

LIFE HISTORY CHARACTERISTICS OF THREE OBLIGATE
RIVERINE SPECIES AND DRIFT PATTERNS
OF LOWER BRAZOS RIVER FISHES

Dissertation

Presented to the Graduate Council of
Texas State University-San Marcos
in Partial Fulfillment
of the Requirements

for the Degree

Doctor of PHILOSOPHY

by

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San Marcos, Texas
May 2011

LIFE HISTORY CHARACTERISTICS OF THREE OBLIGATE
RIVERINE SPECIES AND DRIFT PATTERNS
OF LOWER BRAZOS RIVER FISHES

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ACKNOWLEDGEMENTS

First, I would like to thank the faculty and staff of the Freeman Aquatic Building and Texas State Biology Department. Most importantly, I would like to thank my major advisor, Tim Bonner. Tim has been very patient and a great mentor throughout my graduate career. He helped instill and feed a need for learning and research, enabling me to make and attain goals that were once inconceivable. In addition, he has been a good friend and I look forward to discussions, debate, and hunting with Tim for many years to come. I would also like to thank my other committee members, Dr. John Baccus, Dr. Alan Groeger, Dr. Butch Weckerley, and Dr. Joanna Curran (now at University of Virginia) for their patience, guidance and valuable input into my research. Dr. Tom Arsuffi, Dr. Weston Nowlin, and Dr. Dave Huffman were all vital parts of my educational experience at Texas State. Janet K. Wisian was always helpful and ready with the answers that I needed.

I also have to give a big thank you to the undergraduate and graduate students of the Freeman Aquatic Building. Over the years, many of my fellow graduate students contributed greatly to this dissertation either through field work, ideas, or simply making the work more fun. First of all, Jackie Watson, Dusty McDonald, and Brad Littrell were there from the beginning. We had a lot of fun, worked and played hard, and managed to teach and learn from one another along the way. During the second year of my field work, Tom Heard was with me every step of the way and I don't think I could have done it without him. Tom also played a major role in sorting of the numerous drift net samples

we collected. Josh Perkin, Cooper Knight, David Tinsley and numerous others also aided in the completion of my field work.

This work would not have been possible without the support of my parents and other family members. I thank my parents, Doug and Connie Williams, for instilling in me a proper work ethic and a great love of the outdoors, and for encouraging me to pursue my dreams of making a living by doing something I love. I also would like to thank my family at First Baptist Church San Marcos for their support and encouragement. Julie and Mitch Hoffman, Ross and Martha King, and Jimmy and Janet Scott are the finest group of people I have ever known and have always been there to support and encourage me.

Last and most importantly, I would like to thank my wife Carla and boys Dempsey and Liam. Completion of this degree would not have been possible without their unconditional love, support, encouragement and sacrifices. Hopefully, we can now begin to enjoy the benefits of their sacrifices and I look forward to spending all of my extra time with them. Finally, I thank God for blessing me with the opportunity, ability, and support needed to reach this goal.

This manuscript was submitted on December 9, 2010.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.....	v
LIST OF TABLES.....	ix
LIST OF FIGURES.....	x
ABSTRACT.....	xii
CHAPTER	
I. LIFE HISTORY CHARACTERISTICS AND LARVAL DRIFT PATTERNS OF THREE OBLIGATE RIVERINE SPECIES IN THE LOWER BRAZOS RIVER, TEXAS.....	
	1
Abstract.....	1
Introduction.....	2
Methods.....	5
Study Area.....	5
Fish Collection.....	6
Laboratory Methods.....	7
Results.....	11
Population Structure.....	11
Reproductive Characteristics.....	11
Larval Drift.....	12
Food Habits.....	13
Discussion.....	15
Acknowledgements.....	22
Literature Cited.....	23
II. TEMPORAL AND SPATIAL DRIFT PATTERNS OF LOWER BRAZOS RIVER FISHES.....	
	41
Abstract.....	41
Introduction.....	42

Methods.....	45
Study Area	45
Fish Collection	46
Laboratory Methods.....	47
Analysis.....	49
Results.....	51
Substrate Spawners	52
Pelagic Broadcast Spawners	54
Adhesive Broadcast Spawners.....	55
Discussion.....	57
Implications for Conservation.....	62
Acknowledgements.....	64
Literature Cited	65

LIST OF TABLES

Table	Page
1.1. Mean (\pm SD) maximum length for three age classes of shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005	31
1.2. Total and seasonal mean percentage by weight and percent occurrence (in parentheses) of diet items for adult and juvenile shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005	32
2.1. Relative abundance and drift densities for six reproductive guilds of fishes collected from three sites on the lower Brazos River during 2004 and 2005	75
2.2. Simple main effects tests for larval drift density differences of substrate, pelagic broadcast and adhesive broadcast spawners.	76

LIST OF FIGURES

Figure	Page
1.1. Daily mean discharge rates for the lower Brazos River from two time periods: January 1, 2004 - December 31, 2004; January 1, 2005 - December 31, 2005.....	33
1.2. Location of three collection sites on the lower Brazos River, Texas sampled monthly and/or bimonthly from January 2004 until December 2005.....	34
1.3. Monthly mean (\pm SD) length for three age classes of shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005	35
1.4. Mean monthly gonadosomatic index (GSI; \pm SD) for females and males and monthly ovarian condition (% of females examined) for shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005	36
1.5. Monthly size-frequency distribution for ova diameters from one shoal chub, ghost shiner and silverband shiner per month collected during the 2004 reproductive season from three sites on the lower Brazos River	37
1.6. Mean (\pm SD) clutch size estimates for shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005 (numbers above error bars represent monthly n values)	38
1.7. Length versus estimated clutch size relationship for shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005	39
1.8. Larval drift densities for four life stages of shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from July – September 2004 and May – September 2005	40

2.1.	Mean daily discharge rates for the lower Brazos River from 2004 and 2005	77
2.2.	Mean (\pm SD) monthly drift densities for larval and juvenile life stages of substrate, pelagic broadcast and adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005	78
2.3.	Mean diel drift proportions for larval and juvenile substrate, pelagic broadcast and adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005	79
2.4.	Mean daily night time and day time drift densities for larval and juvenile stages of substrate, pelagic broadcast and adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005	80
2.5.	Day time and night time distance from shore drift densities for substrate spawners collected from three sites on the lower Brazos River during 2004 and 2005	81
2.6.	Day time and night time distance from shore drift densities for pelagic broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005.....	82
2.7.	Day time and night time distance from shore drift densities for adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005.....	83

ABSTRACT

LIFE HISTORY CHARACTERISTICS OF THREE OBLIGATE RIVERINE SPECIES AND DRIFT PATTERNS OF LOWER BRAZOS RIVER FISHES

by

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May 2011

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I examined various life-history characteristics of the shoal chub *Macrhybopsis hyostoma*, ghost shiner *Notropis buchanani* and silverband shiner *Notropis shumardi* from the lower Brazos River, Texas. Monthly or bimonthly collections were made from three sites on the lower Brazos River during January 2004 through December 2005. Shoal chub, ghost shiner and silverband shiner have similar life history characteristics, including rapid growth, short life spans and early reproductive maturity. In addition,

these species produce multiple cohorts of eggs during prolonged spawning seasons lasting from early spring until late fall. Diets of the shoal chub and silverband shiner consisted primarily of aquatic invertebrates, while ghost shiners consumed aquatic invertebrates and a large proportion of detritus. The life history characteristics of the shoal chub, ghost shiner and silverband shiner allow survival in highly variable aquatic systems such as the lower Brazos River.

I also examined larval and juvenile drift patterns of substrate, pelagic broadcast and adhesive broadcast spawning guilds in the lower Brazos River during 2004 and 2005. Relatively higher drift densities were observed during the high flow year for all reproductive guilds and among life stages within reproductive guilds. Substrate, pelagic broadcast and adhesive broadcast spawners also had higher drift densities at night and in near shore areas. Increased metalarvae and juvenile drift densities indicated higher survival and recruitment of larval fishes during the high flow year. Similar night time and near shore drift density patterns demonstrated concurrent use of habitat and resources among life stages and reproductive guilds, suggesting biotic factors such as competition may influence survival of larvae and recruitment of riverine fish.

CHAPTER I
LIFE HISTORY CHARACTERISTICS AND LARVAL DRIFT PATTERNS OF
THREE OBLIGATE RIVERINE SPECIES IN THE
LOWER BRAZOS RIVER, TEXAS

ABSTRACT

I examined various life-history characteristics of the shoal chub *Macrhybopsis hyostoma*, ghost shiner *Notropis buchanani* and silverband shiner *Notropis shumardi* from the lower Brazos River, Texas. Monthly or bimonthly collections were made from three sites on the lower Brazos River from January 2004 through December 2005. Shoal chub, ghost shiner and silverband shiner have similar life history characteristics, including rapid growth, short life spans and early reproductive maturity. In addition, these species produce multiple cohorts of eggs during prolonged spawning seasons lasting from early spring until late fall. Diets of the shoal chub and silverband shiner consisted primarily of aquatic invertebrates, while ghost shiners consumed aquatic invertebrates and a large proportion of detritus. The life history characteristics of the shoal chub, ghost shiner and silverband shiner allow survival in highly variable aquatic systems such as the lower Brazos River.

INTRODUCTION

Declining populations of riverine fish species are frequently associated with anthropogenic modifications of stream systems. Obligate riverine species are often the first affected by habitat and flow modifications due to adaptations for riverine habitats during all or a portion of their life cycle. Unfortunately, flow regime alterations continue and are necessitated by the needs for human water supply, hydropower, agriculture, flood control, and recreation (Poff *et al.*, 1997; Warren *et al.*, 2000; Jelks *et al.* 2008). As alterations continue, development of flow regulations suited to the ecological requirements of obligate riverine fishes will be necessary for conservation of native riverine fish assemblages. However, species-specific information needed to develop adequate flow regulations and conservation strategies are often lacking, especially for fish species inhabiting large rivers. The shoal chub *Macrhybopsis hyostoma*, ghost shiner *Notropis buchanani* and silverband shiner *Notropis shumardi* are obligate riverine species inhabiting main stem habitats of large rivers in central North America (Gilbert and Bailey, 1962; Underwood *et al.*, 2003) and, although these species are somewhat wide spread, little detailed information is known about their life history characteristics.

Members of *Macrhybopsis* are short-lived species inhabiting large to medium-size rivers and spawn semibuoyant eggs that drift downstream while developing. Historically, the shoal chub was considered a wide-ranging subspecies of *Macrhybopsis aestivalis* but was elevated to species status (Eisenhour, 1999, 2004). The shoal chub typically inhabits swift flowing run habitats consisting of sand or gravel (Luttrell *et al.*, 2002) in main stems of medium to large rivers of the Mississippi River drainage and westward along Gulf Slope drainages to the Colorado and Brazos Rivers in Texas (Eisenhour, 2004).

Shoal chubs reproduce from early May to mid August in Tennessee (Etnier and Starnes, 1993) and feed primarily on adult and larval aquatic insects (Starrett, 1950; Etnier and Starnes, 1993). Maximum life span is estimated at 1.5 years (Starrett, 1951) and maximum total length is 76 mm (Etnier and Starnes, 1993). Although considered currently stable by Warren *et al.* (2000), the shoal chub was extirpated from or exhibited population declines in several areas of the historical range including portions of the Arkansas River (Luttrell *et al.*, 1999), Tennessee River (Boschung and Mayden, 2004), upper Kansas River (Sanders *et al.*, 1993), Cumberland River (Etnier and Starnes, 1993), Big Blue River in Kansas (Gido *et al.*, 2002) and the Sabine River in Texas (Runyan, 2007).

The ghost shiner inhabits Mississippi River tributaries from Louisiana to Minnesota and Wisconsin, and westward in Gulf Slope drainages to the Rio Grande drainage in Texas. In addition, northern populations disjunct from the Mississippi River and Gulf Coast populations exist in streams of southwestern Ontario, Canada (Holm and Houston, 1993; Kott and Fitzgerald, 2000). The ghost shiner inhabits reservoirs and slow flowing pools and backwaters of clear to turbid rivers and streams consisting of silt, sand, and gravel substrates (Pflieger, 1997; Boschung and Mayden, 2004). One and two year old individuals spawn over riffles of fine gravel or sand beginning as early as April in Missouri (Pflieger, 1997) and continuing until as late as August in Oklahoma and Kansas (Cross and Collins, 1995; Miller and Robison, 2004). Ghost shiners reach a maximum total length of 66 mm (Etnier and Starnes, 1993) and diet is unknown (Pflieger, 1997). Declines in ghost shiner populations have been associated with habitat loss and reservoir construction in Ohio (Trautman, 1981) and Tennessee (Etnier and Starnes, 1993) and are

considered extirpated from Wisconsin (Lyons *et al.*, 2000) and endangered in Pennsylvania.

The silverband shiner occupies large rivers of the Mississippi River drainage from Louisiana to the Missouri River in South Dakota (Gilbert, 1978). Populations also occur in the Trinity, Brazos, Colorado and Lavaca Bay drainages of Texas disjunct from Mississippi River populations. Based on morphological characteristics, Texas populations were once described as a separate species, *Notropis brazosensis* (Hubbs and Bonham, 1951). Gilbert and Bailey (1962) later refuted this evidence and considered Texas populations as *Notropis shumardi*. Silverband shiners often inhabit areas of fast current over sand and gravel substrates (Ross, 2001). Reproductively mature individuals have been collected from June to August in Louisiana and observed spawning over hard sand and fine gravel (Suttkus, 1980). Diet is unknown. Silverband shiners are considered stable by Warren *et al.* 2000 but are listed as threatened in Kansas (Haslouer *et al.*, 2005) due to population declines associated with habitat loss.

Life history information available for the shoal chub, ghost shiner and silverband shiner is mostly anecdotal and collected piecemeal over large geographic areas. Additional descriptions of life history characteristics are needed to develop adequate conservation strategies and prevent further population declines of these and other similar riverine species. Herein, I describe various life-history characteristics for the shoal chub, ghost shiner and silverband shiner from the lower Brazos River, Texas. Specifically, I assess annual growth rates, age and length relationships, reproductive seasons, minimum length for reproduction, clutch size, oocyte diameters, food habits, and annual drift patterns of larvae for these three species.

METHODS

Study Area

The Brazos River in Texas is one of the largest and most altered river drainages of the western Gulf Slope drainages (Connor and Suttkus, 1986). The Brazos River originates near the New Mexico-Texas border and flows approximately 1,700 km southeast across Texas to a confluence with the Gulf of Mexico. Geographically, the Brazos River basin is separated into three sections: upper, middle and lower Brazos River. The upper and middle reaches are highly regulated by 17 main stem and tributary reservoirs. In contrast, the lower reach is relatively unregulated and flows unimpeded approximately 330 river km from Brazos Lake Dam in Waco to the Gulf of Mexico near Freeport, Texas (Runyan, 2007). Dam construction and resulting habitat fragmentation in the upper and middle reaches have been associated with population declines in several native obligate riverine species including the chub shiner *N. potteri* (Perkin *et al.*, 2009) and two Brazos River endemics, the sharpnose shiner *N. oxyrhynchus* and smalleye shiner *N. buccula* (Runyan, 2007). Currently, the lower reach supports stable populations of shoal chubs, ghost shiners and silverband shiners (Runyan, 2007).

Discharge rates of the lower Brazos River varied greatly relative to the historical hydrograph and between 2004 and 2005. Historical trends in discharge rates of the lower Brazos River generally increased during late spring (April), began decreasing during mid-late summer (July), and showed a gradual increase during fall and winter (Fig. 1.1). Mean (\pm SD) daily discharge rates for 2004 (378 ± 454 m³/s) ranked in the 94th percentile of the historical daily mean flow (214 ± 95 m³/s). Mean daily discharges during 2005

($192 \pm 234 \text{ m}^3/\text{s}$) was substantially lower, ranking in the 41st percentile of the historic mean daily discharge rate.

Fish Collection

I collected shoal chubs, ghost shiners and silverband shiners monthly from three sites on the lower Brazos River from January 2004 through December 2005. In June 2004, only the upstream site was sampled because of excessive stream discharge. I increased sampling effort to bimonthly collections during the reproductive period from May through August 2005. Sample sites were located along a 227 km segment of the lower Brazos River at Hwy 290 near Hempstead ($30^{\circ}08'08''\text{N}$, $96^{\circ}11'32''\text{W}$), upstream from Hwy 723 ($29^{\circ}36'11''\text{N}$, $95^{\circ}50'22''\text{W}$) in Rosenberg, and Hwy 1462 near Rosharon, Texas ($29^{\circ}21'12''\text{N}$, $95^{\circ}34'28''\text{W}$; Fig. 1.2).

At each site and sampling period, I seined (1.2 m X 9.1 m, mesh size: 3.2 mm; 1.2m X 3.7 m, mesh size: 3.2 mm) all wadeable habitat types (main channel, channel bank, eddy, and backwater areas) accessible from point sand bars. I measured total length (TL; mm) of 30 or more randomly selected individuals of three target species when available. I anesthetized up to 10 adults and 10 juveniles of each target species with a lethal dose of MS-222 (80 mg/L) and preserved them in a 10% formalin solution for reproductive and food habit analysis. I released all other individuals unharmed.

