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Habitat Usage by the Page Springsnail, *Pyrgulopsis morrisoni* (Gastropoda: Hydrobiidae), from Central Arizona

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Abstract. We measured habitat variables and the occurrence and density of the Page springsnail, *Pyrgulopsis morrisoni* (Hershler & Landye, 1988), in the Oak Creek Springs Complex of central Arizona during the spring and summer of 2001. Occurrence and high density of *P. morrisoni* were associated with gravel and pebble substrates, and absence and low density with silt and sand. Occurrence and high density were also associated with lower levels of dissolved oxygen and low conductivity. Occurrence was further associated with shallower water depths. Water velocity may play an important role in maintaining springsnail habitat by influencing substrate composition and other physico-chemical variables. Our study constitutes the first empirical effort to define *P. morrisoni* habitat and should be useful in assessing the relative suitability of spring environments for the species. The best approach to manage springsnail habitat is to maintain springs in their natural state.

INTRODUCTION

The role that physico-chemical habitat variables play in determining the occurrence and density of aquatic microinvertebrates in spring ecosystems has been poorly studied. This field deserves more attention because microfauna play critical roles in energy flow and nutrient cycling in the spring environment, and the sustainability of ecosystems depends upon their persistence (New, 1998). Locally endemic invertebrates such as springsnails (Hydrobiidae), riffle beetles (Elmidae), and amphipods (Amphipoda) can be excellent environmental indicators of aquatic conditions because their presence or absence is often associated with particular chemical and physical conditions (Greeson, 1982; Hershler, 1998).

Numerous invertebrate species are imperiled, particularly those inhabiting aquatic environments. As of November 1, 2004, there were 32 species of snails (aquatic and terrestrial), 70 species of clams, and 21 species of crustaceans listed as threatened or endangered under the Endangered Species Act within the United States (U.S. Fish and Wildlife Service, 2004a). Despite the recognized status of such species, the availability of empirical information on the ecology and biology of these organisms to assist resource managers in developing and implementing effective conservation and recovery programs is limited.

The Page springsnail, *Pyrgulopsis morrisoni* (Hershler & Landye, 1988), is medium-sized relative to other congeners, 1.8 to 2.9 mm in shell height, endemic to the Upper Verde River drainage of central Arizona (Williams et al., 1985; Hershler & Landye, 1988; Hershler, 1994), with all known populations existing within a complex of springs located along Oak Creek near the town of Page Springs, Yavapai County. The species is a candidate for listing as threatened or endangered under the Endangered Species Act (U.S. Fish and Wildlife Service, 2004b). What little is known about the ecology and biology of this species has been obtained through agency status reviews, anecdotal observations, and inferences drawn from literature on other springsnail congeners.

Hydrobiids are strictly aquatic, relying on an internal gill for respiration. Their primary food source is periphyton, and they generally graze on exposed surfaces (Taylor, 1987; Mladenka & Minshall, 2001). *Pyrgulopsis* snails are known to be oviparous. Raisanen (1991) surmised that *P. morrisoni* lay eggs during an annual period of reproduction in the winter. Mladenka & Minshall (2001) found that the Bruneau hot springsnail, *P. bruneauensis* (Hershler, 1990), exhibited recruitment year-round. Among most prosobranchs, the veliger stage is completed in the egg capsule, and upon hatching, individuals emerge into their adult habitat (Brusca and Brusca, 1990). No information is available on death and birth rates. Significant migration is undocumented although other small aquatic snails have been known to disperse by becoming attached to the feathers or the mud on the feet and legs of waterfowl and shorebirds (Dundee et al., 1967). Predators may include waterfowl, shorebirds, amphibians, fishes, crayfish, leeches, and aquatic insects. No specific information on disease or parasites is available, but other aquatic snails have been known to serve as the intermediate hosts for trematodes.

