Aquatic Habitats and Fish Communities in the Lower Mississippi River

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ABSTRACT

The Mississippi River ecosystem is, and probably has been for millions of years, home to a large and diverse community of freshwater fishes. The river is also an important inland artery for commerce, and its floodplain supports extensive agriculture and many urban and commercial areas. The ecosystem and the distribution and abundance of its aquatic habitats have changed greatly over geological history. Recent attempts to control the river have also produced changes in the ecosystem, and in many ways these changes are different from those that occurred naturally over the history of the river. Managing the aquatic ecosystem of the river requires an understanding of its ecological habitats, the biotic communities, and their interrelationships. This article examines the state of our knowledge of the lower Mississippi River ecosystem; it also delineates the aquatic habitats of the river and describes the communities of fish associated with them.

I. INTRODUCTION

"The Mississippi is well worth reading about. It is not a commonplace river, but on the contrary is in all ways remarkable."[283]

Mark Twain was not merely being romantic in describing the river, for it ranks among the world's giants in many respects.[71] The Mississippi is the world's third largest river in terms of drainage area (nearly 3.25 million km^2), the third longest (6019 km from the headwaters of its Missouri River tributary to the sea), and the eighth greatest in terms of discharge (about 475 billion m^3 of water sent to the sea annually). The river system contains over one third of the 40,000 km of navigable rivers and lakes in the U.S.[119,191] It drains nearly 41% of the contiguous U.S. and a portion of Canada (Figure 1), and receives the input of mountain torrents, arid plains streams, vast grasslands, and swamps. The subject of this review is the focal point for all these inputs, the lower Mississippi River from the Ohio River to the Gulf of Mexico.

Streams of all sizes comprise a mosaic of recognizably distinct aquatic habitats defined by more or less characteristic arrays of features such as current speed, substrate, depth, amount of debris (or cover), and water chemistry.[5,104,132,198,210] The kinds, amounts, and distributions of habitats directly and indirectly influence the occurrence and abundance of fishes, and

FIGURE 1. The Mississippi River drainage basin.

to varying degrees distinct fish communities can be associated with the habitats.

Here, we examine the aquatic habitats and the resident freshwater fish fauna of the lower Mississippi River. We describe the processes that formed the river and its physical features and outline recent changes to these features brought about by man. Aquatic habitats of the river are defined in terms of their physical and chemical attributes, habitat interrelationships are described, and changes in the distribution and abundance of habitats throughout time are examined. Finally, the fish communities associated with the habitats are delineated.

II. THE LOWER MISSISSIPPI RIVER ECOSYSTEM

A. General Features

The lower Mississippi River and its alluvial valley lie within the Mississippi Embayment, a part of the Central Gulf Coastal Plain.[131] The valley is 40 to 200 km wide, extends nearly 1000 km from just north of the Ohio River confluence to the Gulf of Mexico,[89] and encompasses an area of nearly 130,000 km^2. Much of the valley is bordered by abrupt bluffs (Figure 2) which gradually decrease in height southward and finally disappear beneath the Louisiana coastal marshlands. The valley walls are breached only where major tributary valleys merge with that of the Mississippi. The greatest river bed elevation, in the valley's northern end, is only about 100 m above mean

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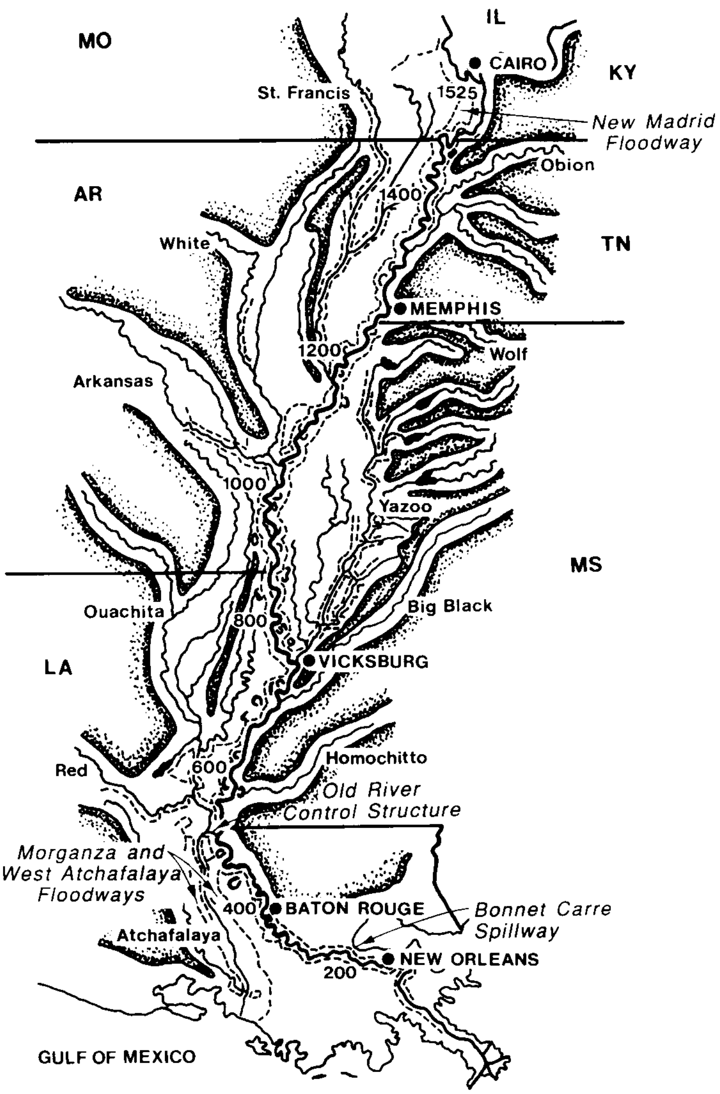


FIGURE 2. The lower Mississippi River alluvial valley. Shown are major tributaries, major cities, control structures, and floodways. Numbers indicate river kilometers above Head of Passes, LA. Solid, heavy line indicates lower Mississippi River; dashed lines indicate levees; shaded areas with stippling indicate the valley margins.

sea level.[285] The aquatic resources of the area include the mainstem Mississippi River, 26 tributary streams, and 242 lakes >8 ha in surface area.[229,285] Since completion of the levee system, much of the original floodplain has been isolated from the river ecosystem.

Mean annual discharge at Vicksburg (RK 704),* midway between the Ohio River and the Gulf, is about 15,637 m^3/s.[180] Variation in discharge is also impressive, ranging from an average of 26,855 m^3/s in April to 7393 m^3/s in September; an estimated maximum flow of 64,532 m^3/s occurred during the 1927 flood.[282] The difference in river stage between the minimum and maximum average monthly discharges is often >8 m, and river stage may fluctuate more than 14 m during a single year (Figure 3).

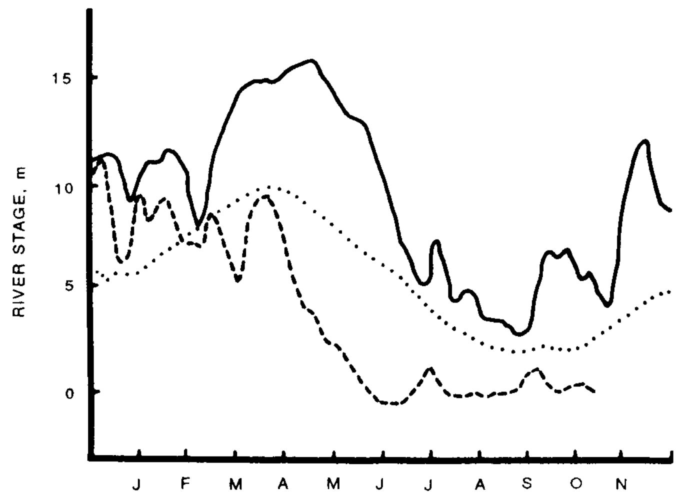


FIGURE 3. Annual hydrographs for the lower Mississippi River at Vicksburg, Mississippi, showing a high-water year (1973, solid line), a low-water year (1988, dashed line), and the average stage (1931 to 1987, dotted line).

The lower Mississippi River comprises two quite distinct sections:[281] that traversing the Alluvial Valley from Cairo, IL (RK 1536) to Baton Rouge, (RK 378), and that flowing across the Deltaic Plain from Baton Rouge to Head of Passes (RK 0). In the upper section, the thalweg* is quite variable, and often very shallow at crossings.[183] River slope averages about 0.24 m/km. There is about 0.6 million ha within the levees and bluffs (ca. 517 ha/RK), which range from about 0.1 km to over 10 km from the river. About 56% of this area is forested, 21% crops-grasslands, and 23% aquatic. Approximately 55% of the aquatic habitat is deep, swift channel and 45% slackwaters. Both dikes and revetments are commonly found manmade features.

The river ecosystem undergoes a distinct change in the lower 378 km below Baton Rouge.[285] River slope is very low, averaging only 0.08 m/km. The channel is deeper and narrower because of the relatively erosion-resistant soil,[145,146] and also because a 12-m deep channel is maintained for ocean-going traffic. Large meander loops are infrequent. Levees are situated nearly at the river's banks along both shorelines, and floodplain habitats are almost nonexistent; only 52,000 ha of land remains

* Mileage on the lower Mississippi River follows the navigation channel from River Mile zero at Head of Passes, Louisiana (the point at which the river divides into its three major channels to the Gulf of Mexico) to River Mile 953.8 at the confluence of the Ohio river. In this article, mileage has been converted to river kilometers (RK).

* The thalweg is the line connecting the deepest points along a waterway; it is generally the center of the navigation channel.[285] Crossings occur where the thalweg shifts from one bankline to the other.

within the levees, or about 137 ha/RK. Aquatic habitat comprises over 53% of this area, with forests and crop/grassland dividing the remainder nearly equally. Over 85% of the aquatic habitat is swift, deep channel.[285] Islands or sandbars, and their associated secondary channels, are nearly absent. Revetments are extensive in this section, but dikes such as those found upstream are not used. River stage fluctuations are small compared to more upstream areas (8 m annually at Vicksburg, but only 3.5 m at New Orleans). The river bottom is below sea level in this section, and the river acts somewhat like an estuary at low flows.[229]

The ecosystem can be divided into the area within the main river banks (mainstem) and the area beyond the banks (floodplain).[55,58] The mainstem contains both the deep, swift, main flow paths of the river and slackwater areas associated with sandbars, islands, and some manmade features. The slackwater areas comprise a diversity of ecologically important aquatic habitats.

The floodplain of the lower Mississippi is one of the largest in the world. It is composed of flood-borne sediments deposited over a wide area as the river changed courses repeatedly.[236,237] The floodplain includes a diverse mosaic of landforms[243] and terrestrial communities.[253] Natural levees, backswamps, abandoned flow courses, point bar ridges (high spots) and swales (low spots), manmade bodies of water, and tributaries are all characteristic features of the floodplain environment. Natural levees are relatively high ridges formed parallel and close to the river as coarse sediment is deposited during floods. They slope gradually away from the river, merging into the backswamps. Backswamps are low, wet areas away from the river in which characteristically fine sediments (silts and clays) support distinctive vegetation types such as Tupelo-Cypress stands.[143,253] Backswamps usually have areas in which water stands for most of the year. Ridges and swales are remnants of former point bars formed at the inside of bends during meandering. Ridges usually have sandier soils that swales, and the two areas support different vegetation.[143,193] Swales may hold water during much of the year.

B. Geological History

The Mississippi River system may have formed as long as 50 to 60 million years BP (before present), in the Paleocene or early Eocene.[78] Prior to this time, the continent was drained by westward-trending rivers emptying into a western sea. Drainage to the south was prevented by an extension of the Appalachian Mountains along what is presently the Gulf Coast. The uplift of the Rocky Mountains, the demise of the Gulf Coast extension of the Appalachians, and the subsidence of the Gulf Coastal Plain caused the major interior drainage of the continent to flow south instead of west. Subsequently, transgression of the Gulf of Mexico onto the Coastal Plain repeatedly inundated much of the present lower Mississippi River. During these transgressions, other, more northern, large rivers persisted,[16,42,70,268] and a more moderate climate brought temperate conditions as far north as Hudson Bay. At the time of the final, continuous appearance of the lower Mississippi River, the system was much smaller than at present.[222] Until perhaps 2 million years BP, much of the upper and middle Missouri River system may have drained north toward Hudson Bay,[42] and much of the west-central plains drainage may have flowed southward via the Ancestral Plains River[70] directly into the Gulf instead of eastward into the Mississippi River. The Mississippi River system may not have assumed its present great size until 1.5 to 2.2 million years BP when midwestern streams were diverted southward by advancing glaciers.[42,237]

Although channel patterns of the lower Mississippi are extremely difficult to reconstruct with certainty for the time preceding the most recent (Wisconsin) glaciation, probable patterns have been ascertained for the subsequent periods.[7,14,144,235,237] Because similar processess probably operated prior to the last glaciation,[7] earlier channel patterns can be inferred on the basis of geological, vegetational, and climatic data indicating previous environmental conditions.[72,247,248] Available evidence indicates that the lower Mississippi River, and undoubtedly many other larger North American rivers, have repeatedly alternated between a braided and meandering channel pattern over the past 1.5 to 2.2 million years, and possibly longer. Differences in channel patterns are associated with differences in discharge, amount and character of transported sediment, and ultimately, climate.[250,299]

Channel pattern changes have a dramatic impact on habitat composition in river systems. Braided rivers are relatively wide and shallow. They contain numerous midstream bars which divide the flow into relatively small chutes that are shallow and have swift currents.[188] The bars and chutes are unstable, often changing size and position over days. Meandering rivers are comparatively deep and narrow with relatively stable islands and sandbars. During meandering they build extensive, well-developed floodplains that contain many large, deep backwaters, cutoff oxbows, and other slackwater habitats only infrequently associated with braided rivers. Thus, braided rivers offer a limited number of primarily swift, shallow, coarse substrate habitats, while meandering rivers offer a diverse array of both channel and floodplain habitats.

The lower Mississippi River has probably shifted between a braided and meandering form at least twice during the last glacial period. Massive deposits of glacial outwash early (80,000 to 60,000 years BP) in this period built an extensive valley train that may have extended to the Gulf of Mexico and caused the river to assume a braided form.[7,237] Following this aggradational period, as glaciers waned and sea levels rose, the ratio of glacial outwash to meltwater volume declined, and valley degradation commenced. During the succeeding interglacial stage a lesser, but more constant and finer-grained sediment load promoted the change from braided to meandering form. There is evidence that the mid-Wisconsin interglacial may have been too short for the entire river to have attained a meandering form,[7] although the lower portion may have done so.[237] Thus, a braided stream form may have predominated from about 35,000 to 70,000 years BP, followed by at least partial meandering until about 25,000 years BP.

The second major Wisconsin glacial advance, ending about 18,000 years BP, caused another large-scale deposition of outwash in the valley and presumably again produced a predominantly braided river. During the period of glacial retreat the river again evolved toward a meandering form. Postglacial periods were almost certainly times of neither gradual nor unidirectional change, however.[249] During the final glacial retreat, for example, the lower several hundred kilometers of the Mississippi River abruptly changed from a braided to a meandering form (11,000 to 12,000 years BP).[238] This change coincided with a loss of meltwater as glacial retreat opened a path to the east through the St. Lawrence River.[14,144] Another decline in discharge (to 40 to 60% of present) may have occurred about 4000 to 5000 years BP.[238] In contrast, several relatively sudden increases in discharge occurred in response to drainage of large proglacial lakes.[14] The meandering character of the present-day river may not have fully developed until about 5000 to 6000 years ago.

Changes in channel pattern did not occur simultaneously in all parts of the valley. In the Mississippi River itself, meandering undoubtedly began near the coast and proceeded irregularly upvalley.[7] Some tributaries may have been begun meandering sooner than the Mississippi River following episodes of braided stream form. For example, the oldest Arkansas River meander belt is thought to be 2000 to 3000 years older than that of the Mississippi.[7,237] Watershed vegetation was also quite different among the various tributaries,[144] and this may have caused them to respond differently to changing climates during and following glacial periods. The Ohio-Tennessee Valley, for example, was mostly wooded,[42] and streamflow and sediment discharge would have responded quite differently there to changes in precipitation than in the upper midwest tall-grass prairie or the western short-grass prairie. Sediment yields from forested lands are generally much lower than those from grasslands, and a change in sediment-to-discharge ratio is thought to be among the most important variables influencing river channel pattern.[248]

Changes in channel pattern imply changes in the kinds and proportions of habitats, which in turn imply changes in ichthyofaunas.[69,176,264,278] Based on the fossil record, however, it appears that sufficient suitable habitat for a wide variety of fishes has existed within the Mississippi River system as a whole for many millions of years.[52,102,263] The Mississippi River system has provided a relatively stable environment for fishes since it formed.[222] Though there have been rather dramatic climatic changes, including the Pleistocene glaciations, there have been relatively few extinctions.[263] In contrast, many of the major groups have undergone extensive speciation. Most present families and many genera of fishes found in the Mississippi River system date back to at least the Miocene Era (5 to 25 million years BP), and some are considerably older. Fossil ictalurid catfishes, and a catostomid very closely resembling present-day *Ictiobus cyprinellus*, are known from the Eocene (37 to 55 million years BP).[105] Gars, bowfin, paddlefish, and sturgeons are even more ancient.[263] In some cases even present-day species, e.g., channel and flathead catfishes,[164,165] are recognizable from the Miocene. Thus, though the lower Mississippi River itself may have changed dramatically at times (or even disappeared under an encroaching Gulf of Mexico), the river system as a whole has provided a sufficient diversity of habitats to allow continued survival of most major taxa.