I sampled larval fish monthly from July through September 2004 and twice monthly from May through August 2005, and once in September 2005. At each site, I collected larval fish from wadeable sand bars with 0.45 X 0.25 m, 500 μm mesh drift nets, tapered on one end and connected to a removable sample cup. Nets were anchored

on each side by metal fence T-posts driven into the substrate. Drift nets were placed at four stations in a line perpendicular to the shore. Stations were arranged from near shore, shallow water areas to areas of increasing depth and current velocity in far shore areas. Two near shore, shallow stations consisted of one net and far shore, deeper stations contained two nets stacked vertically. Near shore nets were sufficient to sample all or the majority of the water column. At far shore stations, upper nets sampled the upper 0.25 m of the water column and lower nets sampled the middle or lower 0.25 m of the water column (total depth < 2 m). I washed the contents of each net into individual Whirl-Pac bags and preserved them in a 10% formalin solution every 3 h for a 24-h period. I measured current velocity (Marsh-McBirney Flowmate Model 2000 flow meter) in the center of each drift net opening at the beginning and end of each 3-h interval. I used beginning and ending current velocity measurements to calculate a mean current velocity through the center of the net during the 3-h interval.

Laboratory Methods

From preserved adults, I examined three randomly selected males and three females of each species from each site and sampling date. I measured total length (mm) and weighed (mg) each individual and removed gonads and intestinal tract through an incision made from the isthmus to the urogenital opening. I used a dissecting microscope (30X) to determine the sex of each fish and stage of ovarian development was determined for females *{i.e., immature or resting, developing, mature, spent; Phillip, 1993; Williams and Bonner, 2006}*. Gonads were cleaned of adipose and connective tissues and weighed. From somatic and gonad weights, I calculated a gonadosomatic index (GSI; [gonad

weight / fish weight]*100) for each fish. I pooled GSIs by sex and across sites for each date and calculated mean GSIs for males and females.

I measured oocyte diameters of three sexually mature females from each month of the 2004 reproductive season to examine patterns in oocyte development. The left ovary of each individual was placed into a clear Petri dish and oocytes were separated by stirring and teasing with small forceps. Using a digital micrometer, I measured the largest and smallest diameters of 100 randomly selected oocytes and used these measurements to calculate a mean oocyte diameter (Heins and Baker, 1989). I grouped oocyte diameters into 0.05 mm increments and constructed size frequency histograms to demonstrate clutch development throughout the reproductive season. Oocytes belonging to the most advanced clutch (mature or maturing) within an individual were separated based on size and coloration and counted. Assuming oocyte production was equal in both ovaries, I doubled the oocyte count from the left ovary to estimate total clutch size. Based on oocyte size and color patterns for 2004 specimens, I counted mature or maturing oocytes and estimated clutch size for three females of each species during each month of the 2005 reproductive season.

I constructed length frequency histograms from total length (TL) measurements to estimate number of age groups in the population, age and length relationships, age class structure, mean yearly growth rates of each age class, and maximum age of each of the three species (Devries and Frie, 1996). Total lengths were pooled across sites for each month, grouped into 2-mm length increments and used to construct frequency histograms. I used modal class progression analysis, Bhattacharya method (FiSAT II,

Version 1.2, Food and Agriculture Organization, 2005) to estimate monthly mean lengths and annual growth in each age group of these species.

For food habit analysis, I examined contents of the alimentary tract from three randomly selected adults and three juveniles for each month when available. The digestive tract was removed from selected individuals and contents from the esophagus to the second loop of intestine were removed. I identified and separated gut contents into broad taxonomic groups (i.e., aquatic insects, terrestrial insects, crustaceans and intestinal parasites), sand, algae, and detritus. Detritus or “bottom ooze” (Starrett, 1950) was defined as sediments consisting of diatoms and very fine sand particles and mud/silt. Taxonomic groups were further segregated into the lowest practical taxon. Wet weights (mg) were then determined for each food group or item after gently blotting with a paper towel to remove excess moisture. Items or groups weighing < 0.1 mg were assigned a weight of 0.1 mg. Percent weight of each food item was calculated for each individual. Monthly samples were pooled across years and grouped into four time intervals to reflect seasonality: January through March (Winter); April through June (Spring); July through September (Summer); October through December (Fall). Seasonal mean percent weight and percent occurrence were determined for each food group. Adult and juvenile food habits were analyzed separately to determine possible ontogenic shifts in diet.

The contents of each drift net sample were rinsed, sorted, and larval and juvenile fishes were identified and counted. I removed contents of each drift net sample from the 10% formalin solution and rinsed with deionized water for approximately 15 minutes. I then placed the sample into a sorting pan and separated all contents into two groups, detritus/macroinvertebrates and fish. Fish were placed in labeled vials and stored in 4%

formalin (Kelso and Rutherford, 1996). I next identified each individual or a sub-sample of individuals from each sample to species and determined developmental stage. Larval identification was based on published larval keys and morphological descriptions for described species (Auer, 1982; Fuiman *et al.*, 1983). Life stages (protolarvae, mesolarvae, metalarvae and juvenile) were determined based on the following characteristics (Snyder *et al.*, 1998): Protolarvae, lack of dorsal, anal, and caudal fin spines and/or rays; Mesolarvae, at least one dorsal, anal or caudal fin spine or ray but lacking a full set of adult soft rays in at least one median fin or lacking pelvic fin buds or pelvic fins; Metalarvae, full complement of principal soft rays in all median fins and pelvic fin buds or pelvic fins. Juveniles, young of year fishes with full complements of adult median and paired fin rays and spines. Due to large numbers of individuals in some samples (>500), I subsampled larger samples (See Chapter 2). The amount of water filtered through each net was calculated by multiplying mean current velocity through the net (m/s), net area (m²; width X submerged portion of net), and time (s). I calculated daily drift densities (#individuals/100 m³) for each species life stage by dividing the sum of all individuals by the total water filtered during each 24-h period. Annual daily drift densities were compared with two-tailed *t* tests ($\alpha = 0.05$). Prior to analysis, data was log transformed [$\log(x+1)$].

All work was conducted under Texas State University-San Marcos IACUC #04-39C297D2 and Texas Parks and Wildlife Permit #SPR-0601-159.

RESULTS

Population Structure

Shoal chub, ghost shiner and silverband shiner populations in the lower Brazos River consisted of three age classes within each year. Age 2 individuals of each species were collected during the early part of each year, however, monthly relative abundances were < 15% and no age 2 individuals were collected after June (Fig. 1.3). Age 1 was the most abundant age class until the reproductive season when age 0 fish abundance increased. Age 1 abundances declined steadily as the year progressed, resulting in few individuals entering into their second winter. Thus, high mortality was exhibited during the second summer and maximum age of all three species was 2.5 years. Age 0 shoal chub, ghost shiner, and silverband shiner exhibited relatively rapid growth, reaching total lengths equal to 45-65% of maximum length during the first summer and fall (Table 1.1).

Reproductive characteristics

Shoal chub, ghost shiner, and silverband shiner reproduced during prolonged spawning seasons lasting from early spring until late fall. Mean monthly GSIs for female shoal chubs were elevated (> 3.5%) and mature ovaries were present from April through October with some females remaining mature through November (Fig. 1.4). The smallest shoal chub female exhibiting gonadal maturation was a 39 mm individual collected in early September 2004. Female ghost shiners exhibited elevated GSIs (> 2.5%) and mature ovaries from May through September. The smallest female ghost shiner to exhibit mature ovaries was a 31 mm individual collected in August 2005. Elevated monthly GSIs (> 3%) and mature ovaries were present in silverband shiners from April

through September. The smallest female to exhibit gonadal development was a mature 41 mm individual collected during August 2004. Trends in mean monthly GSIs for males of all three species was similar and positively correlated with mean monthly female GSI values {shoal chub ($r = 0.86$; $P < 0.01$), ghost shiner ($r = 0.79$; $P < 0.01$), silverband shiner ($r = 0.81$; $P < 0.001$)}.

Shoal chubs, ghost shiners and silverband shiners exhibited trimodal distributions of oocyte diameters throughout the 2004 reproductive season, indicating these species produce multiple cohorts of oocytes during a single reproductive season. For each species, oocyte diameters consisted of three general size groups including small (< 0.3 mm) previtellogenic oocytes, and medium ($> 0.3 - 0.6$ mm) and large (> 0.6 mm) vitellogenic oocytes representing developing and mature oocytes (Fig. 1.5). Estimated mean clutch size for mature shoal chubs was 198.75 (SD = 155.8; $n = 32$) and ranged from 34 to 680 oocytes (TL range = 39 – 70 mm; Fig. 1.6). Ghost shiner mean clutch size was 232.6 (SD = 193.5; $n = 27$) and ranged from 32 to 952 oocytes (TL range = 31 - 49 mm). Mean clutch size for mature silverband shiners was 387.3 (SD = 188.5; $n = 27$) and ranged from 144 to 750 oocytes (TL range = 47 -76 mm). Clutch size was positively related to total length of mature females for shoal chubs ($F_{1,30} = 49.5$, $P < 0.001$), ghost shiners ($F_{1,25} = 23.0$, $P < 0.001$) and silverband shiners ($F_{1,25} = 15.7$, $P < 0.001$; Fig. 1.7).

Larval Drift

Shoal chub, ghost shiner and silverband shiner daily larval drift densities were highly variable but similar among years for protolarvae and generally higher during 2004 than 2005 for mesolarvae, metalarvae and juveniles. Across years, daily combined larval

and juvenile drift densities (# fish/100m³) ranged from 0.005 – 6.71 for shoal chub, 0.02 – 5.14 for ghost shiner, and 0.004 – 4.61 for silverband shiner. High variability across and within years was associated with increased drift densities corresponding to peak GSIs (Fig. 1.8). Mean (\pm SD) daily protolarvae drift densities (fish/100m³) were similar between years for shoal chub (2004, 0.52 \pm 0.75; 2005, 0.23 \pm 0.55; $t_{34} = 1.52$, $P = 0.14$), ghost shiner (2004, 0.92 \pm 1.32; 2005, 0.65 \pm 0.69; $t_{34} = 0.35$, $P = 0.73$) and silverband shiner (2004, 0.33 \pm 0.62; 2005, 0.14 \pm 0.16; $t_{34} = 0.99$, $P = 0.33$). Mesolarvae mean daily drift densities were higher during 2004 for shoal chub (2004, 0.25 \pm 0.36; 2005, 0.05 \pm 0.12; $t_{34} = 2.62$, $P < 0.02$) and silverband shiner (2004, 0.19 \pm 0.24; 2005, 0.04 \pm 0.05; $t_{34} = 3.30$, $P < 0.001$) but similar between years for ghost shiner (2004, 0.21 \pm 0.40; 2005, 0.09 \pm 0.12; $t_{34} = 1.41$, $P = 0.17$). Metalarvae mean daily drift densities were higher during 2004 for shoal chub (2004, 0.8 \pm 0.52; 2005, 0.02 \pm 0.06; $t_{34} = 4.23$, $P < 0.001$), ghost shiner (2004, 0.12 \pm 0.18; 2005, 0.01 \pm 0.01; $t_{34} = 3.44$, $P = 0.002$) and silverband shiner (2004, 0.42 \pm 0.74; 2005, 0.01 \pm 0.06; $t_{34} = 3.51$, $P = 0.001$). Juvenile mean daily drift densities were higher during 2004 for shoal chub (2004, 0.58 \pm 0.72; 2005, 0.002 \pm 0.005; $t_{34} = 4.67$, $P < 0.001$), ghost shiner (2004, 0.09 \pm 0.16; 2005, 0.005 \pm 0.01; $t_{34} = 2.78$, $P < 0.01$) and silverband shiner (2004, 0.42 \pm 0.82; 2005, 0.001 \pm 0.003; $t_{34} = 2.89$, $P < 0.01$).

Food Habits

Stomach contents of adult and juvenile shoal chubs, ghost shiners and silverband shiners included aquatic and terrestrial insects, crustaceans, sand and detritus. Food items of adult shoal chubs (by % weight) consisted primarily of aquatic insects

[Trichoptera (24%), Chironomidae (17%), Ephemeroptera (7%), and unidentified aquatic insects (14%)], sand and detritus (Table 1.2). Aquatic insects occurred most often [% occurrence; Chironomidae (45%), Trichoptera (38%) and Ephemeroptera (13%)] and comprised > 70 % by weight of shoal chub food items during spring and fall. Terrestrial insects were an uncommon food item. Unlike adults, detritus comprised the largest percent by weight of juvenile shoal chub food items, followed by sand, aquatic insects and small crustaceans (Ostrocooda). By percent weight, food items of adult ghost shiners consisted primarily of detritus, aquatic insects [Trichoptera (5%), Diptera (3%), Hemiptera (3%), unidentified insects (14%), and < 1% Plecoptera, Ephemeroptera, and Coleoptera] and sand. Occurrence of detritus was consistent across seasons and among adults and juveniles, occurring in 89% of adults and 85% of juveniles and comprising > 60% by weight of adult and juvenile ghost shiner food items. Digestive tract contents of adult silverband shiners consisted primarily of aquatic insects [percent weight; Trichoptera (15%), Ephemeroptera (12%), Diptera (5%), Plecoptera (2%), and Hemiptera (< 1%)], detritus, algae, terrestrial insects, sand and < 1% crustaceans. Aquatic insects were the most common food item in adult silverband shiners with a peak in seasonal occurrence (89%) during summer. Trichopterans were the most common aquatic insect, occurring in 28% of adult silverband shiners. Terrestrial insects were present but uncommon (7% occurrence) throughout the study period. Similar to adults, aquatic insects comprised the greatest percent by weight of juvenile silverband shiner food items, followed by detritus, sand, crustaceans and algae. Although not considered a food item, cestodes were present in digestive tracts of adult and juvenile shoal chubs and silverband shiners but absent from ghost shiners.

DISCUSSION

Many aspects of life history characteristics are shared among shoal chubs, ghost shiners and silverband shiners. These three species are fast growing and exhibit short life spans and early maturation with reproduction beginning during age 1, or during the second summer of life. Patterns in GSI and ovarian development suggest these fishes reproduce during protracted spawning seasons in which multiple cohorts of eggs are produced during each reproductive season. Based on clutch size estimates and production of multiple egg cohorts during the reproductive season, individuals of these species exhibit high fecundity rates during a spawning season and lifetime.

Shoal chubs are benthic invertivores that reach a maximum age of 2.5 years. The shoal chub population in the Brazos River consists of three age classes with only a few individuals surviving into the third spring or summer (age 2) and is similar to the Des Moines River population (Starret, 1951). Patterns in GSIs and ovarian development of age 1 and older adults indicate shoal chubs began reproducing in April of each year and continued until November of 2004 and August of 2005. These findings are consistent with populations in Wisconsin (May or June until August; Becker, 1983) and Kansas (May until August; Cross and Collins, 1995). Reproduction may have continued into fall 2005 but was not documented due to low sample sizes during July, September, October and November 2005. Scarcity of adults was common during the reproductive season of both years, requiring extra sampling effort to collect sufficient numbers for analysis. Although reproductive behavior was not observed directly, shoal chub reproductive behavior is probably similar to that of *Macrhybopsis tetranemia*, which move into and spawn in deeper waters (Bottrell *et al.*, 1964). If this assumption is correct, larger

individuals may have been in water too deep to be collected by my sampling methods. The trimodal distribution of oocyte diameters exhibited by shoal chubs is a characteristic of species producing multiple cohorts of oocytes during a reproductive season (Heins and Rabito, 1986). In these instances, distinct cohorts of vitellogenic oocytes are recruited from a supply of small, previtellogenic oocytes. Adult diets in the Brazos River were numerically dominated by Chironomidae similar to shoal chubs in Iowa (Starrett, 1950) and Tennessee (Etnier and Starnes, 1993). Although sand was common and abundant within gut tracts of both adults and juveniles, the presence of sand is probably a result of incidental consumption due to bottom feeding strategies by the shoal chub (Davis and Miller, 1967).

Ghost shiners are invertivore/detritivores that reach a maximum age of 2.5 years and reproduce from May through September of each year. Consistent with Missouri populations (Pflieger, 1997), the ghost shiner population in the Brazos River was composed of three age classes. Most adults collected were in their second summer (age 1), but the occurrence and abundance of older individuals decreased during and after the spawning season, leaving few individuals to survive into the third spring or summer (age 2). The extended reproductive period exhibited by the ghost shiner in the Brazos River mirrors populations in Missouri (April through July; Pflieger, 1997), Kansas (May to August; Cross and Collins, 1995) and Oklahoma (late spring through August; Miller and Robison, 2004). Food habits of juvenile and adult ghost shiner were similar, consisting primarily of detritus and a small proportion of aquatic insects (Chironomidae and Trichoptera). Although uncommon in *Notropis* species, detritivory has also been

documented in the redlip shiner *Notropis chiliticus* (Jenkins and Burkhead, 1994) and sand shiner *Notropis stramineus* (Starrett, 1950; Stegman, 1969; Mendelson, 1975).

Silverband shiners are invertivores that reach a maximum age of 2.5 years and spawn early spring until late summer. The silverband shiner population consisted of three age classes with few individuals surviving into the third year. Patterns in GSIs, ovarian development and oocyte diameter distributions indicated the reproductive period of silverband shiners in the Brazos River extended from April or May until September. Previous reports suggested similar reproductive periods throughout the range of the silverband shiner (as early as April in the Red River, Robison and Buchanan, 1988; June – August in the Mississippi River, Suttkus, 1980). Juvenile and adult silverband shiner gut contents consisted primarily of aquatic insects and detritus with an increase in aquatic insects in adults.

Although overall life history traits and patterns were generally similar within each species between years, yearly variation in traits may be associated with differences in yearly flow. Ghost shiners exhibited relatively higher GSIs and a higher percent of mature females during 2005 than 2004. Female silverband shiners became reproductively mature a month earlier (April) during 2004 than in 2005 (May). Possible between year differences in shoal chub reproductive season could not be determined due to low abundances during the end of the 2005 reproductive season. Reproductive activity and increased recruitment in stream fishes has been associated with increased stream flows resulting from seasonal runoff or weather patterns (Platania and Altenbach, 1998; Marchetti and Moyle, 2000). My findings suggested a possible increase in reproductive effort (length of spawning period, increased egg production) within species based on

yearly flow, specifically an increase in ghost shiner reproductive effort during low flow years and an increase in silverband shiner reproductive effort during high flow years. Unfortunately, my study methods did not allow me to directly explore these patterns of yearly variation in reproductive effort.

