current flow, contained the largest number of turtles both in absolute numbers and when corrected for differences in collecting effort (Table 3). This suggests to us that protection of backwater habitats from alteration and maintaining their riverine nature is important in maintaining species diversity and density among aquatic turtles. Previously Starret (1972) suggested that draining backwaters and floodplain lakes of the Illinois River led to reduced population sizes for *Chelydra serpentina* and *Apalone spinifera* in the Illinois River but an increase in the

number of painted turtles. His findings are consistent with our suggestion that maintaining backwater integrity is important and with our observation that diversity indices for backwater habitats are low due to dominance of various emydid species.

One major impact of alteration of the hydrology characteristic of impoundments and to some extent the tailwater zones may be to alter the nature of the flood pulse that formerly characterized UMRS habitats (Theiling, 1995; Theiling et al., 1996). At least one species of turtle, *Trachemys scripta elegans*, that we examined appears to time both nesting and hatchling emergence from nests with the flood pulse as it existed before construction of locks and dams (Tucker et al., 1997; Tucker, 1997). Alteration of the flood pulse could increase the incidence of nest inundation (Tucker et al., 1997) or cause hatchlings to have to cross longer expanses of terrestrial habitats to reach aquatic environments (Tucker, 1997). Either effect could reduce recruitment in this and other species that nest in UMRS habitats.

The general tendency for species diversity to decline from north to south along the length of the UMRS is an important finding (Fig. 14). We suggest that the decline in species diversity index parallels an increase in human modification of habitats associated with increased river regulation from north to south. The declining species diversity overall is actually an indirect measure of species diversity in backwater habitats because except for Reach 5 most specimens were collected in backwaters. Moreover, diversity within backwaters declined more abruptly than diversity overall. For instance, diversity index for Reach 1 backwaters was relatively high (0.72) but decreased to 0.48 in Reach 2 backwaters and 0.40 in backwaters in Reaches 3 and 4.

Although maximal diversity index overall and for backwaters occurred in Reach 1, Reach 2 had maximal diversity indices for the other four habitat types (i.e., impoundment = 0.72, main channel border = 0.65, side channel

border = 0.63, tailwater = 0.75). Reach 5, which had no collections from backwaters, had the lowest diversity index for main channel borders (0.21) and a low value for side channel borders (0.34). Only Reach 3 had a lower value for side channel borders (0.16) but we collected only eight specimens of two species in side channel border habitats in Reach 3. Thus, we believe that the decline in diversity indices from north to south is not limited to backwaters. North to south reduction in species diversity apparently also occurs in the other UMRS habitat types but is obfuscated by the small number of specimens collected in nonbackwater habitats.

The north to south reduction in diversity indices is not due to decreased number of individual turtles collected as CPU is highest for the two southern most reaches (Table 1; Fig. 14). Rather, we found that turtle communities in the two southern reaches (Reaches 4 and 5) were less even than those of other reaches. The increased number of turtles caught resulted from increases in only one or two of the species collected rather than increases in all species.

Reduced diversity from north to south is contrary to what we initially expected given that more turtle species occur in the southern portion of the UMRS than in the northern reaches (e.g., Ernst et al., 1994) and that we actually caught more species in southern reaches than northern ones.

Overall and reach by reach the species diversity indices we found were lower than the 0.88 reported by VanDeWalle and Christiansen (1993) who also reported more species (11 species) than do we (10 species). However, their methods, which relied on museum collections as well as turtles specifically collected for their study, differ greatly from those that we used. Nonetheless, the difference in species lists is instructive. They report three species, *Emydoidea blandingii*, *Macroclemys temminckii*, and *Kinosternon flavescens* that we did not encounter. We collected two species (*Graptemys ouachitensis* and *Pseudemys concinna*) that VanDeWalle and Christiansen (1993) did not find in Iowa.

Only one of the species reported only by VanDeWalle and Christiansen (1993), the alligator snapping turtle (*M. temminckii*), is actually typical of

