Conference Proceedings. Spring-fed Wetlands: Important Scientific and Cultural Resources of the Intermountain Region, 2002.
http://www.wetlands.dri.edu

Connectivity in Desert Aquatic Ecosystems: The Devils Hole Story

Alan C. Riggs
U.S. Geological Survey
ariggs@usgs.gov

James E. Deacon
University of Nevada, Department of Environmental Studies,
Department of Biology, Las Vegas
deaconj@nevada.edu

Abstract

Devils Hole, a skylight to the water table (and beyond) in one of the harshest North American deserts, is a prime example of how perennial desert waters tend to be at the intersection of aesthetic and cultural appreciation, economic and legal conflict, and scientific study. Devils Hole is a fissure, opened by regional tectonic extension of Paleozoic carbonate rocks, that acts, in concert with innumerable other similarly formed fissures, as a subterranean drainage network that transmits rain water and snowmelt, primarily from the relatively well-watered upper elevations of the Spring Mountains, to arid basin-floor spring-discharge oases. The water passing through Devils Hole is supersaturated with calcium carbonate, which has precipitated on its walls in a number of morphologies, each of which precipitated under a unique set of conditions. The distribution and age of the different calcium carbonate morphologies record multiple aspects of the history of Devils Hole and the region, including an indication that Devils Hole opened to the surface about 60,000 years ago. There is also evidence that, probably primarily in response to climate change, the water level in Devils Hole has moved up and down but has had a net downward trend, and has apparently never been high enough to overflow the lip in the last 116,000 years. These historical insights are important to Devils Hole's best-known inhabitant, the Devils Hole pupfish, because if water never overflowed the lip, there is no apparent way for the pupfish to have colonized the Hole. Beyond that, pupfish life in Devils Hole has built-in problems. The water in Devils Hole is almost too warm for successful pupfish reproduction, and limited dissolved oxygen exacerbates the problem. In addition, the narrow fissure above the Devils Hole pool limits the amount of sunlight available to power primary productivity, and hence the amount of food available to pupfish and the other aquatic biota. Nonetheless, pupfish survived, apparently without problem, until the late 1960s when the Devils Hole water level and the pupfish population began to fall precipitously in response to pumping of nearby irrigation wells. The decline set off a classic values conflict between conservationists, who wanted the pumping stopped to prevent extinction of the fish, and many in the local population interested in the potential economic expansion made possible by development of the ground water resource. The conflict over water rights played out on the national stage and escalated to the U.S. Supreme Court, where it was resolved in favor of the conservationists. So, the pupfish live on but so does the pressure to develop the limited water resources of one of the driest areas of the country.

Introduction

Devils Hole, a skylight to the water table (Figure 1) in one of the harshest deserts in North America, has fascinated humans from time immemorial, has yielded an astounding amount of scientific information, is the focus of one of the classic environmental controversies of our time, and is likely to influence water-supply decisions needed to support the growth of Las Vegas over the next 50 years. A powerful Native American mythological character is said to reside there; the first Euro-Caucasians to see the place remarked on its "magical" qualities; calcite deposits on its walls sequester the longest continuous continental paleoclimate record yet recovered; it is the smallest habitat in the world to harbor the entire population of a vertebrate species; and a U.S. Supreme Court decision favoring preservation of that species over economic development helped build public support for the groundbreaking environmental legislation of the 1970s, stimulated creation of a national wildlife refuge, aided the transition of Death Valley to national park status, and helped shift the course of western water law. Devils Hole, located on the edge of Ash Meadows, where discharge from the regional ground-water flow system supports the largest oasis in the Mojave Desert (Figure 2), dramatically exemplifies the powerful cultural, social, scientific, and environmental importance of desert wetlands. This paper describes the interaction of these forces over time.

Figure 1. **Devils Hole, a skylight to the water table**. View down and to the NE. The 0-to->1-m-deep shallow shelf, which is important to pupfish survival, extends from the closest visible extent of the pool to the white water-level recorder housing; beyond, the pool floor drops abruptly to 6 m, then stairsteps down to about 23 m depth (see Figure 4A). The NE end of the pool is hidden in the shadows beyond the breakdown blocks under the overhang. Owls often roost and/or nest in upward-sloping fissures under the overhang, or on a ledge more than half way up the cliff face above the shallow shelf in a location that may at other times shelter a beehive. The full width of the sloping apron to the left of the pool is obscured by bedrock in the foreground. The obscured section of the slope rolls over until it is nearly level before meeting the bottom of the left wall. Pool width gives an idea of how far the fissure has pulled open. The greater width of the Hole above the pool surface is primarily due to collapse of the left wall. Smaller collapse blocks were swallowed by the fissure, sinking to depths greater than 150 m, but larger blocks, such as the shallow shelf, the blocks that appear to form the NE end of the pool, and others noted in the text are wedged in the fissure where they will stay until continuing tectonic spreading widens the fissure enough for them to fall deeper. The white matrix surrounding the dark cobbles, at the lowermost right, is mammillary calcite (described in text) precipitated during higher stands of water table long before Devils Hole opened to the surface.

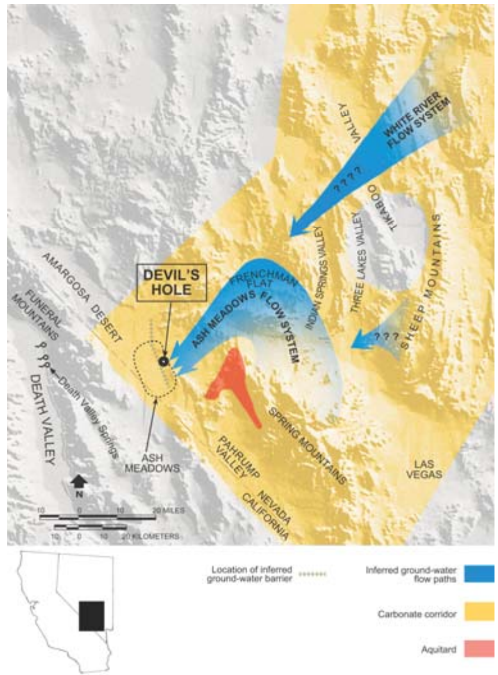


Figure 2. **The Ash Meadows flow system.** Devils Hole in relation to the inferred location of the Ash Meadows flow system and the region. The base topography is modified from Edwards and Batson (1990); the location of the carbonate corridor is taken from Dettinger (1989), who did not map its extent in California; the main flowpath of the Ash Meadows flow system is a schematic representation simplified from Winograd and Thordarson (1975); the possible contributions from the White River flow system are inferred from information in Riggs *et al.* (1994).

The Socio-cultural Dimension

The earliest known human occupants, the Nevada Springs culture, lived in the area near Devils Hole more than 9,000 years ago, leaving only a few artifacts to document their presence (Wallace and Wallace 1978). They were followed by the Southern Paiute branch of the Shoshone, ancestors of the Timbisha people who inhabited the area until largely displaced by Caucasians (Hunt and Hunt 1960; Wallace and Wallace 1979). Evidence of the cultural significance of Devils Hole to these Native Americans was presented by Barbara Durham, an elder of the Timbisha Shoshone Tribe at the Devils Hole Workshop in Pahrump, Nevada on May 29-31, 2002. In her oral communication, she related the myth of Devils Hole "water babies" ready to swallow children (and perhaps even adults) that stayed at the pool too long. Smith (1993) refers to these water babies as well as to a giant, Tso'apittse, who lives near desert springs lying in wait for unsuspecting victims. In spite of those very powerful deterrents, Ms. Durham reported that she and her childhood friends frequently played at Devils Hole because they enjoyed having the pupfish "tickle their toes."

Johnson and Johnson (1987) record impressions of the earliest known Euro-Caucasian visitors, the Death Valley 49ers, who entered Ash Meadows from the east along an Indian trail paralleling the current (2004) dirt road and camped on the night of December 23, 1849, at Collins Springs, about 1.2 km south of Devils Hole. Louis Nussbaumer and his friend Hadapp apparently hiked back to Devils Hole for a private bath, and Nussbaumer recorded his impressions of the place as follows: "At the entrance to the valley to the right is a hole in the rocks [Devils Hole] which contains magnificent warm water and in which

Hadapp and I enjoyed an extremely refreshing bath. The temperature of the water is about 24 to 26°C [75 to 79°F] and the saline cavity itself presents a magical appearance." Nussbaumer almost certainly underestimated the water temperature (see Winograd and Thordarson 1975, and the section on Pupfish Reproduction in this paper). A few years later in 1866, Nevada's first Governor, Henry Goode Blasdel, traversed Ash Meadows, making special reference to his entrance through ".... a range of low coralline limestone hills, with a fine spring [Devils Hole] on the summit, in a cave 30 feet long and 10 feet wide."

Figure 3. **Devils Hole pupfish.** Male (on left) and female (on right) Devils Hole pupfish in spawning position. (Photo by Tom Baugh).

Interest in, fascination with, and recognition of Devils Hole's unique nature continues to the present. Early ichthyologic investigators recognized the Devils Hole pupfish (*Cyprinodon diabolis*, Figure 3) as a unique species (Wales 1930). Carl Hubbs, father of western ichthyology, in an effort to protect the pupfish and the unique geological features, convinced President Harry Truman to designate Devils Hole as a disjunct part of Death Valley National Monument in 1952 "for the preservation of the unusual features of scenic, scientific, and educational interest therein contained" (Truman 1952.) Hoffman (1988) chronicles the many underwater explorations and investigations conducted in Devils Hole, beginning with a hardhat dive conducted by members of the National Speleological Society in June 1950, the first use of scuba to estimate total population size of Devils Hole pupfish in November 1954 (approximately 300), and ending with a first-hand description of the water table oscillations in Browns Room caused by a major earthquake off Adak, Alaska, in 1986 (Figure 4A). The full extent of the Devils Hole cavern system remains unknown. The divers who made the deepest penetration to date (to 133 m [436 ft] below water surface in 1991) could see down the fissure to about 150 m (500 ft) before it angled even more steeply downwards, presumably to even greater depths.

While Devils Hole has always been recognized as a unique place worthy of special protection, care, and even reverence, competing societal values led to resource-allocation conflicts in nearby Ash Meadows. Because of its abundant spring flow, local Euro-Caucasians consistently viewed Ash Meadows as an economic development opportunity. That interest led the U.S. Bureau of Land Management, when charged in the early 1960s with the responsibility of classifying federal land for retention or disposal, to classify most federal land in the Ash Meadows area for disposal (Pister 1991). A corporate farm (Spring Meadows, Inc.) purchased 2,023 hectares (5,000 acres) of federal land, added 2,833 hectares (7,000 acres) of private land, and, in 1968 began to develop ground-water resources for irrigated agriculture in Ash Meadows (Pister 1991; Deacon and Williams 1991). A well drilled within a few feet of the boundary of the 16-hectare (40-acre) Devils Hole reservation (Figure 5) caused an almost immediate decline in water level in Devils Hole when test-pumped. Although never used as a production well, the pumping-induced water level drop caused by that well, more than any other factor, alerted the conservation community to the clear and present danger that ground-water withdrawal posed to the

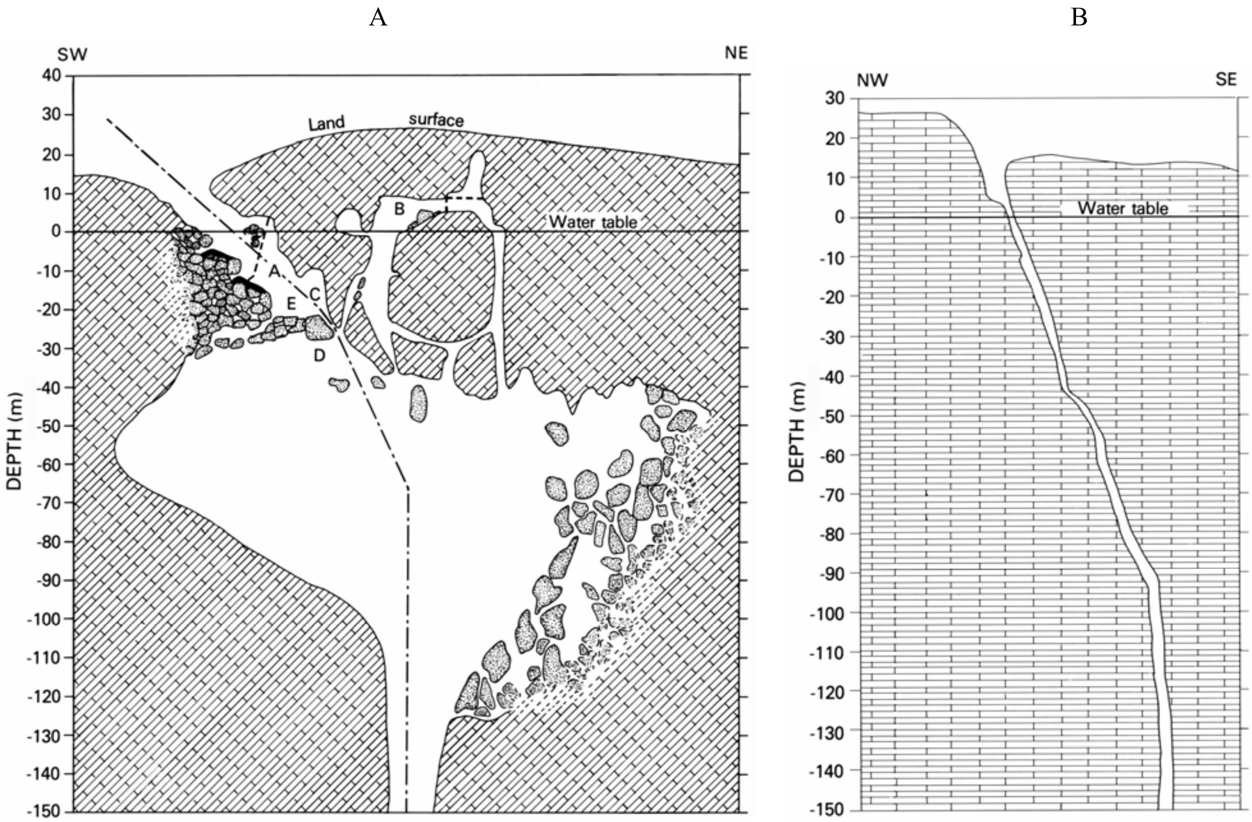


Figure 4. **Sectional views of Devils Hole.** Note the steeply dipping planar shape of the opening. Brick pattern represents Paleozoic carbonate bedrock; stippled pattern represents Paleozoic carbonate bedrock breakdown blocks. Dashed lines mark abrupt changes in chamber width. The dashed-dotted line in **(A)** marks the location of section **(B)**. Elevation datum is the mean 1994 water table (2.03 ft below the copper washer used as an elevation reference for the water-level recorder); horizontal scale equals vertical scale. Below -30 m, sections are sketched from A.C. Riggs' memory, and represent the general form only.

