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Life History Aspects of a Relict Ironcolor Shiner *Notropis chalybaeus* Population in a Novel Spring Environment

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ABSTRACT.—Ironcolor shiner *Notropis chalybaeus* is generally absent from groundwater-dominated systems throughout its range; however, a relict disjunct population occurs within the spring-fed upper reaches of the San Marcos River in central Texas. We conducted monthly seine collections within the restricted 2.2 km headwater range of the species to assess food habits and reproductive life history within a unique spring-run environment. Prey items were dominated by aquatic insects including Diptera (16% by weight), Ephemeroptera (13%), and Odonata (5%), as well as terrestrial insects (9%). The population consisted of four age groups with a maximum life span of 2.5 y. Reproductive ecology showed a protracted spawning season ranging Mar.–Dec. during which multiple clutches were produced. Reproductive maturity was reached at approximately 1 y (36 mm SL), mean mature oocyte diameter was ~0.8 mm, and number of mature oocytes per clutch ranged 46–326. Comparisons between ironcolor shiner populations in the San Marcos River and thermally dynamic Marshalls Creek of Pennsylvania revealed mature female size was larger ($T_{38} = 10.48$, $P < 0.01$) and mature oocyte diameter smaller ($T_{38} = 16.87$, $P < 0.01$) in the upper San Marcos River. Literature accounts regarding ironcolor shiner reproductive ecology suggest a latitudinal trade-off between reproductive season length and oocyte size. Our findings provide further evidence for the roles of photoperiod and water temperature in structuring the reproductive seasonality of spring-dwelling fishes, specifically the lack or delay of terminating cues in stenothermal waters. In this manner, aquifer depletion and alteration of thermal regimes threaten spring-dwelling fishes by disrupting naturally occurring reproductive cues.

INTRODUCTION

Ironcolor shiner *Notropis chalybaeus* is a small-bodied cyprinid occurring in Atlantic coast streams from New York to Florida and tributaries to the Mississippi River from the southern Great Lakes region south to Texas (Page and Burr, 1991). Throughout this range, the species is considered imperiled (Jelks *et al.*, 2008) because of declines in abundance and distribution in Arkansas, Iowa, Louisiana, Mississippi, Missouri, Oklahoma, Texas, and Wisconsin (Douglas, 1974; Robinson *et al.*, 1974; Robinson, 1977; Becker, 1983; Page and Burr, 1991; Pflieger, 1997; Williams and Echelle, 1998; Ross, 2001; Warren *et al.*, 2000; Hubbs *et al.*, 2008). Though specific causes for decline remain poorly understood (Williams and Echelle, 1998), many imperiled listings correspond with disjunct or narrowly distributed populations (Leckvarcik, 2001). Disjunct populations of *N. chalybaeus* become increasingly frequent toward the peripheries of its range (Swift, 1979) and ecology of these disjunct populations remains poorly studied. In fact, ecology and life history of *N. chalybaeus* have been investigated only in contiguous portions of its range, including Florida (Marshall, 1947; Swift, 1970), Arkansas (Robertson, 1977), and Pennsylvania (Leckvarcik, 2001). Furthermore, *N. chalybaeus* is apparently absent from spring-dominated streams within

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contiguous portions of its range (*e.g.*, Florida; Swift, 1970) leading to paucity of life history data for *N. chalybaeus* in these types of habitats.

The upper San Marcos River of central Texas (Hays County) represents a novel environment among streams inhabited by *Notropis chalybaeus*. Swift (1970) considered the upper San Marcos River population the relict of a historically broadly distributed population that was likely contiguous with eastern drainages circa glacial times (~10,000 y ago). During warmer and drier periods of the Holocene climatic optimum (Toomey *et al.*, 1993; Al-rabab'ah and Williams, 2004), continual streamflow from the San Marcos Springs likely allowed for the persistence of a disjunct population of *N. chalybaeus*, which was once considered a unique species (Baughman, 1950). Swift (1970) noted unique meristics for the upper San Marcos River population but concluded the population was not sufficiently different from eastern populations to merit species or subspecies rank. Environmental variables within the upper San Marcos River differed from Florida streams inhabited by the species, including year-round stenothermal water temperature and turbidity was generally lower (Swift, 1970). Groeger *et al.* (1997) characterized the water chemistry in the upper San Marcos River as having slightly acidic pH (6.5), low turbidity (<1 NTU), and stenothermal water (22.3 C). Conversely, Arkansas, Florida, and Pennsylvania streams inhabited by *N. chalybaeus* are characterized by fluctuating water temperatures (annual ranges: 0–25 C, 8–25 C, –0.5–22.3 C, respectively) and higher turbidities due to tannin staining and a lack of spring discharge influences (Marshall, 1947; Robinson, 1977; Leckvarcik, 2001). *Notropis chalybaeus* historically inhabited headwater reaches of streams in Wisconsin but have not been collected since the mid-1920s (Becker, 1983). Consequently, to our knowledge the upper San Marcos River population of *N. chalybaeus* represents the only extant population confined to a spring-dominated stream with stenothermal water (Swift, 1979).

The disjunct population of *Notropis chalybaeus* in the headwater reaches of the San Marcos River of central Texas (Thomas *et al.*, 2007) has been separated from other populations for approximately 10,000 y and by three Western Gulf Slope drainages (~400 km; Swift, 1970) and represents an opportunity to assess the ecology and life history of *N. chalybaeus* in a spring-dominated system. The purpose of this study was to assess the life history of an *N. chalybaeus* population in a novel spring-dominated stream environment. Specifically, we sought to assess: (1) longitudinal distribution within the upper San Marcos River; (2) gut content frequency of occurrence, percent composition, and seasonality; (3) fundamental traits of reproductive ecology including age at maturation, maximum age, length of reproductive season, and number and size of oocytes; and (4) influence of environmental variables on reproductive ecology. Leckvarcik (2001) suggested water temperature was a driving determinant of reproductive season for *N. chalybaeus*, and we hypothesized that reproductive ecology within the upper San Marcos River would differ from streams with variable thermal regimes, such as Marshalls Creek, Pennsylvania, for which detailed life history data exist (Leckvarcik, 2001).