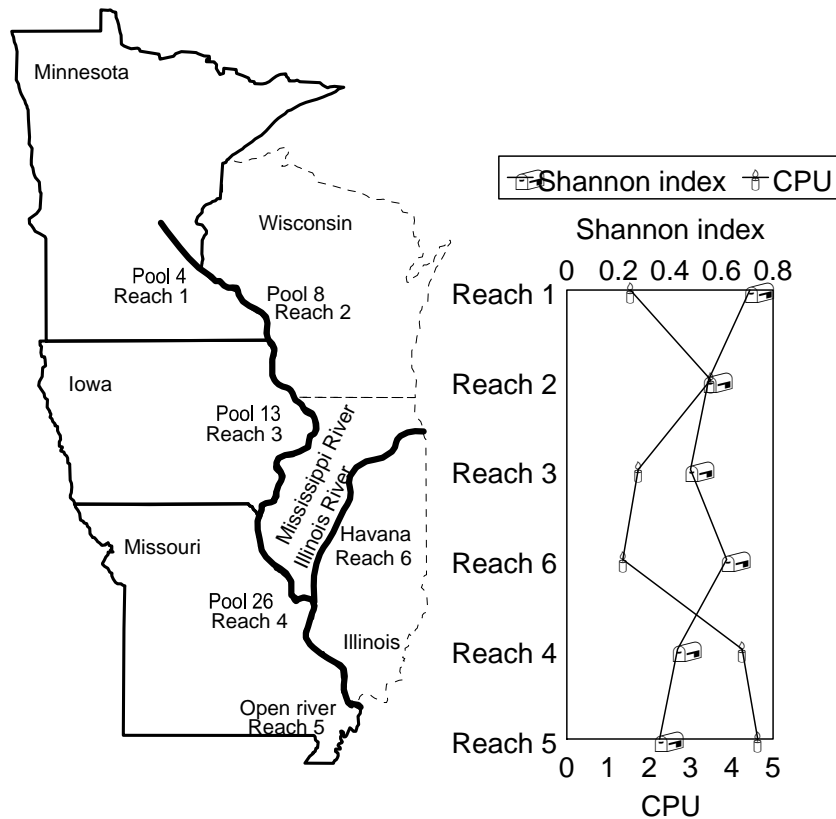


Figure 14. Variation in catch per unit effort (CPU) and Shannon diversity index from reach to reach.

riverine habitats and like the current study, they observed no newly captured specimens of this species. This species is rare in the UMRS (i.e., Smith, 1961; Johnson, 1987; Christiansen and Bailey, 1988) and its absence in our extensive survey underscores that rarity. The other two species are more characteristic of wetland habitats and would be unlikely to be encountered in the sorts of habitats sampled by LTRMP (i.e., Smith, 1961; Christiansen and Bailey, 1988). Of the species that only we report from the Mississippi River, one (*Pseudemys concinna*) does not occur in Iowa (Ernst et al., 1994) and the other (*Graptemys ouachitensis*) was only sporadically collected by our sampling

but did include a single specimen from Iowa (Table 1).

The numerical dominance of emydid turtles that we observed in the UMRS is consistent with findings of VanDeWalle and Christiansen (1993) and Gritters and Mauldin (1994) from the Mississippi River in Iowa and Pool 13 (Reach 3), respectively. Moreover, studies of other sites from eastern North America from both lotic and lentic habitats (reviewed by Bury, 1979) invariably found emydids making up more than 50% of all turtles collected. Thus, emydid turtles tend to dominate faunas region wide.

This finding has certain implications for habitat preservation previously noted by VanDeWalle and Christiansen (1993) because emydids share certain traits. In general, emydids are all basking turtles and are most often found in habitats with moderate to little current. Thus, removal of basking sites (i.e., logs and snags) or increasing current velocity would likely negatively impact their numbers (VanDeWalle and Christiansen, 1993). Moreover, adults and particularly adult females, become largely herbivorous in several of these species (reviewed by Ernst et al., 1994). Consequently, preservation or enhancement of aquatic vegetation in backwater habitats should be an important consideration in conservation plans that include species of emydids.

The temporal variation in size suggested by results for several species is a unique finding whose biological significance is uncertain. In part, the larger size observed in 1994 and 1995 may be an effect of changing our sample design from one of subjectively selected sites to a stratified random design.

Moreover, the number of hoop net sets increased in 1994 and 1995 compared to 1992 and the flood affected 1993 season. Hoop nets tend to catch larger turtles than do fyke nets. Consequently, additional turtles contributed by hoop nets tended to be large ones. The temporal variation we found demonstrates the need for long-term studies of turtle populations along with the importance of understanding gear biases in collections.

The variation in size from month to month that we observed is also a

unique finding. Because most turtles were collected in backwater habitats, this finding suggests that larger turtles were more likely to be collected there from June-August than in other months that we sampled. This finding might be associated with movements of adults in association with nesting. Turtles are known to congregate near suitable nesting habitats prior to nesting (e.g., Vogt, 1980; Tucker, 1997). Thus, collections made during the nesting season (i.e., June-July) in backwater habitats might be expected to contain relatively more mature females and more courting adult males than collections made when turtles are no longer nesting.

