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Early life history dynamics of the fish community in the Atchafalaya River Basin

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**EARLY LIFE HISTORY DYNAMICS OF THE FISH COMMUNITY IN THE
ATCHAFALAYA RIVER BASIN**

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Renewable Natural Resources

by

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August 2010

DEDICATION

This manuscript is dedicated to the following individuals:

James Francis Halloran, Joe Moore, Laurie Guess, Theodore Votteler, M.D., Phil Junghans,
Richard Hunter, Mary Winn Starr, Wishy Halloran, Minerva Waites,

and
Bud and Bern

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TABLE OF CONTENTS

DEDICATION.....	ii
ACKNOWLEDGEMENTS.....	iii
ABSTRACT.....	viii
CHAPTER 1: GENERAL INTRODUCTION.....	1
DISSERTATION OVERVIEW.....	7
LITERATURE CITED.....	7
 CHAPTER 2: THE DISTRIBUTION OF AGE-0 FISHES IN TEMPORARY BACKSWAMP HABITATS IN THE ATCHAFALAYA RIVER BASIN.....	 12
INTRODUCTION.....	12
METHODS.....	16
RESULTS.....	21
DISCUSSION.....	35
LITERATURE CITED.....	42
 CHAPTER 3: EVALUATING THE LEVEL OF SYNCHRONOUS OVERLAP BETWEEN MICROCRUSTACEAN ZOOPLANKTON AND ICHTHYOPLANKTON IN A TEMPERATE RIVER-FLOODPLAIN SYSTEM.....	 47
INTRODUCTION.....	47
METHODS.....	49
RESULTS.....	56
DISCUSSION.....	75
LITERATURE CITED.....	81
 CHAPTER 4: INTRADAY DENSITY AND MEAN LENGTH COMPARISONS OF LARVAL SUNFISH AND SHAD.....	 89
INTRODUCTION.....	89
METHODS.....	90
RESULTS.....	93
DISCUSSION.....	98
LITERATURE CITED.....	102

CHAPTER 5: GENERAL SUMMARY AND CONCLUSIONS.....	107
LITERATURE CITED.....	111
VITA.....	114

ABSTRACT

Seasonal overbank flooding in systems like the Atchafalaya River Basin (ARB) provides the opportunity for fishes in the mainstem to access off-channel areas on the floodplain. Typically, newly inundated floodplain habitats allow adult fishes to add biomass, avoid predation, and potentially, to reproduce. However, in systems like the ARB, the timing, duration, and magnitude of flooding infrequently coincides with known reproductive periods of many fishes assumed to be floodplain-dependent.

To quantify the level of floodplain-exploitative fish reproduction in the ARB, I collected larval and juvenile fish with a variety of sampling gear that allowed estimates in both ultra-shallow (≤ 2 -m) and continuously-inundated habitats (headwater lakes, canals, and bayous). A suite of water quality parameters, river stage, flow, and hours of daylight were used to gauge the influence of environmental phenomena on age-0 abundance during both inundation and drawdown. The results of the 19-month study suggest that many taxa do not rely on the floodplain to ensure high survivorship. Interestingly, the reproductive ecologies of many ARB fishes appeared to be largely independent of widespread connectivity. Although an increasing hydrograph appeared to enhance reproductive output, the interannual timing and intensity of spawning showed limited variability.

Larval densities were also contrasted with the microcrustacean zooplankton (copepods and cladocerans) population to assess if a potential food limitation existed in the weeks and months following hatching. During the study, increased zooplankton abundance was typically preceded by elevated river-floodplain connectivity. Conversely, as floodwaters receded during the summer, zooplankton abundance declined to lowest levels observed during the study. Overall, there was limited synchronous overlap between the hatchlings of most fish taxa and

their zooplankton prey. This could have potentially resulted in starvation and reduced annual recruitment. Yet, my analysis of the factors that regulate larval fish abundance in the ARB suggest that the density of zooplankton was highly significant although high numbers of larvae and zooplankton rarely coincided.

Finally, I compared the intraday (morning vs. afternoon) density and mean length of larval fish at fixed sample sites. The results suggest that once-daily ichthyoplankton collections may fail to provide accurate density and length measurements for young fish populations.

CHAPTER 1. GENERAL INTRODUCTION

Over the last century, the flow regimes of many large temperate rivers have been interrupted by impoundments, diversion projects, and extensive levee systems that have altered the timing, duration, and predictability of the annual hydropulse (Belt 1977; Fleming et al. 1989; Dynesius and Nilsson 1994; Sparks 1995; Schramm et al. 2000; Schramm et al. 2009). The effects of these anthropogenically-induced changes have been particularly pervasive in the Northern Hemisphere, where numerous biogeographically diverse fluvial systems have experienced disruptions that have: (1) altered the deposition rate of sediments; (2) lessened the ability of a river to serve as a corridor for migrating organisms; (3) reduced sinuosity; (4) impoverished riparian zones; and, (5) fragmented upstream-downstream aquatic populations (Dynesius and Nilsson 1994; Ward and Stanford 1995; Nilsson et al. 2005).

Conversely, in the tropics, large-order river systems generally have not experienced the same degree of degradation (Dynesius and Nilsson 1994). The combination of widespread overbank flooding coupled with a predictable precipitation pattern and limited temperature variability results in relatively consistent system-wide conditions for many months (Goulding 1980; Welcomme 1985). These environmental factors are believed to be the principal evolutionary force responsible for biodiversity, reproductive ecologies, and recruitment (the survival of a fish to a specific time in its life cycle) dynamics of tropical fish communities (Junk et al. 1989; Rodríguez and Lewis 1997; Lewis et al. 2000; Hoeinghaus et al. 2003).

Increasingly, theoretical concepts based on observations in equatorial rivers have been extended to explain the behavior and life history strategies of fishes in non-tropical

ecoregions. Currently, floodplain ecology relies on the flood pulse concept (FPC) to interpret a broad range of interactions between a river and its floodplain (i.e., nutrient cycles, development of off-channel macrophyte communities, formation of plankton assemblages; Junk et al. 1989). The FPC framework proposes that sustained connectivity between the mainstem and the floodplain allows fishes to exploit seasonally-inundated habitats to add biomass, avoid predation, and reproduce (Goulding 1980; Welcomme 1985). It is unclear, however, if isolated low-flow temperate backswamps serve as critical nursery habitats for fish larvae in systems that are characterized by extremely intermittent connectivity. Further, there is evidence that changes in the arrival and pattern of discharge have altered both water temperatures (Schramm and Eggleston 2006) and nutrient dynamics (Schramm et al. 2009).

Outside of the tropics, robust off-channel recruitment typically occurs when the reproductive cycle of a particular fish species overlaps with sustained flooding and high temperatures. If the majority of warmwater riverine fishes are obligate flood-exploitative, then the peak spawning periods of these taxa should be coincident with periods of high connectivity. Yet, given the irregular hydroperiods of low-gradient temperate river systems (Winemiller 2004), there may be limited opportunity for adults in the mainstem to access the inundated floodplain and reproduce. Additionally, episodic flooding often produces unstable post-flood conditions in backswamps that could serve as nursery areas for many taxa (Killgore and Baker 1996; Fontenot et al. 2001; King et al. 2003; Jackson 2005). Although ichthyoplankton can probably withstand multiple stressors (e.g., sub-optimal physicochemistry, invasive fish species, persistence non-native vegetation, unpredictable floodplain connectivity), intermittent flooding may

reduce the benefit of off-channel spawning, because fry may become stranded in isolated backswamps as floodwaters recede (Killgore and Baker 1996; Fontenot et al. 2001; King et al. 2003).

Few studies of larval fish populations in temperate rivers have documented consistent use of temporary habitats outside of the main channel (Turner et al. 1994; Kilgore and Baker 1996; King et al. 2003). Some researchers have concluded that many fishes, termed flood-quiescent (see Galat and Zweimüller 2001), do not appear to exploit increasing river stage but instead respond to pulses by emigrating from isolated floodplain lakes and sloughs back to the mainchannel (Ross and Baker 1983). Surveys within flooded backwater habitats have failed to locate ichthyoplankton diversity represented by the adult population in the mainstem (Turner et al. 1994; Killgore and Baker 1996; Humphries and Lake 2000; Fontenot et al. 2001; King et al. 2003; Miranda 2005). The inability to document many taxa that could potentially invade the floodplain in the aftermath of inundation, suggests that although pulses may provide subtle reproductive cues that initiate reproduction, access to newly flooded areas may not be absolutely necessary for strong recruitment for many species. Further, fishes that concentrate spawning in phase with a rising hydrograph may experience reduced post-flood larval survivorship because seasonal overbank flooding often fails to create stable, long-term spawning and nursery habitats (see Humphries et al. 1999; Fontenot et al. 2001).

Another poorly understood element of freshwater fish ecology are the predator-prey dynamics that influence the earliest stages of life. As fry transition to exogenous foraging, the abundance of zooplankton prey could strongly influence the year-to-year

survival of age-0 individuals. It has been suggested that successful recruitment is regulated largely by the overlap of developing larvae in conjunction with elevated plankton biomass (Cushing 1990). Cushing (1972; 1990) proposed that the survivorship of age-0 fishes in temperate oceanic systems was related to the level of primary and secondary productivity in the weeks and months following hatching. This concept, the match/mismatch hypothesis (MMH; Cushing 1972), postulates that fixed spawning and variable plankton blooms combine to produce recruitment variability. Under this premise, optimal spawning strategies “forecast” primary production to ensure adequate food resources for pre-recruits. Any environmental factor, however, that suppresses the onset of planktonic production may impact year-classes by starving young fishes (Rothschild 1986; Cushing 1990).

While the flood pulse transports sediment-rich floodwaters that sustain periodic plankton blooms, initially, inundation destabilizes both phytoplankton and zooplankton communities (Welcomme 1985). In the weeks following flooding, the diversity and biomass of zooplankton tends to increase, especially when widespread flooding coincides with increasing hours of daylight, but both population size and composition have been linked to consistency of seasonal river-floodplain connectivity (Schemel et al. 2004; Grosholz and Gallo 2006). Consequently, floodplain-exploitative fish reproduction may not occur in concert with peak primary and secondary production, especially in areas that experience episodic connectivity. In contrast, increased zooplankton productivity in the mainstem generally occurs in phase with a declining hydrograph (Basu and Pick 1997). Under these conditions, reduced flows create slack-water habitats that larvae have been found to utilize, especially during the summer (Humphries et al. 1999; Schiemer 2001).

This enables developing fishes to exploit the prey-rich, low-flow conditions within the main channel and avoid being passively entrained and transported to sub-optimal nursery areas.

Study Site

In the southeastern United States, bottomland hardwood forests (BLH) are among the most diverse and productive ecosystems in North America (Hefner and Brown 1985; Harris and Gosselink 1990; Sharitz et al. 1993). The productivity associated with these areas results from seasonal flood pulses that reset microbial and nutrient cycles as floodwaters inundate previously disconnected areas (Fleming et al. 1989; Bayley 1995). Since the 1720s there has been a concerted effort to control and redirect flows in the lower reaches of the Lower Mississippi River Valley (LMRV), which has significantly altered the hydrologic cycle of the entire system (Belt 1977; Fleming et al. 1989). Presently, water management projects and land-use practices in the LMRV, aimed primarily at controlling its dominant fluvial feature, the Mississippi River, have reduced the floodplain land area by at least 90% and diminished the level of lateral connectivity (Belt 1977; Fleming et al. 1989). As with other alluvial systems, there has considerable effort to isolate the LMRV floodplain to prevent catastrophic overbank flooding in urban and agricultural areas that border the main channel (Dynesius and Nilsson 1994; Sparks 1995).

The Atchafalaya River Basin (ARB; Figure 1.1) is the largest remaining BLH floodplain system in North America (Reuss 2004). Although mainstem flows are regulated, much of the floodplain still includes a mosaic of habitats (e.g., headwater lakes, bayous, and swamps) that could be suitable reproductive habitats for the

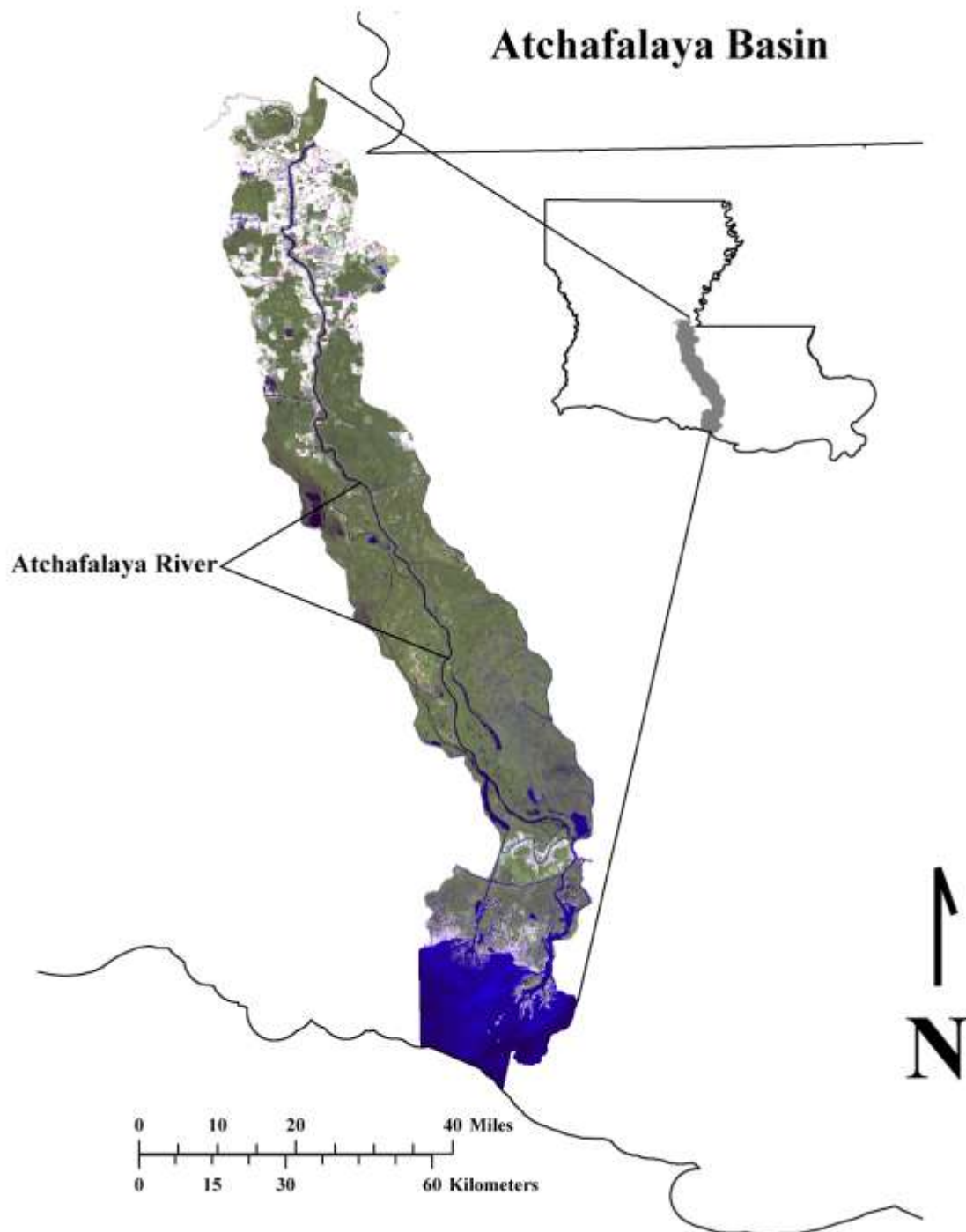


Figure 1.1 — The Atchafalaya River Basin in south-central Louisiana, USA.

community of 100-resident freshwater fish species that is associated with the system. Typically, the ARB hydropulse includes extensive periods of springtime connectivity (Bonvillain et al. 2008) that overlap with the known spawning periods of many fishes that would be capable of exploiting off-channel microhabitats. Thus, the ARB offers the opportunity to examine some of the assertions that fisheries ecologists have advanced regarding the early life history dynamics of warmwater fishes in temperate river-floodplain systems.

DISSERTATION OVERVIEW

There are three components to this dissertation. First, I characterize the annual distribution and abundance of age-0 fishes in seasonally-inundated backswamps in relation to multiple physicochemical and environmental parameters, including mainstem discharge (Chapter 2). Also, I compare the density of zooplankton and ichthyoplankton to establish the degree of seasonal, synchronous co-occurrence between the two groups. Additionally, I examine which water quality conditions coincide with the most common-occurring fish larvae in the ARB (Chapter 3). Finally, I contrast the temporal (morning vs. afternoon) differences in density and mean length of sunfish and shad larvae and assess the statistical confidence of replicates used to derive the abundance of pre-recruits (Chapter 4). The final chapter is a summary of the dissertation and its findings as well as suggestions for further research in the ARB (Chapter 5).

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CHAPTER 2. THE DISTRIBUTION OF AGE-0 FISHES IN TEMPORARY BACKSWAMP HABITATS IN THE ATCHAFALAYA RIVER BASIN

INTRODUCTION

In riverine systems continuous or episodic flooding allows organisms access to off-channel environments as waters rise and systems shift from dry to lotic to lentic. Because floods affect a broad range of important subsidies between a river and its floodplain, it is believed that aquatic biota have evolved to exploit the predictable seasonal advance of floodwaters (Goulding 1980; Welcomme 1985), and further, that the annual flood pulse in subtropical and temperate floodplain ecosystems is the primary agent shaping freshwater fish communities, including spawning (Junk et al. 1989). If the degree of floodplain-dependent fisheries reproduction primarily relies on significant, widespread inundation, then larval fish densities should peak as a consequence of increasing floodplain connectivity with the mainstem. However, evidence of speciose ichthyoplankton communities on the inundated floodplain of non-tropical riverine systems remains elusive (Humphries et al. 1999; Fontenot et al. 2001; King et al. 2003).

The duration, magnitude, and timing of flood pulses in equatorial systems (e.g., Amazon, Zaire, and Orinoco rivers) shape the diversity, abundance, and migratory behavior of fishes (Goulding 1980). In particular, predictable large-scale flooding has been observed to be the determining factors influencing spawning behavior and larval survivorship in the tropics (Welcomme 1985). Consequently, it has been hypothesized that native fish populations outside of the tropics might also rely on inundation, especially springtime floods, to ensure successful reproduction (Junk et al. 1989). However, aperiodic flooding coupled with unpredictable precipitation patterns often

produces limited discharge to areas that are adjacent to the mainstem (Humphries et al. 1999; Benke et al. 2000; Humphries et al. 2002; Winemiller 2004). In many sub-tropical and temperate regions, the greatest reproductive effort sometimes appears to be independent of inundation, occurring during periods when mainstem flow, water quality, and river-floodplain connectivity are diminished (Humphries et al. 1999; King et al. 2003).

Although the Flood Pulse Concept (FPC; Junk et al. 1989) predicts that overbank flooding should be the primary agent structuring the abundance of young-of-the-year (YOY) fishes, a strong correlation between the extent of inundation and successful year-to-year recruitment has been difficult to observe in low gradient rivers (Fontenot et al. 2001; King et al. 2003). Increasingly, research suggests that ichthyoplankton abundance and species composition in many temperate riverine systems is regulated by an intricate combination of: 1) physicochemical processes (Fontenot et al. 2001); 2) zooplankton assemblages (Chick and Van Den Avyle 1999); 3) hydrologic cycles (Killgore and Baker 1996; King et al. 2003); and 4) reproductive strategies (Humphries et al. 1999; Garvey et al. 2002). Accordingly, post-hatching survival could be considerably enhanced by the ability to tolerate a wider, often subtle, suite of such environmental conditions that follow annual peaks in the hydrograph (King et al. 2003).

