Effects of Agricultural Conservation Practices on Oxbow Lake Watersheds in the Mississippi River Alluvial Plain

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Abstract

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Agricultural lands are considered to be a major source of nonpoint source pollutants such as sediment, pesticides and nutrients in the United States. Conservation practices have been tested for their effectiveness in reducing agricultural related pollutants on smaller scales, but farm watershed scale assessments of these practices are limited and few of these have evaluated the impacts on downstream ecology. Several projects focused on oxbow lake watersheds in the Mississippi River alluvial plain were designed to utilize working farms to evaluate primary pollutants in water resources and to identify conservation practices that are most effective in reducing the transport of those pollutants in surface and ground water on a watershed scale. Major findings of these studies include: (1) conservation practices reduced sediment in oxbow lakes, resulting in improved water clarity, plankton growth, and fish stocks; (2) total phosphorus in lakes decreased between 39–50% following application of conservation practices; (3) conservation tillage and cover crops reduced NO_3-N losses by 73%, sediment losses by 70; and (4) riparian areas mitigated the transport of sediment in runoff and enhanced the degradation of pesticides.

Keywords: limnology; management systems evaluation area; nutrients; pesticides; sediment; water quality

Agricultural activities are a significant source of nonpoint source pollution in the United States that have been documented in various agricultural regions like the Midwest, (Pereira & Hostettler 1993). In cultivated watersheds, nutrients in runoff have been tied to eutrophication in oxbow lakes (Rebich 2004; Heatherly *et al.* 2007; Dubrovsky *et al.* 2010). Cooper and McHenry (1989) demonstrated that agricultural activities within the watershed increased sedimentation in oxbow lakes. Miranda *et al.* (2001) found that deposition of suspended sediments to be the most significant contributor to secession in oxbow lakes and further demonstrated that deposited sediments profoundly affect temperature and dissolved oxygen. Legislation such as the 1987 Clean Water Act recognized the effectiveness of agricultural conservation practices, also known as, Best Management Practices (BMPs) in reducing nonpoint source pollutants include sediment, pesticides and nutrients (Meade 1995; Mueller *et al.* 1995).

In the early 1990's, the Management Systems Evaluation Areas (MSEA) program was begun to provide a research framework to (a) assess agricultural conservation practices that reduce overdependency on agricultural chemicals and reduce non-source pollutants; and (b) facilitate technology transfer and implementation of promising conservation practices (Council for Agricultural Science and Technology 1992).

The humid, subtropical and intensively farmed Mississippi Delta provided an opportunity within the National MSEA program framework to evaluate agricultural nonpoint source pollution and corresponding conservation practices in an ecoregion quite different from those located in the Midwestern United States. This new locale for MSEA research was called the Mississippi Delta (MDMSEA) project (Rebich & Knight 2001; Locke 2004).

The MDMSEA was designed to evaluate the effects of conservation practices on downstream water quality and ecology as well as to identify conservation practices that were most effective in reducing transport of pollutants to surface and ground water (Rebich & Knight 2001; Locke 2004).

This manuscript reports the results of the MDMSEA research focused on conservation practice effects, lake water quality and ecology from 1995 to 2004–2005 and updates previous reports through 1999 (Knight & Welch 2004; Nett *et al.* 2004; Cullum *et al.* 2006). The purpose of this research was to determine if conservation practices established in an agricultural watershed could have a positive effect on water quality in the Mississippi Delta by reducing agricultural related contaminants and if these effects would elicit an ecological response.

MATERIAL AND METHODS

Three oxbow lake watersheds located in two Mississippi counties were chosen as site locations for the MDMSEA project (Figure 1) (Rebich & Knight 2001; Locke 2004; Nett *et al.* 2004). Oxbow lake watersheds offered several research benefits. Because they were separated from their parent river or stream, oxbow lake watersheds are closed systems, with all of the runoff from the watershed draining directly into the lakes. Additionally, oxbow lake watersheds provided an opportunity to easily conduct both edge-of-field sampling and receiving-water (oxbow lake) sampling.

The three oxbow lake watersheds selected were Thighman, Beasley, and Deep Hollow (Figure 1). Watershed and lake characteristics may be found in Table 1. The Sunflower River levee defined the Beasley Lake watershed boundary on the northern side, and a large riparian area was located on the eastern side of the lake. Beasley Lake watershed differed from the other two MDMSEA watersheds in that the elevation difference from the north watershed boundary to the lake was about 5.5 m as opposed to elevation ranges of about 1.5 m within the other two watersheds. Deep Hollow Lake watershed also had a large riparian area located between the Yazoo River levee and the lake (Rebich & Knight 2001; Locke 2004; Nett *et al.* 2004).

In order to make comparisons among watersheds, edge-of-field and within-field management practices of interest were assigned to the MDMSEA (Table 1). Conservation practices were selected based on erosion and sedimentation control primarily; however, pesticide and nutrient management and socioeconomic factors were also considered as selection criteria (Rebich & Knight 2001). Practices chosen for the project were general designed to reduce runoff water velocity thereby reducing energy available for erosion and transport of soil. The edge-of-field practices were either structural, such as slotted-board risers and slotted inlet pipes, or vegetative, such as grassed filter strips and turn rows. Within-field agronomic practices in cotton and soybeans included conservation tillage, winter cover crops, and precision application technology.