Because the same mix of hoop and fyke nets were used from month to month, the temporal variation by month is unlikely to be due to some undetected bias due to gear. However, another possible explanation is that during the early part of our sampling season aquatic vegetation is not fully developed. Thus, larger, more herbivorous turtles might be more attracted to the fishes in our nets than that they are later in the season once aquatic vegetation is fully developed. Consequently, our observation might reflect a seasonal variation in the likelihood that larger turtles will enter nets. Regardless, this finding further underscores the importance of maintaining integrity of backwater habitats in the UMRS.

We also found variation in the number of turtles collected from year to year with larger numbers collected in 1994 and 1995 compared to 1992 and 1993 for most reaches. Previously, Gritters and Mauldin (1994) attributed increased number of turtles collected in 1989 compared to 1990-1992 in Reach 3 to the effects of drought in 1989, which caused turtles (and collecting effort) to be concentrated in the few backwaters that remained available to both turtles and investigators. Our collections from Reach 3 though relatively higher in 1995 (Table 2-119 individuals) did not approach the 313 turtles caught there in 1989 suggesting that the explanation offered by Gritters and Mauldin (1994) has ecological relevance. However, drought cannot

account for increased numbers of turtles caught in 1994 and 1995 in all reaches because 1994 and 1995 were certainly not affected by drought conditions. The difference in number of turtles is not due to variation in collecting effort since the number of turtles caught in 1994 and 1995 are greater than those caught in 1993 and 1992 even after correcting for variation in collecting effort. One possible explanation may be that the 1993 flood disrupted aquatic vegetation in backwater habitats (i.e., Sparks, 1996). Reduced availability of aquatic vegetation may have made our nets, which are after all designed to catch fish more attractive to turtles in the years following the 1993 flood. Although the proximal cause or causes for the increased number of turtles caught in 1994 and 1995 are not obvious, the temporal variation in numbers of turtles caught during our study also demonstrates the importance of long-term monitoring of turtle populations in the UMRS.

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APPENDIX: Natural history summaries for turtle species collected by LTRMP. In this section, we briefly summarize previously published natural history details for each species that was collected by LTRMP. These were primarily drawn from Ernst et al. (1994).

Family Emydidae

Chrysemys picta (Schneider, 1783)

Painted turtles (*Chrysemys picta*) primarily live in shallow, often vegetated habitats. They are typical of more lentic than lotic habitats. Although we found painted turtles in many of the habitat types that were sampled in Reaches 1-4 and 6, they were most commonly collected in backwater habitats. They dominated collections from backwaters in Reaches 1-3 but became progressively less important in more southerly reaches and had virtually disappeared from our collections from Reach 5.

We found that as *Trachemys scripta elegans* and *Graptemys pseudogeographica* became more common in Reaches 4-6 that painted turtles declined in numbers (Fig, 4A). *Graptemys pseudogeographica* also occurs in Reaches 1-3 but is only really important in habitats such as main channel and side channel borders where painted turtles are less common (Fig. 4B). This finding supports the conclusion of Moll (1973) who suggested that the small size of the southern painted turtle (*C. p. dorsalis*) might be an adaptation to competition with other emydids that are more common in the southern United States. The difference in size that we found between the larger turtles from Reach 1-3 and those from more southerly reaches (Reaches 4-6) is consistent with latitudinal variation in size noted by Moll (1973).

Painted turtles are omnivorous but tend to depend more on aquatic vegetation after sexual maturity. In contrast, small specimens are largely carnivorous and prey on a variety of small vertebrate and invertebrate animals. Dietary studies were reviewed by Ernst et al. (1994) but most of these are based on specimens from the eastern and southeastern United States.

Presumably, dietary habits are similar in the UMRS.

Reproduction in the painted turtle has been extensively studied from many locations (reviewed by Ernst et al., 1994). Reproductive effort varies by latitudinal in this species (Moll, 1973; Christiansen and Moll, 1973) and can vary within limited geographic contexts (Tucker, 1978). In general, females from the northern and western portions of the range of the species are larger. They lay more eggs per clutch but the eggs are relatively smaller given the large size of the females compared to females from more southern locations (Moll, 1973).