METHODS

Monthly seine collections targeting *Notropis chalybaeus* were conducted at three sites on the upper San Marcos River (Hays County, Texas) during Jan.–Dec. 2007. Sampling locations were Site 1: near Snake Island downstream of the Ranch Road 12/East Hopkins Street crossing (29°52'56"N, 97°56'05"W), Site 2: just downstream of the Cheatham Street crossing (29°52'37"N, 97°56'00"W), and Site 3: 0.2 km upstream of the Interstate Highway 35 (IH-35) crossing (29°52'38"N, 97°55'51"W). These sites were within a 1 km urbanized

stretch of the San Marcos River and were chosen based on historical collections. Collections were made using a 2.4 m by 1.8 m common sense seine (3.2 mm mesh) and a maximum of 12 individuals were opportunistically retained each month to reduce consumptive sampling. Retained individuals were anesthetized in a lethal dose of MS-222 (80 mg/l) and preserved in 10% formalin for laboratory examination. Habitat parameters were recorded for each site and date, including geomorphic units sampled (*i.e.*, run, riffle, pool, eddy), relative current velocities and depths, substrate composition and presence and type of aquatic macrophytes. Additionally, we reviewed historical museum collections taken between the San Marcos River headwaters and mouth (133 km total length) during 1938–2006 to assess longitudinal distribution.

In the laboratory, standard lengths (SL) in mm and total weight (g) of each individual were recorded prior to dissection removal of entire digestive tracts and gonads. To assess reproductive ecology, gonad weights were divided by somatic weights and then multiplied by 100 to yield gonadosomatic indices (GSI) for each individual. Mean (\pm SE) GSI were plotted by month for male and female *Notropis chalybaeus* to illustrate reproductive seasonality. Reproductive activity of female *N. chalybaeus* was assessed by measuring 100 randomly selected oocytes within the left ovary of reproductively active females collected during each month of sampling. Oocyte diameter (mm) was the mean of the longest and shortest cross-sectional lengths of each oocyte, using a compound microscope and stage micrometer (Williams and Bonner, 2006). Frequency distributions of oocyte diameters were plotted to detect modal progression of multiple cohorts using bin frequencies calculated using the Sturges (1926) equation. Mean oocyte diameter and fecundity were estimated by calculating the mean oocyte diameter and mean number of vitellogenic oocytes in 20 reproductively active female *N. chalybaeus*. Vitellogenic oocytes were identified as cloudy to yellow without a definable nucleus.

Reproductive ecology of *Notropis chalybaeus* in the upper San Marcos River was compared to *N. chalybaeus* studied in Marshalls Creek, Pennsylvania (Leckvarcik, 2001). Reproductive ecology of ironcolor shiner from Marshalls Creek, Pennsylvania collected during 1999–2000 were analyzed using methods similar to those described above (Leckvarcik, 2001), which allowed for direct comparisons of detailed oocyte information. Mean SL and mean diameter of mature oocytes were compared for 20 reproductively mature females from each population using *t*-tests ($\alpha = 0.05$) and raw data obtained directly from the author (Leslie Leckvarcik, Juniata College, unpubl. data). Differences in the relationship for SL and (1) number of mature oocytes and (2) mean oocyte diameters were tested among the same 20 reproductively mature females using analysis of covariance (ANCOVA). For ANCOVA, river location was used as the covariate and relationships were plotted to test for similarities/differences in slopes. We placed the findings of these comparisons into a broader context by evaluating similarities in reproductive season lengths and oocyte diameters with previous reports dispersed across the eastern United States.

Population structure and longevity of *Notropis chalybaeus* in the upper San Marcos River were described using SL of all individuals collected. Modal progression analysis was conducted using the program Fish Stock Assessment Tool, Version 2 (FiSAT II; Food and Agricultural Organization, 2001) following the methods of Perkin *et al.* (2009). Mean (\pm SD) SL that corresponded with modes identified using FiSAT II were plotted by month to illustrate age classes and longevity. Modal progression results were compared with the smallest observed SL of a reproductively mature female to estimate minimum age at maturity. Longevity was estimated using the last month the maximum age group was detected.

To assess dietary habits, digestive tracts between the esophagus and the anus were removed from each individual, and contents from the esophagus to the second bend in the intestine were extracted. Gut contents were identified to the lowest practical taxonomic level, enumerated, and weighted to the nearest 0.1 mg. Items weighing less than 0.1 mg were assigned a weight of 0.1 mg. Frequency of occurrence (percentage of fish that contained each food item) and mean percent by weight (taxon weight/total content weight * 100) were calculated for each prey item (Bowen, 1996). Seasonal dietary habits were assessed by calculating diet niche breadth (Levins, 1969) by season, where seasons were defined as fall (Sep.–Nov.), winter (Dec.–Feb.), spring (Mar.–May), and summer (Jun.–Aug.). Seasonal shifts in insect prey items were illustrated by calculating mean percent weight of four broad functional categories (*i.e.*, predatory insects, terrestrial insects, herbivorous insects, and other) by each season.