Springsnails occur in springs, seeps, marshes, spring pools, outflows, and diverse lotic waters, though the most common habitat for *Pyrgulopsis* is a rheocrene, or a spring emerging from the ground as a free-flowing stream (Hershler and Landye, 1988; Hershler, 1998). Springsnails seem to prefer firm substrates such as cobble, rocks, woody debris, and aquatic vegetation, and are rarely found on or in soft sediment (Hershler, 1998; Raisanen, 1991; O'Brien and Blinn, 1999). Distribution of *Pyrgulopsis* within springs has been hypothesized as a function of stable temperature, water chemistry, and flow regime characteristic of the particular aquatic environment within which they occur (Hershler, 1984 and 1998). For example, O'Brien and Blinn (1999) found that dissolved free carbon dioxide plays a significant role in the distribution of the Montezuma Well springsnail, *P. montezumensis* (Hersler and Landye, 1988), and Mladenka and Minshall (2001) found water temperatures influence density and growth rate of *P. bruneauensis.*

Although the current literature provides general insight into ecological conditions suitable for hydrobiids, species-specific information is needed due to the potential for significant inter-specific variation in physiological requirements. Accordingly, the objective of our study was to evaluate associations between habitat variables and occurrence and density of *P. morrisoni* to provide a basic understanding of the species' habitat usage.

STUDY AREA

The Oak Creek Springs Complex includes a number of spring heads located along Oak Creek (Landye, 1973, 1981; Williams et al., 1985; Arizona Game and Fish Department, 1988; Hershler and Landye, 1988). We gained access to Page/Cave Spring, Bubbling Spring, Bass Spring, and an unnamed spring (Figure 1). These aquatic environments are essentially isolated, mid-elevational, permanently saturated, spring-fed aquatic communities commonly described as ciénegas (Hendrickson and Minckley, 1985).

Elevation in the Page Springs area is approximately 1070 meters. Riparian vegetation associated with Oak Creek and the springs complex includes velvet ash, *Fraxinus velutina*; Fremont cottonwood, *Populus fremontii*; Arizona sycamore, *Plantanus wrightii*; willows, *Salix* sp.; and mesquite, *Prosopsis* sp. Aquatic vegetation associated with fine grained sediments, includes macrophytes such as watercress, *Nasturtium officinale*; duckweed, *Lemna minor*; water parsnip, *Berula erecta*; water pennywort, *Hydrocotyl verticillata*; water speedwell, *Veronica anagalli aquatica*; dock, *Rumex verticillatus*; waterweed, *Elodea occidentalis*; and pondweed, *Potamogeton gramineus*; and algae such as *Rhizoclonium hieroglyphicum* and *Oscillatoria rubesens.*

METHODS

We measured density of *P. morrisoni* in the Oak Creek Springs Complex over four sampling periods during the summer of 2001. Initially, 35 modified Hester-Dendy artificial substrate samplers were placed randomly within the aquatic environment of accessible spring heads, spring runs, spring ponds, and spring pond outflows to quantify springsnail density. Artificial substrate samplers collect springsnails at densities comparable to those found in nearby natural substrata (O'Brien and Blinn, 1999). Samplers were constructed of round plates of masonite fastened together with an eye bolt. Each was composed of four round plates 75.49 mm in diameter and six round spacers 24 mm in diameter, all 1 cm thick, resulting in an effective sampling area of 330.86 cm^2 (Figure 2). Sampling periods were as follows: March 23 to May 10, May 10 to June 21, June 21 to August 2, and August 2 to September 25.

At the end of each sampling period, we used a Hydrolab Surveyor II to measure water temperature (°C), pH, dissolved oxygen (mg/L), and conductivity (μS/cm @ 25°C) adjacent to the sampler. We measured water depth with a meter stick or ruler (cm). We placed benthic fauna from each sampler into Whirl-Paks with 70% isopropyl alcohol or 95% ethyl alcohol, and transported them to the lab. We used a Stereozoom 7 Microscope to identify and count springsnails.

After data collection, we returned each sampler to the aquatic environment. Over the course of the four sampling periods, several samplers were unrecoverable. As a result, the initial 35 samplers provided 94 independent samples for each variable.

We classified substrate into one of four categories based on the predominant ($>$50%) composition surrounding the sampler. Substrate categories were modeled after a modified Wentworth classification system for particle size (Cummins, 1962; McMahon et al., 1996). Initially, we established three substrate categories with the following particle size range (mm): silt and sand ($<$2); gravel and pebble (2 to 64); and cobble (64 to 256). Later, we observed that in certain areas dominated by silt and sand, the leaf structure of water pennywort often provided a surface area atypical of other aquatic macrophytes. Accordingly, we split the silt and sand category into two sub-categories to capture potential differences provided by water pennywort. Those sub-categories are presented as silt and sand, and silt and sand with water pennywort.

