12-2014

# Relationship between stream velocity & depth and snail size distribution & density of the balcones elimia, elimia comalensis (pilsbry, 1890) (gastropoda: pleuroceridae) in comal springs, texas

Kathryn E. Perez
*The University of Texas Rio Grande Valley*, kathryn.perez@utrgv.edu

Russell L. Minton

Scott A. Reese

David M. Haye



## Recommended Citation

Perez, K. E., Minton, R. L., Reese, S. A., & Hayes, D. M. (2011). Relationship between Stream Velocity & Depth and Snail Size Distribution & Density of the Balcones Elimia, Elimia Comalensis (Pilsbry, 1890) (Gastropoda: Pleuroceridae) in Comal Springs, Texas. Texas Journal of Science, 63(3/4), 183–198.

TEXAS J. OF SCI. 63(3):183-198 AUGUST, 2011 (PUBLISHED DEC 2014)

# RELATIONSHIP BETWEEN STREAM VELOCITY & DEPTH AND SNAIL SIZE DISTRIBUTION & DENSITY OF THE BALCONES ELIMIA, *ELIMIA COMALENSIS* (PILSBRY, 1890) (GASTROPODA: PLEUROCERIDAE) IN COMAL SPRINGS, TEXAS

**Kathryn E. Perez[1], Russell L. Minton[2], Scott A. Reese[3] and David M. Hayes[4]**

[1]*Department of Biology, University of Texas Pan American*
*Edinburg, Texas 78539*
[2]*Department of Biology, University of Houston Clear Lake*
*Houston, Texas 77058*
[3]*Department of Biological and Physical Science, Kennesaw State University*
*Kennesaw, Georgia 30144*
[4]*Department of Biological Sciences, Eastern Kentucky University*
*Richmond, Kentucky 40475*

**Abstract**.–Pleurocerid snails are important components of aquatic ecosystems and the majority of species are threatened or endangered. This study describes aspects of the life-history of *Elimia comalensis*, specifically population density in relationship to water velocity and depth, and seasonal change. Also examined are spatial segregation of different *E. comalensis* age groups and the relationship of snail size (proxy for age) to flow, depth, and seasonal change. The study was carried out in the lotic portion of spring run 3, Comal Springs, New Braunfels, Texas, by quadrat sampling at 10 m intervals from the spring head to Landa Lake in Fall, Winter, and Spring 2005-2006. The length of snails was strongly influenced by physical characteristics of the stream with stream depth, water velocity, and distance from the spring head accounting for ~43% of the individual variability for shell length ($p < 0.001$). A significant relationship between snail size, stream depth and water velocity was found, with spatial segregation of juvenile snails into the deepest, fastest moving water. Snail population densities did not change across sampling seasons ($p = 0.285$).

---

Pleuroceridae is a highly endangered family of freshwater gastropods with >50% of the species endangered or extinct (Brown et al. 2008). Threats to pleurocerids include water extraction, impoundments, point-source pollution, and invasive species (Brown et al. 2008). Pleurocerids are also significant functional components of aquatic ecosystems affecting periphyton community structure, abundance and diversity of other macroinvertebrate taxa, and populations of predators (Brown et al. 2008). As such, pleurocerids represent a threatened and important component of stream ecosystems, but specific life history information for many species is lacking.

*Elimia* is the most diverse genus of pleurocerid snails with over 100 species ranging from Texas northward into the Midwest and northeastern United States and Canada (Brown et al. 2008). *Elimia* species are periphyton grazers and detritus shredders (Mulholland et al. 1985) that reproduce perennially (Dillon 2000) and may show sexual dimorphism (Dillon 1984a). *Elimia* species inhabit both lakes and rivers with species preferring lotic habitats.