In Deep Hollow Lake and Beasley Lake watersheds, structural and vegetative methods of reducing water velocities included slotted pipes, slotted-board risers, grass buffer strips, and grassed waterways. Slotted-board risers were expected to play a dual role by reducing water velocities and by providing a sheet of water over exposed soil to reduce the effects of raindrop impact. In Deep Hollow Lake watershed, cultural practices such as conservation tillage (reduced tillage in cotton and no-tillage in soybeans) and cover crops were also used to help

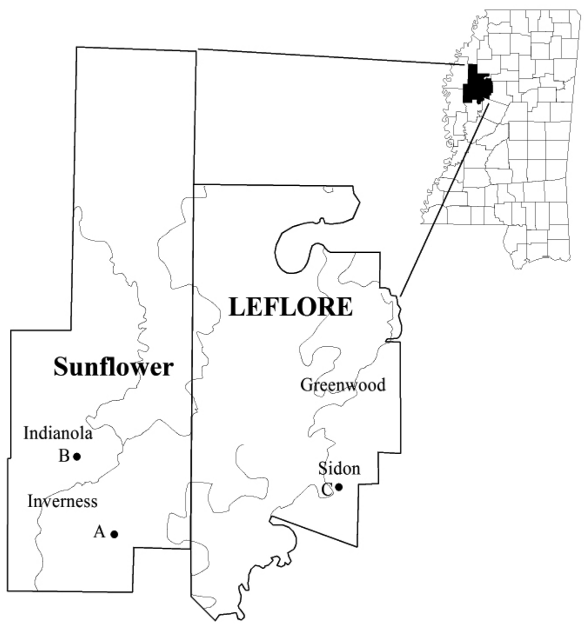

Figure 1. Oxbow lake watershed locations for the Mississippi Delta Management Systems Evaluation Area (MDMSEA) project; A – Thighman; B – Beasley; C – Deep Hollow

reduce the erosive effects of water flow and raindrop impact. It was anticipated that the residues from conservation tillage or cover crops would dissipate energy and reduce water velocities, providing a barrier between the soil and flowing water.

Components of each watershed were monitored and evaluated as to their role in pollutant fate and transport. While in some cases individual practices were evaluated, the project was specifically designed to evaluate the impact of an entire farming system on water quality, ecological processes, and fisheries resources. Lake water quality monitoring was begun in February, 1995, prior to installation or implementation of conservation measures, and continued through 2004–2005. Three replicate sites within each watershed were sampled.

Automated water quality monitoring equipment (Yellow Springs Instruments, Model 6000, YSI Incorporated, Yellow Springs, USA, http://www.ysi.com/index.php) was used to obtain hourly measurements of temperature (°C), pH, dissolved oxygen (mg/l) and conductivity (mmohs/cm^2) for the first two years of the study. The instruments rapidly became bio-fouled, and the data collected in the second year of the study were deemed unreliable by the authors. Therefore, field procedures for maintaining the instruments were changed so that data collection became more reliable. Eventually, all automatic sampling was replaced with biweekly sampling using hand held instruments. Surface water quality was sampled biweekly for total, suspended, and dissolved solids (mg/l), total phosphorus (mg/l), filterable ortho-phosphate (mg/l), ammonium nitrogen (mg/l), and nitrate nitrogen (mg/l), chlorophyll (mg/l), coliform and enterococci bacterial counts (No./l) and Secchi visibility (cm) (American Public Health Association 1992; Rebich 2004).

Preliminary fisheries investigations of the oxbow lakes indicated the fish community was dominated by high sediment and low dissolved oxygen tolerant species (Rebich & Knight 2001). Additionally, relative abundance of sport and food fishes were low. In order to compare the fish community response of the lakes to the application of conservation practices all three lakes were renovated using 5% rotenone solution and restocked with sports fish species (Nielsen & Johnson 1984). This is a standard practice in the United States for establishing a sports fishery (Swingle 1950, 1956; Nielsen & Johnson 1984; McComas 2003).

Pre-management standing stock and other fisheries characteristics were estimated for each oxbow by sub-sampling fish from approximately 0.56 ha of block netted lake. Fish were weighed, measured for total length and identified to species.

Each lake was re-stocked with largemouth bass (*Micropterus salmoides*), a mix of bluegill (*Lepomis macrochirus*) and redear sunfish (*Lepomis microlophus*), and channel catfish (*Ictalurus punctatus*) at rates of 50, 500 and 150 per acre, respectively. The bluegill-redear sunfish mix and channel catfish were introduced in the fall of 1996 followed by largemouth bass in the spring of 1997 (Swingle 1950, 1956; McComas 2003). Sampling was accomplished using a boat mounted Coffelt Model VVP-2C electroshocker (Company no longer in business) operating at 250 V. Sampling effort was limited to one hour of electrofishing time per lake providing adequate survey coverage while minimizing damage to recovering populations. Captured fish were placed in holding tanks until they could be weighed, measured, and released. Capture mortality was generally limited to smaller individuals.

