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APPLICABILITY OF THE FLOOD-PULSE CONCEPT IN A TEMPERATE FLOODPLAIN RIVER ECOSYSTEM: THERMAL AND TEMPORAL COMPONENTS

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ABSTRACT

Annual growth increments were calculated for blue catfish (*Ictalurus furcatus*) and flathead catfish (*Pylodictis olivaris*) from the lower Mississippi River (LMR) to assess hypothesized relationships between fish growth and floodplain inundation as predicted by the Flood-Pulse Concept. Variation in catfish growth increment was high for all age classes of both species, and growth increments were not consistently related to various measures of floodplain inundation. However, relationships became stronger, and usually direct, when water temperature was integrated with area and duration of floodplain inundation. Relationships were significant for four of six age classes for blue catfish, a species known to utilize floodplain habitats. Though similar in direction, relationships were weaker for flathead catfish, which is considered a more riverine species. Our results indicate the Flood-Pulse Concept applies more strongly to temperate floodplain-river ecosystems when thermal aspects of flood pulses are considered. We recommend that future management of the LMR should consider ways to 'recouple' the annual flood and thermal cycles. An adaptive management approach will allow further determination of important processes affecting fisheries production in the LMR. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: flood-pulse concept; regulated rivers; floodplain; Mississippi River; catfishes

INTRODUCTION

Contemporary models of river-floodplain ecosystems predict that fish production is positively related to some measure of inundated floodplain habitat (Junk *et al.*, 1989; Welcomme, 1985). Although conceptualized as a model for large floodplain rivers in general, support for this 'Flood-Pulse' Concept (Junk *et al.*, 1989) largely emanates from studies of little-altered, tropical river systems. In these systems, floodplain inundation tends to be spatially expansive, protracted and temporally consistent (Goulding, 1980). The hydrographs in these rivers are mostly unchanged from historical conditions and water temperatures are relatively stable and sufficient for high rates of food intake and growth by most fishes throughout the year (Humphries *et al.*, 1999). Conversely, most rivers in temperate zones are highly altered systems with respect to channel alignment, annual flow regimes, and floodplain connectivity (Sparks, 1995a,b; Poff *et al.*, 1997). Because of these characteristics, temperate rivers also may exhibit a general asynchrony between annual flood pulses and water temperatures suitable for feeding and growth of many temperate fishes (Schramm *et al.*, 2000; Eggleton and Schramm, 2004).

There is considerable interest in restoring large floodplain-river ecosystems (Gore and Shields, 1995), and the Flood-Pulse Concept provides ample guidance for restoration efforts. However, many candidate rivers for restoration are in temperate regions. Evaluations of the Flood-Pulse Concept in temperate rivers have not provided compelling evidence for its applicability in these systems. In the upper Mississippi River, growth of floodplain-dependent fishes was greater during a year of extensive summer flooding compared to other years while growth of a

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riverine species did not differ during that year (Gutreuter *et al.*, 1999). However, studies in the lower Mississippi River (LMR) have failed to detect expected positive relationships between growth and abundance of young fishes and measures of floodplain inundation (Rutherford *et al.*, 1995). Additional studies in the LMR also suggested that catfish (Ictaluridae) growth was not significantly related to area or duration of floodplain inundation (Mayo, 1999; Schramm *et al.*, 2000). However, positive relationships emerged between catfish growth and extent of inundation when water temperature exceeded 15°C, a threshold temperature for active feeding and growth by catfishes (Schramm *et al.*, 2000). Although these results are compatible with the 'thermal coupling' hypothesis offered by Junk *et al.* (1989), validation over a longer time frame is needed before thermal coupling can be considered a viable restoration objective for the LMR.

The objectives of this paper are to (1) evaluate relationships between growth of ictalurid catfishes and temporal, spatial and thermal measures of floodplain inundation associated with annual flood pulses in the LMR, and (2) propose an adaptive management strategy that should benefit LMR fish production and allow further evaluation of the habitat conditions affecting it. Results will enable a better understanding of river-floodplain linkages in highly altered large rivers that are commonplace in the temperate region.

METHODS

Study site

The LMR is the 1,600 km segment of the Mississippi River from the confluence of the Ohio River to the Gulf of Mexico. The LMR has received extensive bank armouring and placement of large-rock wing dikes to control channel alignment and maintain sufficient depth for commercial navigation (Fremling *et al.*, 1989; Schramm, 2004). Although regulated, the LMR remains free-flowing throughout and flooding regime varies annually. During the period 1940–2001, which reflects the current state of regulation, significant floodplain inundation occurs annually from mid-March through mid-May, though flooding may begin as early as January and continue into summer (Schramm, 2004). Annual stage fluctuations average about 8 m per year, but may exceed 15 m (Baker *et al.*, 1991). Extensive levee construction during the last 150 years has separated approximately 93% of the historical floodplain from the main river channel (Sparks *et al.*, 1998). This reduction in river-floodplain connectance has had unknown, but presumed negative, effects on riverine fishes and fisheries. However, at present, more than 6,000 km^2 (average 3.8 km^2 per river km) of active, annually inundated floodplain remains (Schramm *et al.*, 1999).

