

ALGAE OF DEVILS HOLE, NEVADA, DEATH VALLEY NATIONAL PARK

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ABSTRACT.—We examined algal flora in the aquatic system of Devils Hole, Nevada. The water is seasonally warm, near neutral in pH, and rich in dissolved carbonate, indicative of deeply circulating groundwater flowing through carbonate rock. Most algae were benthic, with only a few planktonic representatives. Eighty-four terminal identifications in 44 genera were recorded, with diatoms and blue-green algae the most speciose groups. Diatoms were major contributors to the grazing food web. Large, mat-forming filamentous algae have an important influence on the physicochemical and general structure of the benthic substrates in Devils Hole.

Key words: Death Valley, Devils Hole, algae, Cyanobacteria, Bacillariophyta, Chlorophyta, thermal springs, desert.

Devils Hole is the collapsed top of a stretch fault leading to a flooded cave system. Carr (1988) and Riggs et al. (1994) discuss the geological development of Devils Hole. The water surface, which is about 15 m below the immediate land surface, is the hydrologic head of the regional Ash Meadows groundwater flow system. In many ways Devils Hole is quite similar to the spring ecosystem of Montezuma Well, Arizona (Boucher et al. 1984, Blinn et al. 1994). Over the last 25 yr, Devils Hole aquatic ecosystem has been studied primarily as it relates to the Devils Hole pupfish (*Cyprinodon diabolis* Wales), which is federally listed as endangered, while other facets of the ecosystem have received limited attention. The National Park Service and the United States Fish and Wildlife Service are now supporting broader studies of the Devils Hole aquatic ecosystem. A logical first step is to summarize what is known about the algal community, hence this paper. Then more in-depth work can build upon this base.

DESCRIPTION OF DEVILS HOLE

Devils Hole, part of the Great Basin Desert, lies in a disjunct portion of Death Valley National Park in southwestern Nevada (36°25'31"N, 116°17'28"E; 2400 ft elevation). The surface configuration of Devils Hole is that of an elongate rectangle with the long axis oriented northeast-southwest (Fig. 1). At the water's

surface its dimensions are approximately 22.0 × 3.5 m (Gustafson and Deacon 1998). Distance to the water, its vertical walls, and orientation of the walls restrict direct insolation to 0–4 h per day (United States Fish and Wildlife Service 1980), depending on the season. The south end of the near-surface water overlies a shallow shelf. This “upper shelf” (Fig. 2) is actually a large breakdown boulder wedged between walls of the fault. The shelf is usually at least partially covered with gravel and cobble, especially along its west side where it meets the west wall of the fault. Dimensions of the upper shelf are approximately 3.0 × 6.3 m, with water depth ranging from 0.0 m at the south end to 0.8 m at the north end. Along the west, north, and east sides of Devils Hole, walls are essentially vertical and extend down to approximately 9 m below the water's surface. The walls have a microtopography of grooves and pits which greatly increases their surface area and facilitates algal colonization (Burkholder 1996). Below the upper shelf is the “lower shelf” (Fig. 2) that slopes downward into the cave. Water depths over this shelf are 5.0–9.0 m (Gustafson and Deacon 1998). From the north end of the lower shelf, the cave system drops to unknown depths; the deepest recorded penetration (using SCUBA, 15 August 1991) was to 133 m without reaching the bottom. In the explored portion of the cave system are several branches of the cave that allow deeply circulating groundwater (Fig. 3). One

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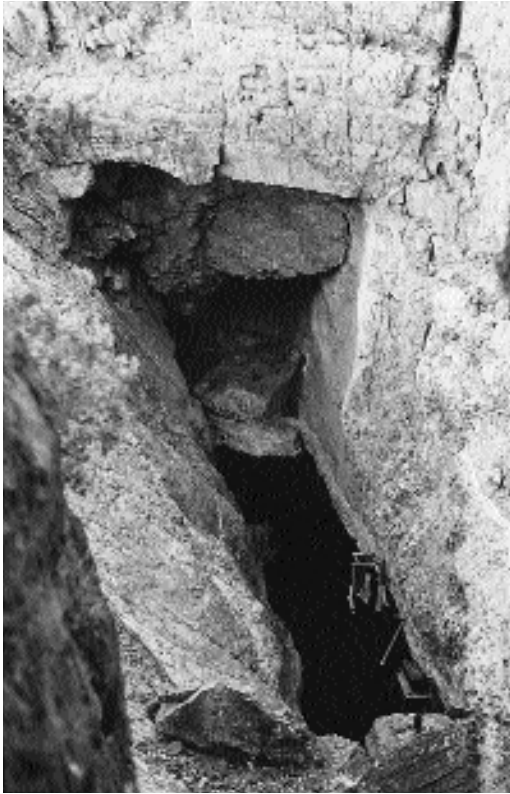


