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Habitat and phenology of the endangered riffle beetle *Heterelmis comalensis* and a coexisting species, *Microcylloepus pusillus,* (Coleoptera: Elmidae) at Comal Springs, Texas, USA

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With 5 figures and 4 tables

Abstract: Habitat characteristics and seasonal distribution of the riffle beetles *Heterelmis comalensis* and *Microcylloepus pusillus* were studied at Comal Springs, Texas, during 1993–1994, to aid in developing sound recommendations for sustaining their natural populations. Comal Springs consists of four major spring outlets and spring-runs. The four spring-runs are dissimilar in size, appearance, canopy and riparian cover, substrate composition, and aquatic macrophyte composition. Habitat conditions associated with the respective populations of riffle beetles, including physical-chemical measurements, water depth, and current velocity, were relatively uniform and varied little among sampling dates and spring-runs. However, the locations of the beetles in the respective spring-runs were not well correlated to current velocity, water depth, or distance from primary spring orifices. Factors such as substrate size and availability and competition are proposed as possibly influencing their respective distributions. Maintaining high-quality spring-flows and protection of the physical habitat of *Heterelmis comalensis* presently are the only means by which to ensure the survival of this endemic species.

Key words: Conservation, habitat conditions, substrate availability, competition.

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Introduction

The Comal Springs, located in Comal County, Texas, issue from the Edwards (Balcones Fault Zone) Aquifer. This artesian spring system is the largest in Texas (BRUNE 1981) and from 1930 to 1999 annual mean discharge was approximately 8 m^3/sec (GANDARA et al. 2000). However, current anthropogenic demands and various additional disturbances on the Edwards Aquifer place spring-flows and their resident biota at significant risk of extirpation (BOWLES & ARSUFFI 1993). Comal Springs have ceased flowing in the past following extended periods of drought, but, for the period of record from 1882 to present, spring-flows had not fallen below 5.7 m^3/sec prior to the drought of the early 1950s (BRUNE 1981). The springs were dry in 1956 for 5 months, and they were partially dry during 1984 and 1990 (CROWE & SHARP 1997). During another drought in 1996, spring-flows at Comal Springs were severely reduced. In recent years, low spring flows due to drought are exacerbated by pumping of water from the aquifer for various human uses (BOWLES & ARSUFFI 1993). Nearly 2 million people in central Texas rely on water pumped from the Edwards Aquifer, and the human population in this area continues to grow. Because of this increasing demand for water, the springs likely will again run dry during periods of drought.

The Comal Springs riffle beetle, *Heterelmis comalensis* BOSSE, TUFF and BROWN (1988) (Coleoptera: Elmidae) is known primarily from Comal Springs. BARR (1993) collected a single specimen of *H. comalensis* from the impounded spring-fed headwaters of the nearby San Marcos River, Hays County, Texas, but additional collections of this species have not been made at this location. Because of the imminent threat of habitat destruction of a geographically limited species, *Heterelmis comalensis* was listed as endangered by the United States Fish and Wildlife Service (1997). As a result of this listing, conservation agencies such as the Texas Parks and Wildlife Department and the U.S. Fish and Wildlife Service are developing baseline ecological information for *H. comalensis* and other rare species occurring at Comal Springs. Such baseline information ultimately will be used to develop management plans for conserving these species and their native habitat, and possibly to establish refugia stocks for replacing extirpated wild populations.

Other species of *Heterelmis* known to occur in Texas include *Heterelmis obesa* SHARP, *Heterelmis glabra* (HORN), and *Heterelmis vulnerata* (LECONTE). The latter species is widespread in the eastern one-half of the state while *H. obesa* and *H. glabra* are known from Culberson and Brewster counties, respectively, in western Texas (BROWN 1972, BOSSE et al. 1988). The Comal Springs riffle beetle appears to be most closely related to *H. glabra*, (BOSSE et al. 1988) from which its populations are disjunct by approximately 450 km. *Heterelmis vulnerata* has been collected from the San Marcos River

(BOSSE et al. 1988), and we have examples of this species from the Guadalupe River both upstream and downstream of the confluence with the Comal River. Another elmid, *Microcylloepus pusillus* (LECONTE), also commonly occurs at Comal Springs and elsewhere in Texas and the U.S. westward to Colorado and Utah (BURKE 1963, BROWN 1972).

Few studies have reported on the biology of elmids occurring in Texas streams (BURKE 1963, BROWN 1987, BOSSE et al. 1988, PHILLIPS 1997 a, 1997 b). BURKE (1963) reported collecting examples of *M. pusillus* in central Texas from May to October on submerged stones in the main currents of streams. BROWN & SHOEMAKE (1964) reported that in Oklahoma representatives of the genus *Microcylloepus* often are found under rocks, beneath bark of submerged logs, or in dead leaves and debris caught on snags in streams, and BARR & CHAPIN (1988) reported *M. pusillus* from submerged roots and aquatic moss in Louisiana. The adults and larvae of most species of *Heterelmis* are known to occur in the benthos, and on water-logged wood and other woody debris (BROWN & SHOEMAKE 1964, PHILLIPS 1995). BOSSE et al. (1988) reported finding the greatest population densities of *H. comalensis* at Comal Springs from February through April. Although the former study provided baseline ecological information for *H. comalensis* and *M. pusillus* at Comal Springs, it did not provide detailed information on habitat characteristics and seasonality. A basic assessment of the habitat of the Comal Springs riffle beetle was presented by CROWE & SHARP (1997) who concluded that "... the riffle beetle appears to inhabit areas of gravel substrate, swift flow rate, and little to no vegetation ...". However, the findings of CROWE & SHARP (1997) are vague and were not supported by specific data. This paucity of information on the habitat of *H. comalensis* has presented a substantial detriment to developing a sound management plan for sustaining its natural population at Comal Springs.

The purpose of this study was to determine the seasonal distributions of *H. comalensis* and *M. pusillus*, characterize their habitats, and provide information on the phenology of their respective life stages.

Methods

Study site

We conducted this study at Comal Springs located in Landa Park, New Braunfels, Comal County, Texas (N 29° 42′ 49.6″, W 98° 8′ 12.6″, Garmin® GPS 45). This spring system consists of four major spring outlets and spring-runs named Comal 1, 2, 3, and 4, respectively, which flow into an impounded area known as Landa Lake (Fig. 1). Many other smaller springs and seeps discharge along the lengths of these primary spring-runs and from within Landa Lake. The major springs in the Comal system are

