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Effects of Habitat Utilization on the Life Histories of Two Imperiled, Sympatric Dionda (Cyprinidae) in the Rio Grande Basin, Texas

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ABSTRACT.—The genus Dionda consists of at least 12 species, of which most inhabit spring-dominated streams within the western Gulf slope drainages of North America and demonstrate some differences in habitat selection within these systems. The purpose of this study was to assess the influence of stenothermal spring or eurythermal stream habitat selection on the life history strategies of the stream-associated Dionda argentosa, a population of Dionda diaboli restricted to the spring influenced portions of Pinto Creek (Kinney County, Texas), and a population of D. diaboli utilizing stream habitats in the Devils River (Val Verde County, Texas). While differences in spawning seasons between the two species were noted, all three populations displayed life histories characteristic of opportunistic strategists including early maturation, long spawning seasons, production of multiple batches of oocytes, and short lifespans (<3 y). Differences in reproductive season between the spring- and stream-associated Dionda were consistent with the hypothesis stenothermal waters of springs lack terminating cues to induce gonadal quiescence in fishes.

INTRODUCTION

Fishes inhabiting karst landscapes are classified as spring- or stream-adapted forms (Hubbs, 1995, 2001). Spring-adapted fishes are located within close proximity to spring outflows and are subject to relatively stable physical and chemical environments when compared to their river-adapted counterparts. Differences in life history strategies have been documented for congeners inhabiting spring versus stream habitats (Hubbs, 1985; Perkin et al., 2012). Factors such as temperature regime and productivity have been shown to affect life history traits (Hubbs, 1985; Gotelli and Pyron, 1991), two things that often vary between stream and spring habitats of karst systems.

Species within the genus Dionda (Cyprinidae) predominately inhabit karst landscapes within western Gulf Slope drainages of North America. Many Dionda species have been classified as spring-adapted or spring-associated (Hubbs, 2001; Hubbs et al., 2008; Kollaus and Bonner, 2012); however, for at least one species that classification may not hold true. The federally threatened Devils River Minnow Dionda diaboli (USFWS, 1999) has historically been classified as having an association with spring habitats (Hubbs and Garrett, 1990; Edwards, 1999; USFWS, 1999). While this species is restricted to spring-fed streams, recent research has shown it sometimes inhabits eurythermal sites away from spring outflows in the Devils River (Val Verde County, Texas) (Kollaus and Bonner, 2012), which is not in keeping with the definition of a spring-associated species.

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**Dionda diaboli** is one of the few *Dionda* species known to have an overlapping distribution with its congeners. *Dionda diaboli* co-occurs with the imperiled Manantial Roundnose Minnow *Dionda argentosa* in the Devils River and San Felipe Creek (Val Verde County, Texas; Bender *et al*., 2005; Hubbs *et al*., 2008). While there have been no published comparisons of habitat use for these species in San Felipe Creek, *D. diaboli* and *D. argentosa* have been documented to partition habitats in the Devils River (Kollaus and Bonner, 2012). When stenothermal spring habitats and eurythermal stream habitats are concurrently accessible in the Devils River, *D. diaboli* selects stream habitats and *D. argentosa* selects spring habitats (Kollaus and Bonner, 2012).

*Dionda diaboli* also occur in one stream within the United States outside of the range of other *Dionda* species (Pinto Creek: Kinney County, Texas). In Pinto Creek *D. diaboli* are limited to the headwaters region, in close proximity to multiple spring outflows (Brune, 1981; Garret *et al*., 2004). While there have been no quantitative habitat utilization studies for *D. diaboli* in Pinto Creek, due to the creek’s small size and numerous spring outflows, it is presumed the habitats *D. diaboli* utilizes there are stenothermal. Therefore, differences in habitat availability between the Devils River and upper Pinto Creek offer a unique opportunity to elucidate life history strategies among *D. diaboli* inhabiting spring versus stream habitats. The Devils River also offers the opportunity to document differences in life history strategies between two congeners, *D. diaboli* and *Dionda argentosa*, in a karst system where they concurrently have access to stream and spring habitats.