Published life history studies of *Elimia* have been limited to a few species (Dillon & Davis 1980; Dillon 1984b; Huryn et al. 1994; Huryn et al. 1995; Huryn & Denny 1997), and only one (Tolley-Jordan & Owen 2008) includes *E. comalensis*, the subject of this study. The Balcones Elimia, *Elimia comalensis* (Pilsbry 1890), is the only pleurocerid known from Texas and one of the few to occur west of the Mississippi River. This study describes some aspects of the life-history of *E. comalensis* in Comal Springs, New Braunfels, Texas. Specifically, this study examines *E. comalensis* population density in relationship to water velocity, water depth, and seasonal change. Previous work in other *Elimia* species, including *E. comalensis*, suggested significant relationships between water velocity and depth on population density (Johnson & Brown 1997; Huryn & Denny 1997; Tolley-Jordan & Owen 2008). In addition to those factors, this study examined spatial segregation of different age groups of *E. comalensis* and the relationship of snail size (proxy for age) to water velocity, depth, and seasonal change.

Recent molecular work on *E. comalensis* revealed this species is native to the Comal River drainage, but widely distributed in West Texas springs through human-mediated introductions in the early 20th century (Hayes et al. 2007). Hayes et al. (2007) observed significant differences in morphology among populations occupying different drainage basins, but with no apparent population genetic structure distinguishing these populations. Minton et al. (2007) found that difference in morphology between two populations of *E. comalensis* appeared to be related to differences in the size (proxy for age) at which individual growth began to slow. Reduction in growth rate resulted in different adult morphologies.

One potential determinant of snail shape is habitat usage (Minton et al. 2007). However, habitat usage over various seasons by juvenile and adult *E. comalensis* is relatively unknown. Cheatum & Mouzon (1934) showed that different sized individuals of *E. comalensis* in Comal Springs exhibited different spatial distributions, but with no indication of factors driving any spatial segregation. The current study attempts to fill this gap in knowledge by examining the relationship of population density and snail size to stream velocity, depth, and seasonality.

## MATERIALS AND METHODS

*Study site*.–Comal Springs, the largest outflows of the Edwards Aquifer, emerge at an elevation of 190 m and form the Comal River in Comal County, Texas. The river flows 1.6 km to its confluence with the Guadalupe River. In the middle 1800's the Comal River was dammed, forming Landa Lake, and a new channel was constructed to divert water for industrial use. Four of the springs emerge at a slightly higher elevation than the dams controlling lake surface elevation, and thus have short spring runs. In modern times, the lake and associated springs serve as a recreation area and groundwater source.

Average annual water properties for the springs and riverine system are pH 7.4, water temperature of 23.3°C, dissolved oxygen of 9.1 mg/L, and 309 mg/L dissolved solids (Fahlquist & Slattery 1997). Spring run 3, where this study occurred, has an average discharge of 0.3-0.6 $m^3/s$ (Crowe & Sharp 1997), a length of 138 m, and an average width of 8 m. Substrates vary from boulders and bedrock at the head of the spring, to gravel in the middle reaches, and silt in the tail reach (Crowe & Sharp 1997). There is little vegetation near the spring head due to the substrate and heavy riparian cover, while the middle reaches have patchy areas of *Ludwigia repens* and *Pomatogeton illinoisensis* (cf. Crowe & Sharp 1997). The tail reach is densely covered with *Cabomba caroliniana*, *Sagittaria platyphylla*, and *Vallisneria americana* (cf. Crowe & Sharp 1997).

Data were collected during three separate trips to the spring run of Comal Springs 3 (Figure 1a) 2-5 September 2005 (Fall), 6-9 January 2006 (Winter), and 17-20 April 2006 (Spring). Beginning at the bedrock wall at the head of spring run 3, single meter-wide transects were sampled across the upper half of the run channel using plastic 0.25 $m^2$ quadrats (101 quadrats sampled total). Data from seven transects were collected, with a 10 m gap between transects. Within each quadrat, stream velocity and depth were measured using a Global Water FP111 flow probe once in the center of each transect at midheight in the water column. In all quadrats each individual *E. comalensis* was collected and transferred to a tray for measurement. Snails were collected via snorkeling and submerged vegetation was searched for snails, and algal mats were examined for snails. Following collection, each individual snail's length (apex to anterior lip of aperture) was measured using vernier calipers to the nearest 0.01 mm (Figure 1b). *Elimia comalensis* in Comal Springs does not show any shell apex erosion, therefore length was treated as a descriptor of growth. After measuring, individuals were returned to their quadrat of origin.

