Mesohabitat Associations of the Devil Tryonia, Tryonia diaboli (Gastropoda: Truncatelloidea: Cochliopidae)

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REGULAR ARTICLE

MESOHABITAT ASSOCIATIONS OF THE DEVIL TRYONIA, *TRYONIA DIABOLI* (GASTROPODA: TRUNCATELLOIDEA: COCHLIOPIDAE)

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ABSTRACT

The Cochliopidae of Texas include both stygobitic species, those that occupy only underground habitats, and epigean species, those living only in aboveground habitats. The devil tryonia, *Tryonia diaboli*, was described from the Devils River of Texas from river wrack, without additional habitat information. This species has been largely ignored since its description, so details of its habitat and ecology are obscure. In Dolan Springs and Finegan Springs, flowing into the Devils River, we sampled macroinvertebrates at five sites that form a gradient from the aquifer to the mainstem Devils River. We found the highest abundances of *T. diaboli* in aquifer samples, decreasing sharply downstream from the spring orifice. Our findings indicate that *T. diaboli* is stygophilic, occupying a transitional area including the aquifer as well as aboveground portions of springs.

KEY WORDS: stygophilic, spring snail, Devils River, aquifer, conservation

INTRODUCTION

Texas has a largely endemic groundwater- and aquifer-dependent snail fauna (Hershler and Thompson 1992; Hutchins 2018) that are of conservation concern (Johnson et al. 2013). Many species occupy different mesohabitats within the aquatic ecosystems and consequently have varied habitat requirements. They also may vary in their susceptibility to changes in spring flow, such as decreases or cessation of flow. Animals that occupy only groundwater, cave, and aquifer systems are referred to as stygobionts. Stygobitic gastropods typically have morphological adaptations to underground habitats, such as reduced size or pale-colored shells and depigmented bodies (Hershler and Liu 2017). In contrast, stygophiles such as *Fontigens nickliniana* (Hershler et al. 1990) and *Cochliopina riograndensis* may occupy both surface (epigean) and underground habitats and may vary in these morphological features. A recent review on the origins of stygobitic gastropods (Osikowski et al. 2017) summarized many independent and ongoing invasions of subterranean aquatic habitats; however, gastropods occupying both above- and belowground aquatic habitats are uncommon, although this may reflect sampling methods rather than the actual habitat occupancy of the organisms.

The stygobitic snail fauna of Texas includes ∼12 extant species (Johnson et al. 2013; Hutchins 2018), all now considered members of the Cochliopidae (Clark 2019): *Balconorbis uvaldensis*, *Phreatoceras taylori*, eight species of *Phreatodrobia*, *Stygopyrgus bartonensis*, and *Texapyrgus longleyi* (Thompson and Hershler 1991). No members of *Tryonia* are reportedly stygobites. *Tryonia* includes 31 extant species that are broadly distributed across the southwestern United States and Mexico, one species in Florida, one species in Guatemala, and five species endemic to Texas springs. Most *Tryonia* are found in thermal, mineralized springs although a few are found in lakes and one in hypersaline, coastal waters (Hershler 2001). The *Tryonia* of Texas are found in mineralized, but not thermal or hot, springs (Hershler 2001). However, the generic placement of *Tryonia diaboli* has not been reevaluated since it was described in 1906 and former members of the genus *Tryonia* have been removed to

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Figure 1. Image of *Tryonia diaboli* from Finegan Spring, Devils River State Natural Area, Val Verde County, Texas, August 2009. Collected by Randy Gibson. Individual is 1.09 mm in length.

Ipnobius, *Pseudotryonia*, and *Juturnia* (Liu et al. 2001; Hershler et al. 2011b). *Tryonia diaboli* was not included or considered in the most recent systematic revision of the *Tryonia* (Hershler 2001) so its generic placement is uncertain.