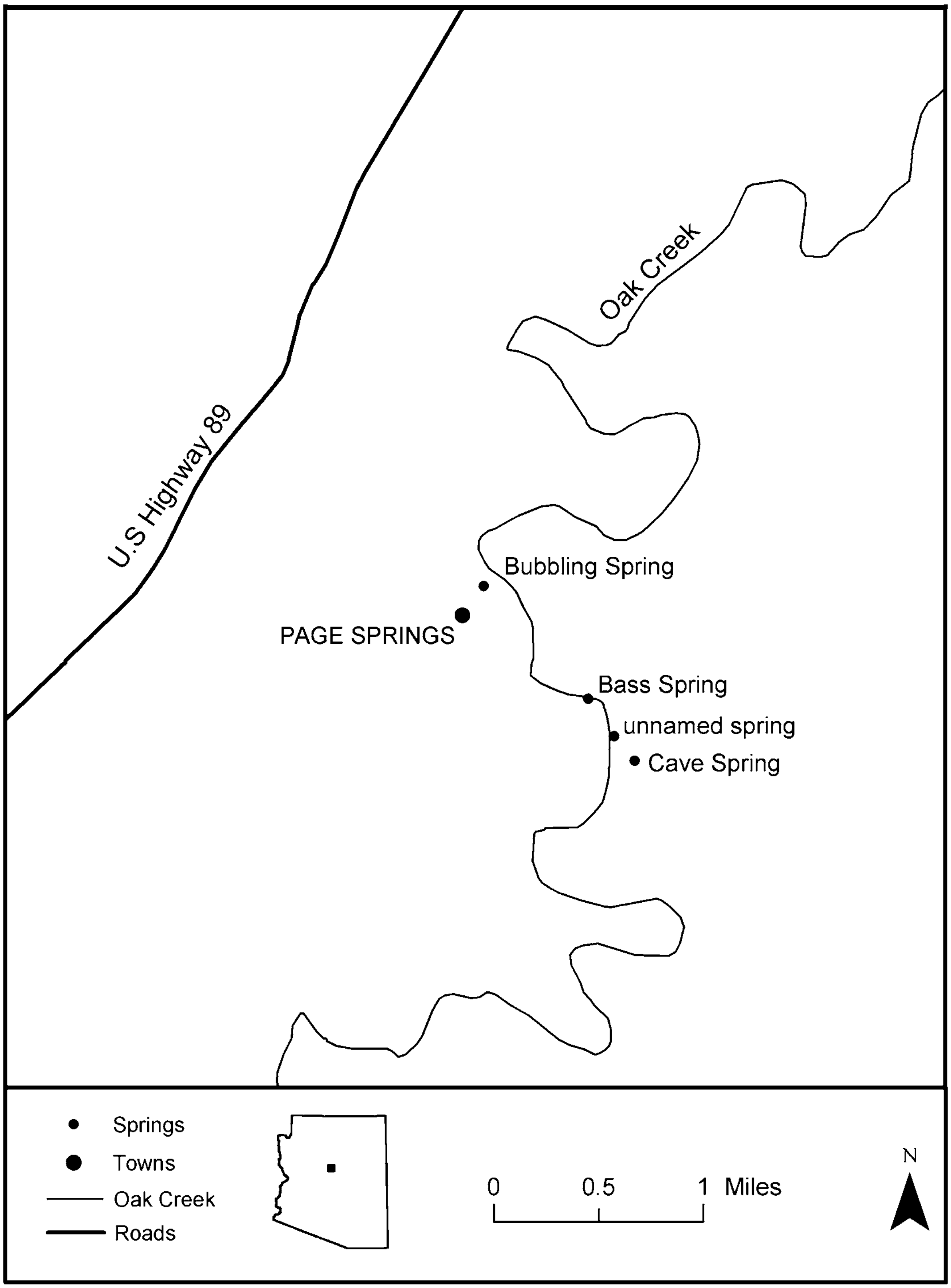

Figure 1. Page springsnail study area, Yavapai County, Arizona.