RESULTS

During monthly seine collections in 2007, 118 *Notropis chalybaeus* were taken from the upper San Marcos River. Water quality in this section of the San Marcos River was characterized by low turbidity, stenothermal water temperature (*i.e.*, ~22 C) and high abundance of submerged aquatic macrophytes. *Notropis chalybaeus* were generally taken from slack-water or eddy-type habitats adjacent to run geomorphic units with depths of approximately 1 m over gravel substrate with moderate flow. Individuals were associated with submerged aquatic vegetation, dominated by grassy arrowhead *Sagittaria platyphylla*, and were rarely collected from habitats lacking vegetation or patches dominated by other macrophyte types (*i.e.*, hydrilla (*Hydrilla verticillata*), Illinois pondweed (*Potamogeton illinoensis*)). *Notropis chalybaeus* was frequently taken with Texas shiner *Notropis amabilis*, another species that uses mid-water column depths.

LONGITUDINAL DISTRIBUTION

Our samples and the historical data suggest that *Notropis chalybaeus* occurs within a 2.2 river km stretch of the upper San Marcos River, between the outflow of Spring Lake and the IH-35 crossing (Fig. 1). Carl Hubbs captured *N. chalybaeus* in the San Marcos River at two points in 1938: (1) immediately downstream from the dam of Spring Lake (University of Michigan Museum of Zoology, UMMZ #120244), and (2) approximately 1.7 km downstream at the present day Cheatum Street crossing (UMMZ #120258). More recently, 16 collections were taken from the San Marcos River between these two points (Perkin, 2009). We found low seasonal variation in abundances of *N. chalybaeus* between the Cheatum Street crossing and 0.2 river km upstream of the IH-35 crossing, and the species generally constituted 5–25% of the sampled assemblage. Exploratory sampling associated with concurrent research within a 0.8 km reach just downstream from IH-35 during 2007 and 2008 yielded no *N. chalybaeus* (Folb, 2010). Furthermore, *N. chalybaeus* was not detected between IH-35 and the mouth of the San Marcos River in 72 museum collections taken during 1949–2006 (*see* Appendix III of Perkin, 2009).

FOOD HABITS

Insects dominated gut contents among 118 *Notropis chalybaeus* examined for dietary habits. Dipterans, chiefly chironomids, occurred in 62% of individuals and constituted 16% of gut tract contents by weight (Table 1). Ephemeropterans were second most abundant (30% occurrence, 13% by weight), followed by terrestrial insects (20%, 9%), and trichopterans (18%, 4%). Vegetation and algae occurred in 8% of individuals and constituted 3% by

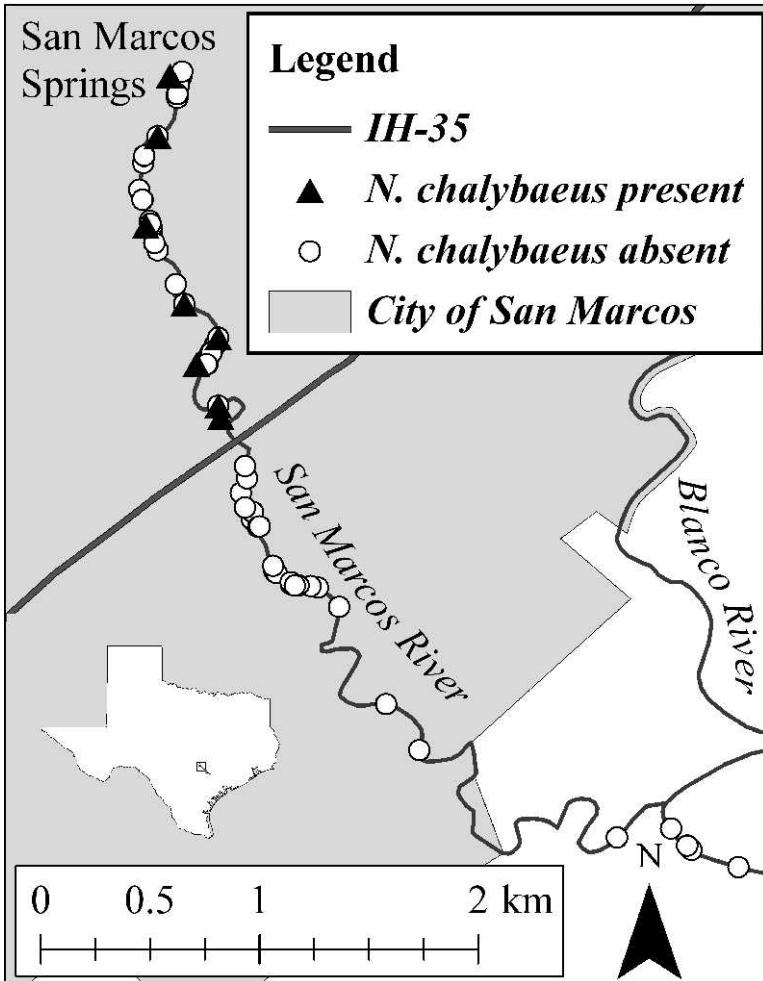


FIG. 1.—Longitudinal distribution of *Notropis chalybaeus* in the upper San Marcos River, Hays County, Texas. Symbols represent collections taken between 1938 and 2006 in which *N. chalybaeus* were present (black triangles) or absent (open circles). Collections are reported in Appendix III of Perkin (2009)

weight. Empty gut tracts were found for eight individuals and cestodes were found in four gut tracts. Diet niche breadth (NB) was greatest during the winter ($n = 23$; $NB = 0.48$), intermediate during fall ($n = 26$; $NB = 0.38$) and spring ($n = 32$; $NB = 0.31$), and lowest during summer ($n = 29$; $NB = 0.13$). During fall, winter, and spring, percent weight of herbivorous insects (*i.e.*, Ephemeroptera, Diptera, Lepidoptera, Trichoptera, and Coleoptera) was greatest (fall = 43%, winter = 34%, spring = 49%) followed by terrestrial insects (*e.g.*, mainly winged Hymenoptera; 16%, 18%, 21%) and predatory insects (*i.e.*, Hemiptera and Odonata; 5%, 3%, 8%). During summer, percent weight of stomach contents was dominated by organic detritus and algae (85%), followed by herbivorous insects (13%).