A. This SW-NE sectional view is modified from one by W.L. Acree, U.S. National Park Service, May 1973, library, Death Valley National Park, Death Valley, CA. Letters identify the location of important features: A - main chamber extending from the surface to about -23 m. B - Browns Room. C - area where big slabs and flakes were sheared off the NW wall by spreading of the opening; the largest sheared-off slab extended to the dashed line to the left of A and wedged in the opening. D - Anvil Rock, a sheared-off slab, is just above D. E - the floor of the main chamber below E is actually a plug of breakdown blocks, as is the shallow shelf (just barely submerged at the SW end of the pool) and the two other shelves stairstepping down to the floor of the main chamber. The black mantles on the shelves below the shallow shelf are piles of sediment and rock debris washed into Devils Hole by rainstorms. Battery Rock is the solitary block to the left (SW) of the dashed-dotted line at a depth of 40 m.

B. This NW-SE sectional view shows the narrow fissure form. The width of this section is typical of the width of most of the Devils Hole fissure except for the area to the right (NE) of the dashed-dotted line in Panel **A** of this figure and between -50 and -90 m, where the chamber is as much as 4 m wide.

Figure 5. **Devils Hole in relation to local features.** Aerial photo of Devils Hole and vicinity, looking roughly WNW. Devils Hole, marked by an arrow slightly to the right of center, is near the SW end of Devils Hole Ridge. The location of the well that galvanized the conservation community into action is marked by a star below Devils Hole. The Amargosa Desert (a Mojave Desert basin) extends from Devils Hole Ridge to the Funeral Mountains in the far distance. Ash Meadows is the light-colored area with scattered patches of phreatophytes that extends from Devils Hole Ridge to the middle distance. Death Valley lies beyond the Funeral Mountains.

survival of the Devils Hole pupfish, the integrity of the Devils Hole ecosystem, the survival of the many endemic species in the Ash Meadows area, and the integrity of Ash Meadows' aquatic, riparian, and phreatophytic biotic communities. By November 1969, conservation biologists had developed an action plan designed to ensure the survival of the endemic species and the integrity of the ecosystem. The plan led to formation of a Pupfish Task Force by the U.S. Department of the Interior in May 1970, formation of the Desert Fishes Council in November 1970, and extensive coverage of the conflict in values by local, regional, and national media. One of the most effective programs, the hour-long NBC documentary "Timetable for Disaster," aired in July 1970, contained a 15-minute segment about the immediate danger to Devils Hole, and won the 1970 "Best Documentary" Emmy Award (Deacon and Williams 1991).

Media attention associated with the Devils Hole controversy helped create public support for the groundbreaking environmental legislation of the 1970s (Rothman, in preparation) and for a lawsuit brought by the U.S. Department of Interior against Spring Meadows, Inc., in August 1971 (Deacon and Williams 1991). The suit alleged that ground-water withdrawal threatened survival of the Devils Hole pupfish, whose preservation had been a major reason for creation of the 16-hectare (40-acre) Devils Hole reservation as a disjunct portion of Death Valley National Monument. The quantity of ground water being withdrawn by Spring Meadows, Inc., was therefore infringing on a federal water right that was essential to conserve Devils Hole "....unimpaired for the enjoyment of future generations" (The National Park Service (NPS) Organic Act of August 25, 1916, 39 Stat. 535). Local conservationists displayed a bumper sticker declaring "Save the Pupfish." Local supporters of economic development countered by displaying a bumper sticker declaring "Kill the Pupfish" (Figure 6).

Figure 6. **Bumper stickers.** The conflict in values reached a local peak in the early 1970s. (Photos by E. Phillip Pister, Executive Secretary, Desert Fishes Council).

During the litigation leading to a decision by the U.S. Supreme Court, the

Court of Appeals for the Ninth Circuit held that "...the fundamental purpose of the reservation of the Devils Hole pool was to assure that the pool would not suffer changes from its condition at the time the Proclamation [reserving Devils Hole as a disjunct part of Death Valley National Monument] was issued in 1952...." (United States v. Cappaert 1974a), and then remanded the case back to the United States District Court for the District of Nevada to "determine whether, on the facts developed during the pendency of this appeal, the lower water level [1.01m below the copper washer] may be adequate to preserve the pupfish." (United States v. Cappaert 1974b). While those facts were being determined, the case moved on to the U.S. Supreme Court, which on June 7, 1976, affirmed the appellate court decision and declared: "We hold, therefore, that as of 1952 when the United States reserved Devils Hole, it acquired by reservation water rights in unappropriated appurtenant water sufficient to maintain the level of the pool to preserve its scientific value.... " (Cappaert v. United States, 1976). On December 22, 1977, the United States District Court for the District of Nevada, having held an evidentiary hearing, concluded that the United States had "....established by a preponderance of the evidence that the minimum water level at Devils Hole necessary to preserve the pupfish there is 2.7' [0.82m] below the copper washer." (United States v. Cappaert 1977). Significantly, in its Findings of Fact and Conclusions of Law (March 24, 1978), the Court affirmed its ".... continuing jurisdiction to modify the injunctive relief ...." (United States v. Cappaert 1978), making it clear that the water right held by the United States is to whatever amount is required to preserve the scientific value of Devils Hole (including its pupfish population). While the preponderance of the evidence has established that level to be -2.7', if evidence developed in the future shows that level to be insufficient to preserve the scientific value of Devils Hole, the district court has the jurisdiction and the authority to require a higher level. Based on scientific evidence, the water level could be set at any level up to -0.37 m, the mean daily water level at Devils Hole during 1962 to 1967 prior to initiation of major groundwater pumping (see caption, Figure 17).

The Supreme Court decision has, not surprisingly, had numerous ramifications. It reaffirmed the principle, previously established in Winters v. United States (1908), that when the federal government reserves land, by implication it also reserves sufficient water rights to accomplish the purposes of the reservation. Previously, this principle, referred to as the Winters doctrine, had been applied to surface waters; the Devils Hole case was its first application to ground water. The Supreme Court pointed out that in this case there was no important distinction between surface and ground water, and that the federal government had a right to sufficient water to maintain the pool at or above a particular level. The Supreme Court decision, following a complex series of events described by Deacon and Williams (1991), led to creation of the Ash Meadows National Wildlife Refuge, and played a role in justifying the transformation of Death Valley National Monument into a National Park (Rothman, in preparation).

The National Park Service Organic Act of August 25, 1916 (39 Stat. 535) requires the agency to manage parks, monuments and reservations so as to ".... conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." To discharge this responsibility with respect to the Devils Hole pupfish, it is necessary to understand the species' habitat requirements, as well as habitat changes over past millennia. As a result, considerable research has been directed at answering the questions: How did pupfish get into Devils Hole and, in addition to maintenance of water table above a minimum level, what are their fundamental habitat requirements?

How Did Pupfish Get Into Devils Hole?

About 135 million years ago (Ma), during the late Jurassic and early Cretaceous, pupfish ancestors are thought to have occupied the western Tethys Ocean. As North America and Europe drifted apart, part of the population persisted on the developing Atlantic coastline of the North American plate (Parker and Kornfield 1995). Their dispersal southward along the developing Caribbean coastline put them in a position to move up the Rio Grande River and into the interior of North America. From the Rio Grande system, pupfish moved into the Guzman Basin in Mexico, and through a series of stream captures and interbasin transfers moved across northern Mexico and southern New Mexico into the Gila River, down the Gila, up the Colorado and into the Death Valley area by the late Pliocene less than 3.4 Ma (Miller 1981; Minckley *et al*. 1986; Smith and Miller 1986; Echelle and Echelle 1998; Smith *et al*., 2002).

Extensive studies of the four pupfish species in the Death Valley/Ash Meadows region and the nearby Owens Valley region reveal little genetic differentiation, but clearly identify two separate lineages. One lineage, represented by the Owens pupfish (*Cyprinodon radiosus*) is more closely related to the lower Colorado River pupfish (*Cyprinodon macularius*) than to its geographically closer relatives (*Cyprinodon salinus, Cyprinodon nevadensis, Cyprinodon diabolis)* in Death Valley and Ash Meadows (Echelle and Dowling 1992; Echelle and Echelle 1993). Using a creative analysis of sequence divergence, Smith *et al*. (2002) estimate that the Death Valley pupfishes probably diverged from the lower Colorado/Owens Valley pupfishes about 3 Ma. Existence of separate Death Valley/Owens Valley pupfish lineages suggests that there were multiple connections from Mexican drainages, through the Colorado River, and into the Death Valley system during Plio-Pleistocene time (approximately 2 Ma). Analysis of sequence divergence also suggests that the Salt Creek pupfish (*Cyprinodon salinus*) differentiated from its Amargosa River relatives (*Cyprinodon nevadensis and Cyprinodon diabolis*) a little more than 1 Ma. Smith *et al*. (2002) further suggest that, despite a number of traits that make it one of the most distinctive of all pupfishes (small body size, lack of pelvic fins, rounded caudal fin, reduced sexual dimorphism, and a lack of male territorial behavior) (Liu 1969; Soltz and Naiman 1978), the Devils Hole pupfish (*Cyprinodon diabolis*) and the several subspecies of Amargosa pupfish (*Cyprinodon nevadensis*) diverged about 0.2 to 0.6 Ma. Smith *et al*. (2002) conclude that divergence of the Devils Hole pupfish as recently as 10,000 years ago, as suggested by Hubbs and Miller (1948) and Miller (1981), would have required unrealistically rapid sequence divergence. While Smith *et al*. (2002) have given us the most objective estimate of divergence time for Devils Hole pupfish to date, it must be remembered that dating recent events using DNA is extremely difficult because the DNA records divergence of molecules, not necessarily divergence of species. Furthermore, molecular divergence always precedes species divergence and the time discrepancy apparently increases as a function of the size of the ancestral population (Edwards and Beerli, 2000). This means that estimates of divergence time made by Smith *et al*. (2002) are more likely overestimated than underestimated.

Whether it diverged from its closest relative more than 200,000 years ago or less than 10,000 years ago, the Devils Hole pupfish is young in the geological sense. If, as seems likely, it evolved into a distinct species after it became isolated in Devils Hole, its age can be constrained by figuring out how old Devils Hole is. To get an idea of Devils Hole's age requires an understanding of regional hydrology, geology, and geochemistry, i.e., the earth-science perspective.

The Earth Science Perspective

The earth-science story begins in the Paleozoic (approximately 570 to 225 Ma) when a large part of what is now central Nevada was continental shelf (Fiero 1986).

For hundreds of millions of years, the calcium carbonate shells of marine organisms, along with lesser quantities of other sediments, accumulated on the shelf, ultimately forming a layer that was locally as much as 12,000 m thick. Even as new sediments were accumulating on the ocean floor, deeper sediments were lithifying into limestone and dolomite interbedded with smaller quantities of a variety of other rock types. Accretion of newly arrived land masses oceanward of the continental shelf progressively blockaded the thick layer of marine carbonate rocks into the continental interior. The carbonate section experienced its first major deformation from late Mesozoic to probably early Tertiary time when compression and uplift thickened the section by folding and by widespread large-scale, low-angle thrust faulting, which repeated the section in some places and dismembered it elsewhere (Winograd and Thordarson 1975). The uplift intensified erosion that exposed the carbonate rocks over large areas, thinned them, and even stripped them down to the underlying Precambrian aquitard (= confining unit; a body of relatively impermeable material that tends to block the flow of ground water) in places, thus reducing the continuity of the carbonate section. In mid-Tertiary time, the region began to extend east-west, thinning the carbonate section and causing the widespread normal block faulting that gave rise to the prominent north-south mountain ranges characteristic of the Basin and Range today (Winograd and Thordarson 1975). Less apparent is that extension concurrently caused predominantly north-south-oriented fractures and joints throughout the brittle limestone and dolomite deposits to progressively pull open, forming extensive interconnected networks of subterranean openings extending a thousand meters or more below land surface (Riggs *et al*. 1994). By the time extension slowed and rotated to its present northwest-southeast orientation 10 to 5 Ma (Zoback *et al*. 1981; Carr 1984), the modern topography of southern Nevada was largely in place. The carbonate section, which had originally been up to 12,000 m thick and continuous across most of southern and eastern Nevada, was so deformed and dismembered that only a 110-to-160-km-wide corridor of contiguous carbonate section, extending south from east-central Nevada through the Spring Mountains, remains (Dettinger 1989) (see Figure 2).

When the effects of rain- and snowfall are taken into account, the reason for focusing on the carbonate corridor becomes clear. With its extensive system of deep and still-widening interconnected fractures, the corridor is preadapted to function as a regional-scale drainage network potentially capable of quickly transporting large volumes of ground water anywhere within the contiguous corridor, with little reference to surface topography or drainage patterns. Of course, ground water cannot go just anywhere. The most conductive flowpaths tend to be along the northeast-southwest-oriented fractures (including the subterranean fissure that ultimately became Devils Hole), slowly opening perpendicular to the present direction of extension (Riggs *et al*. 1994). However, as a result of the diversity, extent, and magnitude of tectonic disruption the carbonate section has endured, the contiguous corridor is hardly homogeneous. The corridor includes interbedded rocks that flow instead of fracturing when deformed, holes where non-carbonate mountains poke through, and discontinuities where faulting has slid other rock types up against the carbonate section. Any of these features can impede or block ground-water flow. So while the contiguous corridor is excellent host rock for an aquifer on the large scale, there are many local exceptions, and the actual flowpaths taken by ground water are the lowest resistance combinations of interconnected fractures that link high-elevation, high-precipitation recharge area(s) (average annual precipitation approaches a meter at the highest elevations of the Spring Mountains) to low-elevation discharge area(s) (average annual precipitation on the low-elevation basin floors surrounding the Spring Mountains is 10 cm or less). The fall-off in precipitation with decreasing elevation understates the change in moisture availability with elevation, as the high temperatures and low humidities on the basin floors suck most of the limited rainfall back to the atmosphere before it can infiltrate below the root zone.

The Ash Meadows flow system is one of several such drainage systems ringing the Spring Mountains (Las Vegas and Pahrump valleys had oases similar to Ash Meadows, fed by flow systems similar to the Ash Meadows flow system, prior the middle of the 20th century, when extensive ground-water pumping needed for the communities' explosive growth intercepted the water before it could discharge to the surface [Harrill 1976, 1986]). The Ash Meadows flow system originates with the infiltration primarily of snowmelt (Winograd and Riggs 1998) through the lush (by southern Nevada standards) vegetation and into the shattered and karstified rock and thin soils of the relatively well-watered upper elevations of the Spring Mountains (Figure 2). From there, the water flows down and north-to-northeast through underground fracture conduits to the general vicinity of Indian Springs Valley, then turns northwest to the vicinity of Frenchman Flat, possibly picking up additional flow from the Sheep Range and a distributary from the White River flow system along the way (Figure 2). From Frenchman Flat, a high-transmissivity zone ushers the water quickly past Devils Hole to discharge at the springs in Ash Meadows (Winograd and Thordarson 1975).