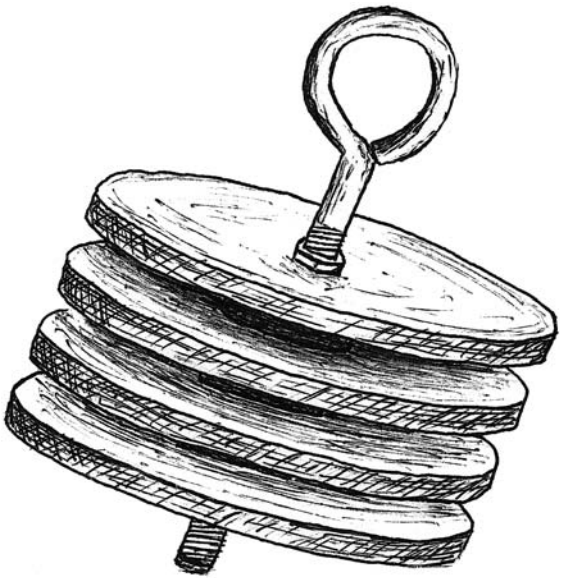

Figure 2. Modified Hester-Dendy artificial substrate sampler.

We did not encounter snails in the cobble category, largely because we did not collect a sufficient number of samples within cobbly areas (n = 6). Thus, for tests comparing snail density and presence between different substrate categories, we did not include the cobble classification.

Prior to statistical analyses, we used Pearson's correlation coefficients to evaluate the independence of pH, water temperature, dissolved oxygen, depth, and conductivity. Temperature and pH were correlated with dissolved oxygen ($r > 0.60$), and thus eliminated from further analyses. We kept dissolved oxygen instead of the former two variables because dissolved oxygen can be an important limiting factor for aquatic invertebrate respiration (Pennak, 1989). Moreover, although temperature differences as small as 4°C increased the production of viable freshwater snail eggs in other studies (Dillon, 2000), we do not suspect that temperature was a significant factor in our study since 96% of our temperature data varied less than 4°C.

Dissolved oxygen and conductivity were not highly correlated with one another ($r = 0.331$) and were both used as independent variables. Depth showed a fairly high correlation ($r = 0.564$) with conductivity, but the relationship between the two variables is unclear because our range of depth measurements did not appear broad enough to influence water quality through thermal stratification. Thus, depth was assessed along with the other independent variables. We pooled data between sampling periods, as a modified-Levene equal variance test showed the variances in snail density between periods to be equal ($F = 0.188$, df = 3, 90, $P = 0.904$) and there were no differences in snail densities between periods ($F = 0.13$, df = 3, 90, $P = 0.942$).

We pursued generalized tests, seeking differences in springsnail habitat between locations where springsnails were present and absent. We tested the following null hypotheses with respect to springsnail presence/absence: There is no difference according to substrate category, depth, dissolved oxygen levels, and conductivity levels.

We used a 3×2 contingency table to test whether snail presence was independent of substrate category, and Mann-Whitney *U*-tests to assess differences in habitat variables between occupied and unoccupied locations.

While our first hypotheses strove to characterize springsnail habitat in general, we also sought to characterize habitat quality by comparing snail densities among substrate categories, and between different levels of the continuous independent variables. We created low, medium, and high categories for each of the independent variables (dissolved oxygen, conductivity, and depth) using the lower, middle, and upper 33rd percentiles of data within the independent variables. Using these categories, we tested additional null hypotheses with respect to springsnail density: There is no difference according to substrate category, depth, dissolved oxygen, or conductivity.

We used the Kruskal-Wallis one-way ANOVA on ranks to test the above hypotheses, and the Kruskal-Wallis multiple comparison *z*-value test for post-hoc comparisons (Hintze, 2000).

NCSS (Hintze, 2000) was used for all statistical tests. We used nonparametric tests since the data generally lacked normality, and transformations were unsuccessful. For all tests, significance was considered $P \leq 0.05$ and results are presented in the form ($\bar{x} \pm$ SE).

RESULTS

For all 94 samples, springsnail density averaged 0.069 ± 0.0137 per cm^2, ranging from 0.0 to 0.680 per cm^2. We found springsnails in 48 samples, and where springsnails were found, their density averaged 0.135 ± 0.023 per cm^2. Throughout the study area (for locations with and without springsnails), dissolved oxygen levels averaged 8.694 ± 0.273 mg/L, ranging from 5.78 to 18.5 mg/L; conductivity levels averaged 431 ± 8.192 μS/cm, ranging from 128 to 524 μS/cm; and water depth averaged 28.225 ± 4.304 cm, ranging from 0.33 to 91.5 cm.