TABLE 1.—Frequency of occurrence and mean percentage by weight of gut contents for 118 *Notropis chalybaeus* collected from the upper San Marcos River during 2007

Taxon	Frequency of occurrence (%)	Mean percentage by weight (%)
Ephemeroptera	29.6	12.9
Baetidae	6.5	1.9
Heptageniidae	0.9	0.1
Isonychiidae	0.9	0.2
Leptophlebiidae	3.7	0.7
Unidentified	17.6	10.0
Diptera	62.9	16.4
Chironomidae	62.0	16.4
Tipulidae	0.9	<0.1
Lepidoptera	7.4	2.6
Pyrilidae	7.4	2.6
Hemiptera	4.6	1.4
Macroveliidae	0.9	0.0
Naucoridae	2.8	1.1
Veliidae	0.9	0.3
Trichoptera	17.7	4.3
Glossosomatidae	0.9	0.1
Hydrobiosidae	2.8	1.4
Hydroptilidae	2.8	0.4
Leptoceridae	0.9	0.1
Philopotamidae	2.8	0.2
Polycentropodidae	1.9	0.9
Unidentified	5.6	1.2
Odonata	7.4	5.0
Coenagrionidae	7.4	5.0
Coleoptera	7.4	4.4
Hydrophilidae	7.4	4.4
Acari	2.8	0.1
Hydrachnidia	2.8	0.1
Terrestrial insects	20.4	9.0
Insect parts	12.0	5.3
Vegetation/algae	8.3	2.8
Cestoda	3.7	2.0
Digested matter	45.4	33.9

POPULATION STRUCTURE

Mean SL (\pm SD) was 41.9 (\pm 4.4) mm and ranged 31–52 mm. Monthly modal progression analysis indicated *Notropis chalybaeus* in the upper San Marcos River lived approximately 2.5 y. Four age groups (ages 0–3) were present with mean (\pm SD) SL of 33 (\pm 1) mm for age 0, 39 (\pm 3) mm for age 1, 44 (\pm 3) mm for age 2, and 49 (\pm 1) for age 3 (Fig. 2). Age-0 individuals reached a maximum SL of 35 mm, Age-1 reached 46 mm, Age-2 reached 50 mm, and Age-3 reached 52 mm. *Notropis chalybaeus* exhibited growth during spring and summer, but SL had low variation among months during fall and winter.

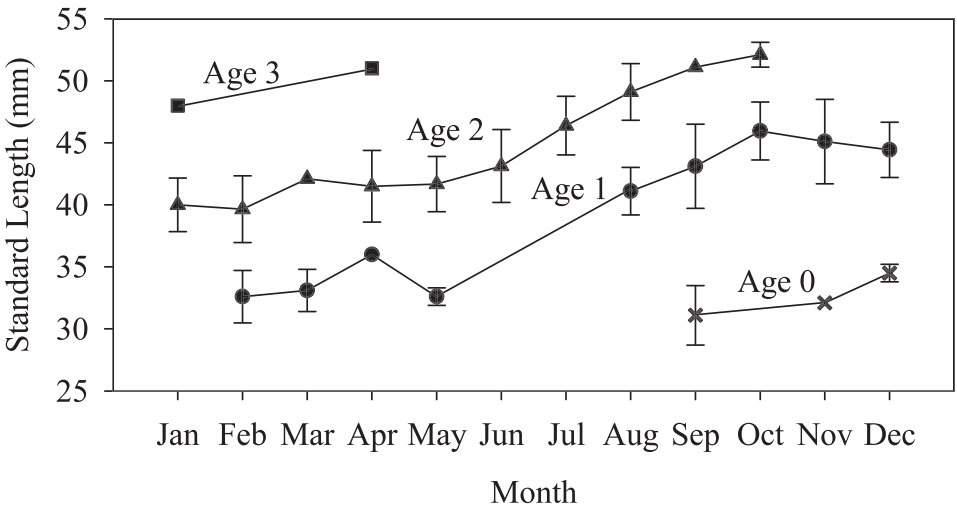


FIG. 2.—Monthly mean (\pm SD) standard lengths (mm) for Age 0, Age 1, Age 2, and Age 3 *Notropis chalybaeus* collected from the upper San Marcos River during 2007

REPRODUCTIVE ECOLOGY

The overall ratio of male to female *Notropis chalybaeus* collected was 0.5:1 and differed significantly from the expected ratio of 1:1 ($X^2_1 = 10.9$, $P < 0.01$). Temporal patterns in mean GSI and oocyte diameter collectively suggested a prolonged spawning season ranging Mar. to Dec., when multiple clutches were spawned. Elevated mean GSI for males (*i.e.*, $>0.5\%$) ranged Apr.–Dec. and peaked at 1.6% during Jul. Elevated mean GSI for females (*i.e.*, $>3.0\%$) ranged Mar.–Dec. and peaked at 8.0% during Jun. (Fig. 3). Minimum SL at sexual maturation was 36 mm for a female collected during Mar. 2007, suggesting age at maturation was approximately 1 y. Frequency distributions of 100 randomly measured oocytes indicated multiple modes within individuals, and mature oocytes (minimum mean diameter = 0.63 mm) were present in reproductively mature females during Mar.–Dec. (Fig. 4). Mean (\pm SD) mature oocyte diameter was 0.78 (± 0.1) mm among 20 mature females (SL range: 39–52 mm) included in measurements.

