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Published in *Transactions of the American Fisheries Society*, Vol. 137, Issue 1 (January 2008) at doi: 10.1577/T06-188.1

Recommended Citation

Csoboth, Laura A. and Garvey, James E. "Lateral Exchange of Larval Fish between a Restored Backwater and a Large River in the East-Central USA." (Jan 2008).

Transactions of the American Fisheries Society 137:33–44, 2008
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DOI: 10.1577/T06-188.1

[Article]

Lateral Exchange of Larval Fish between a Restored Backwater and a Large River in the East-Central USA

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Abstract.—Exchange of larval fish between a river's main channel and its floodplain backwaters is compromised by sedimentation. Restoration projects to reduce sediment loading are being implemented in large rivers of the midwestern United States to curb backwater habitat loss and restore backwater-to-river connectivity. During 2004 and 2005, drift nets were set bidirectionally (with and against the flow) within a constructed channel between the Illinois River and an adjacent, 1,100-ha restored backwater, Swan Lake, to investigate the interplay between life history strategies and lateral drift on a diel and seasonal basis. Ambient larval density and species composition within the river and backwater also were quantified. Drift was positively correlated with water velocity in the main stem during 2004, and an estimated 32.3×10^6 larvae drifted at the surface of the channel into Swan Lake. In the absence of a flood in 2005, the density and composition of the larval fish assemblage in Swan Lake and the Illinois River appeared to drive larval drift timing, magnitude, and composition. Swan Lake's restoration has maintained some river connectivity and lateral drift functionality for resident fish, but its functionality compared with natural, connected river–backwater systems remains unknown.

The propensity of small aquatic organisms to drift in streams and rivers represents an evolutionary response (Eckblad et al. 1984; Kennedy and Vinyard 1997). In fish, drift is usually restricted to early life stages, such as seasonal larval fish drift in lotic systems, and largely influences spatiotemporal patterns in larval density (Holland 1986). Drift in riverine larval fish is typically downstream, but also can transport larvae laterally into slack-water habitat, where these fish may be exchanged between river and off-channel habitats (Humphries et al. 1999). This exchange has been hypothesized because of ichthyoplankton (hereafter termed larvae) density differences among slack-water and main-river habitats (Sheaffer and Nickum 1986; Brown and Coon 1994; King 2004) and because of downstream larval drift from tributaries to main-channel areas (Eckblad et al. 1984; Muth and Schmulbach 1984). However, the extent of lateral larval drift into and out of backwaters relative to downstream drift in rivers is currently undocumented and may be valuable in determining origins and destinations of larval fish.

We define lateral drift as the movement of organisms between a river's main channel and its adjacent floodplain waters. When connected to the river, these backwaters provide a lentic–lotic gradient whereby fish and other aquatic organisms find spawning grounds, structural refuge, food resources, and overwinter habitat (Junk et al. 1989). Slack-water areas have been recognized as a critical component in the early life history of fish (Holland 1986), but the biological interplay these habitats have with the main channel is largely unknown. These areas may be a productive source of age-0 fish, as evidenced by the higher larval densities downstream of backwater outflow (Sheaffer and Nickum 1986) and large migrations of juveniles to the main channel from backwaters (Molls 1999). However, the contribution of river larvae to backwaters may also be significant and a vital process bringing riverine-spawned larvae to productive nurseries (de Graaf et al. 1999). Larval exchange is probably complex, given the nature of these backwater–river confluences, the periodicity of inflow to the backwater and outflow to the river, and the stagnation of waters following high water outflow (Brown and Coon 1994). These flow patterns at the confluence are apt to drive the ability of backwaters to function as nursery habitat for larval and juvenile fish (Brown and Coon 1994).

Most investigators have focused on the patterns of downstream drift but not how timing and behavior shape trends in lateral exchange. Fish spawning

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Received August 10, 2006; accepted August 16, 2007

behavior dictates temporal patterns in larval drift, where drift duration increases with the duration of spawning (Reichard et al. 2001); rising water temperatures and spring floods that cue spawning often result in peak larval drift densities (Carter et al. 1986; de Graaf et al. 1999; Auer and Baker 2002). Depending on the species, larval metamorphosis into exogenously feeding fish can either initiate or cease drift behavior (Carter et al. 1986; Dudley and Platania 2000) or have no influence on the species' presence or absence in the drift (Auer and Baker 2002). Downstream drift into nursery habitats with amenable growing conditions scatters the cohort, may reduce competition for food and space, and should serve predator avoidance (Bardonnet 2001). The interplay of abiotic and biotic factors determines the drift timing and duration and the drift taxa, but their influence on lateral exchange is unknown.

Fish larvae have diurnal, nocturnal, or crepuscular drift patterns that depend on species developmental stage (Gale and Mohr 1978; Muth and Schmulbach 1984; Gadomski and Barfoot 1998). These photokinetic responses may change in some species as larvae age (Bulkowski and Meade 1983), possibly a result of ontogenetic diet changes or predation susceptibility. However, diel patterns in drift can be contradictory; that is, fish species of the same life stage have exhibited significant nocturnal drift in some water bodies and diurnal drift in others (Muth and Schmulbach 1984; Smith and Brown 2002).

Management decisions aimed at improving nursery and spawning habitats and the survival of early life stages may fall short because of gaps in our understanding of lateral larval drift timing and behavior. All riverine fish exhibit certain life history strategies based on their relative dependence on flowing water. Some are specialized for riverine environments and are adapted for downstream drift; others require flowing water for a portion of their life history and involve habitat changes that probably entail lateral movement. Generalists, however, occupy mostly lentic areas and should be less prone to entering the drift. We investigated the interplay of life history strategies with lateral drift dynamics on a diel and seasonal basis within a restored backwater lake. This enabled us to investigate the role of backwaters as larval fish nurseries in large rivers and to address the influence of habitat alterations on larval fish assemblages among backwater lakes and river reaches. Specifically, we wanted to (1) quantify bidirectional drift between the restored backwater and its adjacent river both among seasons and within days and (2) relate drift patterns to abiotic conditions (e.g., temperature, water flow) and ambient larval densities in the backwater and river.