Based on annual larval drift densities, reproductive output is independent of water year although survival of larvae and recruitment varies among years. Protolarvae drift density peaks were associated with increases in monthly GSIs but densities were similar between years for all species. Assuming protolarvae densities correspond to egg production, successful egg production was constant between years. In contrast, mesolarvae, metalarvae and juvenile drift densities increased during the high flow year, suggesting greater larval and juvenile survival.

Short life spans, early maturation, prolonged spawning period, multiple spawning bouts and high fecundity are common traits among obligate riverine species. Evolution of this suite of traits has allowed species to overcome the unpredictability of living in temporally variable riverine environments (Winemiller and Rose, 1992). For example, extended reproductive seasons increase the probability that reproductive activity will occur during adequate environmental conditions during each reproductive season (Winemiller and Rose, 1992; Rinchar and Kestemont, 1996), allowing populations to overcome short-term disturbances that may increase yearly reproductive failure. Similarly, early maturation and short life spans of these fishes contribute to rapid population turnover rates, allowing these populations to quickly recover from declines, reproductive failure or high mortality rates of young associated with temporary or annual disturbances (Winemiller and Rose, 1992; Winemiller, 2005). Similar opportunistic life

history traits (Winemiller and Rose, 1992) are common among other *Notropis* and *Macrhybopsis* (Platania and Altenbach, 1998; Williams and Bonner, 2006) species, including two Brazos River endemics, the sharpnose shiner *N. oxyrhynchus* and smalleye shiner *N. buccula* (Durham, 2007).

The reproductive strategy of broadcast spawning, and for some species, downstream drift of semibuoyant, nonadhesive eggs and larvae is associated with obligate riverine species (Platania and Altenbach, 1998). Broadcast spawning is the release of eggs over open substrate and is a common reproductive strategy for North American cyprinids (Johnston and Page, 1992). High turbidity precluded direct observations of spawning activity during this study; however, previous observations suggest the shoal chub (Platania and Altenbach, 1998), ghost shiner (Pflieger, 1997) and silverband shiner (Suttkus, 1980) each employ the broadcast spawning strategy for reproduction. Drift of semibuoyant eggs or larvae potentially results in rapid downstream dispersion (Bestgen *et al.*, 1989) and deposition of larval fishes in adequate nursery areas, thereby, increasing survival of young. Although spawning behavior was unobserved, drift of larvae was documented and supported previous conclusions identifying shoal chub, ghost shiner, and silverband shiners as pelagic broadcast spawners.

Life history traits associated with obligate riverine species can become detrimental in aquatic systems modified by humans. As human modifications decrease the hydrologic variability of riverine environments, the benefits of extended spawning periods may become invalid, specifically if regulated flows are inadequate for reproductive success (Cross *et al.*, 1983; Dieterman and Galat, 2004). Short life spans of these species increase their susceptibility to long-term disturbances resulting in

reproductive failure or disruption of source/sink population interactions, potentially resulting in rapid population declines or extirpations (Winston *et al.*, 1991; Luttrell *et al.*, 1999). Successful drift of eggs and larvae are also dependent upon uninterrupted lengths of riverine habitat (Platania and Altenbach, 1998; Bonner and Wilde, 2000; Dieterman and Galat, 2004). Fishes employing drift are therefore susceptible to fragmentation of aquatic habitats in which stream reaches become disjunct or too small to provide adequate drifting distance (Platania and Altenbach, 1998; Dieterman and Galat, 2004). In addition, fragmentation can disrupt the equilibrium of downstream displacement and upstream recolonization necessary to maintain upstream populations of some species, resulting in extirpations of sink populations (Bestgen and Platania, 1991; Winston *et al.*, 1991; Platania and Altenbach, 1998; Luttrell *et al.*, 1999; Guenther and Spacie, 2006).

Based on life history characteristics described herein, shoal chubs, ghost shiners and silverband shiners are adapted for the highly variable environment of the lower Brazos River. Current stability of these populations (Runyan, 2007) supports this conclusion and is likely related to the similarity of historic and current flow regimes. Thus, the benefits of these opportunistic life history traits are sustained in these populations. Similar to declines in other riverine species, population declines of these species are associated with loss of habitat (Trautman, 1981; Luttrell *et al.*, 1999; Haslouer *et al.*, 2005) and fragmentation (Trautman, 1981; Luttrell *et al.*, 1999) in parts of their native ranges. Thus, stability of the lower Brazos River populations of shoal chubs, ghost shiners and silverband shiners is supported by and, based on declines in other populations, dependant upon the variability and connectivity of this environment.

Species specific information provided in this study and other similar studies increase our ability to predict potential direct effects of anthropogenic modifications on obligate riverine fishes. However, indirect effects of human alterations are poorly understood and may lead to unpredictable outcomes. Reservoir construction and river regulation can result in introductions or colonization of exotic or introduced species, increased predation pressure and competition, and habitat changes negatively affecting native species (Winston *et al.*, 1991; Herbert and Gelwick, 2003). In some instances, even native species can become dominant in modified systems, thereby increasing competitive interactions with historically abundant species (Bonner and Wilde 2000; Scott and Helfman, 2001; Guenther and Spacie, 2006). Unfortunately, potential effects such as these cannot always be recognized or predicted. For example, the chub shiner *Notropis potteri*, sharpnose shiner *Notropis oxyrhynchus* and smalleye shiner *Notropis buccula* are obligate riverine species that once occupied the lower Brazos River along with the study species. In contrast to shoal chubs, ghost shiners and silverband shiners, these species have experienced severe population declines. Although fragmentation of habitat has been blamed for these declines (Winston *et al.*, 1991; Moss and Mayes, 1993), causal mechanisms are poorly understood. This lack of understanding is especially evident when most life history characteristics of “declining” obligate species are compared and appear similar to those obligate species with “stable” populations in the lower Brazos River.

Conservation efforts directed toward these and other imperiled fish species should be based on known and predictable information, and efforts altered to incorporate additional effects that appear. General life history characteristics can initiate the

development of basic conservation measures and can be used to identify obvious current and potential effects on fishes of conservation concern. However, life history information is limited and is not necessarily a strong indicator or predictor of various anthropogenic alterations and species interactions. Further population and species monitoring and additional research to identify possible indirect effects on imperiled fishes are necessary to implement adequate conservation efforts.

Acknowledgements.--Texas Water Development Board provided partial financial support for this project. Additional funding was provided by the National Science Foundation, Project Flowing Waters. T. C. Heard, J. M. Watson, J. S. Perkin, B. M. Littrell, and D. L. McDonald assisted in field collections. Three anonymous reviewers improved the quality and strength of this manuscript.

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Table 1.1. Mean (\pm SD) maximum length for three age classes of shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005.

Species	Year	Total length (mm) at age				
		0		1		2
		mean	s.d.	mean	s.d.	max.
Shoal chub	2004	38.8	7.3	57.0	0.8	69
	2005	36.9	5.6	55.1	2.4	68
Ghost shiner	2004	33.8	4.9	38.8	1.18	53
	2005	31.7	5.1	45.5	0.07	49
Silverband shiner	2004	41.0	8.5	66.5	4.7	86
	2005	37.0	10.8	64.0	2.2	77

Table 1.2. Total and seasonal mean percentage by weight and percent occurrence (in parentheses) of diet items for adult and juvenile shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005.

Species	Season	N	Mean Total Weight (mg)	Aquatic	Terrestrial	Crustaceans (%)	Detritus (%)	Algae (%)	Sand (%)	Cestoda (%)	
				Insects (%)	Insects (%)						
Shoal chub	Adult	Total	64	6.01	61.5 (81)	1.9 (6)	-	9.6 (19)	-	27.1 (66)	(19)
		Winter	20	5.13	54.0 (75)	3.1 (5)	-	10.0 (20)	-	32.9 (60)	(14)
		Spring	18	8.79	72.0 (94)	-	-	14.0 (22)	-	14.0 (67)	(5)
		Summer	14	5.48	50.5 (57)	0.4 (14)	-	1.4 (7)	-	47.7 (79)	(35)
		Fall	12	3.94	70.9 (93)	4.2 (7)	-	11.8 (27)	-	13.1 (53)	(6)
	Juv	Total	42	0.33	24.9 (38)	-	10.9 (19)	36.3 (60)	-	27.9 (55)	(33)
		Spring	8	0.39	46.0 (63)	-	9.4 (25)	37.5 (50)	-	7.1 (25)	(22)
		Summer	16	0.28	20.4 (38)	-	-	49.5 (81)	-	30.1 (63)	(28)
		Fall	18	0.36	19.4 (28)	-	21.3 (33)	24.1 (44)	-	35.2 (61)	(44)
		Ghost shiner	Adult	Total	70	2.36	25.6 (43)	-	2.9 (11)	64.4 (89)	-
Winter	19			1.21	12.6 (32)	-	0.3 (5)	64.7 (95)	-	22.3 (53)	-
Spring	17			2.36	38.2 (59)	-	5.9 (6)	55.7 (88)	-	0.2 (6)	-
Summer	17			3.59	32.9 (59)	-	0.9 (12)	63.3 (88)	-	3.0 (24)	-
Fall	17			2.66	20.4 (24)	-	4.9 (24)	73.9 (82)	-	0.8 (18)	-
Juv	Total		41	0.56	30.5 (54)	-	2.4 (7)	60.2 (85)	-	6.8 (15)	-
	Spring		8	0.51	44.2 (63)	-	-	55.8 (75)	-	-	-
	Summer		16	0.72	15.8 (38)	-	3.1 (6)	73.6 (88)	-	7.5 (13)	-
	Fall		17	0.44	38.0 (65)	-	2.9 (12)	49.7 (88)	-	9.3 (24)	-
	Silverband shiner		Adult	Total	67	20.92	56.0 (72)	4.7 (7)	0.8 (4)	30.5 (49)	5.6 (8)
Winter		17		13.75	45.2 (65)	0.6 (6)	-	46.0 (59)	5.9 (6)	2.3 (12)	(5)
Spring		17		34.91	64.7 (65)	17.6 (18)	-	11.8 (18)	-	5.9 (12)	-
Summer		18		21.75	69.8 (89)	0.2 (6)	<0.1 (6)	13.5 (39)	15.3 (22)	1.1 (28)	(11)
Fall		15		12.18	42.0 (67)	-	3.4 (13)	54.5 (87)	-	<0.1 (7)	-
Juv		Total	34	1.41	48.4 (71)	-	2.9 (15)	41.1 (74)	2.1 (9)	5.4 (26)	(9)
		Spring	3	0.80	100.0 (100)	-	-	-	-	-	-
		Summer	13	1.76	48.6 (69)	-	-	44.7 (85)	-	6.7 (23)	(8)
		Fall	18	1.25	39.6 (67)	-	5.6 (28)	45.3 (78)	4.0 (17)	5.5 (33)	(11)

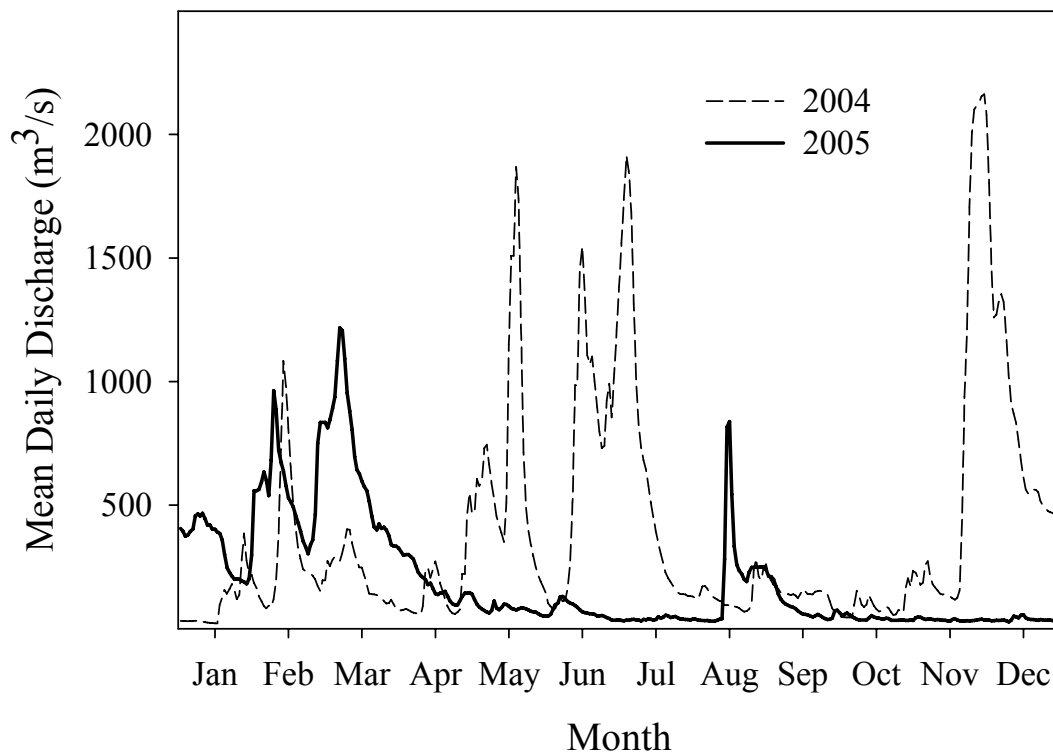


Figure 1.1. Daily mean discharge rates for the lower Brazos River from two time periods: January 1, 2004 - December 31, 2004; January 1, 2005 - December 31, 2005. Discharge data from United States Geological Survey (USGS) gauging station #08114000 located near Richmond, Texas.

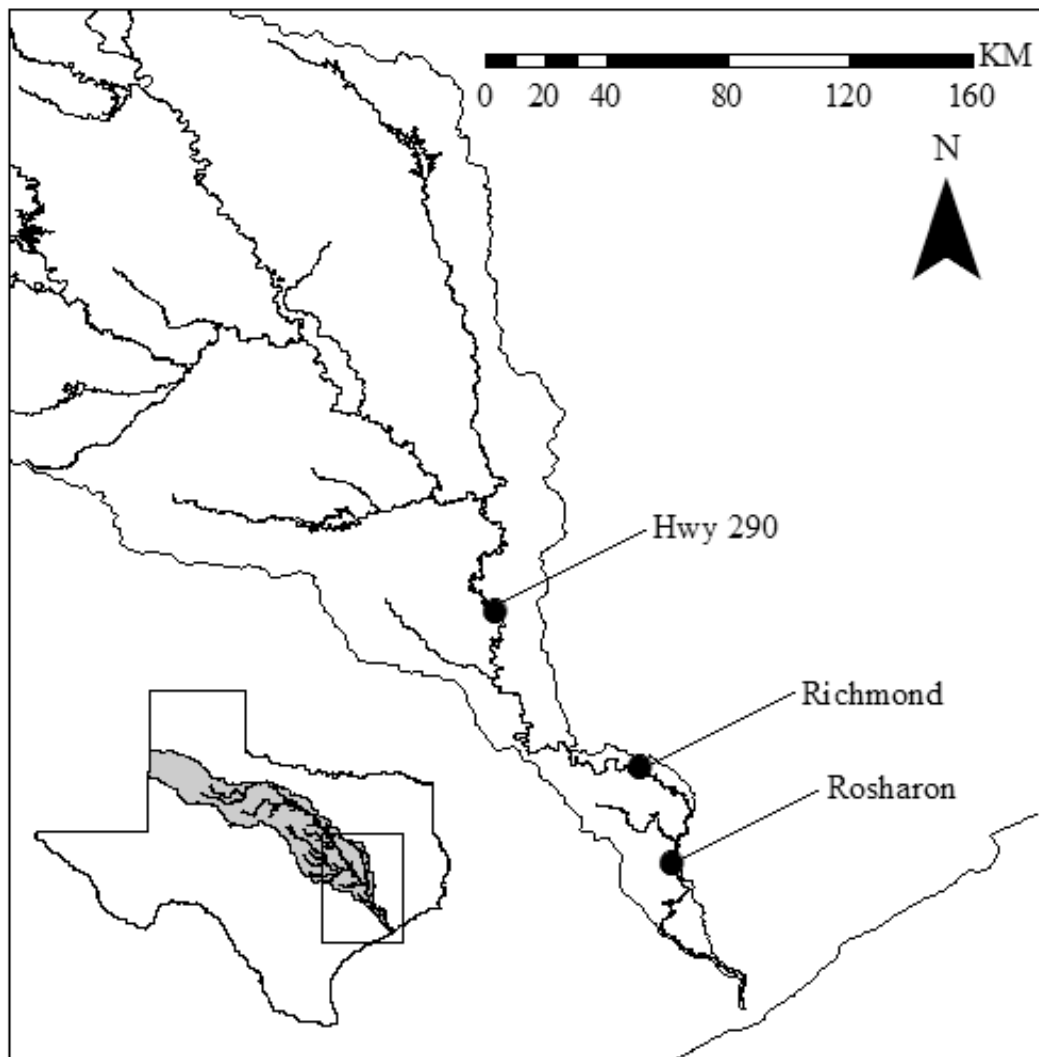


Figure 1.2. Location of three collection sites on the lower Brazos River, Texas sampled monthly and/or bimonthly from January 2004 until December 2005.