Although the systematics of the painted turtle have been extensively studied and four relatively well marked subspecies are accepted by most authors, subspecific identification of painted turtles in the UMRS is complicated by hybridization between the western painted turtle (*Chrysemys p. bellii*) and the midland painted turtle (*C. p. marginata*). Authorities generally identify painted turtles in most of the UMRS as hybrids between these two subspecies. Painted turtles examined in Reach 4 are strongly influenced by *C. p. bellii* in that many have well developed plastral figures that cover more than half of the plastron and extend out along the plastral seams. However, some turtles have small plastral figures and appear to be typical *C. p. marginata*.

The difference in size that we found between larger turtles from Reach 1-3 and those from more southerly reaches (Reaches 4-6) is consistent with latitudinal variation in size noted by Moll (1973). Although we found sexual size dimorphism among our sample of this species consistent with the findings of others (i.e., Gibbons and Lovich, 1990), we also collected one exceptionally large male (230 mm carapace length) from Reach 3.

Graptemys geographica (Le Sueur, 1817)

The common map turtle (*Graptemys geographica*) is typically found in larger lakes and large rivers. Although it ranges through much of the UMRS

(Ernst et al., 1994), we found it most commonly in the northern portion of our study area (Reaches 1-3, Table 1). Our findings are consistent with the range map published by Conant and Collins (1991), which excludes the Mississippi River below Pool 26 from the range of the species. In contrast, our findings are inconsistent with the generalized range map in Ernst et al. (1994) where the species is shown occurring in the Mississippi River to southern Tennessee. We also caught most specimens in backwater habitats rather than main channel or side channel habitats in contrast to *G. pseudogeographica* which was most often collected in side channel and main channel habitats (Table 3).

The common map turtle is largely molluscivorous though other food items are found in the diet (dietary studies were reviewed by Ernst et al., 1994). We made no observations on reproduction in this species but reproductive life history was reviewed by Ernst et al. (1994). Vogt (1980) found that Wisconsin females laid two clutches of 8-19 eggs (mean 13.6 eggs) per year.

Sexual size dimorphism is pronounced in this species with males generally smaller than females. Ernst et al. (1994) listed 160 mm and 273 mm as maximal carapace lengths for males and females, respectively. We found several males that exceeded 160 mm carapace length (Fig. 12B). Although field identification of sex in turtles by personnel primarily trained as fisheries specialist can be difficult (see below), we think it is unlikely that all of these turtles were misclassified. Males of this species have elongated claws on the front feet and are generally easily identified as males in the field. Apparently males reach larger maximal sizes than is generally recognized.

Graptemys ouachitensis Cagle, 1953

The Ouachita map turtle (*Graptemys ouachitensis*) typically occupies large rivers and river-bottom swamps. We collected this turtle only sporadically and most commonly in Reach 2 (Table 1, Fig. 4A). In contrast, Vogt (1981a) found the species to be the most common (66% of total) among three species of *Graptemys* that he collected in Wisconsin. However, Vogt used different

collecting methods specifically designed to catch turtles. Most specimens collected by LTRMP were from backwaters (Table 5).

Unlike the common map turtle, the Ouachita map turtle is omnivorous rather than molluscivorous (Vogt, 1980 and 1981a). Reproduction in this species was reviewed by Ernst et al. (1994), who reported a mean clutch size of 6 to 15 eggs.

We collected one specimen of this species in Iowa. This specimen was collected in the Mississippi River near the northern end of Harrington Slough in Jackson County, Iowa at river mile 555.4 (Reach 3). The species was not included among turtles known to occur in Iowa by Christiansen and Bailey (1988) but should be expected to occur in Iowa given the range reported by Ernst et al. (1994).

Graptemys pseudogeographica (Gray, 1831)

The false map turtle (*Graptemys pseudogeographica*) is characteristically found in large streams and generally occupies lotic habitats. Our findings are highly consistent with that summary. We collected most specimens in main channel and side channel habitats (Fig. 4B) particularly in Reach 5 (Fig. 4A) where this species dominated collections (Table 5). Relatively few specimens were collected in backwater (Fig. 5B) or impoundment (Fig. 6A) habitats in other reaches. Our findings differ from those of Timken (1968), Vogt (1981b), and Christiansen and Bailey (1988) all of whom suggested that this species is most common in habitats with little current.

This species is a general omnivore (Vogt, 1981a). Vogt (1980) found clutch size ranged between 8 and 22 eggs with larger females producing larger clutches.

Graptemys pseudogeographica is a polytypic species (Ernst et al., 1994).