Methods

Study area.—Swan Lake is a 1,100-ha backwater of the Illinois River located between river kilometers (rkm) 8 and 21 that is vitally important for fish of the Illinois and Mississippi rivers (USACE 1991). It is the largest connected backwater lake for more than 100 rkm on the Illinois River and within 30 rkm upstream or downstream of its confluence with the Mississippi River. Because Swan Lake was rapidly losing connectivity due to sedimentation, a Habitat Rehabilitation and Enhancement Project through the federal Environmental Management Program was initiated to improve connectivity and increase habitat heterogeneity (USACE 1991). The downstream portion of the backwater, lower Swan Lake (LS; 567 ha), was managed to be continuously connected to the Illinois River through a water control structure. Historically, Swan Lake was connected to the Illinois River through a 0.5-km-wide opening at LS, and, during flood events, had multiple lateral connections with the river. Restoration of the backwater complex restricted the river connection to the width of a stop-log water control structure, about 5-m wide, which was nested within a rip-rap lined channel about 50 m long and 12 m wide. The backwater's natural levee with the river was heightened to stabilize water levels for wetland plant growth and to give managers more control over water-level fluctuations. During normal pool stage, the stop-log structure at LS is the only avenue through which larval fish movement between the backwater and river occurs, making the stop-log structure the focal point of our study site.

Fish sampling.—To quantify the bidirectional larval drift between LS and the Illinois River, three conical drift nets (0.5-diameter, 2 m long, 500-μm mesh) were attached to a floating, anchored polyvinyl chloride frame and fished from late March to July 2004 and from March to August 2005 (Figure 1). We sampled larvae for 15 min at the surface (approximately the upper third of the channel depth) every 2 weeks on the lake side of the stop-log structure. During each sampling event, nets were set either facing the lake or the channel and then the direction was changed. Two directional net sets, one sampling larvae potentially moving into LS (channel-facing) and one set sampling larvae leaving LS, were conducted at dawn, midday, dusk, and midnight within 36 h. During flooding, sampling frequency was increased to weekly, but fewer night sets were taken.

At each sampling time (dawn, midday, dusk, and midnight), we quantified surface water temperature and

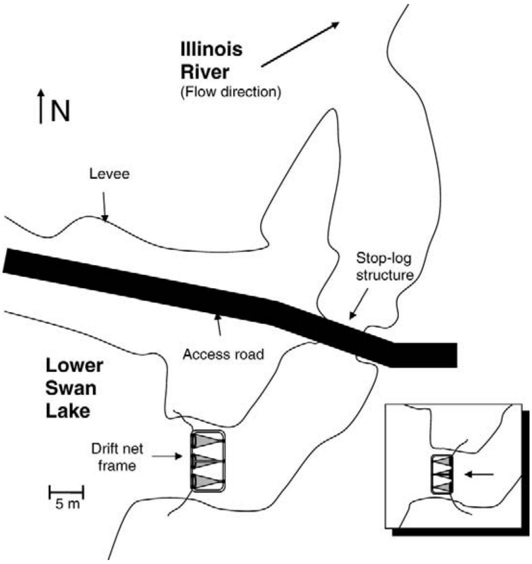

FIGURE 1.—Fixed drift net site at the confluence of the Illinois River and a restored backwater, lower Swan Lake (LS). Three tandem nets suspended on a floating polyvinyl chloride frame were fished during 2004 and 2005 on the LS side of the stop-log structure. The main portion of the schematic depicts the nets positioned to sample ichthyoplankton drifting out of LS, the inset nets positioned to sample ichthyoplankton drifting into LS.

dissolved oxygen (YSI Model 52 dissolved oxygen meter; Yellow Springs Instruments, Yellow Springs, Ohio), Secchi depth, surface water velocity (Flo-Mate Model 2000; Marsh McBirney, Frederick, Maryland), and average wind speed and direction (Kestrel 1000; NFS–Radiation Protection Systems, Groton, Connecticut) at the water control structure. A Doppler bidirectional velocity meter (Model 6526–51 Starflow; Unidata America, Lake Oswega, Oregon) anchored to the bottom of the water control structure recorded temperature, depth, and mean water velocity twice an hour. River stage data from Hardin, Illinois, were obtained from the U.S. Army Corps of Engineers. No Swan Lake depth data were collected from September to November 2004, and no water velocity data were collected from October 2004 to April 2005.

Upon completion of each drift net set, the contents were flushed into the net's cod end and preserved in 95% ethanol. Each sample was split to approximately 200 fish using a Folsom plankton splitter (Aquatic Research Instruments, Hope, Idaho). All age-0 fish were counted, identified to the lowest possible taxon (typically genus), and classified to a developmental stage (i.e., yolk sac, larval, or juvenile) using descriptions and keys (Soin and Sukhanova 1972; Auer 1982; Murty et al. 1986; and Tweb et al. 1990) and voucher specimens from Southern Illinois University (i.e., Fluid Vertebrate Collection; B. Burr, Carbondale, Illinois) and Colorado State University (Larval Fish Laboratory; D. Snyder, Fort Collins, Colorado). For each net, a subsample of 10 fish from each taxon and life stage were measured (total length [TL]; mm) using Scion Image software (calibrated to 0.5 mm) or metric calipers.

Larval densities also were quantified in LS and the Illinois River to characterize the taxa and abundance within each site and compare larval densities to drift. We used paired, bow-mounted ichthyoplankton nets (0.5 m diameter, 2 m long, 500-μm mesh) to sample these habitats on the same dates as drift nets were set. Four randomly chosen transects within LS and two randomly chosen transects in the river at rkm 8.0 were sampled weekly. We stratified backwater transects into two inshore and two offshore tows, and river tows were conducted within 1 km upstream and 1 km downstream of the LS–Illinois River confluence.

At each transect, nets were towed at the surface for 5 min at a constant speed; a calibrated mechanical flowmeter (Model 2030R; General Oceanics, Miami, Florida) mounted in the mouth of one net was used to standardize sampling effort (i.e., volume sampled). Inshore backwater tows followed the shoreline, offshore backwater tows were straight transects, and river tows were straight transects conducted perpendicular to flow direction. River tows started at the main-channel border, continuing across to the opposite main-channel border. If 5 min had not passed, the direction was reversed with nets still in the water, and sampling continued until 5 min was reached. Tow samples were preserved, processed, and identified the same as drift net samples.