Snail densities were calculated for individual quadrats. Spatial and seasonal variations in snail density, snail length, and stream characteristics (stream depth, water velocity, and distance from the spring) were examined using analyses of covariance (ANCOVA). The stream characteristics were used as covariates when looking at snail variables and when looking at other stream characteristics. A multiple regression analysis was used to determine the relative

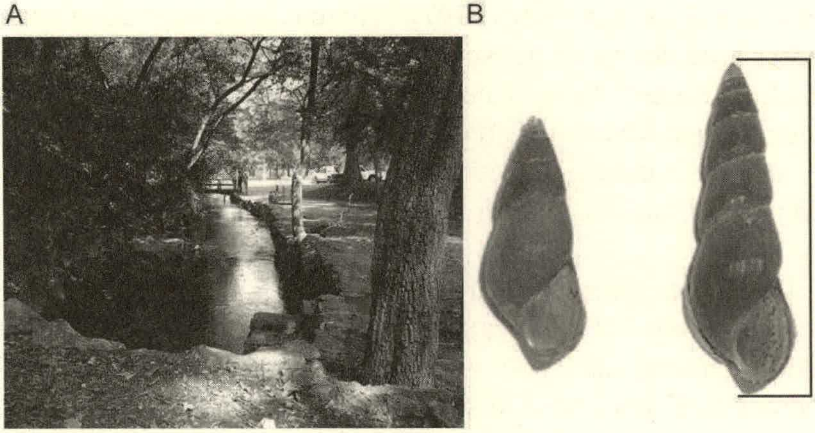


Figure 1. (a) Comal Springs, Spring Run 3. (b) Shell of *E. comalensis* with total length measurement indicated.

influence of the stream characteristics on snail distribution and morphology. Significant differences were reported at the $\alpha \leq 0.05$ level.

## RESULTS

There was a steady increase in stream depth with distance from the spring (Fig. 2a). This resulted in a ~0.2 m increase in depth from the first transect to the final one 63 m downstream ($p \leq 0.001$); there was no change in stream depth across sampling dates ($p = 0.234$). The pattern of stream depth changes and the distance from the spring were equally able to account for ~22 % of the variation seen in water velocity ($r^2 = 0.221$, $p < 0.001$) with the range of stream depth (0.9 m) able to account for a 0.45 m/s increase in stream velocity, while the distance from the spring accounts for a 0.44 m/s increase in stream velocity (Fig. 2b). Controlling for these covariates still yielded a higher stream velocity during the winter sampling period