The objective of this study was to quantify aspects of life histories (i.e., reproductive period, oocyte size, fecundity) for two populations of *Dionda* utilizing spring habitats (*Dionda argentosa*, Devils River; *Dionda diaboli*, Pinto Creek) and one population of *Dionda* utilizing stream habitats (*D. diaboli*, Devils River). Species residing in spring habitats have often been shown to have prolonged or continuous spawning due to the lack of temperature cues to terminate reproduction; therefore, we predict the *D. diaboli* population restricted to spring-influenced waters of Pinto Creek and the spring-associated *D. argentosa* would have similar life history strategies, including a longer reproductive season than the population of *D. diaboli* utilizing eurythermal habitats of the Devils River.

**METHODS**

**STUDY SITES**

The study site on Pinto Creek (site 3) was located on private land in Kinney County, Texas (Fig. 1). Pinto Creek is approximately 55 km in length, spring-fed, and part of the Rio Grande drainage. The upper reaches of Pinto Creek are fed by at least four major spring outflows, known collectively as Pinto Springs, which originate from the Edwards Aquifer (Ashworth and Stein, 2005). The upper two springs did not flow during the study period; therefore, the headwaters of Pinto Creek came from the downstream spring outflows, located just upstream of the study site. The lower half of Pinto Creek is supplied by a different aquifer, has greater total dissolved solids than the upper reaches, and supports a different fish community (Brune, 1981; Garret *et al*., 2004). *Dionda diaboli* are restricted to the upper portions of Pinto Creek (Garrett *et al*., 2004), which is one of two stream segments identified as critical habitat (Pinto Creek Unit, Kinney County, Texas and San Felipe Creek Unit, Val Verde County, Texas) by the United States Fish and Wildlife Service (2008). The upper reaches of Pinto Creek lack a continuously monitored stream gage; however, observations made during this study and previous studies indicate portions of Pinto Creek are intermittent with some outflows within the Pinto Springs complex occasionally ceasing to flow (Schindel *et al*., 2007; USFWS, 2008; TWDB, 2009). Historically, Pinto Springs has
had discharge sufficient to maintain enduring pools and some flowing water habitats containing persistent populations of *D. diaboli* and other fishes (Garrett *et al.*, 2004).

There were two study sites on the Devils River, both located near the Texas Parks and Wildlife Department-Devils River State Natural Area Del Norte Unit. The upper site was located about 1 km upstream from spring outflows (site 1, N 29.903577°, W -101.005907°) and the lower site was adjacent to Finegan Springs (site 2, N 29.90002°, W -100.998281°), a large spring complex flowing into the Devils River (Brune, 1981; Fig. 1). The Devils River, also in the Rio Grande drainage, is approximately 95 km in length and fed through multiple spring sources along its length (Brune, 1981). Due to the river’s large size and numerous spring inputs, the Devils River contains more heterogeneous habitats, a more stable water supply, and a more diverse fish community than Pinto Creek (Garrett *et al.*, 2004; IBWC, 2006; Kollaus and Bonner, 2012).

**COLLECTIONS**

*Dionda diaboli* were collected from site 1 on the Devils River site and from site 3 at Pinto Creek (Fig. 1). *Dionda argentosa* do not occur in Pinto Creek and occurred only in low abundance at site 1 on the Devils River during the study; therefore, they were primarily collected from the downstream Devils River site (site 2). All fishes were collected monthly from September 2009 to August 2010. At each site, short seine hauls (less than 5 m in length) were conducted until either 100 individuals of each species were captured, or

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**FIG. 1.—Map of study sites.** The Devils River upper (1) and lower (2) sites were located at the Devils River State Natural Area in Val Verde County, Texas. The Pinto Creek site (3) was located on private property in Kinney County, Texas.
a minimum of 20 individuals of each species were captured and 1 h of effort was expended. Among fish collected 10 fish of estimated reproductive size (>25 mm SL; Harrell, 1980) of each species were retained for reproductive analysis, euthanized using tricaine methane-sulfonate (MS-222), and fixed in 10% formalin. A maximum of 10 fish was retained per species, per site, in order to minimize negative impacts on the populations of these imperiled species. Remaining individuals were measured for total length (mm) and released unharmed. At each location of fish capture, water temperature was taken and used as a surrogate for spring influence. With increasing spring influence, a decrease in the range of annual temperatures was noted.

