MONTEZUMA WELL

OVERVIEW

Montezuma Well Endemic Species

Montezuma Well, a natural sinkhole in the Verde Valley of north-central Arizona, is home to a rich diversity of endemic (found nowhere else in the world) species that are adapted specifically to the Well's distinctive water chemistry. Five of these organisms have been formally described, several others have been only recently identified, and others still are suspected of being endemic, but are, as of yet, unproven as such.

Environment

Montezuma Well is a near constant aquatic environment. The Well formed when the limestone collapsed sometime between 12 and 15 thousand years ago. Water is fed into the Well through several vents at the bottom, and exits the Well through a swallet and cave system, with the outlet draining into a prehistoric irrigation canal. Both the water level and temperature are nearly constant throughout the year, with the first fluctuating by only 16 cm and the latter averaging 70 degrees F (Blinn 2008). The water also has a stable pH because of high alkalinity and an excessive amount of dissolved carbon dioxide, which enters the well from the bottom vents in concentrations in excess of 500 mg per liter, more than 100 times higher than normal (Blinn 2008). These extreme chemical conditions mean that no fish can survive in the Well, and that organisms living in the water have had to adapt in order to survive.

Endemic Species

Endemic species, both known and suspected, include diatoms, a water scorpion, a spring snail, leeches, amphipods, pondweed, and possibly a mud turtle. Each of these species has adapted to the water chemistry of the Well, and several have adapted to each other in a food web found only in Montezuma Well.

Diatoms

Diatoms are photosynthesizing algae (phytoplankton) with intricate silicate cell walls. Three diatom species found in Montezuma Well are endemic: *Caloneis latiuscula* var. *reimeri*, *Cyclotella pseudostelligera* f. *parva*, and *Gomphonema montezumse*, which is thought to have first appeared in the Well around 8,000 years ago (Blinn 2008; Czarnecki and Blinn 1979). A fourth diatom may also be endemic, but has yet to be formally described (NPS 1992).



Montezuma Well.

Water Scorpion

The endemic Montezuma Well water scorpion (*Ranatra montezuma*) lives in the weed bed along the shore of the Well, entering the open water at night to feed. It uses a sharp beak to pierce and suck internal body fluids from its adult prey, which is another endemic species: the amphipod *Hyalella montezuma* (Blinn 2008; Blinn et al. 1982). Swimming is considered an unusual behavior for this type of organism, but behavioral changes such as this are common amongst Montezuma Well's endemic species.

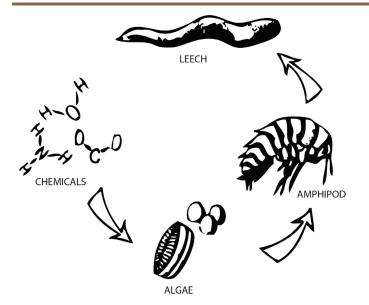
The stick-like body of *R. montezuma* is long and narrow, mimicking pondweed stems (Blinn 2008). This is also the smallest of the four *Ranatra* species known in Arizona and California (Blinn et al. 1982). *R. montezuma* buries its eggs in soft, partially decayed plant tissue to hide them from predators during the months of March through November, and hibernates in limestone cracks around the shoreline during the months of December through February (Blinn 2008).

Spring Snail

Pyrgulopsis montezumensis, the spring snail endemic to Montezuma Well, lives in the swallet and associated limestone and moss habitats along the shoreline (Blinn 2008). This species is currently considered vulnerable and until recently, were potentially threatened by the red-ear slider turtles introduced to the Well in the late 1960s or 1970s (Cordeiro 2012). This particular snail also cannot survive outside the Well, requiring at



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The simplied food chain of Montezuma Well, after Wagner and Blinn (1987). The Montezuma Well water scorpion also feeds on the amphipods.

least 50 mg per liter of carbon dioxide in the water – ten times that found in most standing waters (Blinn 2008).

Amphipods

Two species of amphipod (freshwater scud or side-swimmers) are endemic to Montezuma Well: Hyalella montezuma and H. azteca. Both co-occur along the weedy margins of the Well, but only H. montezuma swims in open water, and only H. azteca is found in the outlet stream (Cole and Watkins 1977).

H. montezuma is the dominant zooplankton in the Well, and is the only planktonic filter-feeder known in North America (Blinn 2008). H. montezuma eats planktonic algae and possibly other zooplankton, and swims in open water, which is an unusual behavior for amphipods. Although light sensitive and habitually 2-4 meters under water, H. montezuma has three times the carotenoid pigment found in H. azteca - a result of exposure to ultraviolet light while free-swimming (Blinn 2008).

H. azteca lives along the shore and does not swim in open water (Blinn 2008). H. azteca remains sedentary in the submerged shoreline vegetation, consuming the toxic compounds of the roots of water parsnip (Berula sp.) as a defense against predatory insects (Blinn 2008).