Reproductive ecology of *Notropis chalybaeus* populations differed in a comparison of the upper San Marcos River of central Texas and Marshalls Creek of eastern Pennsylvania. Mean diameter of vitellogenic oocytes differed ($T_{38} = 16.87$, $P < 0.01$) between the San Marcos River (mean \pm SD = 0.78 \pm 0.1; range = 0.63–1.02) and Marshalls Creek (mean \pm SD = 1.26 \pm 0.1; range = 1.16–1.39; Leckvarcik, 2001). Standard length of reproductively mature females also differed ($T_{38} = 10.48$, $P < 0.01$) between the upper San Marcos River (mean \pm SD = 44 \pm 3; range = 40–52) and Marshalls Creek (mean \pm SD = 32 \pm 4; range = 26–41). However, the number of mature oocytes in reproductively mature females did not differ ($T_{38} = 1.57$, $P = 0.1$) between the upper San Marcos River (mean \pm SD = 95 \pm 43; range = 46–326) and Marshalls Creek (mean \pm SD = 121 \pm 58; range = 40–290). Whereas SL of mature females was generally larger and mean mature oocyte diameter smaller in the San Marcos River, the relationship (*i.e.*, slope) between SL and number of mature oocytes did not differ among populations (ANCOVA $F_{1,37} = 0.03$, $P = 0.9$; Fig. 5a) nor did the relationship between SL and mean mature oocyte diameter (ANCOVA $F_{1,37} = 2.29$, $P = 0.14$; Fig. 5b).

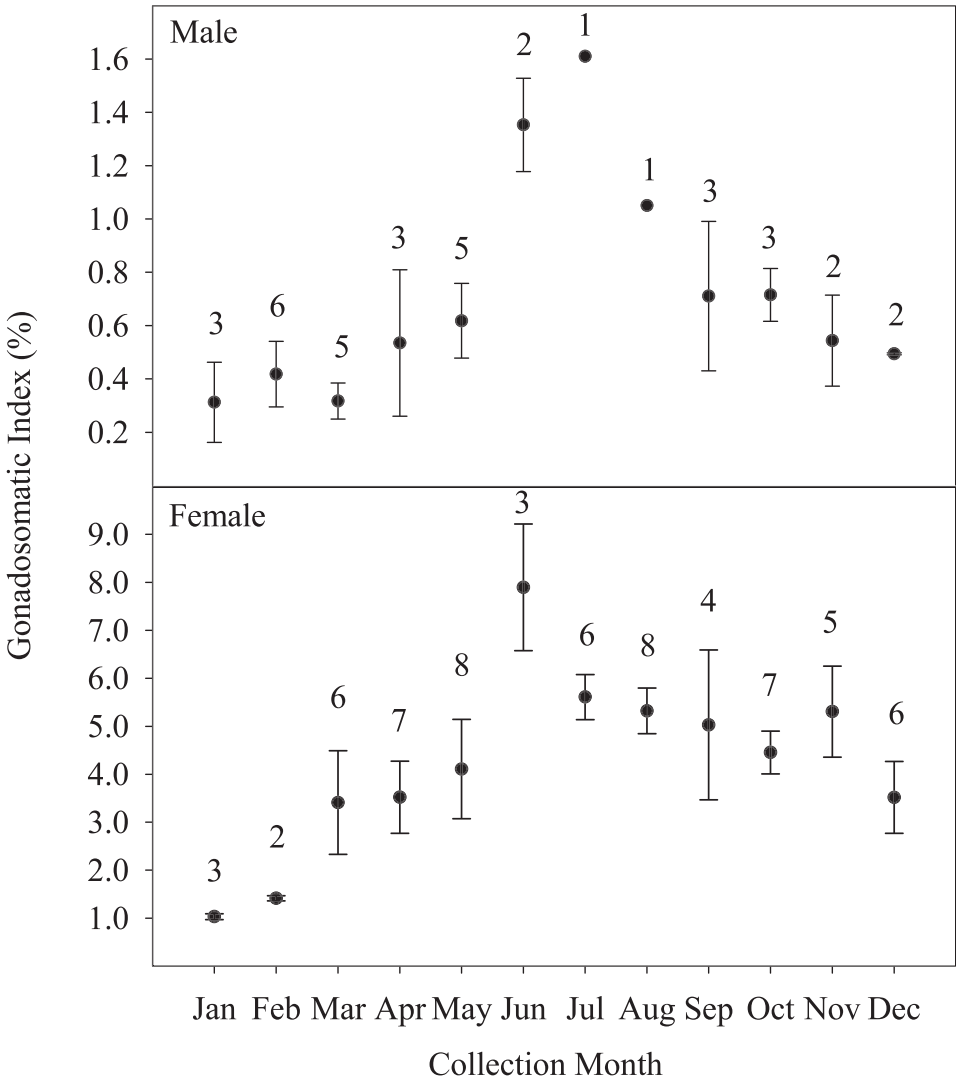


FIG. 3.—Mean (\pm SE) gonadosomatic indices for male and female *Notropis chalybaeus* collected from the upper San Marcos River during 2007. Numbers above error bars represent number of individuals (Age-0 individuals were removed from analysis)

Population-level comparisons of reproductive ecology for locations other than Marshalls Creek were restricted to available published literature. Consequently, comparisons were limited to reproductive season length and oocyte diameters. Accounts of reproductive season lengths among eight localities suggested a latitudinal pattern in reproductive season length. Seasons were relatively shorter among northern populations sampled in Michigan (Jun.–Jul.; MNTC, 2007) and Illinois (late May–Jul.; Smith, 1979) but generally increases in a southerly direction for populations in Pennsylvania (May–Jul.; Leckvarcik, 2001),

