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THE UNIQUENESS AND VALUE OF THE MONTEZUMA
WELL-DITCH SYSTEM AS A RESEARCH RESOURCE

by

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INTRODUCTION

When Hyaella montezuma first appeared in print as a new species probably endemic to Montezuma Well (Cole and Watkins, 1977), an amphipod-expert friend expressed the opinion that probably there were many places in the West like the Well, and that Hyaella montezuma might exist elsewhere. I remember this because I felt at the time that he was wrong. Now I'm sure he was. His experience had been largely in well-watered regions where lakes and streams are close together, and connected to a great extent. To him, the idea of a body of water as an isolated island was alien, and he focussed on the species rather than the deme (population). The cenotes of Yucatán have been compared with Montezuma Well, but in that cryptorheic part of Mexico there may be a great deal of subsurface connection among the cenotes, and isolation is not pronounced. Montezuma Well and its effluent stream constitute a unique system that deserves further study, accompanied by rigorous protection. There are countless problems to be performed by conscientious students and their professors. Material for Masters and PhD theses and dissertations is nearly unlimited. In time, Montezuma Well could rate first among those National Parks and Monuments where research has been carried out.

We know the Well is a fairly simple ecosystem. A list of its organisms is relatively short. There are comparatively few species, but a great abundance is shown by some individual species. In some respects this is typical of a polluted or a hypersaline situation; in

another sense it recalls many spring habitats. If there is a pollutant involved, it probably is free CO_2 or unusually high concentrations of bicarbonate. These two (especially the gaseous CO_2) may be responsible for the absence of certain animals that "should" be there, as well as the supposedly low Shannon-Weaver diversity index (never calculated for communities in the Well system!).

In recent years it has become evident that cosmopolitanism among freshwater organisms is far less than has been believed for the past century (Frey 1982). Accompanying this notion we can say that there is more diversity among these organisms than commonly believed and endemism in isolated habitats such as Montezuma Well may be striking. In addition to the biota of Montezuma Well and its effluent ditch the abiotic factors of the ecosystem have some unique properties and deserve further study and protection.

A surprising feature of Montezuma Well is the lack of certain organisms. The absence of planktonic diaptomid copepods, cladocerans, and rotifers is especially puzzling. There is, however, a chydorid cladoceran in the weed beds, referable to the genus Alona and designated no more specifically in the literature on the Well. David G. Frey (in litt., 1975) stated that the specimens I sent him that year are "...quite definitely Megard's Alona setulosa." Robert Megard described A. setulosa from specimens collected in Lake Itasca, Minnesota. It is significant that about the time Frey wrote to me he was becoming aware of the fact that, despite two centuries during which the idea of cosmopolitanism among the Cladocera prevailed, there is a much reduced geographic range for each species and there is far more world-wide diversity among these

microcrustaceans than had been previously believed. Single ubiquitous species of the past have become many species, each with a rather restricted range (see Frey, 1982). The Alona species in the marginal weed beds might be another endemic (in my mind's eye I see Alona montezuma sp. nov.!).

It is the purpose of this report to discuss various aspects of the Well ecosystem, pointing out the problems that are still awaiting study, biological as well as geologic, chemical and physical. Much of the presentation will be in an anecdotal style -- an unpardonable thing in this day of scientific writing. There may be repetition also, as I use different examples of questions that await answers.

The basis of much of this goes back to the first work starting in the summer of 1960 and summarized in the Final Report to Montezuma Castle National Monument of Investigations of Montezuma Well (Cole, 1965). The report contains much information about the system, but we were not able to solve completely some of the problems we attacked.