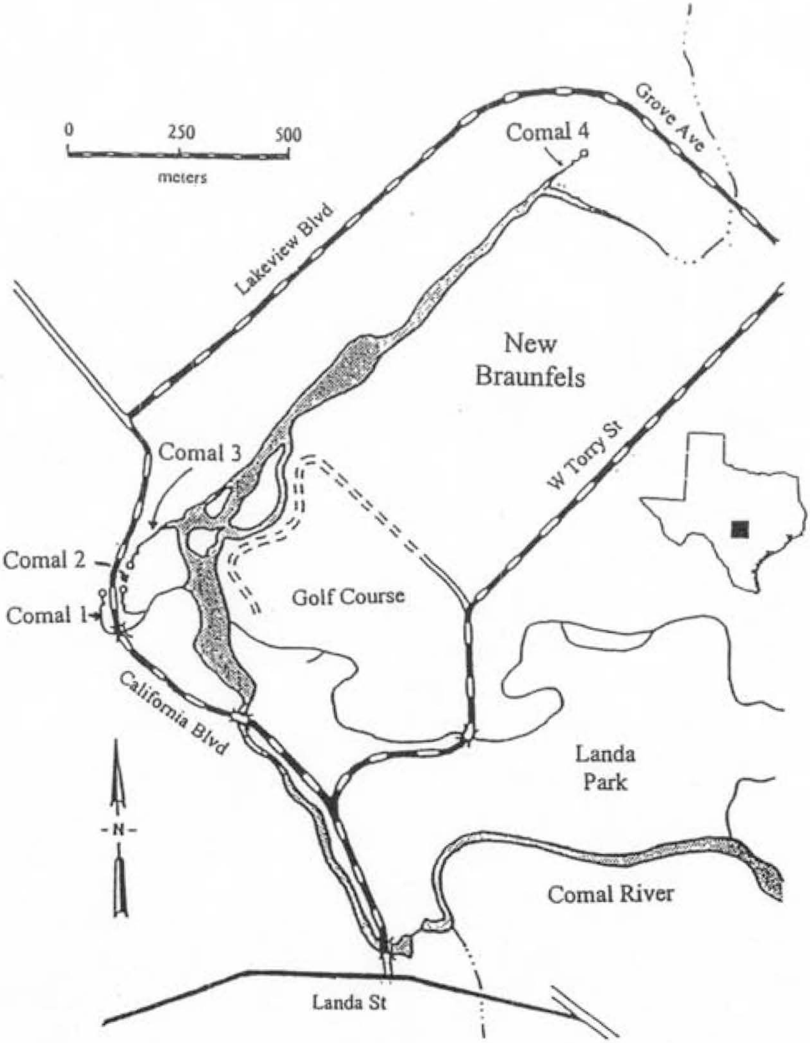

Fig. 1. Map of Comal Springs, Texas (modified from Ogden et al. 1985).

not all hydraulically connected and largely act independently of each other (Crowe & Sharp 1997). The four spring-runs are dissimilar in size, appearance, canopy and riparian cover, substrate composition, and composition and relative abundance of aquatic vegetation. Comal 1 ranges from 9–13 m in width along its length and flows approximately 230 m before entering Landa Lake. Comal 2 ranges in width from 2–3 m and flows 66 m from its source before entering a shallow, concrete-sided wading pool (14 × 21 m). This spring-run then discharges into the lower end of Comal 1. Comal 3 ranges in width from 4.5–8 m and flows 130 m before entering Landa Lake. Comal 4 is approximately 3 m wide over most of its 65 m course before its confluence with Landa Lake. Only about the first 20 m of Comal 4 bears any similarity to the other spring-runs because the lower reach of this spring-run becomes sluggish and silt-laden due to the lentic influences of Landa Lake. Comal 1, the largest of these spring-runs, has an average discharge of approximately 0.6 m^3/sec while the smallest (Comal 2) averages about 0.3 m^3/sec (CROWE & SHARP 1997). SPANGLER & BARR (1995) presented additional descriptions of the four spring-runs. Mean combined discharge for Comal Springs, measured in the Comal River, was 11.29, 9.71, 9.96 and 9.42 m^3/sec during July and October 1993 and January and April 1994, respectively (GANDARA et al. 1994, 1995). However, many other small springs underlying Landa Lake contribute up to 80 % of the total flow of the Comal Springs system (GEORGE OZUNA, U.S. Geological Survey, personal communication). Landa Park is situated in an urban setting and humans have variously modified the springs during the past 150 years, but their resident biota remains diverse and water quality remains excellent (BOWLES & ARSUFFI 1993, CROWE & SHARP 1997).

Sampling techniques

We studied randomly selected 1 m^2 sampling areas (cells) at the four spring-runs during July and October 1993, and January and April 1994. To determine cells to be sampled, a 1 m^2-scale grid was overlaid on a map of each spring-run, and each possible cell within the spring-runs was numbered sequentially from upstream to downstream. Cell numbers were randomized with study cells being selected from among the total possible cells in order of occurrence following randomization. Samples were collected from selected cells from downstream to upstream in order to minimize disturbance to other cells, and only cells falling entirely within the wet area of the spring-runs were sampled. The number of random cells selected for each spring-run represented approximately 10 % of the total number of possible cells that were available for sampling on a given sampling date. With these selection criteria, we collected a total of 278 semi-quantitative benthic samples during the course of this study. Samples were collected by placing a catch-net (Wildco® stream drift net, 363 µm mesh netting; net mouth 300 × 460 mm) on the downstream side of the sample area and then agitating the substrate using a hand-held garden cultivating tool. Large stones were washed by hand into the net to remove attached invertebrates. One-half of the sample area was collected in this fashion and the collecting net was then moved to complete the remaining one-half of the sample area. We preserved samples with 95 % isopropyl alcohol in the field. In the laboratory, samples were sorted and all riffle beetles were removed, identified, counted, and stored in 70 % isopropyl alcohol.

Other species of riffle beetles found at Comal Springs were not included in this study because they were rarely collected. These include a single, unidentified adult female of *Stenelmis* and a few specimens each of *Phanocerus clavicornis* SHARP and *Stygoparnus comalensis* BARR and SPANGLER. The water penny *Psephenus texanus* BROWN and ARRINGTON (Psephenidae), abundant at Comal Springs (CARROLA 1978), also was not addressed in this study.

On each sampling date, we measured dissolved oxygen concentration, conductivity, pH, and temperature at the upper, middle and lower portion of each spring-run using a calibrated Hydrolab Scout® 2. We then averaged physical-chemical readings for each spring-run. We measured depth (m) in the approximate center of each cell sampled using a calibrated, top-setting wading rod, and we determined current velocity (m/sec) at approximately substrate level using a Marsh-McBirney® velocity meter (Gordon et al. 1992).

We visually estimated the relative dominant particle size composition of the surface substrate for each cell sampled using the Wentworth Scale for substrate classification (Wentworth 1922). We also visually determined if sample cells contained aquatic vegetation. Species identifications of vascular hydrophytes were according to Correll & Correll (1975) and Angerstein & Lemke (1994).

Statistical analyses

We consider the spring-runs to be independent, but the samples taken within the respective spring-runs and sampling dates to be pseudoreplicated (Hurlbert 1984). Lack of independence, confounded by the inherent difficulties of sampling a single population from one ecosystem, prevented the proper use of comparative, parametric statistics in the analysis of the data we collected. In addition, benthic samples were collected semi-quantitatively given constraints of the collecting device and technique thus producing variability that could confound statistical analysis. Therefore, we have used only non-parametric tests for statistical analyses including Friedman's test with Tukey multiple comparison, Chi-square goodness-of-fit test, and Kendall's Tau estimate of correlation ($\alpha = 0.05$) (Conover 1980, KWIKSTAT version 4.62). We selected Kendall's Tau over other non-parametric measures of correlation because its distribution more closely approaches a normal distribution, and it offers a direct and simple interpretation (Conover 1980).