Analytical and chemical methods were based on procedures from APHA (American Public Health Association 1992). Calculation of means and statistical analysis was completed using SAS statistical software (SAS Institute 1999). All parameters were tested for differences at the 5% level of significance.

Further details of sampling regimes and protocols, physical and chemical parameters measured, chemical analysis procedures and statistical testing

Table 1. Characteristics of the three Mississippi Delta Management Systems Evaluation Areas (MDMSEA) watersheds

	Location		
	Thighman	Beasley	Deep Hollow
County	Sunflower	Sunflower	Leflore
Watershed size (ha)	1500	915	202
Lake surface area (ha)	9	25	8
Primary soil types	loam to heavy clay	loam to heavy clay	loam
Management practices	none	edge of field	edge of field and within field

for the project varied with the different aspects of the project and are described elsewhere (Rebich & Knight 2001; Locke 2004; Nett *et al.* 2004; Rebich 2004).

RESULTS AND DISCUSSION

Pre-management conditions

Monthly mean values for temperature, conductivity, pH and dissolved oxygen are found in Figures 2–5. Temperature followed seasonal trends and was very similar for all three oxbow lakes. Given their close proximity, significant differences in temperature would not be expected. Thighman Lake had the highest conductivity followed by Deep Hollow. The instruments used to measure conductivity did not produce reliable results from September 1996 through December 1999 and was thus excluded from analysis. No discernible pattern or relationship was found in the pH data that varied for all three lakes between 9.0 and 6.0 during the course of the study. Dissolved oxygen varied for all the lakes prior to implementation of conservation measures. Thighman Lake exhibited the greatest range of dissolved oxygen concentration ranging from 0.0 and 16.0 mg/l. Wedemeyer *et al.* (1976) reported that concentration of less than 2 mg/l of dissolved oxygen is considered lethal to most warm water species of fishes. In North American freshwater fishes 5 mg/l of dissolved oxygen is the minimum concentration required for optimal fish health (Jones 1952). Richards *et al.* (2009) provide a summary of the effects of hypoxia on fishes.

Suspended and total solids data collected prior to implementation of conservation practices indicated that all three MDMSEA lakes were stressed and ecologically damaged due to excessive sediment. Adverse effects of sediment on phytoplankton negatively impacted fisheries as indicated by low primary and secondary productivity. Runoff samples from sites draining conventionally tilled fields had the highest concentrations of suspended-sediment throughout the study period. Suspended-sediment concentration in edge-of-field runoff was approximately three times higher than that measured in the lakes. Sediment accumulated in the three MDMSEA lakes at an average rate that ranged from 0.5 to 2.3 cm/year during the study period (Rebich & Knight 2001). Wedemeyer *et al.* (1976) also reported that concentrations of 80–100 mg/l are considered to be the maximum that most species of fish can tolerate on a continual basis without causing gill damage. Long term exposures to concentrations of 200–300 mg/l were linked to pathological changes is gill structure in addition bacterial tail and fin rot in salmonids (Herbert & Merkins 1961).

Average nitrate concentrations in the three lakes in 1996 were much lower than the drinking water standard of 10 mg/l. Average nitrate concentrations in the three MDMSEA lakes prior to application of management practices were 1.16, 0.53, and 0.39 mg/l for Thighman, Beasley, and Deep Hollow respectively. Less than 10% of the runoff samples from the untreated site had nitrate concentrations greater than 6 mg/l. Average ammonia concentrations in the three MDMSEA lakes prior conservation practice application were 0.168 mg/l for Thighman, 0.123 mg/l for Beasley, and 0.089 mg/l for Deep

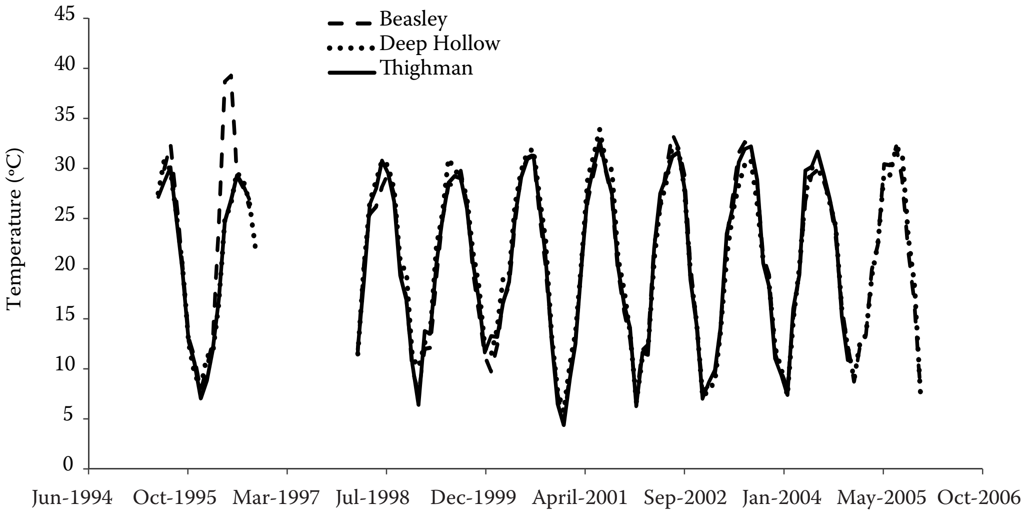

Figure 2. Monthly mean temperature for Management Systems Evaluation Areas (MSEA) lakes from 1995 to 2005