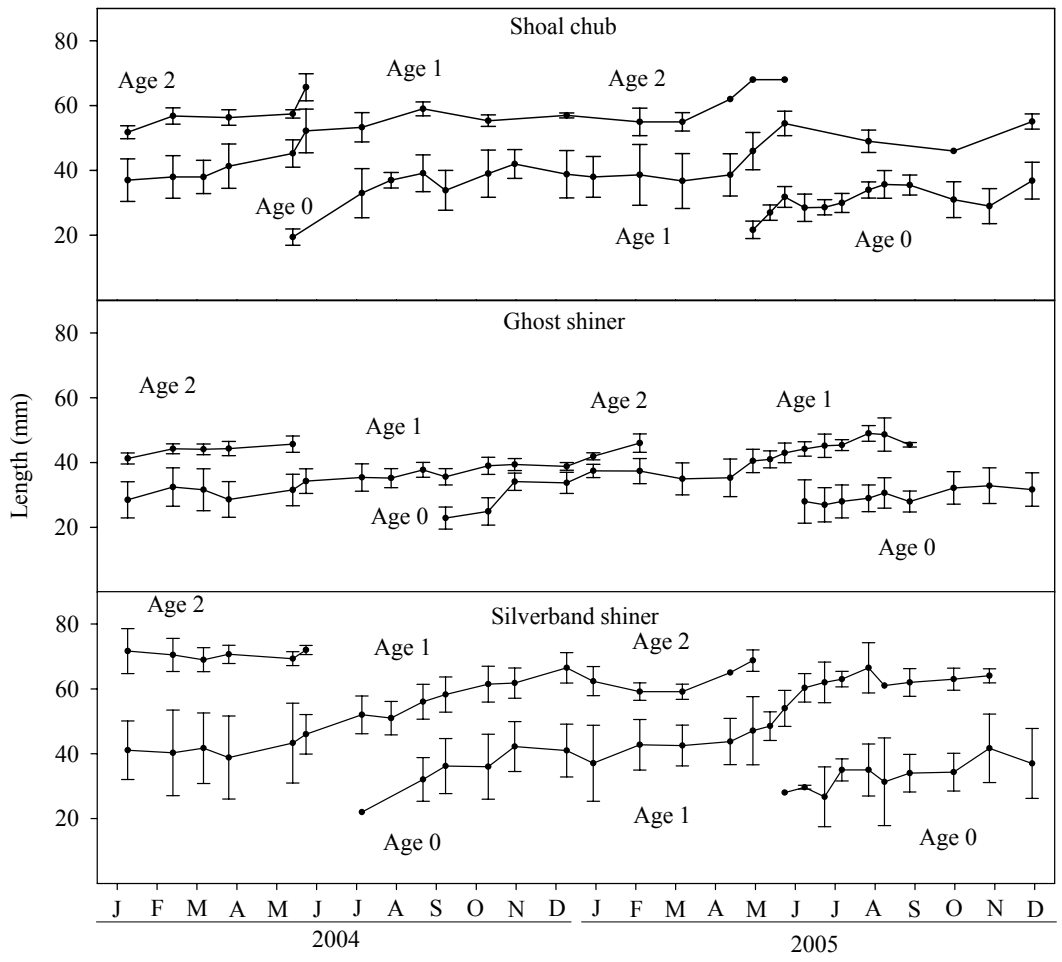


Figure 1.3. Monthly mean (\pm SD) length for three age classes of shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005

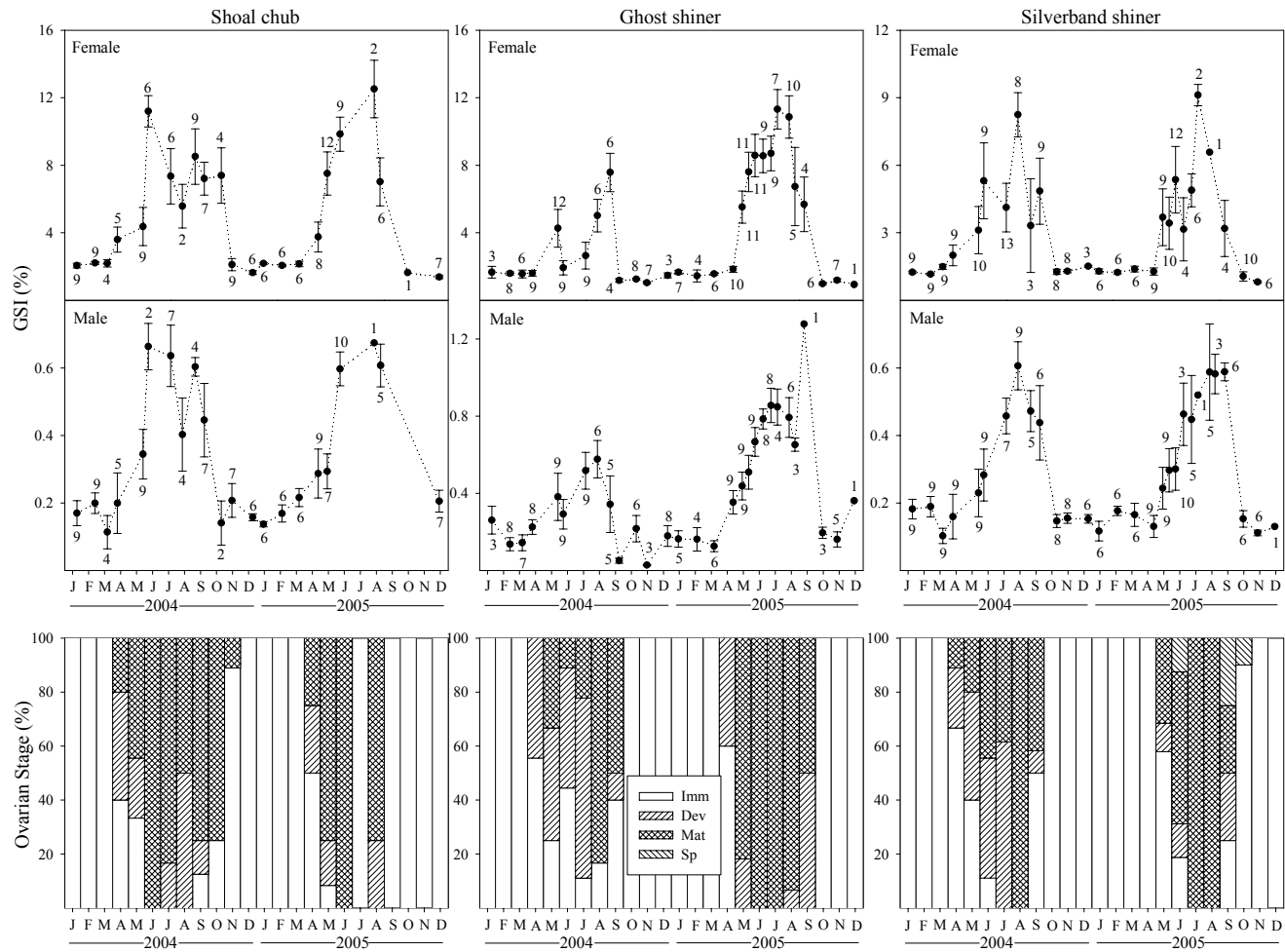


Figure 1.4. Mean monthly gonadosomatic index (GSI; \pm SD) for females and males and monthly ovarian condition (% of females examined) for shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005. Numbers corresponding to monthly means and SD represent n values.

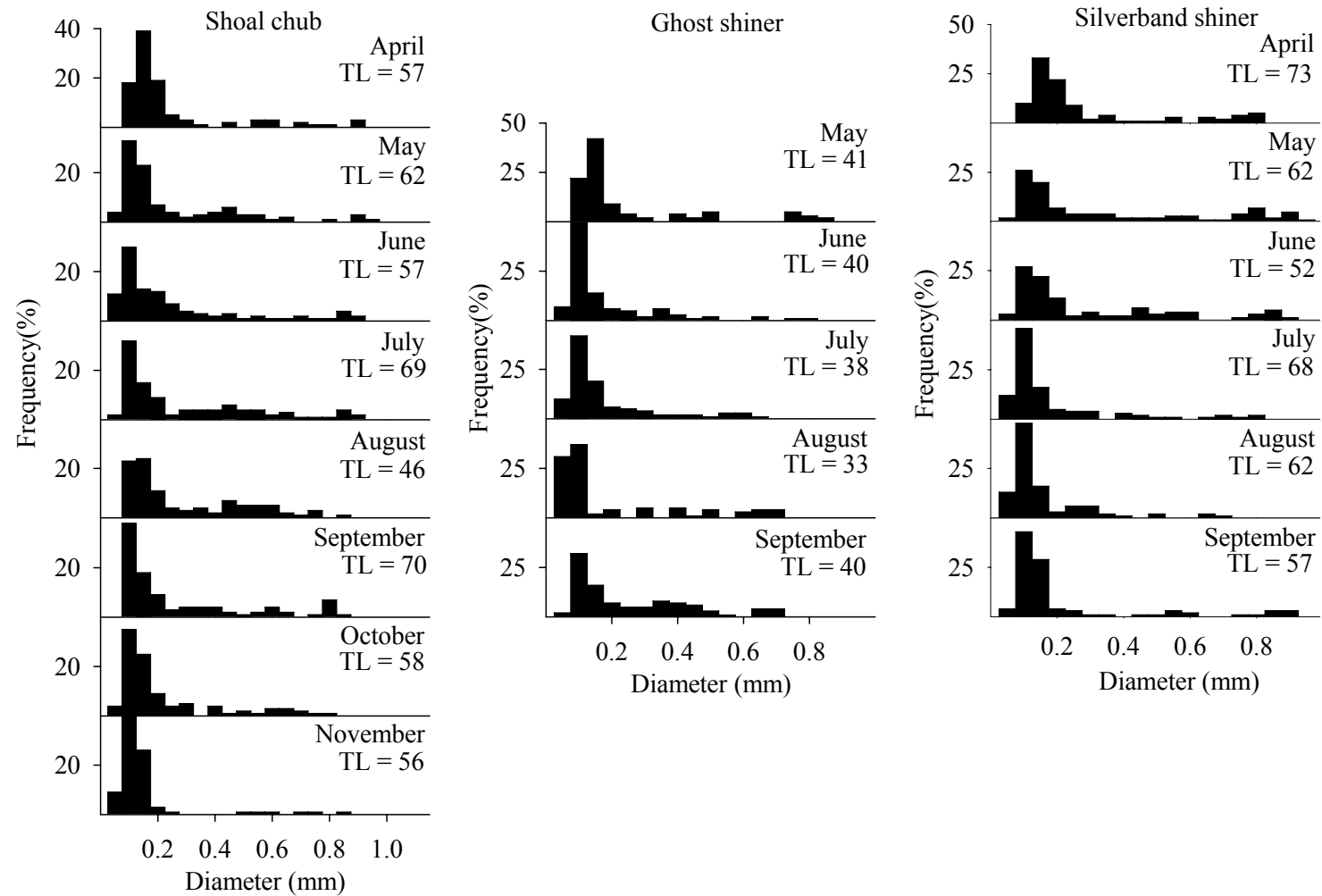


Figure 1.5. Monthly size-frequency distribution for ova diameters from one shoal chub, ghost shiner and silverband shiner per month collected during the 2004 reproductive season from three sites on the lower Brazos River.

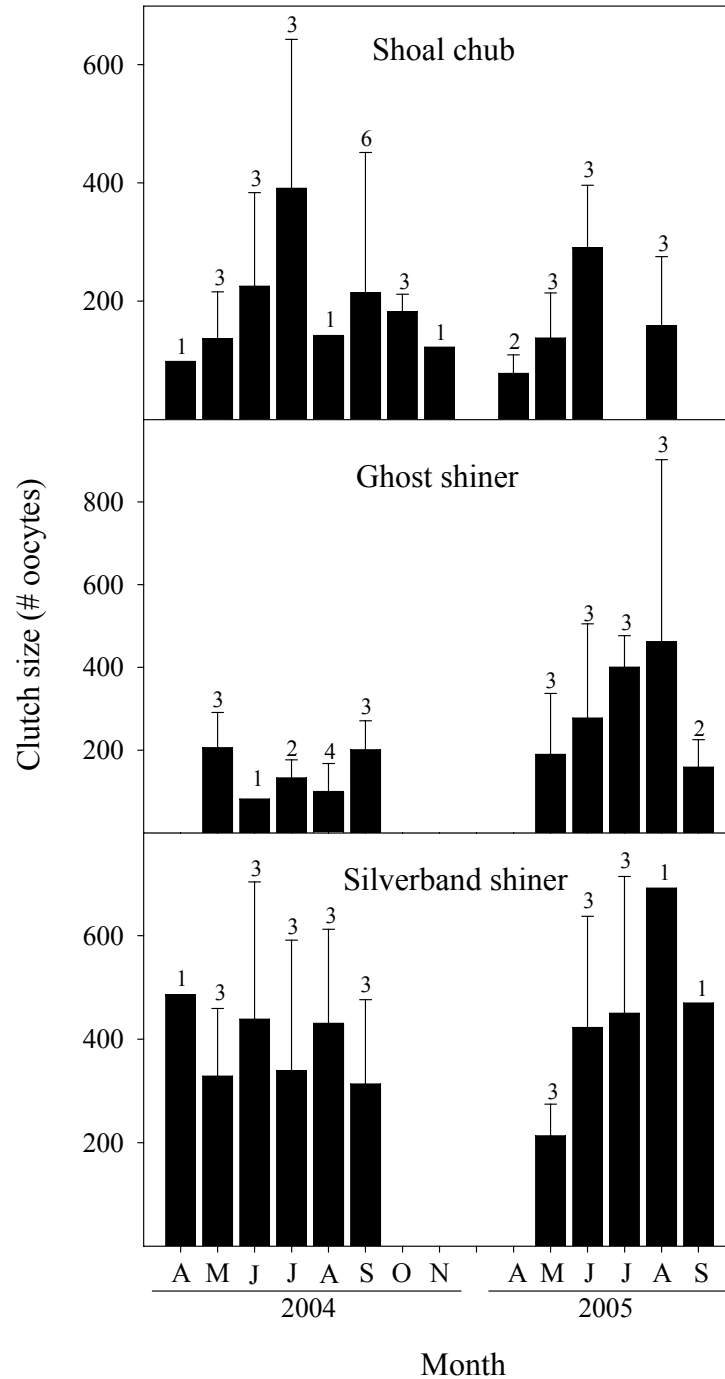


Figure 1.6. Mean (\pm SD) clutch size estimates for shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005 (numbers above error bars represent monthly n values).

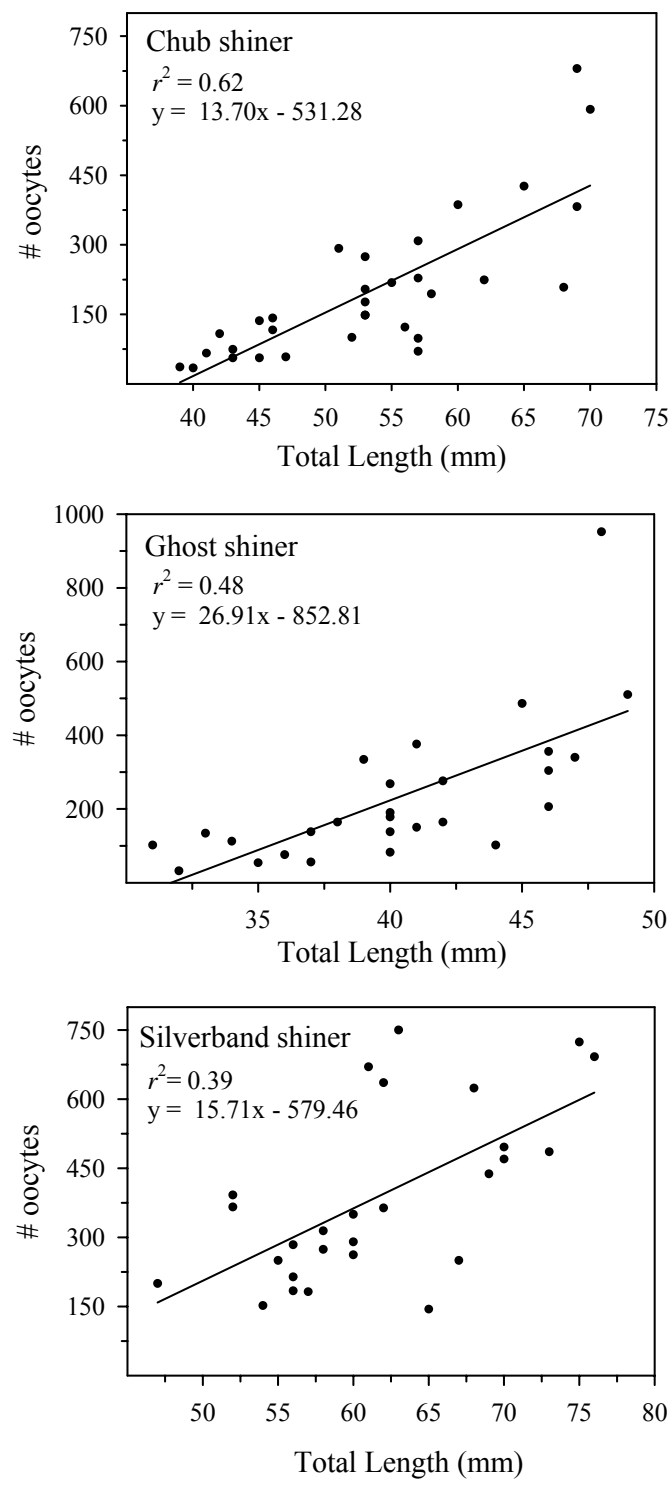


Figure 1.7. Length versus estimated clutch size relationship for shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from January 2004 until December 2005.