C. River Modification

The Mississippi has long been a major route for commerce. As early as 1705, a cargo of furs and animal hides was floated down the Ohio and Mississippi Rivers bound for markets in France.[179] Flatboats and rafts, built for one-way, downstream trips, soon gave way to keelboats, which could navigate the river in both directions. The invention of the steamboat in 1811 accelerated the growth of river commerce by reducing the time for trips to a fraction of their former lengths,[77] and the advent of powerful diesel engines increased the tonnage of cargo moved on the river as rapidly as steamboats had decreased the time. The 27 million metric tons of cargo carried on the river in 1940 increased to over 91 million by 1972, and to over 400 million metric tons by 1985.[182] Commercial vessels are projected to carry nearly 2.6 billion metric tons by the year 2000.[74] As navigation promoted settlement, a number of important riverport cities were founded, and the overall population of the floodplain grew dramatically. An especially interesting and informative narrative relating to historic names and places on the lower Mississippi River is presented by Bragg.[26]

Even though the existence of the river was critical to the development of the area, the Mississippi presented many problems for both settlement and navigation, and man soon began to rework the river and its floodplain. Early work was mostly privately funded and local in scope.[120] However, as river-related problems increased, recognition that control of such a powerful river could only be accomplished through a national effort was inescapable. The following paragraphs outlining the history of this national effort are summarized from several sources.[83,186,189,229,285]

As early as 1837 the Corps of Engineers (CE) had studied the navigation potential of the lower Mississippi River and recommended deepening the channel by dredging. Following the disastrous 1851 flood, the CE again studied the river, producing the first comprehensive topographic and hydrographic studies. These studies led Congress to establish the Mississippi River Commission (MRC) in 1879, directing it to draw up a plan for permanently locating and deepening the navigation channel, protecting banks, preventing flooding, and promoting and facilitating commerce. Following the devastating floods of 1912 and 1913, the MRC submitted a report to Congress considering a combination of levees, tributary reservoirs, cutoffs, outlet and diversion channels, and reforestation for preventing flooding on the lower Mississippi River. Congress took no action until 1917, when the first Flood Control Act specifically authorized levee work for the purpose of flood control. A second Act, in 1923, authorized additional work, but still did not incorporate an overall strategy. Finally, following the most disastrous Mississippi River flood in recorded history in 1927, Congress passed the Flood Control Act of 1928, committing the federal government to a comprehensive plan of flood control, channel stabilization, and river regulation known as the Mississippi River and Tributaries (MR&T) Project. Subsequent legislation (e.g., the River and Harbor Act of 1899 et seq.) has significantly expanded and modified this initial plan, but its major features have been retained.

The MR&T Project incorporates:

1. Levees for containing flood flows
2. Floodways for the passage of excess flows past critical reaches
3. Dredging to maintain channel depths
4. Revetments and dikes to train and stabilize the navigation channel
5. Tributary basin modifications[285]

The Project is primarily responsible for the present physical, hydraulic, and ecological features of the river.

1. Levees

Levees represented man's initial attempts to control the river.[120] Soon after the founding of New Orleans, levees were constructed to diminish the nearly annual flooding of parts of the city, and by 1735 the levee line extended along both sides of the river from about 48 km above to 19 km below New Orleans.[285] Levees were considered so essential that in 1743 the French colonial government required landowners to complete their levees within the year or forfeit their lands.[116] By 1844, the levee system was nearly continuous along the west bank from 32 km below New Orleans to the Arkansas River, and as far as Baton Rouge on the east bank.

Up to this time, the building of levees had been almost entirely local in scope.[120] The destructive floods of 1849 and 1850 damaged many levees and focused national attention on control of the Mississippi River. The Swamp Acts of 1849 and 1850 granted the states all unsold swamp and overflow land within their borders and provided that all funds from the sale of these lands be allocated to drainage, reclamation, and flood control.[285] During the Civil War most work ceased, and flooding destroyed hundreds of miles of levees. Following establishment of the MRC, levee work began in earnest in 1882, and culminated in a coordinated levee system for the entire lower Mississippi River.

The natural floodplain of the lower Mississippi River has been narrowly circumscribed by more than 2560 km of levees and associated structures. Another 960 km of levees are in place or authorized on tributaries.[285] Levees run continuously down the west side of the river except at the confluences of the St. Francis and Arkansas-White Rivers, and levees and high natural bluffs alternate on the east side. The 0.60 million ha of floodplain remaining within the levees[143] represents only about 10% of the area inundated during extremely high floods.[117,179] The clearing of nearly 80% of the extensive floodplain forests lying outside the levees, but still draining into the Mississippi via tributaries,[92,166] has increased the sediment input from these lands manifold.[140] However, tributary modifications (see below) have offset this increase to some degree.[117,140]

Levees have steadily increased in height,[116] from about 2.75 m in 1882 to 9.25 m at present,[229] to accomodate increasing flood stages.[19,191,262] The increased stages are the direct result of river constriction, not increasing discharges; both average and maximum discharges have remained essentially unchanged since river gauging began over 130 years ago.[262]

2. Cutoffs

Two types of cutoffs occur naturally in the lower Mississippi River. Neck cutoffs occur when a river breaks through a narrow strip of land separating the upstream and downstream ends of a meander loop.[97] The cut usually becomes the new channel and the abandoned loop becomes an oxbow lake. The river temporarily decreases slightly in length, and increases in slope, but over time the original conditions are restored as new meanders form. Point bar (chute) cutoffs occur when the river cuts across a point bar during floods.[262] The fate of point bar cutoffs is variable. The new chute channel may enlarge to become the main channel, it may remain relatively stable, or it may gradually fill with sediments and become a backwater. Point bar cutoffs do not shorten the river as dramatically as do neck cutoffs. Meandering rivers naturally create cutoffs. However, man has greatly increased the rate of cutoff formation to create shorter, more direct channels and to increase discharge capacity to reduce flood heights. From 1929 to 1942, 16 cutoffs occurred in the lower Mississippi River,[171,297] most artificially constructed by the CE. The cutoff loops ranged from 6.8 to 27.2 km in length, for a total shortening of 245 km (16%) in 14 years. During the previous 162 years, only 18 natural cutoffs occurred, which shortened the river by 454 km, or about 30%. The artificial cutoffs decreased river length by nearly 17.5 km/year, and the natural cutoffs by only 2.8 km/year.

Cutoffs can affect river character considerably.[248] Increased current speed causes greater erosion of the bed and banks, and a river may change from a meandering to a braided channel pattern to move the increased bedload.[157,247,251,265] This may have happened in the lower Mississippi River, as the number of divided flows in the general vicinity of Vicksburg increased from 41 to 78 following the artificial cutoffs.[297]

3. Floodways and Control Structures

Although the levees and channel works now largely prevent the lower Mississippi River from flooding extensive areas, occasionally even these features do not provide sufficient protection.[172] To pass excess flows past critical reaches, a system of floodways has been constructed (Figure 2). Floodways are large expanses of land beyond the mainstem levees across which excessive floodwaters can be diverted.[285] With the recent exception of the Bonnet Carre Spillway, floodways are rarely used. Although much of the land devoted to the floodways was originally flooded regularly by the river, these areas now provide aquatic habitat only rarely and for a very short time.

The Mississippi and Atchafalaya Rivers are in close proximity in the lower part of the study area, and historically the latter river, and other smaller ones, acted as Mississippi River distributaries during floods.[248] During this century, the Atchafalaya has been capturing a larger share of the Mississippi's flow, and to forestall the ultimate switch of the Mississippi River into the Atchafalaya channel,[158] the CE built the Old River Control Structure (Figure 2). This facility passes a controlled amount of water from the Mississippi at all times, but it is particularly important during floods. About one half of the water moving down the river during extreme floods can be diverted through the control structure to the Morganza and West Atchafalaya floodways (Figure 2).[285] Farther downstream, the Bonnet Carre Spillway provides additional protection to New Orleans by diverting up to 7082 m^3/s into Lake Pontchartrain.

4. Snagging

Prior to the large-scale land-use changes of the past 200 years, the lower Mississippi River basin was almost completely forested.[92,147] As a result, the river contained great numbers of sunken trees and logjams.[67,77] Growing commercial use of the river, especially following invention of the steamboat, brought complaints about the impediment and danger snags presented. Nearly 150 steamboat wrecks on the Mississippi River are known, many caused by snags,[229] and between 1821 to 1825 losses attributed to snags totaled nearly $1.5 million.[77] In 1824, the War Department contracted for removal of snags in the Ohio and Mississippi Rivers, but early attempts depended on manual labor, which was inadequate for the job. It was not until the invention of the steam-powered snagging boat in the late 1820s[77] that most of the drowned forests that had plagued river navigation were removed. Because badly eroding banks continued to plunge large numbers of trees into the river, snagging continued to be a common navigation improvement method until nearly 1930.

5. Dredging

Despite its size, the need for dredging has been relatively great in the lower Mississippi River to maintain adequate depths for navigation. Dredging occurs mostly at crossings, of which there are some 200 between Cairo (IL) and Baton Rouge. Crossings tend to fill during floods and scour during succeeding lower flows,[19,150] though often not fast or deeply enough for navigation needs. During the 1970s, periodic dredging was being performed at more than 100 sites within the river, with 32 to 81 million m^3 of material being excavated annually.[140] Dredging in the reach from Cairo to Memphis almost always greatly exceeded that from Memphis to Baton Rouge, often by several orders of magnitude. Annual dredging below Baton Rouge is also substantial, due in part to maintenance of a 12-m deep channel. Revetments and dikes (see next section) have eliminated some of the need for dredging, although approximately 60 million m^3 of sediment are still removed annually.[140] Dredged material is sometimes deposited in nearby river slackwaters because it is more difficult and costly to pipe the material over the longer distances required to reach land sites. "In-water" disposal is avoided whenever possible because slackwaters are among the most ecologically valuable areas within the river.

6. Revetments

Revetments restrict river meandering by protecting banklines from erosion. Timber and brush mattresses, wooden or wire fences, rock and wire gabions, tires, and even automobile bodies have been used.[141] These materials were unable to withstand the forces generated by the Mississippi River. Asphalt paving and rock riprap gave better results, but they were still less successful than desired. Since about 1945, articulated concrete mattress revetment (ACM), with riprap used only on the upper banks or to repair minor damage to the ACM, has been used almost exclusively in the lower Mississippi River. A more detailed description of revetments, and ACM in particular, is presented in the section on aquatic habitats.

The latest river maps[183] show approximately 250 individual revetments ranging in length from about 0.8 to 13 km, with a typical revetment being 4 to 6 km long. Nearly 2000 km of revetment are authorized, with over 1700 km already in place.[87] When complete, revetments will have covered nearly 50% of the original bankline,[203] and nearly 80% of the steep, eroding banks.

7. Dikes

Dikes are relatively impermeable structures placed in a river to constrict the width and increase the depth of the main channel at low flows, reduce divided flow conditions, adjust channel alignment, and increase channel stability.[180] From original placement in the 1880s until about 1960, dikes were constructed of wooden pilings. Most are now built of limestone rocks.[141] Three types of dikes are used in the lower Mississippi River: transverse dikes (Figures 4A and B) extend perpendicularly from the bankline toward the main channel; L-head dikes are transverse dikes with a downstream-oriented extension at the tip; vane dikes (Figure 4C) are not connected to the bank and are sited obliquely to the flow axis. Several dikes are typically placed within the same river reach, forming a dike field, or dike system.[58,59]

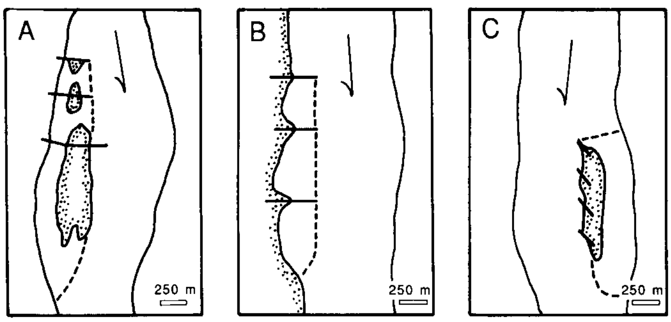


FIGURE 4. (A) Transverse dikes, showing environment downstream when a middle bar forms. (B) Transverse dikes, showing environment downstream when no middle bar forms. (C) Vane dikes. In all figures heavy, solid lines are dikes; lighter, solid lines with stippling indicate areas of sand accretion; dotted lines indicate approximate limits of dike system pools.

Dike systems are now common features of the river. Over 330 km of dikes were completed as of 1985, with 475 km authorized.[181] Recent navigation maps[183] show nearly 125 separate systems, most consisting of three or more dikes. Dike systems are not distributed evenly throughout the river. In one investigation,[59] the total length of dikes found in individual 24-km long study reaches ranged from 0 to >11,900 m. As many as 20 dikes were found within some study reaches, while others contained none. In the entire river below about RK 376 there are no dikes like those upriver. There are riprap structures termed foreshore dikes,[285] but they are parallel to and very near the shoreline and thus function more like revetments.

Dikes are enormous structures (Figure 5). Average dike length, excluding the portion tying the dike to the shoreline, is 630 m,[59] with individual dikes ranging from <110 m to >3650 m. Crown (top) widths may be as great as 10 m, with bottom widths several times this large.

The environment downstream of a dike may include several features: a shallow to deep pool; a natural steep bank; and a sandbar.[58,59] A sandbar typically forms downstream of dikes. If it forms near the outer edge of the dike the pool will be between the river bank and the sandbar (Figures 4A, 4C; 5A). If the sandbar is continuous with the bank the pool will be adjacent to the channel (Figure 4B). The pool often includes a very deep scour hole just downstream of the dike. Characteristics of dike systems vary markedly with river stage.[9,17,59,202] When river stage exceeds the controlling elevation of the dikes, strong flow through the pool may scour fine sediments, leaving only relatively coarse sand and/or gravel substrates. At river stages below the elevation of the dikes slackwater conditions are encountered and fine silt-clay sediments rapidly accumulate.[9,17] Similarly, at low stages an extensive sandbar may exist, while at high stages it may be under many meters of water.

8. Tributary Alterations

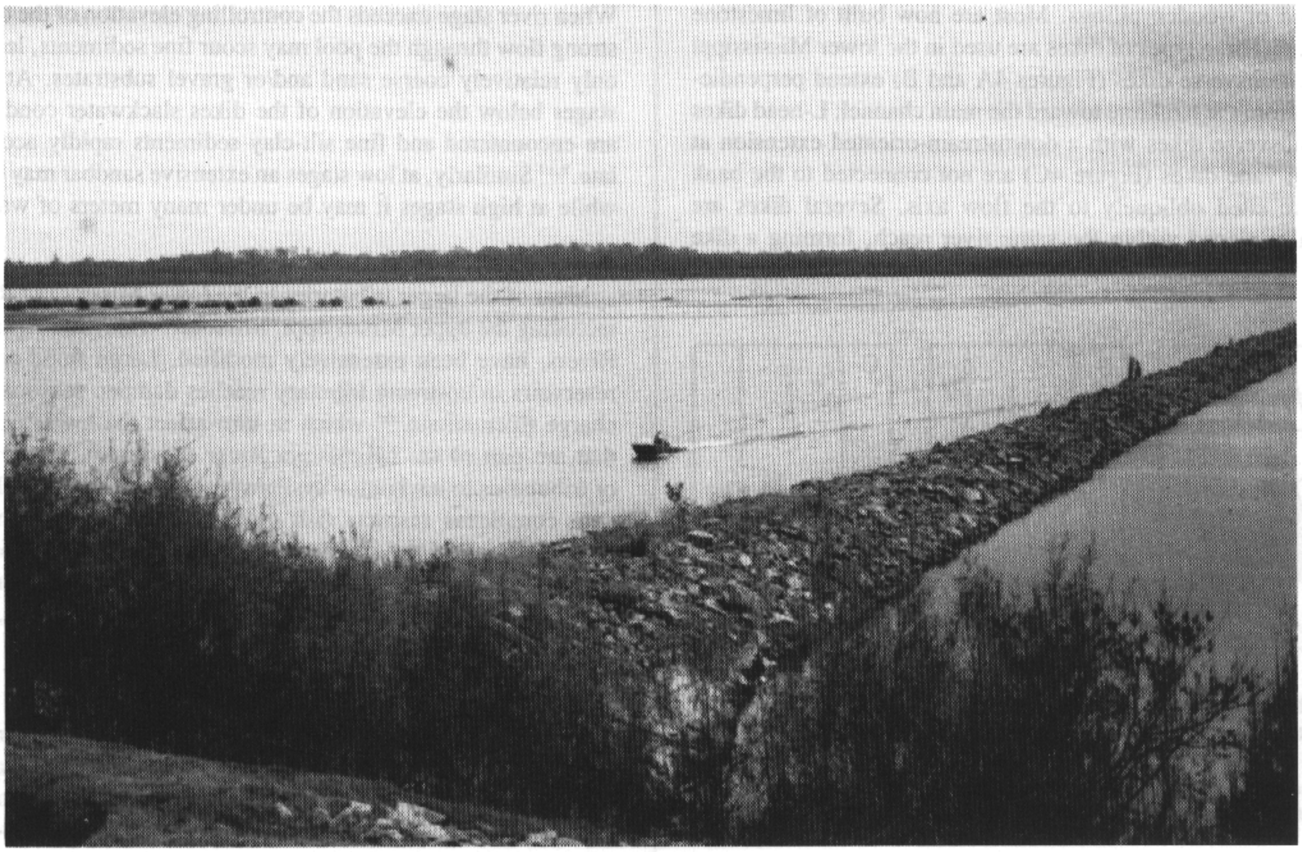
Most of the larger tributaries to the lower Mississippi River, including the upper Mississippi, Missouri, Ohio, and Arkansas Rivers, have been extensively modified. Large flood-control reservoirs in upstream tributary reaches dampen seasonal discharge fluctuations,[205] which in turn affect the lower reaches that are part of the Mississippi River ecosystem. Conversion of tributaries to navigation systems by construction of lock and dam complexes restricts fish movement and changes water quality. Many of the smaller tributaries (e.g., Yazoo, White, Homochitto, Obion-Forked Deer Rivers) have also been extensively modified by levee systems and channelization, particularly in their lower reaches.[8,12,285,296]

D. Summary

The vast Mississippi River system has repeatedly undergone natural changes of great magnitude. However, the changes have apparently not affected the entire system simultaneously, and large-river habitats suitable to fishes much like those occurring today have probably existed for million of years. Natural changes in river channel pattern have been gradual, occurring over at least centuries, if not millenia. However, over the past 150 to 200 years man has drastically altered the aquatic environment, not only of the lower Mississippi River, but of its tributaries. The ecological effects of such rapid, widespread, and dramatic changes have been documented in several others rivers;[30,36,96] for the lower Mississippi the effects are less well understood.