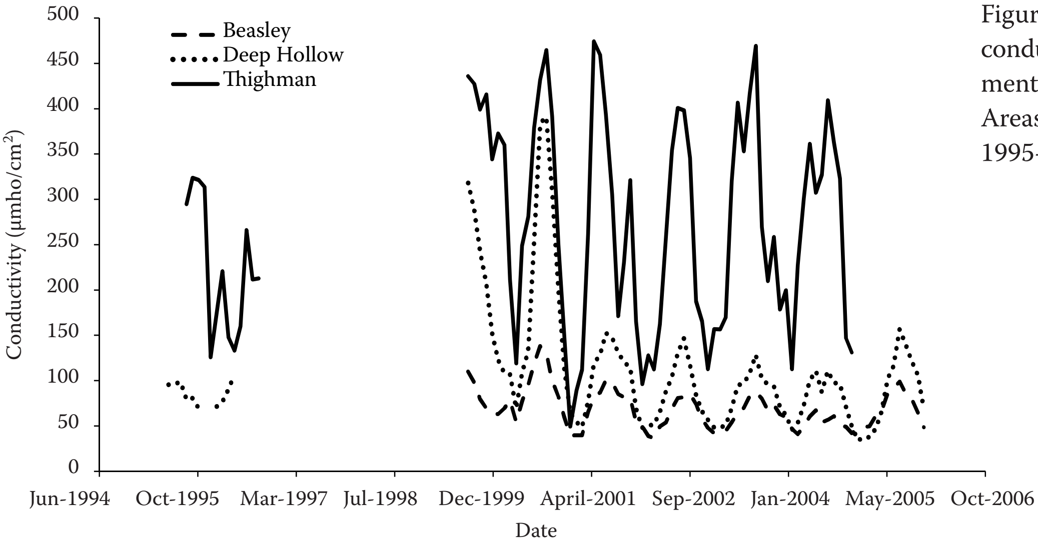

Figure 3. Monthly mean conductivity for Management Systems Evaluation Areas (MSEA) lakes from 1995–2005

Hollow which was much lower than EPA aquatic health criterion. The median ammonia concentration in runoff samples from the untreated site was comparable to that reported within the lakes.

EPA recommended total phosphorus levels during the time of the study were approximately 20 times lower than those observed in MDMSEA lakes (USEPA 1987) Pre-treatment average total phosphorus concentrations in the three MDMSEA lakes were 0.437 mg/l (Thighman), 0.496 mg/l (Beasley), and 0.522 mg/l (Deep Hollow). Additional applications of phosphorus are not typically necessary for crops in the Delta, thus naturally occurring phosphorus bound to sediment resulted in concentrations of total phosphorus above EPA criteria. MDMSEA research indicated that both nitrogen and phosphorus concentrations in lakes and runoff were higher than some recommended criteria. However, these concentrations caused no measurable detrimental effects to aquatic systems. Results suggested that oxbow lakes play an important role in processing nutrients.

Post management – runoff

Two runoff sampling sites were installed to determine the effects of a slotted-board riser and the combination of slotted-board risers and filter strips on runoff. Risors reduced suspended-sediment loads by 30%, however, slotted-board riser alone did not reduce nitrate in runoff since nitrate is water soluble and moves easily in solution. Runoff nitrate concentrations were reduced at sites with combinations of slotted-board risers and filter strips as well as riparian sites. Neither slotted-board risers nor the combination of slotted board risers and filter strips played a significant role in reducing phosphorus concentrations in measured runoff. Riparian areas however were