CHARACTERISTICS OF THE WELL AND DITCH

The Well is a limnocrene fed by artesian waters arising from two or three deep fissures near the center. Cole and Barry (1973) presented a bathymetric map and a table of morphometric data applying to the Well basin. Other details that may facilitate further research are presented here (Table 1). The water pours out of this spring lake from a point at the southeast border. Many years ago this outlet was dubbed the swallet by Monument personnel. It is also called the inner outlet. The water disappears into a limestone cave for about seven minutes' flow

TABLE 1. SOME MORPHOLOGIC AND MORPHOMETRIC DATA
FROM MONTEZUMA WELL, ARIZONA

Area	0.76 ha	1.88 acres
Maximum length	112 m	367.5 ft.
Ashoreline	322 m	1,056.4 ft.
Shoreline - development index	1.04	1.04
Volume	50,842 m ³	13,432, 456 U.S. gallons
Volume - development index	1.18	1.18
Maximum depth	17 m	55.8 ft.
Mean depth	6.7 m	22.0 ft.
Relative depth	17.3%	17.3%
Slope 0-4 m	19°10'	34.4%
Slope 4-8 m	55°10'	142.8%
Slope 8-12 m	37°54'	77.8%
Slope 12-16 m	21°03'	38.5%
Mean slope	22°50'	42.1%

TABLE 1. SOME MORPHOLOGIC AND MORPHOMETRIC DATA FROM MONTEZUMA WELL, ARIZONA
(cont.)

Depth, m	Area, ha	% of total	Stratum, m	Vol, m ³	% of total
0	0.7583	100	0-1	6,576	12.9
1	0.5618	74.1	1-2	5,057	9.9
2	0.4465	58.9	2-3	4,260	8.4
3	0.4057	53.5	3-4	3,940	7.8
4	0.3821	50.4	4-5	3,717	7.3
5	0.3615	47.7	5-6	3,543	6.9
6	0.3472	45.8	6-7	3,418	6.7
7	0.3364	44.4	7-8	3,280	6.5
8	0.3196	42.1	8-9	3,094	6.1
9	0.2991	39.4	9-10	2,887	5.7
10	0.2785	36.7	10-11	2,629	5.2
11	0.2476	32.7	11-12	2,330	4.6
12	0.2188	28.9	12-13	2,011	3.9
13	0.1840	24.3	13-14	1,659	3.3
14	0.1484	19.6	14-15	1,338	2.6
15	0.1197	15.8	15-16	870	1.7
16	0.0540	7.1	16-17	232	0.5
17	0.0028	0.4			

before emerging at the outer outlet (ca. 5 m lower altitude). This heads an effluent stream called simply the ditch. Under natural conditions the outer outlet would pour into Wet Beaver Creek (designated hereafter simply as Beaver Creek). The ditch is man made and served originally as an Indian irrigation canal. A calibrated Parshall flume or "weir", present a few meters downstream, served for making rough estimates of water entering the Well daily, without taking into account evaporation and unknown losses from the Well elsewhere.

The upper reaches of the ditch are very high in free CO_2 , but by the time the flow reaches the Monument picnic grounds (about 40 minutes later, and roughly one kilometer from the outer outlet) much CO_2 has been lost, and the biota has changed. Very conspicuous changes have occurred by the time the water reaches Station III of Cole and Batchelder (1969). This is 1.57 km from the outer outlet and very near the boundary of Monument property. It is an hour's flow from the outlet. During the last 20 minutes' flow from the picnic grounds, about 89 kg (almost 196 lbs) of CaCO_3 are precipitated each day.

The upper part of the ditch differs from most rheocrenes and cave streams in limestone regions by having exceptionally high CO_2 tensions, and the preponderance of ancient carbon in the CO_2 and $\text{Ca}(\text{HCO}_3)_2$. Thirty mg of CO_2 per liter is a very high concentration in natural waters. At the outer outlet the lowest amount we ever found was 73.5 ppm, and the highest was 864.5 mg CO_2 /liter.

Thus the Well system provides four distinct aquatic habitats: the lake or limnocrene; the unexplored watery cave; the upper part of the ditch; and the lower ditch. There are within the Well proper other

distinct habitats, their communities, and subdivisions of them: the pelagic; the benthic; and the fringing, littoral habitat and its community.

The adjacent terrestrial environment is also varied. Clark and Burgess (1966) studied the differences in vegetation patterns on the slopes external to the rim of the depression that holds the Well. Marked contrasts can be found also within the rim on the steep cliffs that bound the Well, depending on what compass direction is faced. Early studies (Cole, 1965) on solar radiation at the Well surface and its subsequent penetration, have been surpassed by more sophisticated treatment by Dean W. Blinn and his students (pers. commun.). Further information that could have been derived from the data presented in the 1965 Final Report, and by Cole and Barry (1973), are presented here in Table 2.