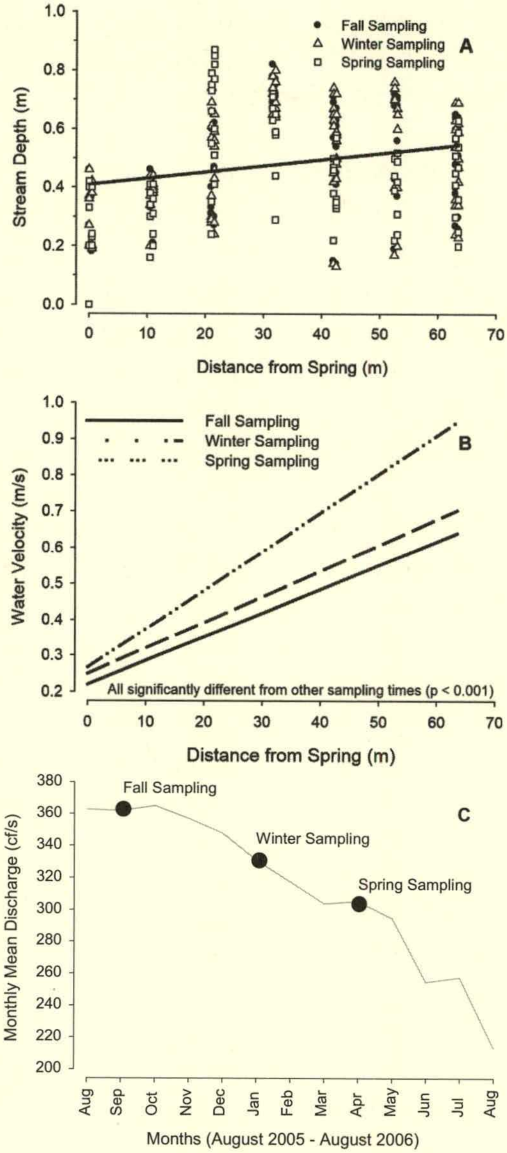


Figure 2. Stream characteristics for a 70 m stretch of Comal Springs starting at spring run 3. Fall samples were collected in September 2005; Winter samples in January 2006; and Spring samples in April 2006. (a) Stream depth (m) (b) Water velocity (m/s) (c) Monthly mean discharge (cf/s) from USGS gage (Hydrologic Unit Code 12100202). 29.705833'W, 98.122222'N; NAD27.

and higher still the following spring ($p < 0.001$). These increases in stream velocity are especially interesting given the decreases in stream discharge during that sampling time (Fig. 2c).

The density of snails along the sample site did not change across sampling seasons ($p = 0.285$). Average snail density for Fall was 78.1 snails/$m^2$, Winter – 70.8 snails/$m^2$, Spring – 51.5 snails/$m^2$. The stream physical characteristics were only able to account for ~15 % of the variation seen across quadrat densities (Figs. 3a-c; $r^2 = 0.151$, $p < 0.001$). Increasing water velocity yielded lower snail densities and the range of velocities (0.8 m/s) across our study site accounted for a 43 snail/$m^2$ lower density (Fig. 3a). Increasing stream depth resulted in higher snail densities and the range of depths across this study site accounted for a 92 snail/$m^2$ higher density (Fig. 3b). Moving from the spring head toward the lotic end of the study site resulted in an increasing snail density (Fig. 3c), though this only accounted for a 35 snail/$m^2$ increase over the entire length.

The length of snails along the study site was strongly influenced by the physical characteristics of the stream with stream depth, water velocity, and the distance from the spring head accounting for ~43 % of the individual variability for shell length (Figs. 4a-c; $r^2 = 0.434$, $p < 0.001$). Of the physical characteristics, stream depth and distance from the spring head affected shell length equally, though in opposite directions ($\beta$ = -0.419 and 0.434, respectively; Figs. 4b & c). Increased stream velocity decreased shell length, though this variable influenced shell length less than the other physical characteristics ($\beta$=0.221; Fig. 4a). The effect of all physical characteristics was significantly lower during the spring sampling trip ($p < 0.001$).