Fig. 1. Looking into Devils Hole, Nevada. Northeast is to the top of the photo.

branch extends above the water level to ground surface (Devils Hole No. 2), but at a distance that precludes light reaching the water. There is no conclusive evidence that water ever flowed out of Devils Hole. There is visual evidence that, in prehistoric times, the water level possibly was at least 1 m below the current level (Hoffman unpublished data).

Physicochemical characteristics of the water in Devils Hole are remarkably stable because the water source has been a huge regional aquifer for thousands of years (Winograd et al. 1997). The physicochemistry has been reported by many authors (Walker and Eakin 1963, Brown and Feldmeth 1971, Bateman et al. 1974, Garside and Schilling 1979, Deacon and Baugh 1985, Hershler and Sada 1987, Gustafson and Deacon 1998). Following is a summary of their measurements: temperature = 32–33°C; pH = 7.1–7.5; dissolved oxygen = 2.0–8.1 mg L⁻¹; total dissolved solids = 410–870 mg L⁻¹; conductivity = 820 μ S cm⁻¹; SiO₂ = 21–23.5 mg L⁻¹; NO₃ = below detection to



Fig. 2. Longitudinal cross section of the upper 10 m of Devils Hole viewed from the east. The horizontal line is the current water level. US = upper shelf; LS = lower shelf (redrawn with permission from Gustafson and Deacon 1998).



Fig. 3. Longitudinal cross section of the upper 60 m of Devils Hole, viewed from the east, showing conduits that allow for deeply circulating groundwater. The horizontal line is the current water level (redrawn with permission from Gustafson and Deacon 1998).

0.5 mg L⁻¹; P = below detection to 0.024 mg L⁻¹; Ca = 46–51 mg L⁻¹; HCO₃ = 300–311 mg L⁻¹. Deep waters are uniform annually and dielily, while shallow waters over the upper shelf have greater variability (Gustafson and Deacon 1998). This variation is due to the high surface area-to-volume ratio, which favors gas and heat flux, and to the greater photosynthesis that occurs on the upper shelf. Variability is greater at the south end (shallowest water) and along the west wall (greatest insolation) of the shelf. The principal source of chemical constituents of Devils Hole water is probably largely from parent rock through which groundwater courses. However, external sources of chemicals, particularly inorganic and organic nutrients, include inputs from rainwater runoff and owl pellet deposits (Deacon and Baugh

1985) as well as from wind- and insect-transported material, dead animals (owls, mice, bees, and ants), and bat guano.

The single paper on the algae of Death Valley (Durrell 1962) does not include any samples from Devils Hole.

The indigenous fauna of Devils Hole is relatively limited, although little examined. Animals reported from Devils Hole include a pupfish (*Cyprinodon diabolis* Wales), riffle beetle (*Stenelmis calida* Chandler), amphipod (*Hyaella azteca* [Saussure]), snail (*Tryonia variegata* Hershler and Sada), planarian (*Dugesia* sp.), and unidentified copepods, ostracods, and protozoans. Recent collections have disclosed other previously unidentified animals including 3 insects, oligochaete worms, gastrotrichs, nematodes, and ciliated protozoans. These additional animals are important because many are from groups known to feed on microalgae (Bott 1996).

METHODS AND MATERIALS

Ten algal collections were made over a period of 14 yr (1984–1998). Mat-forming filamentous macroalgae were collected by SCUBA divers, whereas benthic algae were collected by scraping from rock surfaces and by incubating microscope slides in the water. Sets of 10 slides each were left for 6 months on the upper and lower shelves and suspended on the west wall. In addition to field collections, algae were identified from gut contents of the riffle beetle. Two water samples were collected for phytoplankton analysis, 1 from 3 m deep in the deep-water area, and the other from the water overlying the center of the upper shelf. Each was collected in a 2.2-L Beta Plus horizontal bottle. The sample was divided into 250-mL bottles and preserved in Lugol's solution.