III. RIVER HABITATS

The term "habitat" describes the place or conditions in which an organism normally lives. The term has been used to classify the features of aquatic environments into categories distinguishing varying levels of organization and detail. For example, those interested in the regional landscape may classify the entire river as a habitat type.[82,208] Those interested only in the aquatic environment[43,66] may refer to the river as a system, or aquatic subsystem, with the term habitat referring to specific, smaller-scale features. Even so, there is often considerable variation in the habitats recognized. Several studies,[178,229,271] for example, have recognized habitats such as "main channel border" and "slackwaters" that, while relatively specific, are still a mixture of distinctly different conditions. Recently, Cobb[56] has used the term "aquatic zones"



A

FIGURE 5. (A) Photograph of dike from river bank, moderate river stage, flow from right to left in photo; dike tip (not visible) is ca. 500 m distant, crown width is ca. 8 m at wooden pilings. Note partially submerged middle bar downstream of dike tip, pool habitat downstream of dike between bank and middle bar. (B) Closeup of dike.

in a somewhat similar context. Our definition of habitat is equivalent to what many[13,86,103,227] have termed "microhabitats"; i.e., units of the environment defined by unique sets of physical and chemical features. A similar approach has recently been used in the upper Mississippi River.[252]

Within fish communities, segregation of species along environmental gradients (i.e., "resource partitioning") has been widely documented.[224,244] Habitats, as defined here, are simply multivariate combinations of discrete levels of environmental variables. Thus, even though a large proportion of resource partitioning studies do not specifically delineate habitats in the way that we do, these studies nonetheless support the validity of the habitat concept. It is now widely recognized that changes in the kinds and distributions of aquatic habitats produce changes in biotic communities,[30,104,169,189,241,242] and a voluminous literature has emerged dealing with stream habitat improvement methods.[80] Indeed, habitat-based evaluation methodologies are in wide use by state and federal agencies concerned with environmental changes.[25,118,155,232,275,286,287]

To be useful in evaluating changes in biotic communities associated with changes in river systems, habitats must be delineated on the basis of variables and their gradations which are relevant to the organisms. Early descriptions of large rivers focused on geomorphic and hydraulic attributes such as depth contours and flow patterns, properties important to navigators, but not necessarily to organisms. Secondary channels, for example, were geomorphologically recognizable at all times, even though they might be strongly flowing at one river stage and slack at a lower stage,[58] and sandbars could be located whether they were emergent or under many meters of water. When viewed in this manner, as fixed places within the river, habitats often had very broad and ecologically overlapping attributes. To be appropriate for ecologists concerned with changes in the river ecosystem, habitat classifications had to be improved.

A. Lower Mississippi River Aquatic Habitat Classifications

The earliest lower Mississippi River classifications[178,229] listed only very general habitats, such as main channel, steep clay banks, and slackwater areas (Table 1). Cobb and Clark[58] im-

FIGURE 5B

proved these early categorizations considerably and provided an ecosystem-wide approach to habitat classification that guided a large number of subsequent biological and limnological studies. However, habitats were still defined as much on geomorphological as on ecological criteria. Main channel habitat, for example, was defined as "that portion of the river encompassing the thalweg and lying riverward of the minus 10-foot LWRP* contour on the convex bank and the toe (typically the minus 30-foot contour) of the bank on the concave shoreline."[58] This method was useful for engineers and others who were attempting to "manage" the river because it partitioned the ecosystem into fixed, mappable units whose extent and distribution could be related to river management activities. In doing so it sacrificed biological reality in two ways. First, habitats often had very broad attributes (e.g., current speed ranging from 0 to over 1 m/s). Cobb and Clark,[58] in fact, recognized that some of their habitats were actually composites in an ecological sense. Second, it defined habitats as existing in particular, fixed places even though physical and chemical conditions were often markedly disparate at different river stages. The classification of Nunnally and Beverly,[194,195] though omitting some habitats that others[9,12,58] considered ecologically distinct, was important for recognizing that particular areas within the river often provided an ecologically distinct habitat at different river stages, and that this should be reflected in their terminology (e.g., "some sloughs would be classified as chutes at higher stages").

More recent studies of the lower Mississippi River,[9,12] recognized the composite nature of some river habitats as previously delineated and showed that these physically and chemically unique areas supported distinctive fish communities. In a refinement and enlargement of his 1981 classification (Table 1), Cobb[55] also considered this concept. Baker et al.[9,12] subsequently concluded that some of these areas were equivalent to other accepted habitats, while others were distinctive enough to warrant separate classification.

The following section describes what appear to us to be ecologically meaningful aquatic habitats found within the lower Mississippi River ecosystem. Habitats are delineated largely on the basis of specific variables, including depth, current speed, substrate type, instream structure (irregular bottom, fallen

* The Low Water Reference Plane (LWRP) is the river level corresponding to a discharge that is exceeded 97% of the time based on the 20-year period of record from 1954 to 1973. This elevation is assigned a value of 0 ft, and river stages are referenced to this standard. Zero LWRP does not correspond to zero on the various lower Mississippi River gauges.

Table 1
Lower Mississippi River Aquatic Habitat Classifications

Mississippi Power & Light Co.[178]	Ryckman, Edgerley, Tomlinson & Assoc.[229]	Cobb & Clark[58]	Nunnally & Beverly[195]	Cobb[55]	Present classification
Main channel	Main channel >5 ft deep	Main channel	Main channel	Main channel	Channel
	Chute	Permanent secondary channel	Secondary channel	Permanent secondary channel	
		Temporary secondary channel	Chute	Temporary secondary channel	
Steep clay bank	Main channel <5ft deep	Natural bank		Natural steep bank	Natural steep bank
		Revetment		Revetment	Revetment
		Natural sandbar		Sandbar	Lotic sandbar
		Dike field sandbar		Dike system sandbar	
Slackwater areas	Slackwater	Dike field pool	Pool	Dike system pool	Pool
		Sandbar pool		Sandbar pool	Lentic sandbar
		Abandoned channel (2 types)	Slough	Abandoned channel (2 types)	Contiguous slough
	Lake & borrow pit	Oxbow lake		Oxbow lake	Isolated slough
				Scour channel lake	Oxbow lake
				Crevasse lake	
				Batture lake	
				Manmade lake	
				Floodplain depression lake	
		Levee borrow pit		Levee borrow pit	Levee borrow pit
				Port access channel	
				Port turning basin	Floodplain ponds
		Inundated floodplain		Inundated floodplain	Seasonally inundated floodplain
				Tributary	Tributary

trees and brush, inundated vegetation), position within the ecosystem (within the mainstem of the river, or on the floodplain), and water quality (dissolved oxygen, turbidity, nutrient and plankton levels, etc.). These variables have been identified as important in structuring biological communities in a variety of stream ecosystems.[13,103,104,173,175,227,301] To delineate habitats a multivariate approach was employed. First, all potentially relevant variables were listed and their overall ranges of values within the entire river ecosystem were determined. Some variables were continuous (e.g., current speed, depth), while others (e.g., amount of instream cover) were categorical. The range of values for each variable was divided into categories based on our own field experience, and on extensive discussions with other fishery biologists. Variables and categories were displayed in matrix form to generate the set of "all possible habitats", and the river ecosystem was surveyed to determine which matrix cells (or habitats) actually occurred.

A paucity of food habit data for lower Mississippi River fishes made it impossible to ascertain whether food type might determine habitat use for any species. Also, many invertebrates in the river drift in enormous numbers, and thus food items identified in fish stomachs will not necessarily reflect habitat use. Therefore, rather than considering invertebrate communities to be a potentially relevant "environmental variable" affecting fish distributions, we have simply listed the major invertebrate taxa of each habitat, along with abundance estimates.

B. Aquatic Habitat Descriptions

Thirteen aquatic habitats are delineated (Table 1). Six habitats occur within the river mainstem, and seven are found on the floodplain. Typical associations of habitats in the lower Mississippi River are shown in Figures 6 and 7. Physical and limnological characteristics are presented in Tables 2 and 3, and invertebrate data are summarized in Table 4. Insofar as it was achievable we have quantified variables when describing habitats; for some variables this was neither possible nor desirable. The ecologically relevant variables often change gradually, and not always consistently or concurrently, between adjacent habitats, creating rather wide transition zones in some instances. As a consequence, habitat descriptions are not always precise, partly because we still have much to learn about the physical and chemical environment of the river, but also because fish may not perceive sharp boundaries among many habitats.

In their natural state, large, alluvial rivers such as the lower Mississippi are not static. Erosion and deposition act constantly to shift their courses; banks recede, islands and sandbars are built, and meander bends are cut off to form oxbow lakes. Although individual sites are frequently modified by the river, the variety, distribution, and characteristics of the habitats remain relatively constant over time, unless the river undergoes a fundamental change in either flow or sediment load.[188,215,248]

1. Channel

Channel habitat includes portions of two areas generally recognized as separate habitats by earlier workers:[12,17,58,195,201,202] main channel and secondary channel (known also as side channel, chute, running slough). When the flow of the river is divided, the larger of the two flow paths is designated as the main channel[157] and the smaller as the secondary channel. Secondary channels have been categorized as permanent (having substantial flow at all river stages) or temporary (carrying strong flow only at higher stages).[58] However, from an ecological perspective, either type would be characterized as channel habitat when flowing, and thus we have

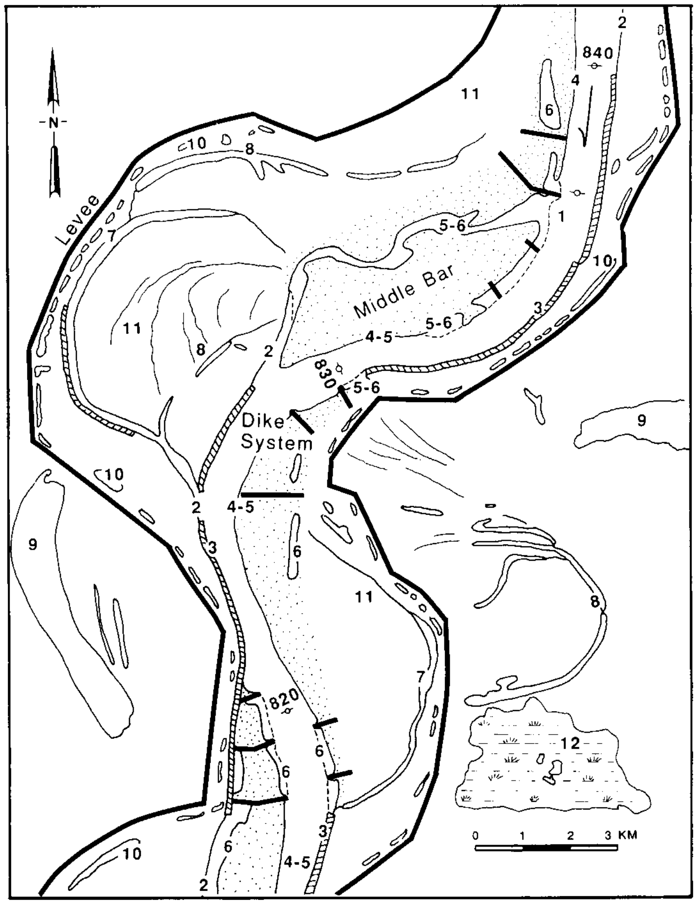


FIGURE 6. Typical association of aquatic habitats, fluvial and terrestrial landforms, and manmade features in the lower Mississippi River between Memphis and Vicksburg. Habitats are (1) channel, (2) natural steep bank, (3) revetment, (4) lotic sandbar, (5) lentic sandbar, (6) pool, (7) contiguous slough, (8) isolated slough, (9) oxbow lake, (10) levee borrow pit, (11) seasonally inundated floodplain, (12) floodplain ponds; tributaries not present in this reach. Note oxbow lakes and several isolated sloughs that are outside the present levees as well as the revetment on lower portion of contiguous slough; until 1933 the river made a large bend in this area (at bulge in levee), and the revetment was on the main channel. Area labeled as pool habitat between large island and sandbar shoreline (upper center of figure) becomes channel habitat at high river stages.

neither identified secondary channels as a separate habitat nor distinguished between the two previously recognized types.

Physically, channel habitat changes little with season or river stage. Current speeds are always high, ranging from 0.9 to 2.4 m/s under low to moderate discharges[12,230] and often exceeding 5.0 m/s during high discharges.[180] Substrates almost uniformly consist of sand and/or gravel.[12,170] In addition, the substrate is constantly shifting; bedload movement in the vicinity of Vicksburg, MS, is estimated to be 0.8 million m^3 of sediment per day.[140] Suspended sediment transported by the river averages 145 million metric tons/year, with most of the transport occurring in the channel habitat.

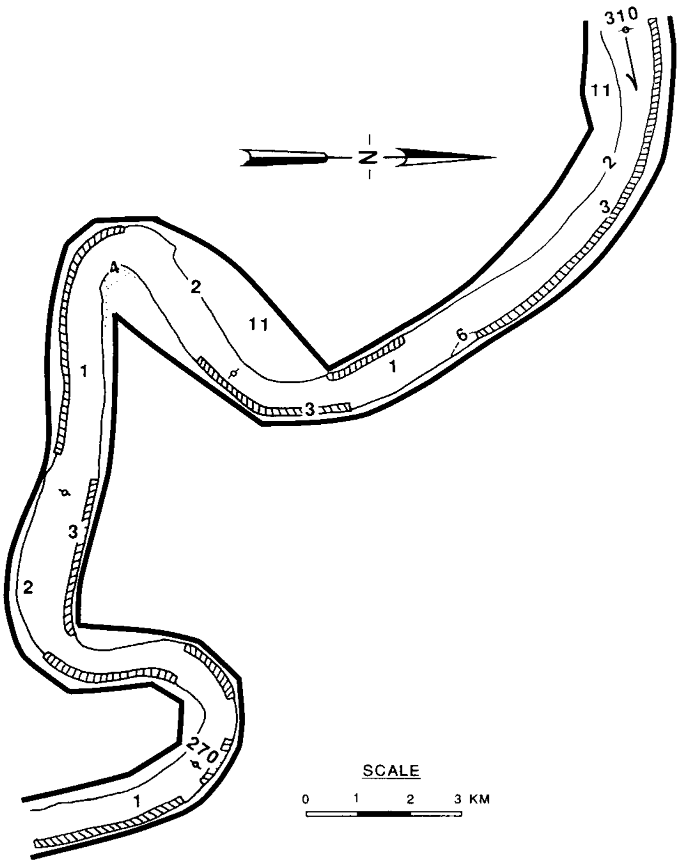


FIGURE 7. Typical association of aquatic habitats in a river reach downstream of Baton Rouge. Note levees nearly at river banks in entire reach, and the consequent lack of floodplain habitats. Note also the large amount of revetment. Numbering of habitats is as in Figure 6.

In large, strongly flowing channels with mobile bed materials the river bottom is seldom flat. Bedforms ranging from ripples to dunes occur,[28,188] and eddies form behind them due to flow separation.[29] Dunes may be quite large, up to 10 m in height and 250 m in wavelength in the Mississippi River[46,215,288] (Figure 8), and they must considerably modify the local characteristics of the channel habitat in their vicinity.[188] Current speed in channels generally decreases from the surface toward the bottom, with the greatest decrease occurring very close to the substrate.[157,188] Current speeds in the bottom 30 cm of the Columbia River, for example, were about 0.5 m/s or lower, whereas surface currents were nearly 1.5 m/s.[239] Although we have no comparable data from the main channel of the lower Mississippi River, measurements from within secondary channels[12] and well offshore along natural steep banks and revetted banks[10] showed a similar phenomenon.

Channel habitat is characterized by relatively cool temperatures, high turbidities, high suspended solids, high levels of most nutrients, and low algal biomass.[75,170,230] Despite high nutrient levels, the high turbidity limits the photic zone to <0.3 m, and as a result, primary productivity is low.[9] Predictable fluctuations occur seasonally and with river stage, but compared to other habitats, changes in the channel appear to be minor.

Macroinvertebrate communities of the channel habitat were until recently thought to exhibit low diversity and abundance.[12,17,18,170,291] Samples generally contained a mixture of lotic and lentic taxa concentrated in silt-clay accumulations, suggesting that the fauna was derived primarily from drift.[170] Recently,[1] a unique assemblage of very small organisms (three chironomids, nematodes, aeolosomatid worms, and microturbellarians) has been found in very high densities in sand substrates.