Except for seven specimens initially identified as *G. pseudogeographica kohnii* in Reach 2, all others were initially identified as *G. p. pseudogeographica* based on head patterns. Except for seven specimens with

'*kohnii*' head patterns from Reach 2, our findings would be consistent with the general finding that *G. p. kohnii* occurs mostly west of the Mississippi River (Ernst et al., 1994). The few specimens that we identified initially as *G. p. kohnii* were included with the many *G. p. pseudogeographica* in the analyses above. Nonetheless, our initial results demonstrate the difficulty in field identification of subspecies in general and for *Graptemys* in particular.

Pseudemys concinna (Le Conte, 1830)

The river cooter (*Pseudemys concinna*) is a large emydid turtle characteristic of large river habitats (Ernst et al., 1994). However, the species is uncommon in Illinois (Moll and Morris, 1991) and Missouri (Johnson, 1987). Our collection of a single specimen of this species among more than 4,400 individual turtles from collections made in habitats typical for the species demonstrates that rarity (Table 1). The single specimen that we did collect was collected in the Little River Diversion Canal near its mouth at mile 48.8 (Cape Girardeau County, Missouri) on 14 October, 1993. The specimen was released at the collecting site. We collected no specimens in Reach 4 where it had been previously reported by Smith (1961).

In part, our collections may have over-estimated the rarity of this species due to its peculiar life-history. Unlike most of the turtles that we collected, *P. concinna* is essentially herbivorous throughout its life (Ernst et al., 1994; Thomas et al., 1994; but see Cahn, 1937 for a contrary opinion). Other turtle species that we collected are omnivores or carnivores and likely were attracted to nets because they contained fish.

Trachemys scripta elegans (Wied-Neuwied, 1839)

The red-eared slider (*Trachemys scripta elegans*) has probably received more attention from biologists than any other turtle world wide and its physiology has been intensively studied in the laboratory. Despite this remarkably few studies of its natural history in the UMRS have been published. The most important of these include studies by Cagle (1950) and Thornhill

(1982). Other studies were reviewed by Ernst et al. (1994). In general, this is a turtle of large rivers and their associated habitats but may be found in lentic habitats both large and small (Smith, 1961; Johnson, 1987).

This turtle is closely adapted to the variable hydrologic pattern found in rivers. The importance of a spring flood pulse to this species was demonstrated by Tucker (1997) who found that nesting occurred on the falling flood and that hatchling emergence occurred at or near the normal flood pulse peak. Moreover, Tucker et al. (1997) showed that immersion in water for 24 to 48 hours induced complete egg failure in eggs containing embryos of two ages. Thus, the long distances that some females travel before nesting (i.e., Tucker, 1997) can be explained as a method to avoid loss of eggs to predictable flooding. These results bear directly on the impact of human alteration of the flood pulse in the UMRS (i.e., Theiling, 1995; Theiling et al., 1996) on turtle populations (see above).

Family Chelydridae

Chelydra serpentina (Linnaeus, 1758)

The common snapping turtle (*Chelydra serpentina*) is a large species that may reach a carapace length of 494 mm (Ernst et al., 1994). It occurs in a broad range of habitats from large rivers to swamps, ponds, and lakes. We collected the species in all habitat types surveyed in the UMRS. However, it was most common in backwater habitats (Table 3). Like many of the turtle species that we collected this turtle is omnivorous but large specimens may feed more heavily on aquatic vegetation (Budhabhatti and Moll, 1990). Dietary habits were reviewed by Ernst et al. (1994).

Numerous studies on reproduction of this species have been published and were reviewed by Ernst et al. (1994). Typical clutches contain 20 to 40 eggs and clutch size may increase with increasing latitude (Ernst et al., 1994). In the UMRS, hatchlings of this species emerge in late summer or fall shortly after hatching (Tucker pers. Obs.).

Family Trionychidae

Apalone mutica (Le Sueur, 1827)

The smooth softshell (*Apalone mutica*) is a large softshell turtle that occurs throughout the UMRS (Ernst et al., 1994). In our collections from the UMRS, we found it in each reach surveyed but it was less common than its congener, *A. spinifera*, in each reach except Reach 5 (Table 1). Moreover, *A. mutica* was more commonly collected in the more lotic main channel and side channel habitats than it was in backwater or impoundment habitats (Table 5, Fig. 4B). Thus, the greater frequency of *A. mutica* in Reach 5 can probably be attributed to the absence of backwater collections in that Reach.

The smooth softshell is largely carnivorous and feed heavily on aquatic invertebrates as well as small vertebrates (Williams and Christiansen, 1981; reviewed by Ernst et al., 1994). Usual clutch size ranges between 18 and 22 eggs (Ernst et al., 1994).