The focus of this study is *T. diaboli*, a smooth-shelled species by original description (Pilsbry and Ferris 1906); however, there are several similar gastropods described from the region, differing in shell sculpture. *Texapyrgus longleyi* (Thompson and Hershler 1991) was described as a fully stygobitic species with the animal blind and unpigmented. This species was characterized by having strong spiral lines on the shell and was described from an unnamed spring on the Devils River, just downstream from Slaughter Bend, ~32 km N of Del Rio. Snails were collected using a net across the spring outflow and were not collected on the surface, although the surface rheocrene was sampled (Thompson and Hershler

1991). Another similar and nearby species with strong spiral shell lines is *Tryonia circumstriata* (Leonard and Ho 1960), described from late Pleistocene fossil deposits in the Pecos River, 0.25 mi N of Independence Creek and later discovered living in the lower Diamond Y spring and draw (Pecos River drainage) (Taylor 1987). *Tryonia circumstriata* is distinguished by distinctive shell sculpture of raised spiral threads; however, this trait is variable with some individuals having no spiral sculpture present (Taylor 1987; Hershler and Thompson 1992). This species was documented as epigean, living on soft mud, in a spring run, and it was described as having a pigmented body and head. In this paper, we do not conduct a taxonomic study, but rather describe the habitat associations of individuals that conform to the original description of *T. diaboli*. Therefore, we included in this study only shells that are minute, smooth in sculpture (no spiral lines), with rounded, deeply incised whorls, and with a continuous lip that is barely adnate (touching) with the body whorl at the upper end (Fig. 1). All *T. diaboli* collections were made from the same watershed as the original description (Pilsbry and Ferris 1906). Sampling sites were about 26 km by air or 37 km by river upstream from the type locality of *Te. longleyi* and 220 km SW of the known localities for *T. circumstriata* in the Pecos River drainage.

Except for inclusion on taxon lists (e.g., Burch 1982; Johnson et al. 2013), *T. diaboli* has been ignored since its description, so the details of its habitat are obscure. It was described from "drift débris of the Devil's River, about four miles from its mouth," Val Verde County, Texas, providing no aquatic habitat information. A second locality "on the Rio San Filipe near Del Rio same county" also was mentioned (Pilsbry and Ferris 1906). The shells were described as dead and bleached, from river drift (meaning river wrack, not in drift nets), leaving the mesohabitat associations of the snail unknown.

Tryonia diaboli has a Natureserve conservation status rank of G1 indicating it is globally imperiled (Johnson et al. 2013), but it does not have U.S. federal protection and lacks all pertinent information to support consideration for listing. A recent review of the conservation status of groundwater-dependent Texas invertebrates concluded that spring sites along the Devils River did not have good viability (Hutchins 2018) primarily due to regional groundwater extraction for proposed municipal (Diaz et al. 2018) and industrial purposes (Industrial Economics Incorporated 2008), although elevated nutrient concentrations are also a concern (Moring 2012). In addition, declining flows in nearby springs have led to the extinction (Hershler et al. 2014) of one cochliopid snail, *Juturnia brunei* (Taylor 1987), and the recent federal listing of gastropods at those sites (U.S. Fish and Wildlife Service 2013). Another nearby species, *Tryonia oasiensis*, may be extinct (Hershler et al. 2011a). Spring sites along a 5-kilometer stretch of the lower Devils River and San Felipe Springs in Del Rio are the entirety of the known range of the devil tryonia. In this study, we present localized occurrence records and describe mesohabitat associations for *T. diaboli*.

METHODS

Sampling was conducted in the Devils River, Dolan Creek, and along Finegan and Dolan spring complexes (Fig. 2); the latter are permanent springs flowing into the Devils River in Val Verde County, Texas. Vouchers from Dolan aquifer samples are deposited in the Smithsonian Institution, USNM 1571310. To examine the habitat occupied by *T. diaboli* we sampled across five hydrologically connected ground and surface water zones: aquifer (water flow emerging from spring orifice), spring orifice substrate (substrate up to 1 m directly below the spring orifice), transition zone (the part of the spring run below the spring orifice and traveling toward a river or creek), Dolan Creek, and Devils River. Each one of these zones was considered a mesohabitat, or biologically and physicochemically distinct habitat (Pardo and Armitage 1997), within the overall ecosystem.