Why does the water surface at Ash Meadows when Death Valley, the ultimate sump in North America, lies just across the Funeral Range from the Amargosa Desert? Why does Spring Mountain ground water not flow directly to Ash Meadows, but instead flows in a giant counterclockwise loop? The flow system loops because a big block of aquitard comprising the northwest end of the Spring Mountains (Figure 2) forces ground-water flow to detour around it. Flow system water wells to the surface at Ash Meadows (and apparently has done so for at least the last 2 to 3 million years [Hay *et al*. 1986]) because beneath Ash Meadows, the carbonate section is inferred to be faulted up against an aquitard along a front trending NNW-SSE down the southern arm of the Amargosa Desert (Winograd and Thordarson 1975) (Figure 2). Unable to penetrate the aquitard, the ground water discharges to the surface as a 15-km-long string of large, sparklingly clear, glory-hole springs surrounded by a broad halo of marshes and capillary fringe discharge areas that, together, comprise the Ash Meadows oasis (Figures 2 and 5). Total annual discharge from all of Ash Meadows' springs, marshes, and capillary fringes is estimated to be about 18,000 to 21,000 acre-feet (Laczniak *et al*. 1999). (Note that the Southern Nevada Water Authority (SNWA) filed applications for water rights in Three Lakes and Tikaboo valleys in 1989, and on March 22 - 26, 2004, the Nevada State Engineer held a hearing on their request to exercise those rights by pumping approximately 17,000 acre-feet of ground water annually from wells to be developed in those valleys (Southern Nevada Water Authority 2004; Vogel 2004). Then, on May 12, 2004, SNWA filed applications with the State Engineer for rights to pump 16,000 acre-feet of ground water annually from Indian Springs Valley (Breen 2004). All three valleys are thought to be in the Ash Meadows ground-water basin (Winograd and Thordarson 1975). Indian Springs Valley may overlie the path of the Ash Meadows flow system well upgradient from Devils Hole and Ash Meadows.)

There is some evidence that not all the Ash Meadows flow system water discharges at Ash Meadows. North of Ash Meadows, the inferred fault is thought to have progressively less offset, and may incompletely block flow of ground water into the western Amargosa Desert. The subsurface hydrogeology of the western Amargosa and the Funeral Range is poorly known and thus what actually happens is a matter of conjecture, but the chemistry of spring waters discharging from the Death Valley springs shown in Figure 2 is sufficiently similar to that of Ash Meadows waters that they might be at least partly derived from the Ash Meadows flow system

(Hunt and Robinson 1960; Hunt *et al.* 1966).

In the otherwise unrelenting desert of the basin floors, the persona of the oases depends on local circumstance and the rate and distribution of ground-water discharge. Slow, diffuse capillary fringe discharges support only phreatophyte communities or wet playas; greater but still slow discharges support marshes and Mojave-style riparian environments; whereas large focused discharges surface as springs, flow down a spring run, and are ultimately lost to evapotranspiration as the spring run anastomoses into a terminal marsh. In fact, all ground water in the Great Basin, beyond that stored in underground openings and that which escapes the Basin underground, is ultimately lost to evapotranspiration, its solutes left behind as various types and morphologies of precipitated minerals. Three morphologies of precipitated calcite store records of past environmental variations that can be used to reconstruct the history of Devils Hole. Mammillary calcite and folia precipitated from ground water onto the walls of Devils Hole below and at the water table, respectively, while flowstone precipitated on the above-water walls of Browns Room from down-percolating water.

Pupfish have been in the Death Valley area since the late Pliocene (3 to 2 Ma) and Devils Hole has existed as a subterranean fissure in which mammillary calcite has been precipitating for more than 500,000 years. So, when and how might pupfish have colonized Devils Hole? Could they have made their way there by swimming through the maze of cracks, faults, and fissures making up the Ash Meadows ground-water flow system? While some fish species have adapted to subterranean conditions, there is no evidence that any pupfish species has this capability, hence it must be assumed that pupfish could not have survived in Devils Hole until it opened to the surface, and sunlight could stimulate production of a food base capable of supporting a much richer aquatic community than is possible in the relatively sterile aquifer environment. So the question is, when did Devils Hole open to the sky?

Strictly speaking, no one knows when Devils Hole opened, but the best guess, based on circumstantial evidence, is that it happened approximately 60 ka (this idea was first proposed in Riggs 1992; subsequently, both the idea and the dating have been refined). The rationale is as follows: mammillary calcite precipitated uninterruptedly in Devils Hole for half a million years, then stopped abruptly 60,000 years ago and never restarted (Winograd *et al*. 1992). Stop and think about it: mammillary calcite precipitated continuously for 500,000 years; precipitated continuously through the climatic vicissitudes of more than four glacial cycles; precipitated continuously for 500,000 years despite tectonic disturbances and a whole range of perturbations that, though vanishingly unlikely in daily life, become highly probable over the course of half a million years. Then 60,000 years ago, at a time otherwise unremarkable in the history of the region, mammillary calcite suddenly stopped precipitating, even though the water in Devils Hole continues to be slightly supersaturated with calcite right up to the present. What happened? The inference is that the ceiling of the subterranean proto-Devils-Hole fissure collapsed, opening Devils Hole to the earth's surface and a startlingly different set of conditions than it had previously experienced. Where previously there had been a remarkably stable environment of perpetual darkness, constant temperature, and 100 percent humidity above the surface of a reservoir of crystal clear water of virtually constant chemistry, now there was low humidity, intermittent dust influxes, sediment-laden surface-water inputs, wildly varying air temperature, and daily doses of sunlight fueling the development of an algal, cyanobacterial, protozoan, and bacterial aquatic community clinging to the walls of the newly opened Devils Hole. It is widely recognized that small concentrations of certain cations or organic compounds in solution can bind to the active sites in the calcium carbonate lattice, inhibiting any further precipitation of calcium carbonate, even in the face of high carbonate supersaturation (e.g., Reddy and Hoch 2000). That something of this nature is happening in Devils Hole at present is indicated by the timing of weight increases of very carefully weighed calcite crystals placed in various underwater locations in Devils Hole for as long as 3.5 years. The crystals initially gained weight as calcite precipitated on them, then stopped gaining weight as precipitation was inhibited (Plummer *et al*. 2000). Therefore, it seems plausible that mammillary calcite precipitation stopped in response to the drastic change in conditions, particularly the suddenly more diverse chemical inputs and surface-bound aquatic community attendant to Devils Hole's opening to the earth's surface. In fact, on submerged surfaces that intercept direct sunlight, photosynthetic endolithic borers now slowly eat away the mammillary calcite coat (Figure 7A-B), and, to a lesser extent, the underlying bedrock. If Devils Hole had always been open, mammillary calcite is unlikely to have precipitated in it in the first place, and any that had managed to precipitate on its illuminated surfaces would have been removed by endolithic borers. Hence, until more compelling findings favor a different date for the opening of Devils Hole, it seems appropriate to provisionally accept 60,000 years ago as the earliest that pupfish could reasonably have colonized Devils Hole and survived. Is it possible to identify when and how colonization occurred?

Remember, the Ash Meadows flow system has been around at least since late Pliocene, and discharge from nearby interconnected springs and marshes must have supported pupfish populations within a kilometer of Devils Hole throughout the late Pleistocene. All that is required to get pupfish into Devils Hole is that sometime during the past 60,000 years water level rose high enough to spill over the rim of Devils Hole, connecting it to one of those springs or marshes. When did that happen? A wonderfully complex assemblage of calcium carbonate morphologies (Figure 8A-B) deposited on the walls of Browns Room (Figure 4A), an air-filled chamber connected to Devils Hole, stores a record of the variations in water level over the past 116,000 years. To understand how the water-level record was developed requires some background material.

Dense, white, billowy coatings of mammillary calcite originally precipitated on all of Devils Hole's underwater surfaces, as calcium-carbonate-supersaturated aquifer water circulated through it. The mammillary calcite coating is as much as 40 cm thick in places and is the material that Winograd *et al*. (1992) analyzed to develop a continuous 500,000-year-long continental paleoclimate record. Other calcium carbonate morphologies, including folia and flowstone, precipitated in Devils Hole, but in different locations and under different circumstances. Folia precipitate on the walls of Browns Room, a perpetually dark air-filled chamber (Figure 9). Foliar growth is stimulated by Devils Hole's mixed semidiurnal tide (caused by small changes in aquifer volume as the moon's and sun's gravitational forces cyclically distort the aquifer) that alternately wets and exposes a small band of wall around mean water level twice a day (maximum spring tide amplitude is about 12 cm). The film of water left on the wall as the tide drops outgases CO_2 and precipitates a distinctive form of calcite, resembling flights of white bracket fungi on vertical-to-overhanging sections of the wall within a few cm of mean water table (Figure 9). Folia are readily recognizable, and their

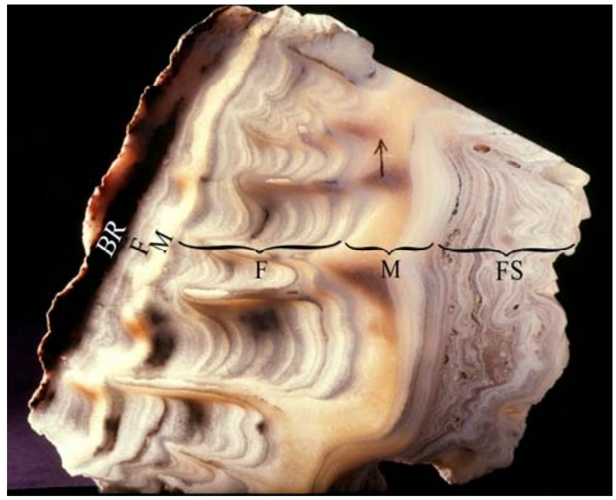
A B

Figure 7. **Planing of mammillary calcite by endolithic borers.** Endolithic borers are apparently algae or cyanobacteria that burrow shallowly into translucent mammillary calcite in locations where light intensity is sufficient to support their photosynthesis. Over time, their burrowing completely permeates the mammillary surface, eroding it back at a rate that is, qualitatively at least, proportional to the intensity of the illumination. In a deep narrow fissure like Devils Hole, sunlight strikes most underwater surfaces at a glancing angle, and the borers progressively plane the well-illuminated mounds off the mammillary surface, while leaving the shadowy hollows largely unaffected. The resulting readily recognizable topography is a powerful tool that can be used to identify surfaces that were once illuminated, even though they may now be in perpetual darkness.

A. An approximately 30-cm-high section of Devils Hole's NW wall about 5 m below water, where surface removal by endolithic borers is presently active. Direct sunlight strikes the whole of the reddish-purple area at the upper left, causing the surface to be planed flat, probably by the organisms with the reddish-purple pigment. The contour-like lines in the planed-off area mark layers of differing susceptibility to boring in the mammillary calcite. Below the pigmented area, the billowy mammillary surface has not been planed down by endolithic borers except for the three flats where billows in the mammillary surface stand high enough to catch sunlight spilling past the reddish-purple surface. The dark nodular surfaces on the mammillary calcite are areas covered by rock varnish.

B. An approximately 1-m-high section of the NW wall of Devils Hole that is now perpetually shaded by the 20-ft shelf. The dark bands form a virtual contour map of the original topography of the mammillary surface that was planed off by endolithic borers when sunlight illuminated this surface before the 20-ft shelf blocks fell into place.

A



B

Figure 8. **Calcium carbonate layers in Browns Room.** The walls of Browns Room are coated with a layer of precipitated calcium carbonate formed of sublayers of mammillary calcite, folia, and flowstone.

A. The NE wall showing the overall aspect of the coating. The coating has sheared off of the right third of the wall, probably as a result of tectonic shifting and now lies shattered, but still largely in formation, on the floor. The dark fissure running across the floor in the foreground has opened since the water table fell below floor level (approximately 20,000 years ago), indicating that extension is still opening Devils Hole. The height of the section of wall shown is about 2.5 m.

B. An approximately 15-cm-wide cross section of the wall coating in Figure 8A. The dark band along the left side of the section is bedrock (BR); to the right of the bedrock, the thin, wavy, intermittent greyish zone is a layer of folia (F) that precipitated when water table was at the level of the section (~6 m above present water table); to the right of the foliar layer is a thin, light-colored layer of mammillary calcite (M) that precipitated when water table was above this section; to the right of M, a thick, wavy, second layer of folia (F) marks a prolonged stand of water table at the elevation of the section; to the right of the foliar layer, a moderately thick, light-colored, second layer of mammillary calcite (M) marks a prolonged water-table stand above the level of the section; to the right of the mammillary layer and extending all the way to the right edge of the section is a series of jumbled flowstone (FS) layers, possibly with small amounts of folia and mammillary calcite mixed in. Because each of the different carbonate morphologies (F, M, FS) precipitated under a different set of conditions, the progression of morphologies shows whether the water table was at, above, or below the elevation of the section as the layers precipitated. The arrow points upwards when the sample is oriented as it was when it formed.

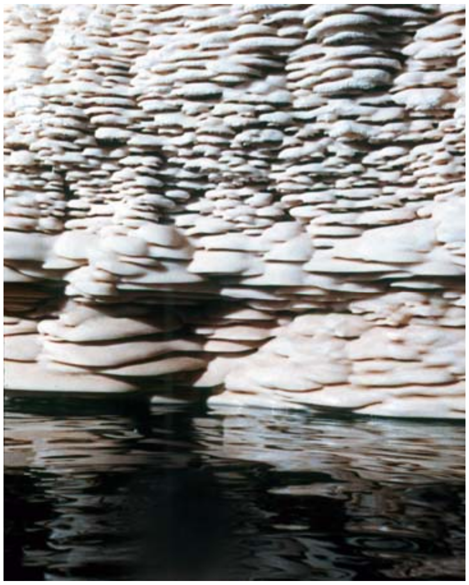


Figure 9. **Folia show past water levels in Browns Room.** In Browns Room, folia precipitate on vertical-to-overhanging walls within a few cm of the mean water level. The roughly half-m-high section of folia pictured here documents higher past water-level stands. The degree of development of the folia seems to result, in part, from the length of time the water table stood at a particular level. The discontinuity about a third of the way up from the water surface is probably due to an abrupt change in water table.

presence both above and below present water level clearly marks the paleo-water level at the time they precipitated. Flowstone is a common speleothem type found in many caves, including Browns Room. It typically occurs as a coating or drape extending downward over a wall, or as hanging or free-standing stalactites, stalagmites, and columns. Water percolating down through the soil zone and carbonate bedrock above a cave dissolves CO_2 and carbonate (just as in the recharge area in the Spring Mountains). When that water seeps into a cave, the excess CO_2 outgases, causing calcite to precipitate from the film of water. The form of the precipitating flowstone is determined by the path the film of water follows as it flows down through the air-filled chamber. In Browns Room, the water flowed down the walls in thin films, forming thin layers of flowstone that mark areas that were above the water table at a time when there was enough rainfall to support recharge to the water table in the vicinity of Devils Hole.