Fish collection

We selected blue catfish (*Ictalurus furcatus*) and flathead catfish (*Pylodictis olivaris*) to assess relationships between fish growth and floodplain inundation measures. While longitudinal movement of these fishes in rivers has been studied (Graham, 1999; Jackson, 1999), little information is available about lateral, river-floodplain movements. In the LMR, blue catfish extensively use the floodplain, but flathead catfish largely remain in the main river channel and adjacent habitats (e.g., side or secondary river channels) (Eggleton and Schramm, 2004). The widely different life-history strategies of these two species may help unravel fish-floodplain relationships in the LMR.

We collected 899 catfishes 250–700 mm total length by 15-Hz pulsed D.C. boat-mounted electrofishing from main river channel habitats. Samples were taken between river km 716–942 during July–October 1996–1997 and September 2000–2003. All fishes were measured for total length, and a pectoral spine was removed before the fish were released. Following the method of Lee (1983), individuals were aged by microscopic examination of articulating process cross sections, with annular measurements obtained from basal recess cross sections perpendicular to the axis of the spine.

Data analyses

Lengths at age were backcalculated by direct proportion (Schramm *et al.*, 1992). The possibility of a Lee effect (i.e., backcalculated lengths that do not accurately represent the lengths at earlier ages) was tested by comparing the slope of lengths at age 1 regressed against age for four cohorts for each species. A zero slope would indicate no

Lee effect. For blue catfish, two cohorts had slopes that did not differ from zero, one cohort had a positive slope, and the other cohort had a negative slope. Identical results were obtained with analyses of four cohorts of flathead catfish. Thus, we concluded no consistent Lee effect and backcalculated lengths from all annuli were considered accurate representations of catfish lengths at the time of annuli formation.

Annual growth increments were estimated from the backcalculated lengths at the time of annuli formation. Age-0 growth was the backcalculated length at the first annulus, age-1 growth was the backcalculated length at age 2 (second annulus) minus the backcalculated length at age 1, and so forth. Blue and flathead catfishes in LMR form annuli on their pectoral spines during May–July (Mayo, 1999). Thus, the growth year for both catfishes was assumed to be 1 July–30 June. Since the annual flood pulse generally began in March of each year, potential energetic benefits could be realized by the end of the July–June growth year or at the beginning of the succeeding growth year. As analyses proceeded, results indicated that environmental conditions in the spring (March–June) often showed better association with environmental conditions during the succeeding summer-fall (July–November) period than the preceding summer, which constituted a different growth year. Therefore, relationships between growth increment and environmental conditions were evaluated both for growth year (GY, July–June; e.g., 1992 growth year was July 1991–June 1992) and calendar year (CY, January–December). Measures of floodplain inundation for both growth and calendar years were the sum of spring and summer-fall measures (i.e., inundation during December–February was excluded).

Floodplain inundation metrics tested for association with catfish growth increment included variables that depicted river stage, river water temperature, total areas of inundated floodplain habitat, duration of floodplain inundation, and lengths of the growing season for catfishes (i.e., days when water temperature was $\geq 15°C$). Several of these variables were combined to depict multidimensional variables (Table I). For instance, total area of inundated floodplain and duration of floodplain inundation were combined into a single variable termed ‘area-days of flooding’, which reflected a measure more ecologically meaningful to fishes. Daily river stages were obtained from the U.S. Army Corps of Engineers, Vicksburg District. River water temperatures were obtained from the U.S. Geological Survey and U.S. Army Corps of Engineers. Area of inundated floodplain at different river stages was calculated using Geographic Information Systems technology on a LMR spatial data set provided by the U.S. Army Corps of Engineers (Schramm *et al.*, 1999). Floodplain water temperatures generally ranged 1–4°C higher than temperatures in the main river channel (Eggleton, 2001). Thus, a temperature of 15°C in the river approximated a temperatures range of 16–20°C in floodplain habitats, which are threshold temperatures at which ictalurid catfishes resumed active feeding and growth (Stickney, 1988; Tucker and Robinson, 1990).

Differences in annual growth increments were tested among years for six age classes of blue catfish and five age classes of flathead catfish by one-way completely randomized analysis of variance (ANOVA). Results were judged statistically significant at $\alpha = 0.05$. Relationships between environmental variables (Table I) and growth increment were assessed by Spearman rank correlation analyses. Only cohorts with nine or more fish in an age class were included in correlation analyses. Correlations were considered significant at $\alpha = 0.10$. The higher α was chosen because of smaller sample sizes (years served as replicates in the correlation analyses) and to ensure that possible growth-environmental relationships were not overlooked due to statistical power issues.