Each mesohabitat was sampled using the most appropriate method to accurately quantify its invertebrate community. Compared to epigean habitats, an aquifer provides restricted access to the available habitats within the system. Therefore, sampling for aquifer species requires passive collection of animals over a time interval. The animals captured using this method are living at some unknown depth of the aquifer and have been dislodged or otherwise caught in the water flow exiting the aquifer. Epigean substrates are more easily accessible and require "snapshot" (not time-interval) methods using a frame and net (Surber and Hess samplers [Bioquip Products, Inc., Rancho Dominguez, CA, USA]) to capture benthic aquatic invertebrates living in and on the substrate.

We sampled the aquifer community (stygobites) using 250-µm mesh drift nets installed over the water flow of an undisturbed spring orifice for about 3 d in August, October, and November 2016. Locations for drift netting were selected randomly. All spring sites were mapped using a Trimble Nomad and a Pro XT receiver (Trimble Navigation Limited, Corvallis, OR, USA). Benthic aquatic invertebrate samples were taken using Surber or Hess samplers, as appropriate depending on water depth. Spring orifice substrate and transition zone samples were taken using a Surber sampler with 500-µm mesh and 0.092-m^2 area in February, April, May, October, and November 2016. Spring orifice substrate and transition zone samples were collected at nearby spring openings that were different than the aquifer samples and were distributed along the length of each spring complex. These springs were nearby but not identical due to disturbance from other collection activity conducted at the same time as this sampling. Spring orifice substrate samples were collected directly below the orifice and up to 1 m downstream. For sampling, large cobbles were cleaned inside the sampler and removed from inside the sampled area. Then, for 45 s, the substrate was disturbed to dislodge invertebrates into the net. Finally, due to their increased depth, creek and river samples (Dolan Creek, Upper and Lower Devils River) were taken repeatedly from within the same riffle using Hess samplers with 500-µm mesh in February, April, July, and November 2016. Creek samples were collected starting in the down-stream section of a riffle or shallow run and were taken from cobble and gravel substrates.

For each creek sample, basic water chemistry was collected using a Hydrotech compact DS5 (Hydrotech ZS Consulting, Round Rock, TX, USA). Flow (FH950; Hach, Loveland, CO, USA) and depth were also recorded at each creek sample. All samples were collected and placed into 95% isopropyl alcohol and sorted under microscopes. We counted or measured only shells with tissue. To compare shell sizes, sets of *T. diaboli* from aquifer ($n = 34$) and creek ($n = 30$) samples were photographed and measured. The shell measurements taken were maximum length along the columellar axis and maximum width at right angles to the columellar axis. The shell measurements were compared using a *t*-test in JMP Pro 13.0.0 (SAS Institute Inc., Cary, NC, USA).

To determine mesohabitat associations of *T. diaboli* and other common community taxa, the mesohabitats were coded 1–5 (1 = aquifer sample, 2 = spring orifice substrate sample, and continuing downstream) and an indicator analysis (Dufrene and Legendre 1997) was conducted in R with the package "labdsv" (Roberts 2013).

RESULTS

Over 72,000 invertebrates, including 640 *T. diaboli,* were collected from 132 samples from all mesohabitats (Table 1). The contribution of aquatic invertebrates from each meso-habitat is as follows: aquifer = 13,175; spring orifice substrate = 6,734; transition zone = 11,678; Dolan Creek = 23,237; and Devils River = 16,787. *Tryonia diaboli* were most abundant in aquifer samples, with an average of 9.35 individuals per sample, comprising 2.62% of macroinvertebrates collected (Table 1). Spring orifice substrate and transition samples had lower abundances, averaging 4.22 and 4.26 individuals per sample, respectively. The lowest abundances, at 3.75 individuals per sample or 0.14 per site, were found in the Devils River sample. Creek samples from Finegan Springs resulted only in three individuals and were not analyzed or further presented here. Indicator analysis found *T. diaboli* to be significantly ($P < 0.05$) associated with the aquifer samples (Table 2). The aquifer and creek sites where *T. diaboli* were collected had similar water chemistry values (Table 3).