Habitat-use classes.—Fish collected were grouped by family into one of three generalized classes to better explain the trends observed between years and treatment groups (Galat and Zweimuller 2001): fluvial specialists, fluvial-dependent fish, and macrohabitat generalists. Fluvial specialists are fish that inhabit streams and rivers throughout their entire life and rarely enter floodplain habitats (Galat and Zweimuller 2001). Fluvial-dependent species regularly use lentic backwater or reservoir habitats, but certain life history traits depend on lotic environments (Galat and Zweimuller 2001). These species are typically broadcast spawners, where developing eggs and larvae are semibuoyant and passively drift in wind-induced or downstream currents (Holland 1986). Adult fluvial-dependent fish also may make lateral migrations into slow-flowing lentic areas to spawn—activities probably corresponding with increasing temperatures and rising water levels (Junk

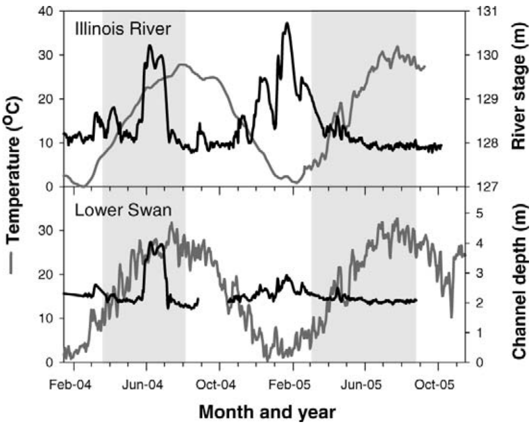

FIGURE 2.—Mean daily temperature (light lines) and depth data (dark lines) for the Illinois River at Hardin, Illinois, and the Lower Swan backwater in 2004 and 2005. Shaded regions represent fish larvae sampling periods.

et al. 1989). Macrohabitat generalists include species commonly found in reservoirs and off-channel habitats that do not depend on lotic systems (Galat and Zweimuller 2001). When these fish use the river, it is typically as a corridor to move among backwaters (Junk et al. 1989; Dettmers et al. 2001). Spawning usually occurs in off-channel habitats and offspring generally do not leave this habitat until the juvenile stage (Holland 1986). We grouped families based on Galat and Zweimuller (2001; taxonomy from Nelson 1994), the only deviation being Sciaenidae, which we classified as fluvial dependent based on life history descriptions (Dettmers et al. 2001) and strong positive correlations between young-of-year catch and flood pulses (Koel and Sparks 2002).

Data analysis.—We investigated directional (i.e., into or out of the backwater), diel, seasonal, and between-year patterns in drift data as well as correlations with abiotic factors and ambient larval densities within each habitat. Larval drift reflected larval exchange between the backwater and river and was standardized as a rate (fish/min). Some fish were caught in nets set opposite to the direction of flowing water when velocities were 0.1 m/s or greater (e.g., frame positioned to catch fish drifting out of LS while water flowed into LS at 0.11 m/s; Figure 1). Because these fish had to actively swim into the net mouth to become entrained, they were not considered to be drifting (Scheidegger and Bain 1995) and were excluded from the analyses. Total larval production from tow data (fish/m^3) were calculated as the sum of weekly densities during each sampling season. Similarly, we summed the rates of larvae drifting both into and out of the channel each year to determine gross movement through time. All data were log-transformed ($\log_{10}[x + 1]$) to meet assumptions of normality.

Two-way repeated-measures analysis of variance (ANOVA, proc MIXED; SAS Institute 1999) tested for differences among treatments over time (Hurlbert 1984): (1) biweekly drift catch rates into and out of the backwater, (2) biweekly drift catch rates at dawn, day, dusk, and night, and (3) weekly mean densities of tow data between sites.

We also determined overall trends within and between years for larval densities. Nonzero drift catch rates were regressed (multiple regression, proc REG; SAS Institute 1999) for each direction and year against environmental data collected from the Doppler device and corresponding to the time and date of drift (e.g., depth, temperature, and velocity); for significant relationships, environmental data were used to estimate the total amount of larval drift for each season. A one-way ANOVA tested how larval density and catch rates differed between years. To control for experimentwise error rates, we used Tukey–Kramer analysis (Sokal and Rohlf 1995). Relationships between larval production and lateral drift were determined using linear regression on untransformed data.

The size of fish may have differed between tow sites, drift direction, or year or among diel time points. The proportions of fish per 1-mm total-length group were used to compare treatments. Kolmogorov–Smirnov cumulative distribution tests compared (1) the size distributions of fish drifting into versus out of LS each year, (2) the total size structures of fish drifting during 2004 and 2005, (3) the size structures of fish collected from tows, and (4) between-year differences for LS and Illinois River tow data. Multiple pairwise comparisons determined size structure differences among the times of day sampled (dawn versus night, dawn versus day, dawn versus dusk, etc.; Bonferroni adjusted α-values were $0.05/6 = 0.008$).

Results

Abiotic Patterns

Larval production and lateral exchange were related to the different flood regimes in the lower Illinois River in 2004 and 2005. A moderate flood pulse occurred in 2004, water levels in the lower Illinois River rising above flood stage for approximately 5 weeks during June (Figure 2). During the 2005 sampling season, water levels remained at or below normal pool level (128 m). Water temperatures in the river gradually rose and fell during 2004, peaking in late July at 28°C, but varied more during 2005, rising to over 30°C twice that season. Lower Swan Lake mimicked the river, although water temperatures were higher and more variable due to shallower water levels (Figure 2).

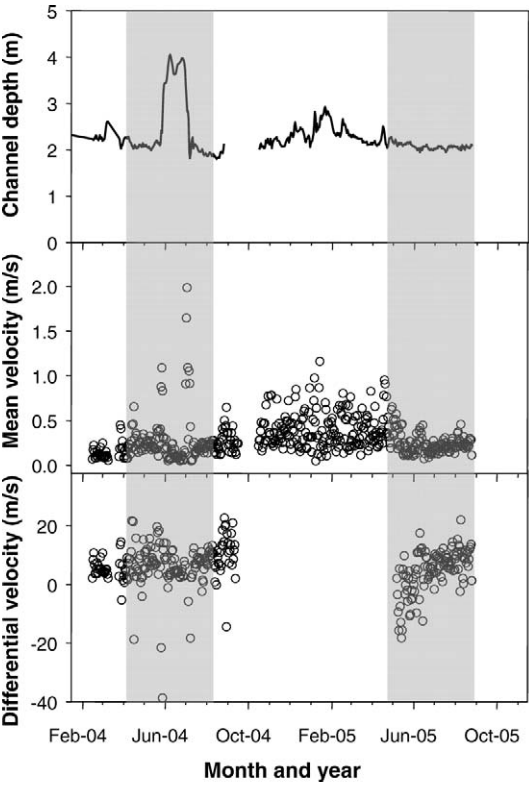

FIGURE 3.—Mean daily depth, mean velocity, and differential velocity in the channel between Swan Lake and the Illinois River. Velocities are averaged across 48 daily observations without respect to direction. Differential velocity was calculated as the sum of the 48 channel velocities; positive values represent net inflows of water into Swan Lake, negative values net outflows to the river. Continuous data were recorded using a submerged device anchored at the stop-log structure. No depth or velocity data were collected from September through November 2004, and no directional velocity data were collected from October 2004 through April 2005. Shaded regions represent the sampling periods.