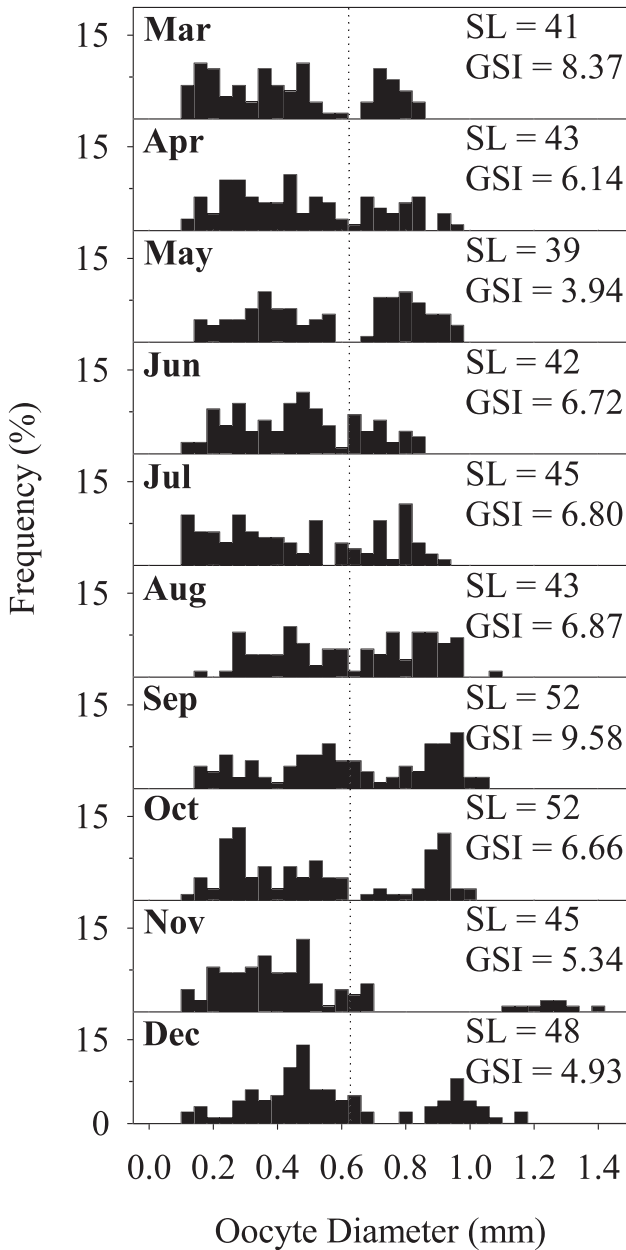


FIG. 4.—Oocyte distributions for reproductively mature female *Notropis chalybaeus* collected from the upper San Marcos River during 2007. SL represents standard length measured in mm; GSI is gonadosomatic index (see text for calculation). Histograms were created from randomly measured oocytes (n = 100) in the left ovary of reproductively mature females. Vertical dotted line represents the smallest observed mean diameter of vitellogenic oocytes (*i.e.*, 0.63 mm; see Fig. 5b)

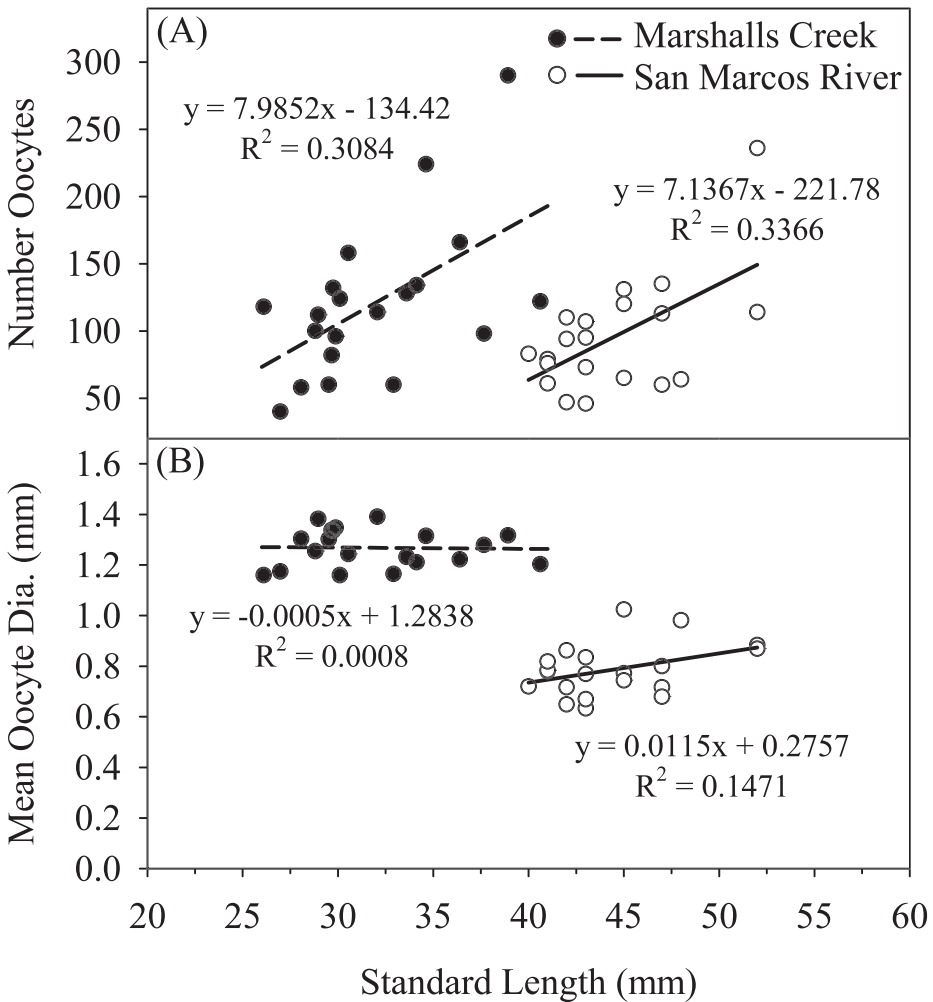


FIG. 5.—Number of mature oocytes (A) and mean mature oocyte diameter (B) as functions of standard length for 20 female *Notropis chalybaeus* collected from the upper San Marcos River, Texas during 2007 and Marshalls Creek, Pennsylvania during 2000. Values for Marshalls Creek are from Leckvarcik (2001; with permission)