Specimen deposition

Representatives of *Heterelmis comalensis* and *Microcylloepus pusillus* collected during this study are deposited in the Texas A & M University Entomological Collection, College Station, Texas.

Results

Habitat analysis

We found that temperature, specific conductance, and pH were essentially constant at Comal Springs (Table 1), and there were no significant differences among these parameters among sampling dates or spring-runs (Friedman's test, $\chi^2 \geq 5.31$, $P \geq 0.062$). Water temperature ranged from 23.2 to 23.8 °C, pH ranged from 6.9 to 7.2, and conductivity ranged from 518 to 551 µmhos/cm. The only parameter demonstrating appreciable variation among spring-runs and sampling dates during this study was dissolved oxygen concentration which was significantly different between spring-runs 1 and 3 only (Friedman's test, $\chi^2 = 12$, $P = 0.008$; Tukey multiple comparison, $Q = 4.68$). In all instances, dissolved oxygen concentrations were above 50 % saturation (Wetzel 1975).

Table 1. Physical-chemical measurements for Comal Springs, Texas, 1993–1994[1].

Sampling Date	Spring-run	Temperature (°C)	Conductivity (µmhos/cm)	Dissolved Oxygen (mg/L)[2]	pH
July	1	23.39 (0.32)	546 (1.15)	4.74 (0.14)	7.12 (0.02)
		23.36–23.45	545–547	4.66–4.90	7.10–7.13
	2	23.46 (0.07)	546 (1.15)	4.49 (0.18)	7.14 (0.02)
		23.38–23.50	545–547	4.36–4.70	7.12–7.15
	3	23.53 (0.02)	546 (0)	4.54 (0.31)	7.17 (0.01)
		23.52–23.56	N/A	4.33–4.90	7.16–7.18
	4	23.78 (0.01)	550 (1.41)	4.21 (0.41)	7.14 (0.04)
		23.77–23.79	549–551	3.92–4.5	7.12–7.17
October	1	23.29 (0.02)	538 (0.56)	5.67 (0.22)	6.96 (0.02)
		23.27–23.32	538–539	5.53–5.76	6.93–6.98
	2	23.31 (0.13)	538 (2.89)	5.02 (0.22)	7.01 (0.01)
		23.16–23.41	535–540	4.84–5.15	7.00–7.02
	3	23.32 (0.13)	537 (2.08)	5.3 (0.19)	7.01 (0.02)
		23.18–23.43	535–539	5.08–5.42	6.99–7.03
	4	23.52 (0.18)	543 (2.00)	5.15 (0.55)	7.04 (0.03)
		23.34–23.70	541–545	4.70–5.77	7.00–7.06
January	1	23.31 (0.09)	523 (1.00)	5.78 (0.45)	7.06 (0.02)
		23.21–23.38	522–524	5.41–6.28	7.04–7.09
	2	23.06 (0.28)	522 (0.57)	5.35 (0.46)	7.13 (0.04)
		22.75–23.31	522–523	5.08–5.88	7.08–7.17
	3	23.31 (0.20)	522 (3.41)	5.69 (0.25)	7.09 (0.04)
		23.08–23.45	518–525	5.43–5.94	7.05–7.13
	4	23.27 (0.13)	525 (1.41)	5.61 (0.41)	7.15 (0.03)
		23.32–23.50	524–526	5.32–5.90	7.13–7.17
April	1	23.33 (0.04)	540 (3.21)	5.32 (0.25)	7.26 (0.02)
		23.28–23.36	538–542	5.03–5.47	7.23–7.28
	2	23.38 (0.12)	541 (1.15)	4.85 (0.12)	7.26 (0.004)
		23.24–23.46	540–542	4.73–4.96	7.25–7.26
	3	23.36 (23.18)	552 (2.31)	5.25 (0.11)	7.24 (0.02)
		23.16–23.50	538–542	5.18–5.38	7.21–7.26
	4	23.54 (23.12)	552 (2.31)	4.80 (0.31)	7.49 (0.03)
		23.41–23.64	549–553	4.57–5.16	7.46–7.51

[1] Values are means followed by standard errors in parentheses, and range. Sample size is 3 for each paramenter on each sampling date.

[2] Means for spring-run 1 are significantly different (Friedman's Test, $\alpha = 0.05$, $P = 0.007$).

Water depth and current velocity varied little among sampling dates and was relatively uniform throughout the respective springs-runs (Table 2). Maximum and minimum mean water depths recorded during this study were 0.98 m (Comal 2, January) and 0.09 m (Comal 2, October), respectively. When viewed across all sampling dates and spring-runs, *H. comalensis* were collected from significantly shallower water depths in comparison to all sample cells measured and those containing *M. pusillus* (Friedman's test, $\chi^2 = 10.97$, P

Table 2. Current velocity and water depth for all samples collected and those containing either *Microcylloepus pusillus* or *Heterelmis comalensis*, Comal Springs, Texas, 1993–1994[1].

Spring-run	Sampling Date		Current Velocity (m/sec)			Depth (m)		
			All Samples	*Microcylloepus*	*Heterelmis*	All Samples	*Microcylloepus*	*Heterelmis*
1	July		0.26 (0.05)	0.08 (0.02)	0.28 (0.02)	0.31 (0.04)	0.31 (0.02)	0.28 (0.02)
			0–1.48	0–0.45	0.01–0.45	0.06–1.4	0.06–0.94	0.06–0.43
		N	31	31	20	31	31	20
	October		0.32 (0.04)	0.32 (0.04)	0.33 (0.05)	0.28 (0.02)	0.28 (0.02)	0.28 (0.02)
			0–0.91	0–0.91	0–0.91	0.09–0.58	0.09–0.58	0.09–0.58
		N	30	30	25	30	30	25
	January		0.22 (0.02)	0.22 (0.02)	0.24 (0.02)	0.25 (0.02)	0.26 (0.02)	0.24 (0.02)
			0–0.50	0–0.50	0–0.05	0.09–0.64	0.09–0.64	0.09–0.43
		N	30	30	24	30	30	24
	April		0.3 (0.04)	0.3 (0.04)	0.32 (0.05)	0.29 (0.02)	0.29 (0.02)	0.27 (0.19)
			0–0.88	0–0.88	0.05–0.88	0.15–0.52	0.15–0.70	0.15–0.52
		N	31	31	20	31	31	20
2	July		0.02 (0.003)	0.01 (0.003)	0.02 (0.01)	0.51 (0.06)	0.53 (0.15)	0.34 (0.16)
			0.01–0.04	0–0.91	0.01–0.04	0.08–0.79	0.27–0.79	0.08–0.79
		N	14	3	4	14	3	4
	October		0.03 (0.01)	0	0.07 (0.03)	0.5 (0.07)	0.09 (0)	0.54 (0.13)
			0–0.03	0	0.01–0.13	0.01–0.73	0	0.30–0.73
		N	10	1	3	10	1	3
	January		0.01 (0.005)	0.002 (0.002)	0.01 (0.005)	0.62 (0.08)	0.64 (0.12)	0.61 (0.09)
			0–0.03	0–0.01	0–0.03	0.46–0.98	0.46–0.98	0.46–0.98
		N	6	4	3	6	4	3
	April		0	0	0	0.49 (0.03)	0.55 (0.09)	0.43 (0.03)
			0	0	0	0.4–0.7	0.46–0.64	0.40–0.46
		N	10	2	2	10	2	2

Table 2. Continued.