The unique physico-chemical features of the aquatic segment of the Well ecosystem deserve further study by limnologists. In addition, the adjacent atmospheric and terrestrial environments have proved tantalizing to geographers and climatologists. At the Nineteenth Annual Meeting of the Arizona Academy of Science, Brazel and Barnett (1975) presented the results of a topoclimatic survey of the Well. Their attempt to construct a complete energy budget for the Well system showed some unusual features. Evaporation is suppressed threefold, and sensible and latent heat exchanges are greatly reduced at the water surface because of the depressed and protected nature of the lake. As a result, Montezuma Well's impact on the immediate atmospheric environment is less than would be expected. Brazel and Barnett also found microclimatic contrasts between the cliff faces as related to their compass aspects.

TABLE 2. SOME OPTICAL DATA FROM MONTEZUMA WELL, ARIZONA

DATE	TIME	Secchi Disc m	Euphotic Zone Limit, m	$\frac{EZ}{SD}$	$k',$ $\log_e$	k'' $\log_{10}$	% transmittance per m	$\frac{X}{SD} = k'$
10 Aug. 60	1000	3.5	-	-	-	-	-	-
7 Sept. 60	1625	-	9.5	-	-	-	-	-
17 Sept. 60	1330	2.3	9.04	3.9	0.509	0.221	60.1	1.17
7 Oct. 60	1830	1.9	-	-	-	-	-	-
8 Oct. 60	1310	2.8	-	-	-	-	-	-
5 Nov. 60	1345	2.9	9.6	3.3	0.479	0.208	61.9	1.39
3 Dec. 60	1205	4.25	10.1	2.4	0.456	0.198	63.4	1.94
27 Dec. 60	1400	4.0	9.7	2.4	0.475	0.206	62.2	1.90
11 Feb. 61	1300	2.75	8.5	3.1	0.542	0.235	58.2	1.49
28 March 61	1110	3.1	9.9	3.2	0.465	0.202	63.4	1.44
14 May 61	1020	2.75	9.1	3.3	0.506	0.220	60.3	1.39
21 June 61	1505	2.5	7.2	2.9	0.639	0.274	52.8	1.60
24 July 61	1155	3.5	10.0	2.9	0.461	0.200	63.1	1.61
16 Aug. 61	1220	3.6	11.5	3.2	0.400	0.174	67.0	1.44
30 Sept. 61	1200	2.75	9.73	3.5	0.473	0.205	62.3	1.30
28 Oct. 61	1447	3.0	9.1	3.0	0.506	0.220	60.3	1.52
10 Feb. 62	1400	2.75	8.8	3.2	0.523	0.227	59.3	1.44

We sometimes found very abrupt changes in the Well water level and in flume readings that indicated lesser or greater amounts of water leaving the outer outlet. Table 3 does not show these sharp changes. It does, however, contain a dozen "readings" through the years taken at irregular times. There was some interest in the sudden changes, perhaps unwarranted, because it was thought by some Monument personnel in the 1960s that barometric pressure changes might affect the flow. There may be many data in the files at Monument headquarters that would have some bearing on this. This may be "science fiction", or it may be another example of the unusual interactions between the Well and the adjacent atmospheric-terrestrial environment.

The ^{14}C Anomaly

Probably nowhere in North America is there a ^{14}C Carbon anomaly as great as that in the water that enters and leaves Montezuma Well. It was first reported by Damon et al (1964) that there is approximately more than 25,000 years' difference between the CO_2 in the atmosphere and the apparent age of the CO_2 in the water. This alone would make the Well unique. Modern experiments and testing might be more easily performed than they were 20 years ago. Modern ultrasensitive mass-and-charge spectroscopy involving use of high-energy accelerators could introduce much more precision in the analyses than the work done earlier. Furthermore, less than a milligram of sample is adequate for this, and the process takes a few hours rather than days.

An original investigation into the trophic organization of Montezuma Well communities would be based on the ^{14}C anomaly there. This would be

TABLE 3. OUTFLOW FROM MONTEZUMA WELL AS CALCULATED FROM
OCCASIONAL FLUME READINGS AT THE OUTER OUTLET.