The walls of Browns Room are coated with a wonderfully complex interlayered accumulation of mammillary calcite, folia, and flowstone (Figure 8A, B). Because mammillary calcite only precipitates underwater, folia within a few cm of the mean water level, and flowstone subaerially, dating the different calcite morphologies from different heights on the walls of Browns Room allowed Szabo *et al*. (1994) to develop a chronology of Devils Hole water-table fluctuation during the last 116,000 years (Figure 10). Surprisingly, the Browns Room water-table chronology indicates that in the last 116,000 years, the water table has never risen more than approximately 9 m of the 17 m required for Devils Hole to overflow and form a continuous surface connection with nearby springs and marshes. In addition, there is no sign of a channel breaching the lip on the downhill side of Devils Hole. Hence, there is no evidence of a surface-water connection that would have permitted pupfish to invade Devils Hole after it is thought to have opened to the surface some 60,000 years ago! On the other hand, lack of evidence that Devils Hole has not overflowed since it opened to land surface falls well short of proving that it never overflowed. Even a cursory examination of Figure 10 will detect that there is considerable uncertainty as to the exact height and timing of water table high stands from 116,000 years ago to 20,000 years ago. The primary reason for the uncertainty is that, in Browns Room, water evaporates from the warm pool surface and condenses onto the cooler ceiling, corroding away precipitated carbonate deposits and bedrock alike. The intensity of condensation corrosion is correlated with height above the water table: it is minimal near the pool surface, but has heavily etched folia on the ceiling 9 m above the water table. Above 9 m, the bedrock is heavily corroded, and almost

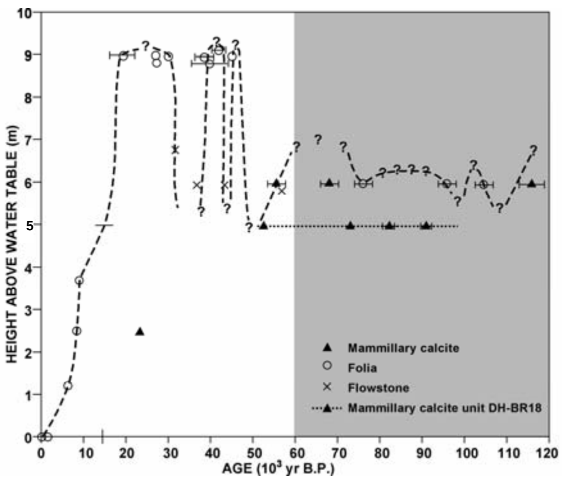


Figure 10. **Changes in Devils Hole water level over the past 116,000 years.** The dashed line marks the water level; the gray shading indicates the time prior to the inferred collapse of Devils Hole's roof. Note that, particularly prior to 20,000 years ago, there is considerable uncertainty as to the exact location of water level (Before Present [B.P.]). Modified after Szabo *et al.* 1994.

nothing in the way of folia, mammillary calcite, or flowstone remains. Hence, if there were ever stands of water high enough to overtop the lip, the deposits they left were subsequently dissolved away by condensation corrosion. To date, there has been no specific effort to answer the overflow question, but the available evidence argues against a continuous aquatic connection between Devils Hole and other perennial surface water during the last 60,000 years. So while there is good evidence that pupfish and their ancestors made a remarkable 100-million-year-long journey from the western Tethys Ocean, along the Atlantic and Caribbean coasts, up rivers, over mountains, and through the desert into the Death Valley area, there is no obvious way for them to have jumped the apparently dry last kilometer to get into Devils Hole!

How do Devils Hole Pupfish Survive?

While the pathway for invasion of pupfish into Devils Hole is uncertain, there is little question that they have lived there for thousands of years. The story of how they managed to survive for so long is also one to capture the imagination. It is a story of a species literally living on the edge, the edge of a cavern in the smallest vertebrate habitat in the world, near the upper limit of its temperature tolerance and the lower limit of its oxygen tolerance, where each spring sunlight peers over the edge of the cliff just in time to grow enough food to support a new generation before the previous year's young die of old age. Devils Hole pupfish survival strategies and ecological relations have been studied for 75 years by numerous investigators interested in understanding the conditions essential to the species' survival. Many of the studies have been supported by the U.S. National Park Service in an effort to understand how to leave them ".... unimpaired for the enjoyment of future generations" (The NPS Organic Act of August 25, 1916, 39 Stat. 535).

Pupfish survival is tied directly to the structure of its habitat, a critical characteristic of which is the availability of shallow water where pupfish spawning and most of the primary productivity that supports the aquatic community occurs. The sloping apron along the northwest side of the Hole (Figure 1), along with the breakdown slope at the southwest end of the Hole (Figure 4A), ensured availability of shallow water habitat during the water level high stands 60,000 to 20,000 years ago. The net trend towards increasing aridity in southern Nevada during the last 20,000 years (e.g., Spaulding 1990, 1995) is mirrored by a continuous lowering of water level in Devils Hole (Szabo *et al.* 1994) that left the apron high and dry, and drained all of the breakdown slope except its lowest block, the shallow shelf (Figures 1, 4A, 10). The shallow-water habitat over a relatively level bottom essential for the survival of Devils Hole pupfish is present today only over the shallow shelf. In the many ways described below, the shallow shelf is the foundation on which survival of the species depends.

Energy Inputs

The shallow shelf offers the substrate over which most of the primary production in Devils Hole occurs, and on/in which most of the invertebrate community dwells. Pupfish population dynamics are largely controlled by annual cycles of energy input (from either sunlight [autochthonous productivity] or organic material carried in from the surrounding area [allochthonous productivity]), and the mechanisms by which various members of the aquatic community share that energy with pupfish. James (1969) first noted a positive correlation between sunlight intensity and duration, algal density on the shallow shelf, and pupfish population size. Deacon and Deacon (1979), using data collected at approximately monthly intervals from May through October, noted an approximately two-month lag time between increasing sunlight and increasing pupfish populations and an approximately one-month lag time between increases in primary productivity and increases in pupfish populations. Correlation coefficients, respectively, of 0.76 ($r^2 = .57$) and 0.86 ($r^2 = .75$) at the 95 percent confidence level suggest relatively strong correlations. Wilson *et al*. (2001) attempted to measure how solar energy entering the Devils Hole ecosystem gets stored by algae and is then divided among the snails, flatworms, beetles, fish, and other creatures living in Devils Hole. Because Devils Hole pool lies in a narrow fissure (Figures 1, 4B) approximately 17 m below the land surface, there is a huge annual variation in solar energy input. Direct sunlight never reaches the water surface in the winter. It begins to strike the surface for just a few minutes in mid-February, increases to a maximum of four hours per day in June, and then decreases back to zero by late November. Sky light and sunlight reflected from Devils Hole's walls, though much less intense than direct sunlight, are more constant energy sources during all daylight hours throughout the year. Total sunlight energy falling on the pool surface is about 21 times greater in June than in November to January (Figure 11). Energy from both direct and indirect sunlight is photosynthetically fixed (NPP in Figure 11) by the filamentous green algae, cyanobacteria (bluegreen algae), and diatoms growing in Devils Hole. The energy stored by the algae is potentially available to pupfish and invertebrates. Because most of the light falls on the water surface from March to September, primary productivity is much greater during spring and summer than it is from October through February. Wilson *et al*. (2001) showed that primary productivity from direct light ranged from a maximum of about 35 mg O_2/m^2/hr in April, to 5 mg O_2/m^2/hr in October (Figure 11). Because no direct sunlight falls on the water surface from November to February, there can be no primary productivity from that source during those months. Primary productivity from indirect light varied from a maximum of about 3.8 mg O_2/m^2/hr in April and December 2000 to a minimum of about 0.3 mg O_2/m^2/hr in August (Figure 11). Thus, there is considerable seasonal variability in primary productivity from both sources of light. Even though direct sunlight falls on the water surface for only a few hours daily from spring through fall, and not at all during winter, annual energy fixation from direct light is about three times higher than from indirect light. While Wilson *et al*. (2001) convincingly demonstrated that lack of sunlight imposes unusually severe limitations on primary productivity in Devils Hole, especially during fall and winter, declining rates of primary productivity from April to August (especially April to June) suggest that other factors (nutrient depletion?) may limit primary productivity through the summer.

Organic material carried into Devils Hole by wind, water, and terrestrial animals is another source of energy for the invertebrate and fish community. Wind-borne input, like algal production, varies seasonally, with greatest input occurring during the late spring and summer months (Figure 11). Organic material carried in by water and terrestrial animals, though intermittently potentially substantial, was not measured. Over the course of a year,

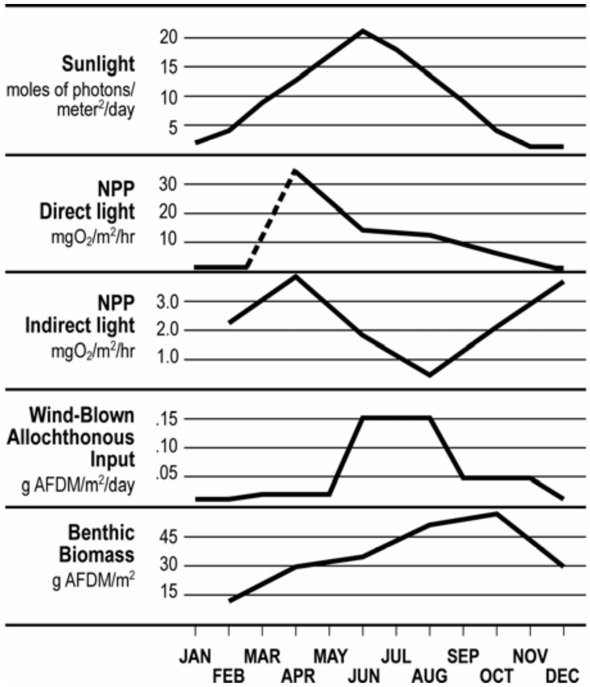


Figure 11. **Annual cycles of energy input and accumulation.** Shows annual cycles of total sunlight energy, net primary productivity (NPP) from direct sunlight, NPP from indirect sunlight, wind-borne allochthonous organic input, and benthic biomass accumulation in Devils Hole. Data are from Wilson *et al*. (2001). Daily light energy was obtained using a terrestrial quantum light sensor placed approximately 1 m above the shallow shelf. Light energy was recorded at 15-minute intervals. Data were transformed to mean daily light energy as moles of photons/m^2/day and summed to get monthly energy values. NPP was estimated by enclosing benthic algae in clear plexiglass chambers equipped with a dissolved oxygen probe. Because direct sunlight falls on the water surface only from mid-February through late November, no measurements of net primary productivity from direct sunlight were made in February or December. Wind-borne allochthonous input was collected in funnel traps placed above the water surface. Organic material washed in during rainstorms or carried in by animals was not measured, but can be substantial. Benthic biomass was collected with a 10-cm-diameter cylindrical stovepipe. Biomass was estimated, after combustion at 500 degrees centigrade for one hour, as ash-free dry mass (AFDM).

food energy available to the aquatic community from windblown sources (approximately 39 g C/m^2/yr) is somewhat greater than energy produced from direct and indirect sunlight (approximately 24 g C/m^2/yr). Furthermore, when primary productivity is at its winter low, windblown input is especially important to the larger aquatic macroinvertebrates (amphipods, beetles, flatworms, snails) which, except for snails, in turn are increasingly important to the well-being of pupfish. Collectively, these autochthonous and allochthonous sources of organic material provide nutrients for the algae, microorganisms, snails, beetles, amphipods, flatworms, other invertebrates, and pupfish of Devils Hole.

The cycles of energy input and fixation result in an annual cycle of accumulation of benthic biomass (allochthonous plants, detritus, cyanobacteria, *Spirogyra*, diatoms, snails, amphipods, beetles, flatworms, etc.) that reaches a peak in the fall and a low point in early spring (Figure 11). Of course, Devils Hole pupfish eat only selected parts of this benthic biomass, but, to the extent to which the selected parts follow the general trend, there is a distinct annual cycle of food availability to the pupfish.

So, to understand how pupfish population density is affected by food availability, it is necessary know not just the general trends of annual variation in net primary productivity (NPP) and benthic biomass, but how the parts of that biomass used by pupfish vary, and whether or not there have been major changes in the abundance of those foods over time. While detail is lacking, some indications are apparent. Wilson *et al*. (2001) report that a substantial majority of the Devils Hole pupfish diet comes from autochthonous sources, and that the winter low in the extreme annual variation in autochthonous productivity puts the Devils Hole pupfish under food stress. One indication of that stress lies in the fact that the average number of macroinvertebrates in pupfish stomachs increases from approximately two in summer to approximately six in winter. Because most macroinvertebrates in Devils Hole are too big to fit into the small pupfish mouth, this increase in the winter suggests that, to avoid starvation, the fish are forced to stuff everything into their mouths that will fit. Another indication is the observation by James (1969) that young adults (15 to 19 mm total length [TL]) were proportionately less abundant in October 1968 than in August 1968. Her analysis concluded that, because young adults were disappearing disproportionately, the population decline she observed from August to October in 1967 and 1968 could not be explained on the basis of fish dying from old age, but was more likely due to starvation. Evidence available therefore suggests that much of the population decline typically seen from late fall to spring is attributable to starvation.

Pupfish Reproduction

While the annual cycles of production and input of organic material appear to be first-order controls on population size, spawning and recruitment (larvae becoming juveniles) also have a strong influence on

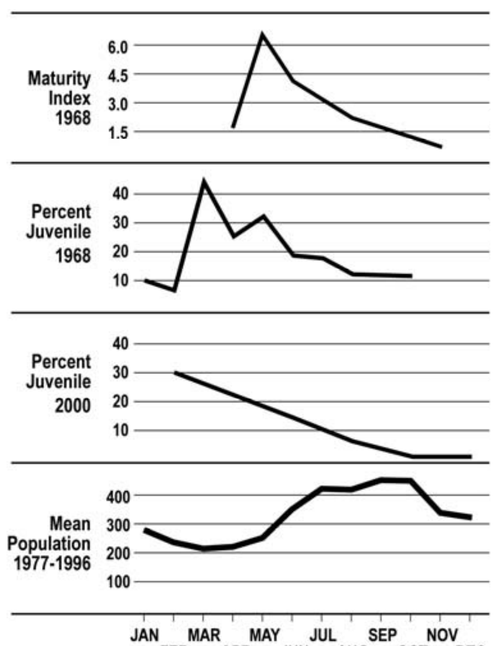


Figure 12. **Annual cycles of reproduction and recruitment.** Annual cycles of ovarian development and juvenile recruitment into the Devils Hole pupfish population. Maturity index (ovary weight as a percentage of body weight) calculated from data collected in 1968 and reported by Minckley and Deacon (1973). Percent juvenile represents the mean value for all collections made during a given month (see Table 1 for variation within a given month) and is calculated from data collected in 1968 by James (1969), and in 2000 by Threloff (2004). Juveniles include fish ≤ 12 mm total length. Mean population is based on 1977 to 1996 data, as presented in Table 2.