Northern Georgia (May–Jun.; Marcy *et al.*, 2005), Alabama (Apr.–Aug.; Boschung and Mayden, 2004), Northern Florida (Apr.–Jul. or Aug.; Swift *et al.*, 1977), and Southern Florida (Apr.–Sep.; Marshall, 1947). The upper San Marcos River population did not follow this trend (Fig. 6). Becker (1983) reported mature oocytes ranged 0.7–0.8 mm in diameter for a single individual collected from an unknown stream in Scott County, Missouri but did not provide an estimate of reproductive season length. Among studies reporting mature oocyte diameters and reproductive season lengths, diameters (mm) were generally larger in populations with shorter reproductive seasons ($n = 4$, $r = 0.86$), including Pennsylvania (3 mo, 1.3 mm; Leckvarcik, 2001), Northern Florida (4 mo, 1.0 mm; Marshall, 1947),

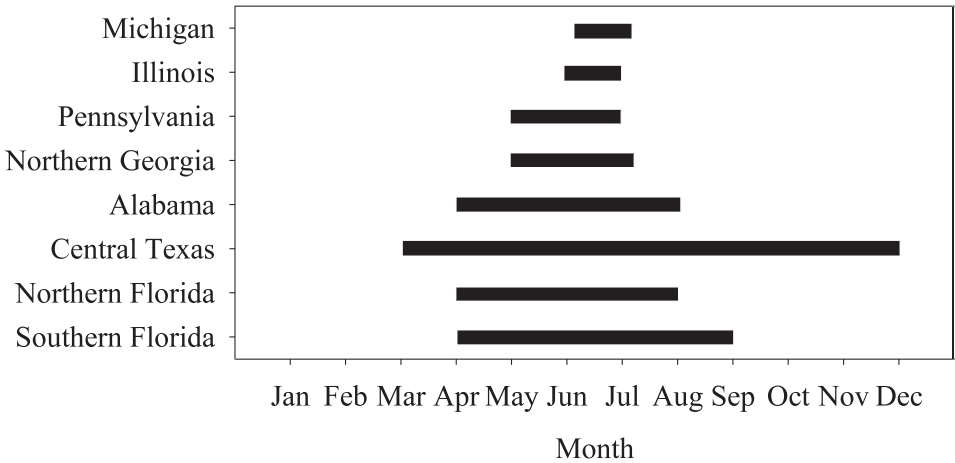


FIG. 6.—Range of reproductive seasons for ironcolor shiner populations sampled from states arranged along a latitudinal gradient. References are Michigan (MNFI, 2007), Illinois (Smith, 1979), Pennsylvania (Leckvarcik, 2001), Northern Georgia (Marcy *et al.*, 2005), Alabama (Boschung and Mayden, 2004), Central Texas (this study), Northern Florida (Swift *et al.*, 1977), and Southern Florida (Marshall, 1947)

southern Florida (6 mo, 0.9 mm; McClane, 1955), and the upper San Marcos River (10 mo, 0.78 mm; this study).

DISCUSSION

Longitudinal distribution of *Notropis chalybaeus* is apparently limited to a 2.2 km reach of the upper San Marcos River, upstream of the IH-35 crossing. Conversations with the late Clark Hubbs (University of Texas) revealed that this distribution closely follows that of the spring-associated largespring gambusia *Gambusia geiseri*. These patterns of restricted range might reflect specific adaptations to water chemistry (*e.g.*, *G. geiseri* is considered stenothermal; Hubbs and Springer, 1957) or habitat parameters that occur only in the spring-dominated upper reaches of the San Marcos River. Furthermore, the dense aquatic macrophyte community in the upper San Marcos River is diverse and likely provides increased habitat heterogeneity in the form of cover and predator refugia (Lemke, 1989; Owens *et al.*, 2001). This may be of particular relevance to *N. chalybaeus* habitat use and reproduction, as individuals in the species seek refuge within submerged aquatic vegetation and spawn adhesive eggs that adhere to gravel or sand substrate adjacent to vegetative stands (Marshall, 1947; Robinson, 1977; Simon, 1999; Leckvarcik, 2001). Greater turbidity and incised and deeper stream channel downstream of IH-35 likely contribute to a decrease in macrophyte abundance (Lemke, 1989; Groeger *et al.*, 1997), which may be an important factor in determining the distribution of *N. chalybaeus* (Robinson, 1977).