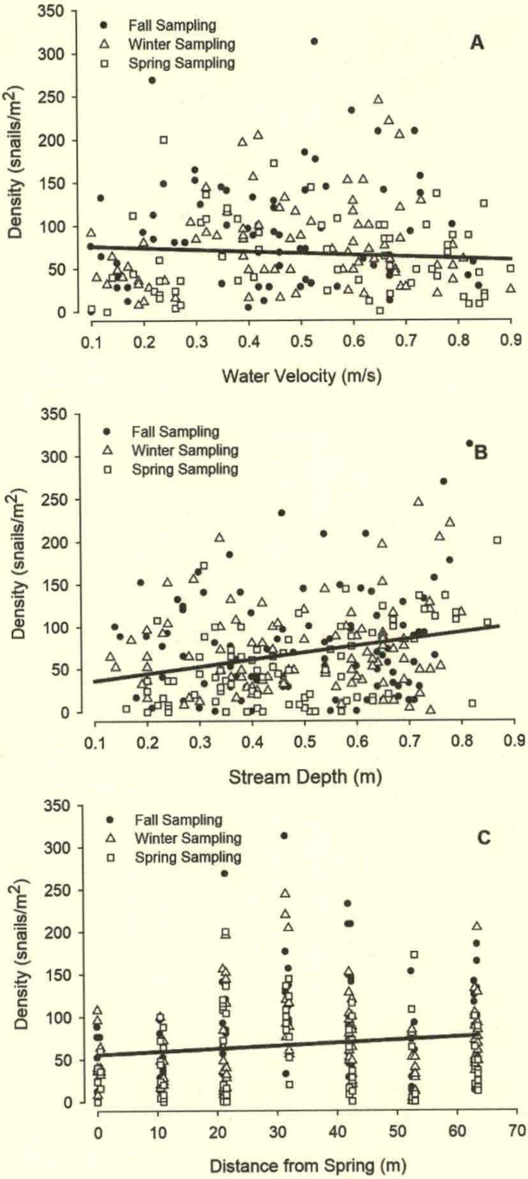


Figure 3. Density of *Elimia comalensis* (individuals/$m^2$) within quadrats sampled along a 70 m stretch of Comal Springs. Fall samples were collected in September 2005; Winter samples in January 2006; and Spring samples in April 2006. (a) Influence of water velocity (m/s) (b) Influence of stream depth (m) (c) Distribution pattern starting at spring run 3.

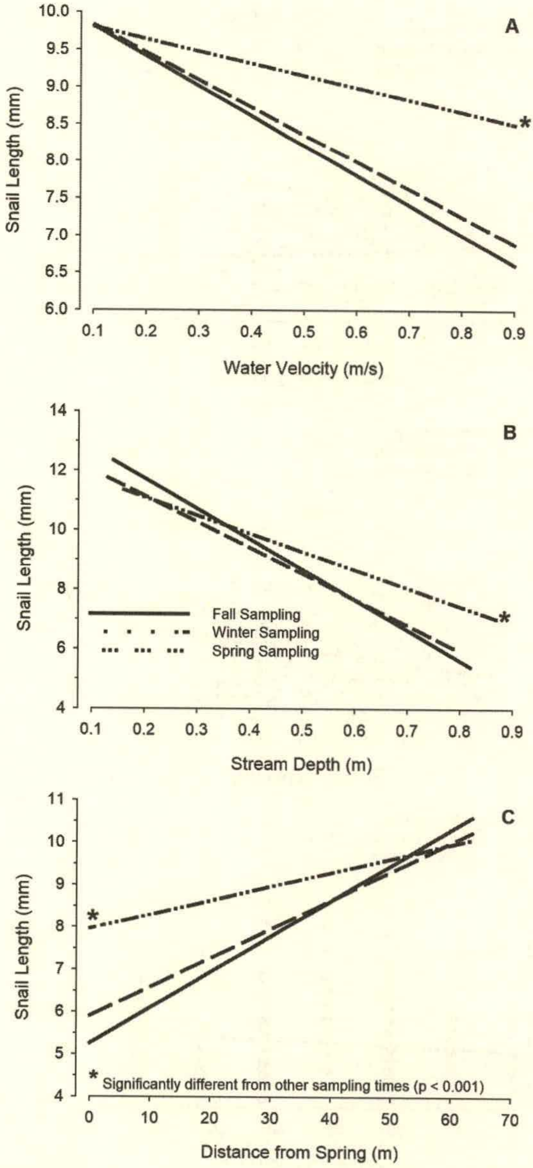


Figure 4. Shell length of *Elimia comalensis* (mm) sampled along a 70 m stretch of Comal Springs. Fall samples were collected in September 2005; Winter samples in January 2006; and Spring samples in April 2006. (a) Influence of water velocity (m/s) (b) Influence of stream depth (m) (c) Distribution pattern starting at spring run 3. An ANCOVA was used to determine differences among sampling seasons.

## DISCUSSION

*Elimia* species are important components of stream ecological processes (Brown & Johnson 2004, reviewed in Brown et al. 2008) with reported influences on the community structure of periphyton (Tuchman & Stevenson 1991; Morales & Ward 2000) and macroinvertebrates (Harvey & Hill 1991). Understanding the ecology of *E. comalensis* is important given that this species occurs in areas detrimentally affected by human activity and has recently spread to previously uninhabited springs (Hayes et al. 2007). The invasive activity of *E. comalensis* raises questions of its impact on native fauna in springs to which it has been introduced.

This study attempts to describe some population ecological parameters of *E. comalensis* as a starting point for further study on species interactions. Other habitat variables such as vegetative cover, stream canopy cover, and competition with other snail or grazing macroinvertebrate species, while potentially contributing to *E. comalensis* population distribution and density are not examined here.