Table 1. **Comparison of mean total length (TL), minimum TL, and percent juveniles in the Devils Hole pupfish population, July 1967 to January 1969, and October 1999 to February 2001.** Juveniles include all fish ≤12 mm total length. N is total number of fish measured. Data are from James (1969) and Threloff (2004). James dip netted fish from the shallow shelf and measured them, whereas Threloff observed the fish by lying on a plank directly above the water surface and measured them by placing a mm rule as near to the fish as possible without disturbing them. The Threloff method probably detected a larger proportion of smaller fish. Threloff (2004) also includes fish observed and measured by scuba divers to a depth of about 30 m. The divers' counts and measurements, like James', probably include a higher proportion of adult fish than Threloff's shallow-shelf data.

Date		N		Mean TL mm		Minimum TL mm		percent Juvenile (≤12 mm)	
1967-1969	1999-2001	1967-1969	1999-2001	1967-1969	1999-2001	1967-69	1999-2001	1967-1969	1999-2001
1-Jul		247		14.1		4.5		44	
29-Aug		169		18.4		8		11	
	15-Oct		151		17		8		19
23-Dec	11-Dec	25	149	15.5	17	12	8	8	17
11-Jan		40		15.6		10		10	
17-Feb	11-Feb	46	165	18.3	15	9	3	7	30
1-Mar		34		15.2		7		32	
22-Mar		46		13.7		5		54	
7-Apr	15-Apr	74	134	16.7	17	5	6	26	22
26-Apr		91		13.1		5		26	
17-May		136		14.8		5		36	
30-May		64		14.9		5		28	
16-Jun	10-Jun	145	145	16.6	17	5	8	19	14
6-Jul		200		17.1		7		16	
23-Jul		117		16.4		5		20	
14-Aug	12-Aug	179	138	17.5	18	8	9	12	7
6-Oct	17-Oct	93	138	17.1	18	5	11	11	2
	9-Dec		122		19		12		2
6-Jan		153		17.5		11		7	
	10-Feb		126		17		3		10

Table 2. **Estimated population sizes of Devils Hole pupfish, 1972 to 2003. Mean and standard deviation are for population estimates made from 1977 through 1996 only.** Population estimates are the sum of the highest numbers counted, respectively, in the deeper waters by scuba divers and over the shallow shelf by surface counters on a given date. Two to six counts were made during the course of a single day. In 13 cases, numbers were taken from J.E. Deacon's files because original data sheets could not be found. In some cases when data are unavailable from a particular month, data collected near the beginning or the end of the previous or subsequent month are entered to represent data from the missing month.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1972				127		248	286		191		199	
1973	252	191	208			184		253			244	
1974		163		143		223	250	286	304	277	250	238
1975	208	159	148	158	201	262	278	294	260	279	261	246
1976		228	180	181	195	203	316	345	410	385		334
1977	324	276	198	210	221	351	330	553	490		381	
1978	296	225	219	184	213	274	324	387	358	441		361
1979	322	263	204	186	202	315		374	345	378	320	267
1980	305	253	165	198	252	333	357	454	386	548	414	352
1981	323	295	283	237	287	408	484	370	470			
1982			229	250				410	349	281	193	246
1983	221	218	220	248		343	481	448				
1984	144	152	143					390	497			
1985			164	174				310	467			
1986									481			
1987				180					484			
1988			236	234					566			
1989				223					463			
1990				244						577		
1991				225						492		
1992				278			466	537	406	319	368	338
1993	284	279	274	226	331	426	528			473		
1994				313					582			
1995				240						548		
1996			257							449		
1997				166					392			
1998			228						329		331	
1999			211					349		322		286
2000		237		227		237		297		294		181
2001		186		163		226		335			277	
2002	164				204			203		206		
2003	126		153			207			303			
mean	277	245	216	226	251	350	424	423	453	451	335	313
1977 - 1996 Std Dev	64	46	44	36	50	52	84	76	75	99	86	53

the amplitude and timing of the annual population cycle. James (1969) observed spawning behavior from March through September, collected young as small as 5 mm from March through July and again in early October, and showed that juveniles made up 26 to 54 percent of the population from March through May, 16 to 44 percent in June and July, and 7 to 12 percent from August through February (Figure 12, Table 1). Threloff (2004) demonstrated that larvae as small as 3 mm were present in February 2000 and 2001, and that juveniles comprised 30 and 10 percent of the population, respectively. The presence of at least some 5-mm pupfish from February through October, some juveniles throughout the year, and mature ova in the ovary of a single female captured December 23, 1967, suggests that limited spawning occurs throughout the year. However, reproduction and recruitment is clearly much greater during the spring than at other times. Increased reproductive success during spring was also found by Minckley and Deacon (1973), who showed that ovaries were most highly developed in May (Figure 12), and by Deacon *et al*. (1995) who showed that Devils Hole pupfish collected in October did not begin spawning in aquaria until late January, but fish collected in May began spawning in aquaria the following day. Once laid, the eggs hatched in approximately 7 to 8 days, and the larvae required another 8 to 10 weeks to grow to juveniles (Deacon *et al*. 1995). The increased recruitment of juveniles during spring would produce a discernible population increase beginning in March if it were not offset by increased mortality of adults. James (1969) showed that during March, April, and May, adult mortality rate increased, probably as a consequence of a combination of old age and stress from spawning. Thus, high egg production in spring, then declining egg production through summer, the lag time required for an egg to become a juvenile, and the increased recruitment of juveniles during spring offset by increased mortality of adults combine to produce an annual population increase through the summer (Figures 12, 13).

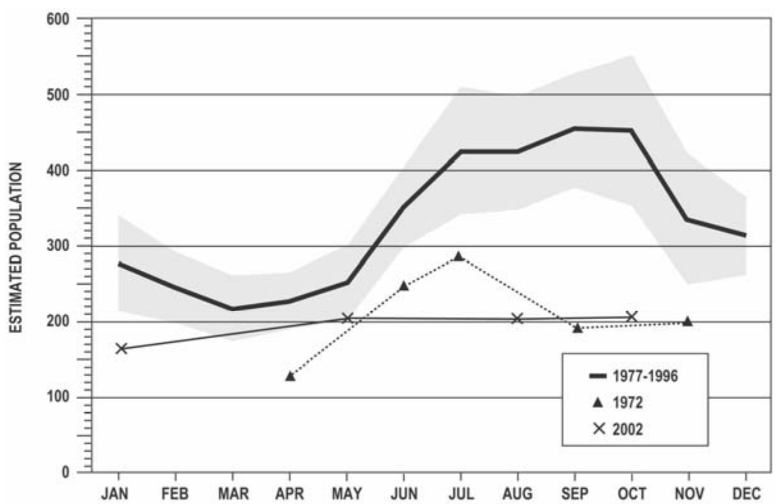


Figure 13. **The annual population cycle.** Monthly mean population size (±1 sd - represented by shaded area) of Devils Hole pupfish during 1977 to 1996 contrasted with population estimates made during 1972 and 2002 to illustrate differences in both numbers and in the annual pattern of population change. This illustration is based on Table 2 data. Data are grouped by month in an effort to show the annual pattern, even though population counts conducted over the years were not taken on the same date each month. In some cases, when data are unavailable from a particular month, data collected near the beginning or the end of the previous or subsequent month are plotted to represent data from the missing month.

The various studies cited above indicate that the peak spawning period for Devils Hole pupfish is February to May. In an environment with water temperature varying by only a few degrees, and with benthic biomass (= potential food) increasing through the summer, why should that be so? Apparently, this is another instance of the pupfish living on the edge, in this case the edge of its reproductive tolerance to temperature and dissolved oxygen (DO) concentration. Much of what is known about the effects of temperature and DO concentration on reproduction in pupfish comes from laboratory studies of closely related pupfish species. Shrode (1975) and Shrode and Gerking (1977) clearly demonstrated that while adult Saratoga Springs pupfish (*Cyprinodon nevadensis nevadensis*) tolerate a wide range of environmental temperatures (approximately 2 to 44°C), the temperature tolerance of eggs, especially during oogenesis, is much narrower. Greatest egg production occurred when females, during oogenesis, were held at any constant temperature from 24 to 30°C. Under those conditions, a normal hatch rate (more than 50 percent of the eggs hatched) was achieved if eggs were either incubated at the same constant temperature or were incubated at daily variable temperatures of 28 to 32 or 28 to 36°C. If temperature during oogenesis and incubation was raised to 32°C, hatching success dropped to about 10 percent or less, even though number of days on which spawning occurred, mean number of eggs per spawn, mean number of eggs per gram body weight per day, and mean yolk diameter were not different. At a constant temperature of 36°C, few eggs were produced and none hatched. In the thermal environment of Devils Hole (33.5 to 34°C throughout most of the area occupied by pupfish), the Saratoga Springs pupfish could therefore be expected to achieve a hatching success of no more than about 10 percent of the eggs produced, provided oxygen saturation was nearly constant at 100 percent (6.8 mg/l). Furthermore, egg production would be severely reduced.

In the Saratoga Springs pupfish, when oogenesis occurred at 28°C and eggs were transferred to other temperatures for incubation, a normal hatch was achieved at any constant temperature throughout a range of 20 to 36°C, or with 12-hr diel fluctuating temperatures of 30 to 38°C, but not at 30 to 39°C. Similarly, Kinne and Kinne (1962a, b) showed that a constant temperature of 36°C was the upper lethal limit of incubation in the desert pupfish (*Cyprinodon macularius*), but that the limit dropped to 28.5°C when oxygen saturation was reduced to 70 percent.

In Devils Hole, while spawning behavior has been observed throughout the area occupied by pupfish, Gustafson and Deacon (1998) documented production of larval pupfish only on the shallow shelf. Fry were not observed on the 20-ft shelf (approximately 5 m below the water surface) where temperature and DO concentration are nearly constant (33.5 to 34°C, 2.3 to 2.6 mg/l). Their data indicate that in 1996 and 1997 more than 50 percent of the larvae were produced on the inner (shallowest) one third of the shallow shelf where diel temperature and DO (Figure 14) variation is greatest, and only approximately 13 percent were produced on the outer one third of the shelf. Larval density was positively correlated with shallow water, gravel/cobble substrate, and length of time that direct sunlight fell on the substrate. Larval density was negatively correlated with *Spirogyra* density.

While temperature of the water throughout the cavern system in Devils Hole is a constant 33.5 to 34°C (Miller 1948; James 1969), Threloff and Manning (2003) document substantial diel temperature variation over the shallow shelf. The variation is especially pronounced from April through September, is greatest over the inner shelf, and decreases toward the outer shelf and deeper water. Perhaps of greatest importance, minimum temperature over the inner shelf frequently dips below 29°C from October to April (Figure 15). Diel variations of 31.5 to 35°C are not uncommon over the inner shelf, where midday temperatures may be elevated for 3 to 3 1/2 hours during June and July. By comparison, middle shelf temperatures seldom drop below 33°C, frequently increase to 36°C or higher, and June and July midday temperatures are elevated for 4 to 5 hours.

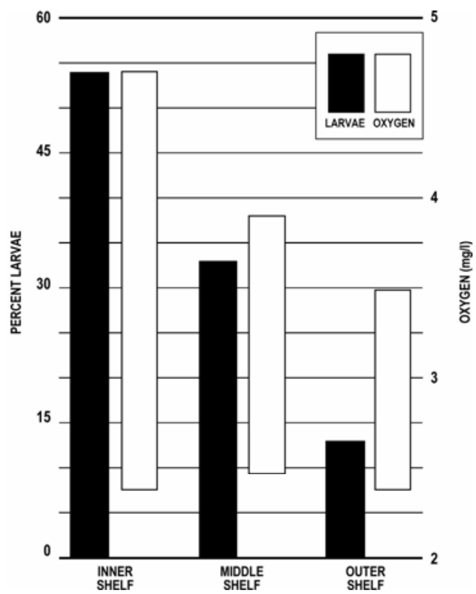


Figure 14. **Larval production in relation to variation in dissolved oxygen concentration.** Percent larval production and mean diel range of DO concentration over the inner, middle, and outer portions of the shallow shelf at Devils Hole in March, April, and June 1996, and May 1997, as reported by Gustafson and Deacon (1998). Plotted DO concentrations are the mean maxima and minima (mg/l) recorded during the 24-hour periods March 30 to April 6, June 19 to 21, 1996, and May 10 to 13, 1997. Larvae are fish ranging in size from 3 to 10 mm total length. During the measurement periods in March, April, and June 1996, DO was also measured over the 20-ft shelf, where it varied only slightly (2.3 to 2.6 mg/l), a concentration range that is probably characteristic of the entire volume of Devils Hole except for the shallow shelf.

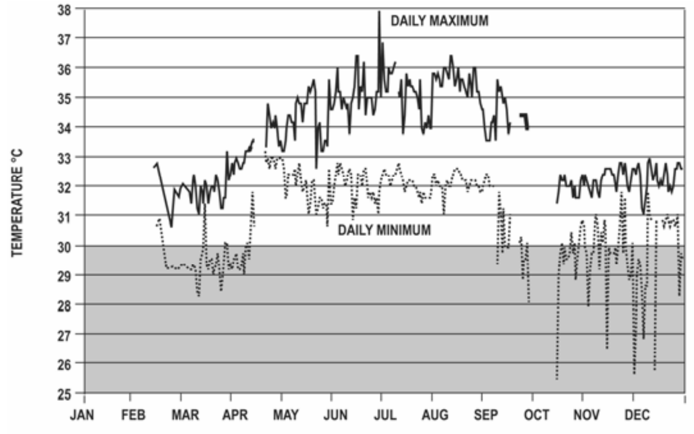


Figure 15. **Daily maximum and minimum water temperatures (°C) over the inner (southwestern) segment of the shallow shelf at Devils Hole, February to December 2001.** Data gaps are caused by a variety of factors, including equipment failure, vandalism, exposure to air as a result of exceptionally low tides, or sensor displacement by floods. For scaling purposes, 25°C is the lowest temperature shown. The only valid sub-25°C temperatures not shown are a rainstorm-induced temperature drop to 24°C for several minutes on September 3, 2001, and two extreme low-temperature excursions, to 17.1°C on December 12, 2001, and to 12.8°C on December 15 to 17, 2001, caused by extreme low tides. The shaded area (<30°C) highlights constant temperature conditions under which eggs of the Saratoga Springs pupfish are able to undergo normal development (see text). Data provided by Doug Threloff, unpublished data.

Temperatures below 33°C are attributable to cooling by cooler seasonal and nighttime temperatures, extreme low tides, evaporative cooling, and floods. Temperatures above 34°C are attributable to high midday air temperatures and intense solar radiation from late spring through early autumn. Constant temperature conditions (33.5 to 34°C) throughout most of the cavern system exceed optimal temperatures (24 to 30°C) for oogenesis of *Cyprinodon nevadensis* eggs. However, fluctuating temperatures on the inner, (Figure 15) and to a lesser extent on the middle, shelf during some parts of the year fall within or near the optimum range for both oogenesis and incubation of eggs. Of course, female Devils Hole pupfish do not stay over the inner shelf throughout oogenesis, and it is possible that optimum temperatures for oogenesis in Devils Hole pupfish are higher than for Saratoga Springs pupfish. Nevertheless, it is pretty clear that temperatures throughout most of Devils Hole are near or above limits of physiological tolerance for oogenesis, and that the inner portion of the shallow shelf during the spring is most likely the most favorable thermal environment for both oogenesis and egg development.