Sexual size dimorphism is pronounced in this species with females reaching a carapace length of 356 mm but males only 178 mm (Ernst et al., 1994). We collected eight specimens identified as males that exceeded this maximum (Fig. 12A). This species has less pronounced sexually dimorphic characters and field identification is more difficult. Some of these larger turtles identified as males could have been immature females.

In Reach 4, where few specimens were collected, all were found in areas of sand substrates. Previously, Williams and Christiansen (1981) found that clean sand was required by *A. mutica*. Moreover, both Goldsmith (1944) and Moll (1980) found that level sandbars or sandy shores free of silt were required as nest sites by this species. Moll (1980) suggested that loss of such silt free sand bars was the proximal cause for declines in numbers of *A. mutica* in the Illinois River. Our sampling indicates that *A. mutica* remains an uncommon species in the portion of the Illinois River that we sampled (Table 1).

Apalone spinifera (Le Sueur, 1827)

The spiny softshell (*Apalone spinifera*) is also a large softshell turtle widely distributed in the UMRS (Ernst et al., 1994). In our collections from the UMRS, we found it in each reach surveyed (Table 1, Fig. 4A). It was much more frequently encountered than its congener, *A. mutica*, in each reach except Reach 5 (Table 1). Unlike *A. mutica*, *A. spinifera* was frequently collected in backwater habitats (Table 5), and less frequently in the more lotic, main and side channel habitats where *A. mutica* was collected (Fig. 4B). *Apalone spinifera* was also found on soft mud substrates in contrast to the apparent preference for sand in *A. mutica*.

The spiny softshell is largely carnivorous (reviewed by Ernst et al., 1994). Males tend to feed more heavily on aquatic invertebrates, whereas females take more vertebrate prey (Williams and Christiansen, 1981). Clutch size ranges from 4 to 39 eggs (Ernst et al., 1994).

Sexual size dimorphism is pronounced in this species, as well, with females reaching carapace length of 540 mm but males only 216 mm (Ernst et al., 1994). We collected 21 specimens identified in the field as males that exceeded this maximum (Fig. 11C). Males and immature females of this species have carapaces with a distinct spotted pattern compared to the more blotched patterns found in mature females. It seems likely that many of the larger specimens identified as males were instead immature females.

We found that sex ratio in our collections were strongly male biases (Table 3). However, other studies of this species have found unbiased sex ratios (i.e., Cagle, 1942; Breckenridge, 1955; Vogt and Bull, 1982). In part, the incongruence of our study and with others may reflect the difficulties in determining sex in the field. This is an active and aggressive turtle that is difficult to handle in the field. It is also possible that the smaller males are more likely to be caught in our gear compared to the larger females.

Family Kinosternidae

Sternotherus odoratus (Latreille in Sonnini and Latreille, 1802)

The stinkpot (*Sternotherus odoratus*) is a small turtle and the smallest collected by us in UMRS habitats. Consistent with previously published range maps (Ernst et al., 1994; Conant and Collins, 1991), we collected it only from Reaches 4-6 (Table 1, Fig. 4A). We found it in all of the various habitats that we sampled in the UMRS (Table 4, Fig. 4B). Although we collected most specimens in backwater habitats, the numbers collected in such habitats only slightly exceeded those collected in the more lotic habitats such as side channels (Table 5). Generally, most references list this species as preferring habitats with little or no current but this might reflect more the absence of collections from rivers because most studies of the natural history of the species have been conducted in ponds or swamps.

The stinkpot is omnivorous, feeding on invertebrates, small vertebrates as well as algae and aquatic plants (reviewed by Ernst et al., 1994). Tinkle (1961) demonstrated that clutch size (but not egg size) varied by latitude with larger clutches being laid by females from more northerly regions. Average clutch size for northern populations averaged 5.5 eggs per clutch similar to the average of 5.8 eggs per clutch for 10 clutches from Pool 26 in the UMRS (Tucker unpublished).

We found roughly equal numbers of males and females among turtles that we identified sex (Table 3). Similar results were reported in a number of other studies reviewed by Ernst et al. (1994). This is a small turtle with a maximal carapace length of 137 mm. We include a turtle reported to have a carapace length of 210 mm, likely an error for 110 mm. We might add that this species does reach greater lengths than previously thought because we collected the carapace of a recently killed stinkpot that measured 154 mm (Tucker unpublished) near Swan Lake in Calhoun County, Illinois (Reach 4) in 1993.