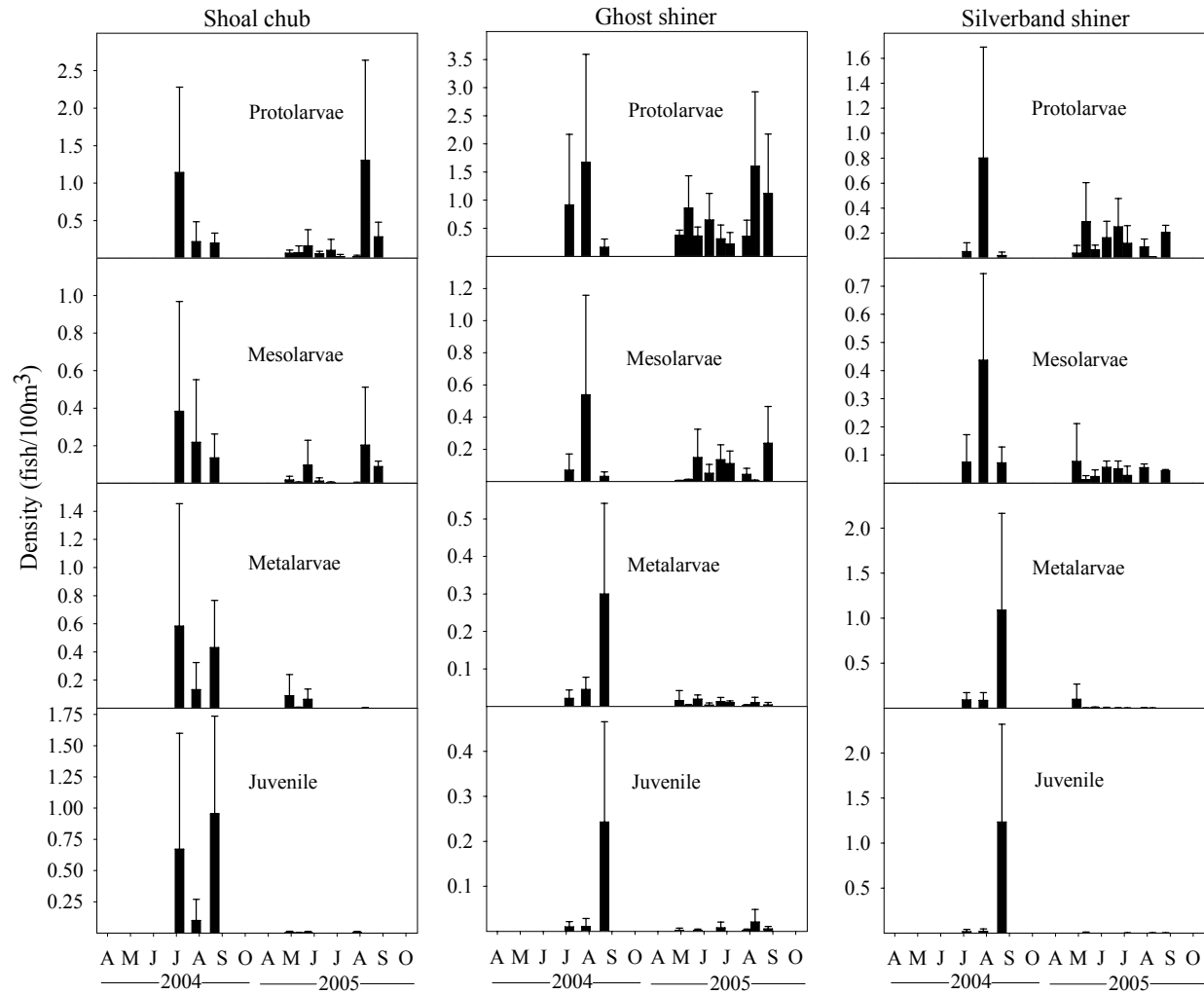


Figure 1.8. Larval drift densities for four life stages of shoal chub, ghost shiner and silverband shiner collected from three sites on the lower Brazos River from July – September 2004 and May – September 2005.

CHAPTER II
TEMPORAL AND SPATIAL DRIFT PATTERNS OF LOWER
BRAZOS RIVER FISHES

ABSTRACT

I examined larval and juvenile drift patterns of substrate, pelagic broadcast and adhesive broadcast spawning guilds in the lower Brazos River during 2004 and 2005. Relatively higher drift densities were observed during the high flow year for all reproductive guilds and among life stages within reproductive guilds. Substrate, pelagic broadcast and adhesive broadcast spawners also had higher drift densities at night and in near shore areas. Increased metalarvae and juvenile drift densities indicate higher survival and recruitment of larval fishes during the high flow year. Similar night time and near shore drift density patterns demonstrate concurrent use of habitat and resources among reproductive guilds, suggesting biotic factors such as competition may influence survival of larvae and recruitment of riverine fish.

INTRODUCTION

Declines in native fish populations are well recognized worldwide (Allan and Flecker, 1993; Leidy and Moyle, 1998) and are common throughout the United States (Moyle and Williams, 1990; Richter *et al.*, 1997; Ricciardi and Rasmussen, 1999; Warren *et al.*, 2000; Jelks, 2008) and similar to those occurring worldwide. For instance, 39% of native fishes in North America are considered imperiled (Jelks *et al.*, 2008). Although population declines are documented in fishes inhabiting many environments (Moyle and Williams, 1990), riverine fishes often require flowing water and unfragmented habitat, making them vulnerable to anthropogenic modifications of riverine habitat such as dam construction, river regulation, dewatering, habitat loss, fragmentation, and increased sedimentation (Winston *et al.*, 1991; Richter *et al.*, 1997; Bonner and Wilde, 2000; Warren *et al.*, 2000; Bunn and Arthington, 2002).

Although direct effects of environmental perturbations on riverine fish populations can be obvious, long-term changes in fish populations and riverine fish assemblages are not always predictable. Direct effects of riverine modification can be more easily identified and predicted than indirect effects. For example, blocking of migration routes leading to spawning grounds can result in rapid and identifiable decreases in reproduction and recruitment leading to declining populations (Luttrell, 1999). In contrast, changes in flow regime can result in slight reductions in spawning success and recruitment, or increases in predation or competition that are not immediately identifiable (Matthews *et al.*, 2001).

In addition, changes in fish assemblages and populations can vary among streams that have undergone similar modifications because of differences in life history

characteristics of species found within individual drainage basins. For instance, pelagic broadcast spawning species migrate upstream as adults, spawn semibuoyant eggs that drift downstream during early larval development, and larvae exit the drift and reside in nursery areas during remaining developmental stages (Moore, 1944; Lehtinen and Layzer, 1988; Taylor and Miller, 1990; Platania and Altenbach, 1998). These species require lotic environments for successful reproduction and recruitment and anthropogenic modifications disrupt this life cycle (Dudley and Platania, 2007). Dams and reservoirs disrupt downstream movement by creating lentic areas in streams which promote settling of eggs and larval fishes into areas inadequate as nursery areas (Winston *et al.*, 1991; Dudley and Platania, 1999; Dudley and Platania, 2007). Eggs and larvae entering reservoirs may also be more susceptible to predation (Platania and Altenbach, 1998). In addition, if drifting eggs and larvae are successful in drifting past instream structures, later upstream migration is inhibited, recolonization of upstream areas by young fish can be disrupted, and extirpation of broadcast spawning species may occur (Wild and Ostrand, 1999; Winston *et al.*, 1999). Channelization of rivers resulting from flow regulation can also decrease the amount of suitable nursery habitat (backwater/slackwater areas) available to larval fishes (Tyus and Haines, 1991). Reduced or regulated flows are believed to interrupt spawning activities by decreasing periodicity of high flow events that act as proximate cues for egg release, thereby reducing the number of eggs spawned during reproductive seasons (Cross *et al.*, 1983; Tyus, 1990). Recent evidence, however, suggests spawning occurs regardless of changes in flow rates (Robinson *et al.*, 1998; Bonner, 2000; Humphries and Lake, 2000; Durham and Wilde, 2006; Durham, 2007), and recruitment is determined by survival of larvae and juveniles (Humphries *et al.*,

2002; Durham, 2007). In contrast to broadcast spawners, facultative substrate spawning species inhabit and successfully reproduce in both lotic and lentic environments.

Consequently, alterations to riverine environments are detrimental to broadcast spawners may benefit substrate spawning species, allowing them to thrive in modified rivers (Scott and Helfman 2001).

In the lower Brazos River, Texas, substantial changes in fish assemblage structure similar to other large rivers have occurred, including declines in obligate riverine broadcast spawning species and increases in facultative substrate spawners. Three obligate riverine broadcast spawners, including *Hybognathus placitus*, *Notropis oxyrhynchus*, and *N. potteri*, have decreased from 33% to < 0.1% of the fish assemblage and *N. buccula*, a Brazos River endemic, has been extirpated (Runyan, 2007). *Notropis buchanani*, *N. shumardi*, and *Macrhybopsis hyostoma* are additional broadcast spawners with currently stable populations similar to historical abundances. During the same period, *Cyprinella lutrensis* and *Pimephales vigilax*, two facultative substrate spawning cyprinids, increased from 16% to 79% of the fish assemblage. *Cyprinella lutrensis* and *P. vigilax* are both capable of spawning in lentic habitats (Parker, 1964; Gale, 1986; Vives, 1993) and *C. lutrensis* populations are known to be negatively affected by variable or high flows.

Declines in broadcast spawning species of the lower Brazos River have been attributed to fragmentation and hydrological changes affecting spawning success (Runyan, 2007). I propose instead of reproductive failure, changes in species abundance are related to larval and juvenile drift and survival. Specifically, changes in hydrologic regime and river morphology have reduced the success of egg and larval drift of

broadcast spawning species, resulting in lower recruitment rates. In contrast, reduced variability in discharge rates have benefited substrate spawner reproduction and recruitment, allowing them to drastically increase in abundance (Scott and Helfman, 2001; Humphries *et al.*, 2002). The purpose of this study was to describe and compare annual, diel and spatial larval and juvenile fish drift patterns among reproductive guilds of the lower Brazos River. Specifically, I sought to compare larval drift patterns of broadcast and substrate spawners to elucidate the relationship between decreasing broadcast spawners and increasing substrate spawners.

METHODS

Study Area

The Brazos River in Texas is one of the largest and most altered river drainages of the western Gulf Slope drainages (Connor and Suttkus, 1986). The Brazos River originates near the New Mexico-Texas border and flows approximately 1,700 km southeast across Texas to a confluence with the Gulf of Mexico. Geographically, the Brazos River basin is separated into three sections: upper, middle and lower Brazos River. The upper and middle reaches are regulated by 17 main stem and tributary reservoirs. In contrast, the lower reach is relatively unregulated and flows unimpeded for approximately 330 river km from Brazos Lake Dam in Waco to the Gulf of Mexico near Freeport, Texas (Runyan, 2007).

Discharge rates of the lower Brazos River varied greatly relative to the historical hydrograph and between 2004 and 2005. Historical trends in discharge rates generally increased during late spring (April), began decreasing during mid-late summer (July), and showed a gradual increase during fall and winter (Fig. 2.1). Mean (\pm SD) daily discharge

rates for 2004 ($378 \pm 454 \text{ m}^3/\text{s}$) ranked in the 94th percentile of the historical daily mean flow ($214 \pm 95 \text{ m}^3/\text{s}$). Mean daily discharge during 2005 ($192 \pm 234 \text{ m}^3/\text{s}$) was substantially lower, ranking in the 41st percentile of the historic mean daily discharge rate.

Fish collection

I sampled larval fish monthly at three sites along a 227 km segment of the Lower Brazos River from July through September 2004 and twice monthly from May through August and once in September 2005. Sample sites were located at Hwy 290 near Hempstead ($30^\circ 08' 08''\text{N}$, $96^\circ 11' 32''\text{W}$), upstream from Hwy 723 in Rosenberg, Texas ($29^\circ 36' 11''\text{N}$, $95^\circ 50' 22''\text{W}$), and Hwy 1462 near Rosharon, Texas ($29^\circ 21' 12''\text{N}$, $95^\circ 34' 28''\text{W}$).

At each site and sampling period, I collected larval fish from wadeable sand bars with $0.45 \times 0.25 \text{ m}$, $500 \mu\text{m}$ mesh drift nets, tapered on one end and connected to a removable cup. Nets were anchored on each side by metal fence posts driven into the substrate. Drift nets were placed at four stations in a line perpendicular to the shore. Stations were arranged from near shore, shallow water areas (Station 1) to areas of increasing depth and current velocity (station 4) in far shore areas. Stations 1 and 2 in shallow water consisted of one net, and stations 3 and 4 in deeper water contained two nets stacked vertically. Nets 1 and 2 were sufficient to sample all or the majority of the water column. Top nets of stations 3 and 4 sampled the upper 0.25 m of the water column and lower nets sampled the middle or lower 0.25 m of the water column (total depth $< 2 \text{ m}$). I washed the contents of each net every 3-h for a 24-h period into individual plastic bags and preserved contents in a 10% formalin solution. I measured

horizontal distance from shore to the center of each drift net (m), total water column depth (cm), depth from the substrate to the bottom of the net (m/s) at the beginning and end of each 3-h interval. Current velocity was also measured (Marsh-McBirney Flowmate Model 2000 flow meter) in the center of each drift net opening at the beginning and end of each 3-h interval. I used beginning and ending current velocity measurements to calculate a mean current velocity through the center of the net during the 3-h intervals.

Laboratory Methods

Contents of each drift net sample were rinsed, sorted, and larval and juvenile fishes were identified and counted. I removed contents of each drift net sample from the 10% formalin solution and rinsed them with deionized water for approximately 15 min. I then placed the sample into a sorting pan and separated all contents into two groups, detritus/macroinvertebrates and fish. Fish were placed in labeled vials and stored in 4% (larvae and juveniles; Kelso and Rutherford, 1996) or 10% (adults) formalin for later species identification.

I next identified each individual or a sub-sample of individuals from each sample to species and determined developmental stage. Larval identification was based on published larval keys and morphological descriptions (Auer, 1982; Fuiman *et al.*, 1983). Life stage (protolarvae, mesolarvae, metalarvae or juvenile) was determined based on the following characteristics (Snyder, 1998): Protolarvae, lack of dorsal, anal, and caudal fin spines and/or rays; Mesolarvae, at least one dorsal, anal or caudal fin spine or ray but lacking the full set of adult soft rays in at least one median fin or lacking pelvic fin buds

or pelvic fins; Metalarvae, full complement of principal soft rays in all median fins and pelvic fin buds or pelvic fins. Juveniles were young of year fishes with full complements of adult median and paired fin rays and spines.

Due to large numbers of individuals in some samples, I subsampled larger samples, and therefore, performed the following procedure to determine the appropriate subsampling methodology required to account for both species and larval stage abundance within samples. I first divided a 25.4 mm square dish into 10 equal squares, giving each square a numerical label (1-10). All fishes from a sample were evenly distributed in a pan with water. I next removed and identified the fishes located in one randomly selected square (10% of the sample) to species and categorized the larval stage of each individual. After identification and classification of all fishes located in the first square, another square was randomly selected and the process repeated until individuals in all 10 grids were processed. This procedure was then repeated for five samples ranging in size from 272 to 1,897 individuals per sample. For each sample, percent similarity was determined between cumulative subsamples (10%, 20%, 30 %, etc.) and total samples using the Bray-Curtis similarity index (Primer 6.1.6). Through this analysis, I determined that for samples consisting of more than 400 individuals, a 40% subsample provided > 90% similarity for the full sample of both species and larval stages. Therefore, I identified each individual in samples with < 400 individuals and identified approximately 40% of samples with over 400 individuals.

Analysis

Drift densities were calculated daily for individual species and reproductive guilds. Total water filtered through each net was calculated by multiplying mean current velocity through the net (m/s), net area (m²; width X submerged portion of net), and duration of sampling (s). The number of individuals of each species or reproductive guild was then divided by the volume of water filtered and multiplied by 100 to represent calculated densities as individuals/100m³ of water. For stations 3 and 4, densities were calculated based on pooled values for individuals collected and water filtered in the two vertically stacked nets. Prior to all analyses, drift densities were log transformed [$\log(x + 1)$] to help meet the assumptions of normality and homoscedasticity. Analyses were conducted for each life stage within each reproductive guild. Initially, relative abundances and drift densities were calculated for all species and life stages within and across years. Adult fishes comprised only 0.2%, and damaged, unidentifiable larval fishes comprised 7.9% of all fish collected. Thus, adult and unidentifiable fishes were excluded from further analyses. For reproductive guild analysis, species were placed into reproductive guilds based on Simon (1999). Drift densities for reproductive guilds were calculated from pooled values of species within the reproductive guild.

Year and month drift density differences were examined for the most abundant reproductive guilds in the drift and included substrate, pelagic broadcast and adhesive broadcast spawners. Daily drift densities for July, August and September of 2004 and 2005 were examined with a 2-factor ANOVA ($\alpha = 0.05$) and significant main effects were further tested using a Fishers least significant difference test (LSD; $\alpha = 0.05$) to identify pairwise differences in year and month. If significant Month X Year interactions

were detected, I used tests of simple main effects to examine month within year and year within month differences in drift densities, followed by Fishers LSD for pairwise comparisons. In addition, a one factor ANOVA was used to assess monthly differences among all months sampled during 2005.

Day time and night time drift densities for abundant reproductive guilds were calculated and examined. Each 24-h period was divided into day time and night time phases based on sunrise and sunset; therefore, time periods varied among sampling dates. For day time and night time periods, the number of individuals per reproductive guild and total water filtered were pooled across all nets and drift densities were calculated. A paired *t*-test (day as subject) was conducted to examine differences in day time versus night time drift densities for each life stage of abundant reproductive guilds ($\alpha = 0.05$). If no individuals were collected for a life stage or reproductive guild during a 24-h period, densities (0 individuals/100m³) were excluded from the corresponding life stage X reproductive guild analysis.