In the southeastern and southcentral United States, coastal floodplains consist primarily of bottomland hardwood (BLH) forests (Benke et al. 2000; Hupp 2000), experience intermittent winter and springtime flooding that typically lasts a few weeks (Taylor et al. 1990; Turner et al. 1994; Killgore and Baker 1996; Fontenot et al. 2001; Bonvillain et al. 2008). Previous studies documenting ichthyoplankton dynamics in BLH

floodplains have suggested that many taxa concentrate their reproductive efforts in seasonally disconnected backwaters (Finger and Stewart 1987; Killgore and Baker 1996; Fontenot et al. 2001). These systems contain diverse fish communities that include species capable of using off-channel areas to reproduce (Risotto and Turner 1985; Fremling et al. 1989; Jackson 2005). During drawdown, as water levels stabilize and drop, dissolved oxygen (DO) levels on the inundated floodplain may fall rapidly because of high bacterial decomposition rates. As a result, poor water quality, which approaches the lethal tolerances of many fishes, often characterizes the later stages of the flood pulse (Rutherford et al. 2001). Although adult fishes can escape these conditions, larval fishes may become stranded in hypoxic (hereafter DO levels ≤ 2.0 mg/L) nursery habitats as floodwaters recede and eventually evaporate. Consequently, the benefits of spawning in backswamps could be negligible, if newly hatched fry are unable to survive physicochemical variability as floodwaters recede.

The BLH and cypress-tupelo swamps within the Atchafalaya River Basin (ARB), in southcentral Louisiana, regularly experience a 2 – 3 m spring flood pulse (Sabo et al. 1999a), which provides large areas recognized as being potentially suitable floodplain spawning habitat for a resident 100-species fish community (Fremling et al. 1989). However, anthropogenic modifications to the ARB have altered the annual flooding regime resulting in spatially extensive and temporally persistent hypoxia across the floodplain (Sabo et al. 1999b; Rutherford et al. 2001).

This research focused on the seasonal extent of backwater microhabitat use by spawning ARB fishes and the relationships between floodplain water quality and larval fish abundance. Specifically, this study examined seasonal ichthyoplankton composition

in transient backwater areas of the inundated floodplain, particularly those that were thought to provide adequate nursery habitats (Fontenot et al. 2001; Engel 2003), to determine which abiotic factors influenced age-0 fish abundance prior to and following the annual springtime flood pulse.

Study Area

The 5,000 km² ARB is the largest remaining floodplain swamp in North America (Reuss 2004). It is composed of a complex system of headwater lakes, natural bayous, man-made canals, and overflow areas (Lambou 1990). Before the construction of the Old River Control Structure in 1963, swamps and lakes in the ARB received water primarily from the Red River or seasonal Mississippi River discharges (Reuss 2004). Currently, the Atchafalaya River receives 30% of the combined flows of the Mississippi and Red rivers on an annual basis (Fremling et al. 1989; Reuss 2004). Water management practices have included considerable bank stabilization projects along with the creation of an elaborate levee system designed for flood control (Reuss 2004). In order to facilitate water and sediment movement in the main channel, several distributaries from the mainstem of the Atchafalaya River to the floodplain have been closed (Sabo et al. 1999b). Also, petrochemical exploration and extraction, as well as timber harvesting, have resulted in numerous canals that bisect large portions of the floodplain. Spoil banks associated with these canals have been shown to disrupt water flow on the inundated floodplain and contribute to the widespread hypoxia that often occurs during drawdown (Sabo et al. 1999a; Sabo et al 1999b; Fontenot et al. 2001).

METHODS

Sample Locations

Three sampling locations, Buffalo Cove (BC), Lake Fordoche (LF), and Department of Energy/Twenty-one inch Canal (TWI), were selected based on geographic location on the floodplain, dissimilar distances from the mainstem, and varying degrees of historic hydrologic connectivity (Figure 2.1). Typically, these locations intermittently receive water from the Atchafalaya River but continuous, widespread flooding is infrequent (Lambou 1990; Reuss 2004). As a result, water quality and river-floodplain connectivity tends to be highly variable, especially during the optimal reproductive periods of many ARB fishes (Lambou 1990; Rutherford et al. 2001; Fontenot et al. 2001; Bonvillain et al. 2008).

Field Collections

Sampling was conducted from 21 February to 18 August 2005 and from 22 February to 27 July 2006. Depending on the degree of inundation, I sampled one location per week and attempted to sample each location at least one time every four weeks for the duration of the study. During 2005, both TWI and BC were sampled six times while LF was sampled seven times. Because of the limited degree of overbank flooding in the spring 2006, BC was inaccessible until the first week of April, consequently, TWI and LF were sampled six times and BC was sampled three times. Annual sampling was terminated once all respective floodplain locations became inaccessible with a shallow-draft boat. Throughout the study, I deployed individual surface and subsurface (1 m) quatrefoil light traps (Floyd et al. 1984; Secor et al. 1992; $n = 713$ in 2005 and $n = 331$ in 2006) in transient backwater areas that normally have a

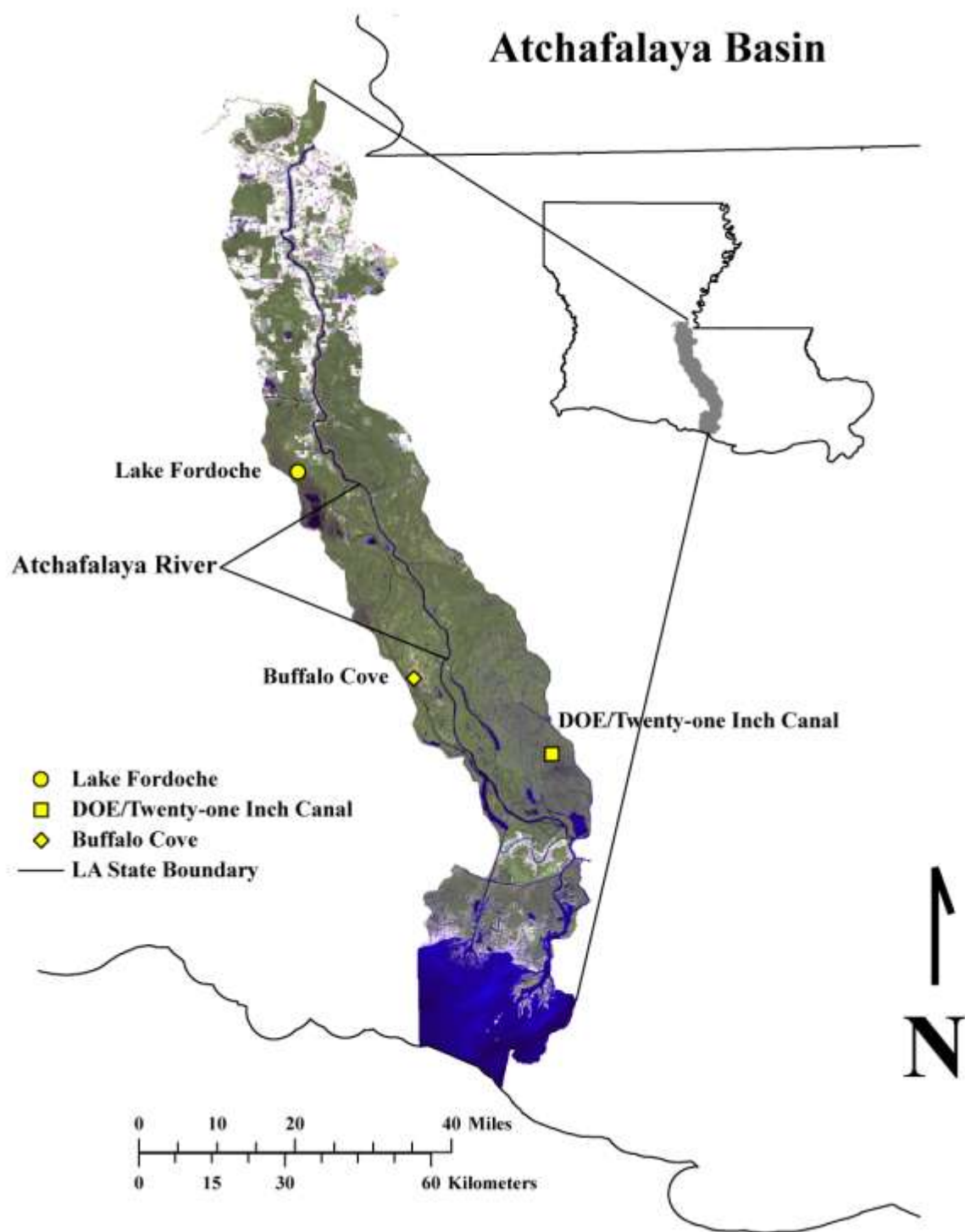


Figure 2.1 — Sampling locations in the Atchafalaya River Basin.

consistent dry-out period (2 - 5 months), as well as backwater lakes and bayous that experience variable seasonal hydrologic isolation. Typically, clusters of 4 to 5 sampling units were non-randomly placed ≥ 2 km apart at each of the BC, LF, and TWI locations. For statistical analysis, a sampling unit on a specific sampling date consisted of a cluster of 3 to 5 individual light traps (30.5 cm x 30.5 cm and 15 cm high with a 500- μ m mesh cod end) within close spatial proximity. All traps were deployed at least 10 m apart to avoid any potential sampling overlap. The light source for all traps was a green Duralume® chemical stick (Lindgren-Pitman, Pompano Beach, FL).

At each sampling unit, I measured surface temperature ($^{\circ}$ C), pH, specific conductance (μ S/cm), turbidity (NTU), and dissolved oxygen (mg/L and % saturation) with a hand held water quality multiprobe (Hydrolab, Hach Environmental, Loveland, CO). To characterize conditions for sub-surface light traps, the same set of physicochemical parameters were also taken when floodplain depth was ≥ 1 m. Surface water movement was measured with a SonTek flowmeter (cm/sec; YSI, Inc., Yellow Springs, OH). Traps were fished for 12 - 14 hours beginning about one hour before sunset. Following retrieval of the traps, fishes were preserved in 90% ethanol and identified to the lowest practical taxonomic level with a binocular compound microscope. Total larval fish length (TL) was measured to the nearest 0.1 mm with an ocular micrometer. The majority of taxa were identified to genera with the aid of a voucher collection at Louisiana State University, as well as the keys found in Houge et al. (1976), Auer (1982), Wallus et al. (1990), Kay et al. (1994), and Simon and Wallus (2006).

Data Analysis

To assess the level of floodplain inundation in relation to the historic hydropulse, I compared the monthly mean stage height (hereafter stage) of the Atchafalaya River at Butte La Rose, LA (United States Geological Survey, gage 07381515) on a month-by-month basis with yearly average (1959 - 2004), and contrasted inter-annual differences in stage over the sampling period. All comparisons were done with analysis of variance (ANOVA), with a Tukey-Kramer *post hoc* adjustment (PROC MIXED, SAS Institute, Cary, North Carolina, vers. 9.1.3). To evaluate the degree of physicochemical variation on the inundated floodplain, I compared DO and temperature (both were log-transformed) at the surface and bottom during each sample year in separate mixed model ANOVAs (PROC MIXED).

Larvae were separated into four categories, yolk sac, preflexion, flexion, and postflexion, based upon developmental changes in the caudal fin (Ahlstrom et al. 1976). To test for differences in the vertical distribution of ichthyoplankton, I compared the abundance of newly-hatch fishes (yolk sac + preflexion) in relation to more ontogenetically advanced larvae (flexion + postflexion) in surface and sub-surface light traps (PROC LOGISTIC). Also, because some light traps included juvenile and adult fishes, as well as larvae, stomach contents of juvenile/adult fishes in 30 randomly selected traps from each year (60 in total) were examined to assess the potential importance of post-capture larval predation.

After reviewing the annual distribution of fishes, backswamp physicochemistry, and stage, I decided that an analysis of the relationship between conditions on the floodplain and age-0 fish abundance should be conducted over two periods, inundation

(all sample dates prior to June 1, hereafter inundation) and drawdown (all samples after June 1, hereafter drawdown). To test for spatial and temporal differences in the overall abundance of larval and juvenile fishes during each field season, I compared the abundance of each group in separate annual ANOVAs (PROC MIXED) with location and Julian day as fixed factors. A *post hoc* assessment was performed on both groups with a Tukey-Kramer adjustment. All poeciliids were excluded from the analysis because of the advanced development of their young in relation to other ARB taxa collected during the study.

The most abundant age-0 taxa collected in the study were separated into three groups based on spawning characteristics. Centrarchids (sunfishes *Lepomis* spp., black basses *Micropterus* spp., and crappie *Pomoxis* spp.) were grouped based on nesting and parental guarding behavior (Carlander 1977; Pflieger 1997). Clupeid broadcast spawners (*Dorosoma* spp.) were grouped because they rely primarily on mainstem transport of developing eggs and hatchlings to low-flow nursery areas (Wallus et al. 1990). Percids were also grouped, because most of the commonly occurring darters *Etheostoma* spp. in the ARB (Fremling et al. 1989; Lambou 1990) have low fecundity and deposit adhesive eggs in the benthos (Page 1983).

I used a mixed model ANOVAs (PROC MIXED) on the log-transformed numbers of larval and juvenile centrarchids, clupeids, and percids collected from each sampling unit on a specific sampling date during the study to assess the affects of water quality and photoperiod on the abundance during inundation and drawdown. The model included river stage (on a specific collection date), flow, water temperature, mean monthly hours of daylight, pH, specific conductance, and DO (fitted as a quadratic

function) as fixed factors on each sampling date. In addition, I included mean river stage at 3, 6, 9, and 12 days prior to sampling (by lagging) to account for the potential influence of inundation on larval and juvenile fish abundance. To control for the affects of Julian day and location, these variables were random (blocked) factors in the model throughout the analysis.

Because of the post-flood paucity of percids and clupeids throughout sampling, a drawdown analysis was conducted only on larval and juvenile centrarchids. Typically, floodplain connectivity is substantially diminished when the Atchafalaya River stage is < 2.8 m (Hupp et al. 2008). Consequently, I concluded that lagging during drawdown was unnecessary because stage was almost continuously ≤ 2 m (2005 range = 0.7 - 2 m; 2006 range = 0.6 - 1.8 m).

RESULTS

Floodplain Physicochemistry

A comparison of the 2005 hydrograph with the historic monthly means at Butte La Rose indicated that stage during January and February was higher ($p < 0.01$) than expected. However, from March - August, which included the springtime flood pulse, the stage was significantly lower ($p < 0.01$). Throughout the entire 2006 sample period (February - July), stage was consistently lower than the preceding 45-year monthly record ($p < 0.01$). A month-by-month (February - August) comparison between the two sample years indicated that monthly stages were dissimilar ($p < 0.01$), except in May ($p > 0.15$) and August ($p > 0.47$). Comparisons of surface DO ($F_{2,53} = 0.22$, $p = 0.80$) and temperature ($F_{2,53} = 1.65$, $p = 0.20$), as well as, bottom DO ($F_{2,46} = 0.58$, $p = 0.56$) and temperature ($F_{2,46} = 0.95$, $p = 0.39$) indicated homogenous physicochemistry among all

three locations in 2005. In 2006, both surface DO ($F_{2,81} = 2.9, p = 0.06$) and temperature ($F_{2,81} = 0.9, p > 0.39$) and bottom DO ($F_{2,21} = 1.29, p = 0.29$) and temperature ($F_{2,21} = 1.15, p = 0.33$), respectively, were also similar across locations.

In 2005, water temperatures (mean = 25.91°C, range = 9.98 - 34.11) dropped rapidly with the arrival of the early seasonal flooding. Although connectivity was highest in January and February, there were two major peaks in stage, occurring approximately six weeks apart starting in early March that coincided with the peak reproductive periods of many ARB fishes (Figure 2.2). Initially, during the first period of springtime flooding, DO levels (mean = 5.23 mg/L, range = 0.74 - 16.08) increased. However, subsequent discharge peaks prior to drawdown tended to coincide with hypoxic conditions on the floodplain. There were very few prolonged stage increases during drawdown yet there was some level of river-floodplain connectivity throughout sampling. The lack of flow on the floodplain in the first year of sampling suggests that it took several weeks before system-wide inundation occurred. Throughout 2005, flows were ≤ 2 cm/sec on 66% of the sampling dates with the greatest variability occurring primarily during reduced periods of summertime river-floodplain exchange (Figure 2.3). During drawdown, stage was continuously ≤ 2 m, and although temperature remained relatively constant; DO showed substantial variability. There were two subsequent DO peaks (Figure 2.3) about a month apart, 21 June and 18 July, which corresponded with a brief rise in the summer hydrograph.

In the spring of 2006, stage was consistently < 3.7 m, consequently, the extent of overbank flooding in many areas was minimal but in early February and late March peaks in the hydrograph resulted in some widespread inundation. However, unlike 2005,

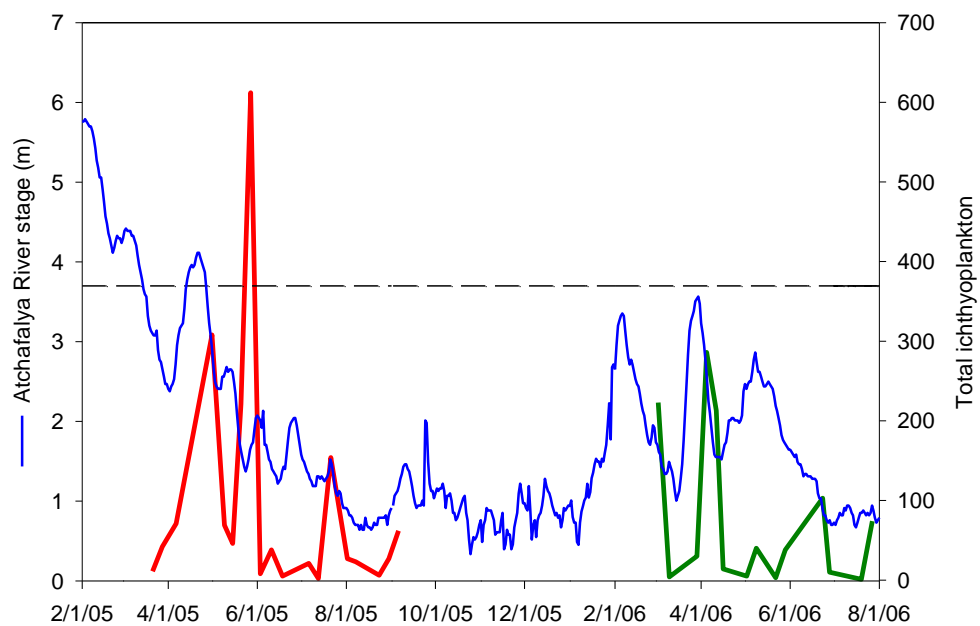


Figure 2.2 — Mean daily Atchafalaya River stage levels (Butte La Rose, LA.) and total number of ichthyoplankton collected on the floodplain during 2005 (—) and 2006 (—). Floodplain inundation is indicated by the dashed line at 3.7 m.