The water depth and bidirectional velocity in the narrow channel separating LS from the Illinois River varied markedly between years. Aside from the 2004 flood pulse, which increased the channel depth to 3.98 m, channel depth remained above 2 m for most of 2004 and averaged 2.04 m after May 2005 (Figure 3). Movement of water through the LS water control structure frequently changed direction during the day, and velocities varied greatly. This movement was probably influenced by many factors, including river stage, river velocity, wind, and barge traffic. On average, water was moving into LS, 86% of the differential velocity values being positive (i.e., into the lake; Figure 3). Mean channel velocities were typically (97% of the data points) less than 1 m/s during the two sampling seasons. In 2004, velocities flowing into LS peaked at 2.2 m/s during the rise in floodwaters, dropped to near zero at flood crest, and flowed out at peak recession velocities of 1.5 m/s. Near-zero velocities occurred during low-water periods, particularly those occurring during summer 2005, differential velocity values being tightly positioned around zero.

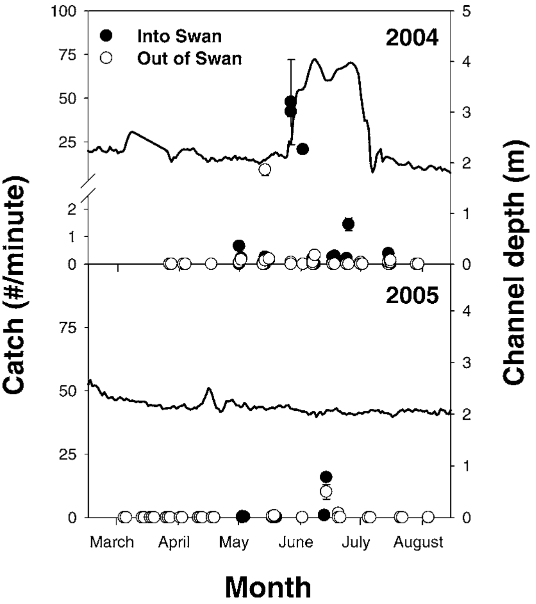

FIGURE 4.—Drift of ichthyoplankton (mean catch per net set) into and out of lower Swan Lake in 2004 and 2005 and continuous depth data recorded at the backwater's stop-log structure (solid lines). Error bars represent the SEs for the mean of each net set.

Seasonal Patterns

Fish larvae were taken in the drift nets from 1 May through mid-July 2004 and, in a more protracted period, from 26 March through late-August 2005 (Figure 4). Total production of larvae, garnered from summing tow data, began in the Illinois River during mid-April each year, whereas production in LS began during late March 2004 and occurred 3 weeks later in 2005 (Figure 5). A major pulse of fish drifted into LS during late May 2004 as floodwaters rose (Figure 4); a synchronous pulse of larvae occurred in tows in June 2004 during floodwater inundation (Figure 5). During 2005, a smaller, discrete peak of larvae drifted between LS and the river that was 3 weeks later and less than half the magnitude (Figure 4). In 2005, larvae peaked 2 weeks later in the river than in LS (Figure 5).

The mean rates (larvae/min) of fish drifting into LS during 2004 varied in a complex way through time;

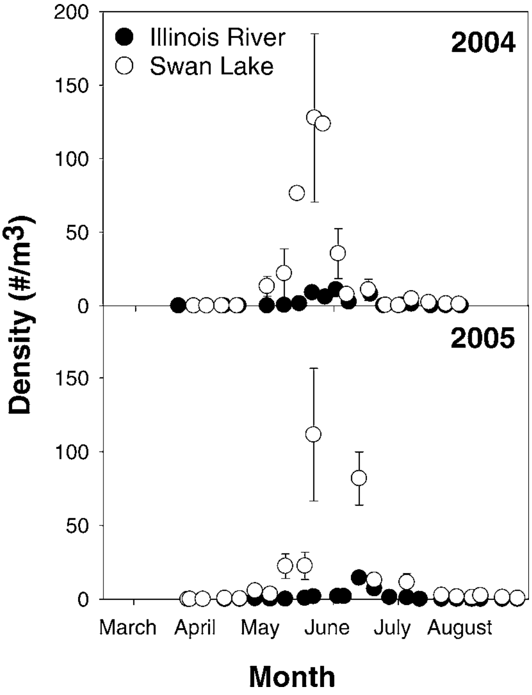

FIGURE 5.—Mean density of larval fish caught per day in the Illinois River and lower Swan Lake during 2004 and 2005. Error bars represent the SEs of mean transect density.

TABLE 1.—Drift net catches of fish during 2004 and 2005 in lower Swan Lake. Catches per set are averaged by time period.

Year	Time of day (hours)[a]	Net sets	Number	Catch number/min (mean ± SE)
2004	Dawn (0450–0711)	24	1,956	1.80 ± 1.76
	Day (1215–1500)	24	2,551	2.38 ± 2.00
	Dusk (1815–2050)	22	1,137	0.96 ± 0.94
	Night (0000–0110)	20	112	0.12 ± 0.08
2005	Dawn (0450–0640)	24	490	0.45 ± 0.42
	Day (1145–1435)	23	77	0.07 ± 0.05
	Dusk (1815–2110)	26	70	0.06 ± 0.04
	Night (2340–0110)	20	869	0.93 ± 0.79

[a] Night net sets were not conducted during rising flood waters during 2004, which reduced the net set count and probably mean night catch rates.

differences over time and an interaction between drift direction and time occurred (Figure 4; direction: $F_{1,11}$ = 18.53; week: $F_{1,11}$ = 7.67; direction × week: $F_{1,11}$ = 8.2; all $P < 0.01$). Ingress and egress of ichthyoplankton were similar in 2005 (Figure 4; $F_{1,11}$ = 3.8, P = 0.10). The peak rate of larval movement was higher in 2004 (47.6 larvae/min) than in 2005 (15.8 larvae/min; Figure 4). However, mean daily drift rates of larvae by direction did not differ between years (two-way ANOVA: $F_{3,132}$ = 1.6, P = 0.21; means were 4.2 larvae/min in 2004 and 0.5 larvae/min in 2005). The nonsignificant between-year result was due to high within-year variance and similar rates of larvae drifting out of the backwater between years (0.4 fish/min each year).