POPULATION STRUCTURE AND REPRODUCTIVE CHARACTERISTICS

Length frequency histograms were constructed by pooling total length data from all fish captured by species, site, and month. Lengths were put into 2 mm bins and plotted as histograms. Length frequency histograms were visually assessed and assigned age groupings based on methods from Murphy and Willis (1996). This method assumes total lengths for fish of the same cohort will be unimodally distributed; therefore, multiple modes from a given sample represent multiple age classes of fish. Modal class progression analysis, the Bhattacharya method (FiSAT II, Version 1.2), was used to validate assigned age groupings and determine mean monthly lengths for each age classification of each species at each site.

In the laboratory gonadosomatic indices (GSI) [(gonad weight/total weight)*100] were calculated for all retained Dionda, and ovarian condition (i.e., immature, developing, mature, spent) was determined for females using methods from Williams and Bonner (2006). The presence of elevated GSIs and mature, vitellogenic oocytes was used to estimate reproductive season in weeks for each population of fishes. GSIs were pooled by species, site, sex, and month to assess reproductive trends. A Pearson product moment correlation (α = 0.05) was used to determine if average monthly male and female GSIs for each species and site combination were correlated and, if so, the nature of the correlation. To assess fecundity and oocyte development, up to three mature females of each species were randomly selected from each site during each month when reproductively mature females were present and oocyte diameters were measured. Following methods from Williams and Bonner (2006), the left ovary was removed from each female and placed in a petri dish with water. If the left ovary was remarkably reduced in size, the right ovary was used in its place. Forceps were used to separate oocytes and then the dish was swirled to uniformly distribute them throughout the dish. Using a disecting microscope with a digital micrometer, oocytes were measured along their longest axis to the nearest 0.05 mm. Histograms were constructed to assess the size distribution of oocyte diameters in each female. Batch fecundities were estimated by counting all the mature, vitellogenic oocytes in the left ovary of each of the selected females. This number was then extrapolated using total gonadal weight to get a total batch fecundity estimate using the weights of the ovaries. Analysis of covariance was used to assess differences in clutch sizes between the three populations of Dionda using fish total length as a possible confounding factor. All tests were considered significant at alpha = 0.05.

RESULTS

From September 2009 to August 2010, total lengths were taken from 1350 Dionda diaboli (Pinto Creek: 644, Devils River: 706) and 713 Dionda argentosa. Populations of D. diaboli consisted of two age groups (ages 0 and 1) and D. argentosa consisted of three (ages 0, 1 and 2; Fig. 2). Age 0 fish were first detected in March and April for all three populations.
Gonads were extracted from 234 *Dionda diaboli* (Pinto Creek: 113, Devils River: 121) and 122 *Dionda argentosa*. Reproductive seasons occurred primarily from winter to summer among *D. diaboli* and year-round among *D. argentosa* (Fig. 3). The onset of the reproductive season coincided with increased photoperiod and water temperature and reproductive season termination coincided with extreme warm summer water temperatures (> 27°C) for both *D. diaboli* populations (Fig. 4). Reproductive season for *D. argentosa* did not terminate during the period of this study. It was noted that a higher proportion of mature females with high GSIs was collected in waters at or near spring temperatures (i.e., October, February, March, April, May; Fig. 4). Developing or mature ovaries occurred as late as August and September in Pinto Creek and the Devils River among *D. diaboli* identified as age 0. With respect to both age groups, the smallest lengths of mature *D. diaboli* were 39 mm in Pinto Creek and 42 mm in the Devils River. Male *D. diaboli* GSIs were positively correlated with female GSIs in Pinto Creek (r = 0.86, df = 9, P < 0.01) and in the Devils River (r = 0.74, df = 9, P < 0.01). The smallest length of mature *D. argentosa* was 45 mm. Male *D. argentosa* GSIs were positively correlated (r = 0.62, df = 9, P = 0.04) with female GSIs.