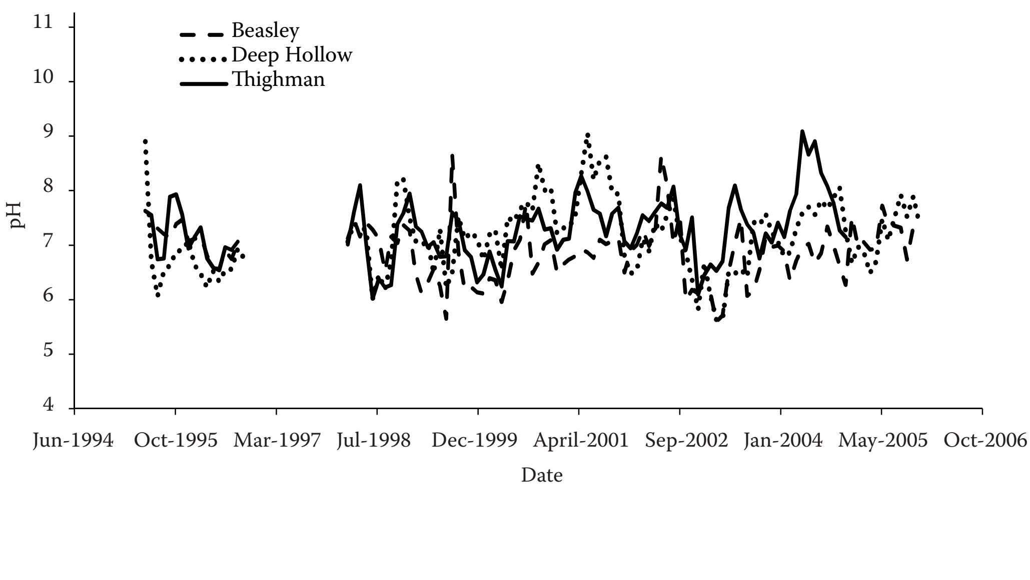

Figure 4. Monthly average pH for Management Systems Evaluation Areas (MSEA) lakes from 1995 to 2005

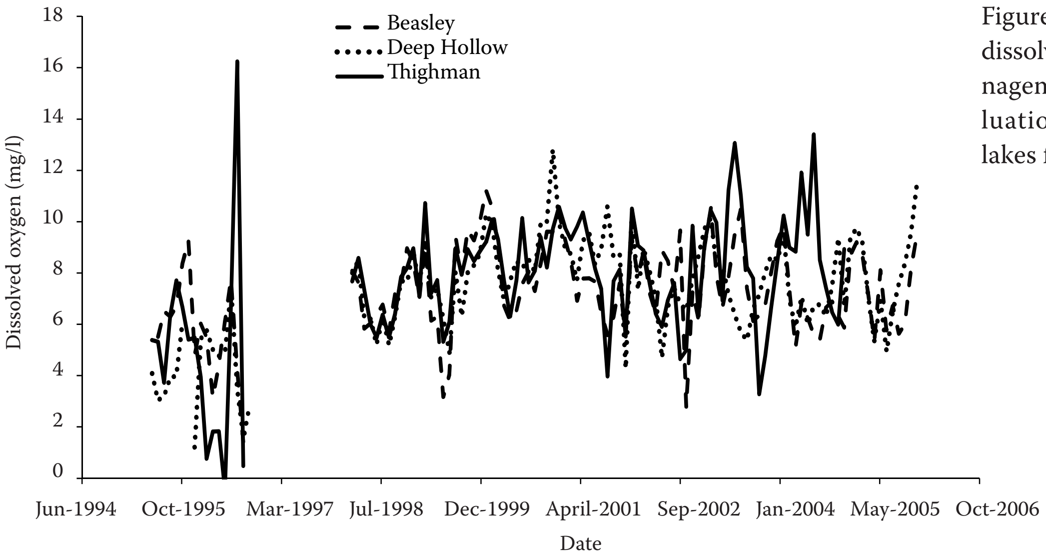

Figure 5. Monthly mean dissolved oxygen for Management Systems Evaluation Areas (MSEA) lakes from 1995–2005

useful in mitigating the transport of sediment in runoff and should be considered part of any plan for reduction of non-point source pollutants. Suspended-sediment concentrations were 84% lower at the exit of the Beasley riparian area compared to the untreated edge-of-field runoff site. Additionally, riparian runoff sites averaged 39% less total phosphorus than the untreated edge-of-field runoff site (Rebich 2004).

In Deep Hollow Watershed conservation tillage with winter cover and conservation tillage with winter cover and a slotted-board riser reduced suspended-sediment concentrations in runoff by 48 and 62%, respectively. Nitrate was shown to be lower in soils of conservation tillage areas than in soils from a nearby conventional tillage area in the Deep Hollow watershed, which may be attributed to binding of nitrogen in organic residues in surface soils of conservation tillage fields. Conservation tillage with winter cover was also effective in reducing both nitrates and total phosphorus in runoff samples (Rebich 2004).

Post management – lake water quality

Cultural and structural management practices reduced total and suspended sediments in all three lakes. The greatest percent reduction in suspended sediment was initially at Deep Hollow Lake (approximately 80%), which featured both cultural and structural practices for erosion control (Figure 6). However, when agronomic practices were applied to Beasley Lake Watershed suspended sediment was reduced by 86%. Reduction in suspended sediment improved water clarity by 22% in Deep Hollow, 57% in Beasley and 28% in Thighman Lake. While Thighman had the lowest average Secchi visibility,

Figure 6. Annual average suspended sediments for Management Systems Evaluation Areas (MSEA) lakes from 1995–2005