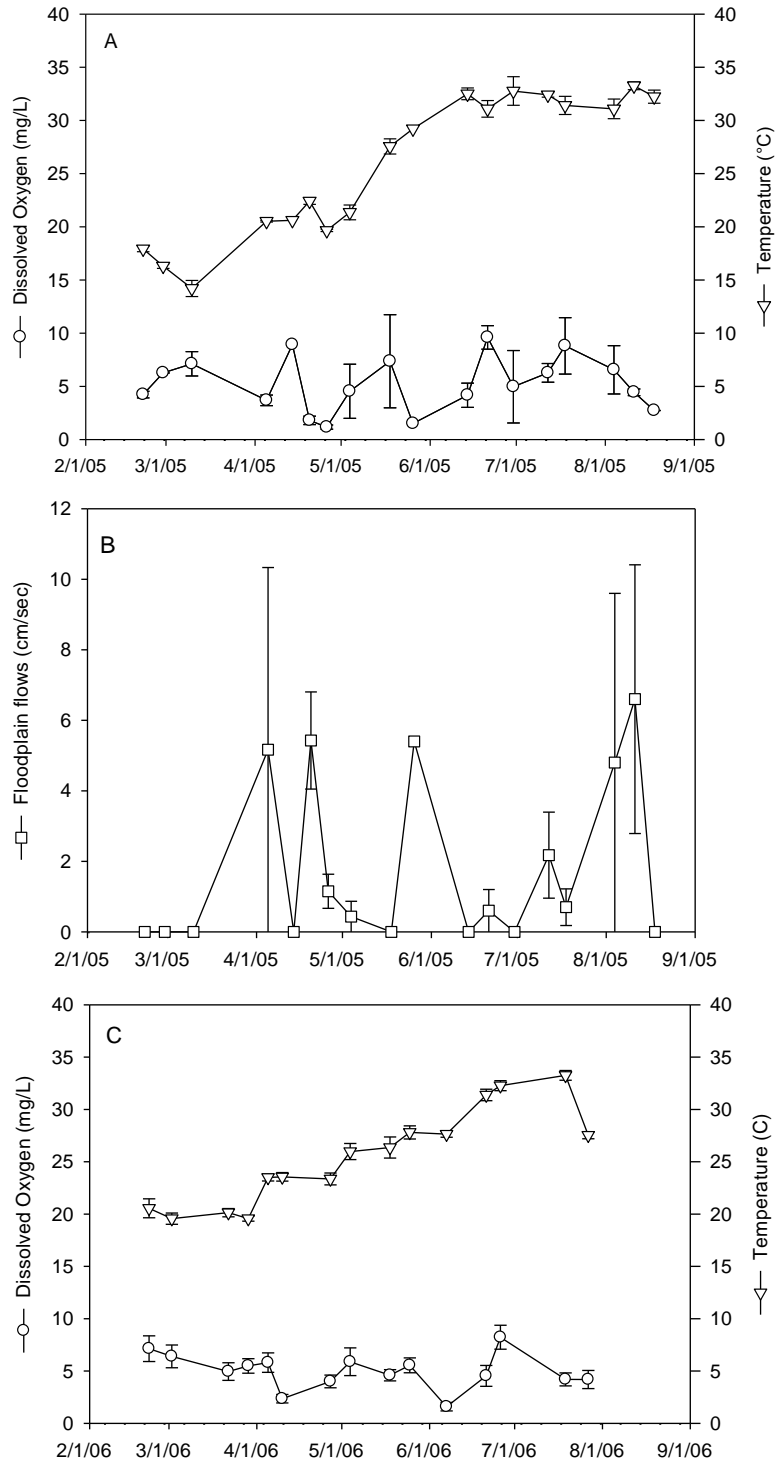


Figure 2.3 — Environmental observations in the Atchafalaya River Basin during 2005 – 2006. Sections A and C include the dissolved oxygen (mg/L) and water temperature (°C) recorded at the surface during each sample season. Section B is the observed water velocity (cm/sec) on the floodplain. Each value represents the daily mean (\pm SE) for each parameter.

connectivity did not appear to significantly alter floodplain physicochemistry, particularly temperature. Floodplain water temperatures (mean = 23.0°C, range = 17.30 - 29.80) gradually increased except for the last sample date in July (Figure 2.3). Despite limited hydrologic exchange with the mainstem, on only one occasion were conditions hypoxic; overall there was nominal week-to-week DO variation (mean = 5.20 mg/L, range = 1.10 - 10.35; Figure 2.3). During the summer of 2006, stage was consistently ≤ 1.8 m and one of the sample locations, BC, completely dried out. Throughout 2006, no floodplain flows were ever detected.

Larval Fishes

I collected a total of 1,739 larvae and 569 juveniles from 11 families in 2005 and 1,044 larvae and 183 juveniles from 10 families in 2006 (Tables 2.1 and 2.2). The most abundant larval taxa for the duration of the two-year study were *Dorosoma* spp. (41.3%), *Lepomis* spp. (19.9%), Percidae (14.1%), *Pomoxis* spp. (10.2%), *Micropterus* spp. (6.1%), and Cyprinidae (5.3%). Juvenile floodplain taxa were comprised of Percidae (34.9%), *Micropterus* spp. (34.7%), *Lepomis* spp. (19.1%), and *Pomoxis* spp. (3.4%). Larval fish abundance in 2005 was dissimilar by both location ($F_{2,1750} = 22.7$, $p = 0.001$) and Julian day ($F_{18,1734} = 42.8$, $p = 0.001$). In the first year of sampling, only pirate perch *Aphredoderus sayanus* appeared to coincide with the highest sustained overbank flooding and lowest water temperatures (range = 14.2 - 17.9°C). Conversely, for other taxa that reproduced in early spring, *Pomoxis* spp., cyprinids, and percids, spawning primarily occurred over a longer period that was bounded by two major inundation peaks, both with a stage > 4 m, which included water temperatures consistently above 20°C. Over a four-week period starting 5 April, which was characterized, in part, by hypoxic

Table 2.1 — Monthly abundance of larval fishes collected in backswamps of the Atchafalaya River Basin during 2005 - 2006.

Taxa	2005							2006					
	Feb	Mar	Apr	May	Jun	Jul	Aug	Feb	Mar	Apr	May	Jun	Jul
Aphredoderidae													
<i>Aphredoderus sayanus</i>	14		5										
Atherinidae													
<i>Labidesthes sicculus</i>			1		2				3				
<i>Menidia beryllina</i>			3						2				
Catostomidae	1		13	1				1	3	3			
Centrarchidae													
<i>Ambloplites</i> spp.	3							1					
<i>Lepomis</i> spp.	1	6	39	59	175	40	80	7	6	21	36	24	75
<i>Micropterus</i> spp.	5		30	100		2		5	25	3	3		
<i>Pomoxis</i> spp.	2	3	30	1				185	64			1	
Clupeidae													
<i>Dorosoma</i> spp.			168	494		6			207	185	2	88	
Cyprinidae	4	12	55	2		2	14		4	15	40		
Fundulidae													
<i>Fundulus</i> spp.			1							2			
Moronidae													
<i>Morone</i> spp.									1				
Percidae	22	50	286	6					24	4	3		
Sciaenidae													
<i>Aplodinotus grunniens</i>									1				
Unknown	1		13				1						
Monthly total	53	71	644	663	177	50	95	199	340	233	84	113	75

Table 2.2 — Juvenile fishes collected in seasonally inundated backwaters of the Atchafalaya River Basin during 2005 - 2006.

	2005							2006						
Taxa	Feb	Mar	Apr	May	Jun	Jul	Aug	Feb	Mar	Apr	May	Jun	Jul	
Aphredoderidae														
<i>Aphredoderus sayanus</i>	1		7	1										
Ameiuridae														
<i>Ameiurus natalis</i>												1		
Atherinidae														
<i>Labidesthes sicculus</i>													1	
Catostomidae			1											
Centrarchidae														
<i>Centrarchus macropterus</i>				5										
<i>Lepomis cyanellus</i>			1	3						2	7			
<i>Lepomis gulosus</i>						2	1					12	13	
<i>Lepomis macrochirus</i>	3		1	9	12	19	5						1	
<i>Lepomis marginatus</i>													1	
<i>Lepomis miniatus</i>					1		3						1	
<i>Lepomis</i> spp.				1	3	1	3	1						
<i>Lepomis symmetricus</i>												9	29	
<i>Micropterus punctulatus</i>											1			
<i>Micropterus salmoides</i>			8	137	1					15		2		
<i>Micropterus</i> spp.			7	24	2				63	1				
<i>Pomoxis annularis</i>				1								2		
<i>Pomoxis nigromaculatus</i>			6	3						2				
<i>Pomoxis</i> spp.			7	1					4					
Clupeidae														
<i>Dorosoma cepedianum</i>						1						1		

Cyprinidae														
<i>Lythrus fumeus</i>							2			5				
<i>Notropis</i> spp.							1							
Esocidae														
<i>Esox americanus americanus</i>	2	1												
Fundulidae														
<i>Fundulus</i> spp.										1		7	1	
Percidae														
			253	4	2	4								
Syngnathidae														
<i>Syngnathus scovelli</i>			5	3		1								
Monthly total	6	1	296	192	21	28	15		1	73	18	3	41	47

conditions, I collected 72% of all ichthyoplankton that occurred throughout the first year of the study. This peak in larval abundance corresponded with a rapid increase in connectivity (stage) but over half of the larvae collected during this period were *Dorosoma* spp. During the final three months of sampling in 2005, only *Lepomis* spp. appeared to consistently exploit the floodplain as both water temperatures and DO levels increased.

In 2006, the first, short-term pulse, lasting less than a week in early February, coincided with the highest levels of percid and *Pomoxis* spp. reproduction. However, once water temperatures reached 23°C, in early April, darter and crappie larvae were infrequent. Overall, larval abundance was different across location ($F_{2,1041} = 69.8$, $p = 0.0001$) and Julian day ($F_{13,1030} = 1201.4$, $p = 0.0001$) in 2006. Although there was little overbank flooding throughout the second year, there was a spike in the hydrograph in late March. During that period, almost 60% of all larvae collected for the entire inundation period occurred but, as in 2005, collections were dominated by clupeids (78%).

Throughout the study, the greatest numbers of larval cyprinids typically followed the first major springtime pulse, with limited evidence of post-flood spawning. As floodwaters receded in the summer, the lone taxon that spawned continuously was *Lepomis* spp., but I did observe a one-time pulse of shad larvae when stage levels were < 2 m in June 2006.

Juvenile Fishes

In the first year of the study, juvenile fish abundance was significantly different among locations ($F_{2,533} = 56.6$, $p = 0.0001$) and Julian day ($F_{17,518} = 16.8$, $p = 0.0001$). The composition and abundance of juveniles during inundation in each year of the study was highly dissimilar. In 2005, percids constituted over 50% all juvenile fishes collected

during the spring, while in 2006 only black basses were abundant (Table 2.2). Conversely, as floodwaters receded in the summer of each year, only juvenile *Lepomis* spp. consistently occurred. In 2005, the peak abundance of larval and juvenile percids occurred during the spring; however, I collected less than 10 juveniles on the floodplain in the months following the springtime spawn. Over the second year of sampling, 90% of all juvenile fishes collected on the floodplain were centrarchids; no other taxa occurred with any regularity in the ARB backswamps. Juvenile taxa were dissimilar by location ($F_{2,180} = 22.9$, $p = 0.0001$) and Julian day ($F_{11,171} = 271.5$, $p = 0.0001$) in 2006 and on two sample dates during inundation I did not observe any juvenile taxa on the floodplain. There was substantially more taxonomic diversity among juveniles in 2005, but there were two juvenile taxa, killifishes *Fundulus* spp. and spotted bass *Micropterus punctulatus*, collected in the second year that I did not document in the prior year of sampling.

Vertical Distribution

A comparison of the distribution of larval fishes in surface and sub-surface light traps indicated that the abundance of yolk sac/preflexion larvae and flexion/postflexion larvae were significantly different ($\chi^2 = 40.97$, $df = 1$, $p = 0.0001$). Although there was an approximately equal distribution of yolk sac/preflexion larvae throughout the water column, 65% of all flexion/postflexion fishes were collected at the surface. Stomach contents of juvenile/adult fishes collected in the light traps revealed no instances of ichthyoplankton consumption.

Centrarchids

During inundation, larval centrarchid abundance was associated by stage 12 days prior to the sample date ($F_{1,19} = 5.7, p = 0.0275$), rising water temperatures ($F_{1,19} = 5.1, p = 0.0346$), and increasing hours of daylight ($F_{1,19} = 14.1, p = .0013$). Throughout the study only 2% of all larval centrarchids occurred when water temperatures ranged between 14 - 18°C. Although the arrival and magnitude of the flood pulse between years was dissimilar, the peak abundance of both larval *Pomoxis* spp. and *Micropterus* spp. (Figures 2.4 and 2.5) occurred over a three to four week period that was preceded by a major rise in the springtime hydrograph. There was almost no evidence (< 1%) of crappie or black bass reproduction over the summer. Conversely, 70% of all larval *Lepomis* spp. were collected during the drawdown period. The highest concentration of *Lepomis* spp. occurred almost two months after the reproductive peaks of all other sunfishes (Figures 2.4 and 2.5). As floodwaters receded, larval centrarchids exhibited a strong positive association with increasing DO ($F_{1,18} = 9.86, p = 0.0057$), even though the average drawdown water temperatures were typically $\geq 31^{\circ}\text{C}$ (Figure 2.3).

Juvenile centrarchid abundance was influenced by increasing hours of daylight ($F_{1,11} = 7.74, p = 0.0178$) during inundation. Throughout drawdown, however, abundance was not correlated with any water quality parameter ($p > 0.15$). The most commonly-occurring juveniles, *Lepomis* spp. and *Micropterus* spp., had different patterns of floodplain abundance in response to the hydrograph (Table 2). Throughout sampling, I collected the majority (98%) of black basses over a two- to three-week period associated with the first rise in springtime stage. Conversely, *Lepomis* spp. occurred primarily

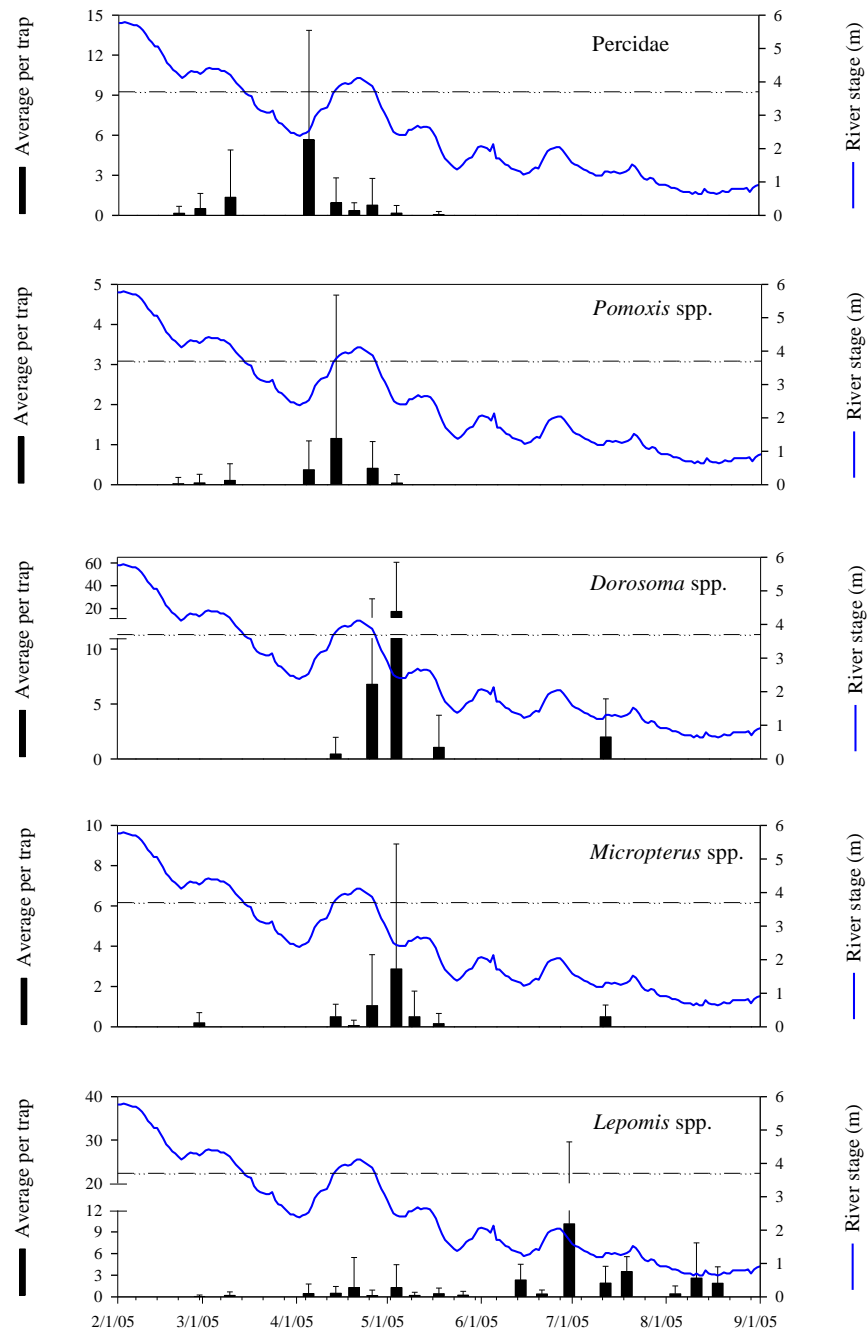


Figure 2.4 — The average number (shaded area) of larval *Pomoxis* spp., *Dorosoma* spp., *Micropterus* spp., *Lepomis* spp., and percidae collected per light trap (\pm SE) in relation to Atchafalaya River stage (obtained from Butte La Rose, LA.) during 2005. Bank full stage of the mainstem is indicated by the dashed line at 3.7 m.

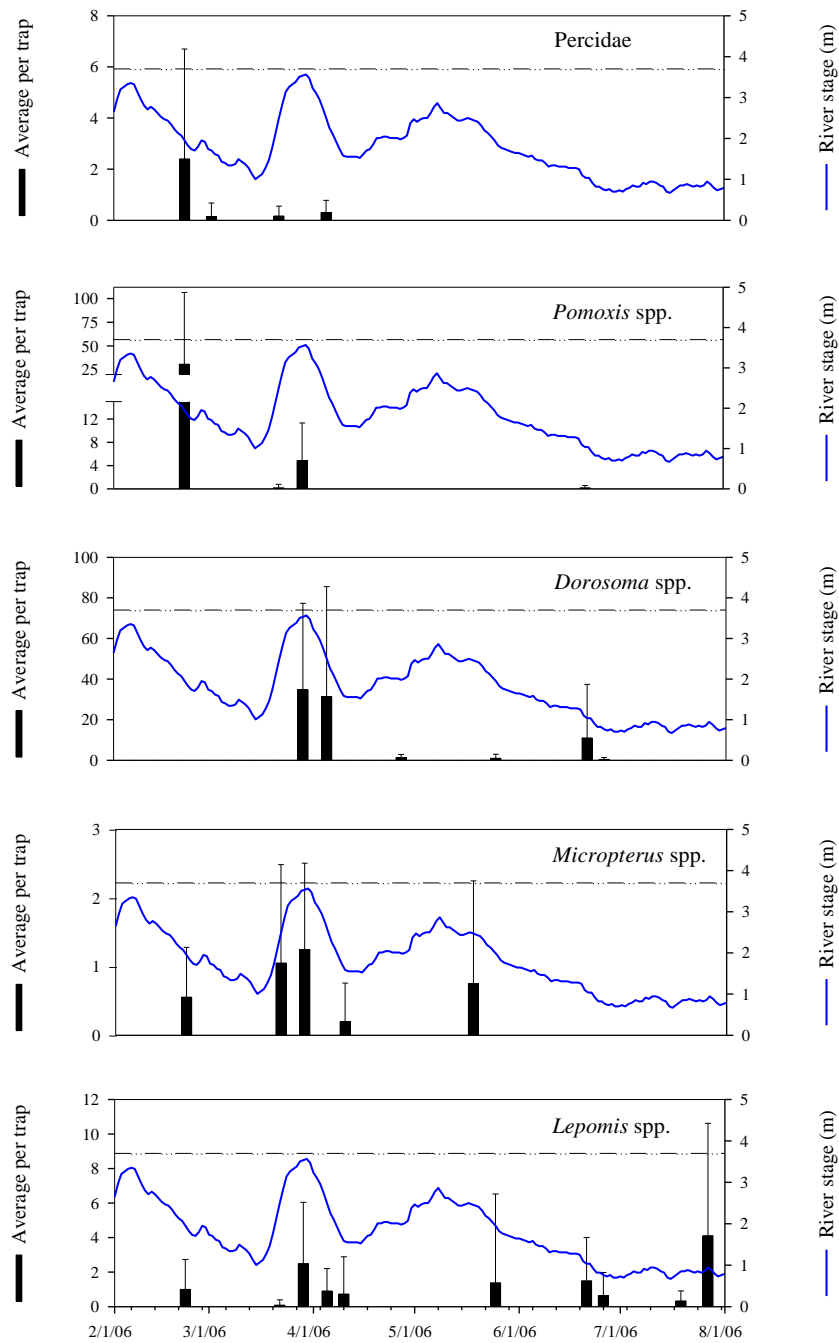


Figure 2.5 — The average number (shaded area) of larval *Pomoxis* spp., *Dorosoma* spp., *Micropterus* spp., *Lepomis* spp., and percidae collected per light trap (\pm SE) in relation to Atchafalaya River stage (obtained from Butte La Rose, LA.) during 2006. Bank full stage of the mainstem is indicated by the dashed line at 3.7 m.