RESULTS

For blue catfish, annual growth increments differed among years for three of seven age classes (Table II). For the age classes of blue catfish that exhibited significant annual differences in growth, GY 1996 (CY 1995) appeared to be a year of consistently greater growth, and mean annual growth increments exceeded long-term averages by as much as 19%. Specifically, growth increments of age-0 fish were significantly greater in GY 1996 than during 5 of 11 other years. During the same growth year, growth increments of age-2 fish significantly exceeded growth during 6 of 10 other years. A consistent but weaker pattern was observed with age-4 fish; although the largest growth increment was measured in GY 1996, this growth increment was significantly greater than only one of the other nine growth years (Table II). Growth increments of age-1, age-3, and age-5 fish in GY 1996 exceeded long-term averages, but the greater growth increments were not significantly different from other growth years. Annual

Table I. Environmental variables tested for association with annual growth increment of blue catfish and flathead catfish in the lower Mississippi River. Growth year is the 12-month time period from July–June; calendar year is the 12-month time period from January–December

Variable (units)	Definition	Minimum	Maximum
Mean stage (m)	Mean river elevation above low-water reference plane	9.7	29.8
Mean temperature (°C)	Mean main river channel water temperature	15.9	18.3
Mean flooded area of floodplain waterbodies (ha)			
March–June, growth year	Mean flooded area during March–June of growth year	134076	900320
March–June, calendar year	Mean flooded area during March–June of calendar year	134076	900320
July–November	Mean flooded area during July–November (same for growth and calendar years)	55680	494222
Annual, growth year	Mean flooded area during July–June	216200	1026822
Annual, calendar year	Mean flooded area during March–November	215840	1375537
Flood days (number of days above flood stage = 7.6 m stage)			
March–June, growth year	Number of March–June days above flood stage of growth year	15	122
March–June, calendar year	Number of March–June days above flood stage of calendar year	15	122
July–November	Number of July–November days above flood stage (same for growth and calendar years)	0	102
Annual, growth year	Number of July–June days above flood stage	194	27
Annual, calendar year	Number of March–November days above flood stage	28	224
Area-days of flooding (cumulative area of flooding through days of flooding)			
March–June, growth year	Cumulative area of days of flooding during March–June of growth year	5	107
March–June, calendar year	Cumulative area of days of flooding during March–June of calendar year	5	107
July–November	Cumulative area of days of flooding during July–November (same for growth and calendar years)	0	68
Annual, growth year	Cumulative area of days of flooding during July–June	9	172
Annual, calendar year	Cumulative area of days of flooding during March–November	9	175
Length of growing season	Number of days with water temperature exceeding 15°C	180	231
Days of flooding when water temperature >15°C (number of days)			
March–June, growth year	March–June days above flood stage when water temperature exceeds 15°C for growth year	6	77
March–June, calendar year	March–June days above flood stage when water temperature exceeds 15°C for calendar year	6	83
July–November	July–November days above flood stage when water temperature exceeds 15°C	0	92
Annual, growth year	July–June days above flood stage when water temperature exceeds 15°C	6	134
Annual, calendar year	March–November days above flood stage when water temperature exceeds 15°C	12	144
Area-days of flooding when water temperature >15°C (area-days above 15°C)			
March–June, growth year	March–June area-days of flooding (defined above) when water temperature exceeded 15°C during growth year	2	72
March–June, calendar year	March–June area-days of flooding when water temperature exceeded 15°C during calendar year	2	72
July–November	July–November area-days of flooding when water temperature exceeded 15°C (same for growth and calendar years)	0	62
Annual, growth year	July–June area-days of flooding when water temperature exceeded 15°C	2	110
Annual, calendar year	March–November area-days of flooding when water temperature exceeded 15°C	4	103

Table II. Mean annual growth increments of blue catfish in the lower Mississippi River. Values in parentheses are number of fish, standard error. Growth year is the annual period from July to June of the succeeding year; e.g., July 1990–June 1991 is growth year 1991. Calendar year is the annual period from January–December

Calendar year	Growth year	Growth increment						
		Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
1990	1991	161^{a} (19, 9.8)						
1991	1992	161^{a} (54, 4.5)	70^{a} (19, 5.8)					
1992	1993	$150^{a,b}$ (55, 4.1)	71^{a} (54, 3.5)	61^{b} (21, 3.3)				
1993	1994	144^{b} (143, 2.6)	80^{a} (55, 3.7)	71^{b} (57, 3.1)	66^{a} (21, 4.3)			
1994	1995	$153^{a,b}$ (51, 4.7)	74^{a} (143, 1.8)	71^{b} (59, 3.6)	75^{a} (57, 2.9)	$63^{a,b}$ (21, 4.8)		
1995	1996	176^{a} (24, 9.2)	82^{a} (51, 3.4)	85^{a} (147, 1.9)	75^{a} (59, 2.9)	76^{a} (57, 2.6)	127^{a} (20, 7.5)	
1996	1997	142^{b} (37, 6.3)	83^{a} (24, 3.3)	$72^{a,b}$ (37, 3.9)	65^{a} (36, 4.2)	54^{b} (17, 4.4)	117^{a} (9, 5.6)	58^{a} (8, 4.1)
1997	1998	$156^{a,b}$ (60, 5.8)	82^{a} (37, 3.7)	66^{b} (24, 3.7)	64^{a} (28, 4.4)	$60^{a,b}$ (24, 4.9)	108^{a} (15, 6.9)	62^{a} (5, 6.5)
1998	1999	$151^{a,b}$ (48, 5.4)	76^{a} (60, 2.9)	$76^{a,b}$ (39, 4.2)	75^{a} (24, 5.5)	$66^{a,b}$ (28, 5.2)	125^{a} (24, 7.3)	59^{a} (15, 6.2)
1999	2000	128^{c} (63, 4.5)	74^{a} (48, 3.4)	66^{b} (61, 3.1)	67^{a} (38, 4.2)	$67^{a,b}$ (24, 5.8)	123^{a} (28, 6.4)	55^{a} (24, 3.6)
2000	2001	141^{b} (38,10.5)	77^{a} (63, 3.4)	$74^{a,b}$ (39, 4.4)	68^{a} (34, 4.5)	$57^{a,b}$ (13, 3.8)	128^{a} (18, 11.9)	54 (18, 4.5)
2001	2002	109^{c} (10, 8.3)	81^{a} (38, 8.0)	69^{b} (44, 3.8)	65^{a} (21, 4.8)	$63^{a,b}$ (20, 5.2)	111^{a} (5, 7.7)	52^{a} (11, 4.6)
2002	2003		94^{a} (10, 4.5)	$77^{a,b}$ (27, 6.3)	69^{a} (37, 5.0)	$68^{a,b}$ (14, 6.6)	137^{a} (13, 12)	40^{a} (4, 1.7)
1990–2002	Mean	148 (602, 5.0)	79 (602, 1.9)	72 (555, 1.9)	69 (355, 1.4)	64 (218, 2.2)	122 (132, 3.4)	54 (85, 2.7)