Aquifer community sampling occurred in late summer through fall (August, October, and November) of 2016 and creek samples were taken in late winter through early summer (February, April, and July) of that year. The average count of *T. diaboli* from both creek and aquifer for Dolan Springs across all sampling periods is shown in Table 4. *Tryonia diaboli* shells from Dolan Springs creek samples taken in winter to early summer were significantly smaller in both length ($P = 0.01$) and width ($P = 0.0034$) than those from the aquifer taken in late summer to fall. In addition, the aquifer (late summer to fall) shells included a larger range of sizes, up to 2.04 mm total length, compared to the largest creek (winter to early summer) snail, measuring 1.34 mm. The average length of individuals sampled from the aquifer (late summer to
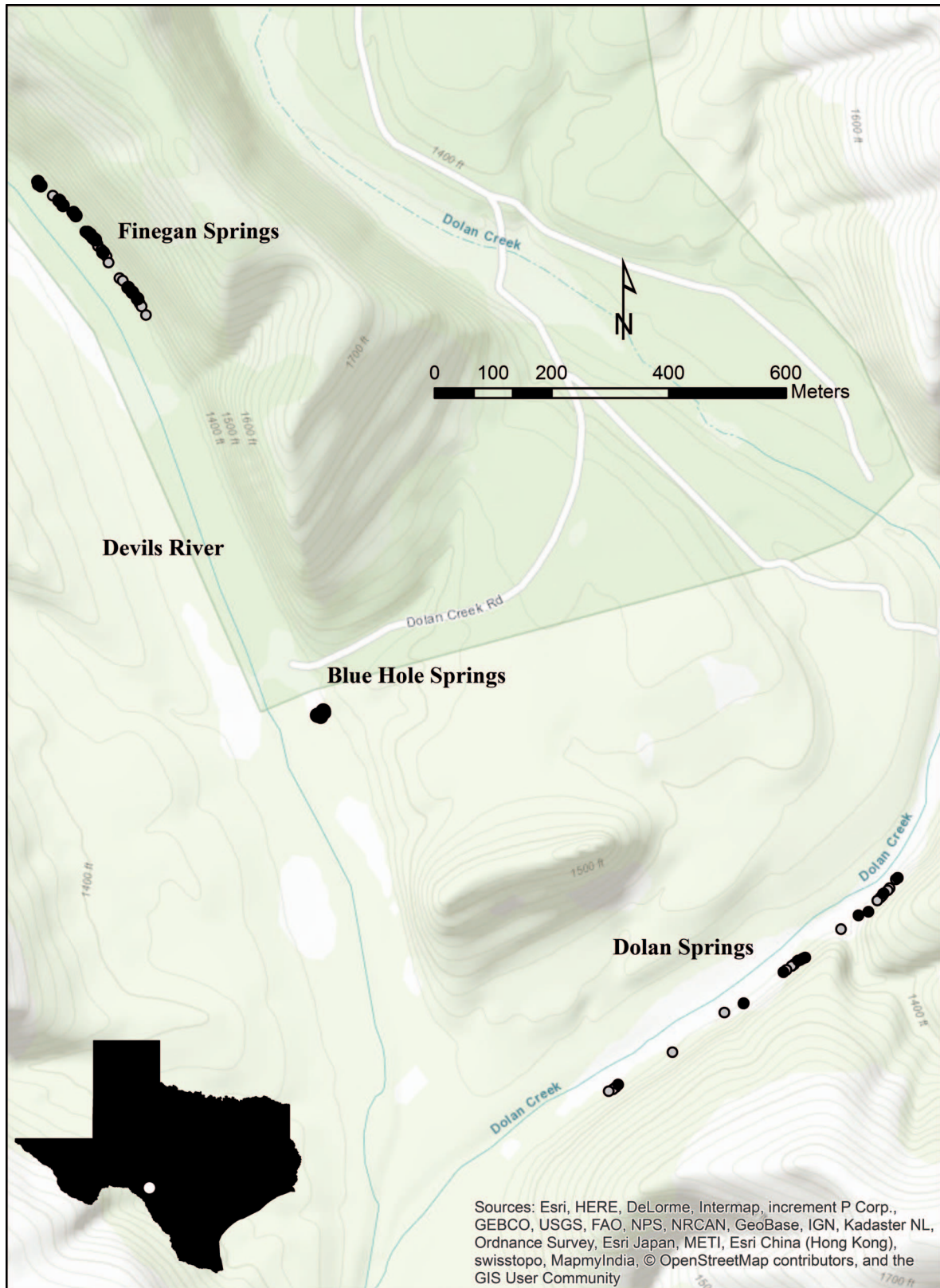
Figure 2. Map of sites. Sites sampled are in black and all other spring outlets are presented in gray.