Identifications were made to the lowest level possible. Some genera were not taken further due to the lack of appropriate keys or to the need for culturing to make identifications. In the results section we use the term *terminal identifications* for whatever identification level is the lowest possible with available keys. Most often this can be considered synonymous with species. However, with a few algae, forms and varieties could be identified. We acknowledge that there will eventually be more terminal identifications in the

future due, in part, to better identification aids and, in part, to more intensive surveys.

In 1986 we collected two 2.2-L water samples to be tested for algal growth potential (Table 3). One was collected at the water's surface and the 2nd at 30.5 m using SCUBA gear. Both samples were filtered through a 0.2- μ m pore-size filter and kept chilled in the dark. Each sample was tested using the following solutions: original sample (= control); sample plus 0.05 mg L⁻¹ phosphorus; sample plus 1.0 mg L⁻¹ nitrogen; sample plus 0.05 mg L⁻¹ phosphorus and 1.0 mg L⁻¹ nitrogen. The test was conducted using the alga *Selenastrum* sp., a species not found in Devils Hole but a common test organism.

RESULTS AND DISCUSSION

Algae represent a diverse component of the biota in Devils Hole, although algal diversity is low compared with other aquatic ecosystems. Studies spanning more than 14 yr have identified 44 genera and 77 terminal identifications in the system (Table 1). In contrast, Kidd and Wade (1963) and Czarnecki and Blinn (1979) reported over 123 algal taxa, some of which are endemic, in the near thermally constant spring system of Montezuma Well, Arizona. Perhaps the low diversity in Devils Hole results from limited substrates and from the limited solar insolation that reaches submerged substrates in the system.

Three different algal groups were found in Devils Hole: Cyanobacteria (blue-green algae), Bacillariophyta (diatoms), and Chlorophyta (green algae). Diatoms constituted the most diverse algal group, with 54 terminal identifications in 18 genera. Mattson et al. (1995) found a similar dominance of diatoms over cyanobacteria and green algae in karst, spring-fed streams in north central Florida. Green algae were represented by the fewest species. Most algal species were present in low numbers. Only 12 species were considered dominant on any particular sample date (Table 2). This observation suggests that animal grazing may control algal diversity. Physicochemical conditions may restrict occurrence of other taxa. Of the recorded dominants, *Lyngbya limnetica* Lemm. was always dominant and *Spirogyra* sp. was dominant in spring. Most algal species were microscopic and benthic. While this physiognomy is associated with habitats

having abundant physical scouring (Peterson 1996), scouring occurs only rarely in Devils Hole. A small group of species was found to be planktonic, but the majority of these were also represented in the benthos. The phytoplankton of Montezuma Well was also predominantly derived from taxa that inhabit substrates (Boucher et al. 1984).

All these algal groups, and many genera and species, found in Devils Hole have been collected in other Great Basin waters and soils (Durrell 1962, Shields and Drouet 1962, Johansen et al. 1981, Ashley et al. 1985). Soils near Devils Hole may serve as a source of periodic algal introductions into Devils Hole.

In Devils Hole algae seem to be the main source of organic carbon (presence and influence of bacteria has not been examined). While this is typical of desert streams (Lamberti 1996), it is not typical of nearby spring pools which have abundant macrophytes.

Cyanobacteria

Cyanobacteria comprised the 2nd most diverse algal group in Devils Hole, represented by 20 genera and 24 terminal identifications. No species were planktonic that were not also present in the benthic community. The lower species diversity of cyanobacteria compared with diatoms is somewhat surprising given the ambient temperature of 32–33°C. DeNicola (1996) cites several examples of cyanobacteria replacing diatoms at elevated temperatures even below 30°C. It may be that overall algal diversity is not evenly spread throughout the photic zone. Also, the circumneutral pH may restrict occurrence of some cyanobacteria.