^{a,b,c}Values in a column with a different letter are significantly different ($p < 0.05$) by least squares means.

growth increment of age-5 blue catfish across all years (mean = 122 mm) was consistently greater than annual growth increment of all other age classes (means 54–79 mm) except age-0.

For flathead catfish, annual growth increments differed among years for three of six age classes (Table III). However, greater growth across the different age classes was not consistently associated with one or more growth year(s). Growth increments of age-0 fish were significantly greater during GY 1998 than during 2 of 10 other growth years. Growth increments of age-1 fish were significantly greater during GY 1996 than during 2 of 10 other growth years. Growth increments of age-4 fish were significantly greater in GY 2003 than

Table III. Mean annual growth increments of flathead catfish in the lower Mississippi River. Values in parentheses are number of fish, standard error. Growth year is the annual period from July to June of the succeeding year; e.g., July 1990–June 1991 is growth year 1991. Calendar year is the annual period from January–December

Calendar year	Growth year	Growth increment					
		Age 0	Age 1	Age 2	Age 3	Age 4	Age 5
1991	1992	$155^{a,b}$ (12, 12.0)					
1992	1993	$160^{a,b}$ (10, 12.3)	60^{b} (12, 7.5)				
1993	1994	$162^{a,b}$ (27, 11.5)	$77^{a,b}$ (10, 11.1)	64^{a} (13, 9.1)			
1994	1995	$156^{a,b}$ (26, 10.5)	72^{b} (27, 5.9)	94^{a} (15, 8.8)	70^{a} (13, 10.6)		
1995	1996	$173^{a,b}$ (13, 10.8)	101^{a} (26, 7.8)	91^{a} (31, 5.6)	85^{a} (16, 9.0)	85^{b} (13, 12.8)	
1996	1997	$171^{a,b}$ (17, 7.4)	$85^{a,b}$ (13, 11.2)	94^{a} (21, 8.5)	72^{a} (16, 9.3)	54^{b} (3, 17.5)	106^{a} (3, 25.4)
1997	1998	183^{a} (33, 11.3)	$77^{a,b}$ (17, 9.5)	71^{a} (12, 11.5)	94^{a} (13, 13.6)	63^{b} (8, 10.0)	141^{a} (2, 24.1)
1998	1999	$156^{a,b}$ (38, 7.3)	$88^{a,b}$ (33, 7.3)	84^{a} (23, 7.5)	91^{a} (12, 18.1)	76^{b} (13, 10.6)	145^{a} (8, 19.6)
1999	2000	$166^{a,b}$ (55, 6.3)	$76^{a,b}$ (38, 5.0)	82^{a} (42, 7.4)	82^{a} (23, 9.0)	82^{b} (12, 13.4)	130^{a} (13, 15.5)
2000	2001	151^{b} (51, 6.0)	$83^{a,b}$ (55, 4.3)	80^{a} (34, 5.6)	86^{a} (27, 6.6)	77^{b} (9, 15.7)	191^{a} (4, 40.6)
2001	2002	134^{b} (15, 7.1)	$87^{a,b}$ (51, 4.6)	83^{a} (38, 7.6)	79^{a} (19, 9.4)	87^{b} (10, 14.2)	115^{a} (3, 26.5)
2002	2003		$98^{a,b}$ (15, 8.8)	97^{a} (26, 9.9)	106^{a} (26, 10.7)	144^{a} (17, 15.7)	180^{a} (8, 20.9)
1990–2002	Mean	161 (297,13.9)	82 (297, 7.6)	84 (255, 8.2)	85 (165, 9.1)	84 (85, 12.5)	144 (41, 20.8)

^{a,b}Values in a column with a different letter are significantly different ($p < 0.05$) by least squares means.

in all 7 years available for comparison. Though not significant, annual growth increments of age-3 and age-5 flathead catfish were 25% greater in GY 2003 than in all other years. As observed for blue catfish, annual growth increment of age-5 flathead catfish (mean = 144 mm) was greater than annual growth increments of ages 1–4 (means 82–85 mm) (Table III).