Drift densities were examined along a distance from shore gradient. For each date, drift nets were grouped into three categories based on the distance from shore to the middle of the drift net. Categories were: 0 – 3 m from shore, 3 – 6 m from shore, and > 6 m from shore (range = 0-37 m). Based on field observations of increased night time densities, drift densities were examined for day time and night time separately. Day time and night time drift densities were calculated by pooling number of individuals within each reproductive guild life stage collected and water filtered within each distance from shore group. If no individuals of a life stage/reproductive guild were collected during a day or night period, that period was excluded from corresponding analyses. Repeated

measures ANOVA was used to test differences among distance from shore drift densities ($\alpha = 0.05$). To compensate for violations of the assumption of sphericity, degrees of freedom (df) for F tests were adjusted using the lower bound Greenhouse-Geisser adjustment. For significant findings, post-hoc analysis was conducted using paired t -tests ($\alpha = 0.05$).

All work was conducted under Texas State University-San Marcos IACUC #04-39C297D2 and Texas Parks and Wildlife Permit #SPR-0601-159.

RESULTS

Approximately 116,990 larval, juvenile and adult fishes were collected in drift nets during 2004 and 2005. Identifiable individuals consisted of 15 families and at least 35 species. Members of family Cyprinidae were most abundant in the drift, comprising > 89% of drifting fish during the two years combined. With the exception of Cyprinidae and Catostomidae (3.5%), all other families each comprised $\leq 2.5\%$ of drifting fishes. The five most abundant species in the drift were cyprinids, including *Cyprinella lutrensis* (38%), *Pimephales vigilax* (31%), *Notropis buchmanani* (9%), *Macrhybopsis hyostoma* (7%) and *Notropis shumardi* (4%). Protolarvae (56%) was the most abundant life stage in the drift, followed by mesolarvae (14%) and metalarvae (11%). Juvenile fishes comprised 19.1% of the drift across years, 28% in 2004 but only 2.8% in 2005.

Larval and juvenile drift abundance and densities were greatest in substrate spawners (70%) and broadcast spawners (27%; Table 1). Within the open substrate spawning guild, relative abundance was 21% for pelagic spawners and 6% for adhesive spawners across years. Drift abundances and densities of other reproductive guilds with < 2.5% were eliminated from further analyses.

Substrate Spawners

Mean monthly drift densities (# fish/100 m³) of substrate spawners ranged from 0.07 to 13.56 for protolarvae, 0.10 to 4.36 for mesolarvae, 0.03 to 3.70 for metalarvae, and 0.01 to 10.72 for juveniles with highest mean monthly drift densities occurring during 2004 for all life stages (Fig. 2.2). Drift densities differed between years and among months for protolarvae ($F_{5,18} = 6.53$; $P < 0.01$) mesolarvae ($F_{5,18} = 9.70$; $P < 0.01$), metalarvae ($F_{5,18} = 6.97$; $P < 0.01$) and juveniles ($F_{5,18} = 15.88$; $P < 0.01$) with significant ($P < 0.01$) month X year interactions for all life stages. During 2004, drift densities were higher ($P < 0.05$) in August for protolarvae and mesolarvae and in September for metalarvae and juveniles (Table 2). From May through September 2005, monthly drift densities did not differ ($P > 0.05$) for mesolarvae, metalarvae and juveniles across months but were higher for protolarvae ($F_{4,22} = 4.80$; $P < 0.01$) in June. Within months, drift densities were higher in 2004 for protolarvae and mesolarvae in August and metalarvae and juveniles in September.

Drift densities of substrate spawners were higher at night than during day for all life stages except juveniles. Mean night time drift (\pm SD) comprised 91% (10.2) of total daily drift for protolarvae, 87% (23.1) for mesolarvae and 74% (26.9) for metalarvae (Fig. 2.3). Consequently, night time drift densities (mean \pm SD) ranging from 1.1 \pm 2.0 in metalarvae to 6.5 \pm 7.7 in protolarvae was higher than during day for protolarvae ($P < 0.01$), mesolarvae ($P < 0.01$) and metalarvae ($P < 0.01$; Fig. 2.4). Juvenile night time drift densities did not differ from day time drift densities ($P = 0.23$). Though variable,

juveniles did exhibit a general pattern of increased mean night time drift proportions (68.5%) when compared to day time drift (31.5%).

Near shore drift densities of substrate spawners were generally higher than far shore densities. Across all dates and sites, near shore (≤ 3 m from shore) drift comprised $> 88\%$ of drift for all life stages. Mean near shore drift proportions (\pm SD) were highest for protolarvae ($86.9\pm 22.4\%$) followed by mesolarvae ($85.9\pm 26.8\%$), metalarvae ($80.4\pm 24.5\%$) and juveniles (57.5 ± 42.6). At night, mean drift density (\pm SD) ranged from 50.5 ± 78.5 in metalarvae to 233.8 ± 275.0 in protolarvae within 3 m from the shore. In contrast, mean drift density ranged from 1.8 ± 2.6 in metalarvae to 9.3 ± 22.3 in protolarvae within 3 to 6 m from the shore. Drift densities declined even further at distances > 6 m from shore, ranging from 0.2 ± 0.3 in mesolarvae to 0.5 ± 0.8 in protolarvae. Consequently, night time drift densities for all life stages was higher ($P < 0.02$) within 3 m of shore and densities within 3 to 6 m of shore were higher ($P < 0.01$) than those at distances > 6 m from shore (Fig. 2.5). Similar to night time drift patterns, day time densities were generally higher near shore for protolarvae, mesolarvae and metalarvae. Mean day time drift density (\pm SD) ranged from 7.4 ± 11.7 in metalarvae to 25.9 ± 53.1 in protolarvae within 3 m from shore. In contrast, day time mean drift density ranged from 0.2 ± 0.5 in mesolarvae to 4.6 ± 9.6 in juveniles at distances > 3 m from shore. Consequently, day time drift densities for protolarvae, mesolarvae and metalarvae were higher ($P < 0.02$) within 3 m of shore and decreased as distance from shore increased. Juveniles exhibited no difference in distance from shore drift densities ($P = 0.097$).

Pelagic Broadcast Spawners

Mean monthly drift densities (# fish/100 m³) of pelagic broadcast spawners ranged from 0.39 to 2.81 for protolarvae, 0.07 to 1.21 for mesolarvae, 0.004 to 1.84 for metalarvae, and 0.003 to 2.47 for juveniles with highest mean monthly drift densities occurring during 2004 for all life stages (Fig. 2.2). Drift densities were similar between years and among months for protolarvae ($F_{5,18} = 2.06$; $P = 0.12$) and mesolarvae ($F_{5,18} = 2.32$; $P = 0.09$). Metalarvae densities were similar ($P = 0.085$) among months but higher ($P < 0.05$) during 2004 ($F_{1,1} = 18.97$; $P < 0.01$). Juvenile drift densities differed between years and among months ($F_{5,18} = 5.46$; $P < 0.01$) with significant ($P < 0.05$) month X year interactions for juveniles. Juvenile drift densities were similar among months within years and between years among months.

Drift densities of pelagic broadcast spawners were higher at night than day for all life stages except metalarvae. Mean night time drift (\pm SD) comprised 75% (19.3) of total daily drift for protolarvae, 77.9% (17.5) for mesolarvae and 63.6% (40.1) for juveniles (Fig. 2.3). Consequently, night time drift densities (mean \pm SD) ranging from 0.4 ± 0.67 in mesolarvae to 1.8 ± 2.03 in protolarvae was higher than day time densities for protolarvae ($P < 0.01$), mesolarvae ($P < 0.01$) and juveniles ($P < 0.05$; Fig. 2.4). Metalarvae night time drift densities did not differ from day time drift densities ($P > 0.05$). Though variable, metalarvae did exhibit a general pattern of increased mean night time drift proportions (74.2%) when compared to day time drift (25.8%).

In general, drift densities of substrate spawner larvae and juveniles were higher near shore than far shore. Across all dates and sites, near shore (≤ 3 m from shore) drift comprised $> 87\%$ of drift for all life stages. Mean proportions of near shore daily drift

densities (\pm SD) were highest for protolarvae ($82.5\pm 25.9\%$) followed by mesolarvae ($81.8\pm 27.3\%$), metalarvae ($71.2\pm 39.3\%$) and juveniles (63.1 ± 42.4). At night, mean drift density (\pm SD) ranged from 18.8 ± 28.3 in metalarvae to 63.2 ± 111.7 in protolarvae within 3 m from shore. In contrast, mean drift density ranged from 1.3 ± 2.7 in metalarvae to 8.6 ± 24.6 in protolarvae within 3 to 6 m from shore. Drift densities declined even further at distances > 6 m from shore, ranging from 0.1 ± 0.1 in mesolarvae to 0.2 ± 0.2 in protolarvae. Consequently, night time drift densities for all life stages were higher ($P < 0.02$) within 3 m of shore. Protolarvae, mesolarvae and metalarvae densities from 3 to 6 m of shore were higher ($P < 0.03$) than those at distances > 6 m from shore (Fig. 2.6). Juvenile drift densities were similar at distances > 3 m from shore ($P = 0.09$). Similar to night time drift patterns, day time densities were higher near shore for protolarvae, mesolarvae and metalarvae. Mean day time drift density (\pm SD) ranged from 5.5 ± 14.0 in mesolarvae to 6.8 ± 10.3 in protolarvae within 3 m from shore. In contrast, day time mean drift density ranged from 0.07 ± 0.1 in mesolarvae to 0.8 ± 2.1 in metalarvae at distances > 3 m from shore. Consequently, day time drift densities for protolarvae, mesolarvae and metalarvae were higher ($P < 0.05$) within 3 m of shore and decreased as distance from shore increased. Juveniles exhibited no difference in drift densities with distance from shore ($P = 0.13$).

Adhesive Broadcast Spawners

Mean monthly drift densities of adhesive broadcast spawners ranged from 0.01 to 1.27 for protolarvae, 0.00 to 0.25 for mesolarvae, 0.003 to 1.23 for metalarvae, and 0.01 to 1.77 for juveniles. Highest mean monthly drift densities occurred during 2004 for

metalarvae and juveniles and in 2005 for protolarvae and mesolarvae (Fig. 2.2). Drift densities were similar between years and among months for protolarvae ($F_{5,18} = 2.16$; $P > 0.10$) and mesolarvae ($F_{5,18} = 1.84$; $P > 0.15$) but differed for metalarvae ($F_{5,18} = 10.24$; $P < 0.01$) and juveniles ($F_{5,18} = 16.54$; $P < 0.01$) with significant ($P < 0.01$) month X year interactions. Within 2004, drift densities were higher ($P < 0.05$) in July for metalarvae and juveniles (Table 2). From May through September 2005, monthly drift densities did not differ ($P > 0.05$) for metalarvae and juveniles across months. Within months, drift densities were higher ($P < 0.05$) in July 2004 and 2005 for metalarvae and juveniles.

Drift densities of substrate spawners were higher at night than day for protolarvae and mesolarvae but not for metalarvae and juveniles. Mean night time drift (\pm SD) comprised 90% (12.0) of total daily drift for protolarvae and 85% (25.9) for mesolarvae (Fig. 2.3). Consequently, night time drift densities (mean \pm SD) of 0.8 ± 1.0 in protolarvae and 0.17 ± 0.2 in mesolarvae were higher than during day for protolarvae ($P < 0.01$) and mesolarvae ($P = 0.01$; Fig. 2.4). Night time drift densities did not differ from day time drift densities for metalarvae ($P = 0.57$) or juveniles ($P = 0.20$). Though drift densities were variable, mean night time drift proportions were generally increased for metalarvae (69%) and juveniles (69%) when compared to day time drift.

In general, drift densities of adhesive broadcast spawners were higher near shore for protolarvae and mesolarvae while metalarvae and juvenile densities were variable across distances. Across all dates and sites, near shore (≤ 3 m from shore) drift comprised 82-83% of protolarvae and mesolarvae drift, 53% of metalarvae drift and only 5% of juvenile drift. At night, mean drift densities (\pm SD) of protolarvae increased when compared to mesolarvae in all near shore and far shore areas, with densities ranging from

4.0±4.8 to 15.5±20.2 within 3 m of shore, 0.6±0.7 to 1.8±2.5 between 3 and 6 m from shore, and 0.1±0.1 to 0.3±0.5 at distances > 6 m from shore. Thus, night time drift densities for protolarvae and mesolarvae were higher ($P < 0.01$) within 3 m of shore than other distances, and densities within 3 to 6 m of shore were higher ($P < 0.01$) than those at distances > 6 m from shore (Fig. 2.7). Day time drift density patterns were similar for protolarvae with higher ($P < 0.03$) mean drift densities (1.9±3.3) within 3 m of shore when compared to other distances (0.1±0.1 to 0.2±0.5). Juvenile night time drift densities (±SD) between 3 to 6 m from shore (0.3±0.4) were higher ($P < 0.01$) than near shore densities (0.006±0.02) but similar to densities at distances > 6 m from shore (0.2±0.4). Night time metalarvae densities and day time drift densities of mesolarvae, metalarvae and juveniles were similar ($P > 0.10$) for near shore and far shore areas.

DISCUSSION

Drifting larval fishes collected from the lower Brazos River were dominated by substrate, pelagic broadcast and adhesive broadcast spawning fishes. Drift rates of the three dominate reproductive guilds were higher at night, in near shore habitats, and during a high water year. Differences in drift patterns within 24 h, along distance from shore gradient, and between flow years suggested larval drift was not homogenous or random through time and space, and failure to detect differences in drift patterns among the three dominant reproductive guilds suggested drifting larvae behaviors were similar despite differences in egg deposition by adult fish.

Night time drift densities were higher in substrate, pelagic broadcast, and adhesive broadcast spawner life stages. Across reproductive guilds, percent of total drift

occurring at night ranged from 75 - 91% in protolarvae to 64 – 69% in juveniles. Similar patterns of increased night drift were reported in shallow prairie streams (Muth and Schmulbach, 1984) and large rivers (Gale and Mohr, 1978; Oesmann, 2003; White and Harvey, 2003) with seasonal high flows from snowmelt or monsoonal rains (Robinson *et al.*, 1998). At least three possible mechanisms are explain non-random drift of larvae at night: 1) larval drift at night is a predator avoidance response to escape predatory fishes moving into shallow water habitats at night to feed (Clark and Pearson, 1980; Pavlov, 1994), 2) larvae become disoriented under low light conditions, resulting in fish passively entering the drift (Hoar, 1953; Northcote, 1962; Gale and Mohr, 1978; Armstrong and Brown, 1983; Brown and Armstrong, 1985), or 3) larval fish actively enter drift at night to search for food (Armstrong and Brown, 1983; Muth and Schmulbach, 1984; Brown and Armstrong, 1985). During this study, I observed an increase in adult and juvenile predatory fishes [i.e., *Cyprinella lutrensis* (Ruppert *et al.*, 1993) and *Ictalurus punctatus* (Bailey and Harrison, 1945; Goldstein and Simon, 1999)] near shore at night, some of which engorged themselves on larval fish, which weakly supports the predator avoidance hypothesis.

Larval and juvenile fishes consistently drifted near shore during day and night, while generally avoiding far shore habitats. An exception was observed in juvenile adhesive broadcast spawners, which were distributed among near shore and far shore habitats during day. Similar patterns in near shore larval drift have been previously reported in streams and large rivers (Gale and Mohr, 1978; Robinson *et al.*, 1998; de Graaf *et al.*, 1999; Reichard *et al.*, 2004). Increased near shore drift densities can be attributed to predatory avoidance response with larvae seeking refuge in shallow water

(Harvey, 1991) or vegetation (Gerlach and Kahnle, 1981), and energy conservation with larvae seeking refugia in slackwater habitats (Kennedy and Vinyard, 1997; Robinson *et al.*, 1998). Although I cannot directly support or exclude predator avoidance or energy conservation as mechanisms responsible for near shore drift, my results suggest near shore drift is an active phenomenon and a result of a behavioral decision to maintain a near shore position drifting (Carter *et al.*, 1986; Penaz *et al.*, 1992; Robinson *et al.*, 1998; Reichard *et al.*, 2002).

Substrate, pelagic broadcast and adhesive broadcast spawner drift densities were generally higher during the high flow year (i.e., 2004) as compared to the low flow year (i.e., 2005). Total annual drift densities during 2004 were double 2005 drift densities for substrate and adhesive broadcast spawners and triple the drift densities for pelagic broadcast spawners. My findings are consistent with drift studies reporting high flow year drift density increases ranging from 2 to 13 times that of lower flow year densities for substrate spawners (Peterson and Vanderkooy, 1995; Durham and Wilde, 2008), five times those of low flow years for pelagic broadcast spawners (Durham and Wilde, 2008), and almost double low flow year densities for adhesive broadcast spawners (Peterson and Vanderkooy, 1995). Greater drift densities during the high flow year were attributed to larger numbers of metalarvae and juvenile fishes in the drift, which were 4.4 to 160 times those drifting during the low flow year. In comparison, drift densities of protolarval and mesolarval fishes were less different between flow years (high flow year drift densities ranged from 0.5 to 3.4 times those drifting during the low flow year). Collectively, my findings support linkages among higher flows, increased larval survival, and consequently reproductive success (Merigoux and Ponton, 1999; Humphries and Lake,

2000; Humphries *et al.*, 2002), but also suggests which life stages of fish are most susceptible (i.e., metalarvae and juveniles) to decreased survival during low flow years. At least two plausible mechanisms exist to explain greater metalarval and juvenile survival during high flow years. First, high flow years and increased flood frequency generally increase allochthonous inputs and carry greater amounts of nutrients (Spink *et al.*, 1998), which may increase resource availability to fishes shifting into exogenous feeding. Availability of nutrients from first feeding through development is an important factor regulating survival and recruitment of fish populations (Miller *et al.*, 1988). Second, abiotic conditions (i.e., water temperature, dissolved oxygen) are more variable during low flow conditions which can decrease larval fish survival (Schlosser, 1985). Regardless of the specific mechanism, high inter-annual variability in recruitment (i.e., boom-and-bust cycles) are common for fishes and other organisms in variable systems like rivers (Walker *et al.*, 1995; Smith *et al.*, 2005; Bednarski *et al.*, 2008). However, repeated low flow years in modified rivers would have a compounding effect and might explain why a number of stream fish, especially prairie stream fishes in North America, gradually decline in occurrence and abundance through time following implementation of flow controls and diversions (Schlosser, 1985).