*Elimia comalensis* was found to occur in higher densities with greater stream depth and lower water velocity. This disagrees somewhat with the results of Tolley-Jordan & Owen (2008) who found significantly fewer *E. comalensis* in water velocity of 0-0.1 m/s and no difference in *E. comalensis* density among stream samples ranging in velocity from 0.11 to >0.6 m/s. Tolley-Jordan & Owen (2008) found no difference in *E. comalensis* density in depths from 0-1.2 m but found significantly lower density of *E. comalensis* at 1.21 to 1.6 m than in shallower areas.

The observed correlation between snail density and water depth/velocity has been proposed (Johnson & Brown 1997; Huryn & Denny 1997) to be due to a number of potential factors: 1) snails preferring particular depth/velocity regimes and positioning themselves in those areas; 2) the effects of stream flow and spates on snail stream position; and 3) food availability and effects on growth rates.

In Comal Springs, density of *Elimia comalensis* individuals ranged from 43 snails/m$^2$ in shallow, higher water velocity quadrats to 92 snails/m$^2$ in deeper, lower water velocity quadrats. The population density of *E. comalensis* (average 78 snails/m$^2$) was low compared to that of *E. clavaeformis* (1000 snails/m$^2$; Rosemond et al. 1993) from Walker Branch, Tennessee and *E. cahawbensis* (200-550 snails/m$^2$; Richardson et al. 1988) from Alabama. Densities of *E. comalensis* are more similar to those of *E. proxima* (<170 snails/m$^2$; Jeremiah 2007) from Appalachian headwater streams in North Carolina and *E. clara* (60-275 snails/m$^2$; Richardson et al. 1988) from Alabama, and within the ranges found in other pleurocerids (Stewart & Garcia 2002).

In the current study, more juvenile snails were found in higher velocity reaches, while overall snail density was highest in deeper, low velocity areas. Huryn & Denny (1997) showed that juvenile *Elimia* congregate in faster flow reaches because smaller shells are less subject to drag. Johnson & Brown's (1997) work on *Elimia semicarinata* in Kentucky streams also noted that adult density and size was negatively correlated to flow. Other studies on pleurocerids have shown the same correlation between higher snail densities and relatively shallow, low flow areas. This is only true in relative terms as stream pleurocerids are not typically found in depositional and extremely low velocity reaches (Foin 1971; Ross & Ultsch 1980).

Johnson & Brown (1997) suggest that a negative effect of increasing depth on dissolved oxygen concentration limits densities. Only in lentic systems does this trend seem to not apply (Laman et al. 1984). Apparent juvenile preference for higher-flow areas has also been proposed to be due to spate-mediated removal of adults, reduction of feeding rate and growth in high flow environments, or indirect effects on growth of reduced food availability (Johnson & Brown 1997). Due to the spring-fed nature of Comal springs there are times of higher and lower flow, but there are not spates similar to streams. The lack of spates could rule out this possibility as an explanation for the concentration of juveniles in deep, fast water.

*Elimia* are perennial snails with life spans ranging from two to 11 years (Richardson et al. 1988; Huryn et al. 1994). Huryn et al. (1994) summarized the seasonal life-history of *Elimia*, with egglaying from early spring through early summer, followed by spring and summer high growth periods. *Elimia comalensis* population size distribution favors snails of intermediate size, as would be predicted for a relatively long-lived species with a fairly constant population size (Butler 1982). Similar results were found for *E. proxima* (Jeremiah 2007), and *E. cahawbensis* and *E. clara* (Richardson et al. 1988).

One result of this study is an observed difference in the sizes of snails in the April sampling population. Huryn (1994) observed in other *Elimia*, in late summer and fall, one to three overlapping cohorts. The size distribution of *E. comalensis* appears similar to Huryn's (1994) observations, with small snails growing into larger size categories between Spring and Fall.