2. Natural Steep Bank

Natural steep banks occur on the concave (or cut bank) sides of river bends, in secondary channels, and also in some straight reaches. Natural steep banks primarily adjoin channel habitat, and the boundary between these habitats is not always easily determined. Slopes of natural steep banks are usually >30° and often approach vertical in the upper portions of the banks. Substrates are unique among river habitats, consisting primarily of consolidated clays and silts[18] in the form of clay plug and backswamp deposits,[58] although sand and gravel, mud, and point bar deposits also commonly occur.[17,170] Because they are usually located where the main channel current flows against them, natural steep banks are especially subject to erosion. Erosion varies widely with location and season;[94,128,130] published bank recession rates range from 0.6 to 305 m/year.[31,45,138,142,145] Two of five natural steep banks sampled in one study[170] were considered to actively erode during a moderate flow stage. Resistance to erosion correlates highly with the percentage of silt-clay in the banks,[128,246,298] because cohesive forces between the very small silt-clay particles make them more resistant than individually much larger, but noncohesive, sand and gravel particles. For this reason, in the lower Mississippi River erosion rates are generally lowest downstream of Baton Rouge, where silt-clay percentages are highest.[90,94,145] Higher percentages of silt-clay sediments do not always reduce erosion rates; their position within a bankline is also important.[91] When a silt-clay topstratum is underlain by an erodable layer, the topstratum tends to cave infrequently but in relatively large units (slump blocks).[138,281] As much as 4 million m^3 of material may be involved in a single bank failure.[214]

Although current speeds are relatively high along natural steep banks,[58] they vary greatly over relatively small distances as a function of several factors,[10] including water depth and distance from the bank (Figure 9A). This is typical of river channels because of friction with both the bed and banks,[215] scalloping caused by block slumping, irregularities caused by the differential erodability of bank materials, and obstructions such as fallen trees.[10,91,138,281] Current direction relative to the bankline also varies considerably both horizontally and

Table 2
Typical Physical Conditions of Lower Mississippi River Aquatic Habitats[a]

River stage[b]	Channel	Natural steep bank	Revetment	Sandbar Lotic	Sandbar Lentic	Pool	Slough Contiguous	Slough Isolated	Oxbow lake	Borrow pit	Seasonal inundated floodplain	Pond	Tributary
Depth (m)													
Low	6—30	1—15	1—15	1—6	<2	2—20	1—5	<3	5—35	1—5	[c]	<3	1—10
High	6—45	12—25	12—25	1—6	[c]	[c]	3—15	2—6	5—40	3—8	1—10	2—5	10—25
Current (m/s)													
Low	1—3	0.25—1.5	0.5—1.5	0.3—1.5	<0.1	<0.1	0	0	0	0	[c]	0	0—2[d]
High	2—5	1—3	1—3	0.5—1.5	[c]	[c]	<0.3	<0.3	0	<0.3	0—1	<0.3	0—2
Substrate[e]													
Low	CSG	C, S	ACM, S	CSG	S, SS	SS, MM	M	M	M	[c]	M	S, SS	
High	CSG	C, S	ACM, S	CSG	[c]	[c]	M	M	M	M	BS	M	S, SS
Structure[f]													
Low	I, E	B, I, E	I, E	I	I	I, D	B	B	B	B	[c]	B, I	B, I, E
High	I, E	B, I, E	I, E	I	[c]	[c]	B	B	B	B	B, I	B, I	B, I, E

[a] Compiled from References 8—10, 12, 17, 18, 33, 38, 58, 59, 61, 76, 85, 114, 170, 184, 187, 190, 197, 201, 212, 229, 234, 245, 261, 285, 295, and 302.
[b] Low = islands, sandbars and dikes emergent, pools large, flow confined to main channel and largest secondary channels; high = river over banks, islands and sandbars submerged, flow strong in most areas within top banks.
[c] Habitat does not exist at this stage.
[d] Tributary current speeds determined by several factors, including interaction of tributary and Mississippi River stages.
[e] CSG = coarse sand and/or gravel; C = consolidated silt-clays; S = sand; M = mud (flocculent silt-clays with much organic matter); SS = sand-silt; ACM = articulated concrete mattress; BS = backswamp sediments (silt-clays).
[f] B = brush, trees; I = irregular bottom; D = dike structures; E = eddies.

vertically[10] (Figure 9B). Upstream flow (eddies) is common in this habitat,[170] where the eddies may be over 250 m long and extend up to 150 m into the river. Velocity shelters are recognized as extremely important for fish communities of large river systems.[267] Individual natural steep banks often differ considerably, with some reaches being relatively homogeneous, and others being more complex.

Although not quantified, fallen trees and brush are common along many natural steep banks (Figure 10). Due to river regulation, bankline modification, and floodplain clearing, the amount of brush is probably several orders of magnitude less than in the unregulated river. The benefit of woody debris on the quality of aquatic habitat for fish is well established,[104,125,169,267] as is its benefit as a substrate for macroinvertebrate production.[10,17,20,21]

Water quality along natural steep banks[10,170] is similar to that of the channel habitat.[230] Variations among seasons and river stages are also similar.

Benthic macroinvertebrate communities are dominated by caddisflies and two species of mayflies.[17,170] The mayflies are large, burrowing forms that are fairly specific to clay banks;[18] the caddisflies primarily colonize submerged trees and brush, and though they are individually relatively small, they typically occur in very high numbers.[10]

Natural steep banks change little with river stage or season. Current speeds and local turbulence may increase slightly during high flows, and trees and brush may accumulate or be swept away in particular areas by floods. On a long-term basis, however, this habitat type remains relatively constant.

3. Revetted Bank

Revetments are protective materials paced over river banks to prevent erosion. Revetments are typically located on the concave side of bends (Figures 6 and 7), although they are used occasionally in other areas.[141] Because banklines are cleared and graded prior to revetment placement, the slope of revetted banks (usually approximately 25°) is lower and more regular than that of natural steep banks. In smaller rivers revetments are constructed from rock riprap; lower Mississippi revetments are mostly articulated concrete mattress (ACM; Figure 11A) with riprap only near the top bank (Figure 11B).[141] The ACM, formed by linking concrete slabs (Figure 11C) with corrosion resistant wires, is laid over the banks from the top bank to the edge of the channel.

The substrate of revetted bank habitats is not exclusively concrete. Divers surveying the bottom from the bank toward the channel along two revetments[10] found that 42 to 64% of the ACM was covered with sediment (Figure 12), with fine sands and silt-clays predominating. A third revetment, sampled in a separate study by grab samplers rather than divers, appeared to have less sediment.[170] Reports from as early as 1952 mentioned the occurrence of extensive sand deposits over

Table 3
Typical Limnological Conditions in Lower Mississippi River Aquatic Habitats[a]

River stage[b]	Channel	Natural steep bank	Revet-ment	Sandbar Lotic	Sandbar Lentic	Pool	Slough Contig-uous	Slough Isolated	Oxbow lake	Borrow pit	Seasonal inundated floodplain	Pond	Tributary
Temperature (°C)													
Low	18—29	18—29	18—29	18—29	24—36	20—31[c] (16—23)	21—34 (15—22)	21—34 (15—22)	22—32 (14—20)	25—34 (15—22)	[d]	20—30	18—30
High	2—15	2—15	2—15	2—15	[d]	[d]	5—18	5—18	4—17	5—18	2—15	2—15	4—18
Dissolved oxygen (mg/l)													
Low	6—7	6—7	6—7	6—7	5—8	6—16 (2—6)	4—20 (0—4)	4—20 (0—4)	5—12 (1—4)	4—20 (0—4)	[d]	0—6	5—7
High	6—12	6—12	6—12	6—12	[d]	[d]	6—12	6—12	6—12	6—12	6—12	6—12	6—12
pH													
Low	7—8	7—8	7—8	7—8	7—9	7—9	7—9	7—9	7—8	7—9	[d]	5—8	6—8
High	7—8	7—8	7—8	7—8	[d]	7—8	7—8	7—8	7—8	7—8	7—8	5—8	6—8
Turbidity (NTU)													
Low	10—65	10—65	10—65	10—65	7—17	7—17	6—15	6—15	5—15	5—15	[d]	5—10	10—25
High	10—65	10—65	10—65	10—65	[d]	[d]	15—50	15—50	10—40	15—50	45—65	15—50	45—65
Specific conductance (μmho/cm)													
Low	450—500	450—500	450—500	450—500	450—600	500—700	550—675	575—725	300—450	250—450	[d]	550—725	150—450
High	300—400	300—400	300—400	300—400	[d]	[d]	375—450	375—450	300—450	250—400	300—400	300—450	150—400
Suspended solids (mg/l)													
Low	50—75	50—75	50—75	50—75	10—35	10—50	5—50	5—35	<25	<25	[d]	<25	10—50
High	150—200	150—200	150—200	150—200	[d]	[d]	25—50	25—50	10—50	10—50	100—200	50—150	100—200
Dissolved solids (mg/l)													
Low	250—300	250—300	250—300	250—300	300—400	300—450	350—450	350—450	300—400	300—400	[d]	350—450	200—400
High	250—300	250—300	250—300	250—300	[d]	[d]	300—400	300—400	300—400	300—400	300—400	300—450	300—400
Chlorophyll *a* (mg/m^3)													
Low	50—70	50—70	50—70	50—70	50—100	50—75	75—125	75—150	75—125	75—100	[d]	50—150	10—50
High	<10	<10	<10	<10	[d]	[d]	<10	<10	<10	<10	<10	<10	<10
Nutrients[e]													
Low	++	++	++	++	++	−	−	−	−	−	[d]	−	++
High	++	++	++	++	[d]	[d]	++	++	++	++	++	++	++
Zooplankton													
Low	+	+	+	+	++	++	++	++	+	++	[d]	++	+
High	−	−	−	−	[d]	[d]	+	+	−	−	−	−	−

[a] Compiled from References 4, 12 to 19, 33, 53, 61, 75, 76, 85, 93, 114, 161, 168, 170, 178, 187, 190, 197, 229, 230, 232, 245, 279, 285, 293, 295, 302, and 303.

[b] Low = islands, sandbars, and dikes emergent, pools large, flow confined to main channel, and largest secondary channels; high = river over banks, islands, sandbars, and dikes submerged, flow strong in most areas within top banks.

[c] For habitats in which stratification occurs values are presented as surface above; bottom below, in parentheses.

[d] Habitat does not exist at this stage.

[e] ++ = high levels; + = moderate levels; − = low levels.

ACM.[138] In large eddies along revetments 44% of all grab samples contained sediment, compared to only 10% in straight reaches.[302]

Currents along revetments are generally swift;[58] however, individual revetments differ considerably despite the fact that banklines are smoothed prior to being revetted. In one study,[11] current speeds at moderate river stages ranged from 0.05 to 1.75 m/s (mean = 0.62 m/s) along a revetted bank near Natchez, MS (RK 592). Another revetment in the same general river reach (RK 496) had consistently lower currents (0.15 to 1.07 m/s; mean = 0.35 m/s). At low stages, current speeds along the first revetment were unchanged, while those at the second

Table 4
Dominant Invertebrates of Lower Mississippi River Aquatic Habitats[a]

Channel, lotic sandbar	Natural steep bank	Revetted bank	Lentic sandbar	Pool	Tributary, Oxbow lake, Borrow pit, slough	Seasonal floodplain	Pond
Sand-Gravel	**Sand-Gravel**	**ACM**	**Sand-Silt**	**Sand-Gravel**	**Mud**	**Mud, Debris**	**Mud, Debris**
Corbicula Oligochaeta Chironomidae Microturbel laria Nematoda (12,142—658,036)	Ephemeroptera[b] *Corbicula* Trichoptera Amphipoda[f] (12—375)[g]	Trichoptera[c] Chironomidae[e] Ephemeroptera Oligochaeta Amphipoda (87—14,377)	Oligochaeta[d] Ephemeroptera Chironomidae Cladocera Copepoda (N/A)	*Corbicula* Oligochaeta Chironomidae Trichoptera (23—2,693)	Oligochaeta *Chaoborus* *Sphaerium* Chironomidae (1939—7,243)	Lumbriculidae Enchytraeidae Turbellaria Nematoda Oligochaeta Copepoda Isopoda Amphipoda Chironomidae Ostracoda (20,000)	Oligochaeta Copepoda Ostracoda Nematoda Chironomidae Amphipoda Isopoda Odonata *Sphaerium* Turbellaria *Chaoborus* Plecoptera (1,500—18,000)
	Clay Ephemeroptera Trichoptera Chironomidae Amphipoda (62—487)	**Sand** Oligochaeta Chironomidae Nematoda (2,476—30,461)		**Mud-Sand** Oligochaeta *Chaoborus* Chironomidae Ephemeroptera (291—4,519)	**Clay** Oligochaeta *Chaoborus* (1,227—3,961)		
	Snags Trichoptera Chironomidae Oligochaeta (1,562—8,614)			**Clay** Trichoptera Ephemeroptera (109—630)			
				Dikes Trichoptera Ephemeroptera Chironomidae (849—23,642)			

[a] Compiled from References 1, 9, 10, 12, 17, 18, 61, 159, 170, 231, 291, 294, 295, 303.
[b] Mud or silt: *Hexagenia;* clay: *Pentagenia, Tortopus;* dikes: *Stenonema, Baetis;* ACM: *Stenonema.*
[c] *Hydropsyche orris, Potamyia flava.*
[d] Numerous taxa of Tubificidae: *Limnodrilus, Ilyodrilus, Branchiura:* Naididae: *Nais.*
[e] Mud or silt: *Chironomus, Coelotanypus, Cryptochironomus;* sand-gravel: *Robackia, Chernovskiia, Rheosmittia;* dikes: *Polypedilum, Glyptotendipes, Ablabesmyia:* ACM: *Rheotanytarsus, Cricotopus, Orthocladius.*
[f] *Corophium, Gammarus.*
[g] Range of reported mean densities (no./m^2).

averaged considerably higher (0.78 m/s), even though the overall range had increased only slightly (0.15 to 1.22 m/s). Like natural steep banks, current speed along revetments also varies with depth and distance from shore (Figure 9A).[10]

Flow direction varies both horizontally and vertically along many revetments (Figure 9B).[10,302] Revetments are often sinuous (Figure 11) with numerous eddies; in general, eddies appear to be smaller and less well defined at low river stages.[302] Interstitial spaces among the rocks of riprap revetment, and between and under (buckled) ACM slabs, also provide velocity shelters.

Revetment habitat exhibits much the same water quality as channels and natural steep banks.[10,230] Even within large eddies water quality is seldom very different from the remainder of the revetment habitat.[302]

Revetment habitat is colonized by a large number of macroinvertebrate species, and densities are often quite high.[10] Caddisflies are abundant wherever unsedimented ACM is exposed to strong currents. Where sediments cover the revetment, oligochaetes and some chironomids are found. Many revetments formerly were natural steep banks, and the ACM probably prevents colonization by large, burrowing mayflies characteristic of that habitat.[18] However, the ACM is buckled (lifted off the substrate) in places, and where this occurs the underlying substrate is inhabited by these mayflies, and other burrowing taxa.

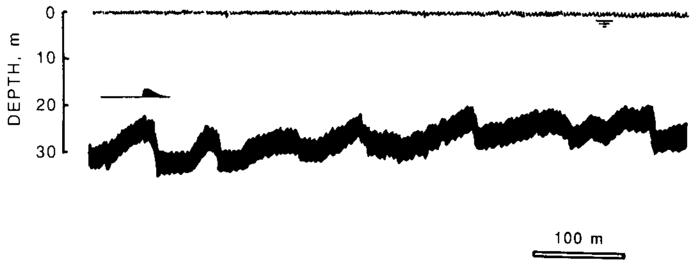


FIGURE 8. Reproduction of hydrograph tracing from the lower Mississippi River showing dunes at the edge of the channel habitat along a natural steep bank. Note difference in horizontal and vertical scales. (Data from Baker et al.[7])

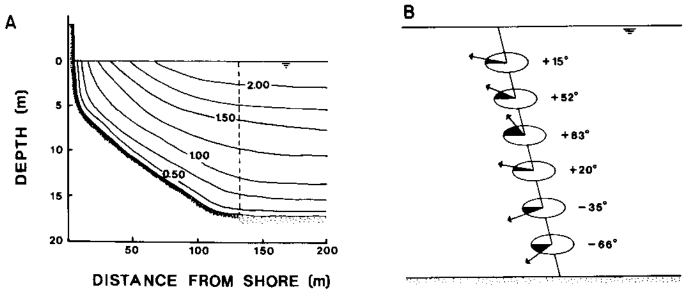


FIGURE 9. Natural steep bank and revetted bank habitats, lower Mississippi River. (A) Typical current speed isovels; dashed line indicates boundary between natural steep bank and channel habitats. (B) Representative variability in current vectors relative to the bankline at 2-m intervals from surface to bottom; +/− indicates current moving toward or away from the bankline, respectively. (Data from Baker et al.[7])

Although individual sites may change, the overall conditions of revetment habitat are relatively constant among seasons and river stages.

4. Lotic and Lentic Sandbars

Sandbars are shallow, gently sloping habitats that occur along point bars (Figure 13A), along the borders of islands and middle bars (Figure 13B), and in association with dike systems (Figure 6). Islands and middle bars are separated from the river banks by water even at low river stages. Though these two landforms cannot be sharply separated, in general, islands have extensive woody vegetation[248,259,260] and are emergent at all but the highest flows, while middle bars have little large woody vegetation and are often submerged at intermediate stages (Figure 13B).[9,58,59] Ecologically, the generally greater elevations of islands permit sandbar habitat to exist along them over a greater range of river stages.

Point bars form along the convex (inside) portions of bends (Figures 6 and 7) and grow toward the eroding concave bank on the opposite side of the river.[97,124,156,174] Point bars usually display a characteristic ridge and swale (high and low areas, respectively) topography;[124,174] the relatively slight elevational differences, on the order of 0.5 to 1.0 m, are sufficient to trigger vegetational differences.[143,193] At low river stages, sandbar habitat exists only along the main channel border of the bar. As point bars grow, high flows tend to cut across them through a swale and form secondary (chute) channels. When flow occurs through this channel, the riverward edge of the point bar becomes an island or middle bar, and sandbar habitat is found along both sides.

Sandbars comprise two habitat types having quite different physical and chemical conditions. Lotic sandbar habitat[9,12,58,59,201,202] (Figure 14A) has moderate to swift currents, a coarse sand or sand-gravel substrate, and chemical conditions much like the adjacent channel habitat. In fact, defining the boundary between channel and lotic sandbar habitat is difficult because these habitats tend to blend. Perhaps because of this, Cobb and Clark[58] defined the riverward limit of sandbar habitat as "the minus 10-ft LWRP contour".