There is probably only 1 dominant mat-forming filamentous macroalga present. The taxon identified as *Plectonema* sp. (Minckley and Deacon 1975) is undoubtedly *Lyngbya* sp. The 2 genera are very similar morphologically and difficult to separate. *Lyngbya* sp. occurs sporadically on the upper shelf, but a dense carpet of this taxon occurs on the lower shelf. In Devils Hole there are 2 species of *Lyngbya*, *L. limnetica* Lemm., and *L. maiuscula* (Dillw.) Harvey. There is little chance of confusing the 2 species since *L. limnetica* has quite narrow cells (1–2 μm) compared to *L. maiuscula* (20–40 μm). Only scant evidence exists that *Lyngbya* sp. is used for food by either the riffle beetle

or the pupfish (Minckley and Deacon 1975). Dense mats of *Lyngbya* sp. on the lower shelf cover much of the substrate. Baugh and Deacon (1983) estimated substrate coverage to be about 80%. This large biomass may be important in locking up available nutrients and releasing them more evenly across time.

Cyanobacteria have been found only rarely in the diet of pupfish and more commonly in the diet of the riffle beetle. These algae may be ingested incidental to feeding on other organisms (Minckley and Deacon 1975). In our April samples of riffle beetles, a large percentage had ingested "unidentified cyanobacterial filaments." These were probably *Oscillatoria* sp., but they may have been ingested incidentally because the food-collecting structures of riffle beetles scrape up benthic algae of a particular size rather than being taxon selective. Even so, the main food of the riffle beetles was a diatom (see below).

The importance of cyanobacteria in Devils Hole is in stark contrast to their absence in the plankton of Montezuma Well (Boucher et al. 1984); Kidd and Wade (1963) reported 11 cyanobacteria at Montezuma Well, with no mention of relative abundance. Perhaps the difference is associated with relatively higher pH in Devils Hole (7.1–7.5) compared to Montezuma Well (6.5).

Bacillariophyta

Bacillariophyta (diatoms) was the most diverse algal group in Devils Hole, with 18 genera and 54 terminal identifications (Table 1). Thirteen genera were monospecific in occurrence. *Nitzschia* sp. and *Achnanthes* sp. were the taxonomically dominant genera, with 11 and 10 species, respectively. These diatom genera were also the dominant algae in the collapsed travertine springmound of Montezuma Well (Czarnecki 1979, Blinn et al. 1994) and in springs and spring-fed streams in Florida (Whitford 1956, Mattson et al. 1995). *Denticula elegans* Kütz, numerically dominant in Devils Hole, is a known Great Basin thermophil found in water and soil (Ashley et al. 1985). Burkholder (1996) reports that *Denticula* sp. is endosymbiotic with *Synechococcus* sp. in nitrogen-poor lakes. Perhaps a similar relationship allows *D. elegans* to dominate in Devils Hole. Diatom dominance at 32–33°C is surprising as they are usually replaced by

TABLE 1. Algal species identified from Devils Hole, Nevada, Death Valley National Park.