(86%) in the late summer when water temperatures were highest and when floodplain connectivity was lowest. Overall, the greatest taxonomic diversity of centrarchids coincided with prolonged declines in the hydrograph.

Clupeids

Larval *Dorosoma* spp. exhibited a strong positive relationship with increasing DO ($F_{1,12} = 8.87, p = 0.0115$), hours of daylight ($F_{1,12} = 8.35, p = 0.0147$), and stage six days prior to sampling ($F_{1,12} = 6.33, p = 0.0271$). Ninety percent of all clupeids occurred approximately seven to ten days after substantial increases in discharge resulted in episodic river-floodplain connectivity (Figures 2.4 and 2.5). As the floodplain became increasingly disconnected during drawdown, there was little evidence of larval or juvenile *Dorosoma* spp. utilizing the ARB backwaters, except for one occasion in 2006. In the summer of 2006, I collected almost 90 larval clupeids on one sampling date; but all the specimens came from a single cluster of traps ($df = 1$). Therefore, I had no abiotic variability, to explain the post-flood abundance. Although shad were the most commonly-occurring larval taxa collected throughout the study, juveniles occurred infrequently, regardless of river stage or time of year (Table 2).

Percids

Overall, the majority of larval percids were concentrated in the earliest months (Figures 2.4 and 2.5). During inundation, larval percid abundance was related to both increasing DO ($F_{1,10} = 8.30, p = 0.0164$) and specific conductance ($F_{1,10} = 5.69, p = 0.0383$) whereas juvenile percids were associated with a combination of declining water temperatures ($F_{1,11} = 8.13, p = 0.0158$) and increasing hours of daylight ($F_{1,11} = 8.35, p = 0.0147$). Although the extent of early seasonal flooding between years was substantially

different, the peak abundance of larvae was associated with the initial rise in stage that produced overbank flooding. Throughout the study, there was no evidence of darter reproduction in the summer. Darters were the most abundant juvenile taxa in 2005; yet, no individuals were observed in the second year.

DISCUSSION

Presently, there are about 100 freshwater species in the ARB (Fremling et al. 1989; Lambou 1990), but there is very limited data on hatchling or juvenile distribution and abundance anywhere in the system. This is the third multi-year survey of the ARB since 1994, encapsulating both inundation and drawdown, using active or passive collection techniques, which has failed to document diverse and speciose larval fish assemblages in limnetic zones (Fontenot et al. 2001), macrophyte beds (Engel 2003) or the floodplain (this study). Prior to this investigation, it was believed that many age-0 species that consistently failed to appear in previous sampling efforts would occur in shallow backwater habitats (Fontenot et al. 2001). Some fishes could be absent due to an early life history strategy that precludes capture (e.g., parental guarding, schooling, precocial behavior of some larvae, daytime drifting, or negative phototactic response). Nevertheless, given the duration of the study, the distance between sampling locations, and the number of traps deployed (~ 1050), I should have detected some instances of reproduction by the majority of floodplain-dependent taxa. However, my results indicate that: 1) the maximum reproductive effort of most fishes in the system did not consistently overlap with widespread flooding; 2) the timing of reproduction for the most commonly-occurring larvae did not vary from year-to-year; and, 3) the highest abundance of both larvae and juveniles for most taxa tended to coincide.

Despite dissimilar inter-annual hydrographs, the timing of reproduction was relatively consistent. However, the magnitude of seasonal inundation appeared to affect the abundance of some taxa on the inundated floodplain. For instance, percid reproduction was primarily concentrated in the weeks following the arrival of the flood pulse. Darter YOY abundance was associated with environmental parameters (i.e., DO, temperature, and specific conductance) that typically oscillate in conjunction with elevated discharge suggesting that the magnitude of flooding influences survivorship. In 2005, spring floods preceded spawning and extended river-floodplain connectivity coincided with post-hatchling development and appeared to enhance both larval and juvenile darter abundance. During the second year, however, mainstem flows were reduced; this resulted in substantially fewer larvae (Figures 2.4 and 2.5). Although percids comprised almost half of all juveniles collected in the first year of sampling, no individuals occurred in 2006 (Tables 1 and 2). By synchronizing reproduction with the first annual spike in the hydrograph, percid recruitment may depend partially on the "assumption" that concentrated spawning will allow fry to develop in concert with increasing post-flood primary and secondary productivity.

As the Atchafalaya River stage reaches 3.7 m most of the floodplain is inundated (Hupp et al. 2008); under these conditions, sheet flow would have likely passively entrained, transported, and deposited pelagic hatchlings in the mainstem to off-channel areas. Interestingly, the presence of some ichthyoplankton on the floodplain, such as shad, was almost always preceded by mainstem flows that approached or exceeded bank full levels. The dominant clupeid species in the system (Fremling et al. 1989), threadfin shad *Dorosoma cepedianum* and gizzard shad *Dorosoma petenense*, are broadcast

spawners that typically spawn in limnetic areas or low-flow zones along the banks of the main channel (Wallus et al. 1990). Clupeids in the ARB have been observed primarily in bayous, floodplain lakes, and canals that receive riverine water except during the lowest flows (Fontenot et al. 2001). Hatchling abundance was linked to stage level six days prior to sampling as well as increasing floodplain DO, which was presumably altered by the arrival of oxygen-rich riverine water. The lack of association with the shortest lag (3 days) probably resulted from the distance between the gauge at Butte La Rose and the sampling locations (Figure 2.1). Elevated numbers of larval shad in off-channel habitats coincided with a declining hydrograph on only one occasion over two sample seasons (Figures 2.4 and 2.5).

Conversely, centrarchids successfully exploited intermittent levels of river-floodplain connectivity during and following the arrival of the annual flood pulse. The reproduction of both *Pomoxis* spp. and *Micropterus* spp. appeared to be facilitated by temporary spikes in the hydrograph during the spring but, *Lepomis* spp. spawned for months as floodwaters receded in the summer. During inundation, centrarchid abundance was associated with increasing water temperatures and a rise in stage 12 days prior to sampling. Because spawning was primarily concentrated during briefs periods of lateral exchange, abundance tended to peak as the floodplain was becoming increasingly disconnected. The lag between flooding and the appearance of larvae is probably an artifact of sunfish spawning behavior. Prior to breeding, many sunfish males build colonial nests and establish territories (Carlander 1977). Following courtship, fertilized eggs usually take 2 - 5 days to hatch, and fry are guarded by the male to protect against

predation until the young leave the nest (Wallus and Simon 2008). As a result, larvae may not venture far from rearing habitats for almost a week following fertilization.

As floodwaters receded, the abundance of *Lepomis* spp. fry was related to a single water quality parameter, increasing DO. Prior research in the ARB found an immediate decline in the density of larval centrarchids that coincided with widespread hypoxia (Fontenot et al. 2001). There were very few instances of lateral exchange with the mainstem after late May that would have altered floodplain physicochemistry, therefore it's probable that DO variability was attributable to the persistence of plankton communities within the isolated backswamps. The biodiversity of phytoplankton communities typically corresponds to the residence time of water on the inundated floodplain (Schemel et al. 2004); consequently, habitats characterized by increased levels of DO may represent stable, prey-rich environments, in which hatchlings would thrive as the floodplain became increasingly disconnected.

Both crappie and black bass (Figures 2.4 and 2.5) reproduced during as rising hydrograph yet the species-specific peaks of each taxa rarely overlapped. Conversely, sunfishes successfully spawned for months across a broader range of physiochemical conditions that were associated with increasing photoperiod and inconsistent summertime connectivity. It is unclear if a protracted spawning strategy in systems where the timing and duration of flooding is irregular results in higher larval survivorship. Studies examining the annual survivorship of YOY *Lepomis* spp. have consistently reported that the greatest numbers of larvae tend to occur in the late spring and early summer, yet the age distribution of juveniles collected in the fall of the same year indicated that the

survivors were comprised of individuals that hatched much later in the season (Garvey et al. 2002; Santucci and Wahl 2003).

In many high-order tropical riverine systems, fisheries recruitment is structured by a series of relatively dependable ecological events (i.e., inundation, adult upstream migration, spawning, hatching, phytoplankton bloom, zooplankton pulse, downstream transport to nursery areas; see Goulding 1980; Welcomme 1985). Conversely, in southeastern warmwater rivers in North America, peak discharge infrequently coincides with the optimal reproductive periods of many riverine fishes (Benke et al. 2000; Hupp 2000). As a result, many taxa display considerable year-to-year variation in the timing and intensity of reproduction that has been linked to the aperiodic arrival and magnitude of the flood pulse (Finger and Stewart 1987; Turner et al. 1994; Killgore and Baker 1996). The ability of some species to rapidly invade the floodplain following brief periods of inundation may allow for some level of off-channel reproduction, however, the benefits of spawning in phase with the mainstem river may not enhance recruitment because of unpredictable post-flood connectivity (Killgore and Baker 1996), low prey densities (Humphries et al. 1999), and unstable water quality (Fontenot et al. 2001).

During springtime, monthly stage was lower than the historic average but widespread overbank flooding coincided with the known spawning periods of numerous fishes thought to be floodplain-dependent in the system, yet, few taxa reproduced during this period. Further, the distribution of the most commonly occurring species was relatively consistent, despite substantial differences in inter-annual river-floodplain connectivity. Although most taxa were collected at different times, a comparison of water quality on the floodplain did not indicate a significant difference at a specific

sampling location that might have influenced abundance. This suggests that ARB fishes that successfully exploit the floodplain do so based on interspecific differences in parental investment, fecundity, and environmental thresholds rather than community-wide responses to the co-occurrence of multiple environmental cues. This is important because it reduces the reliance on the overlap of ichthyoplankton presence and a number of potentially favorable environmental conditions, which, if they do not occur, might otherwise jeopardize spawning opportunities and, consequently, negatively impact survivorship.

In systems like the ARB, ichthyoplankton hatched in transient backwaters run the risk of perishing in ecological sinks if they cannot evacuate the floodplain before the completion of drawdown. The behavior of hatchlings in this study suggests that YOY fishes in temperate floodplains may have evolved to cope with unpredictable post-flood conditions. For instance, the vertical position of newly hatched larvae over the study, as opposed to more developed individuals, indicated that shortly after hatching, more mature individuals, which were typically 8 - 12 mm TL, appeared to aggregate near the surface. In other systems, it has been suggested that this response could enable hatchlings to catch surface flows and eventually be advected and dispersed downstream (Nezdoliy 1984). This would be especially advantageous in BLH systems that have large areas that often become rapidly disconnected following inundation (Taylor et al. 1990; Hupp 2000). Further, the ARB is known to have widespread, subsurface, chronic hypoxia (Sabo et al. 1999b) that is often coincident with the peak abundances of larval fishes in the system (Fontenot et al. 2001). The ability to change position in the water column might allow developing fishes to avoid unstable environmental conditions on the

floodplain. Although for much of this study DO was normoxic, larvae could actively avoid sub-optimal physicochemistry by orienting to the surface where conditions, particularly DO and temperature, would be more favorable.

It has been suggested that the mainstem-river serves as a "highway" that transports adult fishes to key reproductive areas on the floodplain (Junk et al. 1989). Yet, when Galat and Zweimüller (2001) analyzed the habitat use of fishes in a series of temperate rivers in North America and Europe, the authors concluded that many species did not appear to rely on access to the floodplain. While I did not collect larvae in the Atchafalaya River, the results of this study suggest that off-channel habitats maybe of marginal reproductive importance for many taxa. Long-term ichthyoplankton studies (~ 10 years) in the largest riverine system associated with the ARB, the Mississippi River, have documented many of the taxa not observed in this study (W.E. Kelso and D.A. Rutherford, unpublished data). Given the year-to-year variability of the hydrograph in many temperate lotic systems, the highest temperatures and greatest level of river-floodplain connectivity rarely coincide (see Killgore and Baker 1996; Humphries et al. 1999; Hupp 2000; Winemiller 2004). I documented that many native ARB taxa (perchids, black basses, and crappie) were able to synchronize their reproduction to match brief periods of inconsistent inundation. Over the two-year study period, floodplain-exploitative ichthyofauna in the ARB would have encountered highly variable levels of riverine-floodplain connectivity, physicochemistry, and timing of inundation that have limited the amount of suitable rearing and nursery microhabitats. Only one genus, *Lepomis* spp., appeared to the floodplain in the months following inundation, irrespective of the magnitude or timing of the flood pulse. Increasingly, there is evidence that the

reproductive strategies of fishes, like those that frequently occur in the BLH, have evolved to compensate for abiotic variability and may avoid "hedging" on the co-occurrence of multiple environmental factors. The inconsistent nature of year-to-year inundation may require that floodplain-exploitative fishes, like those in this study, be able to synchronize spawning with ephemeral peaks in connectivity or, in fact, have a decreased reliance on floodplain accessibility to ensure high levels of survivorship.

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CHAPTER 3. EVALUATING THE LEVEL OF SYNCHRONOUS OVERLAP BETWEEN MICROCRUSTACEAN ZOOPLANKTON AND ICHTHYOPLANKTON IN A TEMPERATE RIVER-FLOODPLAIN SYSTEM

INTRODUCTION

Historically, fluctuations in marine fish landings indicated that, despite the high fecundity of many target species, the majority of hatchlings failed to reach adulthood (Helland-Hansen and Nansen 1909). Yet, the processes that regulated the survivorship of young fishes were largely unclear until Hjort (1914) explicitly associated successful recruitment with the ability of larvae to find prey during the first few days as fry transitioned from endogenous to exogenous feeding. This trophic relationship was expanded in "match/mismatch" hypothesis (MMH), which proposed that spawning was adaptively linked with springtime plankton blooms in temperate oceanic systems (Cushing 1972; Cushing 1990). The MMH suggests that seasonal timing of fish reproduction is a relatively fixed event and the inter-annual variability in the number of pre-recruits is directly related to the level of primary and secondary productivity in the weeks and months following hatching.

Young fishes that encounter and assimilate plentiful prey benefit from an acceleration in the timing of specific ontogenetic "events" (i.e., formation of internal organs, fin differentiation, jaw development) that leads to rapid growth and development (Balon 1985). Empirical studies have documented that even minute increases in size result in substantially improved visual acuity (Zaunreiter et al. 1991), enhanced swimming and burst speeds (Williams et al. 1996), improved responsiveness to a potential predator (Fuiman 1989), and the ability to withstand starvation (Fuiman 2002). Consequently, it has been suggested that subtle changes in the duration that larvae spend

during the most vulnerable developmental stages prior to metamorphosing to become juveniles results in order of magnitude differences in cohort survivorship (Chambers and Leggett 1987; Houde 1987). Therefore, considerable research has been focused on characterizing the degree of synchronous occurrence of zooplankters and ichthyoplankton in large-scale oceanic systems (e.g., California Current, Lasker 1975, Lasker 1978; Gulf of Maine, Townsend 1992; Gulf of Alaska, Bailey et al. 1995; Kuroshio Current, Oozeki and Zentitani 1996; eastern Nova Scotian shelf, Platt et al. 2003), but our understanding of predator-prey relationships that influence the earliest stages of life in freshwater habitats, especially floodplains, is rather limited.

Globally, sustained overbank flooding regulates microbial, nutrient, and invertebrate cycles (Goulding 1980; Bayley 1995). Additionally, rising floodwaters are believed to act as a reproductive cue for many riverine fishes (Goulding 1980; Welcomme 1985). In many temperate warmwater rivers, however, flooding is often unpredictable and discontinuous (e.g., Murray-Darling River Basin, Australia, King et al. 2003; Brazos River, USA, Zeug et al. 2005; Atchafalaya River, USA, Hupp et al. 2008). As a result, taxa that synchronize reproduction in concert with widespread inundation show considerable year-to-year variation in the timing and intensity of spawning (Fontenot et al. 2001; King et al. 2003). This has been attributed to the arrival and magnitude of the flood pulse (Killgore and Baker 1996). While springtime river-floodplain connectivity increases accessibility to potentially suitable nursery and grow-out habitats for some ichthyofauna (Junk et al. 1989), flood pulses initially tend to destabilize plankton communities in the mainstem (Basu and Pick 1996) and shallow backwater habitats (Schemel et al. 2004). Flooding rapidly alters the distribution and

composition of zooplankters (Groszholz and Gallo 2006), and it may take weeks for the community to reset to pre-flood densities. Consequently, fishes that concentrate spawning during temporary peaks in the hydrograph could face the diminished likelihood of high larval survivorship because of a potential food limitation. Conversely, elevated phytoplankton and zooplankton biodiversity has been related directly to a combination of both increasing photoperiod and residence time of water on the floodplain (Reynolds 1984; Basu and Pick 1996; Wehr and Thorp 1997) and on the floodplain (Groszholz and Gallo 2006; Paidere et al. 2007).

In this study, I evaluated seasonal microcrustacean zooplankton-ichthyoplankton dynamics in the Atchafalaya River Basin (ARB) over a two-year period. The ARB is the largest remaining temperate bottomland hardwood floodplain in North America (Lambou 1990). Although there has been considerable anthropogenic manipulation of the ARB (Reuss 2004), peak periods of inundation primarily occur during the winter and early spring followed by rapid isolation of the floodplain in the summer (Bonvillain et al. 2008). The primary goal of this research was to determine the degree of temporal overlap between zooplankter and larval fish assemblages and evaluate the effects of physicochemistry and mainstem discharge on both populations.

METHODS

Study Area

Over the last century, changes in the hydrology of the ARB have resulted in increased sedimentation (Hupp et al. 2008), variable internal circulation of floodwaters (Sabo et al. 1999a), and sub-optimal physicochemistry that has been linked to structuring both adult (Rutherford et al. 2001) and larval fish (Fontenot et al. 2001) populations. To

reduce the effects of these changes, water management units have been established with the goal of restoring the flow path of water across the floodplain. Despite efforts to reestablish river-floodplain connectivity, the degree of inundation across large portions of the floodplain remains irregular due to the construction of canals, dredging activity, and levees (Hupp et al. 2008; Kaller et al. 2010). Consequently, to accurately estimate the abundance of zooplankton and ichthyoplankton in the system, I reviewed historic data to locate areas that had dissimilar hydrology, connectivity, and distance from the Atchafalaya River (Bryan and Sabins 1979, Sabo et al. 1999a; Sabo et al. 1999b; Rutherford et al. 2001) and selected three locations, Department of Energy/Twenty-one inch Canal (TWI), Lake Fordoche (LF), and Buffalo Cove (BC) (Figure 3.1).

Sampling Locations

The first location, TWI, is a linear pipeline canal that bisects a series of bayous and sloughs in the southeastern portion of the ARB. Flows into this area originate primarily in the Intracoastal Waterway (Sabo et al. 1999a). The Waterway, designed to facilitate barge traffic, transfers main channel discharge to outlying areas in the interior of the floodplain.