The larval densities in LS were 10 times the river densities during both years (Figure 5; two-way repeated measures ANOVA; 2004: $F_{1,20}$ = 66.97; 2005: $F_{1,18}$ = 109.78; $P < 0.01$), although densities differed over time (2004: $F_{21,20}$ = 23.27; 2005: $F_{22,18}$ = 15.11; $P < 0.01$) and also interacted (2004: $F_{1,21}$ = 4.43; 2005: $F_{1,22}$ = 3.74; $P < 0.01$). Separate one-way ANOVAs of larval densities averaged across weeks in 2004 $F_{1,138}$ = 9.56, $P < 0.01$) and 2005 ($F_{1,122}$ = 22.84, $P < 0.01$) confirmed that densities were higher in LS. Total larval production estimates summed across sampling dates were similar between 2004 and 2005, both in the river (respectively, 41.5 and 31.0 larvae/m^3) and LS (434.8 and 530.5 larvae/m^3).

Both LS and the river had spatially homogeneous larval distributions. The differences in LS between inshore and offshore were not significant in 2004 ($t_{1,20}$ = −2.08, P = 0.05) or 2005 ($t_{1,18}$ = −0.66, P = 0.52), nor did upstream and downstream stratified transects in the Illinois River differ in 2004 ($t_{1,21}$ = 0.94, P = 0.36) or 2005 ($t_{1,22}$ = −0.27, P = 0.79).

No diel patterns in catch rates occurred during 2004 (Table 1; $F_{3,11}$ = 0.1, $P > 0.05$). However, a diel drift pattern occurred during 2005; more larvae drifted at night than during other times of day ($F_{3,35}$ = 15.9, P = 0.01).

Grouping families by habitat-use class revealed that macrohabitat generalists were abundant in tows during both years, whereas drift taxa differed between years (Table 2; Figure 6). Fluvial dependents were most abundant taxa drifting into LS during 2004, sciaenids, clupeids, and cyprinids representing 90% of the fish exchange and occurring about equally. Temporal drift patterns varied by habitat-use class, fluvial-dependent taxa peaking in a discrete pulse during rising floodwaters. Furthermore, fluvial-dependent taxa were most abundant in the river tow samples during 2004, which were five times higher than the densities of those taxa in LS. Macrohabitat generalists, composed mostly of clupeids, also drifted in peak rates during the rising floodwaters, beginning in May before the pulse and continuing for 2 months. Macrohabitat generalists were collected in the drift during 2004 and 2005 without much directional difference, making these some of the few taxa that drifted out of LS (Figure 6).

If LS was contributing macrohabitat generalists to the Illinois River, we might expect the downstream larval composition to differ from that at the upstream river site. This did not occur. Conversely, the river did

TABLE 2.—Distributions of fish families caught by drift and tow nets in the Illinois River and lower Swan Lake in 2004–2005, by habitat use class. Drift net catches were 5,756 and 1,506 in 2004 and 2005, respectively; tow net catches were 56,476 and 60,509. No fluvial specialists were caught by either gear.

	2004		2005	
Family	Drift nets	Tow nets	Drift nets	Tow nets
Fluvial specialist	0.00	0.00	0.00	0.00
Fluvial dependent				
Catostomidae	8.37	0.33	1.59	0.24
Cyprinidae	28.82	2.70	1.00	4.85
Moronidae	0.16	0.18	0.00	0.04
Percidae	0.03	<0.01	0.07	0.00
Sciaenidae	31.01	5.04	2.19	0.44
Macrohabitat generalist				
Atherinidae	0.00	0.01	0.00	0.19
Centrarchidae	0.30	1.82	0.73	1.08
Clupeidae	30.59	89.84	92.56	92.52
Gasterosteidae	0.00	<0.01	0.07	0.00
Ictaluridae	0.00	0.00	0.53	<0.01
Lepisosteidae	0.07	0.01	0.00	0.00
Poeciliidae	0.03	0.01	1.20	0.59

appear to influence drift into LS in 2004 because taxa present in tows in the river were similar to those drifting into LS (Figure 6). During the nonflood year 2005, drift rates and density of fluvial dependents were lower than macrohabitat generalists (Table 2; Figure 6). No fluvial specialists were sampled during either year.

Drift rates were correlated with abiotic and biotic factors. Nonzero catch rates of fish drifting into the backwater during 2004 correlated positively (multiple regression model: adjusted $r^2 = 0.92$, $F_{3,13} = 61.83$, $P < 0.01$) with velocity ($t = 13.19$, $P < 0.01$) but not temperature or channel depth. Using the regression model and continuous velocity data, we extrapolated catch rates to the seasonal duration of drift (1 May through 15 July) and channel volume. An estimated 32.3 million fish drifted into LS at the surface during the 2004 sampling season, as estimated using a regression equation (mean catch = 33.86 • velocity − 2.91) and summing mean catch across the channel as predicted by velocity across days. Drift catch rates into LS were weakly positively correlated with river tow-derived densities during 2004 ($r^2 = 0.36$, $P = 0.02$). During 2005, abiotic variables were unrelated to drift. However, drift into LS was positively linearly related to river larval densities ($r^2 = 0.78$, $P < 0.01$), whereas LS larval tow-derived densities probably influenced catch rates of drift to the river ($r^2 = 0.94$, $P < 0.01$,). Therefore, abiotic factors combined with larval density appeared to influence 2004 and 2005 larval drift.