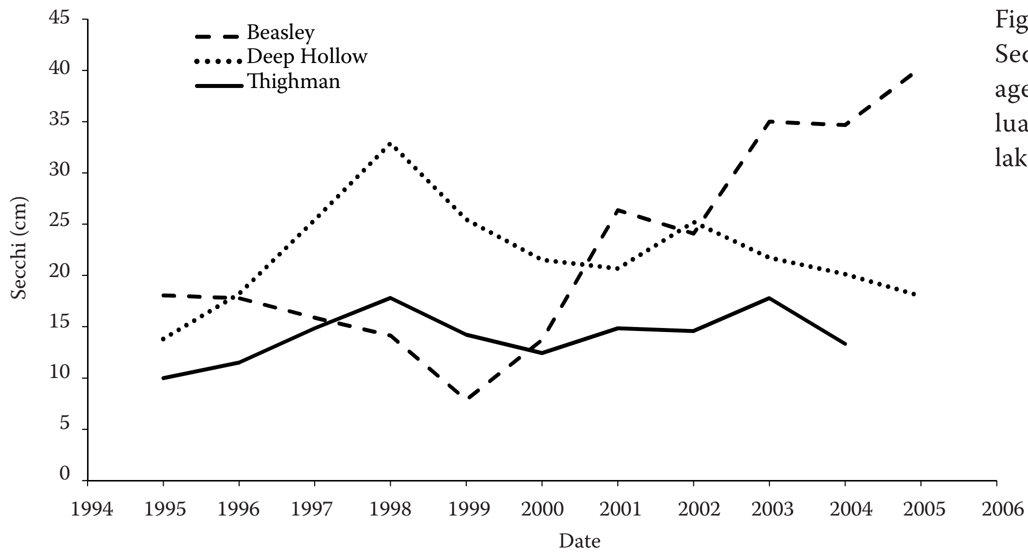

Figure 7. Annual mean Secchi depth for Management Systems Evaluation Areas (MSEA) lakes from 1995–2005

it also had the highest increase in chlorophyll *a* (Figures 7 and 8). While high pre-management suspended sediment levels suppressed chlorophyll concentrations in the MDMSEA lakes, reductions in sediment loadings due to management practices contributed to corresponding increases in chlorophyll and improved productivity. Only slight differences in nitrate and ammonia were observed in the lakes after conservation practices were in place for three years. Nevertheless, nitrate concentrations were 2 to 27% lower in 1999 than those recorded in 1996 prior to BMP installation.

Total phosphorus in the MDMSEA lakes decreased, as a result of conservation efforts, by approximately 60% from 1997–2005. Filterable orthophosphate increased on all MDMSEA lakes during the study period; however, the actual concentrations were less than EPA recommendations for surface waters. Nitrate concentrations in shallow ground water in the three MDMSEA watersheds were low. High rates of denitrification were one possible cause for low levels of nitrate in MDMSEA soils and, ultimately, in shallow groundwater.

Within field and edge of field management practices specifically designed to reduce water velocity and trap sediments reduced total and suspended sediments on all three MDMSEA lakes. This reduction in suspended sediment improved Secchi visibility in all three MDMSEA lakes. Prior to conservation practice establishment, Secchi visibility was exceptionally low averaging less than 12.5 cm for all three lakes. As a result of sediment reductions due to management practices, mean Secchi visibility increased to 19 cm; a 34% increase in wa-

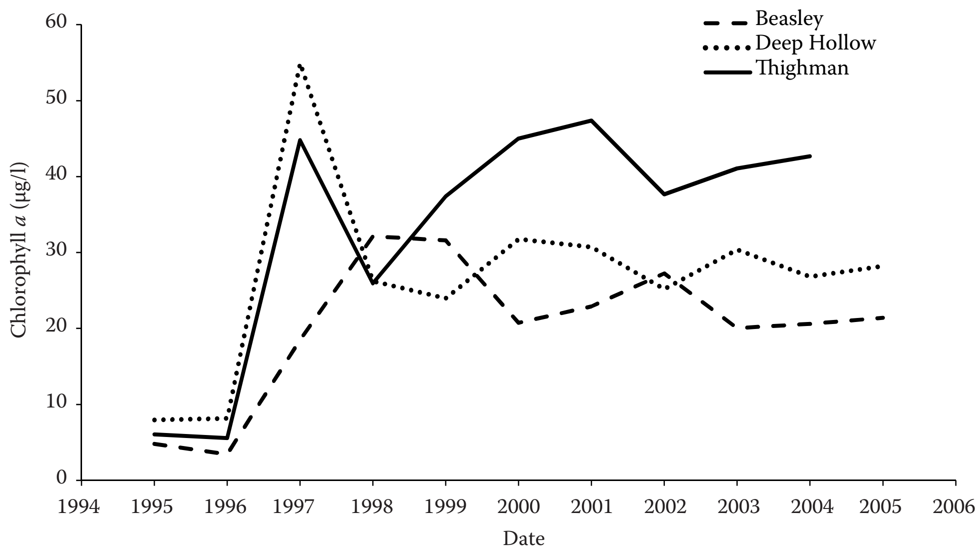

Figure 8. Annual mean Chlorophyll *a* for Management Systems Evaluation Areas (MSEA) lakes from 1995–2005