Fish growth-environment correlations for blue catfish were generally low and nonsignificant for measures of mean stage, mean water temperature, area of flooded floodplain waterbodies, and days of floodplain inundation (Table IV). Annual growth increment was positively related to days of flooding during July–November when river water temperature exceeded 15°C for four of six age classes. Annual growth increment was positively related to area-days of floodplain inundation when water temperature exceeded 15°C during March–June (CY) and during the entire CY for four of six age classes.

Table IV. Spearman rank correlation coefficients between environmental variables and annual growth increments of length of blue catfish. Correlation coefficients in bold are significantly different ($p < 0.10$) from zero. Growth year is the annual period, or portion thereof, from July to June of the succeeding year. Calendar year is the annual period, or portion thereof, from January–December

Environmental variable	Growth increment					
	Age 0 ($n = 12$)	Age 1 ($n = 13$)	Age 2 ($n = 12$)	Age 3 ($n = 11$)	Age 4 ($n = 10$)	Age 5 ($n = 7$)
Mean stage	0.08	0.10	0.10	−0.30	0.01	0.39
Mean temperature	−0.30	0.04	−0.11	0.23	−0.15	−0.32
Mean flooded area of floodplain waterbodies						
March–June, growth year	−0.04	0.20	−0.12	**−0.64**	−0.21	0.14
March–June, calendar year	**0.54**	−0.05	0.08	0.20	0.21	0.14
July–November	0.11	0.27	0.25	0.02	0.30	0.04
Annual, growth year	−0.01	0.21	−0.05	**−0.56**	−0.07	0.14
Annual, calendar year	0.47	−0.05	0.18	0.32	0.35	0.36
Flood days						
March–June, growth year	0.11	0.09	−0.12	**−0.54**	−0.30	0.25
March–June, calendar year	0.35	−0.21	−0.02	0.16	0.33	0.00
July–November	−0.11	0.36	0.44	0.24	0.29	0.13
Annual, growth year	0.07	0.16	−0.02	−0.47	−0.09	0.07
Annual, calendar year	0.25	0.00	0.10	0.17	0.38	−0.04
Area-days of flooding						
March–June, growth year	**0.54**	−0.05	0.08	0.20	0.21	0.14
March–June, calendar year	−0.01	−0.13	−0.20	−0.51	−0.20	0.36
July–November	−0.04	0.20	−0.12	**−0.64**	−0.21	0.14
Annual, growth year	0.29	0.20	0.20	−0.02	−0.01	0.07
Annual, calendar year	−0.09	0.11	−0.11	**−0.61**	−0.21	0.11
Length of growing season (water temperature >15°C)	0.29	0.20	0.20	−0.02	−0.01	0.07
Days of flooding when water temperature >15°C	0.41	0.12	0.56	0.62	0.58	0.68
March–June, growth year	−0.19	−0.12	0.14	**0.56**	−0.06	−0.21
March–June, calendar year	0.07	−0.20	−0.17	−0.45	−0.19	0.36
July–November	0.41	0.11	**0.56**	**0.62**	**0.58**	**0.68**
Annual, growth year	0.32	−0.09	0.24	**0.58**	0.44	0.20
Annual, calendar year	0.40	0.22	**0.53**	0.46	**0.71**	0.54
Area-days of flooding when water temperature >15°C						
March–June, growth year	0.19	0.14	0.08	−0.08	0.13	0.31
March–June, calendar year	**0.56**	0.21	**0.65**	**0.60**	0.38	**0.82**
July–November	−0.07	0.37	0.31	0.15	0.34	0.07
Annual, growth year	0.15	0.26	0.20	−0.02	0.38	0.25
Annual, calendar year	0.45	0.26	**0.64**	**0.57**	**0.59**	**0.79**

Flathead catfish annual growth increment was only weakly related to mean stage, mean water temperature, area of flooded floodplain waterbodies, and days and area-days of floodplain inundation (Table V). Annual growth increment was positively related to days of flooding when river water temperature exceeded 15°C during July–November, but only for age-1 fish. Annual growth increment was positively related to area-days of floodplain inundation when temperature exceeded 15°C during March–June (CY) for two of five age classes, but negatively related to area-days of floodplain inundation when temperature exceeded 15°C during July–November for age-2 fish.

Temporal and thermal aspects of floodplain inundation were highly variable during 1990–2002. A notable flood occurred in the Mississippi River basin during CY 1993; floodwaters remained on the floodplain in much of the LMR from February through September. During this period, water temperatures in the LMR exceeded 15°C for 144 consecutive days (Figure 1). Relatively long periods of floodplain inundation also occurred in CY 1990, 1991, 1994–1999, and 2002. However, periods of floodplain inundation when river temperatures were ≥ 15°C exceeded 90 days only during CY 1990, 1995, and 1998.