The second location, LF, is a relatively isolated backwater lake situated in the upper western reach of the ARB. The hydrology of this area is regulated from the Bayou Courtableau Control Structure. The Control Structure receives flows from both Bayou Teche and a group of borrow pits, used in levee construction, that empty into diversion canals located outside of the western protection levee. Although LF has historically been

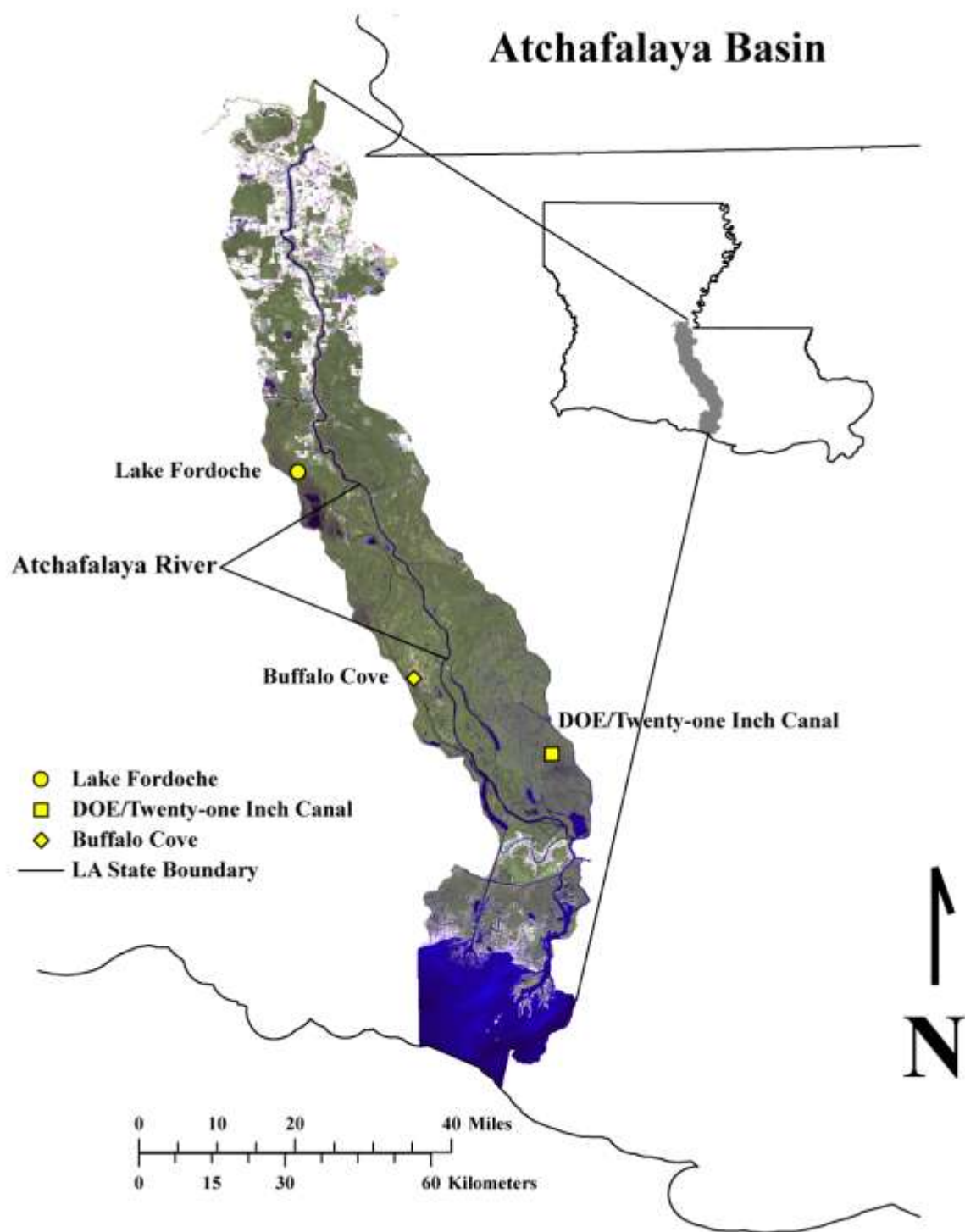


Figure 3.1 — Sample locations in the Atchafalaya River Basin, LA.

impacted by a number of water control projects, it still experiences significant sheet flow as water levels rise in the early spring (Lambou 1990).

The final location, BC, is a chain of interconnected backwater lakes located in the southwest portion of the floodplain. There are three primary artificial distributaries to this area: Si Bon Canal, Gays Slough/Philips Canals and Lake Fausse Pointe Cut as well as a number of smaller bayous that periodically transport water into BC. As with the other two locations, there are numerous petrochemical channels that intersect large parts of the floodplain and affect connectivity (Sabo et al. 1999a; Hupp et al. 2008).

Field Collections

There were three to four fixed sites at each location that were sampled at least one time every four weeks from 21 February 2005 to 29 September 2005 and 22 February 2006 to 30 August 2006. Over the duration of the two-year study, only one sample site became inaccessible by boat because of reduced floodplain connectivity. On each weekly sampling date, physicochemical measurements were taken at every site both at the surface and within 3-5 cm of the bottom. A hand-held water quality multiprobe (Hydrolab, Hach Environmental, Loveland, CO) was used to measure temperature ($^{\circ}\text{C}$), pH, specific conductance ($\mu\text{S}/\text{cm}$), turbidity (NTU), and dissolved oxygen (mg/L and % saturation). Surface water movement was measured with a SonTek flowmeter (cm/sec , YSI, Inc., Yellow Springs, OH) and a secchi disc reading was also recorded. Although there were short-term increases in depth that coincided with spring flooding, typically, the depth at the various sites was ≤ 3 m (range = 1.0 - 5.2).

A small boat, traveling at approximately 1 m/sec, was used to push a pair of bow-mounted push nets placed slightly below the surface. Larval fish were collected from

three replicate runs ($n = 184$ in 2005 and $n = 185$ in 2006), each between 250 - 280 sec, with a 0.5-m diameter net with 500- μ m mesh (Sea-Gear Corporation, Melbourne, FL.). Microcrustacean zooplankters were sampled from a single ($n = 62$ in 2005 and $n = 74$ in 2006) 45 - 60 sec run with a 0.5-m diameter net with 110- μ m mesh (Sea-Gear Corporation, Melbourne, FL.). A flow meter (General Oceanics Inc., Miami, FL.) was placed in the center of each net during every run to measure the volume of water filtered.

Ichthyoplankton were preserved in 90% ethanol and were sorted and identified to the lowest practical taxonomic level with the aid of a voucher collection at Louisiana State University, as well as the keys found in Houge et al. (1976), Auer (1982), Wallus et al. (1990), Kay et al. (1994), and Simon and Wallus (2006). Total length was measured to the nearest 0.1 mm with an ocular micrometer and each fish was classified based upon developmental changes in the caudal fin as yolk sac, preflexion, flexion, or postflexion (Ahlstrom et al. 1976). The total numbers of larval taxa collected from both push nets on each run were combined into a single sampling unit for statistical analysis.

Prior to storage, microcrustacean zooplankton specimens were condensed by filtering the contents of each net through a 100- μ m sieve to remove water. The remaining sample was then fixed in 90% ethanol. The volume of the individual sample was then approximately 80 - 90 ml. Because of the patchy distribution of zooplankton an estimate of the composition collected in each run was based on an examination of > 2% of the contents from each net. Four 1-ml aliquots were taken from each sample with a Hensen-Stemple pipette, and the contents were placed in a Sedgewick-Rafter cell for enumeration and identification. Taxa were identified to lowest practical level with the aid of the following references: Smith (2001), Zimmerman and Hubschman (1990), and

Dodson and Frey (1991). To approximate the abundance of a particular taxon, I averaged the number of each individuals enumerated from the four aliquots. The mean of each individual taxon was then multiplied by the volume of the original sample. This value was divided by the volume of water filtered to obtain a density estimate (m^3) for each taxon occurring in a single run. The abundance of both cladocerans and copepods (including nauplii and copepodites) were combined to provide a zooplankter density estimate.

Statistical Analysis

Analysis of variance (ANOVA) with a Tukey-Kramer *post hoc* adjustment (PROC MIXED, SAS Institute, Cary, North Carolina, vers. 9.1.3) was used to compare the historic (1959-2004) monthly mean stage height (hereafter stage) at Butte La Rose, LA. (United States Geological Survey, gage 07381515) with stage during the study. Monthly stage between sample years was also contrasted with ANOVA (PROC MIXED, SAS, vers. 9.1.3) that included a Tukey-Kramer *post hoc* adjustment.

Akaike's information criterion for small sample size (AIC_C) was used to evaluate multiple working hypotheses (Burnham and Anderson 2002) between candidate models that best approximated the abundance of both microcrustacean zooplankters and specific ichthyoplankton taxa. Candidate parameters included all the surficial physicochemical variables collected at each sample site as well as mean monthly hours of daylight (photoperiod) and the difference in stage on the day of sampling with stage three days prior. To improve the formulation of candidate models (see Burnham and Anderson 2002; Hobbs and Hilborn 2006) and limit the influence of irrelevant variables (see Lukacs et al. 2010), previous ichthyoplankton (Fontenot et al. 2001; Engel 2003) and

microcrustacean zooplankton (Davidson et al. 1998; Kelso et al. 2003) research in the ARB was reviewed in order to construct ecologically meaningful *a priori* relationships. In addition, the early life history dynamics of age-0 fishes in other floodplain systems (Finger and Stewart 1987; Sabo et al. 1991; Turner et al. 1994; Killgore and Baker 1996) were examined to gauge the importance of certain abiotic interactions. Finally, independent variables were compared in principle component analysis (PROC FACTOR, SAS, vers. 9.1.3) to assess the potential of multicollinearity between effects prior to model development. Thirteen *a priori* candidate models were hypothesized to explain the abundance for each ichthyoplankton taxon and 17 models were used to characterize variation in microcrustacean zooplankton abundance.

Two thresholds were used to determine if a particular larval taxon was retained for analysis. The candidate taxon had to occur in $\geq 10\%$ of all push net runs or comprise $\geq 1\%$ of the total number of larvae collected during the study. Effects used to evaluate larval fish abundance included water temperature, surface flow, dissolved oxygen, and total microcrustacean zooplankton density. The effects retained to assess zooplankton abundance were mean monthly hours of daylight, dissolved oxygen, secchi depth, water temperature, and surface flow. The AIC_C models were compared in a generalized linear mixed model framework (PROC GLIMMIX, SAS, vers. 9.1.3) which included both the null (intercept only) and global (all effects of interest) models. Criterion for model selection was based upon ΔAIC_C , Akaike weight (ω_i), and evidence ratios. For each effect, the slope coefficient and standard error along with the 95% confidence level intervals were calculated. The level of support for a given effect was assessed based upon the extent to which confidence intervals overlapped with zero. Effects that included

zero in the 95% confidence level were considered to lack strong support (Burnham and Anderson 2002). Competing models were ranked based on AIC_c scores with the lowest values assumed to be the most explanatory. ΔAIC_c values were calculated by comparing a particular candidate model with the with the lowest AIC_c value among the individual models. An explanatory model was retained for consideration if $\Delta AIC_c \leq 2$ and evidence ratios ≤ 2.7 (Burnham and Anderson 2002). Models were also assessed by contrasting the ω_i (Burnham and Anderson 2002) of a model under consideration in comparison to all models assumed to explain abundance for each taxon. A general information criterion (GIC) was calculated for all models (Wright 1998) to compare the validity of the explanatory models. A r^2 statistic was generated from the following formula: $r^2_{GIC} = 1 - \exp[((GIC_{MODEL} - GIC_{NULL}) / n)]$ where GIC_{MODEL} = an individual model under consideration, GIC_{NULL} = intercept only model, and n = sample size. Because r^2_{GIC} is derived from the same data as AIC_c values, the interpretation is similar to the conventional r^2 with the r^2_{GIC} representing the proportional amount of variability explained in the statistical model compared to its null model (Wright 1998).

RESULTS

Physicochemistry

Stage was consistently lower than the historic average for all months over the study except during February 2005 ($p < 0.01$). A month-by-month comparison of stage (February-August) between sample years indicated that flows in the main channel were only similar in May and August ($p > 0.15$). In the first year, increase in stage was followed by a substantial reduction in discharge of approximately the same duration. As a result, system-wide connectivity was irregular throughout inundation (February - May)

and into drawdown (June - September). In 2006, mainstem flows never produced any periods of overbank flooding but there were two prolonged springtime peaks prior to drawdown. Throughout the study, summertime stage consistently remained ≤ 2 m.

Although widespread flooding was infrequent, several water quality parameters, temperature, dissolved oxygen saturation, and specific conductance, showed considerable variation in relation to the hydrograph. Rapid shifts in physicochemistry occurred primarily during brief periods of fluvial exchange when riverine water reached outlying areas on the floodplain. As floodwaters receded, both temperature (Figure 3.2) and specific conductance (Figure 3.3) steadily increased; however, dissolved oxygen saturation continuously fluctuated between sample dates (Figure 3.4). Generally, elevated springtime river-floodplain connectivity was associated with reduced oxygen levels, but there were episodes of supersaturation that coincided with spikes in the hydrograph. The abrupt change in all water quality parameters on the last sample date in 2005 coincided with post-Hurricane Katrina flood control measures designed to reduce downstream Mississippi River flows to New Orleans.

Larval Fish

A total of 17,346 larvae were collected over the two-year study period representing eight families (Table 3.1). Overall, the most abundant taxa were shad *Dorosoma* spp. (84.3%), sunfishes *Lepomis* spp. (12.8%), and crappie *Pomoxis* spp. (1.2%). Almost all taxa initiated spawning in the spring but once stage dropped to ≤ 1 m during the summer, there was a pronounced reduction, except for sunfishes. Peak reproductive effort for most fishes was relatively consistent between years although the

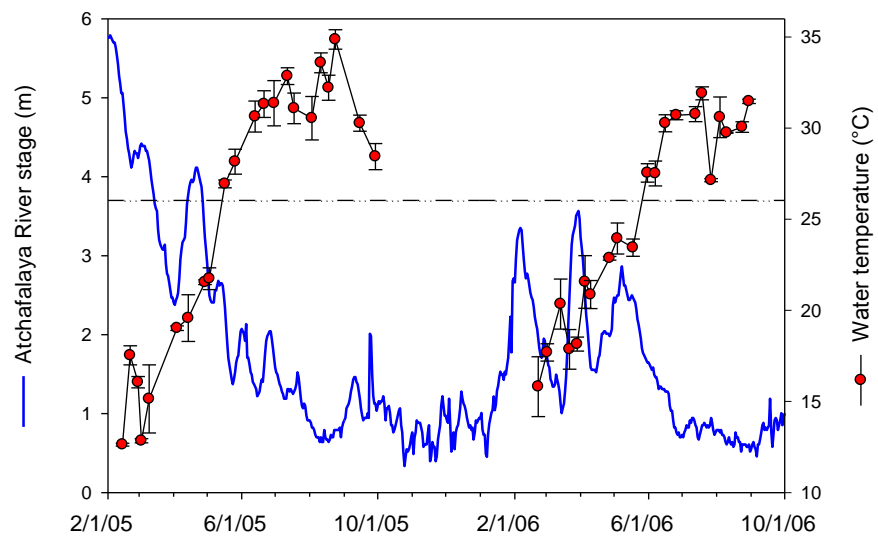


Figure 3.2 — Surface water temperatures (\pm SE) in the Atchafalaya River Basin during 2005 – 2006. The dashed (--) represents the bank full stage of the Atchafalaya River.

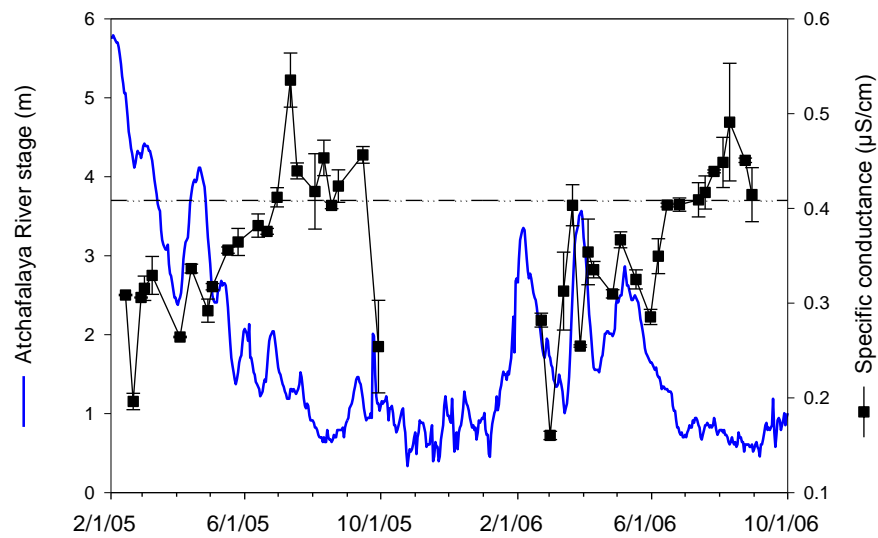


Figure 3.3 — Specific conductance (\pm SE) observed in the Atchafalaya River Basin during 2005 – 2006. The dashed (--) represents the bank full stage of the Atchafalaya River.

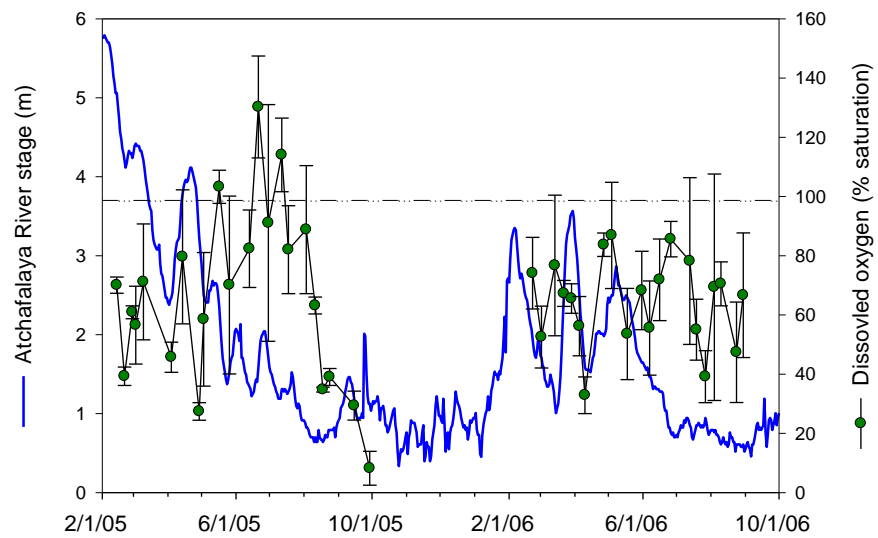


Figure 3.4 — Dissolved oxygen (\pm SE) on the floodplain in the Atchafalaya River Basin during 2005 – 2006. The dashed (--) represents the bank full stage of the Atchafalaya River.

1 Table 3.1 — Ichthyoplankton collected during 2005 – 2006 in the Atchafalaya River Basin.
2

	2005								2006							
Taxa	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Feb	Mar	Apr	May	Jun	Jul	Aug	
Aphredoderidae																
<i>Aphredoderus sayanus</i>																
Atherinidae																
<i>Labidesthes sicculus</i>													1			
<i>Menidia beryllina</i>				2												
Catostomidae	1		11	5	10				18	21	20					
Centrarchidae																
<i>Ambloplites</i> spp.									4							
<i>Lepomis</i> spp.	1		39	177	384	266	190	3	3	2	63	40	900	145	12	
<i>Micropterus</i> spp.		3		1					8	9	1		1			
<i>Pomoxis</i> spp.	2	6	38	1			3		48	68	38	3				
Clupeidae																
<i>Dorosoma</i> spp.	1		336	650	119	102	5	1	1	325	8365	680	3768	268	3	
Cyprinidae		1	4		21				6	3	29	46				
Fundulidae																
<i>Fundulus</i> spp.																
Hidonidae																
<i>Hidon</i> spp.												1				
Moronidae																
<i>Morone</i> spp.																
Percidae		2	39	2						1	1				1	
Sciaenidae																
<i>Aplodinotus grunniens</i>			11	1	1							3	1			
Unknown											1					

Monthly Total	5	12	478	839	535	368	198	4	88	429	8518	773	4671	413	16
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inter-annual hydrograph was dissimilar. For example, the highest densities of black basses *Micropterus* spp., crappie, and catostomids, were concentrated in the early spring when inundation and connectivity was unpredictable (Figures 3.5 and 3.6). Yet, early-seasonal reproduction for these taxa occurred when zooplankton production was among the lowest pre-drawdown levels observed in the study. Clupeid spawning was protracted but most cohorts did not coincide with unusually high zooplankton numbers. Throughout sampling, elevated zooplankton and larval abundance typically corresponded with aperiodic rises in stage however, densities of both groups declined rapidly as floodwaters receded. On only one occasion over the two sample years, did robust zooplankton stocks occur in phase with ichthyoplankton. Sunfishes were the only taxon that continuously spawned during a combination of conditions that included a declining hydrograph and seasonally-reduced zooplankton densities.