Table 2. Slope, intercept and R squares for the relationships between mean annual total sediments (TS), total phosphorus and chlorophyll *a* for the Mississippi Delta Management Systems Evaluation Areas (MDMSEA) oxbow lakes

		Slope	Y-intercept	R^2
Beasley	all data	–0.146	0.981	0.006
	< 150 TS	0.054	1.142	0.001
	> 150 TS	–0.244	0.921	0.011
Deep Hollow	all data	–0.066	1.141	0.011
	< 150 TS	0.106	1.277	0.003
	> 150 TS	–0.238	1.033	0.015
Thighman	all data	–0516	0.993	0.001
	< 150 TS	0.915	1.504	0.344
	> 150 TS	–0.558	0.976	0.074

ter visibility (Figure 7). Cooper and Bacon (1980) reported that at 100 mg/l of suspended sediments, chlorophyll concentration was reduced to less than 20 mg/l. Cooper *et al.* (1995) demonstrated that when suspended sediments were reduced through diversion of sediment laden runoff chlorophyll concentration doubled. Reductions in sediments due to management practices contributed to corresponding increases in chlorophyll on all MDMSEA oxbows, ranging from 61 to 629%, (Figure 8).

Regression analysis of total phosphorus, total sediment and chlorophyll *a* concentrations indicated weak relationships between all three water quality parameters (Table 2). Total phosphorus and total sediment concentrations were positively correlated, while total phosphorus and chlorophyll *a* were either not correlated or weakly negatively correlated in all lakes.

While this relationship seems counterintuitive, further analysis indicates that when suspended solids are less than 150 mg/l there is a weak positive relationship between chlorophyll *a* and total phosphorus. When suspended solids exceed 150 mg/l there is a weak negative relationship between chlorophyll *a* and total phosphorus. It is likely that this negative correlation between phosphorus and chlorophyll *a* is due to both light limitation by sediment and the phosphorus ad-

Table 3. Fisheries characteristics of Management Systems Evaluation Areas (MSEA) lakes prior to implementation of best management practices based on rotenone sampling (Knight & Welch 2004) and electrofishing

		Thighman	Deep Hollow	Beasley
Rotenone sampling				
Catch (kg)		157	163	85
Number		2139	1473	886
No. of species		17	21	15
kg/ha		282	292	152
Electrofishing				
1998	Catch (kg)	35.6	21.4	14.3
	Number	166	178	145
	No. of species	13	15	14
	kg/h	14.26	10.73	4.7
2004	Catch (kg)	43.8	37.7	31.3
	Number	198	227	127
	No. of species	16	17	10
	kg/h	43.89	37.74	31.35

sorbed to clay particles comprising the suspended sediments. While suspended sediments suppress light and thus phytoplankton production, they are also high in phosphorus (McDowell *et al.* 1988). When sediment is reduced and light is no longer limited the relationship between phosphorus and chlorophyll becomes positive.

A comparison of total phosphorus versus chlorophyll a relationships for several lakes in the southeastern United States is found in Figure 9. As can be seen from this figure, the MDMSEA lake phosphorus-chlorophyll *a* relationships are unique in that the slopes are negative for the total data set when sediment concentration exceeds 150 mg/l additionally the relationships for all three lakes have a much higher y-intercept compared to other lakes.

Based on this research, the relationships between sediment, nutrients and chlorophyll *a* must be considered before effective water quality criteria can be established. Mitigation strategies that simply remove sediment may in turn trigger oxygen depletion due to excessive eutrophication in fertile oxbow lakes. Multidimensional management practices designed to remove sediment and nutrients may be necessary to meet water quality goals. Additionally future research that more accurately defines the point at which turbidity no longer limits productivity will be necessary before effective nutrient standards can be established.

Fisheries

Fishery characteristics prior to implementation of conservation measures may be found in Table 3. Fish species collected in the rotenone sampling were characteristic of oxbow lake fauna. Gizzard shad (*Dorosoma cepedianum*), white crappie (*Pomoxis annularis*) and bluegill (*Lepomis macrochirus*) were the most abundant species in Thighman Lake while white crappie, mosquito fish (*Gambusia affinis*) and gizzard shad where dominant in the catch from Deep Hollow. White crappie, gizzard shad and madtom catfish (*Noturus gyrinus*) were the most abundant species in Beasley Lake. Gar (*Lepisosteus* sp.), common carp (*Cyprinus carpio*), white crappie and paddlefish (*Polyodon spathula*) significantly contributed to the catch (weight) in all MSEA lakes.