Taxa	Benthos	Phytoplankton	Diets
CYANOBACTERIA (cyanobacteria)			
(20 genera, 24 terminal identifications)			
<i>Anabaena</i> sp.	X	X	
<i>Anacystis gelatinosa</i> (Henn.) Lemm.	X		
<i>Aphanocapsa</i> sp.	X		
<i>Calothrix thermalis</i> (Schwae) Hansg.	X		
<i>Chaemosiphon</i> sp.	X		
<i>Chroococcus turgidus</i> (Kütz) Nag.	X		
<i>Chroococcus</i> sp.		X	
<i>Gloeocapsa</i> sp.	X	X	
<i>Heterohormogonium schizodichotmum</i> Copeland	X		
<i>Lyngbya maiuscula</i> (Dillw.) Harvey	X		
<i>Lyngbya limnetica</i> Lemm.	X	X	
<i>Lyngbya</i> sp.	X		X ^b
<i>Microcoleus vaginatus</i> (Vauch.) Gomont	X		
<i>Microcystis</i> sp.	X		
* <i>Myxosarcina amethystine</i> Copeland	X		
* <i>Oscillatoria amphibia</i> Ag.	X		
<i>Oscillatoria amphigranulata</i> van Goor	X		
<i>Oscillatoria princeps</i> Vauch.	X		
<i>Oscillatoria</i> sp.	X		
<i>Phormidium purpurascens</i> (Kütz.) Gom.	X		
<i>Plectonema</i> sp.	X		X ^a
<i>Raphidiopsis</i> sp.	X		
<i>Scytonema</i> sp.	X		
* <i>Synechococcus lividus</i> Copeland	X		
* <i>Synechococcus minervae</i> Copeland	X		
<i>Synechococcus</i> sp.	X	X	
<i>Synechocystis</i> sp.	X	X	
* <i>Thalophila imperialis</i> Copeland	X		
Unidentified cyanobacterial filaments			X ^b
BACILLARIOPHYTA (diatoms)			
(18 genera, 54 terminal identifications)			
<i>Achnanthes affinis</i> Grun.	X		
* <i>Achnanthes exigua</i> Grun.	X	X	
<i>Achnanthes exigua</i> Grun. var. <i>heterovalva</i> Krasske	X		
* <i>Achnanthes gibberula</i> Grun.	X		
* <i>Achnanthes grimmer</i> Krasske	X		
<i>Achnanthes hungarica</i> (Grun.) Grun.	X		
* <i>Achnanthes lanceolata</i> (Bréb.) Grun.	X		
<i>Achnanthes linearis</i> (W. Sm.) Grun.	X		
<i>Achnanthes minutissima</i> Kütz	X		
<i>Achnanthes submarina</i> Hust.	X		
<i>Achnanthes suchlandtii</i> Hust.	X		
<i>Achnanthes</i> sp. 1	X		
<i>Achnanthes</i> sp. 2	X		
<i>Anomoeoneis serians</i> (Bréb.) Cl. var. <i>brachysira</i> (Bréb.) Cl.	X		
<i>Brachysira aponina</i> Kutz.	X		
<i>Caloneis ventricosa</i> Ehr.	X		
<i>Caloneis</i> sp.	X		
<i>Cocconeis</i> sp.			X ^b
<i>Coscinodiscus</i> sp.	X		
<i>Cymbella angustata</i> (W. Sm.) Cl.	X		
<i>Cymbella cesatii</i> (Rabh.) Grun.	X	X	
<i>Cymbella delicatula</i> Kütz	X		
<i>Cymbella fonticola</i> Hust.		X	
<i>Cymbella microcephala</i> Grun.	X		
* <i>Cymbella minuta</i> Hilse	X		

TABLE I. Continued.

Taxa	Benthos	Phytoplankton	Diets
<i>Cymbella minuta</i> f. <i>latens</i> (Krasske) Reim.	X		
<i>Cymbella norvegica</i> Grun.	X		
<i>Cymbella</i> sp.			X ^b
* <i>Denticula elegans</i> Kütz	X	X	X ^b
<i>Eunotia arcus</i> Ehr.	X		
* <i>Eunotia pectinalis</i> (Dillw.) Rabh.	X		
<i>Eunotia praeruptia</i> Ehr.	X		
<i>Eunotia</i> sp.			X ^b
<i>Fragilaria arcus</i> (Ehr.) Cl.	X		
<i>Fragilaria vaucheriae</i> (Kütz) Peterson	X		
<i>Fragilaria</i> sp.	X		X ^b
<i>Gomphonema angustatum</i> (Kütz) Rabh.	X		
<i>Gomphonema intricatum</i> Kütz	X		
<i>Gomphonema</i> sp.	X		
<i>Mastogloia smithi</i> Thw. var. <i>lacustris</i> Grun.	X		
<i>Navicula frustulum</i> Hust	X		
* <i>Navicula minima</i> Grun.	X		
<i>Navicula parva</i> (Menegh.) Cl.-Euler	X	X	
<i>Navicula tripunctata</i> (O. F. Müll.) Bory		X	
<i>Navicula</i> sp.			X ^b
<i>Nitzschia amphibia</i> Grun.	X		
<i>Nitzschia denticula</i> Grun.	X		
<i>Nitzschia dissipata</i> (Kütz) Grun.	X		
<i>Nitzschia fonticola</i> Grun.	X		
* <i>Nitzschia frustulum</i> (Kütz) Grun.	X		
<i>Nitzschia hantzschiana</i> Rabh.		X	
<i>Nitzschia kutzingiana</i> Hilse	X		
<i>Nitzschia pales</i> (Kütz) W. Sm.	X		
<i>Nitzschia paleacea</i> Grun.		X	
<i>Nitzschia romana</i> Grun.	X		
<i>Nitzschia vitrea</i> Norman	X		
<i>Nitzschia</i> sp.	X		X ^b
<i>Pinnularia</i> sp.	X		
<i>Stephanodiscus astraea</i> (Ehr.) Grun.			
<i>minutula</i> (Kütz) Grun.	X		
<i>Synedra rumpens</i> Kütz	X		
<i>Tabellaria flocculosa</i> (Roth) Kütz	X		
Unidentified diatoms			X ^a
CHLOROPHYTA (green algae)			
(6 genera, 6 terminal identifications)			
<i>Chlorococcum</i> sp.		X	
<i>Elakatothrix viridis</i> Wille	X		
<i>Gloeocystis</i> sp.		X	
* <i>Oedogonium</i> sp.	X		X ^b
<i>Protococcus</i> sp.	X		
<i>Spirogyra</i> sp.	X		X ^b