Centrarchids

Crappie and black bass spawning occurred over a six to eight week period each spring and there was almost no evidence of post-flood reproduction (Figures 3.5 and 3.6). The extent of wintertime inundation, however, appeared to influence the timing of reproduction of both taxa. In 2005, there were substantial periods of overbank flooding in the months preceding sampling that appeared to delay the start of reproduction. Conversely, in the second year, reduced springtime river-floodplain connectivity seemed to allow reproduction to start almost a month earlier than in 2005 (Table 3.1).

Micropterus spp. occurred too infrequently to assess which environmental parameters influenced age-0 distribution but there were four candidate models that explained

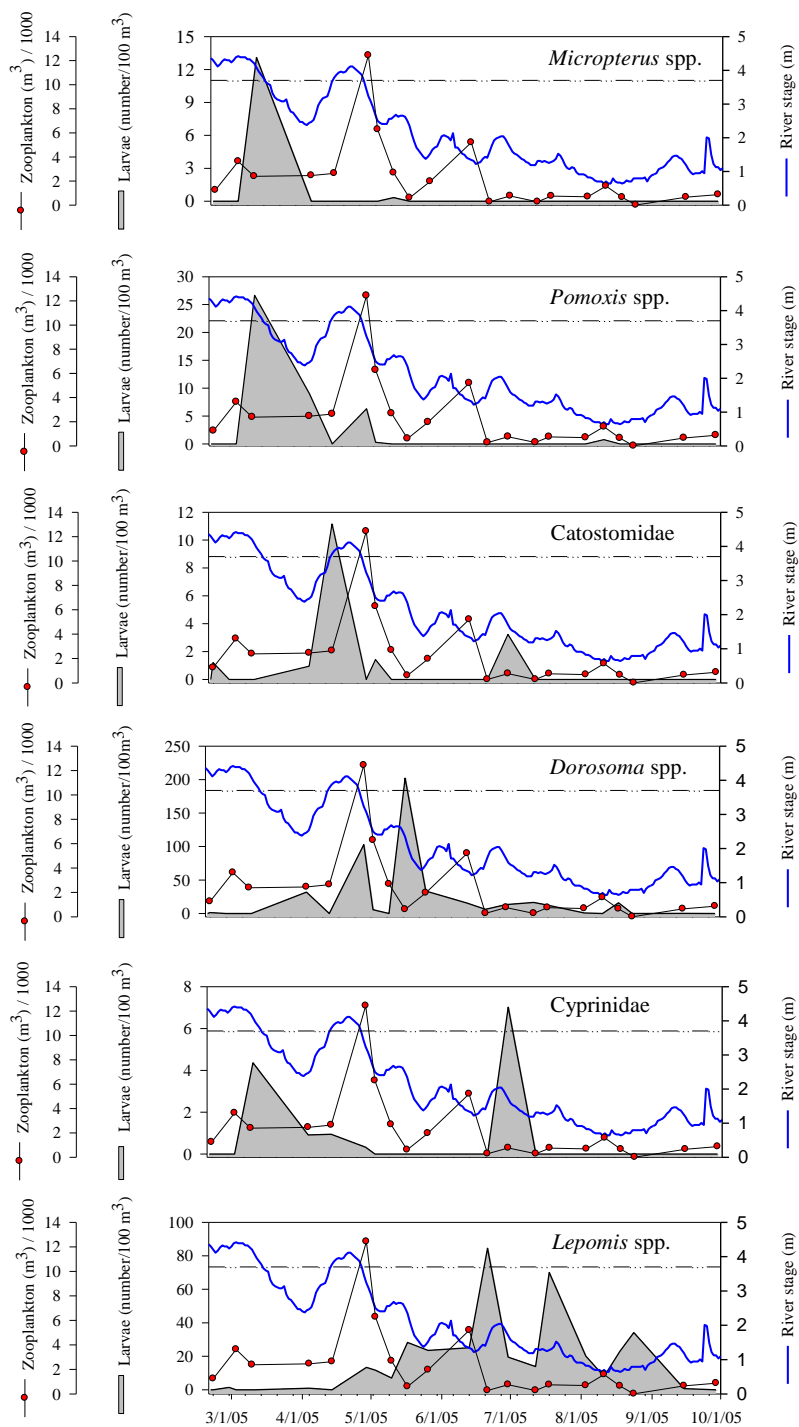


Figure 3.5 — Seasonal densities of multiple ichthyoplankton taxa in relation to microcrustacean zooplankton density in the Atchafalaya River Basin in 2005. The dashed (--) represents the bank full stage of the Atchafalaya River.

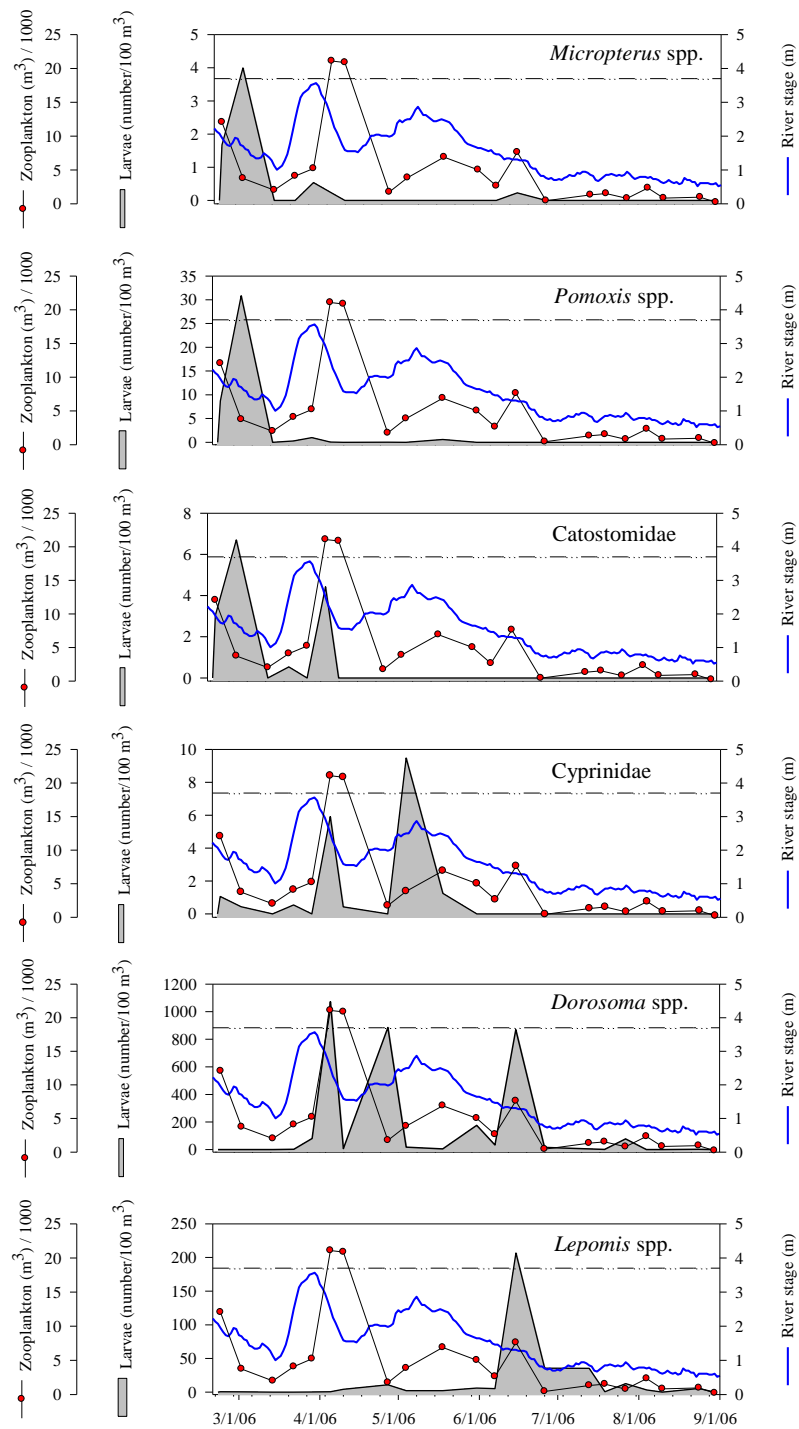


Figure 3.6 — Seasonal densities of multiple ichthyoplankton taxa in relation to microcrustacean zooplankton density in the Atchafalaya River Basin in 2006. The dashed (--) represents the bank full stage of the Atchafalaya River.

Pomoxis spp. abundance and each included a negative association with water temperature (Table 3.2). Among the candidate models, the strongest (lowest AIC_c value) was a negative association with water temperature. The next best approximating model included a negative association with flow. The model with the third highest ω_i was comprised of both decreasing temperature and dissolved oxygen, however, oxygen had limited support (95% confidence level = - 0.160⁻¹ to 0.452⁻²). The final model that deserved consideration was comprised of temperature and zooplankton density, but the slope of the zooplankton effect did not differ from zero (95% confidence interval = - 0.338 to 0.814).

Lepomis spp. concentrated reproduction as the hydrograph dropped and water temperatures increased, but these conditions typically coincided with the lowest zooplankton densities (Figures 3.5 and 3.6). The strongest candidate model was comprised of a positive association with water temperature and zooplankton density (Table 3.3). The two other best approximating models also included the effects from the strongest model; however, the additional parameters in each of the two models did not differ from zero (dissolved oxygen 95% confidence interval = - 0.240⁻³ to 0.131⁻¹; flow 95% confidence interval = - 0.554⁻² to 0.364⁻¹). The fully parameterized model also merited consideration but the ω_i was the lowest of the competing explanatory models.

Clupeids

Spawning typically lasted four months, but densities dropped as mainstem volume declined in the summer (Figures 3.5 and 3.6). At least one shad cohort overlapped with highest annual zooplankton densities. There were two *a priori* models with AIC_c ≤ 2

Table 3.2 — Rankings of AIC_c *a priori* models used to explain larval *Pomoxis* spp. abundance in the Atchafalaya River Basin in 2005 - 2006.

MODEL	K	AIC _c	ΔAIC _c	ω _i	Evidence ratio	r ²
temp	3	86.01	0	0.34	1.0	54.53
temp flow	4	86.95	0.94	0.22	1.56	53.51
temp DO	4	87.79	1.78	0.14	2.46	52.56
temp zoo	4	87.94	1.93	0.13	2.58	52.40
temp flow zoo	5	88.70	2.69	0.09	> 3.00	51.53
temp DO zoo	5	89.82	3.81	0.05	> 3.00	50.22
FULL	6	90.69	4.68	0.03	> 3.00	49.18
zoo	3	115.92	29.91	0.00	> 3.00	7.34
flow zoo	4	117.62	31.61	0.00	> 3.00	3.51
DO zoo	4	117.7	31.69	0.00	> 3.00	3.33
NULL	2	119.12	33.11	0.00	> 3.00	0
DO	3	120.23	34.22	0.00	> 3.00	- 2.69
flow	3	121.05	35.04	0.00	> 3.00	- 4.71

Note: Column headings include, *K* (the number of parameters in model including slope and intercept), AIC_c (small sample size AIC value for each model), ΔAIC_c (the difference between a particular model and the model with the AIC_c lowest value), ω_i (Akaike's weight for each model), evidence (the evidence ratio of a model), and r² statistic. Parameters include temp (water temperature), flow (surface water velocity), zoo (microcrustacean zooplankter density), and DO (dissolved oxygen). Null model (intercept only) and full model (all parameters) are also included.

Table 3.3 — Rankings of AIC_c *a priori* models used to explain larval *Lepomis* spp. abundance in the Atchafalaya River basin in 2005 - 2006.

MODEL	K	AIC_c	ΔAIC_c	ω_i	Evidence ratio	r^2
temp zoo	4	153.76	0	0.28	1.0	35.70
temp zoo DO	5	154.01	0.25	0.24	1.16	35.31
temp zoo flow	5	154.04	0.28	0.24	1.16	35.27
FULL	6	154.78	1.02	0.17	1.64	34.12
temp	3	158.26	4.5	0.03	> 3.0	28.43
temp flow	4	159.19	5.43	0.02	> 3.0	26.82
temp DO	4	159.32	5.56	0.02	> 3.0	26.59
DO	3	171.86	18.1	0.00	> 3.0	1.05
NULL	2	172.31	18.55	0.00	> 3.0	0
flow	3	172.59	18.83	0.00	> 3.0	- 0.67
zoo DO	4	173.01	19.2	0.00	> 3.0	- 1.68
zoo	3	173.92	20.16	0.00	> 3.0	- 3.91
zoo flow	4	173.99	20.23	0.00	> 3.0	- 4.09

Note: Column headings include, K (the number of parameters in model including slope and intercept), AIC_c (small sample size AIC value for each model), ΔAIC_c (the difference between a particular model and the model with the AIC_c lowest value), ω_i (Akaike's weight for each model), evidence (the evidence ratio of a model), and r^2 statistic. Parameters include temp (water temperature), flow (surface water velocity), zoo (microcrustacean zooplankter density), and DO (dissolved oxygen). Null model (intercept only) and full model (all parameters) are also included.

and both included associations with water temperature and zooplankters. The strongest explanatory model was a combination of increasing zooplankton abundance and decreasing water temperature (Table 3.4). In second best model, surface flow, had limited explanatory support (95% confidence interval = - 0.301 to 0.122).

Cyprinids

Annual cyprinid reproduction was variable (Figures 3.5 and 3.6). In 2005, larval density peaked in late June, but this corresponded to substantially diminished zooplankton production. In the second year, spawning closely tracked increases in springtime stage and coincided with the highest observed microcrustacean zooplankter densities over the study. Three competing models all included a negative association with water temperature (Table 3.5). The strongest explanatory model was a combination of a positive association with zooplankton and increasing surface flow. The second best model was comprised of temperature and increasing flow. Although the fully parameterized model was a potential candidate to describe cyprinid abundance, it was over two times (2.11) less likely than the strongest model and had the lowest ω_i among the competing models with AIC_c values ≤ 2 .

Catostomids

Most catostomid reproduction paralleled temporary spikes in the hydrograph. Spawning appeared to be influenced by the arrival and duration of inundation, and as with other early-seasonal reproducing fishes (e.g., black basses and crappie); the timing of spawning was associated with the intensity of the flood pulse. Although spawning in the spring was variable, there was very limited evidence of any summertime reproduction. Overall, catostomid reproduction had some synchrony with zooplankter

Table 3.4 — Rankings of AIC_c *a priori* models used to explain larval *Dorosoma* spp. abundance in the Atchafalaya River Basin in 2005 - 2006.

MODEL	K	AIC _c	ΔAIC _c	ω _i	Evidence ratio	r ²
temp zoo	4	119.62	0	0.43	1.0	68.64
temp zoo flow	5	121.57	1.95	0.16	2.71	67.15
temp DO zoo	5	121.75	2.13	0.15	2.85	67.01
zoo	3	122.24	2.62	0.12	> 3.0	66.61
FULL	6	123.74	4.12	0.06	> 3.0	65.41
zoo DO	4	124.13	4.51	0.05	> 3.0	65.08
zoo flow	4	124.22	4.6	0.04	> 3.0	65.01
temp DO	4	166.19	46.57	0.00	> 3.0	4.95
temp	3	166.33	46.71	0.00	> 3.0	4.63
temp flow	4	168.27	48.65	0.00	> 3.0	0.12
NULL	2	168.32	48.7	0.00	> 3.0	0
DO	3	168.55	48.93	0.00	> 3.0	- 0.55
flow	3	170.02	50.4	0.00	> 3.0	- 4.13

Note: Column headings include, *K* (the number of parameters in model including slope and intercept), AIC_c (small sample size AIC value for each model), ΔAIC_c (the difference between a particular model and the model with the AIC_c lowest value), ω_i (Akaike's weight for each model), evidence (the evidence ratio of a model), and r² statistic. Parameters include temp (water temperature), flow (surface water velocity), zoo (microcrustacean zooplankter density), and DO (dissolved oxygen). Null model (intercept only) and full model (all parameters) are also included.

Table 3.5 — Rankings of AIC_c *a priori* models used to explain larval cyprinid abundance in the Atchafalaya River Basin in 2005 - 2006.

MODEL	K	AIC _c	ΔAIC _c	ω _i	Evidence ratio	r ²
zoo flow temp	5	75.29	0	0.32	1.0	47.08
flow temp	4	75.75	0.46	0.25	1.28	46.50
FULL	6	76.81	1.52	0.15	2.11	45.13
zoo temp	4	77.34	2.05	0.11	2.85	44.43
temp	3	78.15	2.86	0.07	> 3.0	43.35
zoo temp DO	5	78.24	2.95	0.07	> 3.0	43.23
temp DO	4	79.82	4.53	0.03	> 3.0	41.05
zoo flow	4	87.17	11.88	0.00	> 3.0	29.78
zoo	3	90.15	14.86	0.00	> 3.0	24.63
zoo DO	4	90.82	15.53	0.00	> 3.0	23.42
flow	3	97.8	22.51	0.00	> 3.0	9.57
NULL	2	102.02	26.73	0.00	> 3.0	0
DO	3	104.08	28.79	0.00	> 3.0	- 5.04

Note: Column headings include, *K* (the number of parameters in model including slope and intercept), AIC_c (small sample size AIC value for each model), ΔAIC_c (the difference between a particular model and the model with the AIC_c lowest value), ω_i (Akaike's weight for each model), evidence (the evidence ratio of a model), and r² statistic. Parameters include temp (water temperature), flow (surface water velocity), zoo (microcrustacean zooplankter density), and DO (dissolved oxygen). Null model (intercept only) and full model (all parameters) are also included.

abundance (Figures 3.5 and 3.6). Among the three *a priori* models with $AIC_c \leq 2$, the strongest approximating models all included an association with decreasing water temperature and increasing zooplankton density (Table 3.6). The other parameters, flow and dissolved oxygen, in likely candidate models had limited support (flow 95% confidence interval = -0.151^{-1} to 0.584 ; dissolved oxygen 95% confidence interval = -0.462^{-2} to 0.209^{-1})

Zooplankton

Microcrustacean zooplankton abundance showed considerable seasonal variability (Figures 3.5 and 3.6). Abundance tended to increase following elevated periods of springtime river-floodplain connectivity, but flooding did not appear to sustain widespread secondary productivity. Starting in late June, zooplankton numbers began to decline, even though seasonal drops in stage were relatively gradual and all locations continued to receive some flows from the mainstem (Figures 3.2 – 3.4). In fact, increasing hours of daylight generally coincided with reduced densities and stable floodplain physicochemistry. The strongest candidate model describing zooplankton density was comprised of low water temperature, reduced dissolved oxygen, and increasing photoperiod (Table 3.7). The second best model included two parameters, temperature and oxygen, from the strongest model along with a positive association with flow. Flow, however, had little support in explaining abundance (95% confidence levels = -0.227^{-2} to 0.309^{-1}).

Table 3.6 — Rankings of AIC_c *a priori* models used to explain larval catostomid abundance in the Atchafalaya River Basin in 2005 - 2006.

MODEL	K	AIC_c	ΔAIC_c	ω_i	Evidence ratio	r^2
temp zoo	4	71.7	0	0.35	1.0	46.82
temp zoo flow	5	72.89	1.19	0.19	1.82	45.29
temp zoo DO	5	73.42	1.72	0.15	2.34	44.59
temp	3	73.81	2.11	0.12	2.85	44.08
temp flow	4	74.82	3.12	0.07	> 3.0	42.71
FULL	6	74.84	3.14	0.07	> 3.0	42.68
DO temp	4	75.88	4.18	0.04	> 3.0	41.25
zoo	3	84.68	12.98	0.00	> 3.0	27.55
flow zoo	4	85.07	13.37	0.00	> 3.0	26.88
zoo DO	4	86.06	14.36	0.00	> 3.0	25.13
flow	3	97.76	26.06	0.00	> 3.0	1.08
NULL	2	98.22	26.52	0.00	> 3.0	0
DO	3	100.18	28.48	0.00	> 3.0	- 4.79

Note: Column headings include, K (the number of parameters in model including slope and intercept), AIC_c (small sample size AIC value for each model), ΔAIC_c (the difference between a particular model and the model with the AIC_c lowest value), ω_i (Akaike's weight for each model), evidence (the evidence ratio of a model), and r^2 statistic. Parameters include temp (water temperature), flow (surface water velocity), zoo (microcrustacean zooplankter density), and DO (dissolved oxygen). Null model (intercept only) and full model (all parameters) are also included.