The characteristic diamond shape of islands and middle bars,[188] and the crescent shape of point bars,[124,174] causes channel flow to diverge from the sandbar shore downstream.[262] In bends, the thread of maximum current speed moves along the point bar shore when entering the bend and along the opposite bank when leaving;[262] a similar phenomenon takes place when flow is diverted to either side of the islands. In such places, lentic sandbar habitat (Figures 13B, 14), with low current speeds, shallow depths, and finer sediments may be found.[9,12,136,262] Lentic sandbar habitat may also occur where strong currents run close to shore. Flow over sandbars causes the formation of sand ripples[261] running obliquely downstream along the edge of the sandbar and sloping gradually toward the channel. Thus, the shoreline in such areas is not always straight, but often comprises a series of small, linear bays (Figure 14). These bays may be as small as 2 to 3 m long, 1 m wide, and only a few centimeters deep, or they may be >10 m long and >2 m deep. In the bays, the temperature may be 5 to 10°C warmer, and turbidity lower, than in the lotic habitat. Silt-clay sediments accumulate, and densities of algae and small crustaceans may be high. Lotic sandbar habitat frequently occurs only a few meters from the shore, and the transition between these habitats is often abrupt.[9,12,170]

The shifting sand substrate of lotic sandbar habitat is colonized by a diverse array of both lotic- and lentic-adapted invertebrates[170] similar to those in the channel habitat.[1] The lentic habitat may include some taxa (e.g., oligochaetes, chironomids, *Chaoborus*) typically found in more permanent, larger slackwater habitats such as pools and sloughs.[17,170] Although many of the invertebrates are very small, densities may be relatively high. Copepods and other microcrustaceans may also be abundant.

Sandbar habitat, particularly the lentic form, is ephemeral. The lentic form is most distinctive during periods of relatively constant river stage. Very low stages can completely dewater these areas; a small, rapid rise may introduce channel water and change some characteristics (e.g., temperature, turbidity)

FIGURE 10. Natural steep bank on the lower Mississippi River. Note slumping banks and brush and trees in water. Photograph taken at center of large eddy extending ca. 100 m upstream and downstream from point of photo; eddy extends ca. 50 m into river.

considerably; a large, rapid rise may completely eliminate the lentic habitat. Even the lotic sandbar is considerably diminished in extent, although probably not eliminated, when the river stage is high enough to inundate the island or bars.

5. Pools

Pools are relatively deep, slack-, or slow-water areas within the main river banks. Pools may exist downstream of islands, middle bars, and point bars at low river stages (Figures 13A, 13B, 14)[9,136,262] in nonflowing secondary channels,[12,58] and within dike systems at lower flows.[9,58,59] The areas downstream of dikes (Section II.C.7 and Figures 4 to 6) predominantly consist of pool habitat during low river flows. Presently, most of the pool habitat in the lower Mississippi River is associated with dike systems.[59,195]

Pools are characterized by slow or no current, relatively great depths, and generally fine sediments. Coarse sediments and consolidated silt-clays occasionally occur.[18] Pools typically lack substantial amounts of brush or debris.

Pools are usually less turbid, slightly warmer, and have lower nutrient levels than flowing habitats.[9,18] Deep pools often stratify, causing pronounced water quality differences (e.g., bottom water anoxia) between surface and bottom strata.[9,17,76,230] Primary productivity can reach relatively high levels.[9]

The areas and depths of individual pools are closely tied to river stage.[59] At comparable stages, some pools may be shallow while others may be over 15 m deep. Some may increase greatly in surface area following river rises by inundating adjacent sandbars whereas others may enlarge primarily by increasing in depth. Pools that exist only at very low river flows may form and dissipate several times during a single season,[59] while others may exist continuously during the same period. Pools can become completely isolated from the river at times (Figure 6).[59,195]

Pools are most distinctive during low river stages, and they may largely disappear at stages near bankfull. Following periods of high water, pools probably contain relatively coarse sediments.[9,12,17] Fine sand and silt accumulate rapidly following pool formation, however, and may accrete to a depth of more than 0.2 m. Even at low stages, pool characteristics, particularly water quality, can change rapidly as a result of fluctuation in river level[76,230] and wind generated mixing during storms.[231]

Benthic invertebrates of pools typically include most of those found in the lentic sandbar habitat, plus other taxa such as the large mayfly *Hexagenia* more common to sloughs. Areas of

A

FIGURE 11. Revetted banks on the lower Mississippi River. (A) ACM at moderate river stage; note sand deposition over revetment at far left of photo; note also small eddy near shoreline at center of photo, and large eddy (ca. 300 × 150 m) beyond point at right center of photo. (B) High river stage showing rock riprap on upper bank; note ACM patch just visible on point in upper center of photo, and small eddy at stern of boat. (C) closeup of ACM; blocks are 1.22 m × 0.36 m × 7.2 cm and are linked with corrosion resistant wires.

coarse sand or consolidated clay harbor invertebrates characteristic of these lotic sandbar and natural steep banks, respectively.[1,17,170] In addition, dike structures associated with many pools are inhabited by large numbers of invertebrates, particularly caddisflies and chironomids.[9,17]

Pool habitat primarily adjoins lentic sandbar and channel habitat (Figures 6 and 15). Pool habitat can also be isolated on large sandbars, either naturally or due to dike-induced sedimentation. Though pools are deeper, usually more turbid, and somewhat cooler than lentic sandbars, the boundary between these habitats is not always sharply defined. Boundaries between pool and lotic habitats are sharper and more easily delineated.

6. Contiguous and Isolated Sloughs

Sloughs are moderate-sized, slackwater, floodplain habitats. Like oxbow lakes (see below), sloughs are most often remnants of abandoned river channels, but are distinguished by being considerably narrower and shallower, by being much closer to the river mainstem, and by being extensively confluent with the main channel during overbank flows.[58] Other studies[17,18,58,170,201,202,230] have used the term "abandoned channel" for these habitats. However, in the literal sense oxbow lakes are also abandoned river channels. To avoid confusion we prefer the term "slough". In agreement with Cobb,[58] we recognize two types of sloughs (Figures 6 and 16). Contiguous sloughs are connected to the main channel during most river stages; isolated sloughs are confluent with the main channel only during high stages. Contiguous sloughs are often deeper, at least near their connection with the river, and this can produce differences in water quality between the two types.[170]

Delineation of the two types of sloughs and oxbow lakes is sometimes difficult because these habitats form a continuum within the lower Mississippi River ecosystem. Even sites that would easily be categorized as oxbow lakes sometimes have small channels connecting them to the river.[201] As Cobb and Clark[58] point out, all these habitats are formed by the same river processes, i.e., meandering and bend cutoffs.[27,97] Sloughs

FIGURE 11B

may more often be formed by the abandonment of secondary or point bar channels than by neck cutoff of large, main channel meander bends. This would help explain their generally smaller, shallower nature. However, they could also be long-abandoned, mostly filled oxbows to which the meandering river is only just returning.

Lentic conditions exist in sloughs except during periods of overbank flow, when main channel water may enter through the upstream end. Even at these times current speeds are generally too slow to scour the substrate,[18] which consists of flocculent silt-clays, often with large amounts of detritus.[17,159,170] Banks of sloughs are typically wooded, and trees and brush are usually present in the water.

Water quality varies considerably throughout the year.[230] Water temperatures are warmer at all seasons than in mainstem habitats.[18] During summer and autumn, marked thermal stratification may occur in contiguous sloughs.[159,170] Surface water oxygen supersaturation is occasionally observed, and bottom water anoxia often occurs. These conditions are apparently seldom observed in isolated sloughs, perhaps because their shallower depths permit the water to remain well mixed.[170] Turbidity and suspended solids are low, except during severe flooding, and specific conductance is high relative to other habitats. Primary productivity may be relatively high.[9]

The macroinvertebrate community of sloughs is diverse, and densities are greater than in most other river habitats.[18] *Chaoborus*, tubificid oligochaetes, and fingernail clams (*Sphaerium*) generally dominate the community.

7. Oxbow Lake

Oxbow lakes are former river channels that have been isolated by the cutoff of large meander loops.[97] Within the lower Mississippi River ecosystem, oxbow lakes range from 200 to >1600 ha,[229] and they may be up to 25 km long and 1 km wide. They are generally much deeper than sloughs (often >35 m) and have much lower surface-to-volume ratios. The shoreline is typically wooded, and brush is often abundant in the water near shore.

The overall water chemistry of oxbow lakes is similar to that of sloughs. They may stratify in summer, and anoxia may develop below the thermocline;[93,161,168,187] surface oxygen supersaturation is occasionally observed. Oxbow lakes generally receive less main channel water during periods of overbank flow than do sloughs.

FIGURE 11C

The benthos of oxbow lakes is similar to that of other types of lakes, and to that of sloughs.[24,135,170,187,199] *Chaoborus*, oligochaetes, and fingernail clams are the dominant taxa.[20]

8. Borrow Pits

Borrow pits are manmade floodplain habitats formed by excavation of fill material during levee construction. Although borrow pits lie adjacent to the levees (Figure 6), they vary greatly in terms of distance from the main river channel, elevation relative to the river channel, and elevation of the batture (the land between the levees and the river).[38] As a consequence, some are inundated annually, while others are flooded as infrequently as every 5th year.[61] The average annual days inundated by the river for 25 borrow pits studied in 1981[61] ranged from 24 to 117.

Surface areas and depths of borrow pits vary substantially.[38,61,183] Some are little more than shallow ponds, while others may be >20 ha. Except when inundated by floodwaters, lentic conditions prevail in all borrow pits. Substrates are almost entirely flocculent silt-clays similar to those of the sloughs and oxbow lakes.[61] Some borrow pits are wooded on one or more sides (except the levee side), while others have grasses or crops along the borders.

A systematic seasonal study of water chemistry in levee borrow pits has not been made. However, short-term studies performed during the summer and early autumn[9,61] have suggested that water quality is similar in most respects to that of sloughs. Stratification probably exists in most deeper borrow pits during warmer months. Primary productivity may be low compared to other lentic river habitats,[9] possibly due to rapid uptake and retention of available nutrients.

The benthos of borrow pits is similar to that of sloughs and oxbow lakes, with oligochaetes, *Chaoborus*, and chironomids dominating.[61]

9. Seasonally Inundated Floodplain

Seasonally inundated floodplain habitat occurs when high river stages inundate nearby low-lying lands. Even at stages below bankfull, flooding of backswamp areas often occurs via tributaries.[108,184] Originally, floodplain land consisted largely of forests, but due to clearing and draining forest acreage in the lower Mississippi Valley has decreased dramatically.[92,143] Former floodplain land now outside the levees consists primarily of cropland and pastures; second-growth forests and remnants of the original forests are rare. Slightly over 0.6 million ha of land exists within the levees and is still subject

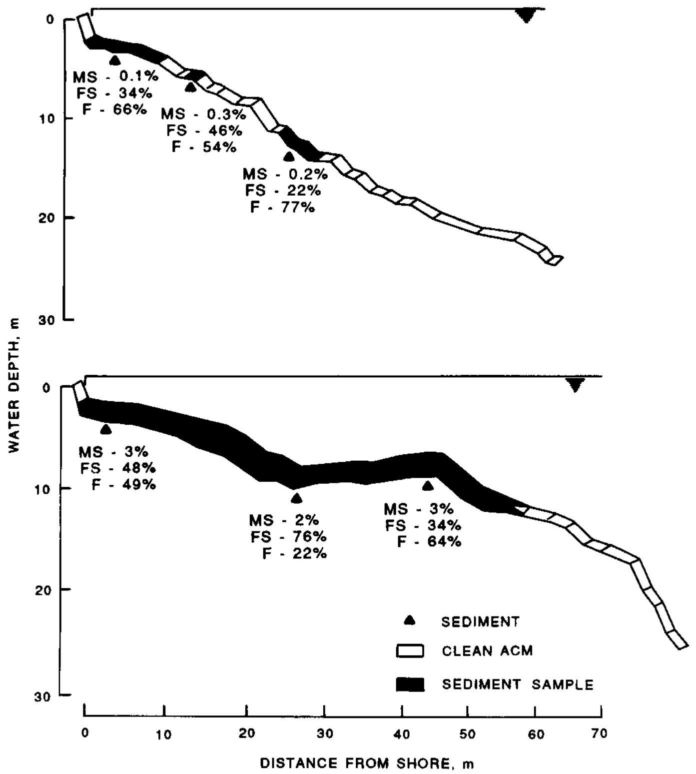


FIGURE 12. Underwater profile and sediment deposition on two reaches of articulated concrete mattress revetment (ACM). Grain-size analysis of sediment samples indicated below black triangles: MS = medium sand, FS = fine sand, F = fines (silt-clays). (From Baker, J. A., et al.[7])

to nearly annual flooding.[143] Approximately 0.4 million ha of this total are forested. Prior to the levee construction, flood waters often inundated an area several times as large for several months per year.[117] In some places, as in northeastern Missouri, floodwaters spread for nearly 80 km.[129] Now, both the extent and duration of this important, seasonal habitat is much reduced.

Conditions on the seasonal floodplain range from strong currents and deep water near the channel to slack, relatively shallow water near the flood periphery. Water quality conditions approximate those of the main channel.

10. Floodplain Ponds

Floodplain pond habitat consists of permanent, but relatively small, shallow, isolated bodies of water located in alluvial river swamps.[184,292-295] They may form in floodways, in low points in intermittent tributaries, in nearly filled abandoned channels,[97] or in backswamp depressions. They are most often associated with Tupelo-Cypress stands, other forested wetlands, or marshes. An excellent photograph and description of floodplain ponds is given by Wharton et al.[285] The major difference between floodplain ponds and isolated sloughs or oxbow lakes is size. Ponds are often less than 500 m^2 in surface area, sometimes much less. Because of this, a relatively high percentage of this aquatic habitat lies along the shoreline (within 1.5 m of the banks). The small size also permits the entire bottom to receive considerable organic input in the form of leaves and stems.[295] Most of the surface is shaded throughout the day.

Ponds have deep, muddy substrates with an abundance of organic debris (usually leaves and sticks), depths typically less than 2 m, and usually no detectable current. Aquatic vegetation, particularly duckweed, may be abundant.[184,295]

During flooding, water chemistry is similar to that of the floodwater from the parent stream (Mississippi River or tributary), but following isolation considerable differences develop between the ponds and their parent rivers.[184,293,295] High summer temperatures may occur despite the shading, and low dissolved oxygen concentrations are probably also common;[184,295,303] concentrations of most nutrients appear to be low.

The macroinvertebrate community of floodplain ponds is diverse. *Chaoborus*, oligochaetes, isopods, amphipods, chironomids, and fingernail clams are typically abundant.[184,200,294,303] In many instances, snails, certain mayflies, microcrustaceans (copepods, cladocerans), and damselflies and dragonflies are also numerous.

11. Tributaries

This habitat consists of the downstream-most portions of tributary streams, near their confluence with the Mississippi River. The upstream limit of this habitat is sometimes difficult to delineate. In general, tributary habitat includes only those reaches of tributaries that flow across the lowest parts of the Mississippi River floodplain and that are influenced by backwater flooding from the Mississippi on a regular basis. Depending upon location within the valley, and stream course relative to that of the Mississippi, the length of tributary stream that would be considered part of the Mississippi River ecosystem can range from approximately 0.5 to 5 km. Tributaries flowing into the lower Mississippi River range from clear streams such as the White River to turbid ones like the Arkansas. Very few tributaries remain unmodified. Most larger ones have flood control dams in the upper parts of their drainages, and many have been channelized for at least part of their length. The largest tributaries (Arkansas, Ohio, Missouri, and upper Mississippi Rivers) have been transformed into navigation systems that are essentially long series of impoundments.

Tributary habitat is predominantly low-gradient, sand-silt or mud-bottomed, and relatively slow-flowing during most of the year.[8,106,112,285] A few tributaries (e.g., White River[11]) are relatively strongly flowing and primarily sand-bottomed at most times. Tributaries typically have much fallen brush and trees in the water along the shoreline. Individual tributaries may change rapidly in response to localized, heavy precipitation, becoming swift and turbid. During high stages on the Mississippi River, tributaries may be dammed and remain sluggish

A

FIGURE 13. Sandbar and pool habitats in the lower Mississippi River. (A) In association with a point bar. Note chute channel between point bar and main river bank on right of photo. Chute would probably be slack at this river stage, and would thus consist of pool habitat in the center with lentic sandbar habitat along the bar. Lentic sandbar habitat would also occur in a narrow strip along the main channel (left, in photo) side of the bar. Lotic sandbar habitat would occur more than around 2 to 3 m from the bar. Pool habitat might also occur between the bar and the main channel along the downstream one third of the bar, where the primary current flow would be deflected away from the bar. Flow from top to bottom of photo. (B) In association with middle bars (unvegetated) and islands. The middle bar in the foreground would be completely inundated by a river rise of only about 2 m; the island behind it rises to a much greater elevation. A large area of pool habitat occurs downstream (left, in photo) of the middle bar in the foreground, at the large indentation, and also at the smaller indentation near the head of the bar. Lentic sandbar habitat occurs in a narrow strip along most of the periphery of this bar, and to a lesser extent along the two islands. Lotic sandbar habitat lies beyond this strip.

(or even flow backwards), even though they are also receiving high discharges from their own drainages.

Water quality in tributaries is a function of discharge, both of the Mississippi River and of the tributary itself. During high discharges water quality is similar to that of channel habitat. During extended low-flow periods, physical and chemical conditions are similar to those of sloughs and pools.

The macroinvertebrate communities are varied. Slow-flowing, silt or mud-bottomed tributaries probably support invertebrates like those of sloughs. Flowing, sand-bottomed tributary mouths probably have faunas more like pools. The submerged brush undoubtedly supports invertebrate communities similar to those described for natural steep banks.