*Previously reported from warm springs

^aPupfish diet (Minckley and Deacon 1975)^bRiffle beetle diet

cyanobacteria above 20°C (DeNicola 1996). Perhaps most diatom diversity is on the upper shelf where temperatures are less stable (Gustafson and Deacon 1998), thereby maintaining thermal refugia.

The majority of diatoms were members of the benthos, many of which are indicative of circumneutral waters with notably high car-

bonates and waters with elevated temperatures (Patrick and Reimer 1966, 1975). Some have also been found to be epiphytic on *Lyngbya limnetica*. Only 4 taxa were found in the phytoplankton that were not in the benthic community.

Both the pupfish (Wales 1930, Minckley and Deacon 1975) and riffle beetle depend

TABLE 2. Dominant algal taxa in Devils Hole, Nevada, on selected dates.

Taxon	Microhabitat	Date
CYANOBACTERIA		
<i>Chroococcus turgidus</i> (Kütz) Nag.	Benthos	April 1998
<i>Lyngbya limnetica</i> Lemm.	Benthos	All sample dates
<i>Oscillatoria princeps</i> Vauch.	Benthos	April 1998
<i>Synechocystis</i> sp.	Phytoplankton	June 1984
BACILLARIOPHYTA		
<i>Cymbella norvegica</i> Grun.	Phytoplankton	November 1986
<i>Denticula elegans</i> Kütz.	Benthos	December 1983 April 1998
<i>Navicula minima</i> Grun.	Benthos	November 1986
<i>Nitzschia amphibia</i> Grun.	Benthos	April 1998
CHLOROPHYTA		
<i>Gloeocystis</i> sp.	Benthos	June 1984
<i>Protococcus</i> sp.	Benthos	June 1984
<i>Spirogyra</i> sp.	Benthos	Every spring

Table 3. Algal growth potential for water from Devils Hole, Nevada, using the test alga *Selenastrum* sp.

Site	Control	+0.05 mg LP ⁻¹	+1.0 mg LN ⁻¹	+0.05mg LP ⁻¹ +1.0 mg LN ⁻¹
Maximum specific growth rate - day ⁻¹				
Surface water	0.77	1.22	0.70	0.90
30.5-m water	0.56	1.12	0.87	1.16
Maximum standing crop - cells mL ⁻¹				
Surface water	1.54 × 10 ⁴	3.48 × 10 ⁴	1.39 × 10 ⁴	3.80 × 10 ⁴
30.5-m water	1.02 × 10 ⁴	3.80 × 10 ⁴	1.15 × 10 ⁴	3.55 × 10 ⁴
Dry weight - mg L ⁻¹				
Surface water	0.31	1.04	0.28	1.01
30.5-m water	0.20	1.14	0.23	0.94

heavily upon diatoms as a food throughout the year. The riffle beetle consumed predominantly *Denticula elegans* and only a few other taxa (Table 1). It is likely that the snails also depend heavily on diatoms as a food.

Chlorophyta

Green algae are relatively minor contributors to algal diversity in Devils Hole. This observation might have been expected since green algae are more sensitive to high temperatures than cyanobacteria (Brues 1929) and require more light. However, DeNicola (1996) suggests that Chlorophyta may dominate at temperatures of 15–30°C. In Devils Hole only 6 genera and 6 terminal identifications of Chlorophyta were found. Four species were benthic and 2 were planktonic.