<u>Date</u>	<u>m³ per minute</u>
16 Aug. 1961	3.565
30 Sept. 1961	3.565
28 Oct. 1961	3.857
5 Nov. 1961	3.857
14 Nov. 1961	3.857
24 Feb. 1962	3.993
10 March 1962	3.702
5 July 1962	4.432
15 Sept. 1962	4.148
15 May 1964	4.890
3 June 1968	4.280
11 Oct. 1968	<u>4.512</u>
Average	4.055 m ³ /minute
Average m ³ /day	5,839.2
Average gallons/day	1,542,716.6

Convert to gallons by multiplying by 264.2;
reciprocal, 0.003785

costly and would involve taking a few protected animals -- turtles, lizards. The kill would be minimal, however, and the experiment would be the first of its kind. Damon et al. (1964) found that the CO_2 evolved from the Well water contains only about 5% modern CO_2 and has, therefore, an apparent age of more than 25,000 years. The stems and other parts of the submerged pond weed Potamogeton illinoensis (?) have approximately the same "age"; the plant utilizes the CO_2 in the water to build its tissue.

In the shallows some Chara plants that are partially emergent (because of fluctuating water levels) showed an apparent age of roughly 17,000 years, implying 12% modern carbon; they had incorporated 7% more atmospheric CO_2 than the pondweeds. A turtle (Kinosternon) revealed an apparent age of 10,000 years, suggesting an intake of much modern carbon in its diet. A fruitful research effort could be made from ^{14}C dating of the major animals in the Well and categorizing them according to their "distance" from the water's ^{14}C and the pondweed's ^{14}C . Thus, Hyaella montezuma is probably a primary consumer (Blinn and Johnson, 1982) although it will eat dead animal matter under laboratory conditions. Its ^{14}C age should be closer to the plants than one of its principal predators, the bug Ranatra montezuma (Blinn et al., 1982). A food web could be constructed for the relatively simple communities in the Well. Of special interest would be the apparent age of the lizards which prey on the emergent damselflies that perch on vegetation at the Well's margins. The terrestrial plants at the water's edge show no evidence of using anything but modern CO_2 in their photosynthesis. The lizards' ^{14}C age would indicate what percent of their food is derived from the

adjacent aquatic communities. This would be a new approach to food-web analyses and it would be of great interest to most ecologists.

As the Well water passes down the ditch toward the picnic grounds gaseous CO_2 is lost and eventually CaCO_3 is precipitated. Does the apparent age of the ditch water decrease? What is the apparent age of the introduced Asiatic clam, Corbicula, which is present in the picnic-ground region? This clam is a suspension feeder, which means it feeds on particulate matter in the water by filtering it out. Much of its food comes from the plankton material that leaves the Well via the swallet and the outer outlet.

Phycologists have been more reluctant to abandon the idea of cosmopolitanism than have freshwater zoologists. Perhaps the means by which algae are dispersed seem more efficacious than those that might move invertebrates from continent to continent. Perhaps the differences between closely related algae are more difficult to detect; cross-breeding experiments are more difficult; and the algal fossil record is poor compared to that of many freshwater invertebrate animals.

According to Czarnecki and Blinn (1979) there are about "80 taxa" of diatoms growing on the mud surfaces and stones near the Well's swallet. They described three new diatoms from this flora, stating that they appear to be restricted to the Well. They considered the three algae to represent a new variety, a new form, and a new species, Gomphonema montezumense. As further taxonomic refinements develop there is little reason to doubt that other diatom taxa will be discovered and, possibly, the new variety and new form will be raised to specific rank.

The bluegreens and greens of the Well -- planktonic, epiphytic, epilithic, and epipellic -- had not been studied intensively until Dr. Dean Blinn and his students began to publish their findings. The early paper of Kidd and Wade (1963) listed 19 species from the Well and the same number from adjacent Beaver Creek.

In our studies of the 1960s we found unusual difficulties in extracting chlorophyll from the phytoplankton, but our estimates of a mean of 17.6 mg/m^3 of chlorophyll a in the water column suggests a substantial population of phytoplankton. This is equal to about 100 mg/m^2 in the open part of the lake, not an especially unusual figure (ten times that is considered high and is rarely found). Our results from chlorophyll analyses may well have been too conservative, however.