C. Habitat Relationships

The 13 habitats can be grouped into several subsets based on their physical and chemical characteristics (Figure 17). These subsets are not based on a complete and rigorous statistical analysis; rather, they reflect our preliminary perceptions based on the literature, our personal field experiences, and those of

FIGURE 13B

other researchers. Swift-current mainstem habitats include channel, natural steep bank, revetted bank, and lotic sandbar; slackwater mainstem habitats are the pool and lentic sandbar. Sloughs, oxbow lakes, and borrow pits form a very similar subset of larger, permanent floodplain habitats. Floodplain ponds, tributaries, and the seasonally inundated floodplain each appear to comprise a unique subset, although tributaries have much in common with several other subsets.

D. Habitat Quantities

Table 5 presents estimates of the amounts of each aquatic habitat recognized in our classification and compares them to estimates for habitats that existed prior to river modification. Estimates for all habitats are not equally accurate. Classifications that define habitats using fluvial landforms or fixed depth contours derived from hydrographic surveys are advantageous to engineers because habitats can be relatively easily and repeatably mapped. The Computerized Environmental Resources Data System (CERDS)[57,62] recently developed for the lower Mississippi River contains one such classification.[60] Our classification, based in large part on variables that may change rapidly over time at a single site, and that cannot be easily determined using large-scale mapping techniques, sacrifices this ease of mapping. For some seasonally discrete, easily distinguished habitats located on the floodplain we can use values from geomorphologically based studies directly. However, mainstem habitats differ more between the two types of classifications, and our habitats (pool, natural steep bank, revetment, channel, and lotic and lentic sandbars) are difficult to accurately delineate on river maps or aerial photos. However, our habitats tend to be associated with particular fluvial landforms, training structures (dikes and revetments), or river configurations; thus, with sufficient field experience one can often predict where they will occur. Similarly, only crude estimates of habitat abundance in the river prior to modification can be derived from early maps. Despite these problems, we believe our estimates are sufficiently accurate to show any significant changes in habitat abundance.

To arrive at area estimates for our habitats, we used information from a number of sources; the CERDS[62] was particularly useful. Some studies examined one or more habitats within the entire ecosystem,[38,194,229,285] and in these cases we used their values. Other investigations dealt with some or all recognized habitats within a particular river reach;[58,59] in these instances we extrapolated their findings to the entire lower Mississippi River as necessary. Because other habitat classi-

A

FIGURE 14. Lotic and lentic sandbar habitats. (A) Oblique view looking downstream along sandbar. Current speed > 1.0 m/s in lotic sandbar habitat (at point of photo, about 25 m from sandbar); current still ca. 0.5 m/s 5 m from shoreline. Lotic sandbar habitat grades into channel habitat behind photographer. Note small bays (lentic sandbar habitat) formed behind ridges on sandbar. (B) Facing view of small bays (lentic sandbar habitat) formed on sandbar by previous high flows. The lentic sandbar habitat here grades into pool habitat approximately 25 m from the sandbar at a depth of about 1.5 m; pool habitat extends about 150 m out to channel behind photographer.

fications do not correspond exactly to ours, we proportionally allocated amounts from some of their habitats to ours based on our own experience or on the results of other investigations. For several short reaches of river we estimated the areas of certain habitats (e.g., pools not associated with dike systems, lotic sandbars) directly from recent river maps[183] based on our field knowledge of where these habitats occurred in those reaches and extrapolated these values appropriately. Finally, for revetments and natural steep banks we used linear amounts derived from CE records[87] and direct planimetry, respectively, and calculated total area by assuming that these habitats extended, on average, 150 m into the river.

A number of distinct changes in the river ecosystem are apparent (Table 5). Most floodplain habitats have decreased dramatically in area due to the development of the levee system. Seasonally inundated floodplain habitat has declined simply because spring flooding is now confined by levees to a small fraction of its original amount. Floodplain pond habitat has been lost because former floodplain lands now protected by levees have been largely drained and cleared. Even when areas have been left uncleared, they are often degraded by poor land use practices in surrounding areas, or by altered hydrologic cycles. In addition, aquatic communities in relatively small tracts may not survive without periodic, natural flooding.

Many oxbow lakes are now outside the present levee system and thus no longer part of the river ecosystem. Sloughs are a natural floodplain habitat that have been created in significant amounts by river regulation activities, especially artificial cutoffs and diking of chute channels; however, the increases have not offset the loss due to constriction of the floodplain by levees. Due to the natural filling of floodplain habitats,[45,97,142] sloughs will eventually be converted to land. Since river meandering has been effectively halted, few new sloughs, and no new oxbow lakes, will be created. At least partial ecological compensation may be provided by the substantial amount of borrow pit habitat that has been created due to levee

FIGURE 14B

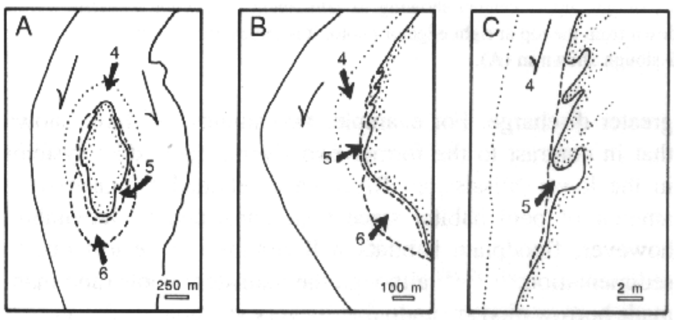


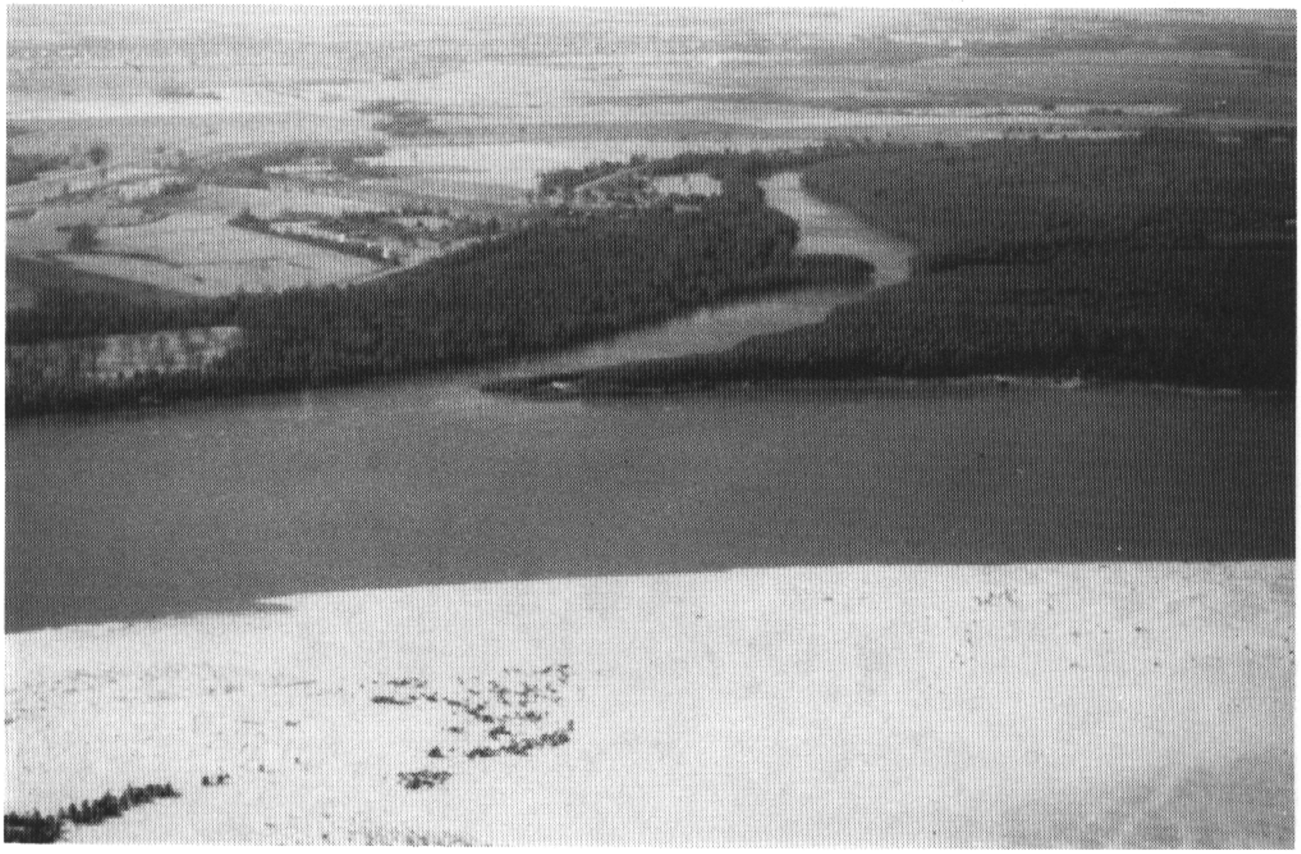
FIGURE 15. Distribution of lotic sandbar (4), lentic sandbar (5), and pool (6) habitats. (A) Associated with islands. (B) Associated with point bars. (C) Closeup of small bays formed behind sand ridges at edges of point bars and islands. See also Figures 6 and 14.

construction.[38,61] However, borrow pits are also subject to ultimate filling.

The relative changes in most mainstem habitats have not been as great as those of floodplain habitats. Channel habitat has apparently declined modestly in extent due to losses from river shortening and to a general constriction of river width by dikes to produce a deeper navigation channel. Lotic sandbar habitat appears to have declined substantially in abundance. Shortening and straightening the river has reduced the number of bends, and concomitantly the number of point bars, areas that consist largely of sandbar habitat. In addition, diversion of most flow through the main navigation channel at low stages has necessitated the diking of many secondary channels. Lotic sandbar habitat is lost by elimination of flow along one side of the island or middle bar. Historic reports[67,77] indicate that 125 or more islands previously existed in the lower Mississippi River, many more than at present. Although dike systems seem to have created a considerable amount of sandbar habitat,[59] dikes are often placed in locations which were already conducive to sandbar formation, and it seems probable that they have not offset losses to a significant degree.

Natural steep banks have declined substantially due largely to construction of revetments.[203] Natural steep bank habitat has also been lost due to dike construction, especially at the upstream entrance to secondary channels, and to the overall shortening of the river that has resulted from navigation and flood control works.

Lentic sandbar habitat has probably decreased slightly in abundance. Although many islands and middle bars, around both sides of which a current typically flowed, are now slack on one side (influenced by a dike), the overall reduction in



A

FIGURE 16. Slough habitat in the lower Mississippi River. (A) Contiguous slough (upper center) showing its permanent connection to main channel. End of small, isolated slough visible about one fourth of the distance down from the top at right edge of photo; it is intermittently connected to the contiguous slough via a narrow channel. (B) Closeup of end of isolated slough shown in (A).

islands and point bars probably offsets any new lentic sandbar habitat created by dikes. In addition, river stages for given discharges are higher now than before,[19,192,262] and thus the availability of lentic sandbar habitat may fluctuate to a greater extent.

A considerable increase in pool habitat can be attributed largely to the construction of dikes.[59,194,195] Pool habitat associated with islands and point bars has been lost, but a much larger amount has been added within dike systems.

Although by any standards the change in lower Mississippi River aquatic habitats has been dramatic, a considerable variety and amount still remains. The magnitude and pace of future changes are controversial, however, and predictions of future habitat change are beyond the scope of this article. Severe reductions in the amount, distribution, and quality of aquatic habitats due to river regulation practices have been well documented for both the middle Mississippi River[134,262] and the lower Missouri River.[96,207] However, it is uncertain whether the same practices will similarly affect the lower Mississippi River, which has a lower slope, lesser sediment load, and greater discharge. For example, two studies[59,195] have shown that in contrast to the former two rivers, many dike systems in the lower Mississippi River have retained a considerable amount of pool habitat since their construction. Inevitably, however, floodplain habitats will continue to be lost due to sedimentation;[97,157,248] although the mainstem pools (and man-made borrow pits) are undoubtedly very valuable slackwaters,[18] they may not be ecologically equivalent to natural floodplain slackwater habitats.

Undoubtedly, the loss of a substantial percentage of floodplain habitats (both permanent and seasonal) has adversely affected the river ecosystem.[101,151] The effects of levee construction were noted long before formal, systematic studies were initiated.[116,117,289] It is now known that mainstem habitats receive a substantial proportion of their energy and nutrient input from the floodplain,[81,184,185] directly, in the form of items consumed by fish, or indirectly, as suspended or dissolved organic matter used by invertebrates. In addition, many mainstem species use floodplain habitats as spawning or nursery areas.[65,98,99,184,294,295]

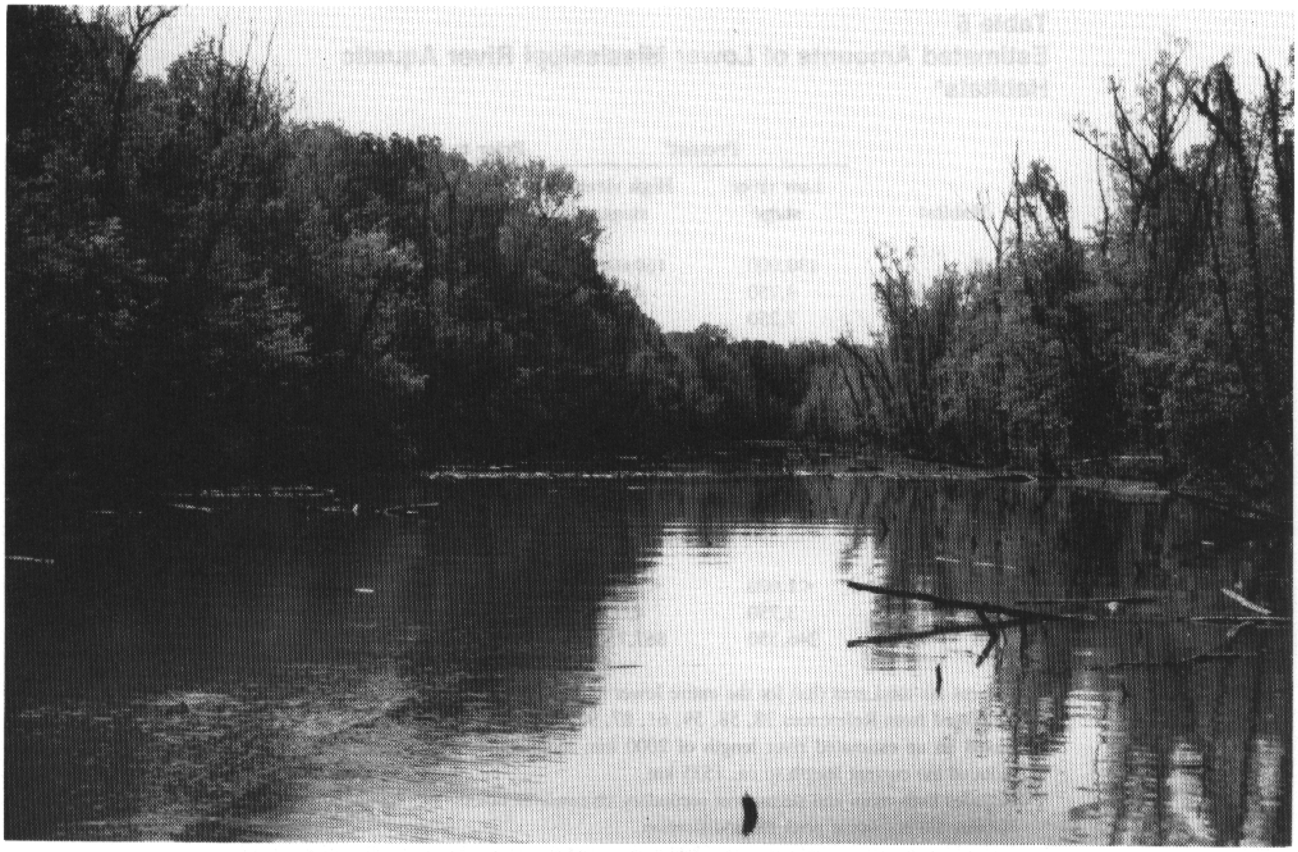


FIGURE 16B

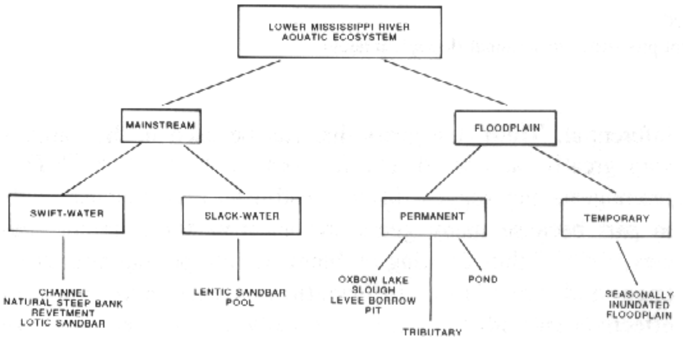


FIGURE 17. Relationships of the 13 aquatic habitats.