Failure to detect differences in drift patterns among the three dominant reproductive guilds was surprising. I expected larval drift patterns to differ between reproductive guilds based on differing requirements for successful reproduction, egg characteristics, and decreases in abundance of broadcast spawning fishes in the lower Brazos River (Runyan, 2007). However, similar drift patterns among the three reproductive guilds suggested innate patterns in larval fish drift do not benefit one reproductive strategy over

others. Consequently, prediction of differences in larval drift could explain large scale changes in the lower Brazos River fish assemblage were not supported. Instead, similar diel and spatial drift patterns across reproductive guilds indicated a concurrent utilization of stream margin habitat. As such, recent population increases in relative abundances of substrate spawning fish (16% to 79% for *P. vigilax* and *C. lutrensis* from 1969 to 2006; Runyan, 2007) might lead to density dependent effects and exploitative competition among larvae and juveniles across these reproductive guilds (Welker *et al.*, 1994; Matthews *et al.*, 2001).

Declines in broadcast spawning fishes of North American rivers are associated with anthropogenic modifications. Environmental modifications have resulted in broadcast spawner declines in a wide variety of lotic environments including large rivers, headwater streams, and spring and snowmelt influenced systems (Cross *et al.*, 1983; Luttrell *et al.*, 1999; Humphries and Lake, 2000). Similar declines in broadcast spawners have occurred in the lower Brazos River, including decreases in *N. potteri* (Perkin *et al.*, 2009) and *Notropis oxyrhynchus*, and the extirpations of *N. buccula* and *Hybognathus placitus* (Runyan, 2007). Population declines in these systems have largely been linked to fragmentation of riverine habitats due to dams, dewatering and especially to hydrological changes altering numbers of eggs released (Moore, 1944; Taylor and Miller, 1990; Platania and Altenbach, 1998) during the reproductive season. However, recent evidence suggests egg release is likely independent of flow regime (Robinson *et al.*, 1998; Bonner, 2000; Durham and Wilde, 2006; Durham, 2007) and based on the results of this study, I propose larval survival is another potential factor for precipitous declines through time (Humphries and Lake, 2000; Humphries *et al.*, 2002).

My study elucidates the importance of adequate flows and unfragmented habitats to successful larval survival and recruitment of broadcast spawning fishes. For instance, sustained low flows or dewatering may mimic the effects of low flow years, resulting in decreased nutrient input (Pringle, 1997; Rosenberg *et al.*, 2000) and increases in competition or predation within and among larval stages. Channelization decreases sandbar habitat (Van Steeter and Pitlick, 1998), reduces the amount of shallow, low velocity habitat near shore and may prevent larval fish from exiting the drift during day, possibly increasing predation risk and increasing the overall drift distance required for larval maturation. Hydropower related releases can cause rapid inundation and receding of edge water and, depending on timing of releases, can result in stranding of fish in unsuitable habitats (Bradford *et al.*, 1995; Higgins and Bradford, 1996). Although the detrimental effects of fragmentation are well documented, the drift of all larval stages and juveniles in my study suggests fragmentation effects may be even more severe on recruitment of stream fishes than previously believed.

Implications for Conservation

The similarities in drift patterns and yearly survival between substrate and broadcast spawning species greatly complicate conservation strategies aimed strictly at imperiled broadcast spawners. Manipulation of regulated flows to provide “required” peak flows or to mimic the natural flow regime is the most often suggested conservation measure to provide reproductive requirements and maintenance of stream fish populations (Stanford *et al.*, 1996; Poff *et al.*, 1997; Marchetti and Moyle, 2001; Matthews *et al.*, 2001). Although management of flows to induce spawning is warranted, adequate flow should

also be maintained to provide flows required for successful egg and larval survival and drift (Humphries *et al.*, 2002; Durham and Wilde, 2009). Increases in periodicity of flow events, especially during the reproductive season, would provide the needed flows for successful reproduction and egg and larval drift and also maintain nutrient input into the system. The near shore distribution of drifting larvae supports the need for periodic channel forming flows (Poff *et al.*, 1997) to maintain the shallow, low flow areas near shore and to prevent incision and channelization.

Although these conservation measures may benefit declining broadcast spawner populations, these efforts fail to address possible biotic mechanisms influencing their decline. Unfortunately, these management strategies will most likely benefit already increasing populations of substrate spawners and, where substrate spawners or other invasive species are dominant, may actually increase competition or predation on already declining broadcast spawners (Scott and Helfman, 2001). In these instances, species conservation or restoration of historic communities may require not only reestablishment of historic environmental conditions but also a physical manipulation of communities (i.e., species removal or supplementation; Fukami and Lee, 2006). Regardless, basin wide management strategies are required to maintain patterns and benefits of drifting larval fishes and should include maintenance of flow variability and high flow events during the reproductive period, reduction in fragmentation, maintenance of nutrient input and cycling, and protection of discharge rates that maintain or restore historical morphological characteristics of riverine environments and maintain adequate habitat heterogeneity.

Acknowledgements.-- Texas Water Development Board provided partial financial support for this project. Additional funding was provided by the National Science Foundation, Project Flowing Waters. T. C. Heard, J. M. Watson, J. S. Perkin, B. M. Littrell, D. L. McDonald, and C. J. Hassan-Williams assisted in field collections and laboratory methods.

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Table 2.1. Relative abundance and drift densities for six reproductive guilds of fishes collected from three sites on the lower Brazos River during 2004 and 2005.

	2004					2005				
	All stages	Proto	Meso	Meta	Juv	All stages	Proto	Meso	Meta	Juv
Relative Abundance	100	34.0	13.7	18.1	34.2		72.5	18.4	6.2	2.9
Substrate Spawners	67.5	23.8	10.0	10.4	23.4	73.0	52.6	13.6	4.6	2.2
Open substrate spawners										
Pelagic eggs	24.8	8.9	3.5	5.2	7.3	17.2	14.3	2.4	0.4	0.1
Adhesive eggs	5.2	1.3	0.2	1.4	2.3	7.7	5.4	1.1	1.0	0.2
Nest Spawners	2.4	<0.1	<0.1	1.1	1.2	2.0	0.2	1.3	0.2	0.4
Brood hidiers						<0.1	<0.1			<0.1
Catadromous						<0.1				<0.1
Burrowers						<0.1				<0.1
<i>N</i> =	48244					46032.2				
Drift Density (# fish/100 m ³)										
Substrate Spawners	11.1	3.8	1.4	1.9	4.1	4.6	3.2	0.8	0.3	0.2
Open substrate spawners										
Pelagic eggs	4.3	1.6	0.6	1.0	1.2	1.3	1.1	0.2	<0.1	<0.1
Adhesive eggs	1.5	0.3	0.045	0.4	0.7	0.7	0.4	0.1	0.1	<0.1
Nest Spawners	0.7	0.006	0.013	0.3	0.3	0.2	<0.1	0.1	<0.1	<0.1
Brood hidiers						<0.1	<0.1			<0.1
Catadromous						<0.1				<0.1
Burrowers						<0.1				<0.1
Water filtered (m ³)	157046.2					426881				

Table 2.2. Simple main effects tests for larval drift density differences of substrate, pelagic broadcast and adhesive broadcast spawners.

	Between Years				Among Months			
	Month	<i>F</i>	df	<i>P</i>	Year	<i>F</i>	df	<i>P</i>
Substrate Spawners								
Protolarvae	July	3.08	1,7	0.1229	2004	14.78	2,6	0.0048
	August	10.42	1,7	0.0145	2005	4.8	4,22	0.0062
	September	15.13	1,7	0.0177				
Mesolarvae	July	3.99	1,7	0.0859	2004	9.39	2,6	0.0142
	August	18.77	1,7	0.0034	2005	2.24	4,22	0.0975
	September	0.07	1,7	0.8038				
Metalarvae	July	0.57	1,7	0.4738	2004	4.07	2,6	0.0763
	August	2.48	1,7	0.1593	2005	0.46	4,22	0.7675
	September	17.51	1,4	0.0139				
Juvenile	July	0.49	1,7	0.5082	2004	16.46	2,6	0.0037
	August	1.9	1,7	0.2107	2005	2.59	4,22	0.0652
	September	15.41	1,4	0.0172				
Pelagic Broadcast Spawners								
Juvenile	July	5.36	1,7	0.0538	2004	2.14	2,6	0.1984
	August	1.86	1,7	0.2144	2005	0.77	4,22	0.5557
	September	4.79	1,4	0.0939				
Adhesive Broadcast Spawners								
Metalarvae	July	14.53	1,7	0.0066	2004	6.2	2,6	0.0347
	August	38.1	1,7	0.0005	2005	1.54	4,22	0.2245
	September	0.33	1,4	0.594				
Juvenile	July	64.22	1,7	<0.0001	2004	8.09	2,6	0.0198
	August	3.49	1,7	0.1039	2005	1.17	4,22	0.3491
	September	2.94	1,4	0.1614				

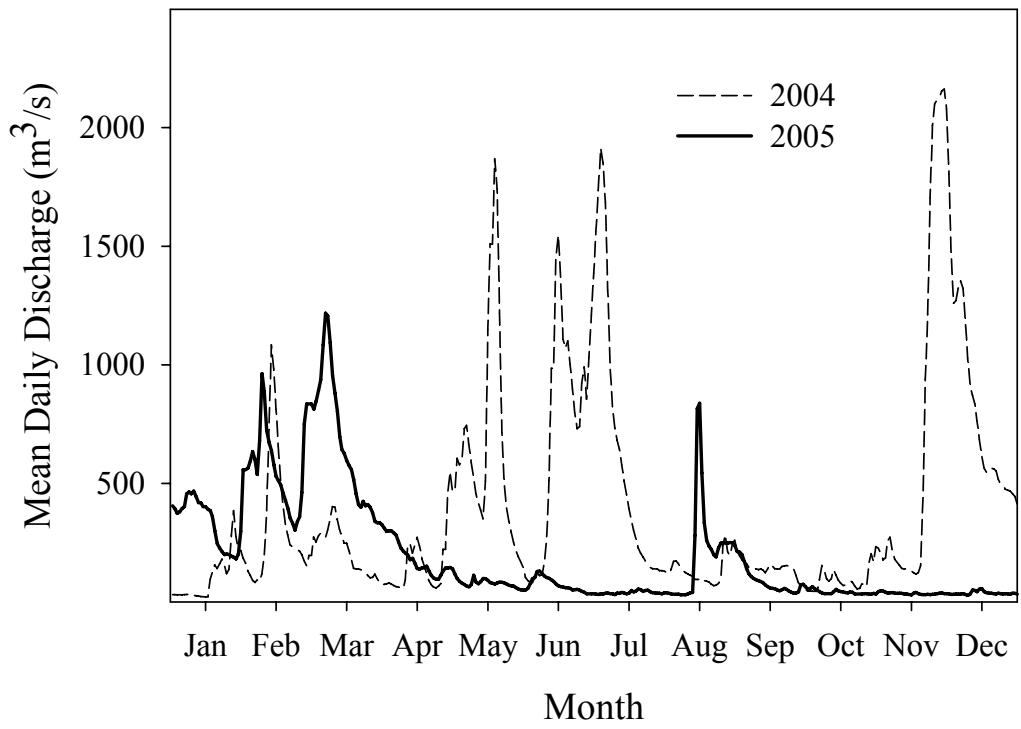


Figure 2.1. Mean daily discharge rates for the lower Brazos River from 2004 and 2005. Data from USGS gauging station near Hempstead, Texas.

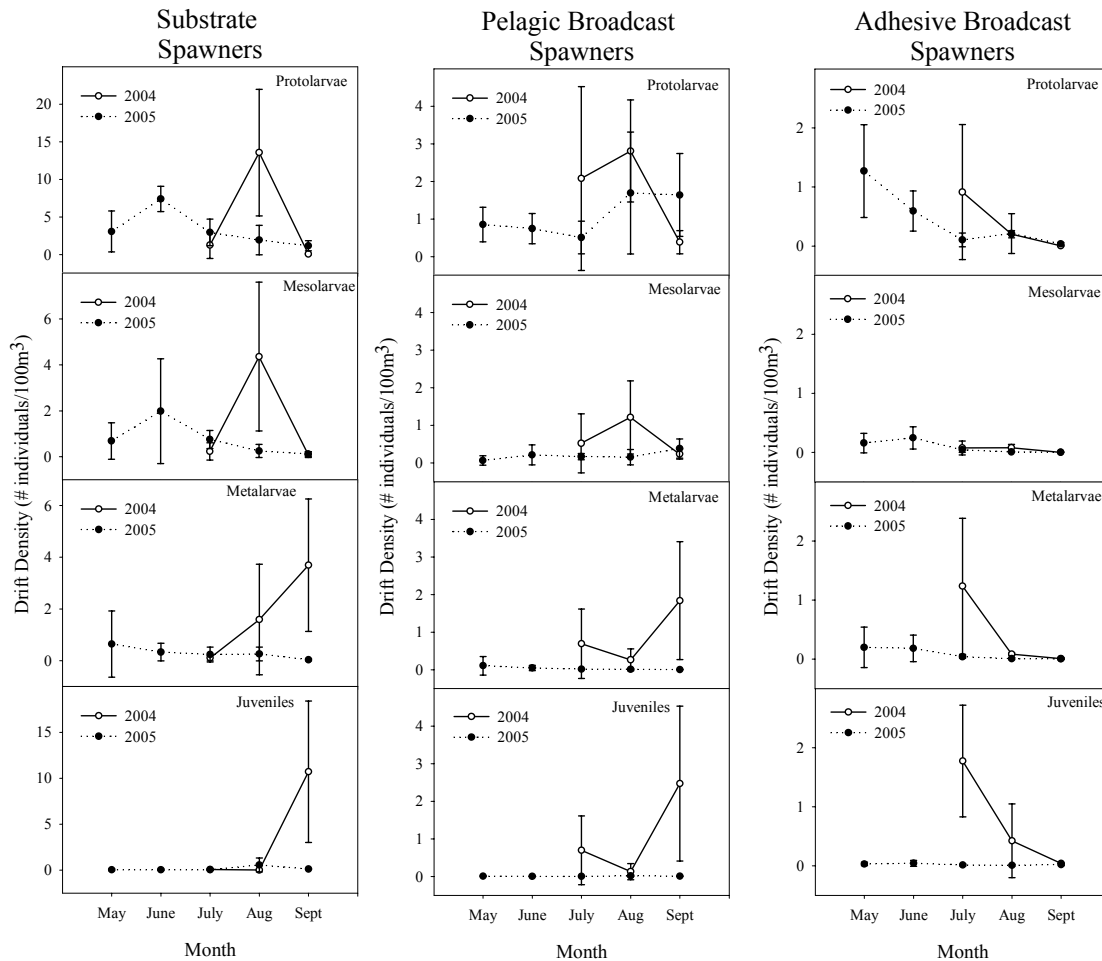


Figure 2.2. Mean (\pm SD) monthly drift densities for larval and juvenile life stages of substrate, pelagic broadcast and adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005.