The red alga, Batrachospermum, would make an interesting study. It occurs in the ditch at and below the outer outlet. It was reported from Beaver Creek by Kidd and Wade (1963) but the probability is great that it was growing only at some place where Well water was seeping into the creek. Batrachospermum requires free CO_2 for photosynthesis, being unable to utilize bicarbonate. I have one record of Batrachospermum extending down the ditch to a point 823 m below the outlet, but its limits have not been studied through the seasons. The part that light plays in its distribution may have been overshadowed by the CO_2 aspects. In the effluent ditch it would be intriguing to see whether the plants seem to become younger downstream, based on ^{14}C analysis.

Aquatic mosses are similar to Batrachospermum in their CO_2 requirements, and are restricted to the upper reaches of cave streams.

The moss at the outer outlet was identified by James McCleary as Fissidens fontanus. Formerly this had been known as F. julianus. I do not know the status of bryophyte taxonomy, but with the development of karyotyping and other sophisticated techniques, it is quite possible the moss is worthy of further taxonomic study. In fact, the entire "upper ditch" community and its downstream limits is an engaging project -- the moss, the red alga, and a macroscopic, colonial ciliate Carchesium (probably feeding on particles swept from the Well) are just part of the community.

The Characeae, although macroscopic and superficially resembling "weeds" are classed with the algae. In Montezuma Well there are at least two species of Chara. Twenty years ago (1962) Arland T. Hotchkiss examined specimens and suggested that they seemed to be Chara contraria (with 28 chromosomes) and C. vulgaris, a smaller form with 14 chromosomes. They were not uniformly distributed in the Well. C. vulgaris was present along the south shore, west of the swallet; C. contraria was found most abundantly at the northern shore in the shallows just east of the peat bed. Hotchkiss wrote me that he had found the two species co-occurring but one other time; that was in a New York pond where temperature differences were extreme because of cold seeps that favored C. vulgaris and left C. contraria to form large beds in the warm central regions of the pond. What are the differences between the microhabitats occupied by the two species in the Well? And, now 20 years later, what is the exact taxonomy of the Chara forms in the Well? Dr. Vernon W. Proctor (of Texas Tech., Lubbock, TX) would be the man to contact on this problem. He has a broad view of the Charales geographically, paleontologically, and taxonomically, and he cultures and breeds Chara spp.

The aquatic macrophytes at the Well are not diverse. Only eight species of submerged and emergent seed plants were associated with the Well-ditch system in the early 1960s. Some work was started on mapping the plants and attempting to determine the reason for occasional bare spots as well as the disjunct distribution of some species. The student lost interest in the project, and it still remains as a potential study that might lead to asking other interesting questions -- or to answering a few.

There is still a provocative problem associated with the big Potamogeton species that is the predominant plant in the Well. It reaches the surface where it is rooted 7.5 m below, marking therefore, the 24.6-foot contour line. Slightly deeper the same plant never reaches the surface, growing only to levels 2.5-3 m below. Now we blithely call it Potamogeton illinoensis Morong, but its serrated leaves and other features are puzzling. (In some instances professional botanists, whose aid had been solicited, keyed it directly to P. crispus and then threw away both the plant and book with disgust, for they knew it was not that European species!) In 1961, the New York State Botanist, Dr. E. C. Ogden stated in litt. that "...this species varies a great deal and it hybridizes with P. gramineus." In the early 1940s he had decided (on the basis of two collections from Montezuma Well) that it was a hybrid between P. gramineus and P. illinoensis, but, "Today [1961] I would call it P. illinoensis." Cross sections of the stem reveal the lower part is like P. gramineus; the upper part is like P. illinoensis. I do not know the recent advances that have been made in botanical taxonomy nor do I know the availability of herbarium specimens. Now, however, more than 20 years after Dr. Ogden's treatment

of the material, the long pondweed might join the growing list of endemics from Montezuma Well.