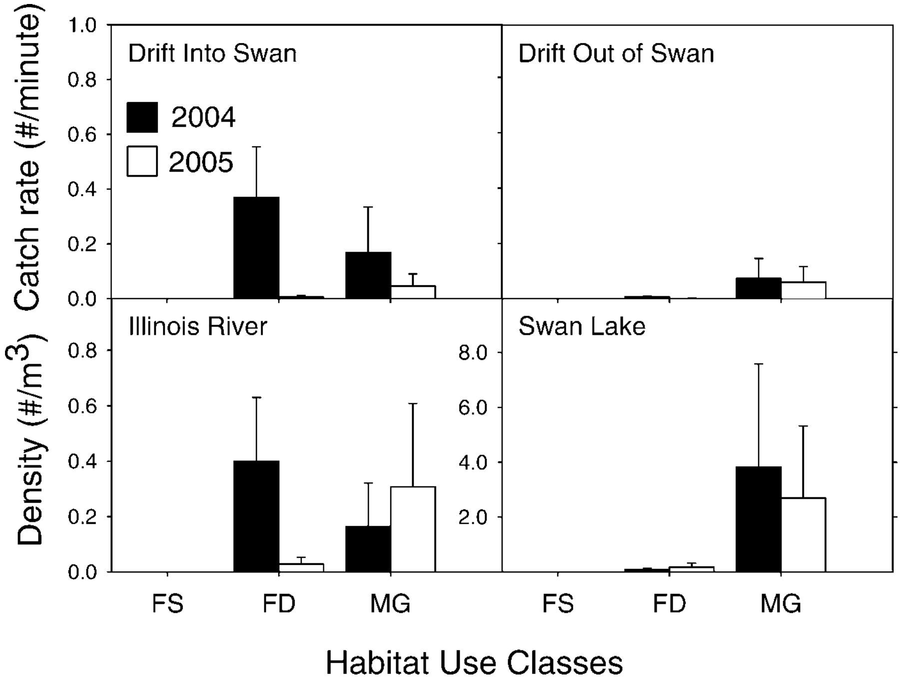

FIGURE 6.—Mean catch rate of fish families drifting into and out of lower Swan Lake and mean density of families in the Illinois River and lower Swan Lake by habitat-use class (Galat and Zweimuller 2001): fluvial specialists (FS), fluvial dependents (FD), and macrohabitat generalists (MG). Error bars represent the SEs of the means.

TABLE 3.—Kolmogorov–Smirnov tests for 2004–2005 pooled diel drift net data and lower Swan Lake (LS) and Illinois River (ILR) larval tow data. The columns headed "Result" indicate treatments that produced significantly larger fish; KS_a = Kolmogorov–Smirnov test statistic.

Treatment	2004			2005		
	KSa	*P*	Result	KSa	*P*	Result
In vs. Out	10.91	<0.01	Out	4.41	0.01	In
LS vs. ILR	8.83	<0.01	LS	5.37	<0.01	LS
Night vs. Dawn	9.48	<0.001	Night	7.78	<0.001	Night
Night vs. Day	9.57	<0.001	Night	11.99	<0.001	Night
Night vs. Dusk	10.93	<0.001	Night	2.55	<0.001	Night
Dawn vs. Day	0.56	0.914	–	9.70	<0.001	Dawn
Dawn vs. Dusk	2.03	<0.001	Dusk	6.06	<0.001	Dusk
Day vs. Dusk	1.48	0.026	–	4.74	<0.001	Dusk

Size Structure

Larval sizes differed between years and among sites. Similarly sized fish drifted into and out of LS during 2004, although fish drifting out were slightly larger. During 2005, larger fish drifted into the backwater than out (Table 3; Figure 7). However, there were no differences in size distribution of larvae caught in tows upstream and downstream of LS. Higher river and channel velocities during the flood pulse did not entrain larger fish into LS, and regardless of net direction larger fish were taken in drift nets during 2005 (Kolmogorov–Smirnov test statistic [KSa] = 8.01, $P < 0.01$). Despite this change in size structure, larval sizes remained larger in the backwater than in the river, regardless of year. Furthermore, both the backwater and river yielded larger larval sizes during 2005 than 2004 (LS: KSa = 2.53, $P < 0.01$; Illinois River: KSa = 10.55, $P < 0.01$).

Lengths varied with time of day. Multiple pairwise Kolmogorov–Smirnov comparisons revealed a propensity for larger fish to drift at night (Table 3). In 2004, fish were similarly sized during dawn, day, and dusk (Table 3; Figure 8). Stronger diel patterns occurred during 2005, night catch collecting the largest fish and dusk, dawn, and day catches each sampling progressively smaller fish (Table 3). Regardless of year, ichthyoplankton drifting at dawn, day, and dusk were predominantly less than 8 mm total length, cumulative percent frequencies being between 74% and 80% for each period in 2004 and between 56% and 82% in 2005. Almost 70% of larvae during night catch were 8 mm or greater (Figure 8).

Discussion

The lateral drift of larval fish at the restored connection between LS and the lower Illinois River followed seasonal patterns shaped by the annual flood pulse and the early life history strategies of the fish species. The flood-pulse concept specifies that increasing water levels and temperatures prompts spawning and yields high recruitment of riverine fish (Junk et al. 1989; Harvey 1987). In our study, fish production differed between LS and the river. Within the backwater and river, larval densities, but not species composition, were similar between two physically contrasting seasons, a flood and a nonflood year. Abiotic conditions apparently induced a change in ambient family densities between years, which may have influenced the between-year variation in magnitude, direction, and composition of lateral larval exchange. During 2004, the large pulse of larvae drifting into LS was timed to the rising floodwaters, and exchange was temporally isolated to that flood (Reichard et al. 2001). In contrast, peak drift rates in 2005 were less than half that of 2004. Only during 2005 were ambient larval densities positively correlated to drift rates, demonstrating a strong biotic influence in the absence of the spring flood.

Abiotic cues probably initiate and drive larval drift within years and influence family composition in the river and drift between years (see Adams 2004). The propensity for fluvial dependents to drift into the backwater during the flood year was probably related to the coupling of temperature and flooding, whereas the relative absence of these species in the drift and the larval assemblage was related to their decoupling during the nonflood year. A lack of a spring flood pulse in 2005 may have resulted in lower reproduction or recruitment of fluvial dependents. These patterns stress the strong reliance of larval early life history on annual flood pulses.