Table V. Spearman rank correlation coefficients between environmental variables and annual growth increments of length of flathead catfish. Correlation coefficients in bold are significantly different ($p < 0.10$) from zero. Growth year is the annual period, or portion thereof, from July to June of the succeeding year. Calendar year is the annual period, or portion thereof, from January–December

Environmental variable	Growth increment				
	Age 0 ($n = 11$)	Age 1 ($n = 11$)	Age 2 ($n = 10$)	Age 3 ($n = 9$)	Age 4 ($n = 5$)
Mean stage	0.39	−0.09	−0.16	−0.07	−0.20
Mean temperature	−0.24	0.06	0.09	−0.05	−0.30
Mean flooded area of floodplain waterbodies					
March–June, growth year	0.33	−0.25	−0.07	−0.30	0.60
March–June, calendar year	0.42	0.04	−0.09	0.25	−0.30
July–November	**0.58**	0.17	−0.47	0.20	−0.60
Annual, growth year	0.37	−0.18	−0.22	−0.27	0.60
Annual, calendar year	0.33	0.13	−0.09	0.33	−0.30
Flood days (stage > 7.6 m LWRP)					
March–June, growth year	0.32	−0.08	−0.09	0.03	−0.10
March–June, calendar year	0.33	0.02	−0.29	0.41	−0.40
July–November	0.41	0.28	−0.40	0.27	−0.70
Annual, growth year	0.42	−0.15	−0.47	0.10	−0.20
Annual, calendar year	**0.57**	0.13	−0.39	0.33	−0.40
Area-days of flooding in March–June					
March–June, growth year	0.42	0.04	−0.09	0.25	−0.30
March–June, calendar year	0.06	−0.15	−0.08	−0.30	0.30
July–November	0.33	−0.25	−0.07	−0.30	0.60
Annual, growth year	0.51	0.03	−0.13	−0.07	−0.10
Annual, calendar year	0.24	−0.24	−0.08	−0.42	0.60
Length of growing season (water temperature > 15°C)	0.51	0.03	−0.13	−0.07	−0.10
Days of flooding when water temperature > 15°C					
March–June, growth year	−0.27	−0.02	0.17	−0.15	−0.60
March–June, calendar year	0.09	−0.14	−0.07	−0.23	−0.10
July–November	0.42	**0.64**	0.44	0.47	−0.30
Annual, growth year	0.18	0.35	0.47	0.27	−0.20
Annual, calendar year	0.50	0.46	0.05	0.30	0.00
Area-days of flooding when water temperature > 15°C					
March–June, growth year	0.06	0.07	0.07	−0.32	0.60
March–June, calendar year	0.37	**0.59**	**0.74**	0.13	0.00
July–November	0.47	0.28	**−0.61**	0.37	−0.67
Annual, growth year	0.25	0.15	−0.24	−0.13	0.50
Annual, calendar year	0.33	0.47	0.16	0.23	−0.30