PRIMARY PRODUCTION

Primary production in Montezuma Well was one of our goals in the early 1960s. Several pages (45-51) in the 1965 Final Report tell of our (somewhat bungling) methods and results. All should be repeated, using modern techniques, by someone who is not trying to investigate everything else in the system! Probably converting annual growth to organic matter -- ash-free dry weight/m² per year (AFDW/m²-yr) would simplify comparisons with the summarized data presented by Teal (1980). The exact growing season must be worked out, and an important accompanying study would be determining the leakage of dissolved organic material from the plants, part of productivity that is usually overlooked. Our standing dry weight crop estimates for Potamogeton (about 810 g/m²) and such estimates as 26 g/m² dry mass growth each day in midsummer, and new spike flowering amounting to 74 g/m² dry mass each year are approximate, but may rate high on a world-wide basis, where maximum annual production, AFDW, is 1300 g/m² for submerged aquatic plants (Teal, 1980). The possible annual fixation of about 0.8 kg of carbon per square meter each year ranks the annual primary productivity of Montezuma Well phytoplankton 16% of the highest known, that of Lake Nakuru, Kenya.

There is one experiment in primary productivity I regret that we failed to try. At the present time this is not a brand new idea, but it would still work nicely and result in a contribution to limnology.

Although we worked with suspended light-dark bottles to establish photosynthetic rates in the open water, we later simplified the procedure to taking samples at different depths at different times for quantifying dissolved O_2 increase or decrease. We finally decided that a sample from a depth of 8 m seemed to be an integrated example of the entire water column at any specific time. One feature that we overlooked, even though experiments showed the water was mixing-circulating-spinning from top to bottom, was the effect of light inhibition or the lack of adequate light on the photosynthetic algae. Is an algal cell but a short time in the bright inhibitory light or, conversely, does it spend some time below the euphotic zone?

In the Well the average depth where one percent of the surface light persists is 9.41 m, ranging from 7.2-11.5m between 1000 and 1400 hours. What proportion of the oxygen in the open water owes its origin to the marginal weed bed? Is there photosynthesis occurring below the so-called euphotic zone? (In the Well the average Secchi disc transparency in m $\times$ 3.03 equals the one-percent light level). How does the euphotic depth change during the day as pertaining to the time a cell spends in the "dark"? With suspended, paired light-dark bottles a great deal could be discovered, if the worker were able to concentrate on this experiment only. One set of bottles suspended at various depths would remain there from dawn to dusk. Another set or sets would be changed so that only a certain time would be spent for any pair of light-dark bottles at any specific depth. Bottles would be moved down and back up to the surface X number of times per day. The stationary

group would be simply shaken at the times the other bottles were moved. Open-water, unconfined samples could be taken for comparative oxygen analyses. Perhaps dawn to noon, and noon to dusk would be adequate and appropriate times for running the test -- a new series of stationary and circulating bottles commencing at noon. Maybe a shorter time interval would be more appropriate. Whatever procedure the researcher might work out, the results would be a relevant contribution.

A different but similar subject, the diurnal-nocturnal vertical migration of the nektonic-planktonic animals presently being investigated by Dr. Blinn will be enlightening. Much of the theory concerning the reasons for such diel migrations has been founded on conditions in fish-containing stratified lakes; sharp vertical differences in temperature and food, and the presence of visually oriented predators have been invoked to explain the rise of animals at night and their retreat at dawn. Montezuma Well, approximately uniform throughout, is a more simplified system and weakens some prevailing ideas about zooplankton and nekton journeys.

ANNELIDA

Oligocheta

The oligochaete fauna of Montezuma Well sediments includes two extremes. In 1974 and 1975 the late Richard P. Howmiller identified them for me and more can be said about them than was submitted in the 1965 Final Report, p. 37. Limnodrilus hoffmeisteri was identified by Dr. Howmiller as the less abundant tubificid in the sediments. He wrote, "Next time send me something a bit more interesting..." Further-

more, he added, "Cosmopolitan, and [is] the most common worm just about anywhere."