Aside from the influence of abiotic cues on floodplain habitat use, the ecological role of the restored backwater, as it contributes to fish reproduction in the river–floodplain, needs to be identified and evaluated. In other systems, slack-water areas contribute larval and juvenile fish to the river, thereby increasing the densities downstream of the backwater–river confluence (Muth and Schmulbach 1984; Sheaffer and Nickum 1986). However, we did not see any difference in river densities upstream or down-

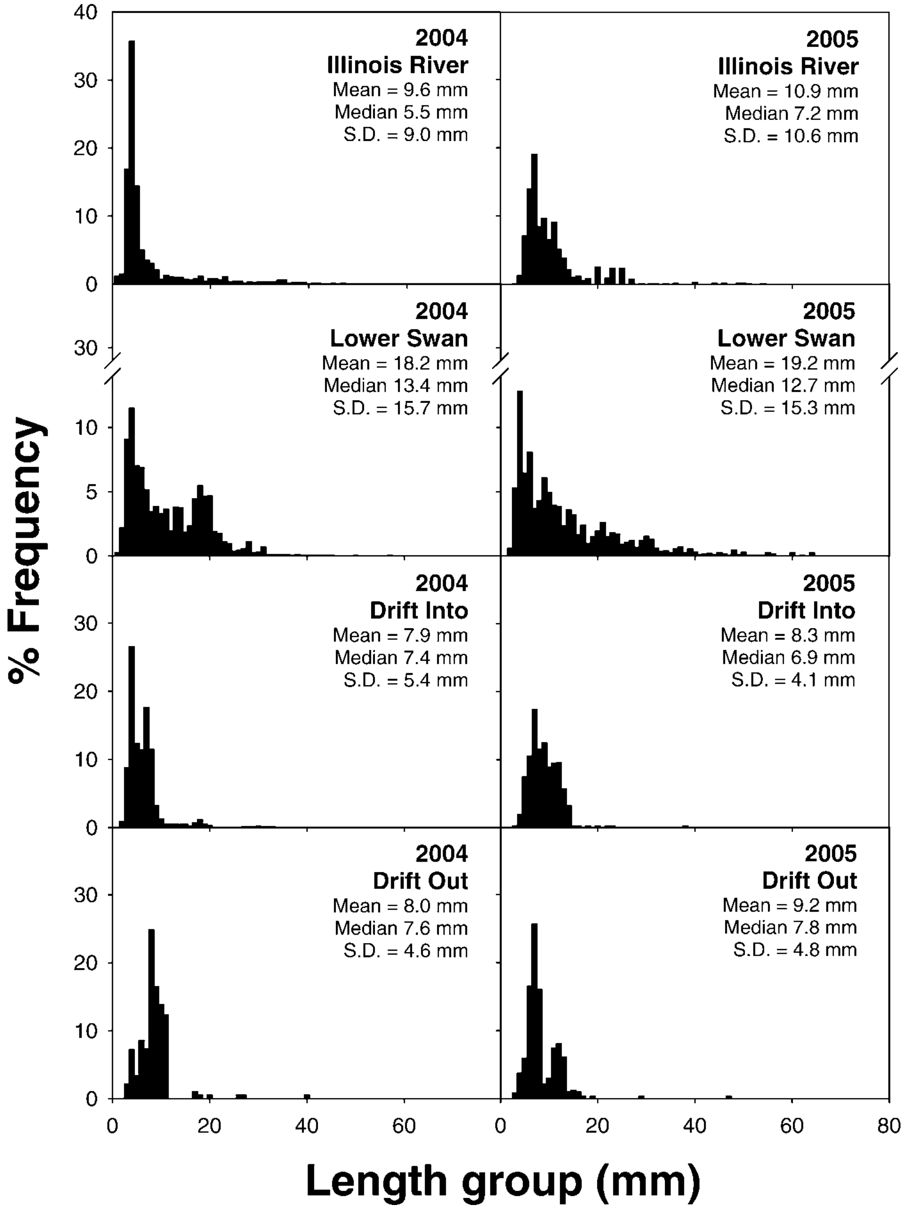

FIGURE 7.—Length frequency distributions of all larval and juvenile fish caught in the Illinois River and lower Swan Lake and drift into and out of the lake, 2004 and 2005. Statistics were calculated from raw length data.

stream of the backwater. Substantial movement of larvae between the backwater and river occurred, even though Swan Lake seemed to neither function as a major sink nor source of larvae. The LS backwater appears to continue to be a vital component of the lower Illinois River and potentially benefits the Mississippi River because of its close proximity (USACE 1991). In particular, LS produced a large proportion of clupeids, which are important prey for piscivorous fish and waterbirds.

The drift rates of macrohabitat generalists suggest a behavioral component to lateral drift, thereby discounting suspicions that LS acts solely as a sink. The predominant taxa in the larval assemblage are commonly found in the drift (Jurajda 1995; Reichard et al. 2001), yet in our study clupeids were less abundant in the 2004 drift than their ambient densities would have