Restricted range within a stenothermal reach of stream likely has implications for the observed protracted spawning season of *Notropis chalybaeus* in the upper San Marcos River. The relative roles of water temperature and photoperiod in structuring reproductive seasons of fishes have been discussed (*e.g.*, de Vlaming, 1974), largely because it is difficult to partition covariation between the two parameters. Hubbs (1985) was among the first to suggest increasing day lengths initiated reproductive activity among three species of

Percidae, and that termination of spawning season was likely driven by reductions in water temperature. Similarly, Leckvarcik (2001) suggested reproductive seasonality for *N. chalybaeus* in Marshalls Creek was initiated by photoperiod and terminated by declining water temperatures. This pattern resulted in inter-annual variation in reproductive season length among the years 1999, 2000, and 2001, when variation in mean summer water temperature corresponded with variation in reproductive season lengths (Leckvarcik, 2001). Consequently, the lack of dynamic fluctuations in water temperature in the upper San Marcos River likely contributed to the observed protracted reproductive season by effectively removing the cue to return to gonadal quiescence. This is particularly evident in the visibly skewed pattern of GSI distributions presented in Figure 3. Rather than a Gaussian distribution, our GSI distributions were skewed toward the latter half of the reproductive season, suggesting prolonged gonadal recrudescence after a peak in reproductive intensity. Distributions of GSI for multiple-clutch spawning cyprinids inhabiting thermally dynamic streams generally exhibit a sharp decline following the height of reproductive intensity (e.g., Williams and Bonner, 2006). Accordingly, we believe the protracted spawning season, and consequently altered reproductive ecology of *N. chalybaeus* in the upper San Marcos River are artifacts of abiotic environmental factors, primarily lack of a terminating cue driven by stenothermal water.

Variations in water temperature likely act to structure reproductive seasonality along a latitudinal gradient and within spring-run environments. Reproductive season length correlated with latitude among 21 species of North American cyprinids analyzed by Gotelli and Pyron (1991), so that season lengths in northern latitudes were shorter. Our findings for ironcolor shiner were consistent with this pattern, with the notable exception of the San Marcos River. These patterns might reflect non-adaptive plasticity in life history attributes arising from responses to environmental characteristics, in this case water temperature. In reviewing the ability of studies to detect adaptive versus non-adaptive plasticity, Gotthard and Nylin (1995) suggested proceeding with additional methodologies including reciprocal transplant of organisms to evaluate responses to environments. Such methods were beyond the scope of this study. However, we believe our findings do allude to evidence for life history adaptation among spring-dwelling fishes that encounter stenothermal water. We detected a trade-off in reproductive season length and size of mature oocyte diameter among ironcolor shiner populations, a pattern that has been reported for fishes in families Cyprinidae (Heins and Baker, 1987), Percidae (Hubbs, 1985; Folb, 2010), and Salmonidae (Lobon-Cervia *et al.*, 1997). In general, fishes inhabiting relatively more thermally stable environments tend to have smaller oocyte or egg diameters. These trade-offs might represent transitional adaptations towards a more equilibrium-type life history strategy (Winemiller and Rose, 1992) because of the inherent stability of spring-fed streams and may provide a basis for why size selection within fishes does not necessarily follow a strict latitudinal gradient (Perez and Munch, 2010; *i.e.*, spring-run environments occur among most latitudes).

Notropis chalybaeus in the upper San Marcos River fed on a diversity of insect prey items that varied with season. In Marshalls Creek, small crustaceans (*i.e.*, Cladocera) constituted >50% of prey items (Leckvarcik, 2001), whereas larger insects constituted >60% by mean weight of prey items over the course of the present study. Insect prey items provide greater energy availability relative to small crustaceans for insectivorous cyprinids such as *N. chalybaeus* (Marshall, 1947) and may have contributed to the greater growth rates, overall size, and potentially greater overall fecundity observed among San Marcos River *N. chalybaeus*. Interestingly, food items consumed during the summer were similar among San

Marcos River and Marshalls Creek populations. Both contained large amounts of detritus and algal material. Marshall (1947) suggested abundance of algae in intestinal tracts of *N. chalybaeus* in Florida was an artifact of algae ingested by crustaceans, which were preyed upon by *N. chalybaeus* during summer months. This conclusion is consistent with our finding of ~85% by weight of algae and detritus in intestinal tracts of *N. chalybaeus* collected between Jun. and Aug. of 2007, and Leckvarcik's (2001) finding that crustaceans constituted 83–85% by number of prey items for *N. chalybaeus* collected from Marshalls Creek during May and Jun. of 2001. *Notropis chalybaeus* are opportunistic invertivore foragers (Goldstein and Simon, 1999), which likely explains supplemental foraging on terrestrial insects and insect parts during fall and spring months in the upper San Marcos River.

Narrowly distributed and disjunct populations of *Notropis chalybaeus* are listed as imperiled throughout the range of the species, including the upper San Marcos River of central Texas (Hubbs *et al.*, 2008; Jelks *et al.*, 2008). Within the upper San Marcos River, long-term stability of *N. chalybaeus* (*i.e.*, 1938–2006; Perkin, 2009) might be related to the close management of the San Marcos Springs as an ecologically sensitive environment and limited aquifer pumping in the region (McCarl *et al.*, 1999). The upper San Marcos River is also inhabited by the endangered fountain darter *Etheostoma fonticola*, which also may require a continually flowing and thermally stable environment (McDonald *et al.*, 2007). Interestingly, Swift (1970) noted fountain darters were historically widely distributed among Western Gulf Slope drainages, but long-term (*i.e.*, circa the last period of glaciation) isolation in the headwater reaches of the San Marcos and Comal rivers resulted in specific divergence. Genetic analysis of *N. chalybaeus* in the upper San Marcos River has not been conducted, but our patterns in life history divergence coupled with morphometric differences from Swift (1970; *i.e.*, additional vertebra and pectoral fin ray) suggest this population may be unique. Although the Endangered Species Act indirectly protects this potentially unique population because of distributional similarities with the fountain darter, future causes for concern exist. Construction of impoundments and alteration of flow and thermal regimes that are not directly associated with aquifer depletion (*e.g.*, watershed and instream impoundments; Perkin and Bonner, 2011) may cause shifts in ecosystem structure that negatively influence the abundance and distribution of *N. chalybaeus* (Hubbs and Pigg, 1976; Bowles and Arsuffi, 1993). Accordingly, continued monitoring of *N. chalybaeus* population trends in the upper San Marcos River is a potentially useful conservation approach.

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