One unmeasured factor which could have a significant effect on snail population density is the effect of competition for space or food. In Comal Springs, two invasive species of freshwater snail have potential to compete with *E. comalensis*. Tolley-Jordan & Owen (2008) found a negative co-occurrence of *E. comalensis* and *Melanoides tuberculatus* that they attribute to these species requiring different habitat types. *M. tuberculatus* requires more lentic habitats due to susceptibility of dislodgement by spates (Giovanelli et al. 2005; Tolley-Jordan & Owen 2008), while *E. comalensis*, similar to other pleurocerids, prefers flowing water habitat (Lindholm & Huffman 1979; Dillon 2000).

More significant for this study, is the positive co-occurrence of *E. comalensis* and *Tarebia granifera*. *Tarebia granifera* can tolerate flowing water, although they also prefer lentic habitat, where densities may be up to 20X higher (Tolley-Jordan & Owen 2008). While competition with *Melanoides* and *Tarebia* could potentially influence the results of the current study, Tolley-Jordan & Owen's (2008) work suggests that the lotic habitat where this studied was carried out minimized the potential effects of such competition.

A final limitation of this study is lack of data on vegetative cover in Comal springs. Tolley-Jordan & Owen (2008) found *E. comalensis* densities were significantly lower in 76-100% vegetative cover but no difference across a range of 0% to 75% cover. In Comal Springs vegetative cover changes somewhat seasonally, the fact that results did not find significant differences in *E. comalensis* density across seasons is perhaps an indication that vegetative cover is less important that depth or current velocity in structuring *E. comalensis* density. However, this can only be demonstrated by further study of *E. comalensis* density incorporating further variables such as vegetative cover, cooccurrence with potential competitors, substrate, and stream canopy cover.

## ACKNOWLEDGMENTS

Funding for this project was provided by a Texas Academy of Science graduate student research grant to ULM and a Howard Hughes Medical Institute undergraduate science education grant to ULM. KEP support by the SPIRE program at University of North Carolina–Chapel Hill (NIH-MORE GM00678), Duke Biology

Department, University of Wisconsin System Institute for Race and Ethnicity Grant, and a University of Wisconsin at La Crosse Faculty Research Grant. We thank Jeff Brooks, Eugene Thibodeaux, and John White for their assistance with field work.

## LITERATURE CITED

Brown, K. M. & P. D. Johnson. 2004. Comparative conservation ecology of pleurocerid and pulmonate gastropods of the United States. Am. Malacol. Bull., 19(1/2):57–62.

Brown, K. M., B. Lang & K. E. Perez. 2008. The conservation ecology of North American pleurocerid and hydrobiid gastropods. J. N. Am. Benthol. Soc., 27(2):484495.

Butler, M. G. 1982. Production dynamics of some arctic *Chironomus* larvae. Limnol. Oceanogr., 27(4):728-736.

Cheatum, E. P. & E. D. J. Mouzon. 1934. Biometrical study of *Goniobasis comalensis* Pilsbry from two diverse habitats. Field and Lab., 1(1):18-23.

Crowe, J. C. & J. M. Sharp. 1997. Hydrogeologic delineation of habitats for endangered species: the Comal Springs/River System. Environ. Geol., 30(1):17-28.

Dillon, R. T. 1984a. What shall I measure on my snails? Allozyme data and multivariate analysis used to reduce the non-genetic component of morphological variance in *Goniobasis proxima*. Malacologia, 25:503-511.

Dillon, R. T. 1984b. Geographic distance, environmental difference, and diversity between isolated populations. Syst. Biol., 33(1):69-82.

Dillon, R. T. 2000. The Ecology of Freshwater Molluscs. Cambridge University Press, Cambridge, UK. 524 pp.

Dillon, R. T. & G. M. Davis. 1980. The *Goniobasis* of southern Virginia and northwestern North Carolina: genetic and shell morphometric relationships. Malacologia, 20(1):83-98.

Fahlquist, L. & R. N. Slattery. 1997. Water quality assessment of the Comal Springs Riverine System, New Braunfels, Texas, 1993-94. U.S. Dept. of the Interior, U.S. Geological Survey, Reston, Va. 6 pp.

Foin, T. C. 1971. The distribution pattern of the freshwater prosobranch gastropod *Oxytrema proxima* (Say). J. Elisha Mitchell Sci. Soc., 87(1):1-10.