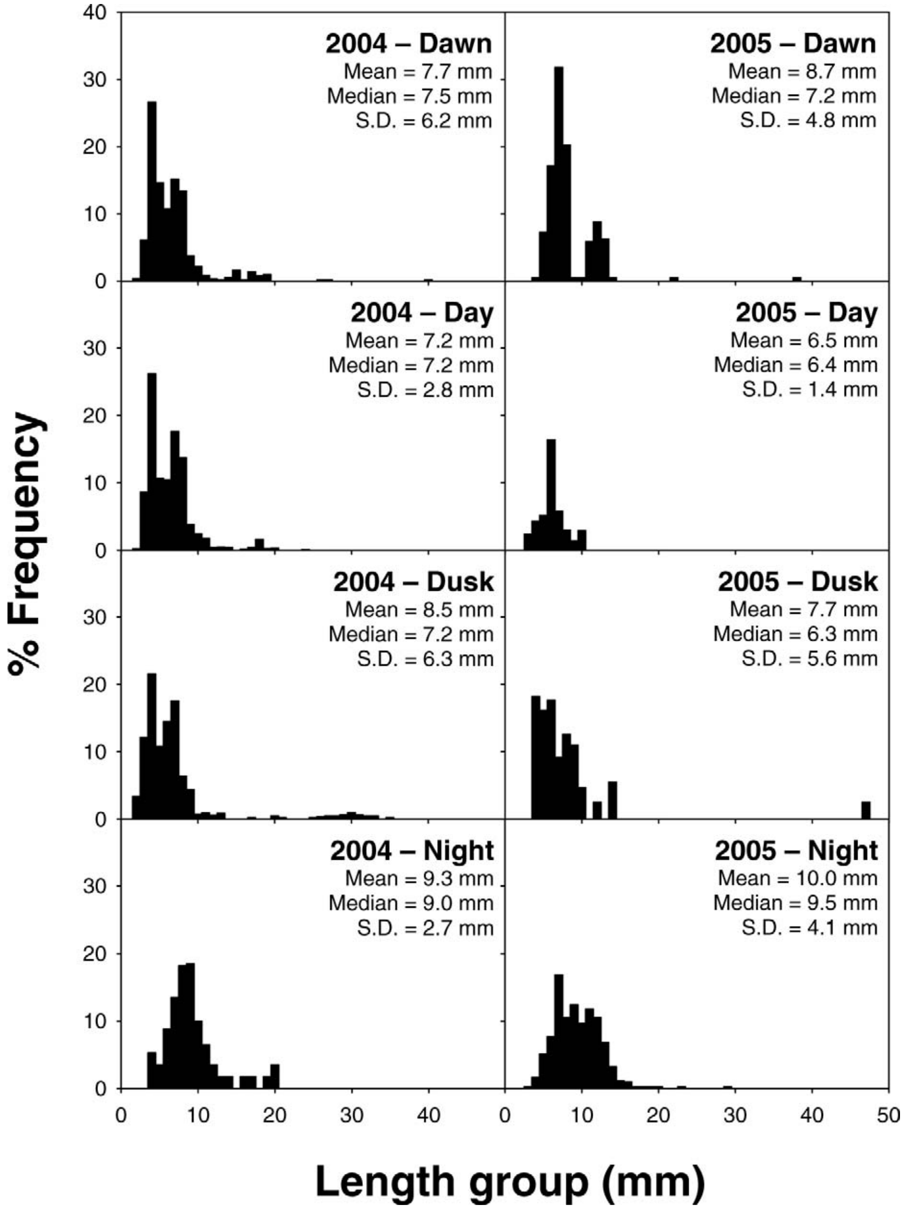

FIGURE 8.—Length frequency distributions of all fish caught in drift samples (percentages of the mean number per set of three net sets over the sampling season) at the mouth of lower Swan Lake by time of day, 2004 and 2005. Statistics were calculated from raw length data.

warranted. Similarly, during 2005, macrohabitat generalists drifted in lower rates despite their higher densities within the river and LS. This underrepresentation of macrohabitat generalists in the drift may reflect drift avoidance (Brown and Armstrong 1985; Reichard et al. 2001). Ultimately, these findings imply a purposeful lateral drift pattern, whereby some families may avoid or are less prone to drift.

The observed diel and size structure patterns of larval drift reflect a behavioral component to drift. Larger larvae drifted at night during both years, but higher catch rates at night only occurred during 2005. Larvae, particularly larger individuals, may innately drift at the bottom during the day and move to the surface at night to feed or evade predation (Gale and Mohr 1978; Muth and Schmulbach 1984; Johnston et al. 1995). Carter et al. (1986) captured larvae drifting in densities almost four times higher at night than during the day. Other abiotic factors, like water clarity, probably drove interannual diel variations; catch rates showed no diel patterns during the flood year but were more apparent during low flows when water transparency was probably greater (Reichard et al. 2001; Araujo-Lima et al. 2001). Therefore, it is possible that diel patterns quantified in LS may result from phototaxic responses and changes in water clarity between years.

The tendency for larger fish to drift out of LS during 2004 supports conventional larval drift hypotheses that backwaters function as nursery habitat that provides ideal conditions for growth and that backwaters are therefore an important source of age-0 fish (Sheaffer and Nickum 1986). Lateral movement during 2005 may not have been necessary as a life history strategy, given that portions of the lower Illinois River during that low-flow year offered amenable habitat similar to backwaters: slower flows, warmer habitat, and high plankton densities (Csoboth 2006). Furthermore, abundant juvenile clupeids emigrated from LS into the river during summer 2004, and juvenile sciaenid and moronid fish followed this same trend during fall 2004 (Schultz 2006). Thus, it is our thought that larvae entering the backwater or spawned in the backwater were able to feed and grow throughout the season, eventually making an ontogenetic habitat shift by exiting the backwater sometime that fall and recruiting to the river fishery (King 2004).

In restored backwaters, continuous connectivity should be maintained where possible because species use the floodplain throughout the spring and summer. Limiting backwater access or reducing river access could impair the recruitment potential of certain fishes, eventually leading to a less diverse riverine fish community (Turner et al. 1994). The LS connection to the Illinois River was about 99% wider than its postrestoration width and probably permitted gradual changes in water level, direction, and velocity. Water levels now lag behind the river, flow direction typically changes multiple times per day, and velocities are dynamically variable and most likely higher through the restricted channel, especially during flood pulses. Although our data suggest that functionality has been maintained to some extent, it is possible that the narrowed connection (via the levee) and the constructed stop-log structure have negatively altered water flow patterns and lateral exchange of fish through the structure.

This study was unique in that to our knowledge no other study has quantified lateral larval drift in a river–floodplain system. Lateral drift is an important component of fish life history in lotic systems, but drift strategies and ontogenetic habitat changes may not withstand the anthropogenic disturbances in streams and rivers. Altered hydrology may affect larval drift ecology and influence recruitment of fish. Lateral drift patterns in the restored LS–Illinois River system were strongly influenced by the flood pulse, but in the absence of a flood the ambient biotic assemblage appeared to drive drift timing, magnitude, and composition. Generally, the Swan Lake Habitat Rehabilitation and Enhancement Project appears to have successfully altered the backwater to reduce sediment input while still maintaining some river connectivity and lateral drift functionality. Ultimately, future conservation efforts aimed at restoring hydrology should not focus on one particular habitat but should equally consider main-channel, floodplain, and tributary habitats (Galat and Zweimuller 2001).

Acknowledgments

We thank the many Fisheries and Illinois Aquaculture Center employees, Department of Zoology at Southern Illinois University, and other individuals for their help with this project, particularly P. Beck, R. Brooks, B. Burr, R. Colombo, K. DeGrandchamp, K. Derr, C. Dolan, R. Lane, M. Lynam, D. Martin, D. Schultz, M. Siepker, and S. Tripp. Funding was provided by the St. Louis District, U.S. Army Corps of Engineers through the Environmental Management Program. Lodging and field help from the U.S. Fish and Wildlife Service Two Rivers National Wildlife Refuge also were greatly appreciated.

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