Defining Habitat Using Presence/Absence

Our contingency table analysis demonstrated that the occurrence of springsnails was not independent of substrate type (Table 1; $\chi^2 = 10.531$, df = 2, $P = 0.005$). The gravel/pebble category contained springsnails more often than expected, and both of the silt/sand categories contained springsnails less often than expected. Locations where springsnails were present were characterized by

Table 1

3 × 2 contingency table showing frequencies of Page springsnail presence and absence on three substrate categories during sampling in the Oak Creek Springs Complex in Arizona, 2001. Expected frequencies in parentheses.

Substrate	Absent	Present	Total
Gravel/pebble	14 (21.4)	33 (25.6)	47
Silt/sand	17 (11.4)	8 (13.6)	25
Silt/sand/water pennywort	9 (7.3)	7 (8.7)	16
Total	40	48	88

significantly lower dissolved oxygen levels (Figure 3A; $Z = -5.268$, $P < 0.0001$), lower conductivity levels (Figure 3B; $Z = -4.732$, $P < 0.0001$), and shallower depth (Figure 3C; $t = 2.135$, df = 41, $P = 0.039$).

Defining Habitat Quality Using Springsnail Density

Springsnail density differed between the three habitat substrates from which we sampled (Figure 4; $\chi^2 = 17.99$, df = 2, $P = 0.0003$). Springsnail density in gravel/pebble was significantly greater than in the silt/sand substrates (both with and without water pennywort). Springsnail density was lower for the highest level of dissolved oxygen (0.005 ± 0.005) compared to the lower two levels (Figure 5A; low = 0.084 ± 0.021; med = 0.069 ± 0.024; $\chi^2 = 26.49$, df = 2, $P < 0.0001$), lower for the highest two levels of conductivity than for the lowest level (Figure 5B; low = 0.124 ± 0.029; med = 0.020 ± 0.010; high = 0.013 ± 0.008; $\chi^2 = 30.32$, df = 2, $P < 0.0001$), and remained unchanged for all levels of water depth (Figure 5C; shallow = 0.074 ± 0.003; med = 0.083 ± 0.037; deep = 0.036 ± 0.019; $\chi^2 = 2.83$, df = 2, $P = 0.242$).