Giovanelli, A., C. L. P. A. C. da Silva, G. B. E. Leal & D. F. Baptista. 2005. Habitat preference of freshwater snails in relation to environmental factors and the presence of the competitor snail *Melanoides tuberculatus* (Müller, 1774). Mem. do Inst. Oswaldo Crus, 100(2):169-176.

Harvey, B. C. & W. R. Hill. 1991. Effects of snails and fish on benthic invertebrate assemblages in a headwater stream. J. N. Am. Benthol. Soc., 10(3):263-270.

Hayes, D. M., R. L. Minton & K. E. Perez. 2007. *Elimia comalensis* (Gastropoda: Pleuroceridae) from the Edwards Plateau, Texas: multiple unrecognized endemics or native exotic? Am. Midl. Nat., 158(1):97-112.

Huryn, A. D., A. C. Benke & G. M. Ward. 1995. Direct and indirect effects of geology on the distribution, biomass, and production of the freshwater snail *Elimia*. J. N. Am. Benthol. Soc., 14(4):519-534.

Huryn, A. D. & M. W. Denny. 1997. A biomechanical hypothesis explaining upstream movements by the freshwater snail *Elimia*. Funct. Ecol., 11(4):472-483.

Huryn, A. D., J. Koebel & A. C. Benke. 1994. Life history and longevity of the pleurocerid snail *Elimia*: a comparative study of eight populations. J. N. Am. Benthol. Soc., 13(4):540-556.

Jeremiah, N. G. 2007. Life History and Secondary Production of *Goniobasis proxima* (Prosobranchia: Pleuroceridae) from Four Appalachian Headwater Streams in Western North Carolina, Virginia Polytechnic Institute and State University, Blacksburg, VA. 31 pp.

Johnson, P. D. & K. M. Brown. 1997. The role of current and light in explaining the habitat distribution of the lotic snail *Elimia semicarinata* (Say). J. N. Am. Benthol. Soc., 16(3):545-561.

Laman, T. G., N. C. Boss & H. D. Blankespoor. 1984. Depth distribution of seven species of gastropods in Douglas Lake, Michigan. Nautilus, 98(1):20-25.

Lindholm, J. T. 1979. The gastropods of the Upper San Marcos River and their trematode parasites, San Marcos, Texas. Southwest Texas State University MS Thesis, 73 pp.

Minton, R. L., S. A. Reese, K. Swanger, K. E. Perez & D. M. Hayes. 2007. Changes in shell morphology of *Elimia comalensis* (Gastropoda: Pleuroceridae) from the Edwards Plateau, Texas. Southwest. Nat., 52(4):475-481.

Morales, J. B. T. & A. K. Ward. 2000. Snail grazers affect the fate of labile dissolved organic C in streams. J. N. Am. Benthol. Soc., 19(4):659-669.

Mulholland, P., J. Elwood, J. Newbold & L. Ferren. 1985. Effect of a leaf shredding invertebrate on organic matter dynamics and phosphorous spiralling in heterotrophic laboratory streams. Oecologia, 66(2):199-206.

Richardson, T. D., J. F. Scheiring & K. M. Brown. 1988. Secondary production of two lotic snails (Pleuroceridae: *Elimia*). J. N. Am. Benthol. Soc., 7(3):234-241.

Rosemond, A. D., P. J. Mulholland & J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology, 74(4):1264-1280.

Ross, M. J. & G. R. Ultsch. 1980. Temperature and substrate influences on habitat selection in two pleurocerid snails (*Goniobasis*). Am. Midl. Nat., 103(2):209–217.

Stewart, T. W. & J. E. Garcia. 2002. Environmental factors causing local variation in density and biomass of the snail *Leptoxis carinata* in Fishpond Creek, Virginia. Am. Midl. Nat., 148(1):172-180.

Tolley-Jordan, L. & J. Owen. 2008. Habitat influences snail community structure and trematode infection levels in a spring-fed river, Texas, USA. Hydrobiologia, 600(1):29-40.

Tuchman, N. C. & R. J. Stevenson. 1991. Effects of selective grazing by snails on benthic algal succession. J. N. Am. Benthol. Soc., 10(4):430-443.

KEP at: perezke@gmail.com