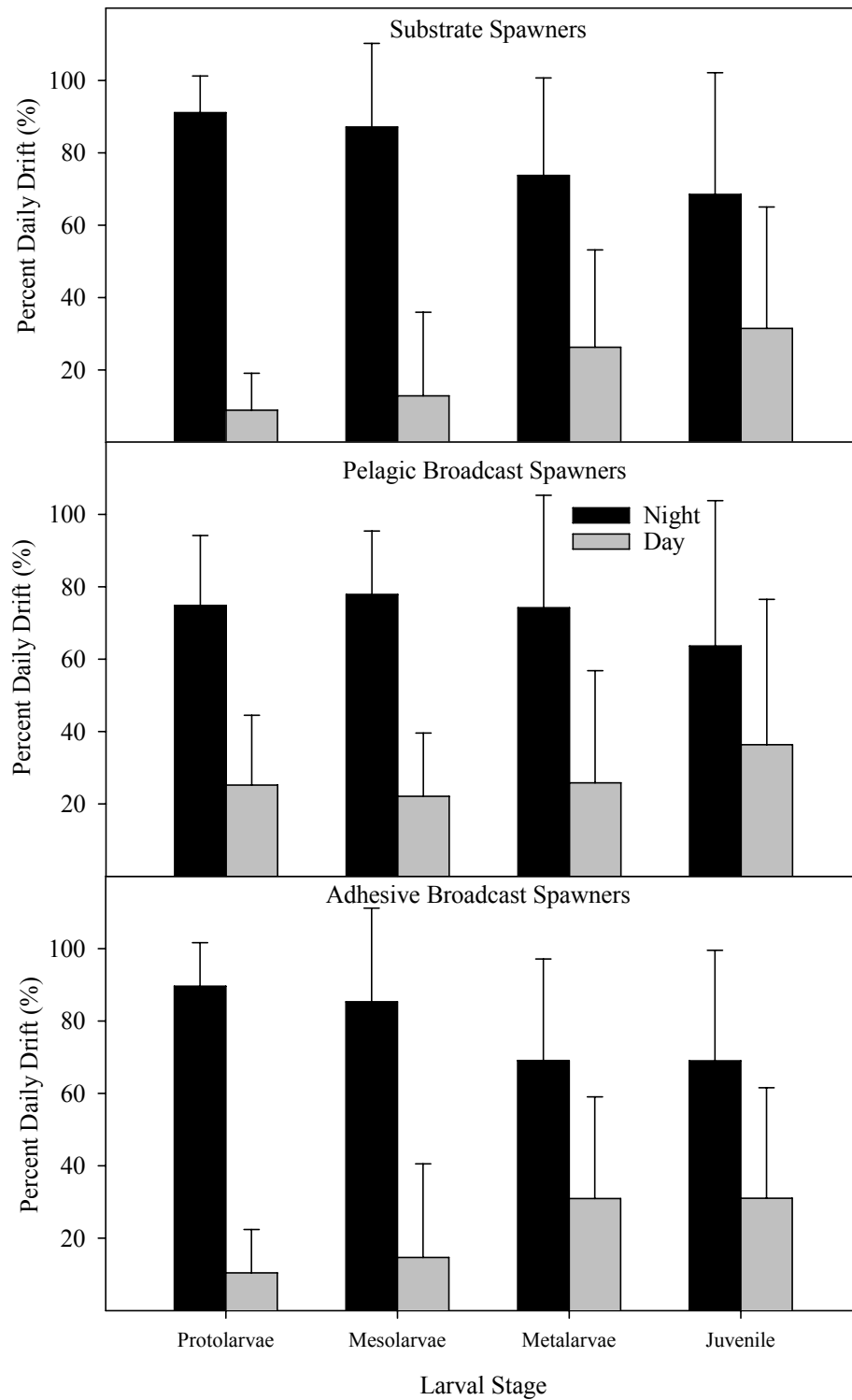


Figure 2.3. Mean diel drift proportions for larval and juvenile substrate, pelagic broadcast and adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005.

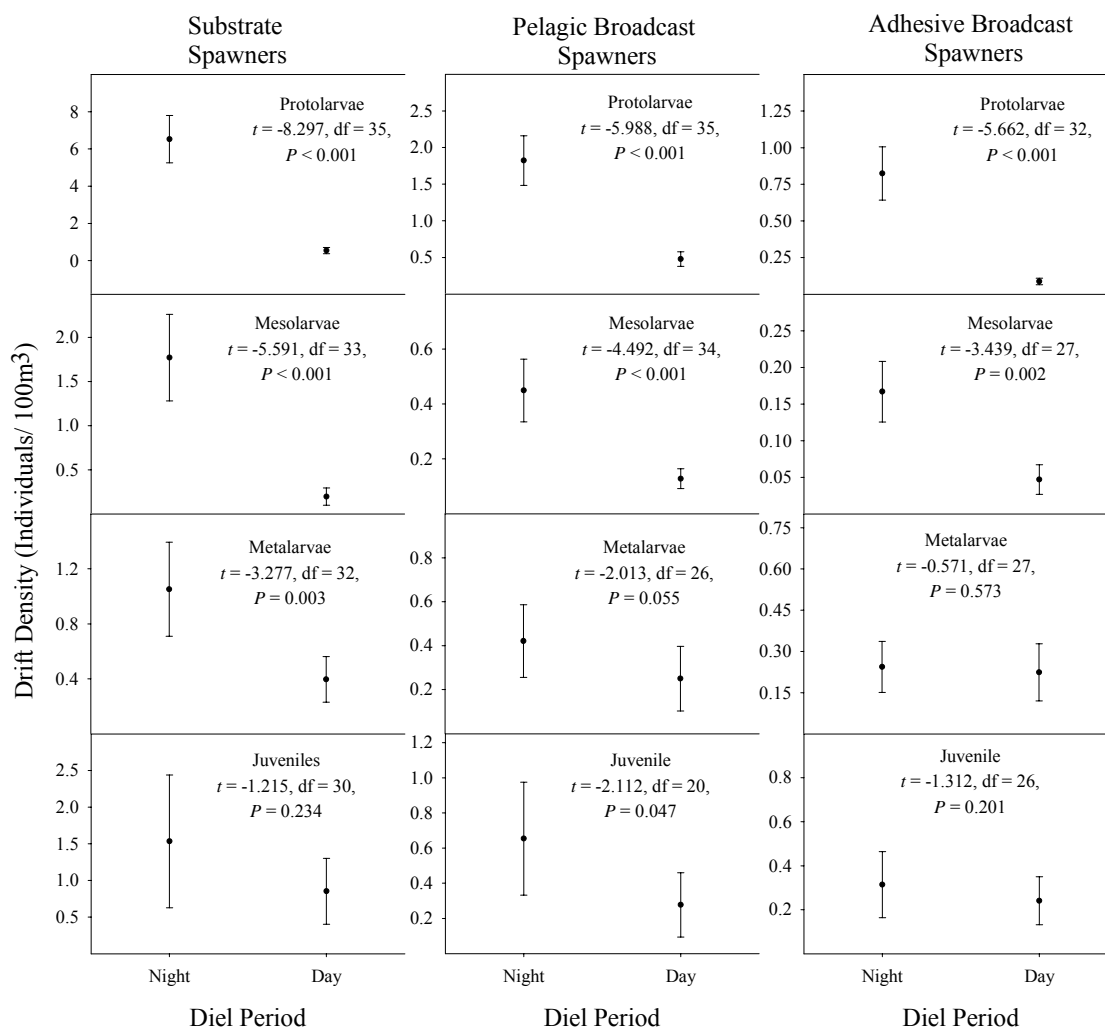


Figure 2.4. Mean daily night time and day time drift densities for larval and juvenile stages of substrate, pelagic broadcast and adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005.

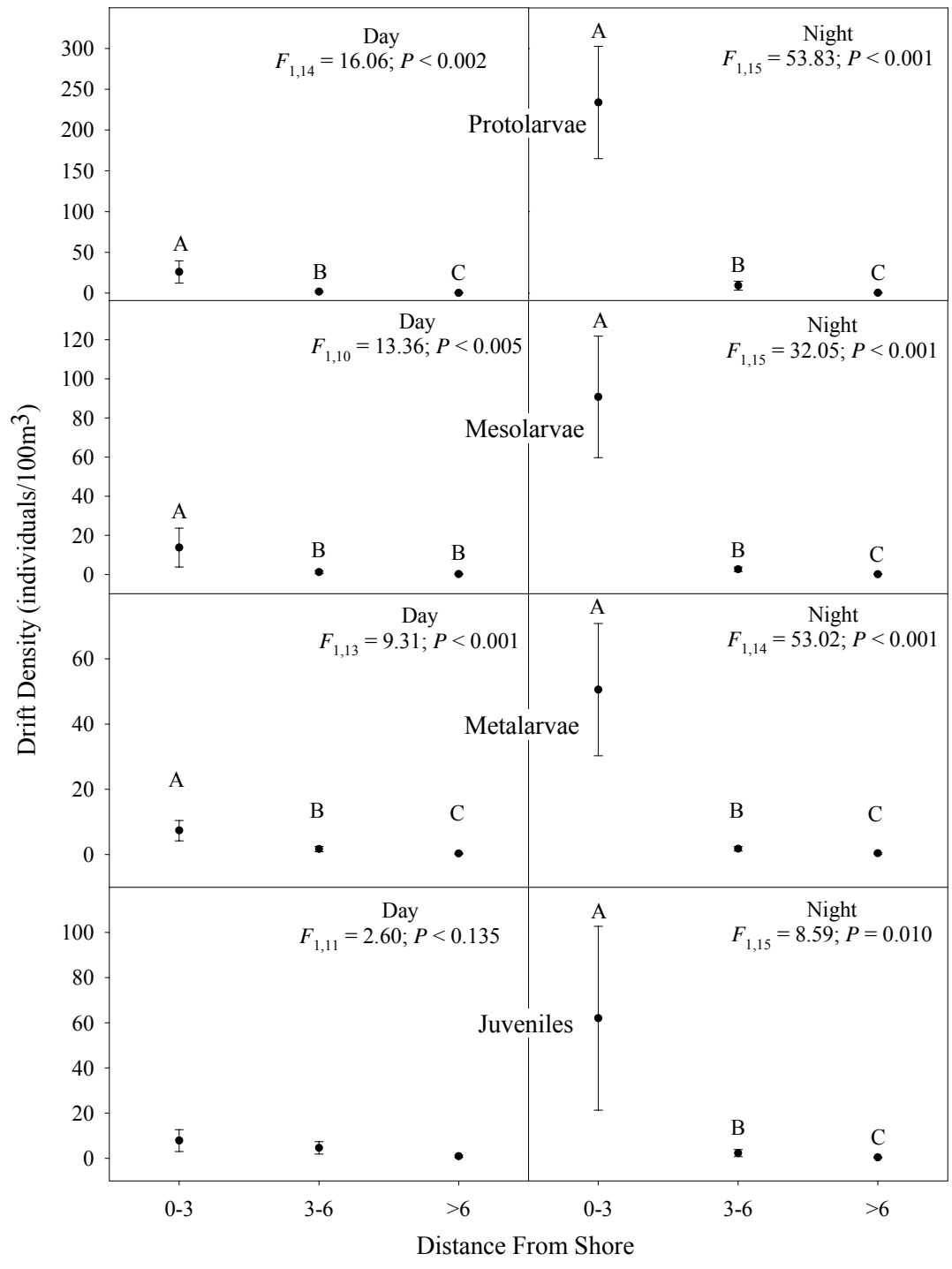


Figure 2.5. Day time and night time distance from shore drift densities for substrate spawners collected from three sites on the lower Brazos River during 2004 and 2005.

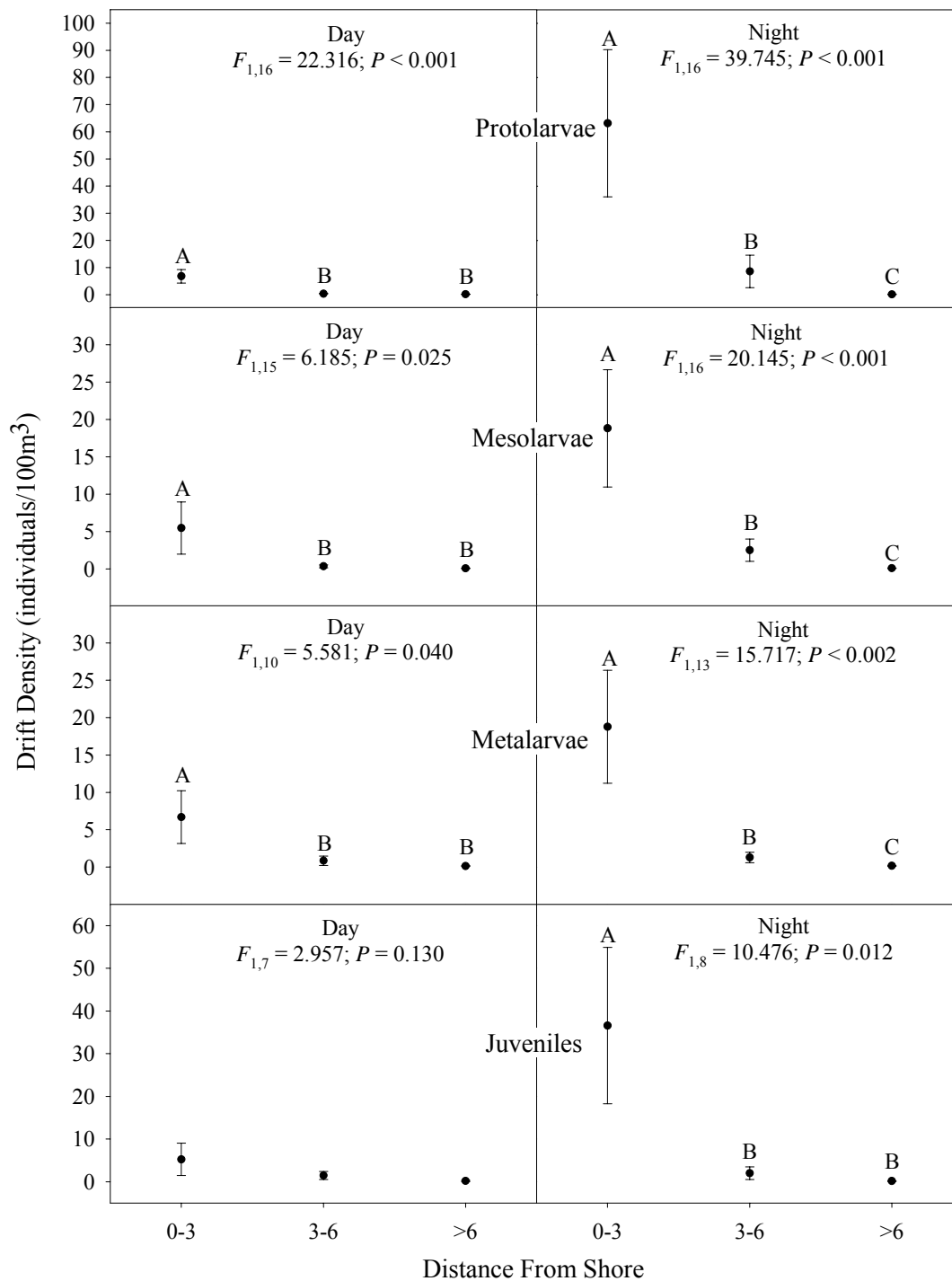


Figure 2.6. Day time and night time distance from shore drift densities for pelagic broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005.

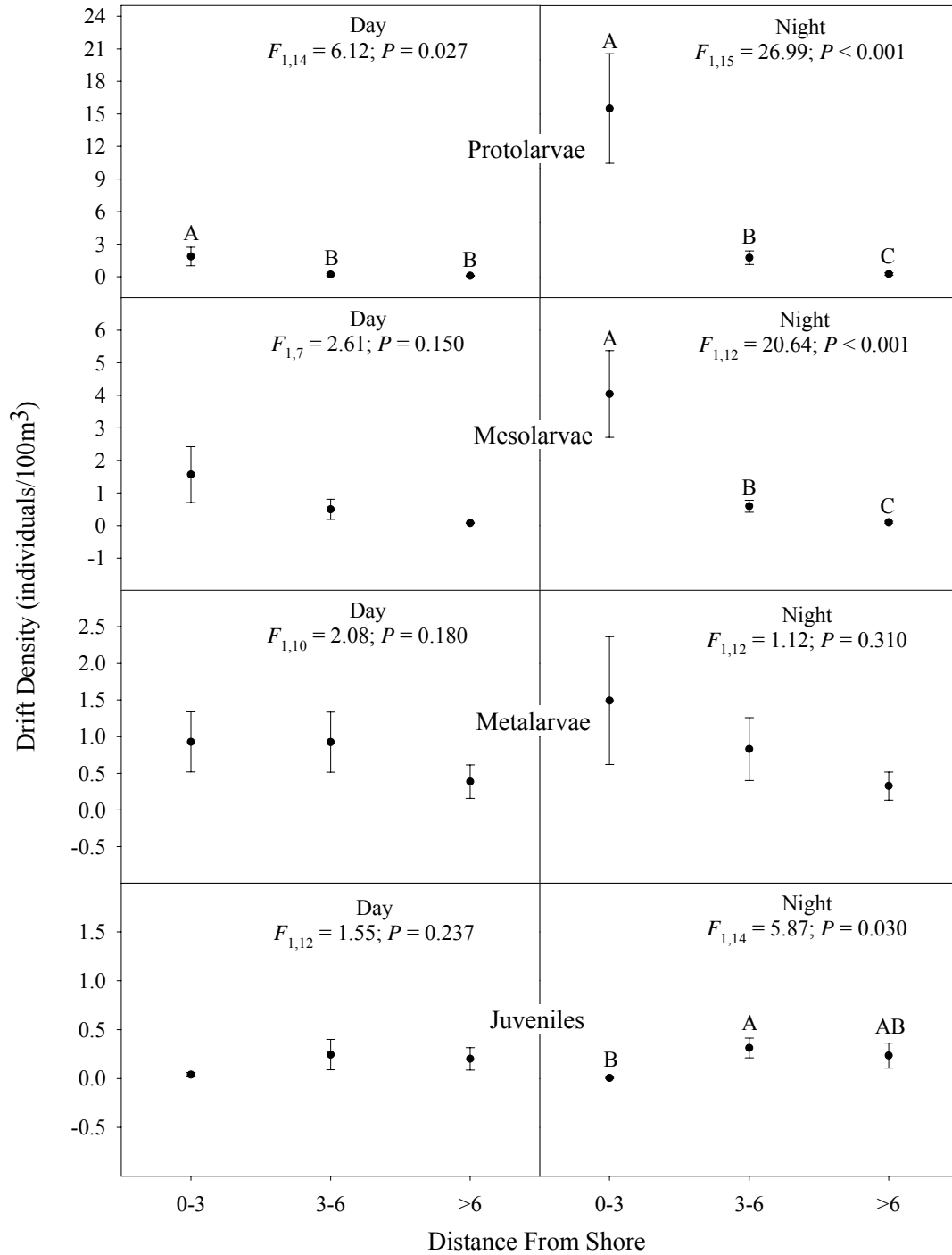


Figure 2.7. Day time and night time distance from shore drift densities for adhesive broadcast spawners collected from three sites on the lower Brazos River during 2004 and 2005.

VITA

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