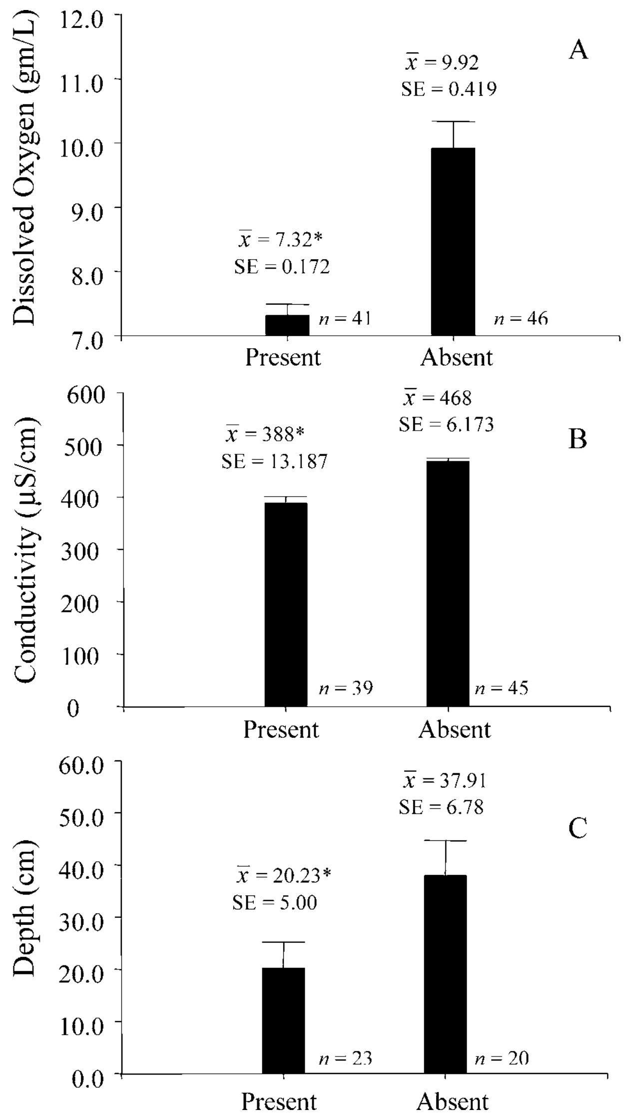

Figure 3. Mean values for three habitat parameters where Page springsnail was present and absent in the Oak Creek Springs Complex in Arizona, 2001. Differences were tested with Mann-Whitney *U*-tests comparing sites with and without springsnails. *$P < 0.05$.

DISCUSSION

We found that substrate particle size was an important factor determining occurrence and density. *P. morrisoni* occurred more often and in greater densities in gravel and pebble substrates. They may prefer larger substrate because it provides a reliable surface for the deposition of egg masses, facilitates mobility, and provides a suitable medium for production of periphyton, the snails' preferred food source. This, in turn, may result in higher recruitment and snail densities.

Mladenka (1992) demonstrated that *P. bruneauensis* preferred gravel to sand because snails used hard surfaces to deposit their eggs. *Pyrgulopsis* females deposit single, small egg capsules on hard surfaces (Hershler, 1998). Larger substrates should be more conducive to oviposition because the surface provides improved stability over smaller, uncoalesced particles such as silt and sand. Moreover, prosobranch snails have a distinct foot with a creeping planar sole and locomotion is facilitated by secretion of a mucous trail over which the animal glides (Brusca and Brusca, 1990). This type of locomotion likely requires less effort over large and stable surfaces. Smaller particles are also more likely to be displaced by water current, possibly burying snails and eggs.

We did not include cobble within our analysis because our sample size in that category was small. However, we

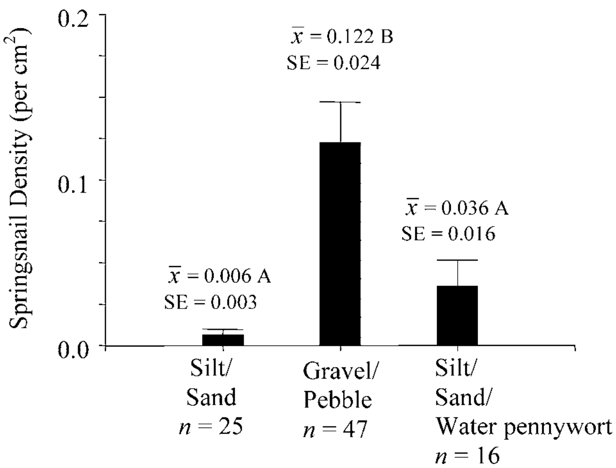

Figure 4. Values for Page springsnail density ($\bar{x} \pm$ SE) in three different substrate types in the Oak Creek Springs Complex in Arizona, 2001. Means with the same letter did not differ when tested with a Kruskal-Wallis one-way ANOVA on ranks at α = 0.05.

do not dismiss cobble as a potentially preferred substrate medium due to its large, stable character. *P. morrisoni* did not show a significant preference for water pennywort as a substrate medium. We found this surprising since anecdotal field observations convinced us that the species was abundant on the leaves of water pennywort. Upon reflection, perhaps our sampling technique did not capture the importance of water pennywort as a substrate medium.

Water pennywort occurred within only one spring that we sampled. That spring, Bubbling Spring, is not a rheocrene, but instead exists as a pond with a maximum measured depth of 91.5 cm. Within Bubbling Spring pond, water pennywort occurred near spring vents and grew to a height of about 15–20 cm within the water column. Because samplers were placed in sediments near the stem base, the snail population present on the leaves may not have been able to access them. Perhaps this could be addressed by using the surface area of the macrophyte itself to quantify snail density as done by O'Brien and Blinn (1999).

Nevertheless, we believe the potential suitability of water pennywort as a substrate medium for *P. morrisoni* deserves further investigation. A substrate-stratified field sampling technique or laboratory experiment may be useful to assess the importance of all substrate types.