Table 1. Total number of *Tryonia diaboli* from 132 benthic aquatic invertebrate samples collected in 2016 from the Devils River and Dolan Creek along with their associated spring complexes. Each column represents a specific ecosystem component sampled to examine mesohabitat associations.

| | Spring Orifice | | | | |
	Aquifer	Substrate	Transitional	Dolan Creek	Devils River
No. of individuals	346	135	81	75	3
% of individuals collected	54.06	21.09	12.66	11.72	0.47
% of invertebrate samples	2.62	2.04	0.69	0.32	0.03
Sample size	37	32	19	20	21

fall) was 1.25 mm (SEM = 0.06 mm) and the length of individuals from creek samples (winter through fall) was 1.09 mm (SEM = 0.02 mm). Average widths from creek and aquifer samples were 0.675 (SEM = 0.026 mm), and 0.588 mm (SEM = 0.0085 mm), respectively. There were no observed differences in animal or shell pigmentation among the samples collected.

DISCUSSION

In this study, macroinvertebrate samples were taken from five mesohabitats on a gradient from aquifer to creek, with the unexpected result that *T. diaboli* was most common (54% of

Table 2. Mesohabitat associations of aquatic invertebrates from indicator species analysis of different ecosystem components. Taxa are ordered by each ecosystem component, from aquifer samples toward downstream, then alphabetically within ecosystem component category.

Taxa	Zone	Indicator	*P* value
Lirceolus sp.	Aquifer	0.921	0.001
Psephenus sp.	Aquifer	0.259	0.067
Tryonia diaboli	Aquifer	0.363	0.005
Heterelmis cf. *glabra*	Spring orifice substrate	0.357	0.005
Heliocopsyche sp.	Transition	0.710	0.001
Hyalella sp.	Transition	0.609	0.001
Microcylloepus pusillus	Transition	0.573	0.002
Phanocerus clavicornis	Transition	0.345	0.034
Allenhyphes vescus	Dolan	0.657	0.001
Chironomini	Dolan	0.650	0.001
Cochliopina riograndensis	Dolan	0.471	0.001
Elimia sp.	Dolan	0.496	0.001
Melanoides tuberculata	Dolan	0.343	0.004
Metrichia sp.	Dolan	0.644	0.001
Orthocladiinae	Dolan	0.534	0.002
Simulium	Dolan	0.547	0.001
Tanytarsini	Dolan	0.491	0.001
Turbellaria	Dolan	0.383	0.004
Chimarra sp.	Devils	0.494	0.001
Corbicula sp.	Devils	0.734	0.001
Fallceon quilleri	Devils	0.487	0.001
Hexacylloepus ferrugineus	Devils	0.800	0.001
Macrelmis sp.	Devils	0.555	0.001
Thraulodes gonzalezi	Devils	0.635	0.001

individuals) in samples taken using drift nets to collect invertebrates exiting the aquifer. Mesohabitats farther from the aquifer and spring source had declining abundances of *T. diaboli*. This finding is supported by both the count and indicator analyses. Indicator analyses determined that the typical stygobitic species *Lirceolus* sp. (water slater) and the spring species *Heterelmis* cf. *glabra* (riffle beetle) also were significantly associated with the aquifer or spring orifice substrate samples. This is a surprising finding as no other *Tryonia* species has been documented occupying stygobitic habitats.