Concern for the integrity of the river ecosystem is manifested in the number and nature of recent studies. Several of these reports have been summarized in this section, concerning the physical and limnological characteristics of the aquatic habitats; fishery studies are examined in the next section. In addition, a number of CE reports have provided guidance to engineers involved in building levees,[133] constructing dikes[39,217,234,255,256] and revetments,[2,6,122,141,234] maintaining channels by clearing and snagging,[257] and removing material to form borrow pits.[3] Several reports summarizing general guidelines for flood control projects have also been published.[196,254,258,276]

IV. LOWER MISSISSIPPI RIVER FISHES

The Lower Mississippi River aquatic ecosystem may support as many as 91 species of freshwater fishes (Table 6). Other studies have listed from 110 to 121 species.[111,114,153,229,285] In this article, species were considered only if they potentially maintained reproducing populations in the river, and thus we have listed fewer taxa. Obvious strays from smaller tributaries, recently introduced species, or invaders from the marine environment are not included.[37,48,64,110,139,274] We have also limited the scope of this article to larger juveniles and adults. The literature on larvae and small juveniles is sufficiently voluminous and complex to warrant its own review. As a general rule, we included species when they became vulnerable to gears such as electroshockers, hoop nets, and seines instead of ichthyoplankton nets. A few species of uncertain distributional

Table 5
Estimated Amounts of Lower Mississippi River Aquatic Habitats[a]

Habitat	Present[b]		Prior to human modification[c]	
	Low river stage	High river stage	Low river stage	High river stage
Channel[d]	130,000	160,000	170,000	185,000
Natural steep bank	3,750	4,500	16,500	18,000
Revetment[e]	7,250	8,250	—	—
Sandbar				
Lotic[f]	28,500	31,500	47,500	47,500
Lentic[g]	3,500	—	6,500	—
Pool	21,000	5,000	15,000	7,500
Slough[h]	21,000	24,500	50,000	60,000
Oxbow lake	11,000	12,500	35,000	37,500
Borrow pit[e,i]	15,600	17,000	—	—
Seasonal inundated[j] floodplain	—	600,000	—	4 million
Floodplain pond	<1,000	<1,000	10,000	10,000
Tributary	3,750	4,000	5,500	6,500
Total	246,350	867,750	356,000	4.372 million

[a] Figures are total area (ha) for the entire lower Mississippi River.
[b] Compiled from References 38, 58, 59, 61, 87, 92, 114, 143, 158, 195, 229, 285.
[c] Based on an estimated river length of 2000 km; modification, especially cutoffs, have reduced the current length to ca. 1535 km.
[d] Includes both main and permanent secondary channels of others.
[e] Habitat did not occur prior to modification.
[f] Two older reports[67,77] indicated ca. 980 km of island shoreline prior to modification, along with 2450 km of other sandbars, primarily point bars; this area has been apportioned among lotic and lentic sandbars and pools, using percentages from present habitats (i.e., 10% pools, 15% lentic sandbar, 75% lotic sandbar).
[g] Habitat does not exist at high river stages.
[h] Both contiguous and isolated sloughs combined.
[i] Only pits filled year-round counted; intermittent pits added to seasonal floodplain habitat.
[j] Habitat does not exist at low river stages.

status that we included may eventually be removed from the list of resident fishes. Species in this category include sturgeon chub,[49,206] sicklefin chub,[50] pallid sturgeon,[47,137] lake sturgeon,[223] and chub shiner.[273] However, it seems unlikely that many species will be added.

In referring fish species to habitats we have used several sources of information, the most important being studies directly linking species to particular habitats.[228] Because fishery studies of large eastern U.S. rivers often defined habitats differently, or not at all, it was sometimes difficult to assign fishes collected in these studies to our habitats. Second, the lower Mississippi River has been sampled relatively poorly because of its great size, depth, and strong currents. Until the early 1970s there had been almost no large-scale fish studies of the river.[63,106] Not surprisingly, habitats have been studied in inverse proportion to the difficulty in sampling them, so that a few have been relatively well sampled (e.g., lentic sandbars, borrow pits, pools) while others (e.g., channel and lotic sandbars) remain virtually unknown. Therefore, assignment of species and relative abundances to some habitats is still largely inferential. Third, the gears that can be used in the habitats vary greatly, as does their effectiveness.[54,95,126,152,201,270] Different gears may suggest different estimates of habitat use,[123,284] in part because many gears are selective for different species,[126,201,270] thus creating problems in interpreting both presence and abundance information. Gears may vary in effectiveness with river stage.[209] Finally, most collections have apparently been made during the daytime, and it is probable that in at least some habitats night collections would differ considerably. Diel differences in habitat use and behavior have been documented for many freshwater fishes.[121,225]

Indirect criteria, including morphological attributes such as body shape, mouth size and shape, and overall size,[100,240] were used to infer habitat use by particular species. These criteria were used primarily where little direct data were available, but they were also useful in substantiating abundance ratings for some species in particular habitats.

The following sections describe the fish communities of lower Mississippi River aquatic habitats in terms of the subsets of similar habitats delineated in Section III.C. This avoids

Table 6
Habitat Distribution and Relative Abundance of Lower Mississippi River Fish Species[a]

Family and species	Channel[b]	Natural steep bank	Revetted bank	Sandbar Lotic	Sandbar Lentic	Pool	Slough[c]	Oxbow lake	Borrow pit	Seasonal floodplain	Pond	Tributary	Overall
Petromyzontidae													
Chestnut lamprey *(Ichthyomyzon castaneus)*	P	P	P	—	—	—	—	—	—	—	—	U	R
Acipenseridae													
Lake sturgeon *(Acipenser fulvescens)*	P	P	P	P	—	P	—	—	—	—	—	R	R
Pallid sturgeon *(Scaphirhynchus albus)*	P	P	P	R	—	P	—	—	—	—	—	R	R
Shovelnose sturgeon *(S. platorynchus)*	C	C	C	C	—	U	R	—	—	—	—	C	C
Polyodontidae													
Paddlefish *(Polyodon spathula)*	U	U	R	U	—	C	T	C	T	P	—	U	U
Lepisosteidae													
Spotted gar *(Lepisosteus oculatus)*	R	R	R	R	R	R	C	C	A	C	C	U	C
Longnose gar *(L. osseus)*	C	C	C	C	C	A	T	C	U	U	R	C	A
Shortnose gar *(L. platostomus)*	A	A	C	C	A	A	A	A	C	C	R	A	A
Alligator gar *(L. spatula)*	R	R	R	R	R	R	U	U	R	R	R	R	U
Amiidae													
Bowfin *(Amia calva)*	—	P	R	R	—	R	A	C	A	C	U	C	C
Anguillidae													
American eel *(Anguilla rostrata)*	U	T	T	U	—	U	—	—	—	R	—	C	U
Clupeidae													
Skipjack herring *(Alosa chrysochloris)*	C	C	C	C	C	A	A	C	R	U	—	C	A
Gizzard shad *(Dorosoma cepedianum)*	U	C	C	C	A	A	A	A	A	A	—	A	A
Threadfin shad *(D. petenense)*		C	C	U	A	A	A	A	A	A	—	A	A
Hiodontidae													
Goldeye *(Hiodon alosoides)*	U	T	T	T	T	C	T	R	R	R	—	T	U—C
Mooneye *(H. tergisus)*	P	R	R	R	—	R	R	—	—	—	—	R	R—U
Esocidae													
Grass pickerel *(Esox americanus)*	—	—	—	—	—	R	U	U	R	C	C	R	R
Chain pickerel *(E. niger)*	—	—	—	—	—	R	U	C	R	U	U	R	R
Cyprinidae													
Common carp *(Cyprinus carpio)*	C	A	A	C	U	C	A	A	A	A	—	A	A

Table 6 (continued)
Habitat Distribution and Relative Abundance of Lower Mississippi River Fish Species[a]

Family and species	Channel[b]	Natural steep bank	Revetted bank	Sandbar Lotic	Sandbar Lentic	Pool	Slough[c]	Oxbow lake	Borrow pit	Seasonal floodplain	Pond	Tributary	Overall
Cypress minnow (*Hybognathus hayi*)	—	—	—	—	R	R	U	U	U	U	U	R	R
Central silvery minnow (*H. nuchalis*)	P	C	C	C	A	C	U	—	—	A	—	A	C—A
Speckled chub (*Hybopsis aestivalis*)	C	C	U	C	T	U	—	—	—	—	—	C	C
Sturgeon chub (*H. gelida*)	P	P	P	R	—	—	—	—	—	—	—	R	R
Flathead chub (*H. gracilis*)	P	P	P	R	—	—	—	—	—	—	—	R	R
Sicklefin chub (*H. meeki*)	P	P	P	R	—	—	—	—	—	—	—	R	R
Silver chub (*H. storeriana*)	P	C	C	C	A	C	—	—	—	C	—	C	C
Golden shiner (*Notemigonus crysocleucas*)	—	R	R	R	U	U	U	C	U	A	A	R	U
Pallid shiner (*Notropis amnis*)	—	R	R	R	R	R	—	—	—	—	—	U	R
Emerald shiner (*N. atherinoides*)	P	A	C	A	A	A	U	C	U	C	—	A	A
River shiner (*N. blennius*)	P	A	C	A	A	C	R	P	R	C	—	C	A
Ghost shiner (*N. buchanani*)	P	U	R	U	U	U	—	—	—	—	—	U	R
Pugnose minnow (*N. emiliae*)	—	R	—	—	R	R	C	C	C	C	C	U	U—C
Ribbon shiner (*N. fumeus*)	—	R	—	—	R	R	C	C	C	A	C	C	U—C
Red shiner (*N. lutrensis*)	—	R	R	R	U	U	R	R	R	U	—	C	R—U
Taillight shiner (*N. maculatus*)	—	—	—	—	R	R	C	U	C	C	C	U	U
Chub shiner (*N. potteri*)	P	P	P	R	P	P	—	—	—	—	—	R	R
Silverband shiner (*N. shumardi*)	P	C	C	C	C	C	R	U	R	C	—	C	C
Weed shiner (*N. texanus*)	—	R	—	—	R	R	U	R	R	R	—	U	R
Blacktail shiner (*N. venustus*)	—	T	T	U	C	C	—	U	—	C	—	C	C
Mimic shiner (*N. volucellus*)	P	C	C	C	C	C	R	R	—	C	—	C	C
Bullhead minnow (*Pimephales vigilax*)	—	U	R	—	U	T	R	U	U	U	—	A	U
Catostomidae													
River carpsucker (*Carpiodes carpio*)	C	A	A	C	A	A	A	A	C	C	—	C	A
Quillback (*C. cyprinus*)	P	R	R	R	R	R	R	R	R	R	—	U	R
Highfin carpsucker (*C. velifer*)	P	R	R	R	R	R	R	R	R	R	—	R	R
Blue sucker (*Cycleptus elongatus*)	A	C	A	C	—	T	—	R	—	—	—	U	C

Table 6 (continued)
Habitat Distribution and Relative Abundance of Lower Mississippi River Fish Species[a]

Family and species	Channel[b]	Natural steep bank	Revetted bank	Sandbar Lotic	Sandbar Lentic	Pool	Slough[c]	Oxbow lake	Borrow pit	Seasonal floodplain	Pond	Tributary	Overall
Smallmouth buffalo (*Ictiobus bubalus*)	A	C	A	C	C	C	C	A	A	C	—	A	A
Bigmouth buffalo (*I. cyprinellus*)	U	T	T	R	—	T	C	A	A	A	—	C	C
Black buffalo (*I. niger*)	U	U	U	R	—	R	R	U	R	U	—	U	U
Spotted sucker (*Minytrema melanops*)	—	R	—	—	R	U	T	T	T	R	R	R	U
Ictaluridae													
Blue catfish (*Ictalurus furcatus*)	A	A	A	A	C	C	T	U	U	R	—	C	A
Black bullhead (*I. melas*)	—	—	—	—	—	P	U	U	C	C	C	R	R—U
Yellow bullhead (*I. natalis*)	—	—	—	—	—	P	U	U	C	A	C	R	R—U
Brown bullhead (*I. nebulosus*)	—	—	—	—	—	—	R	R	R	P	P	—	R
Channel catfish (*I. punctatus*)	C	A	C	C	C	A	A	C	A	C	—	A	A
Tadpole madtom (*N. gyrinus*)	—	—	—	—	—	—	P	P	U	P	P	—	R
Flathead catfish (*Pylodictis olivaris*)	A	A	A	C	U	T	R	U	U	R	—	C	A
Aphrododeridae													
Pirate perch (*Aphredoderus sayanus*)	—	—	—	—	—	—	C	C	C	A	A	U	A
Cyprinodontidae													
Blackstripe topminnow (*Fundulus notatus*)	—	R	—	—	R	R	C	C	C	U	C	U	R—U
Blackspotted topminnow (*F. olivaceus*)	—	R	—	—	R	R	U	U	.C	C	C	C	R—U
Golden topminnow (*F. chrysotus*)	—	—	—	—	—	—	R	U	R	C	C	R	R—U
Northern starhead topminnow (*F. dispar*)	—	—	—	—	—	—	U	U	R	C	C	R	R—U
Poeciliidae													
Mosquitofish (*Gambusia affinis*)	—	R	R	—	R	R	C	A	A	A	A	C	C
Atherinidae													
Brook silverside (*Labidesthes sicculus*)	—	U	R	—	U	U	C	C	A	C	C	C	C
Inland silverside (*Menidia beryllina*)	P	C	C	C	C	C	R	R	A	A	—	C	A
Percichthyidae													
White bass (*Morone crysops*)	U	C	C	C	C	A	U	U	U	C	—	C	C—A
Yellow bass (*M. mississippiensis*)	R	U	R	R	R	U	U	T	C	U	—	C	U
Striped bass (*M. saxatilis*)	T	T	T	T	—	T	R	R	—	—	—	T	R—U

Table 6 (continued)
Habitat Distribution and Relative Abundance of Lower Mississippi River Fish Species[a]

Family and species	Channel[b]	Natural steep bank	Revetted bank	Sandbar Lotic	Sandbar Lentic	Pool	Slough[c]	Oxbow lake	Borrow pit	Seasonal floodplain	Pond	Tributary	Overall
Centrarchidae													
Flier (*Centrarchus macropterus*)	—	—	—	—	—	—	R	R	R	C	A	—	R—U
Banded pygmy sunfish (*Elassoma zonatum*)	—	—	—	—	—	—	R	R	R	C	A	—	R—U
Green sunfish (*Lepomis cyanellus*)	—	R	R	—	—	R	U	U	U	R	R	R	R
Warmouth (*L. gulosus*)	—	U	R	—	—	R	A	A	A	A	A	U	C
Orangespotted sunfish (*L. humilis*)	—	R	R	—	—	R	C	C	A	C	R	U	U—C
Bluegill (*L. macrochirus*)	—	T	U	—	U	T	A	A	A	A	C	A	C—A
Longear sunfish (*L. megalotis*)	—	R	—	—	R	R	—	R	R	R	—	C	U
Redear sunfish (*L. microlophus*)	—	R	R	—	R	R	U	C	U	C	U	U	R—U
Spotted sunfish (*L. punctatus*)	—	—	—	—	—	—	U	U	R	C	C	—	R
Bantam sunfish (*L. symmetricus*)	—	—	—	—	—	—	U	R	R	C	C	—	R
Spotted bass (*Micropterus punctulatus*)	—	—	—	—	—	R	—	R	R	—	—	C	U
Largemouth bass (*M. salmoides*)	—	U	R	—	R	U	C	A	A	C	U	T	C
White crappie (*Pomoxis annularis*)	P	C	U	R	U	C	A	A	A	C	—		C—A
Black crappie (*P. nigromaculatus*)	P	T	R	R	R	T	U	U	T	C	—	T	U—C
Percidae													
Crystal darter (*Ammocrypta asprella*)	P	—	—	P	—	—	—	—	—	—	—	R	R
Scaly sand darter (*A. vivax*)	P	—	—	P	—	—	—	—	—	—	—	U	R
Mud darter (*Etheostoma asprigene*)	—	—	—	—	—	—	U	R	R	C	C	R	R—U
Bluntnose darter (*E. chlorosomum*)	—	P	R	P	U	U	R	—	—	C	C	C	U
Slough darter (*E. gracile*)	—	—	—	—	—	—	R	R	R	C	C	R	R—U
Cypress darter (*E. proeliare*)	—	—	—	—	—	—	R	R	—	C	C	R	R—U
Logperch (*Percina caprodes*)	—	—	—	—	R	R	—	R	R	—	—	U	R
River darter (*P. shumardi*)	P	R	.U	C	R	R	—	—	—	—	—	C	U—C
Sauger (*Stizostedion canadense*)	U	C	C	U	C	C	T	U	U	U	—	C	C

Table 6 (continued)
Habitat Distribution and Relative Abundance of Lower Mississippi River Fish Species[a]

Family and species	Channel[b]	Natural steep bank	Revetted bank	Sandbar Lotic	Sandbar Lentic	Pool	Slough[c]	Oxbow lake	Borrow pit	Seasonal floodplain	Pond	Tributary	Overall
Sciaenidae													
Freshwater drum (*Aplodinotus grunniens*)	C	A	A	C	C	A	A	A	A	C	—	A	A

[a] Derived from References 4, 9—12, 15, 16, 18, 22—24, 33, 35, 40, 44, 47, 49, 51, 53, 61, 68, 73, 79, 84, 85, 88, 106—115, 137, 139, 148, 149, 153, 160, 162, 163, 177, 190, 197, 201—204, 206, 212, 213, 217—223, 229, 231—233, 245, 266, 279, 280, 285, and 294. (A) abundant: usually found in high numbers; (C) common: usually found in moderate numbers; (T) typical: occurs regularly, but in low numbers; (U) uncommon: irregularly found, usually, but not always, in low numbers; (R) rare; seldom encountered, almost always in low numbers; (P) probable; likely to occur, but records lacking or inconclusive.

[b] Habitat virtually unsampled; presence and abundance based on known or suspected habitat use in other rivers and on morphological inference.

[c] Includes both contiguous and isolated sloughs.

considerable repetition, because habitats within the subsets appear to have very similar fish communities (Table 6). Important differences from the general pattern are noted as necessary. In addition, because the fish communities of some habitats are very poorly known, this approach allows us to speculate on their communities without discussing them individually in detail.

A. Fish Communities

1. Mainstem Swift-Current Habitats

This subset includes the channel, natural steep bank, revetment, and lotic sandbar habitats. Natural steep banks and revetments in the lower Mississippi River have been studied often,[10-12,53,111,178,197,201-204] but typically with a rather limited number of gears. Electroshockers and hoop nets have been the primary collecting means, although a few studies have attempted to use seines or trammel nets. Despite this limitation, at least 63 species have been recorded from natural steep banks, and 55 from revetted banks, and other species are likely.