We found that mean dissolved oxygen concentrations differed by more than 2 mg/L in sites where springsnails were present versus sites where springsnails were absent. Moreover, regions with high dissolved oxygen concentrations had significantly lower snail densities than sites with low and medium concentrations. We do not suspect that depressed dissolved oxygen levels limited respiration because we never encountered oxygen-poor conditions (minimum value = 5.78 mg/L). For common species of the pulmonate genus *Physella*, 2 mg/L is about the limiting level for dissolved oxygen to meet respiratory needs (Pennak, 1989). However, we have no reason to postulate that higher levels of dissolved oxygen would directly limit *P. morrisoni* occurrence and density, given that higher levels should more readily meet respiratory requirements. Thus, the negative relationship between dissolved oxygen and snail occurrence and density may be a function of

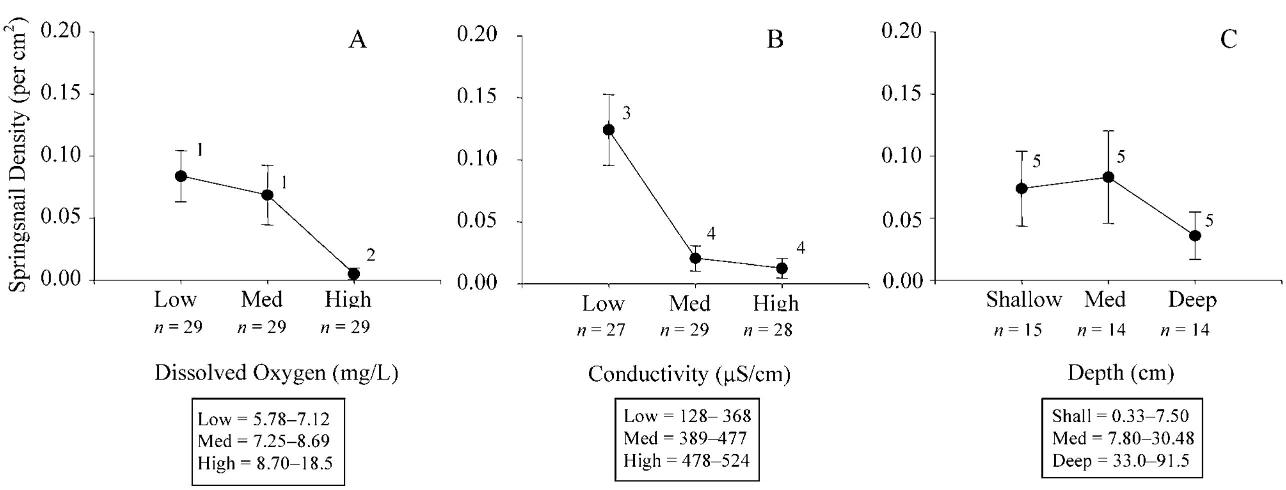

Figure 5. Values for Page springsnail density ($\bar{x} \pm$ SE) in relation to three different environmental variables in the Oak Springs Complex in Arizona, 2001. Values with same number did not differ when tested with a Kruskal-Wallis one-way ANOVA on ranks at α = 0.05. Low, medium, and high categories were created using the lower, medium, and upper 33rd percentiles of data within the independent variables.

other environmental variables that interact with both dissolved oxygen and the snail. These may include the influence of other gases and/or primary productivity.

For instance, it is generally true that dissolved oxygen and carbon dioxide concentrations exhibit an inverse relationship within aquatic environments. Coupled with sunlight, carbon dioxide is the primary element driving photosynthesis. It is possible that regions within the Oak Creek Springs Complex characterized by low dissolved oxygen levels were also characterized by elevated levels of carbon dioxide and primary production, particularly at the periphytic level. Perhaps the relationship between dissolved oxygen and occurrence and density of *P. morrisoni* is tied to the availability of periphyton.

Whatever the mechanism, the proximity of spring vents may play an important role. Hershler (1984, 1998) noted that hydrobiid densities seem to decrease downflow from spring sources. Although our design was not structured to capture this influence, it is important to note that *P. morrisoni* seemed most abundant near spring vents, particularly within Bubbling Spring pond. If dissolved oxygen concentrations nearer spring vents were lower than concentrations away from vents, and springsnails were most abundant near spring vents, we would expect a negative relationship between springsnail abundance and dissolved oxygen. An ad-hoc analysis showed that sampling stations within 10 m of spring vents in Bubbling Spring pond had a mean dissolved oxygen concentration of 7.27 $\pm$ 0.127 mg/L while stations greater than 10 m from vents had a mean concentration of 10.77 $\pm$ 2.79 mg/L (t = 7.17, df = 38.6, $P < 0.0001$). This relationship closely resembles the results of our tests for snail presence and density.