The more abundant worm species in the sediments of the Well, described as "an aberrant tubificid" by Dr. Clarence J. Goodnight (The Final Report, 1965, p. 37) was identified as a species of Haplotaxis, belonging to the family Haplotaxidae. There are said to be two species in North America, both subterranean in habit. The Haplotaxis material sent to Dr. Howmiller was not identified to species, and since that time I showed specimens to a Yugoslavian scientist, Dr. J. A. Šapkarev, who is an expert on oligochaete annelids. He stated that in his opinion the Montezuma Well Haplotaxis represents an undescribed species. In the early 1960s dredge samples showed that the two oligochaetes were extremely numerous in organic sediments from the depths of the Well. Samples from 13.3 m (43.6 feet) in November 1960, revealed 15,800 worms per square meter. At that time the major part of the population was found between 10 and 16m.

Hirudinea

The other annelid worms are the leeches (Class Hirudinea). In the shallows, a leech that could be Helobdella stagnalis (L.) is occasionally found. The common leech, however, has been collected in all communities of the Well: the marginal Potamogeton beds; the Chara beds; the plankton; the sediments beneath the pondweed (0-8 m); and in the sediments beneath the open water (ca. 8-17 m). This form is an active swimmer and certainly has been represented poorly in our samples. Dredge collecting has implied slightly more than 200/m², and vertical net hauls have captured very few. At night we have observed tremendous

numbers of these leeches swimming in the upper layers of the Well, along with Hyalrella montezuma and cyclopoid copepods. With flashlight and dip-net the worms were captured easily.

During bright daylight hours the largest portion of the population may be found in a thick subsurface band (5-8 m below the surface) where dissolved oxygen is at a minimum. The oxygen minimum disappears at night when the leeches (and crustaceans) disperse. Plans to study the role and impact of the leech as a predator in the Well were abandoned because of the difficulties in quantifying their abundance. Some unpublished data show that a leech 4 cm long has a dry weight of 24.9 mg; about 95% of the live weight is owed to water. Our laboratory experiments showed that at 20° C a group of leeches amounting to one gram dry mass would consume roughly 30 g O₂/m³ within a 24 hour period. This might be represented by 40 or 50 animals, depending of course on their sizes.

The leech is, however, remarkable. It is nektonic, preying on another member of the pelagic community, Hyalrella montezuma, and perhaps from all communities of the Well. It may move into the weeds to feed on H. azteca and damselfly naiads. Observations of hirudinean predation on damselflies in glass containers show this is possible.

The taxonomy of the Montezuma leech represents, as typical of the Well's inhabitants, another puzzling situation. Dr. J. Percy Moore was the expert consulted. Parenthetically, he wrote the section on Hirudinea in the 1918 Ward and Whipple's Fresh-water Biology, and also authored the leech chapter in the 2nd edition in 1959 -- the only contributor spanning these 40 years! We had poor luck in getting mature individuals

to Dr. Moore, sending him specimens in 1960 and 1961. He wrote that the leech is assignable to Erpobdella, resembling E. punctata from the eastern United States, but with dorsal crossbarring rather than being longitudinally striped. In that respect it resembles the subspecies, E. p. annulata from British Columbia and some northwestern border states. Later, Dr. M. C. Meyer (at that time from the University of Maine) examined specimens I had deposited in the U. S. National Museum, but I do not know the outcome of his study. Leech experts are scarce. Dr. Kenneth H. Mann, Dalhousie University, Halifax, Nova Scotia, may be the best on our continent, and he has not seen any Montezuma Well specimens. Leeches should be shipped in wet moss (Sphagnum), alive and in breeding condition. In many parts of the nation this would mean collecting in May or June, but the breeding season in Montezuma Well is not clear. Specimens collected in December had "spent reproductive organs" (Moore, in litt., 1960).

CRUSTACEA

Amphipoda

The crustaceans of Montezuma Well became especially noteworthy with the discovery of Hyaletta montezuma (Cole and Watkins, 1977). For the record, the history of this discovery is worth some anecdotal space here. About 1958 someone told me of "golden fairy shrimps" in the Well. Although Arizona has many species of anostracans (perhaps the State can be termed accurately the fairy-shrimp capital of the World!), this type of crustacean is typical of temporary ponds. Therefore, I thought that perhaps the brine shrimp Artemia was being described, and that Montezuma Well might be an hypersaline pool. My first visit to the Well showed me

that its water was fresh, and the "fairy shrimp" was an amphipod crustacean. At that time Hyaella azteca, originally described from Mexican specimens, was considered a single species, ranging from South America to the Canadian tundra. It is the most common malacostracan in lakes of Minnesota and Michigan, for example, where it lurks in the marginal weed beds and is uniformly a blue-green-brown hue (if there is such a color...it's greenish!). At night, when safe from predators that rely on visual cues, it ventures briefly into open water above the weeds.