Measurements indicate that the DO concentration in the vast majority of Devils Hole varies little from the baseline value of 2.3 to 2.6 mg/l (34 to 38 percent saturation). As with temperature, variations in DO concentration are greatest over the inner and middle parts of the shallow shelf where DO concentration reached or exceeded saturation only around noon on rare days (Gustafson and Deacon 1998; Deacon *et al*. 1995). Greatest diel DO variability occurs in May to July, with less variability in March to April and August to September, and almost none in February (probably October to February). Dissolved oxygen concentration over the inner shelf, as a consequence of photosynthetic activity, can increase from a morning low of about 2.5 mg/l (37 percent saturation) to an afternoon high of as much as 8.5 mg/l (124 percent saturation). Elevated midday DO levels over the inner and middle parts of the shallow shelf in Devils Hole are probably crucial to the survival and development of pupfish eggs and larvae, especially in the face of elevated midday temperatures.

Reproductive success (= production of larvae) of Devils Hole pupfish may be greatest in February to May because, during this period, minimum daily water temperatures are relatively low, midday temperature increases are smaller and of shorter duration than in summer, and midday increases in DO concentration, especially in April and May, may be substantial (Figures 14 and 15). During June and July, the increased frequency and duration of high midday temperatures, coupled with diminishing photosynthetically induced rises in DO, make physiological compensation increasingly difficult. This complex pattern of variation in temperature and oxygen over the shallow shelf, especially the inner shelf, may explain why the overwhelming preponderance of larval pupfish appear restricted to the tiny inner shallow shelf section of the Devils Hole pool (Figure 14).

An examination of the percentage of the population occupying the shallow shelf provides further evidence that pupfish of all ages find the shelf less desirable in the summer (Figure 16), perhaps in part because of high midday temperatures. From November through April of 1974 to 2003, a higher percentage of the population appears to have occupied the shallow shelf than from May through October. That behavior pattern puts a higher proportion of the population, during the peak spawning months of February to April, in a location where eggs, once laid and fertilized, are more likely to hatch. The pattern is consistent throughout the 30-year period, even though the monthly mean percentage of the population occupying the shelf appears lower during all months of the year from 1993 to 2003 than from 1974 to 2003, and in December, January, February, April, May, and July that difference is greater than one standard deviation (Figure 16). Over the past decade, the shallow shelf seems to have become less attractive to pupfish.

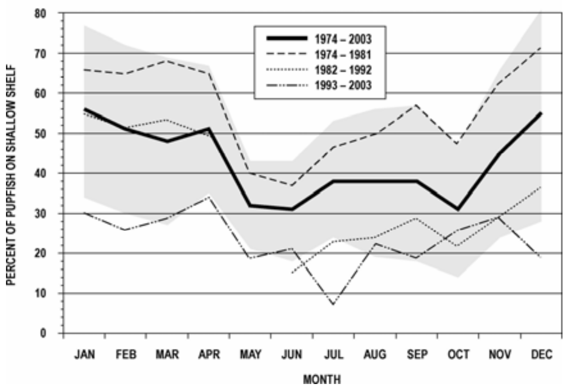


Figure 16. **Monthly mean percentage (± 1 sd - represented by shaded area) of the pupfish population occupying the shallow shelf 1974 to 2003, compared to percent occupancy during the early, middle, and late years of that 30-year period.** Number of observations during each month varied from 8 to 39 during 1974 to 2003; 5 to 15 during 1974 to 1981; 0 to 16 during 1982 to 1992; and 1 to 12 during 1993 to 2003. Note that percentage of the population occupying the shelf tended to be high during the early years and low during the later years, and that during the middle years, percent occupancy was near the 30-year mean in the spring, but tended to be low from June through December.

So, declining food availability seems to be the first-order cause of the normal fall and winter population decline, whereas increased reproductive success in the spring drives the summer population increase. Food availability and reproductive success, in turn, are controlled by a variety of factors, including variations in water temperature and DO concentration, substrate characteristics, density and/or species composition of filamentous algae, duration of sunlight shining on the pool surface, percent of the population occupying the shallow shelf, water depth over the shelf, and disturbance events such as floods and earthquakes. Each of these factors may differentially influence different life stages, and while many are predictable consequences of seasonal variations in solar radiation, others are unpredictable or operate on extra-annual time scales.

Extra-Annual Environmental and Population Variation

Perhaps because the annual oscillations of direct sunlight have such an obvious influence on autochthonous productivity, and therefore food availability, the pupfish population is expected to oscillate on a similarly predictable annual cycle. Major deviations from the "normal" annual pupfish population cycle therefore seem most likely attributable to changes in ecological interactions. Under present (2004) conditions, controlling ecological interactions (composition and abundance of benthic biomass, variations in temperature and DO concentration, reproduction, larval development, substrate characteristics, etc.) on the shallow shelf are quite variable, in part because small changes in water level cause major changes in both water volume and area of submerged substrate (Figure 17). Given the primary importance of the shallow shelf to pupfish survival, it behooves us to evaluate how various short- and long-term changes in the dynamic Devils Hole environment affect the shallow shelf's ability to continue to provide conditions necessary for the species survival.

The primary natural short-term perturbations of the shallow shelf environment are surface water inflows and earthquake-induced water level oscillations (Devils Hole tsunamis!). About once a year on average, a rainstorm on Devils Hole Ridge is large enough to cause surface runoff down the ridge, and into the small channel that drains into Devils Hole. Because the ridge is steep, flow is fast, and the water flushes organic and mineral particulates as large as a basketball into Devils Hole. The inflows have a marked effect on the shallow shelf, first flushing it clean of poorly anchored algal mats and

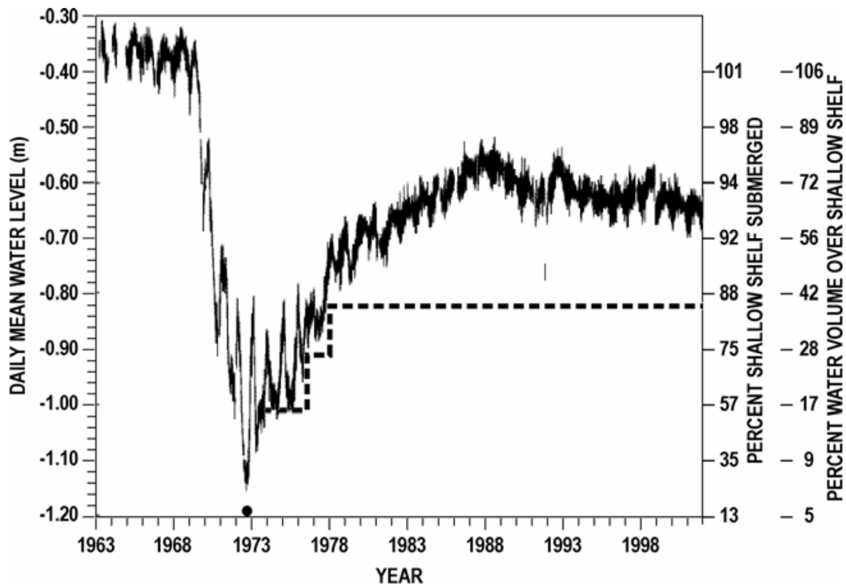


Figure 17. **Daily mean water level in Devils Hole, January 1, 1963-December 31, 2002.** Water level is measured as the distance (m) below a reference marker placed on the southeast wall above the shallow shelf when the water-level recorder was installed by the U.S. Geological Survey in 1962. Using -0.43 m to represent 100 percent, scales along the right margin of the graph indicate respectively, percent submergence of the shallow shelf substrate, and percent volume of water over the shallow shelf. That water level (-0.43 m) was the mean monthly minimum water level from July 1962 through December 1967 prior to initiation of major irrigation pumping, and was used as the standard for 100 percent coverage of the shelf in testimony before the United States District Court. Both parties to that litigation stipulated that -0.37 m was the mean daily water level prior to agricultural pumping, and that pumping could be adjusted to maintain a daily mean water level at any level below – 0.37 m (United States v. Cappaert 1978). The stair-stepping dashed line shows the minimum water level ordered by the Federal Courts as follows: June 1973, -1.01 m; July 1976, -0.91 m; January 1978, -0.82 m. The dot marks the minimum historic water level (-1.19 m), recorded in Devils Hole on September 20, 1972. Field measurements used to calculate percentages were made by Peter Sanchez and Bruce Bessken (NPS), and Gail Kobetich (U. S. Fish and Wildlife Service), and calculations were made by Herb Guenther (U. S. Bureau of Reclamation) using a computer program referred to as "STAMPEDE." The calculations are based on measurements made at 708 points on the shallow shelf.

unconsolidated material, then depositing a layer of sediment on it. After a large inflow, the sediment deposit can be thick enough to make the shelf significantly shallower; in extreme cases, part of the accumulated sediment stands above water level, reducing shelf area. After Devils Hole was fenced, the volume of particulate inputs was reduced somewhat by the access gate placed across the channel into Devils Hole. After one storm, about a cubic meter of sediment was piled against the upstream side of the gate.

The tendency for sediment accumulations to smother the shelf and reduce water depth appears to be counteracted, strangely enough, by earthquakes. Devils Hole is a natural seismograph. Its water level bounces with the passing of seismic waves, sometimes violently. From the height of stranded algal mats in the wake of the Landers earthquake on June 28, 1992, it is estimated that the water level in Devils Hole bounced about 3.6 m (1.8 m above the pre-earthquake water level, and 1.8 m below), flushing all the algal mats and most of the loose sediment off the shallow shelf. Most water level bounces in response to earthquakes are much smaller, but given the active seismicity of the west coast of North

America, it is not unreasonable to expect that most flood deposits on the shallow shelf will be flushed off sooner or later. Indeed, the shallow shelf has probably been loaded with sediment and flushed clean innumerable times during *C. diabolis'* tenure in Devils Hole. Such disturbance may, in fact, be important to maintaining an environment favorable to perpetuation of the species.

Climatically induced changes in the water table, along with fissure spreading due to continuing extension, are probably the primary long-term physical processes affecting the shallow shelf's suitability as pupfish habitat. As previously noted, from about 60,000 years ago until about 15,000 years ago, the water table was at least 5 m higher than it is now. Then, coincident with the end of the last glaciation, it fell rapidly to its present level (Figure 10). During the first 45,000 years after Devils Hole's inferred opening to the surface, the shallow shelf is unlikely to have been important to pupfish survival (assuming pupfish were in Devils Hole that early), first, because at a depth of more than 5 m, it is unlikely to have temperature and DO conditions suitable for pupfish reproduction, and second, because there was potentially a much larger area of shallow, submerged, relatively flat substrate illuminated by direct sunlight for a much longer part of the year. Most of the primary productivity and most of the pupfish's reproductive activities were likely concentrated on this substrate.

As the water table fell from 15,000 years ago to the present, the importance of the shallow shelf to pupfish survival presumably burgeoned, but two potentially sticky details remain. The first is that folia on the southwest wall of Browns Room extend to about a meter below present water table (Figure 18), a sure indication that water table was once roughly a meter lower than at present. How this relates to the importance of the shallow shelf in providing for pupfish needs depends on whether the low stand occurred before or after pupfish colonized Devils Hole. The sub-water-table folia have neither been collected nor dated, so there is no way, at present, to evaluate the significance of the low stand to pupfish survival. If the low stand occurred prior to pupfish colonization, it is of little significance beyond demonstrating that water tables about a meter lower than at present occurred naturally in the past. If, on the other hand, the low stand occurred after *C. diabolis* colonized Devils Hole, the species obviously survived the crisis. Perhaps even smaller near-surface microhabitats offer sufficient temperature and oxygen variability in tiny shelf-like spaces to support enough eggs to sustain the species. Or, perhaps there are just enough eggs able to hatch under constant temperature and oxygen conditions in deeper waters to sustain the species.

Figure 18. **Water level has been lower.** Submerged folia in Browns Room demonstrate past stands of water table down to about a meter below present water level. The floating dead mouse serves as scale.

The second detail is that the shallow shelf is the upper surface of a breakdown block that has not always been in its present location. It fell into place some time after Devils Hole opened to the sky. The evidence for this lies in the fact that the surface of the mammillary coat on the part of the northwest wall of Devils Hole closely adjacent to, and now shaded by, the shallow shelf block (Figure 19) has been eroded by photosynthetic endolithic borers that need relatively bright light to function. The collapse of the shallow shelf block is typical of the continuing evolution of Devils Hole. As extension continues to widen the Hole, blocks of bedrock, both above and below the water table, will break loose and fall. The bigger ones, including the shallow shelf block, Anvil Rock, Battery Rock, and the blocks supporting the floor of the Devils Hole entrance chamber (Figure 4A), hang up in the narrow parts of the fissure until extension widens the fissure enough for them to sink deeper. Smaller blocks will either sink or temporarily accumulate on the big blocks before a disturbance frees them to sink to depths beyond the known extent of Devils Hole (greater than 150 m below water surface). So, as in the past, the blocks forming Devils Hole's shallow shelf, Anvil Rock, Battery Rock, and others will sink, only to be replaced by others falling from above, hanging up, then sinking to the depths in their turn. To persist over the long term, inhabitants of a system as dynamic as Devils Hole must be able to handle substantial and ongoing change.

Figure 19. **The shallow shelf has not always been present.** This figure shows the mammillary surface that was eroded by endolithic borers before the shallow shelf breakdown block fell into its present position. Once the shallow shelf breakdown block fell to its present location, the surface was perpetually shaded, inhibiting further boring. The width of the area in the photograph is about 50 cm.

From about 1977 to 1996, pupfish population numbers at any given time during the year (Table 2), the annual maximum and minimum population sizes (Figure 20), and the annual population cycle (Figure 13) were reasonably consistent in spite of variation of the many environmental variables discussed above. However, pupfish populations, particularly the annual maxima, appear to be unusually small prior to 1977 and after 1996. For example, 79 percent of the counts made during 1972 to 1976 (33 of 42) and 2000 to 2003 (15 of 19) were more than one standard deviation lower than the comparable monthly means from 1977 to 1996 (Table 2). At the greatest extreme in 1972 and 2002, both population numbers and the pattern of the annual population cycle were quite divergent from "normal" (Figure 13). Why?

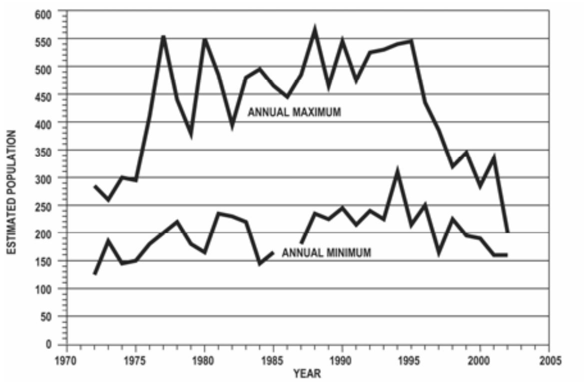


Figure 20. **Annual maximum and minimum population sizes of Devils Hole pupfish, 1972 to 2003.** Data are from Table 2.