Two filamentous green algae occur in Devils Hole, *Spirogyra* sp. and *Oedogonium* sp.

The latter is found only sporadically and is present in the riffle beetle diet. *Spirogyra* sp. is seasonally common, mainly on the upper shelf. This alga has been found in gut contents of both the riffle beetle and pupfish (Minckley and Deacon 1975), but at low levels. *Spirogyra* sp. may be incidentally ingested by the pupfish while it catches invertebrate prey (Minckley and Deacon 1975). Beds of *Spirogyra* sp. are, however, important in their influence on the physical environment of the upper shelf. *Spirogyra* sp. beds can become dense in spring and summer. James (1969) gives an annual chronology of the build-up of the beds, and Gustafson and Deacon (1998) illustrate some monthly and annual differences in percent coverage. *Spirogyra* sp. beds can occupy much of the water column over the upper shelf and cover much of the gravel-cobble substrate. In doing so the beds cover substrate

interstices and contribute to increased water temperatures by reducing mixing of shelf water with deeper water. Both conditions are detrimental to the survival of the larval pupfish (Gustafson and Deacon 1998).

The 2 chlorophyte taxa found in the phytoplankton, *Chlorococcum* sp. and *Gloeocystis* sp., have not been found associated with substrates in Devils Hole. Neither genus has been identified in dietary studies. The riffle beetle diet occasionally did include a considerable amount of unidentified algal cells, however, some of which resembled *Protococcus* sp.

Algae and Water Chemistry

Results from algal growth potential experiments indicate that phosphorus was the most limiting nutrient in Devils Hole. Groundwater typically is low in both nitrogen and phosphorus (van der Kamp 1995). Addition of phosphorus to Devils Hole water increased both algal growth and maximum standing crop (Table 3). Deacon and Baugh (1983) noted that owl pellets dropped into the water increased both O-PO₄ and N-NO₃ and suggested these nutrients would stimulate algal growth.

Deacon and Baugh (1985) provide information on the monthly and annual variability of primary productivity on the inner and outer portions of the upper shelf. They suggested the variability is due to light intensity and duration and the quantity of nutrients available. In the 1970s, when declining water levels (due to excessive groundwater pumping) began exposing the surface of the upper shelf, artificial lighting was used to stimulate primary productivity in Devils Hole (Osborn 1983, Deacon 1985).

Production of oxygen through photosynthesis is important to the survival of pupfish eggs and larvae (Deacon et al. 1995, Gustafson and Deacon 1998). Particularly important is the diel fluctuation in dissolved oxygen. Oxygen production is mostly due to microscopic benthic algae rather than the large, filamentous algae or phytoplankton. Bubbles rapidly appear on the encrusting benthic algae as soon as direct sunlight strikes them.

Threats to the Devils Hole System

A drop in water level beyond the upper shelf will likely impact the algal community by reducing the surface suitable for diatom colo-

nization. This will have effects on both biomass and diversity throughout the ecosystem. On the west wall diatoms may be able to follow dropping water levels down the wall. But there is a limit to their movement because direct insolation occurs only a few meters down this wall due to the geometry of the fault. Beyond that point diatoms may not survive in high densities. A positive effect of dewatering the 1st shelf may be reducing the negative influence of *Spirogyra* sp. upon larval pupfish survival. However, this may never become important because larval pupfish depend so greatly upon substrate interstices to avoid adult cannibalism (Gustafson and Deacon 1998).

Future Research

Desert springs often have stability in most physicochemical characteristics, with only solar input varying (Boucher et al. 1984). They seem to offer a link between the artificiality of laboratory environments and the more variable natural environments. Such springs provide invaluable settings that could be studied more. Boucher et al. (1984) have also shown how these springs are useful in comparing temperate and tropical aquatic ecosystems.

The comparison of ecosystems in Devils Hole and Montezuma Well should be fruitful. They are alike in many ways, but they vary in the amount of solar input due to the smaller opening at Devils Hole. Additionally, the Montezuma Well ecosystem can be compared to that in Crystal Pool, a large spring near Devils Hole with water coming from the same aquifer, but which has marginal macrophyte beds and a water outflow.

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