Spring-run	Sampling Date		Current Velocity (m/sec)			Depth (m)		
			All Samples	*Microcylloepus*	*Heterelmis*	All Samples	*Microcylloepus*	*Heterelmis*
3	July		0.05 (0.01)	0.05 (0.01)	0.06 (0.01)	0.5 (0.04)	0.52 (0.04)	0.41(0.07)
			0–0.06	0–0.15	0–0.11	0.01–0.85	0–0.85	0–0.61
		N	22	21	12	22	21	12
	October		0.2 (0.04)	0.2 (0.04)	0.23 (0.04)	0.49 (0.05)	0.49 (0.06)	0.43 (0.06)
			0–0.68	0–0.68	0.02–0.49	0.09–1.2	0.12–1.22	0.12–0.91
		N	21	21	14	21	21	14
	January		0.14 (0.04)	0.17 (0.04)	0.18 (0.06)	0.46 (0.4)	0.42 (0.05)	0.43 (0.07)
			0–0.55	0.01–0.55	0.01–0.55	0.02–0.85	0.02–0.85	0.02–0.85
		N	21	16	12	21	16	12
	April		0.19 (0.04)	0.22 (0.04)	0.22 (0.05)	0.36 (0.05)	0.35 (0.05)	0.25 (0.05)
			0–0.07	0–0.70	0–0.7	(0.03–0.88)	0.03–0.88	0–0.46
		N	21	20	13	21	20	13
4	July		0.02 (0.01)	0.03 (0.02)	–	0.46 (0.08)	0.28 (0.09)	–
			0–0.12	0–0.12	–	0.07–0.91	0.07–0.52	–
		N	10	5	0	10	5	0
	October		0.05 (0.04)	0.06 (0.05)	–	0.33 (0.10)	0.22 (0.12)	–
			0.01–0.23	0.01–0.23	–	0.01–0.61	0.01–0.52	–
		N	6	4	0	6	4	0
	January		0	0	–	0.39 (0.09)	0.21 (0.13)	–
			0	0	–	0.03–0.73	0.03–0.46	–
		N	7	3	0	7	3	0
	April		0.04 (0.02)	0.08 (0.04)	–	0.31 (0.06)	0.28 (0.17)	–
			0–0.14	0–0.14	–	0.03–0.61	0.03–0.61	–
		N	8	3	0	8	3	0

[1] Values are means followed by standard error in parentheses and range.

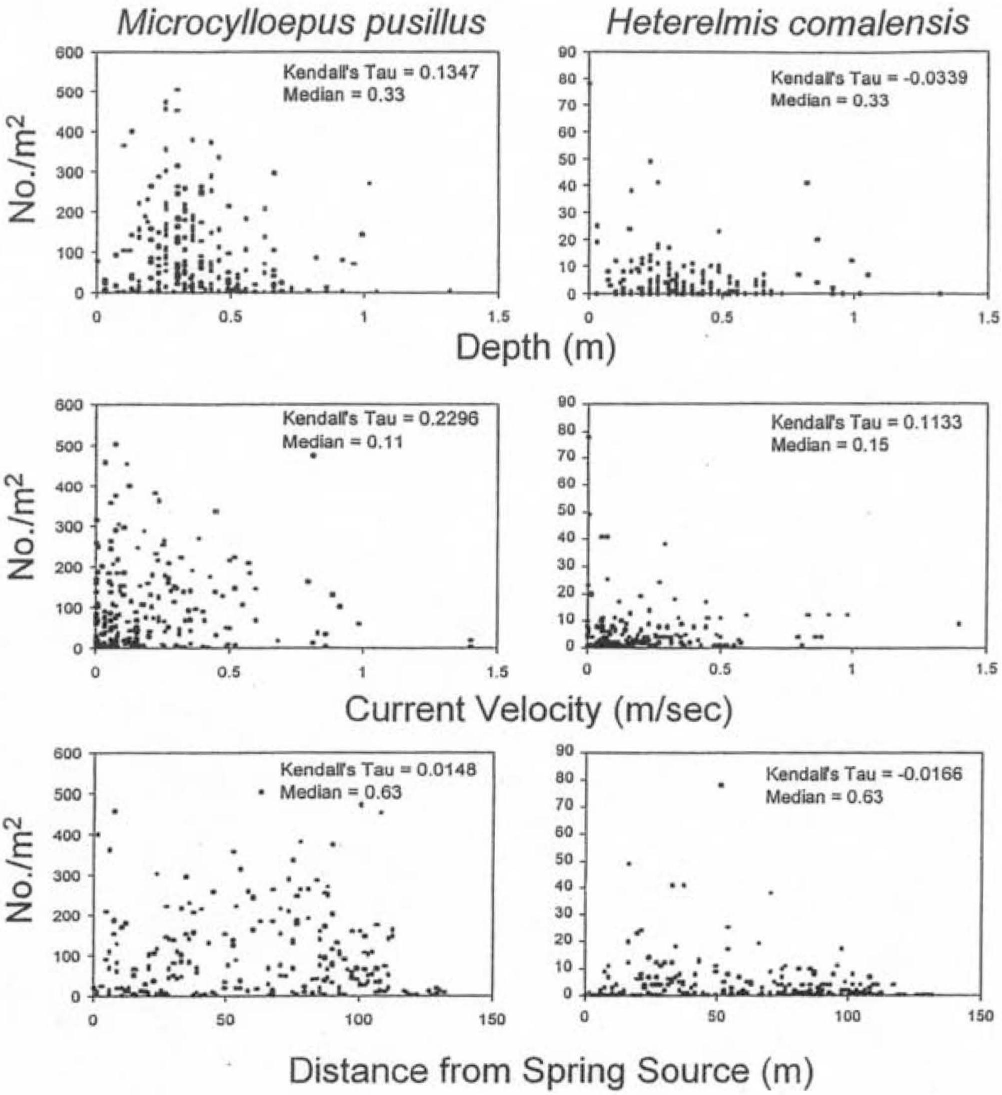

Fig. 2. Correlation of abundance of *Microcylloepus pusillus* and *Heterelmis comalensis* with depth, current velocity and distance collected from primary spring sources at Comal Springs, Texas, 1993–1994.