Both amphipod species are susceptible to parasitic infection by trematodes, or flukes (Microphallus spp.), and by acanthocephalans, or thorny-headed worms (Corynosoma constric*tum*). Both parasites alter the appearance of the amphipods, changing their color from the normal gray-green to bright orange, either in part or completely (O'Brien and van Ripper 2009). These parasitic infections also change the behavoir of

the amphipods, making them slower, less prone to seek camoflauge, and more likely to be found in the nearshore vegetation, where they become food for water bugs, water scorpions, and waterfowl (O'Brien et al. 2002).

H. montezuma is the primary food source for one of Montezuma Well's endemic leeches, Motodbella montezuma. Although normally in the open water of the well, as the leeches rise from below to feed a few hours after sunset, the amphipods move into the near-shore vegetation, thereby escaping the leeches but becoming prey to insects and waterfowl. Waterfowl, the dominate host of both parasites, prefer the orange amphipods, closing the parasitic cycle, which is completed in the intestinal wall of the new host (Blinn 2008).

H. montezuma is a keystone species in Montezuma Well because of its role in the food web.

Leeches

Three species of leech are endemic to Montezuma Well: Motodbella montezuma and two Helobdella species that have not vet been formally described.

Motodbella montezuma, first described as Erpobdella montezuma, has three pairs of eyes, densely pigmented dorsal stripes, and a length of around 71 mm (Mulhern et al. 2012). Like the Montezuma Well spring snail, M. montezuma cannot survive without the high concentrations of carbon dioxide found in the Well (Blinn 2008). These leeches hunt the endemic amphipod *H. montezuma*, ascending to the surface to feed an hour or two after sunset (Blinn 2008). They track their prev by detecting vibrations in the water (mechanoreception or passive sonar) using special structures called sensilla (Govedich and Bain 2005). These structures are so sensitive



A juvenile Motobdella montezuma leech. Courtesy of Shayla Mulhern, Northern Arizona University

Montezuma Well - Endemic Species

that the leeches can selectively hunt, choosing juveniles over adults. Each leech eats between 12-16 amphipods per night, swallowing their prey whole and then using enzymes to digest the internal body fluids. The carcasses are then excreted and can be seen floating on the surface of the water in the morning (Blinn 2008; Govedich and Bain 2005).

M. montezuma are hermaphroditic, allowing males and females to change their reproductive roles when necessary (Govedich and Bain 2005). The adults breed in the swallet of the Well in the late summer and early fall, attaching the cocoons in which the young develop to pondweed stems at depths below five meters to avoid the reach of surface predators (Mulhern et al. 2012).

Two other leech species have recently been found to be endemic as well. These are currently known as Helobdella stagnalis and H. triserialis, both of which have yet to be formally described (Beresic-Perrins et al. 2014). Both are genetically different from their "standard" cousins, and the Montezuma Well H. stagnalis also has brood size, parental behavior, and life history that that is different from other populations (Beresic-Perrins et al. 2014; Elliott et al. 2012).

Pondweed

Like the Montezuma Well spring snail, mud turtles living in the The pondweed most common and visible in Montezuma Well Well were until recently threatened by red-ear slider turtles and is also likely endemic but unnamed (NPS 1992). According other non-native species, which competed for basking space to Cole (1965), the Montezuma Well Potamogeton species and other resources (Drost et al. 2010). Fortunately, the last of has stem anatomy like P. gramineus and upper anatomy like the non-native turtle species was successfully removed from P. illinoiensis. The pondweed in Montezuma Well roots in the Well in 2013, and the National Park Service continues to monitor the Well for new introductions and to track the status sediments as deep as eight meters (about 26 feet) below the surface, which may be the deepest known for a Potamogeton of the native mud turtle population. species (Blinn 2008).

Mud Turtle

The mud turtle currently identified as the Sonoran mud turtle (Kinosternon sonoriense) species may also be endemic



Sonoran mud turtle at Montezuma Well.

Pondweed below the surface of Montezuma Well, 2006.

to Montezuma Well (NPS 1992). If formally recognized, the mud turtles of Montezuma Well will be the third subspecies of K. sonoriense known in the greater Southwest, or perhaps a new species of Kinosternon altogether.

Summary

Montezuma Well is the unique home of at least 12 plant and animal species found nowhere else in the world. "The breadth of species diversity and the complexity of interactions among organisms in this one-of-a-kind ecosystem are only now beginning to be recognized," (NPS 1992:75) and as the recent identification of the two Helobdella species demonstrates, more species endemic to the Well may be described in the future.

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Ducks at Montezuma Well feed on the water scorpions, amphipods, leeches, and pondweed. They also serve as hosts to the same parasites that turn the amphipods orange.

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