Characteristics of the fisheries following implementation of management practices may be found in Table 3. Catch per unit of effort (CPUE), measured

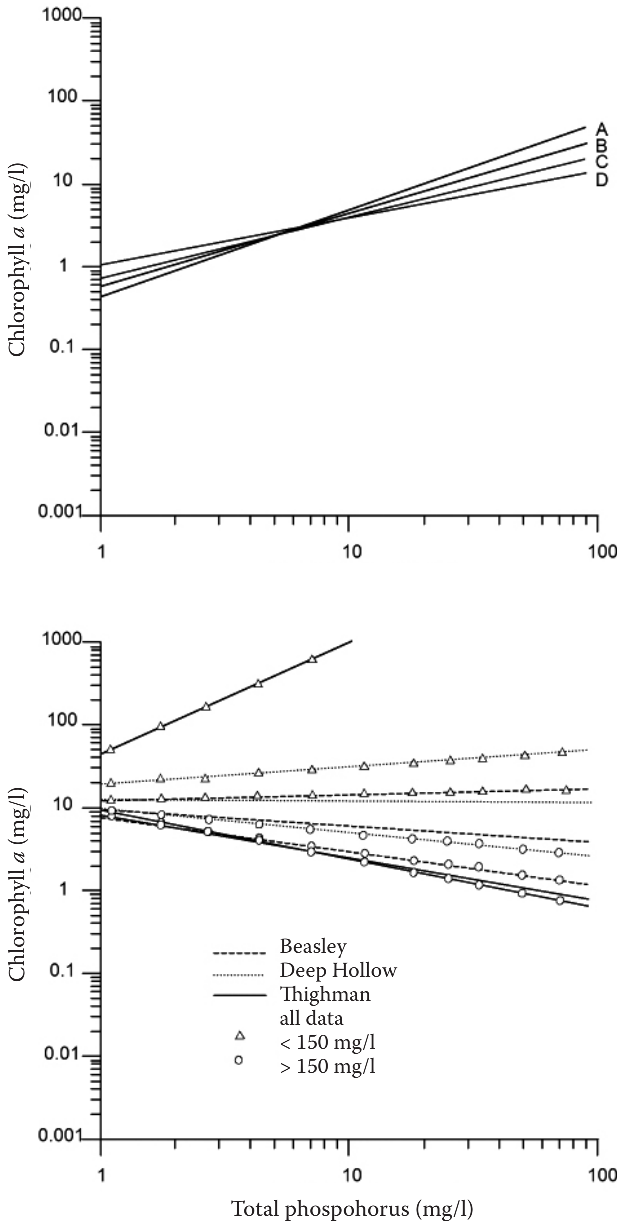

Figure 9. Plots of annual mean total phosphorus versus annual mean chlorophyll *a* for several lakes in the southeastern United States as well as Mississippi Delta Management Systems Evaluation Area (MDMSEA) lakes (lines without symbols represent MSEA data regardless of suspended sediment concentration, triangles represent MSEA data where suspended sediment is < 150 mg/l, circles represent data where suspended sediment is > 150 mg/l); lines on the left are from: A – Brown *et al.* 2000, B – Canfield 1983, C – Ground & Groeger 1994, D – Jones & Knowlton 1993

as kg/h, increased on all lakes between 1998–2004. Beasley Lake had the exhibited the lowest CPUE in 1998 indicating a slower restoration. Cyprinids composed primarily of common carp, *Cyprinus carpio*, were a major component of all catches by weight regardless of gear type or sampling period. Catch by weight of centrarchids from electrofishing increased in all three MSEA lakes from 1998 through 2004.

The greatest percent composition change in centrarchid catch occurred in Beasley Lake where centrarchids were 19% of the catch by weight in 1998 but 54% by 2004. Clupeids which dominated the catch by weight in Thighman Lake in 1998 were also the most abundant by weight in 2004. By 2004, centrarchids, composed of *Lepomis* sp., *Pomoxis* sp. and *Micropterus salmoides* dominated the percent composition by weight in both Deep Hollow and Beasley comprising more than 50% of the catch.

Micropterus salmoides (a popular game species) which were practically nonexistent prior to renovation comprised 5, 27 and 45% of the catch by weight in Thighman, Deep Hollow and Beasley respectively following lake restoration.

In Thighman where catches of largemouth bass were comparatively low, other game fishes such as crappie and channel catfish dominate the catch comprising 22% of the catch by both weight and number.

Based on the above results successful fisheries restoration depends upon improving primary productivity. Primary productivity as measured by concentrations of chlorophyll *a* is dependent upon the availability of both phosphorus and sunlight which has been linked to reductions in sediments. Sediment reduction was most effectively achieved by using a combination of structural and agronomic practices in a systematic watershed wide approach. Therefore, any attempt to restore a sustainable fishery in sediment damaged systems should begin with a watershed wide plan for reducing sediment in agricultural runoff.

CONCLUSION

The MDMSEA project was designed to utilize field-scale working farms to evaluate primary pollutants in Delta water resources and to identify conservation practices that are most effective in reducing the transport of those pollutants in surface and ground water. Three Mississippi Delta oxbow lakes and the surrounding agricultural watersheds were selected for study.

Conservation practices reduced sediment in oxbow lakes, resulting in improved water clarity, plankton growth, and fish stocks. Additionally, total phosphorus in lakes decreased between 39 to 50% following conservation measure implementation. Conservation tillage and cover crops were two of the more effective agronomic practices tested resulting in reduced NO_3-N losses by 73%, and sediment losses by 70%.

This research demonstrates that conservation practices applied in agricultural watersheds can have a positive impact on downstream water quality and ecology.

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