Table 3.7 — Rankings of AIC_c *a priori* models used to explain microcrustacean zooplankton abundance in the Atchafalaya River Basin in 2005 – 2006.

MODEL	K	AIC _c	ΔAIC _c	ω _i	Evidence ratio	r ²
daylight do temp	5	135.23	0	0.40	1.0	59.60
daylight flow temp	5	137.22	1.99	0.15	2.71	57.64
daylight temp secchi	5	137.71	2.48	0.12	> 3.0	57.15
FULL	7	137.84	2.61	0.11	> 3.0	57.02
temp	3	138.53	3.3	0.08	> 3.0	56.31
do temp	4	138.63	3.4	0.07	> 3.0	56.20
temp secchi	4	139.96	4.73	0.04	> 3.0	54.80
do temp secchi	5	140.42	5.19	0.03	> 3.0	54.29
daylight	3	165.65	30.42	0.00	> 3.0	16.65
daylight do	4	166.69	31.46	0.00	> 3.0	14.57
daylight secchi	4	166.87	31.64	0.00	> 3.0	14.21
daylight do flow	5	167.45	32.22	0.00	> 3.0	13.01
flow	3	171.46	36.23	0.00	> 3.0	4.29
do	3	172.15	36.92	0.00	> 3.0	2.71
secchi	3	172.25	37.02	0.00	> 3.0	2.47
NULL	2	173.30	38.07	0.00	> 3.0	0
do secchi	4	173.44	38.21	0.00	> 3.0	- 0.33

Note: Column headings include, *K* (the number of parameters in model including slope and intercept), AIC_c (small sample size AIC value for each model), ΔAIC_c (the difference between a particular model and the model with the AIC_c lowest value), ω_i (Akaike's weight for each model), evidence (the evidence ratio of a model), and *r*² statistic. Parameters include temp (water temperature), flow (surface water velocity), zoo (microcrustacean zooplankton density), and DO (dissolved oxygen). Null model (intercept only) and full model (all parameters) are also included.

DISCUSSION

Zooplankton

In many riverine systems, reduced discharge and lower flows combined with increasing photoperiod stimulate widespread zooplankton biodiversity in the weeks following inundation (Welcomme 1985; Ferrari et al. 1989; Basu and Pick 1996). Surprisingly, this combination of conditions usually overlapped with the lowest levels of secondary productivity observed in this study. Although flooding appeared to facilitate zooplankton blooms, within a two to three week period, densities returned to pre-flood levels. A comparison of copepod and cladoceran abundance with prior research characterizing seasonal microcrustacean dynamics in the ARB (Davidson et al. 1998; Davidson et al. 2000), suggests that this pattern is not uncharacteristic for the system. Typically, reduced river-floodplain connectivity, results in short-term elevated secondary productivity, especially in off-channel habitats that are infrequently inundated (Welcomme 1985; Grosholz and Gallo 2006). In the weeks following widespread inundation, however, ARB zooplankton populations did not appear to benefit from prolonged periods of isolation. It seems unlikely that this study failed to detect widespread secondary productivity given the regularity of sampling and the diversity of habitats (e.g., bayous, headwater lakes, and canals). The association with low water temperatures is probably an artifact of increased planktonic production following the arrival of the cold, nutrient-rich riverine water in the spring. Some environmental conditions, specifically increasing daylight and reduced river-floodplain connectivity, reported to enhance the diversity and abundance of floodplain zooplankton populations (Baranyi et al. 2002; Grosholz and Gallo 2006), tended to coincide with the lowest

observed ARB densities. Another factor that could have influenced secondary productivity is the presence of aquatic macrophytes. Increasingly, introduced exotic macrophytes (e.g., water hyacinth *Eichhornia crassipes*, common salvinia *Salvinia minima*, Eurasian water-milfoil *Myriophyllum spicatum* and *Hydrilla verticillata*) in the ARB have disrupted water quality, especially seasonal DO dynamics (Walley 2007; Kaller et al. 2010). A macrophyte-driven oxygen deficit, resulting from decaying plant matter in the benthos, typically develops across large portions of the ARB floodplain following inundation (Sabo et al. 1999a; Rutherford et al. 2001; Kaller et al. 2010).

In addition, prolific surface and sub-surface macrophyte growth could also inhibit the formation of stable phytoplankton communities by blocking the light necessary for photosynthesis and sequestering limiting nutrients (Schramm et al. 2009). As a result, phytoplankton production could decline and adversely affect zooplankton abundance. All locations, however, remained relatively free of dense macrophyte beds and conditions rarely included any extended periods of hypoxia (≤ 2 mg/L) and there were few instances of any unusual shifts in water quality that might have depressed zooplankton abundance.

Microcrustacean zooplankton numbers observed in this study were lower than other temperate backwater floodplains (Baranyi et al. 2002; Grosholz and Gallo 2006), even though the sampling design specifically targeted littoral habitats suspected of containing robust planktonic communities. One difference between this study and other research characterizing the composition of zooplankton could be the absence of rotifers. Although gear size precluded an accurate estimation of rotifers, past research in the ARB suggests that the distribution (Holland et al. 1983) would not have "matched" the peak spawning periods of many fishes better than other zooplankton taxa collected during

sampling. Further, rotifer densities have been found to be among the lowest annual levels (Holland et al. 1983) that correspond with the known spawning periods of many fishes found to utilize off-channel areas in the system (see Fontenot et al. 2001; Engel 2003).

Ichthyoplankton

While the hydrograph appeared to influence the timing of reproduction and structure the level of secondary productivity, few fishes consistently coincided with seasonally-elevated zooplankton abundance during inundation or drawdown. For black basses, crappie, and catostomids the arrival of floodwaters appeared to influence the timing and intensity of reproduction. The ability to exploit early annual intermittent flooding could potentially confer a significant developmental advantage for the hatchlings of some species but the strategy could jeopardize survivorship because larvae often preceded stable prey numbers. The first cohorts to mature, however, may be in the position to outcompete conspecifics produced later in the year as well as other age-0 fish species. Some fishes could avoid competition for food resources with the larvae of other species by synchronizing reproduction with a rising hydrograph, even if the spikes were unpredictable. Studies have reported that highly fecund species, such as clupeids, may produce enough larvae to reduce available zooplankton prey for other developing fishes (Dettmers and Stein 1992; DeVries and Stein 1992; Hirst and DeVries 1994; Garvey and Stein 1998; Partridge and DeVries 1999). Consequently, the earliest spawners may produce offspring that transition to exogenous foraging without having to encounter a potentially diminished prey base that could be affected by the dominate larval taxa (shad and sunfish) in this study.

Some research (Partridge and DeVries 1999; Claramunt and Wahl 2000) hypothesizes that the growth and mortality of freshwater fish larvae is influenced by the strength of plankton stocks, but evidence documenting this relationship in some aquatic systems is equivocal (see Bunnell et al. 2003). Because the hydrograph in temperate river-floodplain systems is irregular (Winemiller 2004) or tends to peak during periods that are sub-optimal for reproduction (Benke et al. 2000), the opportunity to spawn in off-channel areas that provide optimal reproductive habitat for many fishes may be limited. As a result, the reproductive ecologies of many taxa are probably "fixed" as much to the arrival of springtime flooding as to seasonal zooplankter abundance. Because fish reproduction and elevated zooplankter abundance often followed discharge peaks throughout sampling, some pre-recruits produced during inundation would likely have had the best opportunity to exploit the greatest annual plankton production. This was reflected in the strongest approximating *a priori* models of larval abundance for early spawning taxa, except *Pomoxis* spp., which included an association with both increasing zooplankter density and water temperature. Although at times microcrustacean zooplankton abundance was equivalent to zooplankter densities observed in other aquatic MMH studies (Garvey et al. 2002; Bunnell et al. 2003), overall, fry would have encountered depauperate prey numbers. Yet, postponing reproduction to coincide with zooplankter blooms could reduce the opportunity to spawn, especially as floodwaters began to recede.

Interestingly, reproductive effort of the two most abundant ichthyoplankton, shad and sunfishes, was extended over many months. The strongest models of these fishes suggest that the primary environmental mechanism regulating spawning was water

temperature, yet, the distribution of larvae indicated that there appeared to be temperature-mediated reproductive response for each taxon. As a result, there was relatively limited overlap between the peak abundance of hatchlings of each taxon, especially during the drawdown period that was characterized by reduced zooplankton abundance.

By early April, shad reproduction was continuous and only as the floodplain became increasingly disconnected during the summer did spawning diminish. The abrupt reduction in larval shad abundance appeared to be related to physicochemical fluctuations, particularly increases in water temperatures that accompanied declining discharge (Figure 3.2). By relying on a range of abiotic conditions to stimulate and terminate spawning, broadcast spawners like *Dorosoma* spp. could spawn during a suitable reproductive "window" that occurs over a number of months instead of concentrating reproduction over a shorter time as other fishes did during the flood pulse. Betsill and Van Den Avyle (1997) reported that the growth rate of larval threadfin shad *Dorosoma petenense* did not improve with increasing zooplankton density but instead, as prey availability reached a particular threshold, survivorship was correlated with an optimal range of water temperatures. For some taxa, this strategy would be advantageous, particularly in systems like the ARB, which experience inconsistent seasonal levels of mainstem inundation (Bonvillain et al. 2008) and unpredictable zooplankton abundance (Holland et al. 1983; Davidson et al. 1998). Protracted reproduction might allow at least one larval cohort to develop in concert with the highest seasonal levels of microcrustacean zooplankters that tend to occur in the weeks and months following the highest inundation peaks.

Recently, it has been suggested that some fishes in temperate rivers time their reproduction to occur during periods of reduced flows that typically coincide with rising seasonal water temperatures. The low flow recruitment hypothesis (LFRH, Humphries et al. 1999) postulates that the reproductive strategies of some fishes rely on periods of reduced discharge, which allow fry to develop in a prey-rich environment within the main channel. Despite dramatic drops in stage predicted to enhance recruitment, only *Lepomis* spp. appeared to exploit these conditions, but sunfish reproduction consistently overlapped with the lowest ARB zooplankton densities. Although I did not directly sample the mainstem, the backwater lakes, bayous, and canals, which were the focus of this study included the spatially complex, slackwater habitats postulated to be key nursery areas that enhance recruitment. In addition, prior research suggests that outlying areas on the floodplain undergo similar environmental fluctuations to those in the mainstem, even as floodwaters recede (Bonvillain et al. 2008). Interestingly, taxa that used declining river stage as a reproductive cue were found to spawn over periods that included the lowest annual zooplankton densities. While protracted reproduction may allow young fishes to avoid stochastic physicochemical conditions and irregular periods of river-floodplain connectivity, fry may encounter depauperate foraging conditions during a falling hydrograph. As a result age-0 fishes might not be the appropriate size to over-winter.

Although there was considerable zooplankton variation associated with off channel areas both in this study and in past research within the system (Holland et al. 1983; Davidson et al. 1998), the diversity and abundance of the adult fish population in the ARB (approximately 100 resident species occur, see Fremling et al. 1989) suggests

that secondary production that would regulate the yearly number of pre-recruits, is sufficient to sustain recruitment. Further, it is increasingly unclear what *in situ* prey levels are necessary to ensure high annual recruitment (see Bunnell et al. 2003). Surprisingly, studies examining the affects of zooplankter abundance on recruitment in freshwater systems are equivocal as to the importance of synchronous overlap between predator and prey (Betsill and Van Den Avyle 1997; Garvey et al. 2002). While the larval abundance of almost every taxon in this study was associated with zooplankter density, it is unclear if this relationship was the result of environmental mechanisms that appeared to regulate the density of both. This suggests that the early life history dynamics of many temperate floodplain-exploitative fishes may be more reliant on the hydroperiod then post-hatch zooplankter prey availability.

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CHAPTER 4. INTRADAY DENSITY AND MEAN LENGTH COMPARISONS OF LARVAL SUNFISH AND SHAD

INTRODUCTION

Accurate estimates of ichthyoplankton abundance are critical to characterize the timing and magnitude of reproduction as well as the annual recruitment potential of a particular fish species. Yet, estimating the density, composition, and individual size, can be problematic due to the patchy distribution of larvae and the limited knowledge of optimal nursery and grow-out areas preferred by many taxa. Because a complete understanding of early life history dynamics relies on the ability to document the distribution and behavior of fry, numerous sampling gear have been devised (e.g., push nets, light traps, emergence traps, benthic sleds, pumps) or modified from existing collection methods (e.g., trawling, seining, electrofishing) to obtain larvae from pelagic and demersal habitats (Kelso and Rutherford 1996).

Increasingly, however, fisheries ecologists have recognized that certain techniques and collecting protocols may bias catch rates and estimates of cohort size (Cada and Loar 1982; Bain and Finn 1991; Magnan 1991; Cyr et al. 1992). Consequently, there has been considerable emphasis on comparing the sampling efficiency of gear (Gale and Mohr 1978; Claramunt et al. 2005; Niles and Hartman 2007), quantifying the effects of towing speed (Aron and Collard 1969; Barkley 1972), and contrasting different mesh size (Hale et al. 1995; Isermann et al. 2002). Despite increased attention to identifying the limitations associated with specific gear and sampling methodologies, inadequate emphasis has been placed on addressing potential flaws that may result from once-daily ichthyoplankton estimates. Although the catch

rates of larvae have been found to vary more between habitats of comparable composition than among subsamples from the same sampling location (Holland-Bartels et al. 1995), few studies have addressed whether this trend is consistent; especially between daily collections. Because of the expense and logistical constraints of collecting several daily samples, there is limited understanding of the accuracy of estimates that rely on a single collection event to describe the microdistribution of larvae. The objective of this study was to compare daily differences (morning vs. afternoon) in the density and mean length of specific ichthyoplankton taxon and examine inter-replicate variability at fixed sampling sites.

METHODS

Field Collections

Three locations, Department of Energy/Twenty-one Inch Canal, Lake Fordoche, and Buffalo Cove (see Chapter 3 for description of these locations), in the Atchafalaya River Basin (ARB), were sampled approximately one time every ten days from 29 April 2005 to 24 August 2005 ($n = 12$) in order to characterize larval fish abundance. Each location was comprised of three to four fixed sampling sites ($n = 11$), which included backwater lakes, canals, and bayous. Although inter-site morphometry differed, both the water volume and the amount of aquatic vegetation associated with each site was relatively consistent throughout sampling. Generally, the depth of the floodplain during the study was ≤ 3 m, with the exception of two sites that were located in close proximity to anthropogenic waterways. Most sites were within 2 km (range = 1 - 4 km) of one another and there was always some degree of connectivity between sites throughout the study.

Abundance and length estimates were based upon two daily series of collections at each sample site. The first series occurred from 0830 - 1200 and were designated as morning samples. The second series was collected from 1300 - 1630 and were referred to as afternoon samples. Typically, four hours (range = 4 - 6) elapsed between the intraday collections at each site. To limit the affects of any crepuscular behavior (see Gale and Mohr 1978; Muth and Scmulbach 1984) that might bias intraday estimates (especially with the morning collections), all sampling occurred at least 1.5 hours after sunrise and 2.5 hours prior to sunset.

Ichthyoplankton were collected with paired, bow-mounted push nets (mesh size = 500- μm , mouth diameter = 0.5 m) from a small boat moving about 1 m/sec. I used a retractable frame to position the nets just below the surface. A flow meter (General Oceanics Inc., Miami, FL.) was used to determine the volume of water sampled during each run (mean = $66/\text{m}^3$, SE = ± 3.4). Three replicate runs, each 250 - 280 sec, were completed during both time periods at each site to derive all larval estimates. Push net runs were typically concentrated in the shallowest areas (< 2-m) and if macrophytes were present, I sampled along the margins of vegetation stands. Prior early life history research in the ARB suggested that these structurally complex, near-shore areas were optimal nursery habitat for the fry of many taxa (Fontenot et al. 2001; Engel 2003). In order to limit the effects of differing microhabitats associated with each site, push net runs were repeated in the same area during both sample periods. A hand-held water quality multiprobe (Hydrolab, Hach Environmental, Loveland, CO) was used to measure dissolved oxygen (DO, mg/L), temperature ($^{\circ}\text{C}$), pH, specific conductance ($\mu\text{S}/\text{cm}$) and

turbidity (NTU) at the surface of each site. Physicochemical measurements were taken at each site during both sample periods.

Following capture, all larval specimens were preserved in 90% ethanol and identified to the lowest practical taxonomic level with the keys found in Houge et al. (1976), Auer (1982), Wallus et al. (1990), Kay et al. (1994), and Simon and Wallus (2006) and a voucher collection at Louisiana State University. Larvae were assigned to a specific developmental stage based on ontogenic development of the caudal fin (Ahlstrom et al. 1976). Any juvenile or adult fishes collected over the course of the study were not included in any subsequent analysis. Total length was measured to the nearest 0.1 mm with an ocular micrometer. All undamaged fishes were used to establish mean lengths (mm) for each taxon. Densities were calculated as the number of individuals of a specific taxon per cubic meter of water sampled (number of individuals/m³). The total number of each taxon collected from both push nets on each run were combined into a single sampling unit for statistical analysis.

Statistical Analysis

A nested analysis of variance (ANOVA; PROC MIXED, SAS Institute, Cary, North Carolina, vers. 9.1.3) was used to evaluate intraday taxon-specific larval density and mean length differences at each site on a specific sampling date. I also compared the physicochemistry between sample sites at each location and contrasted replicate runs at each site from the same time series with ANOVA.

RESULTS

A total of 4,480 larval fish were collected which included inland silverside *Menidia beryllina*, brook silverside *Labidesthes sicculus*, freshwater drum *Aplodinotus grunniens*, crappie *Pomoxis* spp., shad *Dorosoma* spp., sunfishes *Lepomis* spp., percids, catostomids, and cyprinids (Table 4.1). Most taxa occurred too infrequently for analysis; therefore diurnal density and mean length comparisons were only preformed on larval shad and sunfish, which comprised 98% of the taxa.

During the study, there was no significant interaction between sunfish density and sample location ($F_{2,171} = 2.58$, $p = 0.079$), but larval catch rates were dissimilar between individual sites on each sampling date ($F_{27,121} = 3.7$, $p < 0.0001$). A comparison of larval densities among the morning ($F_{26,59} = 2.70$, $p = 0.0008$) and afternoon ($F_{27,61} = 4.40$, $p < 0.0001$) replicates on each sampling date indicated that there was statistically significant difference between individual runs over both periods. Overall, sunfish densities ranged from 0 - 7.40/m³ (mean = 0.41 m³) with a mean catch rate in the morning of 0.46/m³ (SE = ± 0.09) and in the afternoon of 0.35/m³ (SE = ± 0.05). The density of sunfish at each site was significantly higher in the morning than in the afternoon ($F_{37,120} = 2.08$, $p = 0.0016$, Figure 4.1). Mean larval length (range = 2.2 - 14 mm) in the morning was 4.33 mm (SE = ± 0.05) and in the afternoon it was 4.15 mm (SE = ± 0.06). There was no significant interaction between mean length and time of day at each site on specific sample dates ($F_{30,931} = 1.33$, $p = 0.1134$; Figure 4.2).

The catch rates of larval shad were dissimilar among the locations ($F_{2,147} = 15.66$, $p < 0.0001$) and between sites on each sample date ($F_{25,102} = 10.26$, $p < 0.0001$). There was also a statistically significant density difference among the morning ($F_{23,49} = 3.88$, p

< 0.0001) and afternoon ($F_{22,53} = 3.11$, $p = 0.0004$) replicates. Shad abundance ranged from 0 - 5.62/m³ (mean = 0.38/m³) with a mean morning density of 0.31/m³ (SE = ± 0.06) and a mean afternoon density of 0.45/m³ (SE = ± 0.10) but there was no significant interaction between catch rate and time of day ($F_{32,102} = 1.34$, $p = 0.1348$; Figure 4.1). The mean length of shad (range = 3.3 - 19.5 mm) collected in the morning was 5.22 mm (SE = ± 0.14) while length in the afternoon was 4.86 mm (SE = ± 0.12). A comparison between the two series indicated that mean length was significantly greater in the morning than in the afternoon ($F_{25,729} = 2.65$, $p < 0.0001$; Figure 4.2).