= 0.004). Only *M. pusillus* was collected at Comal 4, where it generally occurred in samples whose mean depth was less than the mean depth for all samples. In addition, we found that *H. comalensis* occurred in slightly faster current velocities than *M. pusillus* on all sampling dates for Comal 1, 2 and 3 (Table 2; Friedman's test, $\chi^2 = 7.37$, $P = 0.03$). For Comal 4, *M. pusillus* consistently occurred in samples whose mean current velocity was greater than the mean current velocity of all sample cells measured in that spring-run.

We found that total abundance of each beetle species was poorly correlated to water depth, current velocity, and the distance downstream from the pri-

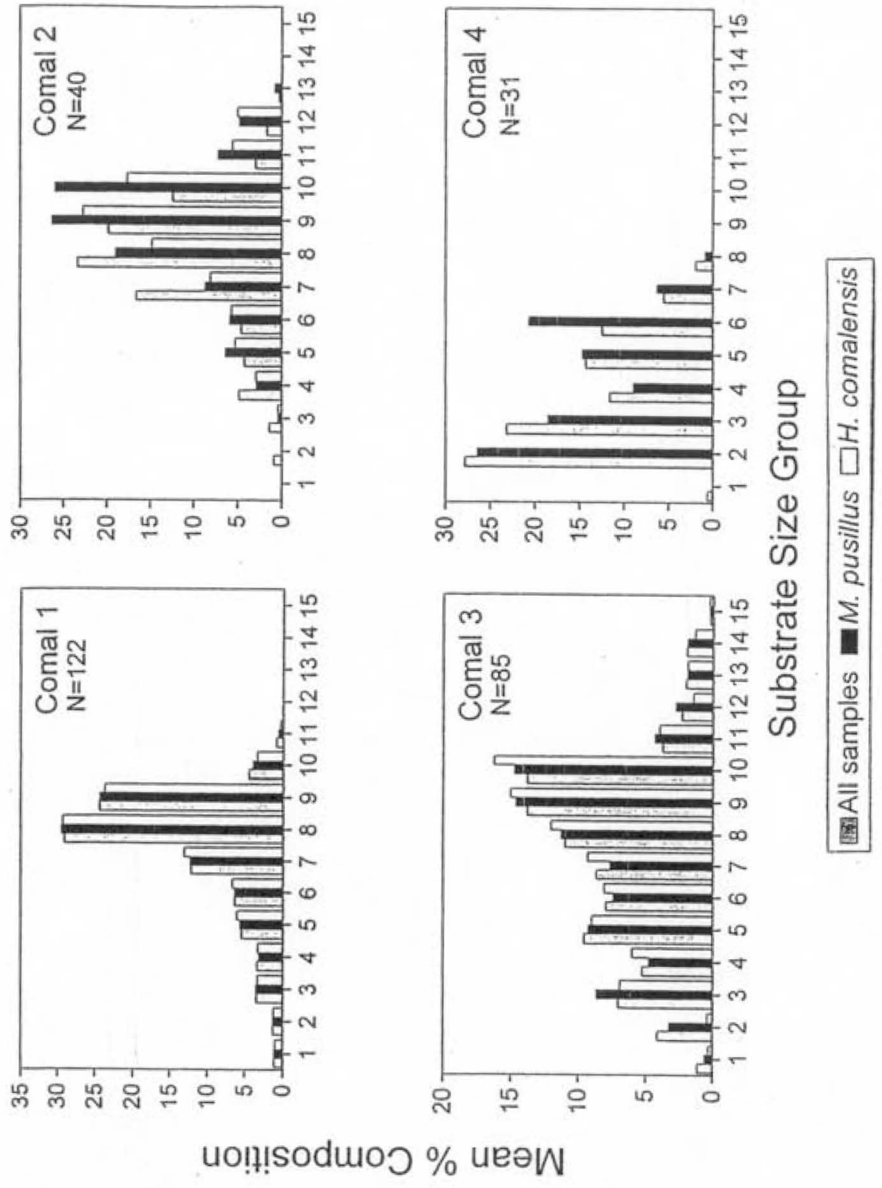

Fig. 3. Mean percentage substrate composition for benthic samples taken at Comal Springs, Texas, 1993–1994. Substrate size group (mm): 1 = <0.004, 2 = 0.004–<0.062, 3 = 0.062–1, 4 = 1–2, 5 = 2–4, 6 = 4–8, 7 = 8–16, 8 = 16–32, 9 = 32–64, 10 = 64–128, 11 = 128–256, 12 = 256–512, 13 = 512–1,024, 14 = >1024, 15 = solid substrate.

mary spring outlets where beetles were collected (Fig. 2). In all instances among sampling dates and spring-runs, estimates of Kendall's Tau for total numbers of *H. comalensis* and *M. pusillus* for each factor were closer to zero than to either –1 or +1 (Conover 1980). Such a poor correlation of beetle densities with these physical factors indicates that they are randomly distributed in the springs-runs.

Riffle beetles of both species were collected from a broad range of substrate sizes in Comal 1, 2, and 3 where the substrate composition of cells was similar and dominated by gravel and cobble (8–128 mm) (Fig. 3). The substrate sizes associated with riffle beetles collected from Comal 3 covered a broader, more even distribution in comparison to either Comal 1 or 2, although the dominant substrate size classes were similar for all three spring-runs. By comparison, silt, sand and small gravel dominated the substrate in Comal 4, and particle size generally did not exceed 32 mm (Fig. 3). Most specimens of *M. pusillus* collected from Comal 4 were taken in samples having a substrate dominated by relatively small particles (≤ 8 mm). Mean percentage composition of substrate size classes among spring-runs 1–3 were not significantly different (Chi-square goodness of fit, $\chi^2 = 5.99$, $T \leq 5.02$) for all sample cells measured compared to samples containing either species of riffle beetle. Organic debris observed in sample cells consisted of assorted leaves, small woody debris, plant roots, and dead and dislodged aquatic vegetation. However, with the exception of Comal 4, organic debris generally was not common and is not addressed further here.

Comal 1 and 3 had the greatest diversity of aquatic vegetation while Comal 2 and 4 supported few species (Table 3). Comal 2 was nearly devoid of aquatic vegetation, supporting only the moss *Leptodictyum riparium* (HEDW.) and small, scattered patches of filamentous algae. Species composition of aquatic vegetation among Comal 1 and 3 were similar with both spring-runs sharing several species in common. For the these two spring-runs, the majority of cells

Table 3. Aquatic vegetation occurring at Comal Springs, Texas during 1993–1994.