We therefore have reason to believe that dissolved oxygen concentrations and occurrence and density of *P. morrisoni* were heavily influenced by proximity to spring vents. Regions nearer spring vents may provide environmental conditions that better meet the species' physiological need. This may be tied to geologic and ecological subterranean processes that determine the nature of water quality near vents. Another factor may be significant diel fluctuations in water quality. Perhaps water further from spring vents exhibits greater variability in extreme conditions due to atmospheric influences while water closer to vents is more stable. A sampling methodology designed to capture the influence of diel fluctuations could provide important insight.

We found differences in mean conductivity concentrations in locations where the species was present versus locations where the species was absent. Sites with high and medium levels of conductivity had lower snail densities than sites with low conductivity levels.

Conductivity is commonly used as an index of dissolved solids, particularly salts. Salts can play a major role in determining mollusk population density and distribution because they are used in shell formation (Pennak, 1989). Though we find the relationship perplexing, lower levels of conductivity seem to be preferred by *P. morrisoni*. Perhaps lower levels of dissolved salts are more readily assimilated. Or, as with dissolved oxygen, perhaps the relationship is tied to other factors, such as proximity to spring vents and their associated stable environmental conditions.

We found that water depth influenced *P. morrisoni* occurrence, and mean water depth was greater in regions where the species was absent versus regions where present. Although depth did not appear to influence springsnail densities, deeper sites had non-significantly lower snail densities than sites with shallow and medium depths. A larger sample size may have shown this definitively.

Water depth can substantially influence aquatic ecosystems. Sunlight can more readily penetrate shallower regions, raising water temperature and boosting photosynthetic rates. Deeper waters are more accessible to a diverse assemblage of organisms, such as fishes, that may act as predators. Although we did not attempt to assess the effect of predation, it is important to note that occurrence and density of aquatic mollusks can be greatly influenced by the presence of predators, particularly fishes.

Experiments conducted by Myler (2000) showed that redbelly tilapia (*Tilapia zilli*) significantly reduced the food availability for *P. bruneauensis* and tilapia actively ate individual snails they encountered. Raisanen (1991) reported shells of *P. morrisoni* in a gut analysis of mosquitofish (*Gambusia affinis*) from Bubbling Spring. The potential influence of water depth on the abundance and foraging habits of predaceous fishes within the Oak Creek Springs Complex deserves more attention.

Our study constitutes the first empirical effort to define *P. morrisoni* habitat and should prove useful in assessing the relative suitability of natural or restored spring environments for the species. It is important, however, to view the structure of an aquatic ecosystem as a complex web of intricate relationships between various biotic and abiotic variables. Benthic organisms can be affected by a multitude of variables, most of which are extremely difficult, if not impossible, to manipulate or control. As such, caution should be used when actively managing spring environments to provide suitable habitat for endemic invertebrates.

Since it is reasonable to conclude that snail density is indicative of habitat quality (cf. Van Horne, 1983), we recommend that management actions focus on providing preferred substrates and water depths. This may be accomplished by ensuring the physical environment facilitates water velocities that promote the maintenance of gravel and pebble substrates. Specifically, the shear stress of flowing water should effectively transport fine sediments out of the system. A rheocrene environment should provide the most appropriate substrate medium and may serve to boost snail recruitment and density.

Although managing water chemistry variables at levels that promote occupancy and high density would be difficult, our results can be used to assess the relative suitability of a spring for the species. This may have practical application for possible reintroduction or transplantation efforts. Until now, little information was available to judge the suitability of sites considered for reintroduction or transplantation.

Directly manipulating dissolved oxygen and conductivity in a spring to levels most conducive to *P. morrisoni* occupancy and high density would probably be impractical. Such efforts would likely be costly with low success rates. As such, we suggest the best approach to provide habitat is to maintain springs in their natural rheocrene condition. This is consistent with Hershler and Williams (1996) who suggested that efforts to maintain springsnail populations should focus on the maintenance of natural spring head integrity, which will improve water quality and conserve springsnails.

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