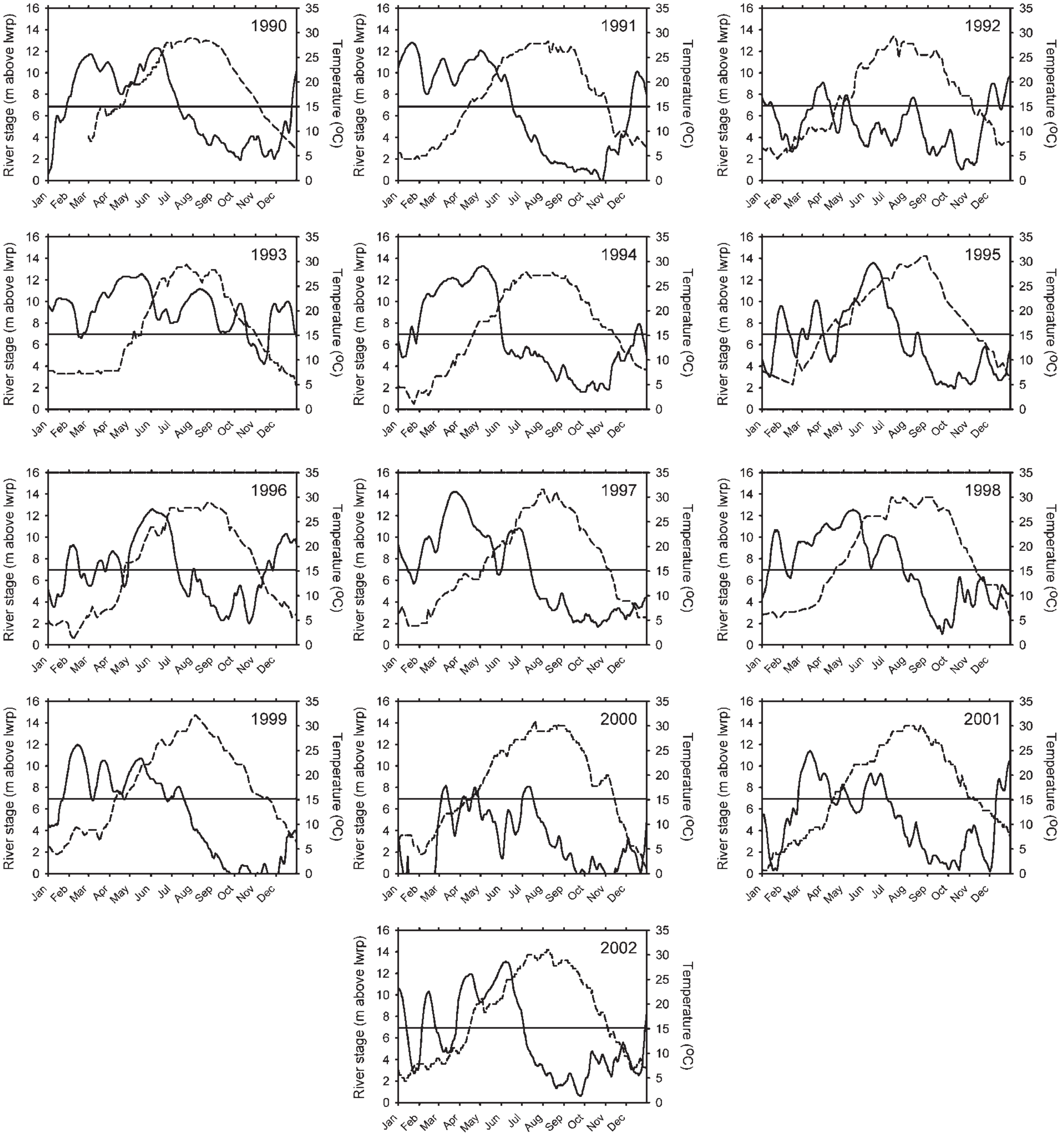

Figure 1. Stage (solid line) and temperature (dashed line) of the Mississippi River measured at Vicksburg, Mississippi for calendar years 1990–2002. Horizontal line is the approximate stage at which water commences to move laterally onto the floodplain; lwrp is low water reference plane, the river stage at which discharge is exceeded during 95% of the time of measurement

DISCUSSION

Annual growth increments varied among years for each age class of both blue catfish and flathead catfish; but, overall, the variation for both species was smaller than we expected in a highly variable environment such as the LMR. The magnitude of the potential variation in growth rate was illustrated by the substantially greater growth increment for age 5 than for other age classes for both species. Nevertheless, some variation in growth occurred among years for both species.

Blue catfish and flathead catfish are native to warmwater rivers of the central United States including the Mississippi River (Graham, 1999; Jackson, 1999). Our expectation was that their growth would be influenced by thermal and hydrological conditions associated with spring flood pulses. We did not detect consistent positive relationships between mean temperature, length of growing season, mean river stage, or areal and temporal measures of inundated floodplain habitat as predicated by basic fish growth-temperature responses (Welcomme, 1979; Weatherly and Gill, 1987) or the Flood-Pulse Concept (Junk *et al.*, 1989). However, for blue catfish, we did find positive relationships between annual growth increment and days or area-days of floodplain inundation when river water temperature exceeded 15°C, a temperature approximating the thermal threshold for active feeding and growth by ictalurid catfishes. Further, growth increment was consistently greater across year classes during GY 1996 (CY 1995), a year of protracted warm-water floodplain inundation. This corroborates previous findings by Schramm *et al.* (2000) and supports the 'thermal coupling' component of the Flood-Pulse Concept proposed by Junk *et al.* (1989).

We did not find consistent positive relationships between temporal or spatial measures of floodplain inundation when water temperature exceeded 15°C for flathead catfish. Unlike blue catfish, which forage extensively on inundated floodplain habitats (Eggleton and Schramm, 2004), we rarely collected flathead catfish in LMR floodplain habitats. Hence, lack of significant positive relationships with floodplain inundation measures is not unexpected. The absence of a year or years of consistently enhanced growth across age classes of flathead catfish, in contrast to the consistently high growth increments across age classes of blue catfish in GY 1996, also suggests differences in use and growth benefit of the floodplain between the two catfish species. Similar results were obtained in the upper Mississippi River where growth of floodplain-dependent fishes was increased during CY 1993, a year of protracted, summer floodplain inundation (Gutreuter *et al.*, 1999). Consistent with our results, no growth response was detected in that study for a more riverine species.

Unlike the results obtained by Gutreuter *et al.* (1999), we did not find increased growth increment associated with the protracted flooding in the LMR during 1993. Growth is one component of fish production, but recruitment also is important. Our sampling was not designed to measure or estimate catfish recruitment rates. However, strong reproduction and recruitment for the 1993 year class of blue catfish can be inferred from the greater numbers of fish of that cohort available for growth increment analyses (Table II).

Implications for conservation and management of the lower Mississippi River

Our results corroborate and expand on an earlier study by Schramm *et al.* (2000), which indicated that growth of catfishes in the LMR was linked to floodplain inundation, but only when water temperatures were sufficient for active catfish feeding and growth. This finding also agrees with greater growth of floodplain fishes observed in the upper Mississippi River during an unusual year (the 'flood of 1993') when floodplain inundation persisted throughout summer, thus providing warm water coincident with floodplain inundation. However, it is apparent from our results is that warm-water floodplain inundation accounts for only a moderate portion of the variation in growth of floodplain fishes. Future studies in the LMR need to address other possibilities, such as annual variation in primary catfish prey items (e.g., fishes, decapod crustaceans, and molluscs; Eggleton and Schramm, 2004), habitat quality and quantity, local nutrient sources, or possible interactions within and between catfish populations (e.g., Edds *et al.*, 2002).