In general, other *Tryonia* species are most abundant at spring heads (Brown et al. 2008), with some species found in the spring run or creek up to about 1 km downstream. In this study, we found *T. diaboli* acting as a stygophile, occupying both stygobitic (aquifer) and near-spring sites, declining in abundance in the creeks, and at very low densities in the main channel. This could be due to a physiological requirement for water characteristics associated with proximity to the aquifer, such as thermal stability or oxygen concentration, or to biotic characteristics such as a preferred food source. It is possible that the decline in abundance that we observe downstream is related to our sampling method, with the cumulative collection of animals over 3 d in aquifer samples being compared to "snapshot" sampling methods in the downstream samples. However, we think the general trend of decreasing abundance downstream is broadly accurate for two reasons. First, the abundance of individuals sampled from the aquifer is two times higher per sample, representing 54% of the total individuals collected across all five mesohabitats. This finding seems unlikely to be entirely due to sampling method. Second, the trend of reduced abundance downstream is also seen across the "snapshot" sampling methods, with reduced abundance in creek and river samples compared to spring orifice substrate and transition zones.

Tryonia typically live in highly mineralized, sometimes thermal, (Hershler and Sada 1987; Hershler 1999; Liu et al. 2001) and even hypersaline environments (Kitting 2015), usually on mud or gravel substrate as well as on vegetation and detritus (Hershler et al. 2011a). If water flow is retained, some species (e.g., *T. chuviscarae*) are able to persist in highly human-impacted springs and streams (Hershler and Sada 1987; Hershler et al. 2011a; Kitting 2015), although at lower abundances (Hershler et al. 2011a). In the epigean sites sampled in this study, we found *T. diaboli* occupying sites that

Table 3. Average and standard deviation (in parentheses) of water physicochemical values for Dolan Springs ($n = 7$ sites, 3 sampling periods) and Finegan Springs ($n = 7$, 3 sampling periods) aquifer creek sites ($n = 6$, 4 sampling periods) where *Tryonia diaboli* was collected.

		Temp. (°C)	Conductivity (mS/cm)	DO (mg/L)	pH	TDS (g/L)	Flow (m/s)
Dolan Springs	Aquifer	22.619 (0.10)	458.460 (3.27)	7.528 (0.43)	7.347 (0.12)	0.291 (0.00)	0.82 (0.29)
	Creek	23.200 (2.97)	444.500 (18.53)	8.120 (1.16)	7.880 (0.07)	0.281 (0.01)	0.55 (0.28)
Finegan Springs	Aquifer	22.472 (0.07)	475.207 (3.93)	7.604 (0.11)	7.307 (0.08)	0.304 (0.00)	1.00 (0.34)

DO = dissolved oxygen; TDS = total dissolved solids.

were characterized as having the following substrates: cobble, bedrock, gravel, rubble, and organic debris. The spring sites occupied by *T. diaboli* were more moderate in temperature, ~22–23°C. Altogether, *T. diaboli* is unusual among the *Tryonia* as it occupies habitats that are nonthermal, not heavily mineralized, and both stygobitic and epigean.