Ovaries consisted of oocytes with multiple size classes in *Dionda diaboli* and *Dionda argentosa* throughout their reproductive season. Estimated mean clutch size (±1 SD) for
D. diaboli was 107 oocytes (±66.4) in Pinto Creek and 147 oocytes (±97.8) in the Devils River. Estimated mean clutch size for D. argentosa was 166 oocytes (±119.9). While total fish length had a significant effect on clutch size (P < 0.001), estimated clutch sizes did not differ between the three populations of Dionda (F2,55 = 2.809, P = 0.069).

**DISCUSSION**

Both species of Dionda matured quickly, were short lived, produced multiple batches of oocytes within a spawning season and had a similar number of oocytes per batch. The major finding of this study was evidence of differences in reproductive season length between species based on the presence of elevated GSIs and mature oocytes. Spring-associated D. argentosa had a longer reproductive season (12 mo) than Devils River D. diaboli taken from eurythermal waters (8 mo) as predicted. Due to drought conditions (National Drought Mitigation Center, 2015) and low spring flows into Pinto Creek (estimated at <1 cfs during portions of the study), D. diaboli in that system were restricted to eurythermal waters throughout the study (13 to 25 C). This prevented testing of the hypothesis that D. diaboli would exhibit differences in life history strategies when utilizing spring versus stream habitats. Instead, the Pinto Creek D. diaboli population served as a replicate of the Devils River D. diaboli population (inhabiting water temperatures of 13 to 28 C) and both displayed similar life history strategies.

No distinct reproductive season occurred in D. argentosa; however, peaks in gonadosomatic indices and the proportion of mature females among total females collected coincided with times when individuals were collected closest to spring temperatures (22-23 C),
suggesting the possibility of an optimal, but not limiting, reproductive temperature (Schenck and Whiteside, 1977; Bonner et al., 1998). The prolonged spawning season of *D. argentosa* was approximately 28 w longer than predicted for cyprinids residing within this latitude (Gotelli and Pyron, 1991). Continuous or near-continuous spawning as shown in this study in *D. argentosa* is a rare reproductive strategy in temperate and subtropical North American freshwater fishes (Folb, 2010). Seasonal spawning (<8 mo) is thought to coincide with periods of abiotic stability, optimal conditions to lessen interspecific competitions, and synchronization of spawning aggregates (Bye, 1984). If reproduction truly coincides with these factors, stenothermal environments, such as spring systems, would negate the need for seasonal spawning and make continuous spawning favorable. While mature *D. argentosa* were found in spring-runs adjacent to spring outflows, a few individuals were collected in eurythermal waters, making it unclear if stenothermal habitats are a necessity for reproduction or are instead selected for as part of an overall life-history strategy to produce more batches of oocytes.