Species	Comal 1	Comal 2	Comal 3	Comal 4
Chlorophyta	X	X	X	X
Cyanophyta			X	
Rhodophyta	X		X	
Leptodictyum riparium (HEDW.)	X	X	X	X
Bacopa monnieri PENNELL	X			
Cabomba caroliniana GRAY				X
Eleocharis macrostachya	X			
Hydrocotyle umbellata L.			X	
Hygrophila polysperma (ROXB.)	X			X
Ludwigia repens FORST.	X			
Nuphar luteum SIBTH. & SM.	X		X	
Potamogeton illinoensis MORONG.	X		X	
Sagittaria platyphylla ENGELM.			X	
Scirpus sp.			X	
Vallisneria americana MICHX.	X			

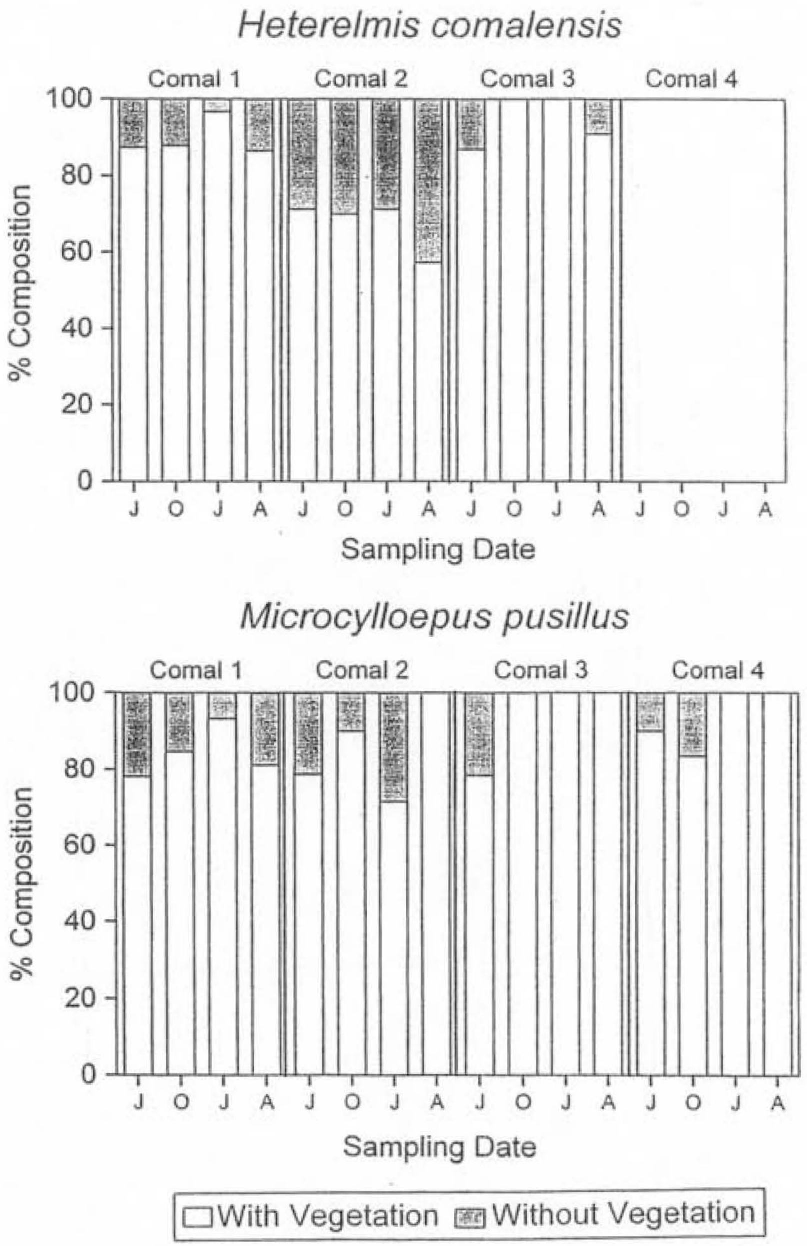

Fig. 4. Percentages of *Heterelmis comalensis* and *Microcylloepus pusillus* collected in sample cells with and without aquatic vegetation.

we sampled contained at least some aquatic vegetation (Fig. 4). For most sampling dates and spring-runs, aquatic macrophytes were present in 70% or more of the samples. Both species of riffle beetles occurred predominately in samples that contained aquatic vegetation compared to those samples that did not (Chi-square goodness of fit, $\chi^2 = 3.84$, $T \geq 22.43$), exlusive of Comal 2 in April ($T = 2.08$). However, due to the constraints of our sampling technique, we were unable to make statistical associations of the beetles with specific hydrophytes and algae, or their assemblages.

Phenology

All life stages, except eggs, of both species of riffle beetles were collected on all sampling dates from Comal Springs (Fig. 5). In general, more larvae of both *M. pusillus* and *H. comalensis* were collected in samples than adults or pupae. However, during July, adults of *H. comalensis* and *M. pusillus* were re-

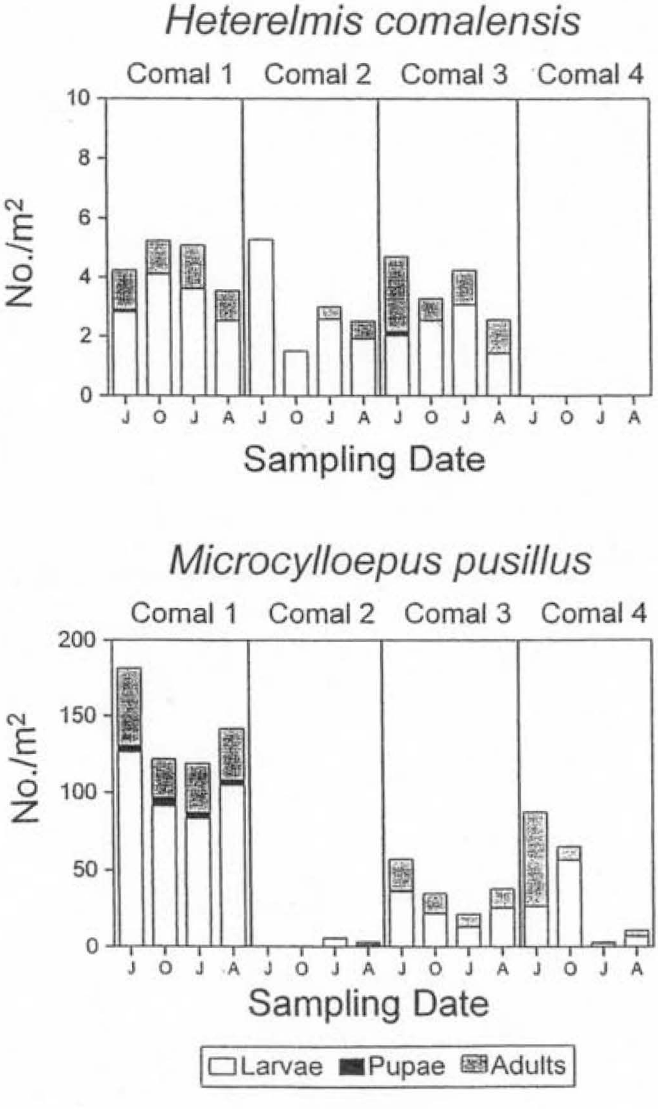

Fig. 5. Mean benthic densities (number/m^2) for *Heterelmis comalensis* and *Microcylloepus pusillus* collected from Comal Springs, Texas, 1993–1994.

Table 4. Percent overlap among occurrencs of riffle beetles in benthic samples collected at Comal Springs, Texas, 1993–1994.