Rutherford *et al.* (1995) suggested that the lack of expected positive relationships between fish growth and floodplain inundation in the lower Mississippi River may have been attributed to the high degree of alteration of this system, particularly the loss of connectivity with more than 90% of the historical floodplain. Evidence from various floodplain-river ecosystems supports the importance of floodplain connectivity (e.g., Welcomme, 1979; Heiler *et al.*, 1995; Ward and Stanford, 1995; Tockner *et al.*, 1999). Although the LMR has lost much of its historic floodplain, an expansive active floodplain still remains.

Considering that a substantial floodplain is still connected to the LMR, attributing lack of energetic and reproductive benefits to historic loss of floodplain may be premature without considering thermal factors. Grubaugh and Anderson (1988) reported that the present-day upper Mississippi River flooded earlier and for shorter duration than it did historically during a period of record exceeding 100 years. They concluded that excessive channelization and flood control practices throughout the basin contributed most to the altered flood pulse. Retention of floodwaters in floodplains, as occurs in an unaltered river-floodplain system, would be expected to moderate water temperatures during annual flood pulses, thereby creating a more suitable thermal environment for warmwater fishes. The consequences of an earlier and abbreviated flood pulse may be exacerbated in temperate rivers, which show distinct warm-cold cycles.

The LMR may fall into this category. During 1933–1942, 16 bendway cutoffs shortened the river by 245 km (Baker *et al.*, 1991). The morphology of the LMR is a product of many influences, precluding cause-effect relationships for an individual factor. However, man-made cutoffs and the associated channel aggradation and degradation, which promote lesser connectance with floodplains, have had the most dramatic effect of any occurrence on channel morphology (Biedenharn and Watson, 1997). Based on river stage data collected at Vicksburg, Mississippi (river km 702, 14 km downstream of our lowermost sampling site), the average period of floodplain inundation was 4–5 months (early February through early July) prior to cut-off construction compared to 2 months (mid-March to mid-May) following cutoff construction (Schramm, 2004). As evident from Figure 1, thermal conditions of these altered flood pulses vary among years, though river water temperatures typically reach 15°C by mid-April. Thus, under the current hydrographic conditions in the LMR, the duration of floodplain inundation when water temperature exceeds 15°C is only about 1 month per year on average. Such a brief period of time may be insufficient for floodplain-foraging fishes like the blue catfish (and other fishes; see Schramm, 2004) to achieve a detectable energetic benefit. The abbreviated period of warm, flooded conditions also would be expected to adversely affect recruitment of numerous warmwater fishes (Schramm *et al.*, 2000).

The alteration of the thermal cycle is compounded by the main line levees in the LMR that constrain floodwaters, resulting in deeper, more swiftly-flowing waters on the floodplain. This hydrological characteristic, likely common in many temperate river systems, may further impede water warming when compared to shallower water spread over an expansive floodplain. Further, the narrower, leveed floodway is more prone to rapid rises and falls, reducing the ‘flood-pulse advantage’ proposed by Bayley (1991). Thus, the cutoffs and levees in the LMR in concert may function to reduce fishery productivity benefits from a more prolonged and thermally desirable flood pulse.

Returning the LMR to historical hydrological conditions is a paramount component of floodplain river restoration (Bayley, 1991; Sparks *et al.*, 1998). In the LMR, this strategy would help ‘recouple’ the natural thermal and hydrological conditions. In the unimpounded LMR, restoring the hydrograph will require restoring the sinuosity (and thus, the length and slope) of the main channel and the width of the floodplain. Because of the importance of the LMR for navigation and flood control, restoring the sinuosity and removing the levees is extremely unlikely.

Gore and Shields (1995) stress the key to the river restoration in the developed world is the partial recovery of some of the river’s ecological values and functions in carefully selected reaches. We suggest that adaptive management of the existing LMR floodplain will enhance fisheries production, and concurrently provide opportunities to further explore the ecological function of temperate floodplain-river ecosystems. Specifically, strategies designed to detain and warm floodplain waters are needed to recouple the thermal and flood cycles. Such strategies should include maintaining or re-establishing connectivity of existing waterbodies within the leveed floodplain. During summer low-water stages, there are approximately 53 300 ha of lakes on the floodplain; however, less than 25% of these lakes remain connected to the river (Schramm *et al.*, 1999). Although important aquatic habitats, these lakes comprise a relatively small area of the LMR and are being steadily lost to sedimentation (Schramm, 2004). Thus, we suggest that restoration of ecological function may also require construction of new floodplain waterbodies. Although such management activities may seem ambitious or otherwise far-fetched, they would require only a small fraction of the resources that have been dedicated to construction projects necessary to maintain navigation and alleviate flooding in the lower Mississippi River-floodplain ecosystem.

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