In contrast both populations of *Dionda diaboli* had a defined reproductive season from winter to summer with reproductive timing correlated to changes in photoperiod and water temperature (Fig. 4). Reproductive season length for *D. diaboli* was within the expected range for the latitude at which they were collected (Gotelli and Pyron, 1991). Reproductive characters of *D. diaboli* support previous qualitative assessments of this species in the wild (Garrett et al., 2002; Lopez-Fernandez and Winemiller, 2005) but differ from laboratory results. In captivity *D. diaboli* spawned at spring-associated temperatures ranging from 18 to 22 C and photoperiods ranging from 10 to 12.5 h of light per day (Gibson et al., 2004; Gibson and Fries, 2005). In the wild we found evidence of reproductive activity at a much wider range of temperatures and photoperiods (16-27 C; 10-14 h/d). The termination of *D. diaboli*’s spawning season in late summer supports the hypothesis that reproduction in some species terminates seasonally in avoidance of extreme warm temperatures which might reduce larval survival (Hubbs, 1985; Houde, 1989; Green and Fisher, 2004). This study supports previous habitat assessments by Kollaus and Bonner (2012) which showed *D. diaboli* is more temperature tolerant than previously thought. It does not appear spring outflows are essential to reproduction in *D. diaboli*, nor were *D. diaboli* found using habitats directly adjacent to them. However, *D. diaboli* are restricted to karst streams, which points...
to the possibility these systems provide *D. diaboli* something necessary for their persistence (Garrett et al., 2004; Schönhuth et al., 2012).

Multiple-modal histograms of oocyte diameter distributions indicate synchronous batch spawning in all three *Dionda* populations. Synchronous batch or group spawning is characterized by females who spawn multiple clutches of eggs during a reproductive season, have a heterogeneous pool of developing oocytes, and have a distinctly larger batch of synchronously developing mature oocytes (Heins and Baker, 1988, 1989; Taylor and Miller, 1990). Synchronous batch spawning is common among fishes found in environments with fluctuating hydrographs or eurythermal conditions and is often attributed to an increased probability that at least a proportion of the total spawn will survive to maturity (Weddle and Burr, 1991; Rinchard and Kestemont, 1996; Durham and Wilde, 2008). However, synchronous batch spawning can also be found in stenothermal waters (Schenck and Whiteside, 1977; Perkin et al., 2012); therefore, selection for this reproductive scheme does not seem to be an adaption to a specific hydrology or temperature regime. Other possible mechanisms for the development of synchronous batch spawning are competition avoidance for favorable reproductive sites (Gale and Gale, 1977) or an attempt to maximize reproductive output in a small-bodied species (Hubbs et al., 1968; Schenck and Whiteside, 1977), either of which could apply to these populations of *Dionda*. Clutch fecundity estimates were not different between the three populations of *Dionda*; however, *Dionda argentosa* produced larger oocytes which accounted for higher GSIs. Due to the extended spawning season of *D. argentosa* and similar batch fecundities between the species, overall reproductive output is likely higher in *D. argentosa* than in *Dionda diaboli*, although this is dependent on spawning frequency which is often constrained by food availability (Williams, 1959; Hubbs et al., 1968; Constantz, 1979). Several previous fish assemblage assessments of the Devils River have reported higher relative abundances of *D. argentosa* as compared to *D. diaboli* (Cantu and Winemiller, 1997; Robertson and Winemiller, 2003; Kollaus and Bonner, 2012), further supporting the hypothesis *D. argentosa* has an overall higher reproductive output.

Overall, both species demonstrated similar life history strategies defined by early maturation, a long spawning season, production of multiple batches of oocytes, and a short lifespan. These characteristics are representative of what Winemiller and Rose (1992) identified as opportunistic strategists. As seen in this study, opportunistic strategists tend to invest more energy into producing multiple batches of oocytes laid over a long spawning season than into parental care to increase the odds of successful recruitment. These short-lived species usually have high population turnover and, as such, each spawning year is critical to maintaining individual populations. With the need to have a successful spawn every year, it is evident habitat partitioning is a potentially important strategy for these two species who otherwise share similar life history traits (Wheeler and Allen, 2003; Robertson et al., 2008).

Results from this study indicate water temperature as a controlling abiotic factor in *Dionda* reproduction. As such, the habitat partitioning between spring and stream habitats seen in *Dionda diaboli* and *Dionda argentosa* plays an important role in the life history strategies of these two species. With drought and increased groundwater demand throughout the ranges of these fishes, the stability of spring outflows in these systems is uncertain. Understanding the habitat uses and life history strategies for these species in spring-flow dependent karst systems will help inform conservation strategies for these populations.

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**LITERATURE CITED**