It's the water level! Deacon and Deacon (1979) attribute the unusual population characteristics of 1972 (and 1973) to water-level decline caused by ground-water pumping. To some extent, the population also was affected by a flash flood and by management actions (removal of loose substrate from the shallow shelf, installation of artificial lights to stimulate photosynthesis) intended to counteract the effects of the declining water level. Water level reached its lowest point (-1.19 m) on September 20, 1972, at which time only 13 percent of the substrate on the shallow shelf was submerged, and the volume of water over the shelf had been reduced to 5 percent of the 1967 volume (Figure 17). It is not surprising that such a drastic reduction in the shelf habitat would be reflected in decreased population size. Some control over the water level (via constraints on the amount of water pumped) was exerted by the federal courts in June 1973, and increasingly more restrictive controls were imposed in July 1976 and December 1977 (Figure 17). Water level gradually rose until about August 1988 and since has been slowly declining (Figure 17). Analysis of population data through 1997 led Andersen and Deacon (2001) to conclude that monthly mean and annual maximum population numbers were significantly lower in 1972 to 1976 than in any subsequent five-year block of time through 1997 (the latest block analyzed, 1991 to 1997, extended over six years). And, annual minimum population size in 1972 to 1976 was significantly lower than in 1991 to 1997, but did not differ significantly from minimum populations in 1977 to 1990. The annual maximum population size throughout the 25-year period was positively correlated with mean water level during the month in which the annual maximum occurred and with mean water level during the month one year prior to the month in which the maximum occurred. Thus, it appears that relatively small changes in water level influence the annual maximum population size, but it takes relatively larger changes in water level to influence the annual minimum population size. However, the marked drop in the annual maximum and the smaller decline in the annual minimum population since about 1995 to 1997 (Figure 20, Table 2), coupled with the failure of the population to increase at all during summer 2002 (Figure 13), despite minimal changes in water level, suggest that something as potent as the water level drop of the early 1970s is adversely affecting pupfish populations.

Earlier, the authors proposed that food was a primary, and reproductive success a secondary, driver of the normal annual pupfish population cycle in Devils Hole. Closer examination of those two parameters might give us some insight into causes of the recent disturbing changes in the pupfish population picture. First, let's look at what changes may have occurred in the Devils Hole pupfish diet over the past 35 years. Stomach contents from pupfish collected in 1967 to 1969 and 1999 to 2000 were analyzed by Minckley and Deacon (1975) and Wilson *et al.* (2001), respectively. Both studies found calcium carbonate crystals the dominant item in stomachs and suggested these crystals were ingested to consume the diatoms growing on their surfaces. The crystals were probably originally parts of floating or sunken carbonate rafts on the shallow shelf, or on other substrates throughout the main chamber. Both studies identified diatoms (*Denticula* and others) as a major food item. These diatoms may colonize rafts very quickly after formation, offering the tiny pupfish convenient bitesize morsels for their dining pleasure. A study of the colonization of rafts by diatoms, and persistence of the colonizers or their replacement by other diatom species when the rafts sink, might reveal a wealth of information about the importance of raft formation to the nutritional well-being of pupfish.

The two studies also show interesting differences in food habits, probably reflecting differences in food availability associated with ecosystem alteration occurring over the 32 years from 1968 to 2000. The 1967 to 1969 study found amphipods (*Hyalella* sp), ostracods, and protozoans to be approximately equally important components of the diet (and second only to diatoms), while the later study found amphipods incidental and ostracods absent (protozoans were not looked for). In addition, in the 1967 to 1969 study, diatoms and the green alga *Spirogyra* were equally common in stomachs on an annual basis, but varied seasonally in a reciprocal manner, with diatoms most important in winter and spring and *Spirogyra* most important in summer and fall. Because it was typically undigested, *Spirogyra* was interpreted to be a feeding substrate from which amphipods and protozoa (and probably also ostracods) were taken. In the 1999 to 2000 study, *Spirogyra* was absent from all diet analyses except in October 1999 where it made up only 1 percent of the items found in gut contents. By contrast, cyanobacteria (*Plectonema wollei* and *Chroococcus*), absent from stomachs in the earlier study, constituted 7 to 19 percent of the items found in guts in August, October, and December, but was nearly absent in February. Although Wilson *et al*. (2001) found *Plectonema* to be a surprisingly good substrate for most invertebrates living in Devils Hole, ostracods were not observed in *Plectonema* mats, in pupfish stomachs, nor anywhere else on the shallow shelf, but rather were seen only in deeper waters. In both studies, beetles (mostly *Stenelmis calida*), flatworms (*Dugesia dorotocephala*), and snails (*Tryonia variagata*) constituted a small but important fraction of the diet, especially in winter. These larger invertebrates are available throughout the year, but are apparently not chosen when smaller, more easily ingested foods are available. It appears that, by contrast to 1999 to 2000, 31 to 32 years earlier (and/or perhaps at any time when *Spirogyra* is abundant), *Spirogyra* was an important summer/fall feeding substrate and the smaller invertebrates likely to be associated with *Spirogyra* (amphipods, ostracods, and protozoa) were more important components of the diet. Thus it appears there have been shifts in food availability (or at least in foods ingested) of the kind that might have an especially strong effect on summer maximum pupfish population size.

What about changes in reproductive success? Threloff (2004), in a study of demographic characteristics conducted from December 1999 to February 2001, found that reproduction and recruitment, as revealed by minimum length, mean length of the population, and percent juveniles in the population, appeared to be more successful in February than in other months. At nearly all other times, the results showed a pupfish population with a greater minimum length, an equal or longer mean length, and a lower percentage of juveniles in the population than James (1969) found in 1967 to 1969 (Table 1, Figure 12). While methods of data collection differed in the two studies, the methods used by Threloff (2004) would have been more likely to detect fish of smaller size. Therefore, at least the data on minimum length make an especially strong case that reproduction in 2000 (and perhaps subsequently) was concentrated earlier in the year (February) than was the case in 1968. Summer recruitment into the adult population from about 1997 to 2003 also appears to have decreased (Tables 1 and 2). An extreme reduction in reproduction occurred in 2002 (Figure 13) when, for the first time in 30 years, there was no summer increase in pupfish population size. No cause has been established for this anomalous situation, but a major shift in Devils Hole's ecological interactions may be responsible, particularly a significant change in algal dominance on the shallow shelf.

From at least the mid 1960s to May 1997, *Spirogyra* tended to be the dominant mat-forming alga in spring and summer, and it frequently covered substantial portions of the inner and middle segments of the shallow shelf (James 1969; Gustafson and Deacon 1998). *Plectonema* was present, sometimes producing filamentous mats extending from bottom to surface on the inner portion of the shelf; but except in winter and early spring, *Plectonema* was seldom present in greater density than *Spirogyra*. No other filamentous alga was observed to dominate the shallow shelf from the late 1960s to the late 1990s, though diatoms frequently grew as a "fuzz" covering the rocky rubble/gravel substrate. During summer 2002, the team conducting the pupfish census noted that a yellow-green algal film had formed a mat closely investing nearly all of the substrate on the shallow shelf, giving the appearance that the entire shallow shelf had been "shrink-wrapped" (Dr. Stanley Hillyard, University of Nevada, Las Vegas, oral communication, August, 2002). Dr. Michael Parker of Southern Oregon University identified the alga as *Oscillatoria*, and noted that, in other locations with which he was familiar, the species tended to form a tough, rubbery mat beneath which conditions often became anoxic. Under these conditions it is unlikely that pupfish eggs could be deposited in the interstices of the gravel and cobble substrate, or if laid, could survive the anoxic conditions. If laid on the surface of this nearly impenetrable mat, the eggs would be extremely vulnerable to predation by invertebrates or other pupfish, to the maximum daily temperatures occurring during midday in the summer, and to damage by ultraviolet light from the sun. While there may be other as yet unidentified causes for the extremely poor reproductive success in spring and summer 2002 and perhaps in previous and subsequent summers as well, *Oscillatoria* is a prime suspect. The role of *Oscillatoria* "shrink wrap" as an inhibitor to successful reproduction was further supported during summer 2003. Rains in May and August 2003 precipitated what may have been the first flood events during reproductive season in about two years. With this disturbance, the *Oscillatoria* mat was broken up, substrate on the shelf was sorted, and *Spirogyra* and diatoms apparently gained a competitive advantage. Whether from these changes or others, the pupfish population increased from July to September 2003 (Table 2).

Whether from being rendered undesirable because of *Oscillatoria* dominance, reduced frequency of natural disturbance, declining water levels, increased frequency of human disturbance (pupfish tend to move into deeper water when people begin moving around on or near the shelf), or from other causes, it is clear that over the past 30 years an ever smaller proportion of the pupfish population has been found on the shallow shelf during the peak reproductive season of February to April (Figure 16). Monthly mean percent of the population on the shallow shelf during February to April population counts from 1974 to 1993 was 49 to 68 percent, from 1993 to 2003 the proportion dropped to 26 to 34 percent, and those means included two counts in March 2003 of 10 percent and 11 percent, respectively. And, as pupfish spend less time on the shelf, egg production (oogenesis) as well as the number of eggs deposited in areas most likely to provide optimal conditions for incubation must diminish.

The apparent shift in the dominant algal species, along with the dietary and behavioral changes discussed above, suggests there have been significant changes in food availability and reproductive success of pupfish in the Devils Hole ecosystem over the past 30 to 40 years. The extensive investigations conducted at Devils Hole result in a description of what some of these changes are, but, except for the nearby water withdrawals of the late 1960s and early 1970s, there continues to be uncertainty as to why they are occurring. If they are human-induced, and the cause can be determined, federal and state management agencies could take appropriate action, or, if necessary, the District Court of Nevada has the authority to order corrections. For example, the shift in dominant algal species may have been caused by installation of the observation platform that permits visitors to look down into the Hole. *Oscillatoria* (and *Plectonema*) are able to grow more vigorously under lower light and higher temperature conditions than can *Spirogyra*. The observation platform casts a shadow on the shallow shelf for part of the afternoon. Perhaps that shadow caused just enough reduction in sunlight illumination to tip the balance in favor of *Oscillatoria* in this system, where duration and intensity of sunlight is already low. If investigation demonstrates that the observation platform is a problem, the platform could be moved.

Ground-water pumping near Devils Hole has been severely curtailed, but pumping further upgradient in the Ash Meadows flow system could lower the water table at Devils Hole. If upgradient pumping now or in the future can be shown to be responsible for reducing water level in Devils Hole, the District Court of Nevada has the authority to curtail that pumping to the extent necessary to preserve the pupfish, or other features of scientific value. Such a scenario seems increasingly probable as interest in developing the Ash Meadows Flow System ground-water resource increases. On the other hand, the gradual decline of the water table at Devils Hole may be attributable to longer-term climatic cycles. So, while a lot is known about Devils Hole, there is much yet to learn.

Conclusion

Devils Hole serves as a prime example of the connectivity of perennial desert surface waters, not so much because it is unusually well connected, but because it is unusually well studied. From the studies, it is known that Devils Hole's origins lie in Paleozoic sedimentation on a continental shelf, that accreting terranes blockaded the sediments into the continental interior, and that tectonism compressed the sediments and then extended them into the modern topography of the southern Great Basin, with high-elevation recharge areas and low-elevation discharge areas connected by a carbonate aquifer comprised of a network of subterranean fracture conduits pulled open by extension. The perennial aquifer discharge that supports low-elevation oases also precipitates datable calcium carbonate deposits of a variety of morphologies on the walls of the conduits. Each carbonate morphology deposits under a specific set of conditions, so the variation in past conditions can be interpreted from the sequence of morphologies making up the carbonate deposits. By about the Jurassic-Cretaceous boundary, pupfish ancestors, who had evolved in the Tethys Ocean, had populated the North American shore of the opening Atlantic Ocean, they then ascended the early Rio Grande, crossed the Continental Divide, and, by late Pliocene time, had colonized the Colorado River and surface waters in the Death Valley region. Devils Hole apparently remained a subterranean branch of the aquifer until about 60,000 years ago, when ceiling collapse opened it to the surface and to colonization by a photosynthetically and detritally powered aquatic community. When and how pupfish joined that community is something of a mystery, because there is no evidence that, since opening, Devils Hole has had a surface-water connection to the perennial Ash Meadows springs. However the pupfish got in, they evolved into a very distinctive species that has had to cope with perilously high temperatures, low DO content, and falling water levels, particularly during the climatic drying concurrent with the change from glacial to interglacial conditions over the last 20,000 years. Under the low-water conditions of the past few thousand years, the pupfish appear to depend on a few square meters of shallow-water substrate as their primary feeding and breeding area. Even in the face of Devils Hole tsunamis and intermittent flash floods, that small patch of habitat served the purpose admirably until development of ground-water resources in the late 1960s and early 1970s exacerbated the natural water-level decline. But, in a water-rights conflict arising from the likelihood of pupfish extinction, the Supreme Court favored preservation of the status quo in Devils Hole. So, the pupfish lives on, it's population decreasing below historic levels for reasons not entirely understood, even as new challenges to its survival loom on the horizon.

For being in such a remote place, Devils Hole's connectivity is impressive, to deep time, a vanished ocean, the vagaries of tectonism, changing climates, evolving aquatic communities, and the increasingly urgent demand for water development, all converging on this small world in a puddle in one of the most inhospitable deserts in North America.

Acknowledgments

This paper, like most, is the culmination of the efforts of many more people than just the authors. We specifically thank Dave Melton, University of Nevada, Las Vegas (UNLV), an illustrator who assembled many of the illustrations, for patiently running through numerous iterations of several of the figures while we muddled about trying to figure out what we really wanted to show and how best to communicate it. Ike Winograd of the U.S. Geological Survey introduced the first author to Devils Hole and the hydrology of the southern Great Basin, with particular emphasis on the Amargosa Desert. Cave divers Ray Hoffman, Peter Kolesar, Sheck Exley, Paul DeLoach, and Guy Bryant all made important contributions to the underwater exploration, sampling, and description of Devils Hole. During 2003 and 2004, Yuri Graves, graduate student in Environmental Studies at UNLV, developed a systems dynamics model of the Devils Hole ecosystem for his Master's thesis. His gracious sharing of ideas, countless hours of work, and fascinating discussions of possible interactions were immensely helpful as we struggled to interpret the data presented here. Dean Blinn, Andrew Martin, Michael Parker, Hal Rothman, Gary Scoppettone, Jim Thomas, Douglas Threloff, and William Van Liew reviewed the manuscript and provided important corrections, improvements, information, and data, thus contributing immeasurably to the depth and breadth of the story presented. April Perry helped illuminate the legal significance of the Devils Hole Supreme Court decision by surveying the mysteries of the legal literature. Don Sada is the unseen father of this collaboration. Had it not been his inspiration to assemble a wildly diverse group of people who shared a common interest in desert springs, this collaboration probably would not have come about. Finally, we thank the Indians, pioneers, explorers, adventurers, drifters, scallywags, miners, farmers, natural historians, politicians, bureaucrats, ordinary citizens, scientists, and tourists for contributing to the sun-bleached and dusty, but still marvelously rich, southern Great Basin tapestry into which Devils Hole is intimately embroidered, and of which this paper, our considerable efforts notwithstanding, captures only a glimpse.