Snail population abundance could vary seasonally for a variety of reasons, for instance, due to seasonal patterns of reproduction or to water level fluctuations. While there is not comparative data for other *Tryonia* species, hydrobioids are generally annual with seasonal recruitment in cold springs (Brown et al. 2008). In *Juturnia kosteri*, there is a three- to four-fold increase in snail density in summer, potentially due to recruitment, decline in water level, or both (Johnson et al. 2019). Aquifer sampling in this study was conducted in summer and fall, with the highest average abundance across sites of 11.9 in August and a drop to 2.2 in November. Creek samples farther downstream and earlier in the year (January through July) found lower abundances, with the highest abundance of 5.5 in April. This finding suggests an increase in abundance in spring and summer and a decline in winter, which aligns with the typical expectation for hydrobioid gastropods. These data on *T. diaboli* are not conclusive, in part because our sampling is not complete across seasons. In addition, while the methods used are the best available to accurately sample these mesohabitats, comparisons between findings using a "snapshot" sampling method and those using a time-interval sampling method must be made with caution.

In the absence of a modern taxonomic reappraisal of *T. diaboli*, *Te. longleyi*, and *T. circumstriata*, we focused this description of mesohabitat associations on individuals conforming to the original description of *T. diaboli*. It is possible that *T. diaboli* and *Te. longleyi* and/or *T. circumstriata* are valid species which are similar in size and shell morphology and which occur in the same watershed or region. Indeed, spring snails tend to be extreme narrow-range endemics. On the other hand, if any of these species were synonymized with

T. diaboli (the name with taxonomic priority), the mesohabitat associations described would still apply and the main finding of this study would still be novel, as neither *Te. longleyi* nor *T. circumstriata* is reportedly stygophilic.

Tryonia diaboli was ranked as imperiled by the most recent evaluation of conservation status of North American freshwater snails (Johnson et al. 2013), based on the limited population extent, as the species was documented only from a small stretch of the Devils River and nearby San Felipe Springs (Pilsbry and Ferris 1906). Except for the current study, there has been a complete lack of research on this organism. The presence of *T. diaboli* in both the aquifer and spring run indicates it could occupy a tremendously greater habitat area than previously understood. Over half the individuals encountered during this sampling came from the aquifer (drift net) samples, eluding to higher numbers underground than at the surface. However, the full extent of the habitat of this species is unclear as we have not determined if this population occupies only the shallower hyporheic zone rather than deeper in the phreatic zone of the aquifer. Future work would need to determine if the species is present in well samples in addition to those underground habitats closely associated with springs.

The question of the potential habitat this species can occupy leads to an important corollary for species conservation; if this species occupies significant belowground habitat, it is possible that it could survive deeper in the aquifer during cessation of flows. Two other closely related, fully epigean species, *Juturnia brunei* and reportedly *T. oasiensis* (Hershler et al. 2011a), have recently gone extinct due to cessation of spring flow (Hershler et al. 2014). *Juturnia brunei* had persisted in the Phantom Lake spring system through extensive human modification of the spring and creek channels for irrigation; however, it appears to have gone extinct when local groundwater levels dropped sufficiently such that the spring where it resided went completely dry (Hershler et al. 2014). This study is a small first step in understanding the

Table 4. Average and standard deviation (in parentheses) of *Tryonia diaboli* individuals collected across sampling period (2016) in Dolan (DS) and Finegan Springs (FS) in aquifer and/or creek samples. Values for n are as follows for aquifer samples (not individuals): August: DS and FS, $n = 7$; October: DS, $n = 7$, FS, $n = 6$; November: DS, $n = 3$, FS, $n = 2$. Values for n are as follows for creek samples (not individuals) at DS: February, $n = 6$; April, $n = 6$ July, $n = 6$.

		February	April	July	August	October	November
Dolan Springs	Aquifer	—	—	—	10.43 (12.53)	8.00 (13.22)	0.67 (0.58)
	Creek	4.17 (6.21)	5.50 (8.48)	2.33 (5.72)	—	—	0.50 (0.55)
Finegan Springs	Aquifer	—	—	—	13.29 (18.74)	5.17 (4.26)	4.5 (2.12)

ecology of *T. diaboli*, a task with some urgency due to local extinctions of related species in similar habitat.

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