Spring-run	Sampling date	Both species	*Microcylloepus pusillus* only	*Heterelmis comalensis* only	Neither species
1	Jul	64.5	35.5	0	0
	Oct	78.8	18.2	0	3.03
	Jan	81.2	9.4	0	9.4
	Apr	67.6	29.7	0	2.7
2	Jul	14.3	7.1	14.3	64.3
	Oct	10	0	20	70
	Jan	57.1	0	14.3	28.6
	Apr	20	10	0	70
3	Jul	50	41.7	0	8.3
	Oct	66.7	33.3	0	0
	Jan	57.1	14.3	0	28.6
	Apr	63.6	27.3	0	9.1
4	Jul	0	50	0	50
	Oct	0	66.7	0	33.3
	Jan	0	42.9	0	57.1
	Apr	0	37.5	0	62.5

spectively the dominant life stages collected from Comal 3 and 4. For the July and October sampling dates at Comal 2, only larvae of *H. comalensis* were collected, and no specimens of *M. pusillus* were collected from Comal 2 during July. Larval benthic densities for *M. pusillus* ranged from 0.28/m^2 (Comal 2, July) to 125.8/m^2 (Comal 1, July). By comparison, benthic densities of *H. comalensis* larvae generally were much less than those of *M. pusillus* and ranged from 1.4/m^2 (Comal 3, April) to 5.3/m^2 (Comal 2, July). Several larval instars of both species were observed in collections taken on all sampling dates, but no attempt was made here to quantify their relative temporal distributions. Pupae were poorly represented in samples. The maximum benthic densities of this life stage for *M. pusillus* and *H. comalensis* were estimated as 5.8/m^2 (Comal 1, October) and 0.2/m^2 (Comal 3, October), respectively. Comparable numbers of pupae were collected on the other sampling dates for each spring-run. Benthic densities of adult *M. pusillus* did not exceed 60.7/m^2 (Comal 4, July) while the greatest benthic density of adult *H. comalensis* was 2.5/m^2 (Comal 3, July).

Most samples taken in Comal 1 and 3 contained examples of both *H. comalensis* and *M. pusillus* (Table 4). Those samples from Comal 1 and 3 containing only one of these species contained *M. pusillus* exclusively. For Comal 2, by comparison, *H. comalensis* was found in most of those samples where only one of the species were found, but a larger proportion of these samples contained neither species. For Comal 4, the spring-run where *H. comalensis* was not collected, the number of samples containing *M. pusillus* and samples containing no beetles were similar across all sampling dates.

Discussion

The physical and chemical characteristics of Comal Springs that we measured were highly uniform and similar to those reported for other studies of this system (CROWE & SHARP 1997, SHERWOOD & SHEATH 1999). Of those measurements that exhibited significant variation (e.g., dissolved oxygen), we offer that such differences may not be biologically significant. Depth and current velocities also were uniform among spring-runs and sampling dates. Our data indicate that *H. comalensis* inhabits shallower water and higher current velocities when compared to all samples measured and those containing *M. pusillus*. However, this apparent difference in habitat selection by *H. comalensis* may be attributed to the smaller number of specimens we collected of this species. Comal 4 had more lentic-like conditions in comparison to the other spring-runs and apparently such conditions are unfavorable as habitat for the Comal Springs riffle beetle because we did not collect this species from this spring-run. The substrate in Comal 4 was dominated by fine sediments and the apparent absence of *H. comalensis* from this location suggests that such fine substrates do not provide suitable habitat for this species although they are apparently adequate for the widely distributed and more ecologically tolerant *M. pusillus*.

Both *H. comalensis* and *M. pusillus* appear to have overlapping, asynchronous generations in Comal Springs. Moreover, the presence of pupae in samples taken quarterly suggests that the respective emergence patterns for both species are non-seasonal as is typical for elmids in springs (SHEPARD 1990). However, we do not attempt to further describe the life histories of these species here because life histories of elmids are notoriously long and complicated (MAITLAND 1967, BROWN 1973, LESAGE & HARPER 1976, WHITE 1978, SEAGLE 1980, STEEDMAN & ANDERSON 1985, TAVARES & WILLIAMS 1990, PHILLIPS 1997 a, 1997 b). For instance, BROWN (1973) found that when larvae of *Microcylloepus* were placed under stressful conditions, they could survive up to two years. Similarly, adults of *H. comalensis* collected in the wild have been kept alive under laboratory conditions for over one year (JOE FRIES, U.S. Fish & Wildlife Service, personal communication). Thus, the life histories suggested by our study may be deceptive given our quarterly sampling regime. A more detailed sampling program will be required to fully elucidate the life histories of *H. comalensis* and *M. pusillus* at Comal Springs.

Microcylloepus pusillus and *H. comalensis* do not appear to be spatially separated in Comal Springs, or at least not completely so. The mechanisms allowing the coexistence of these two species are not fully understood, but factors such as substrate availability and competition with each other and other aquatic species, at least in part, may be influencing their respective distributions. MINSHALL (1968) suggested factors that allow related species to coexist also could include subtle differences in life histories, size differences, and habitat specificity. In particular, the combination of seasonal succession, differences in food habits, and microhabitat preferences can appreciably reduce competition among related species (MINSHALL 1968).

Although our data showed that both species of elmids occurred predominantly in vegetated areas, this difference may simply reflect the dense and diverse vegetation that grows in most of the spring-runs rather than a preference for such habitats by the beetles. This contention is supported by our finding that several sample cells among the four spring-runs did not contain any aquatic vegetation, yet they yielded both species of beetles. Our findings are in stark contrast to those of CROWE & SHARP (1997) who reported that *H. comalensis* occurs in areas with little to no vegetation. Investigations of riffle beetles in Europe have produced conflicting information about the extent to which these insects use aquatic vegetation as habitat. However, some studies have shown the distribution of riffle beetles is positively associated with aquatic vegetation. MAITLAND (1967) found that several species of elmids occurring in Scottish streams were associated with both vegetation and rocky substrates, but the greatest benthic densities for the respective species were on vegetation. Conversely, IVERSEN et al. (1985) found that the riffle beetle *Oulimnius tuberculata* (MÜLLER) was abundant in the benthos of a Danish stream, but it was poorly represented in aquatic vegetation. However, the rarer *Elmis aenea* (MÜLLER) was found equally distributed in both vegetation and the benthos (IVERSON et al. 1985). In a similar study, MALMQVIST & SJÖSTRÖM (1983) found that the abundances of two species of riffle beetles in a Swedish stream were positively correlated with the occurrence of algae and moss.

The uniformity of physical-chemical conditions and habitat at Comal Springs probably serves as the primary foundation for the random, aseasonal distribution of the life stages we observed. Similar aseasonality and uniformity among insect populations occurring in environmentally uniform, large-volume springs previously was reported by SLOAN (1956). The physical microhabitats of *H. comalensis* and *M. pusillus* also likely play a significant role in determining their distributions in the spring-runs, but the specific mechanisms by which their respective populations are regulated are not known and require further investigation. The marked longitudinal zonation downstream of spring sources that has been documented for smaller systems (RESH 1983, McCABE 1998) apparently is not as pronounced for larger, more diffuse systems such as Comal Springs. In addition to the primary spring openings at Comal Springs, each spring-run has numerous smaller seeps and springs that emerge along their respective lengths. Although these smaller springs each produce only a fraction of the flow issuing from the major spring orifices, they may provide additional stability to the habitat conditions in this ecosystem. In addition to the stability they provide, multiple spring sources likely confound interpretation of benthic invertebrate data collected from such systems as Comal Springs (RESH 1983).