References

Andersen, M.E., and J.E. Deacon. 2001. Population size of Devils Hole Pupfish (*Cyprinodon diabolis*) correlates with water level. *Copeia* 2001(1): 224-228.

Breen, H. 2004, May 12. Water Authority Seeks State's Permission to Drill New Wells. *Las Vegas Review-Journal*. www.reviewjournal.com/archive/2004archive.html.

Cappaert v. United States. 1976. 426 U.S. 128, 147 (1976).

Carr, W.J. 1984. Regional Structural Setting of Yucca Mountain, Southwestern Nevada, and Late Cenozoic Rates of Tectonic Activity in Part of the Southwestern Great Basin, Nevada and California. U.S. Geological Survey Open-File Report 84-854.

Deacon, J.E., and M.S. Deacon. 1979. Research on Endangered Fishes in the National Parks with Special Emphasis on the Devils Hole Pupfish. Pages 9-19 In, R. Linn (ed.), *Proceedings of the First Conference on Scientific Research in the National Parks*. U.S. National Park Service Transactions and Proceedings, No. 5.

Deacon, J.E., F.R. Taylor, and J.W. Pedretti. 1995. Egg viability and ecology of Devils Hole pupfish: insights from captive propagation. *The Southwestern Naturalist* 40(2): 216-223.

Deacon, J.E., and C.D. Williams. 1991. Ash Meadows and the Legacy of the Devils Hole Pupfish. Chapter 5 In, W.L. Minckley and J. E. Deacon (eds.), Battle Against Extinction: Native Fish Management in the American West. The University of Arizona Press.

Dettinger, M.D. 1989. Distribution of Carbonate-Rock Aquifers in Southern Nevada and the Potential for their Development: Summary of Findings, 1985-88. *Program for the Study and Testing of Carbonate-Rock Aquifers in Eastern and Southern Nevada*. Summary Report No. 1. Carson City, Nevada. 37 p.

Echelle, A.A., and T.E. Dowling. 1992. Mitochondrial DNA variation and evolution of the Death Valley pupfishes (*Cyprinodon, Cyprinodontidae*). *Evolution* 46(1): 193-206.

Echelle, A.A., and A.F. Echelle. 1993. Allozyme perspective on mitochondrial DNA variation and evolution of the Death Valley pupfishes (Cyprinodontidae: *Cyprinodon*). *Copeia* 1993(2): 275-287.

Echelle, A.A., and A.F. Echelle. 1998. Evolutionary relationships of pupfishes in the *Cyprinodon eximius* complex (Atherinomorpha: Cyprinodontiformes). *Copeia* 1998(4): 852-865.

Edwards, K. and R.M. Batson. 1990. Experimental Digital Shaded-Relief Maps of the Southwestern United States. Miscellaneous Investigations Series, 1:2,000,000 Experimental Shaded Relief, Southwestern United States, Map I-1850, Sheet 2 of 2.

Edwards, S.V., and P. Beerli. 2000. Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution* 54: 1839-1854.

Fiero, B. 1986. Geology of the Great Basin. Reno: University of Nevada Press.

Gustafson, E.S., and J.E. Deacon. 1998. Distribution of Larval Devils Hole Pupfish, *Cyprinodon diabolis* Wales, in Relation to Dissolved Oxygen Concentration in Devils Hole. Final Report to the National Park Service, Death Valley National Park, Death Valley, California 92328.

Harrill, J.R. 1976. Pumping and Ground-Water Storage Depletion in Las Vegas Valley, Nevada, 1955-74. *Nevada Division of Water Resources, Bulletin* 44.

Harrill, J.R. 1986. Ground-Water Storage Depletion in Pahrump Valley, Nevada-California, 1962-75. U.S. Geological Survey Water Supply Paper 2279.

Hay, R.L., R.E. Pexton, T.T. Teague, and T.K. Kyser. 1986. Spring-related carbonate rocks, Mg clays, and associated minerals in Pliocene deposits of the Amargosa Desert, Nevada and California. *Geological Society of America Bulletin* 97:1488-1503.

Hoffman, R.J. 1988. Chronology of Diving Activities and Underground Survey in Devils Hole and Devils Hole Cave, Nye County, Nevada, 1950-86, U.S. Geological Survey Open-File Report 88-93.

Hubbs, C.L., and R.R. Miller. 1948. Correlation between fish distribution and hydrographic history in the desert basins of western United States. Pages 17-166 In, Great Basin, with Emphasis on Glacial and Postglacial Times. *University Utah Bulletin* 38 (20): 1-191 (Biological Series, Vol. 10, No. 7).

Hunt, A., and C. Hunt. 1960. *Archeology of the Ash Meadows Quadrangle*. Special Collections, University of Nevada, Las Vegas.

Hunt, C.B., and T.W. Robinson. 1960. Possible Interbasin Circulation of Ground Water in the Southern Part of the Great Basin. In, Short Papers in the Geological Sciences: U.S. Geological Survey Professional Paper 400-B, pp B273-B274.

Hunt, C.B., T.W. Robinson, W.A. Bowles, and A.L. Washburn. 1966. Hydrologic Basin, Death Valley, California, U.S. Geological Survey Professional Paper 494-B.

James, C.D. 1969. Aspects of the Ecology of Devils Hole Pupfish, *Cyprinodon diabolis* Wales. Unpubl. Masters thesis, University of Nevada, Las Vegas. 70 pp.

Johnson L. and J. Johnson (eds.). 1987. Escape from Death Valley: As told by William Lewis Manley and other 49ers. Reno: University of Nevada Press.

Kinne, O., and E.M. Kinne. 1962a. Rates of development in embryos of a Cyprinodont fish exposed to different temperature-salinity-oxygen combinations. *Canadian Journal of Zoology* 40: 231-253.

Kinne, O., and E.M. Kinne. 1962b. Effects of salinity and oxygen on developmental rates in a Cyprinodont fish. *Nature* 193: 1097-1098.

Laczniak, R.J., G.A. DeMeo, S.R. Reiner, J.L. Smith, and W.E. Nylund. 1999. Estimates of Ground-Water Discharge Determined From Measurements of Evapotranspiration, Ash Meadows Area, Nye County, Nevada. U. S. Geological Survey Water-Resources Investigations Report 99-4079.

Liu, R.K. 1969. The Comparative Behavior of Allopatric Species (Teleostei-Cyprinodontidae: *Cyprinodon*). Ph.D. diss., University of California, Los Angeles.

Miller, R.R. 1948. The Cyprinodont fishes of the Death Valley system of Eastern California and Southwestern Nevada. *University of Michigan Museum of Zoology Miscellaneous Publications* 68: 1-155.

Miller, R.R., 1981. Coevolution of Deserts and Pupfishes (Genus *Cyprinodon*) in the American Southwest. Pages 39-94 In, R.J. Naiman and D.L. Soltz (eds.), Fishes in North American Deserts. New York: John Wiley and Sons.

Minckley, C.O. and J.E. Deacon. 1973. Observations on the reproductive cycle of *Cyprinodon diabolis*. *Copeia* 1973(3): 610-613.

Minckley C.O. and J.E. Deacon. 1975. Foods of the Devils Hole pupfish, *Cyprinodon diabolis* (*Cyprinodontidae*). *The Southwestern Naturalist* 20(1): 105-111.

Minckley W.L., D.A. Hendrickson, and C.E. Bond. 1986. Geography of Western North American Freshwater Fishes: Description and Relationships to Intracontinental Tectonism. Pages 519-614 In, C.H. Hocutt and E.O. Wiley (eds.), Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York, New York.

Parker, A., and I. Kornfield. 1995. Molecular perspective on evolution and zoogeography of Cyprinodontid killifishes (Teleostei; Atherinomorpha). *Copeia* 1995 (1): 8-21.

Pister, E.P. 1991. The Desert Fishes Council: Catalyst for Change. Chapter 4 In, W.L. Minckley and J.E. Deacon (eds.), Battle Against Extinction: Native Fish Management in the American West. The University of Arizona Press.

Plummer, L.N., E. Busenberg, and A.C. Riggs. 2000. In-situ growth of calcite at Devils Hole, Nevada: comparison of field and laboratory rates to a 500,000-year record of near-equilibrium calcite growth. *Aquatic Geochemistry* 6: 257-274.

Reddy, M.M., and A.R. Hoch, 2000. Calcite crystal Growth Rate Inhibition by Aquatic Humic Substances. Pages 107-121 In, Z. Amjad (ed.), Advances in Crystal Growth Inhibition Technologies. Kluwer Academic/Plenum Publishers, New York.

Riggs, A.C. 1992. Geohydrologic evidence for the development of Devils Hole, southern Nevada, as an aquatic environment. *Proceedings of the Desert Fishes Council* XX: 47-48.

Riggs, A.C., W.J. Carr, P.T. Kolesar, and R.J. Hoffman. 1994. Tectonic speleogenesis of Devils Hole, Nevada, and implications for hydrogeology and the development of long, continuous paleoenvironmental records. *Quaternary Research* 42: 241-54.

Rothman, H.K. Draft manuscript. To Ride Alone Forever in an Unpossessed Country: An Administrative History of Death Valley National Park. 82-91.

Shrode, J. 1975. Developmental temperature tolerance of a Death Valley pupfish (*Cyprinodon nevadensis*). *Physiological Zoology* 48: 378-389.

Shrode, J., and S. Gerking. 1977. Effects of constant and fluctuating temperatures on reproductive performance of a desert pupfish, *Cyprinodon n. nevadensis*. *Physiological Zoology* 50: 1-10.

Smith, A. 1993. Shoshone Tales. Salt Lake City: University of Utah Press.

Smith, G.R., T.E. Dowling, K.W. Gobalet, T. Lugaske, D.K. Shiozawa, and R P. Evans. 2002. Biogeography and Timing of Evolutionary Events among Great Basin Fishes. Pages 175-234 In, R. Hershler, D.B. Madsen, and D.R. Curry (eds.), Great Basin Aquatic Systems History. Smithsonian Contributions to the Earth Sciences. No. 33. Washington, D.C.: Smithsonian Institution Press.

Smith, M.L., and R.R. Miller. 1986. The Evolution of the Rio Grande Basin as Inferred from its Fish Fauna. Pages 457-485 In, C.H. Hocutt and E.O. Wiley (eds.), The Zoogeography of North American Freshwater Fishes. New York: John Wiley and Sons.

Southern Nevada Water Authority. 2004. SNWA Water Resource Plan. http://www.snwa.com/html/news_pubs_wr_plan.html. 53pp + appendix.

Spaulding, W.G. 1990. Vegetation dynamics during the last deglaciation, southeastern Great Basin, U.S.A. *Quaternary Research* 33:188-203.

Spaulding, W.G. 1995. Environmental Change, Ecosystem Responses, and the Late Quaternary Development of the Mojave Desert. Chapter 11. Pages 139-164 In, D.W. Steadman and J.I. Mead (eds.), Late Quaternary Environments and Deep History: A Tribute to Paul S. Martin. The Mammoth Site of Hot Springs, South Dakota, Inc. Scientific Papers, Vol. 3, Hot Springs, South Dakota.

Soltz, D.L., and R.J. Naiman. 1978. The Natural History of Native Fishes in the Death Valley System. Science Series No. 30. Natural History Museum of Los Angeles County. Los Angeles. 76 pp.

Szabo, B.J., P.T. Kolesar, A.C. Riggs, I. J. Winograd, and K. R. Ludwig. 1994. Paleoclimatic inferences from a 120,000-yr calcite record of water-table fluctuation in Browns Room of Devils Hole, Nevada. *Quaternary Research* 41: 59-69.

Threloff, D., and L. Manning. 2003. Thermal Environment of the Devils Hole Pupfish (*Cyprinodon diabolis*). Draft report, January 6, 2003. 29 pp. Plus appendix.

Threloff, D. 2004. Demographic Characteristics of the Devils Hole Pupfish between October, 1999 and January, 2003. Unpublished report, 28 pp.

Truman, H.S. 1952. Addition of Devils Hole, Nevada, to Death Valley National Monument -- California and Nevada. Proclamation No. 2961, 3 CFR 147 (1949-1953 Comp.)

United States v. Cappaert. 1974a. 508 F. 2d 313, 318 (9th Cir. 1974).

United States v. Cappaert. 1974b. 508 F. 2d 322 (9th Cir. 1974).

United States v. Cappaert. 1977. United States District Court for the District of Nevada: Unpublished Order, Civil LV_1687 (December 22, 1977).

United States v. Cappaert. 1978. United States District Court for the District of Nevada: Unreported Findings of Fact and Conclusions of Law (D. Nev., March 24, 1978, pp 15 and 16).

Vogel, E. 2004, March 25. Rural Groundwater Sought. *Las Vegas Review-Journal*. www.reviewjournal.com/archive/2004archive.html.

Wales, J.M. 1930. Biometrical studies of some races of Cyprinodont fishes from Death Valley region with description of *Cyprinodon diabolis* n. sp. *Copeia* 1930: 61-70.

Wallace, W., and E. Wallace. 1978. Ancient Peoples and Cultures of Death Valley. Ramona, California: Acoma Books.

Wallace, W., and E. Wallace. 1979. Desert Foragers and Hunters: Indians of Death Valley Region. Ramona, California: Acoma Books.

Wilson, K.P., D.W. Blinn, and D.B. Herbst. 2001. The Devils Hole Energetics/Community Relationships: Death Valley National Park, California. Two-Year Progress Report to Death Valley National Park. Project No. 7530. 52pp.

Winograd, I.J., T.B. Coplen, J.M. Landwehr, A.C. Riggs, K.R. Ludwig, B.J. Szabo, P.T. Kolesar, and K.M. Revesz. 1992. Continuous 500,000-year climate record from vein calcite in Devils Hole, Nevada. *Science* 258: 255-260.

Winograd, I.J. and A.C. Riggs. 1998. The relative contributions of summer and cool-season precipitation to groundwater recharge, Spring Mountains, Nevada, USA. *Hydrogeology Journal* 6: 77-93.

Winograd, I.J., and W. Thordarson. 1975. Hydrogeologic and Hydrochemical Framework, South-Central Great Basin, Nevada-California, with Special Reference to the Nevada Test Site. U.S. Geological Survey Professional Paper 712-C.

Winters v. United States. 1908. 207 U.S. 564 (1908).

Zoback, M.L., R.E. Anderson, and G.A. Thompson. 1981. Cenozoic evolution of the state of stress and style of tectonism in the Western United States. *Philosophical Transactions, Royal Society of London* A300: 407-434.