Twenty-three to 25 species appear to be common to abundant in these two habitats, and 7 or more others typical. The community includes a diverse mixture of fishes ranging from openwater forms, including shads, skipjack herring, goldeye, and white and striped bass, to large, streamlined bottom-dwellers such as shovelnose sturgeon, common carp, blue sucker, buffalofishes, carpsuckers, catfishes, and freshwater drum. Centrarchids, more typical of floodplain habitats, are regularly collected along natural steep banks, but are much less common along revetments. A rather surprising number of small species (e.g., minnows, silversides) have been documented for this habitat, some of them common to abundant. Their numbers are undoubtedly underestimated by present sampling.

Fish distribution along lower Mississippi River natural steep banks and revetments has recently been surveyed using hydroacoustics.[9,10,12] Results suggested that these habitats may harbor larger numbers of fish than indicated previously by more traditional fishery gears. In addition, many of the acoustic targets were rather small (ca. 3 to 30 cm), supporting the conclusion derived from previous studies that the abundance of small fishes is underestimated in these habitats. Fishes were primarily distributed close to the shoreline, near the bottom, or in eddies, although exceptions to this general pattern were common, and distributions often changed with river stage and season.

Sandbars have been studied extensively,[9,11,12,33,49,53,73,106,190,197,201,202] but few investigations have sampled more than the fringe of the lotic sandbar habitat as defined here. At least 49 species occur in this habitat. Typical species are either bottom-oriented (e.g., shovelnose sturgeon, catfishes, blue sucker, smallmouth buffalo, freshwater drum, speckled chub) or capable of swimming against strong currents (paddlefish, skipjack herring, white bass, and sauger). Catch rates appear to be generally low,[9,12,190,201,202] but this habitat has been sampled rather poorly in most studies. Sand ripples, and perhaps also larger sand waves farther offshore, may harbor smaller, bottom-dwelling species such as chubs (*Hybopsis*) and the river darter. It is unlikely that bottom topography offers the same degree of protection from the current as in the channel, and physical conditions may preclude many species from using the lotic sandbar habitat regularly in large numbers.

Fish collections from channel habitat in the lower Mississippi River are essentially nonexistent.[9,12] From what is known of its physical attributes, few species probably could regularly inhabit the upper and middle water column in this habitat. Some larger fishes, such as paddlefish, white bass, and striped bass, and smaller actively swimming fishes such as skipjack herring and goldeye may often occupy this area for feeding or for moving among other habitats.[16,206,213] Even these species presumably spend considerable time in habitats having lower current speeds.

Current speeds are considerably diminished at and very near the river bottom, and the enormous sand dunes probably produce rather large, relatively slow-current eddies.[29] Fishes have been observed using simmilar sites as velocity shelters in smaller streams,[68] and it is probable that larger, bottom-dwelling species such as sturgeons, common carp, buffalofishes, carpsuckers, blue sucker, catfishes, sauger, and freshwater drum could inhabit these areas in the channel habitat, as they do in smaller rivers.[136] It is also possible that relatively small species such as the central silvery minnow, several chubs (genus *Hypobsis*), and the river darter could inhabit the channel due to their bottom-dwelling habits and streamlined forms. Although current speeds are somewhat lower, the main navigation channel of the upper Mississippi River appears to be inhabited by a surprising number of species.[167,272] In all, channel habitat in the lower Mississippi River may be inhabited by 30 or more species of fish.

Hydroacoustics[9,12] has recently indicated that fish abundances in both lotic sandbar and channel habitats may be underestimated by traditional fish collecting techniques. Densities appear to be lower, on average, than in pool, lentic sandbar, and natural steep bank habitats; however, during summer and early autumn the channel and lotic sandbar habitats have rather surprising numbers of fish. Densities were somewhat lower in the lotic sandbar habitat than in channels. In addition, most of the fish detected were relatively small. Fish appeared to be distributed relatively evenly throughout the water column in some channel and lotic sandbar habitats, but were bottom-oriented in others.

Seasonal changes in the swift-current mainstem habitats have not been adequately investigated. Present data suggest little change, although adult threadfin shad show an intriguing increase in abundance along natural steep banks and revetments during spring and early summer, and an almost total absence during late summer and autumn.[18] Bottom-dwelling species have probably been better sampled than mid-water species. Better methods need to be developed for sampling all areas of these habitats.

2. Mainstem Slackwater Habitats

This group consists of lentic sandbar and pool habitats. The community of the lentic sandbar habitat includes over 50 species, including gars, shads, numerous minnows and suckers, catfishes, silversides, sauger, and freshwater drum.[9,12,49,53,106,190,197,201,202] Juveniles of many larger species, such as river carpsucker, freshwater drum, white bass, and channel and blue catfishes are also common. Fish abundance in lentic sandbars probably varies considerably more with season and river stage than in any other habitat. Lentic sandbar habitat is maximally abundant during July through December and is used extensively by large numbers of fish, including the juveniles of many larger species. Catches in seine hauls are typically high during June to September,[9,190] lower in October to November, and lowest from December to May. Unseasonably high stages may eliminate much sandbar habitat and force many species into other habitats,[9] but electroshocking samples suggest that larger fishes may continue to inhabit these areas until conditions become extremely harsh.[9,201]

Pools support a diverse array of species, perhaps 68 or more. Among mainstem habitats, the wide variety and often high densities of fishes found in these habitats may stem from the relatively benign physical conditions of pools (low to zero currents, warm temperatures, high plankton, and benthic invertebrate densities), and their proximity to many swift-water habitats.

Pools have been sampled in many studies with a variety of gears.[9,12,49,127,190,197,201,202,220,221] With the exception of rotenone studies,[9,49,127] areas deeper than ca. 5 m probably have been ineffectually sampled. Because rotenone collections are generally made only in the most isolated areas (e.g., pools behind dikes, and those at least partly separated from the channel by a sandbar[9,127]), they may not be representative of pool habitat as a whole. Pool habitat adjacent to islands (Figures 6 and 13B), for example, has apparently not been sampled by rotenone.

Studies using rotenone and those using more traditional collecting gears (e.g., electroshocking, nets) have yielded fairly comparable species lists and relative abundances. Clupeids (especially *Dorosoma* spp.), carpsuckers, freshwater drum, channel and blue catfish, and several minnows (*Notropis, Pimephales, Hybognathus*) were abundant in both types of collections. Rotenone appeared to sample buffalofishes, sunfishes (especially crappies), and paddlefish more effectively, while gars were apparently more efficiently collected by electroshocking and gill nets.

Because they can be sampled by rotenone, pools are the only mainstem habitat for which standing stock biomass estimates are available. Initial samples suggested that fish biomass averaged 153 kg/ha and typically ranged from 16 to 625 kg/ha. More recent studies utilizing much larger net sets (0.5 to 4.0 ha) have indicated that biomasses may average over 2065 kg/ha, and can reach over 3860 kg/ha.[9,127] The highest biomasses appear to be attributable to extraordinarily high numbers of gizzard and threadfin shad, and to a lesser extent river carpsucker and freshwater drum. Occasionally, large numbers and biomasses of buffalofishes, catfishes, crappies, gars, and white bass occur.[127] Data from electroshocking and net collections suggest that the highest numbers of fish are present in pools during summer and early autumn, coincident with lowest river stages, warmest water temperatures, and the greatest food densities.[9,190,202] However, this conclusion may be biased, since sampling is probably most effective under such conditions; in addition, winter sampling efforts do not appear to have been as intensive as those during summer and autumn. Recent winter samplings of dike pools on the Missouri River,[123] using specialized techniques in some instances, have captured large numbers of several species.

Hydroacoustic studies[9] have shown that fish are often most abundant in the deepest parts of pools. In particular, plunge pools and eddy scour holes downstream of dikes often harbor relatively high densities of fish.

3. Larger, Permanent Floodplain Habitats

Sloughs, oxbow lakes, and borrow pits have been sampled relatively well, often with rotenone. Numerous oxbow lakes within the lower Mississippi River ecosystem have been studied,[93,127,149,159,162,178,201] as have a large number of oxbows on tributaries.[24,148,160,162,163,232,233] Lower Mississippi borrow pits have also recently been intensively surveyed using rotenone,[61] although only during a single summer. Until very recently[49,159] sloughs had been sampled almost exclusively with electroshockers and nets.[170,201,202] Few studies have sampled the smaller species thoroughly (e.g., darters, minnows), although several recent collections[161-163] have given them more emphasis.

The larger, permanent floodplain habitats harbor a fauna of up to 70 species of fish, at least 24 of which are common to abundant. Several of the abundant species are ubiquitous within the river ecosystem, e.g., shortnose gar, gizzard and threadfin shad, skipjack, herring, common carp, river carpsucker, smallmouth and bigmouth buffalofishes, channel catfish, and freshwater drum. A number of species are characteristic of this habitat group, including paddlefish, spotted gar, bowfin, spotted sucker, bullheads, pirate perch, topminnows, mosquitofish, certain centrarchids such as warmouth, bluegill, orangespotted sunfish, largemouth bass and crappies, and perhaps alligator gar.[111,114,159,206] Several of these species may be unique to these habitats.[18] Although few collections made specifically for small fishes are available for oxbows, we expect the presence of many such species (e.g., *Fundulus*, certain *Notropis* and *Etheostoma*, and several small *Lepomis*), based on a knowledge of their habitat preferences elsewhere.[43,68,88,136,177,223,279,294]

The fish community tends to remain stable in oxbow lakes, borrow pits, and isolated sloughs during the low-water season (typically July to December[58,59]), when these habitats are isolated from the river. Changes in the fish community do occur in contiguous sloughs, which are connected to the river at all times; however, with a few notable exceptions changes in contiguous sloughs are minor. Threadfin shad and skipjack herring are common in this habitat during late summer and autumn, but are apparently rare during spring and early summer.[170,201,202] Catches of all species combined appear to be low during spring and high to very high through summer and autumn, although part of this observed difference may be due to sampling bias. In one study,[202] catch rates and numbers of species observed nearly doubled in November (over those of June and September), possibly due to amelioration of poor water quality conditions that often occur in summer and early autumn. Fish communities probably increase in diversity during spring flooding, when all floodplain habitats may be confluent with the river mainstem.

Standing stock biomasses can reach high levels in floodplain habitats. In three apparently isolated sloughs standing stocks ranged from 145 to 939 kg/ha, and averaged ca. 510 kg/ha.[127,159] Species lists and relative abundances were very similar in studies using a variety of gears.[170,201,202] Fish biomasses in lower Mississippi River oxbow lakes appear to range from 162 to 1023 kg/ha, with a mean of ca. 535 kg/ha.[127,149,159] This is somewhat higher than estimates from oxbows on tributaries, where biomasses ranged from 58 to 823 kg/ha, with an average of about 250 kg/ha.[26,148,232,233] Standing stock biomasses in borrow pits ranging from 60 to 3650 kg/ha, and averaging 678 kg/ha, were documented in one study,[61] and over 1700 kg/ha were observed in another.[217] These biomasses are higher than those reported for most similar habitats in the region, apparently being exceeded only in the nearby Atchafalaya River basin.[34]

Because borrows pits are manmade habitats, most are dependent upon flooding by the river for the initial introduction of fishes, although some may also be stocked with a limited number of species. Species can invade from any nearby mainstem or floodplain habitats. The presence of uncommon species in any particular borrow pit may be due largely to chance.

Size distribution of fish in borrow pits may be barometers of success for some species. Bigmouth buffalofishes, for example, spawn primarily on flooded vegetation,[41] a substrate that is especially abundant near many borrow pits. Observed length-frequency distributions[61] suggested that 1978 and 1979 year-class buffalofishes were abundant in many pits, while 1980 and 1981 year-classes were absent. The years in which bigmouth buffalofishes spawned in the pits were ones of relatively prolonged high river stages, and they apparently did not spawn in the two relatively low stage years. The interpretation[61] was that spawning success for this species was excellent when extensive flooding made substantial spawning substrate available, and that this was evidenced by the presence of these year-classes in the borrow pits.

4. Floodplain Ponds

Floodplain ponds support what is undoubtedly the most unusual fish community of all river habitats. Characteristic species include some of the least common fishes within the ecosystem, e.g., chain pickerel; cypress minnow; taillight shiner; golden topminnow; flier; banded pygmy sunfish; spotted and bantam sunfishes; and mud, bluntnose, slough, and cypress darters.[40,43,51,79,112,115,206,223,279,294,295] Other common taxa that are more widely distributed include spotted gar, bowfin, golden shiner, pugnose minnow, ribbon shiner, pirate perch, blackstripe and blackspotted topminnows, mosquitofish, warmouth, and bluegill. There is evidence[154] that at least some of these species can survive long periods of very low oxygen concentration, perhaps explaining their dominance in this habitat. This community varies little except during flooding, when it may be temporarily invaded by fishes utilizing the adjacent seasonally inundated floodplain.

5. Seasonally Inundated Floodplain

In river systems of all sizes on all continents,[32,108,226,290,294,295] a variety of fishes take advantage of seasonally inundated floodplains. Large species such as gars, bowfin, common carp, buffalofishes, river carpsucker, channel and blue catfishes, white bass, crappies, and freshwater drum extensively exploit the floodplain for feeding. Many of these taxa, and a considerable number of others, also spawn on the inundated floodplain, at least in part.[41,101,151,216,269,289,295,300] Many smaller species such as pickerels, minnows, topminnows, bullheads, mosquitofish, and sunfishes probably also actively exploit this seasonal habitat, but documentation for this is less extensive.

6. Tributaries

Tributary mouths harbor as many as 82 species of fish considered to be inhabitants of the lower Mississippi River ecosystem. During nonflood periods most tributaries are inhabited by species typical of sloughs, oxbow lakes, and borrow pits, including gars, bowfin, gizzard shad, common carp, several minnows, carpsuckers, buffalofishes, channel catfish, some topminnows and mosquitofish, many sunfishes including crappies and largemouth bass, a few darters, and freshwater drum.[8,111,112] The few tributaries (e.g., the White River) that remain relatively strongly flowing during the summer and autumn contain fewer slackwater fishes and include many flowing-water forms, such as shovelnose sturgeon, minnows of the chub genus *Hybopsis*, some *Notropis*, blue sucker, blue and flathead catfish, and sauger,[11,113] more typical of pools and the swift-current mainstem habitats.

Seasonal variations probably occur when high flows force slackwater fishes into other areas and allow flowing-water species to invade. Additionally, many Mississippi River fishes may move into tributaries on spawning or feeding migrations.[108,206,211,277] During extended low flows, poor water quality may also affect fish distribution in tributary mouths. However, it is remarkable how little is known about fish movements either into, out of, or within, the river ecosystem. For example, apparently the only information on paddlefish migration into tributaries comes from two fortuitous observations by J. A. Baker in which several thousand recently killed paddlefish were found. The fish had apparently migrated into the tributary (Bayou Pierre) and were killed when heavy rains washed recently applied pesticides into the streams.

B. Fish Community-Habitat Associations

Fish communities largely substantiate the habitat delineations derived independently on the basis of physical and chemical variables. Habitats with similar physicochemical characteristics support similar fish communities, regardless of where they may be located within the river ecosystem. However, for a number of habitats our knowledge of some facets of their fish communities is poor. Channel-inhabiting fish, for example, are especially poorly known, as are the smaller species in habitats such as natural and revetted banks, and sloughs. In addition, our knowledge of the physicochemical attributes of certain habitats is limited. Some of these gaps can be addressed by using currently available technologies; others will require the development of new approaches and techniques.

The definitions and descriptions of the habitats will undoubtedly be improved by future research. However, the present delineation appears sufficient for projecting the responses of the fish community to changes that would occur under various management alternatives. Guidelines are currently available to help engineers incorporate ecological considerations into activities affecting particular subsets of the river ecosystem (e.g., dike systems, revetments). A habitat-oriented approach would provide guidance on an ecosystem-wide scale.

V. SUMMARY

During at least the past several million years, the larger rivers of the Mississippi system, including the lower Mississippi River itself, have presumably fluctuated between two very different channel patterns: braided and meandering. These patterns provide very different types and abundances of aquatic habitats, and the kinds and abundances of fishes must have changed considerably in response to the changes in pattern. Braided rivers are wide and shallow, with many islands and sandbars dividing the flow into numerous small, swift channels. Braided rivers meander little and thus have relatively few long-lived, well-developed floodplain aquatic habitats. Meandering rivers have fewer, larger channels and a greater diversity of quiet-water mainstem and floodplain habitats. In its present form the lower Mississippi River exhibits a meandering pattern. Not all rivers of the Mississippi River system apparently changed similarly or at the same time, and thus a diverse large-river ichthyofauna was able to persist even during times of predominantly braided channel pattern. The habitats of the lower Mississippi River are again changing, this time in response to man's activities, and the changes are different in many respects from those that occurred during geological history.

Protecting the lower Mississippi River aquatic ecosystem requires an understanding of the interrelationships and functioning of its habitats. Until recently, habitats have not been consistently viewed in terms of the variables important to the organisms. In this article, 13 aquatic habitats have been delineated and described on the basis of such variables, and the relationships of the habitats have been examined. Habitats have been grouped into six subsets that reflect their physical and chemical similarities. Most habitats have been decreasing in abundance since river regulation activities began over 250 years ago. The single most deleterious modification has been reduction in the amount of seasonally inundated floodplain due to levee construction. However, channelization works that have prevented the river from meandering to form new slackwater floodplain habitats have also had an overall negative ecological impact.

At least 91 species of freshwater fishes have the lower Mississippi River ecosystem as their primary population center; 30 or more species may be present sporadically. This review has determined the relative abundance of adults of each species in each delineated habitat. Consistent groupings of species collected across a large number of studies substantiates the habitats delineated independently on the basis of physical and chemical features. The recognition of these habitats and their relationships may provide those concerned with river management with a useful tool for projecting ecosystem changes given various management alternatives.

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