Physical mechanisms, such as periodic spates and drought, also may serve to regulate riffle beetle populations at Comal Springs, because they tend to affect the entire system in a similar manner and are not restricted to local or longitudinal variations. The upper portions of the springs-runs at Comal Springs are subject to periodic spates following periods of high rainfall, but the extent to which such events influence the riffle beetle populations is unknown. Other studies of riffle beetles also have concluded that physical factors play key roles in the distribution of populations. For example, physical factors were shown to be the most important determinant in controlling the populations of several species of riffle beetles in a Scottish Stream (MAITLAND 1967). Similarly, TURCOTTE & HARPER (1982) found that elmid density in a non-seasonal Andean stream was regulated by periodic spates. Although aquatic communities are often viewed as being largely controlled by abiotic processes including frequency and intensity of hydrologic events (i.e., flooding and drought), or the broader biological and geological characteristics of the system, recent studies (DOWNES et al. 1998) have suggested benthic communities also can be largely regulated by local processes in the stream. Others contend that when environmental conditions are uniform, population fluctuations are presumed to result primarily from biotic factors, such as life history traits, and community interactions including food availability and predation (VARZA & COVICH 1995). For example, MALMQVIST & SJÖSTRÖM (1983) reported that variables pertaining to substrate, vegetation, current velocity, coarse detritus, and depth partly explained the distribution of two species of elmids in a Swedish stream. However, biotic factors were viewed as being more important in regulating these distributions than were abiotic factors (MALMQVIST & SJÖSTRÖM 1983).

Direct competition between *H. comalensis* and *M. pusillus* cannot be ruled-out as a mechanism regulating their respective populations although we found little evidence that would support this argument. The co-occurrence of *H. comalensis* and *M. pusillus* in the majority of samples collected suggests that they partition their respective habitats at some level to avoid direct competition. Our observations led us to question whether food availability affects the population dynamics of these two species. Although feeding varies among species, and even more among genera, it appears that most elmids feed on microorganisms and debris scraped from the substrate (BROWN 1987, TAVARES & WILLIAMS 1990). Given the highly productive nature of Comal Springs and other spring-systems in central Texas (e.g., HANNAN & DORRIS 1979), we suspect that availability of food resources for these two beetles probably is not a factor limiting their respective populations. This contention is supported by the findings of TAVARES & WILLIAMS (1990) who found that three species of elmids co-occurring in a temperate stream had almost complete dietary overlap. Likewise, MALMQVIST & SJÖSTRÖM (1983) found that *Elmis aenea* (P. MÜLLER) and *Limnius volckmari* (PANZER) had similar diets and coexisted throughout the year indicating niche overlap occurred. However, they cautioned that, if food were overrepresented, then the beetles might be generalists with respect to diet and microhabitat selection (MALMQVIST & SJÖSTRÖM 1983). Interspecific predation and physical displacement likewise could be viewed as regulating factors (BROWN & SHOEMAKE 1969).

The wide distribution of *M. pusillus* at Comal Springs and elsewhere in Texas and throughout the U.S., in comparison to *H. comalensis*, may be partially attributable to morphological differences between the species. Adults of *Microcylloepus* commonly show up at lights suggesting that they are capable of extended flight (LEECH & SANDERSON 1959, BROWN & SHOEMAKE 1969). We found that the *M. pusillus* occurring at Comal Springs are winged and are assumed to be capable of flight. While some species of *Heterelmis* are capable of flight (CHERYL BARR, unpublished data), adults of *H. comalensis* lack functional flight wings, and, correspondingly, do not have the ability to disperse broadly. Because of this limited ability, the single population of *H. comalensis* at Comal Springs could be severely impacted or extirpated if the springs permanently stop flowing. Although Comal Springs were dry for 5 months in 1956 and were briefly dry in 1990, the mechanism by which *H. comalensis* survived this dewatering of its habitat and the extent its population was negatively impacted are unknown. The species may have survived these drought events by retreating into the springs-heads, aquifer, or the hyporheos as spring-flows diminished, or a life-stage specific aestivation may have allowed their survival. The ability of riffle beetles to survive drying of their habitat by burrowing into the substrate is well documented (COLE 1957, BELL 1972, BROWN 1973, 1987). Hyporheic retreats are likely the mechanism by which *H. comalensis* survived previous drying events at Comal Springs, but, given the absence of data documenting this behavior, this contention is entirely speculative. *Microcylloepus pusillus* inhabits a broad range of lotic habitats in Texas (senior author, unpublished data) suggesting that this species could repopulate Comal Springs from nearby aquatic systems if the extant population became extirpated.

Development and maintenance of refugia stocks for endangered species, including *H. comalensis*, from Comal Springs are goals of the United States Fish and Wildlife Service (1995). However, captive breeding stocks of *H. comalensis* are not yet in place because the habitat requirements of these species are extremely difficult to emulate under artificial conditions. Although these beetles can be kept alive under laboratory conditions for over one year, reproduction in such an artificial environment has not yet been demonstrated (personal communication, JOE FRIES, U.S. Fish and Wildlife Service).

Presently, the only means by which to ensure the longterm survival of *H. comalensis* at Comal Springs is to maintain high quality spring-flows, and continue to protect the physical habitat of the spring-runs from anthropogenic disturbances. Although the specific spring-flow requirements necessary to support populations of *H. comalensis* remain largely unknown, the existing habitat for this species suggests that at least the conditions reported herein are required. The U.S. Fish and Wildlife Service (1995) has identified collective spring-flows of approximately 5.7 m^3/sec (200 ft^3/sec) and 4.2 m^3/sec (150 ft^3/sec) for take and jeopardy levels, respectively, for the federally endangered fountain darter (*Etheostoma fonticola* JORDAN and GILBERT) which also occurs at Comal Springs. Take levels are those that damage or destroy individuals while jeopardy levels are those that result in appreciable reduction of survival and recovery of the species. Spring-flow levels necessary to sustain the Comal Springs riffle beetle have not yet been identified. Based on the distribution of the riffle beetles in the spring-runs reported herein, we were unable to determine if the take and jeopardy levels established for the fountain darter are sufficient for *H. comalensis*. Indeed, the data reported here were collected when spring-flows were greater than the historic mean spring-flow. We contend that a range of spring-flows is ideal for sustaining the population of *H. comalensis* at Comal Springs. From a conservation management perspective, this range ideally should reflect the range of spring-flows recorded for the period of record from 1882 to present to the extent that the springs do not stop flowing for extended periods of time or become permanently dry as a result of anthropogenic activities. Reductions in water levels in the Edwards Aquifer to the extent that spring-flows cease likely would have devastating effects on the only known secure population of this species and could result in its extinction.

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