A comparison of mean water quality variables on each sample date indicated significant differences for DO, water temperature, and pH between periods (Table 4.2).

Table 4.1 — Total number of ichthyoplankton (n) and percent (%) of each taxon in the Atchafalaya River Basin from 29 April 2005 to 24 August 2005. All taxa were collected in the shallow littoral zone with paired bow-mounted push nets.

Taxa	n	%
Atherinidae		
<i>Labidesthes sicculus</i>	1	< 0.01
<i>Menidia beryllina</i>	3	< 0.01
Catostomidae	26	< 0.01
Centrarchidae		
<i>Lepomis</i> spp.	2,418	0.54
<i>Micropterus</i> spp.	1	< 0.01
<i>Pomoxis</i> spp.	29	< 0.01
Clupeidae		
<i>Dorosoma</i> spp.	1,967	0.44
Cyprinidae	29	< 0.01
Percidae	2	< 0.01
Sciaenidae		
<i>Aplodinotus grunniens</i>	3	< 0.01
Unknown	1	< 0.01
Total	4,480	

Table 4.2 — Daily comparisons ($n=12$) of water quality parameters (\pm SE) collected during the morning (0830 - 1200) and afternoon (1300 - 1630) at various location in the Atchafalaya River Basin from 29 April 2005 to 24 August 2005. An asterisk (*) indicates a significant difference ($p < 0.05$) for a particular variable.

Physicochemical parameter	Morning	Afternoon
Dissolved oxygen (mg/L) *	4.86 (\pm 0.27)	5.41 (\pm 0.25)
Temperature ($^{\circ}$ C) *	28.75 (\pm 0.13)	29.45 (\pm 0.19)
pH *	7.63 (\pm 0.07)	7.71 (\pm 0.05)
Specific conductivity (μ S/cm)	423 (\pm < 0.01)	422 (\pm < 0.01)

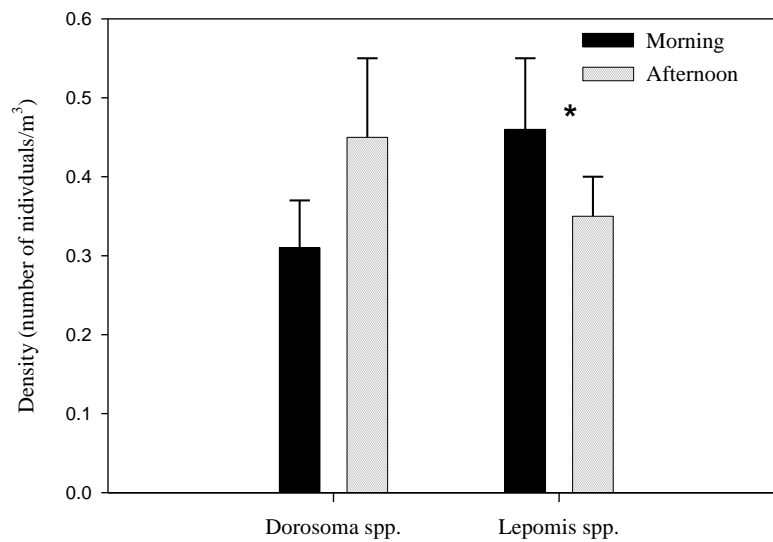


Figure 4.1. — Mean density (\pm SE) of larval shad *Dorosoma* spp. and sunfish *Lepomis* spp. collected in the morning (0830 - 1200) and afternoon (1300 - 1630) in the Atchafalaya River Basin from 29 April 2005 to 24 August 2005. Time of day comparisons for each taxon were based on abundance estimates (morning vs. afternoon) at multiple fixed sample sites. The asterisk (*) indicates a statistically significant difference ($p < 0.05$).

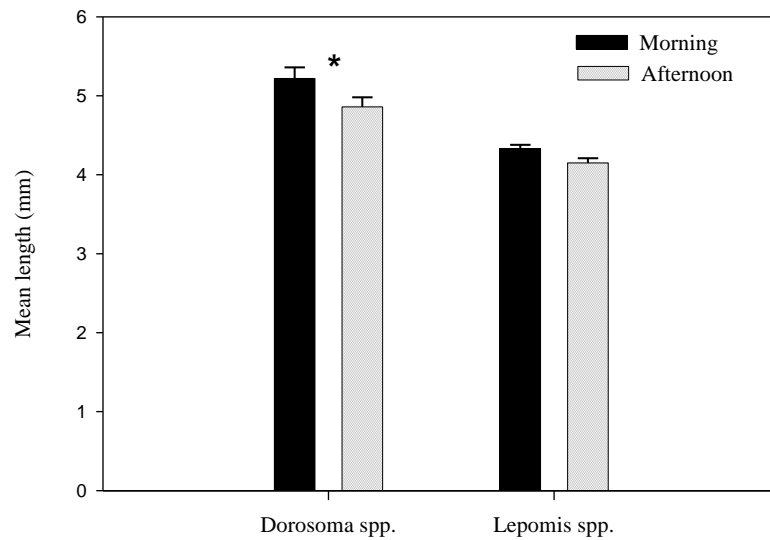


Figure 4.2 — Mean length (\pm SE) of larval shad *Dorosoma* spp. and sunfish *Lepomis* spp. collected in the morning (0830- 1200) and afternoon (1300 - 1630) in the Atchafalaya River Basin from 29 April 2005 to 24 August 2005. Comparisons were based on the length of all undamaged individuals from each taxon from each time period (morning vs. afternoon). The asterisk (*) indicates a statistically significant interaction between mean length and time of day ($p < 0.05$).

DISCUSSION

The timing and duration of centrarchid (Wallus and Simon 2008) and clupeid (Wallus et al. 1990) spawning is known to vary with latitude, photoperiod, water temperature, and habitat type, in the ARB, shad generally concentrate spawning in the weeks following the springtime flood pulse; in contrast, sunfish synchronize reproduction with elevated summertime water temperatures that usually overlap with prolonged periods of reduced discharge (Fontenot et al. 2001; Chapter 2). Flows into the system, however, are highly regulated (Reuss 2004) and this produces substantial annual variability in the hydroperiod (see Bonvillain et al. 2008) as well as reducing periods of widespread sheet flow that would simultaneously inundate much of the floodplain. Internal circulation has also been negatively impacted by the construction of linear canals designed to facilitate small boat traffic into the interior of the floodplain. These channels have altered the deposition rate of riverine sediments resulting in irregular elevation and geomorphology that reduces the level of river-floodplain connectivity (McManus 2002; Hupp et al. 2008). As a result, inter-basin abundance comparisons for early seasonal spawners, such as shad, could be dissimilar due to fluctuating river stage that provides only intermittent access to large portions of the floodplain. Because the majority of clupeid spawning in the ARB is relatively fixed (Chapter 3), seasonally inconsistent inundation may not coincide with the prime reproductive periods for shad, making many large portions of the floodplain inaccessible. Further, the combination of unpredictable flooding and episodic backswamp connectivity probably increases the potential that some nursery and grow-out areas may not persist in the aftermath of spring pulse. Consequently, basin-wide density estimates for taxa that exploit temporary rises in the

hydrograph maybe distinctly different based on distance from the mainstem and geographic location on the floodplain.

Conversely, most ARB sunfish reproductive activity tends to occur during a falling hydrograph (Fontenot et al. 2001). During the summer reduced river-floodplain connectivity tends to produce analogous environmental conditions (although at times sub-optimal) in the ARB (Sabo et al. 1999a; Sabo et al. 1999b; Rutherford et al. 2001). Therefore, even spatially disparate locations (Figure 2.1) may experience a uniform hydroperiod that is largely unaffected by oscillating flows in the mainstem. This could explain the lack of a significant interaction between the inter-locational comparisons examining potential differences in sunfish abundance in this study.

While ichthyoplankton abundance was lower (often by orders of magnitude) than densities reported in other temperate freshwater systems (Holland-Bartels 1995; Claramunt et al. 2005; Niles and Hartman 2007), the observed catch rates in this study are typical for the ARB (Fontenot et al. 2001; Engel 2003). Shad and sunfish are consistently among the most abundant and widespread pelagic fish larvae collected in the ARB (Fontenot et al. 2001; Engel 2003; Chapter 3), but catch rates between sites on each specific sampling date were dissimilar regardless of taxon.

The statistically significant difference in clupeid abundance between sites on a particular date, however, was somewhat unexpected given the high number of hatchlings that have been consistently reported throughout the system regardless (Fontenot et al. 2001; Engel 2003). Site-to-site comparisons also indicated that the distribution of sunfish larvae was dissimilar. It has been suggested that the annual cohort strength of *Lepomis* spp. is regulated by intermittent physicochemical fluctuations (particularly water

temperature and DO) (Fontenot et al. 2001) and as a result, even slight distances have been observed to contain disproportionate numbers of hatchlings (Engel 2003; Chapter 2).

Further research focused on characterizing the early life dynamics in systems like the ARB, should include an emphasis on sampling habitats in close spatial proximity (~ 1- 3 km apart) as well as concentrating sampling in areas that are relatively isolated from one another to ensure equitable comparisons of ichthyoplankton given the variability in mean length and abundance observed in this study. Holland-Bartels and colleagues (1995) examined the spatial pattern of ichthyoplankton in a variety of low-flow riverine areas and concluded that *a priori* habitat designations were often not predictive of larval abundance. Further, environmental factors (i.e., sinuosity, depth, organic concentrations, and shoreline length) have been found to influence the quality of nursery habitats in seasonally-inundated floodplain ponds in the lower Mississippi River Valley (Sabo et al. 1991).

Although greater numbers of shad larvae were collected in the afternoon, only sunfish abundance showed a significant interaction with time of day. Typically, centrarchids excavate nests in shallow, near-shore habitats that include sand and gravel bottoms (Carlander 1977; Wallus and Simon 2008). In the ARB, annual sunfish reproduction coincides with increasing photoperiod and the profusion of floating and submergent macrophyte growth in the littoral zone. The larvae of many species appear to exploit the plant canopy. However, the combination of higher temperatures and reduced discharge in the summer tends to accelerate the decomposition rates of vegetation both in the sub-canopy and in the water column. Consequently, the overall quality of the canopy

varies based on depth and the decomposition rates of organic matter (both aquatic and terrestrial) (Colón-Guad 2003). Despite the considerable diel variability associated with these beds, it has been hypothesized that larvae of some species utilize the canopy as a DO refugia to offset periods of unstable physicochemistry that often characterize the drawdown period in the ARB (Fontenot et al. 2001). It has been documented that the vertical position and location of larvae within the beds tends to be species-specific and changes both with the level of post-hatching development and the distance in relation to the shoreline and canopy edge (Engel 2003). Yet, bacterial-driven respiration in the sub-canopy causes the DO dynamics within the canopy to rapidly degrade in the absence of photosynthetic production (see Frodge et al. 1990). This could produce a DO "squeeze" that forces ichthyoplankton to vertically migrate within the canopy as DO declines.

During the morning, as DO levels begin to increase in the water column, fry may move from the canopy out to the pelagic zone to avoid near anoxic conditions that often prevail within the canopy. Therefore, concentrations of larvae would be significantly higher in the morning collections. Unsurprisingly, there was a significant interaction between time of day and certain physicochemical parameters. Daytime changes in DO and pH are attributable to elevated primary productivity by both phytoplankton suspended in the water column and aquatic vegetation in the littoral zone. As near-shore physicochemical conditions continue to improve, ichthyoplankton may orient back to the plant beds and not be susceptible to push netting later in the afternoon. Ichthyoplankton have been observed to respond to multiple environmental stimuli (tidal fluxes, Aceves-Medina et al. 2008; ultraviolet radiation, Williams et al. 1997; crepuscular activity, Muth and Scmulbach 1984; Gadomski and Barfoot 1998; circulation patterns and pycnocline depth,

North and Houde 2004) by altering buoyancy in the swim bladder (Trotter et al. 2003) or osmoregulatory changes (Kitajima et al. 1993).

Reviews of ichthyoplankton studies (Cyr et al. 1992) have stressed that low-replicate sampling may limit the precision of estimates, yet there is relatively limited knowledge about the precision of studies that rely on single daily estimates to establish larval abundance. Density comparisons between replicates at each site on a specific collection date were always dissimilar regardless of taxon or time of day. Prior research in other systems suggested that larval abundance was more variable between sites of comparable composition than between subsamples from the same site (Holland-Bartels et al. 1995). The results in the study, however, suggest that in order to detect density differences between and within individual sites on the floodplain, there should be separate, multiple daytime collections, especially in microhabitats that are known to undergo rapid environmental shifts. Interestingly, the relatively limited distance between collection sites did not result in comparable estimates. Finally, intraday mean length comparisons were only significant for shad with the largest individuals occurring in the morning. Although there is debate about the importance of size regulating post-hatch survivorship, multiple studies (Houde 1987; Pepin et al. 1992; Fuiman 1994) have reported that even subtle increases in size led to improved physical responsiveness to a multitude of stimuli.

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CHAPTER 5. GENERAL SUMMARY AND CONCLUSIONS

Currently, the dominant paradigm in floodplain ecology (i.e., the flood pulse concept, Junk et al. 1989) emphasizes that the recruitment dynamics of temperate fish communities, in systems like the Atchafalaya River Basin (ARB), are regulated largely by the timing and magnitude of the flood pulse. Although many fishes have been found to invade the floodplain in the aftermath of inundation (Kwak 1988), post-flood connectivity is often irregular and fails to coincide with optimal environmental conditions (e.g., increasing photoperiod, stable physicochemistry; see Winemiller 2004) that enhance the growth and maturation of developing fishes. Consequently, cohorts of young fishes hatched in transitory backswamps may experience disproportionately poor survivorship that effectively reduces the importance of the floodplain as critical nursery habitat. Nevertheless, many species are often presumed to migrate from the mainstem to the floodplain to spawn, despite increasing evidence (Humphries et al. 1999; King et al. 2003) that suggests that the importance of off-channel areas may be marginal.

Prior to this study, it was assumed that many taxa that remained undetected in previous ichthyoplankton surveys (see Fontenot et al. 2001; Engel 2003) would occur in off-channel areas following spring flooding. Although the hydropulse of the Atchafalaya River is manipulated (Reuss 2004; Bonvillian et al. 2008; Hupp et al. 2008), there is still a substantial degree of river-floodplain connectivity that typically coincides with the known spawning periods of many potentially floodplain-exploitative species (Lambou 1990). Consequently, I sought to determine if the floodplain was, in fact, the "epicenter" of fisheries reproduction by sampling seasonally-inundated backswamps, lakes, bayous, and canals. Overall, there were two major components to this research: establishing the

level of floodplain-exploitative fish reproduction and characterizing the synchronous overlap of fish larvae and zooplankton as cohorts of young fishes transited to exogenous foraging.

Chapter 2 describes the distribution and abundance of age-0 during and following the spring flood pulse. Throughout sampling there was relatively predictable connectivity even though mainstem flows were substantially lower than historic levels. To assess which environmental conditions structured the presence of larvae and juveniles on the floodplain, I compared river stage, photoperiod, and water quality during inundation and drawdown. Fluctuations in the timing and intensity of the hydropulse appeared to influence reproduction, but the predominant reproductive trait, regardless of the degree of parental care, appeared to be a temporally consistent spawning. Few taxa appeared to concentrate spawning in the ultra-shallow habitats, especially as floodwaters recede during the summer. The limited number of young-of-the-year fishes collected conflicts with hypotheses that emphasize the importance of overbank flooding in the recruitment strategies of riverine fish species.

In Chapter 3, I compared the abundance of multiple larval species in relation to microcrustacean zooplankton densities and several physicochemical parameters. Water temperatures appeared to be an important reproductive cue that influenced reproduction for all larvae and interestingly, most ichthyoplankton did not occur in phase with the highest zooplankton densities, yet zooplankton abundance was a critical component in the majority of Akaike's information criterion models used to explain the abundance of ichthyoplankton. Both zooplankton and larvae appeared to benefit from episodic increases in stage yet, the densities of each declined rapidly once discharge subsided.

Although it was anticipated that hatchlings and zooplankters would benefit from increasing photoperiod and lower summertime flows (see Humphries et al. 1999, Grozholz and Gallo 2006), both groups were reduced during this combination of conditions. The species-specific spike of each larval species suggests that two major reproductive strategies, concentrated and protracted spawning, may prevent some taxa from competing for resources following hatching.

Chapter 4 was a contrast of daily (morning vs. afternoon) densities and mean length estimates of larval sunfish *Lepomis* spp. and shad *Dorosoma* spp. A comparison of sunfish abundance between the two time series was significant however; there was no interaction between mean length and time of day. Conversely, for shad there was no observed time of day density interaction but mean length was statistically different. Although the sampling locations were selected based on distance from the mainstem and the level of connectivity, a comparison of sunfish density among the three locations was not statistically significant yet, abundance differed between the fixed sample sites at the same location on a given sampling date. In contrast, there was inter-locational and site-to-site density difference for shad. Finally, a comparison of the morning and afternoon replicates at each site for both taxa was statistically different.

Future Research

We now possess a relatively strong understanding of the reproductive ecologies of many ARB fishes (Fontenot et al. 2001; Engel 2003; Chapters 2– 4). I have selected three areas that I believe warrant further investigation. First, an understanding of the proximate bioenergetic composition (i.e., protein, fat, and water) of adult fishes through the use of bioelectrical impedance analysis (BIA, Cox and Hartman 2005) could be

highly beneficial in determining if the peak fitness of adults parallels the highest annual reproductive output. For species that have extended spawning periods (e.g., sunfishes and shad) it is unclear if the fecundity of an individual contributes to the duration of reproduction. In other words, are annual larval cohorts generated, in part, because of seasonal differences in the overall "health" of a particular species or the "health" of individuals within that species that tends to change over time (i.e., reproductive plasticity)? If so, BIA could detect metabolic fluctuations that could forecast the onset and intensity of reproduction.

Secondly, we need to quantify primary productivity in the ARB. Currently, we collect a number of physicochemical and environmental measurements on a weekly basis. However, we lack any knowledge about phytoplankton dynamics. My research found that secondary production collapsed in the months following inundation. This contradicts the findings of many studies (Welcomme 1985; Basu and Pick 1996; Schemel et al. 2004; Grozholz and Gallo 2006) that report a relatively predictable trajectory of post-flood planktonic production. While we have chronicled (Sabo et al. 1999; Kaller et al. 2010) the impacts of acute, widespread hypoxia (≤ 2.0 mg/L dissolved oxygen) on the larval (Fontenot et al. 2001) and adult (Rutherford et al. 2001) fish community in the ARB, there is a lack of information about its affects on other organisms. In addition, it should be important to determine if invasive aquatic macrophyte growth is disrupting phytoplankton production due to a competition for light or nutrients. I suggest that we expanded our daily water quality sampling protocols to include the collection of chlorophyll *a* at multiple locations.

Finally, a survey of ichthyoplankton in the Atchafalaya River is critical. Prior, long-term ichthyoplankton research in the Mississippi River (C. F. Bryan, W. E. Kelso, and D. A. Rutherford unpublished data) suggests that many taxa have limited reliance on the floodplain. These native and introduced species comprise the majority of fishes (e.g., freshwater drum *Aplodinotus grunniens*, grass carp *Ctenopharyngodon idella*, carpsuckers *Carpiodes* spp., shiners *Notropis* spp., buffalo fish, *Ictiobus* spp.) absent in my study but frequently occur in the extensive electrofishing surveys conducted by the department. There is evidence, based on the infrequency of some larvae and the widespread documentation of adults of the same species in the system, that the ARB could be an ecological sink for hatchlings.

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