The surprising things I found in Montezuma Well were that the Hyaella is pelagic, and that a large percentage of them are a golden color. At that time I recalled the excellence of goldfish as fish bait, and that many states have found it necessary to ban their use because fishermen prize them as bait and wild populations eventually become carp-like. The color of a goldfish is much like that of many Hyaella in Montezuma Well, a color that would have no survival value or selective advantage in the presence of fish predators. The principal predators of Hyaella in the Well are the leech Erpobdella (perhaps an endemic species) and the endemic water scorpion Ranatra montezuma (Blinn et al., 1982). Parenthetically, the Kinosternon turtles in the weed beds may prey on Hyaella there; they can be observed picking something from the upper surfaces of the pondweeds or from the water just above. The invertebrate predators may rely on other than visual cues (or may be uninfluenced by the golden color) in capturing Hyaella. Whatever the case, the unusual color presents some research opportunities. First -- what are the genetics involved? Often coupled amphipods (in the so-called precopula embrace) include a greenish member and a golden member. If

these were captured and, if the future generations were studied, would a simple Mendelian inheritance pattern be revealed? In general, it is very easy to rear Hyaella species in the laboratory, although the situation is not so simple in the case of the Montezuma Well amphipods. As CO₂ bubbles out of the water the pH soars, calcite is precipitated and the crustaceans die. Amphipods survive in Montezuma Well water in stoppered or sealed jars. Perhaps bubbling CO₂ into laboratory culturing bowls would make for survival. We tried cross-breeding experiments with the two species of Hyaella collected from the Well and kept them alive in fingerbowls for more than a week. The early shock (from loss of CO₂ and the attendant pH changes) must be guarded against. Dr. Blinn has been working with this problem, and suggests there may be some differences in tolerances between the two species -- another possible research project.

Associated with the genetics experiments could be others to test the negative selective value of the gold color in the presence of fish, and whether the leeches or water scorpions capture the golden and greenish varieties differentially in the dark and light.

Another factor could be involved in the golden amphipods. Is this in any way related to their serving as intermediate hosts for acanthocephalan worms? The adults of these worms are found in the intestines of turtles, muskrats and waterfowl.^{*/} We have found Hyaella individuals with as many as 30 eggs, an extremely high number for such infections. Is the gold color associated with acanthocephalan infection? The color

^{*/} Since the 1965 Final Report I have noted additional waterfowl in the Well -- redhead, bufflehead, and ring-necked ducks (7 March 1975).

seems to vary seasonally, the frequency of gold being low at times. Do the infected Hyalella show abnormal behavior when compared with uninfected members of the population? Gammarus lacustris individuals carrying intermediate stages of duck tapeworms act entirely different (in some Canadian lakes) from the norm. They swim close to the surface and do not shy away from shadows -- the modified behavior favors the completion of the tapeworm's life cycle!

Turning now to another unique problem associated with the Montezuma Well amphipods: the prevailing idea that there is a single species of Hyalella in North America was weakened when Stevenson and Peden (1973) described Hyalella texana from the Edwards Plateau. For almost twenty years the crustaceans from Montezuma Well had not been examined in detail. Sometime in 1975 Dick Watkins (a graduate student at ASU) dissected the mouth parts of a specimen and sketched one of the 1st maxillae. When I saw this picture I knew we had been overlooking an unusual animal. Most previous authors have defined the talitroid amphipods in such narrow terms that the new specimen could not be included with the other members of the family Hyalellidae! Following up Dick's serendipitous discovery we found that there were two distinct types of Hyalella in the Well. Our publication (Cole and Watkins, 1977) was rather detailed, but we in no way finished the story of the Montezuma Well amphipods. We suggested that H. montezuma seemed to have structures for filter feeding; this was followed up by Blinn and Johnson (1982), who ingeniously proved it is capable of such behavior, and the more nearly normal Hyalella in the Well does not filter feed.

Now, about the other Hyalella of the weeds, swallet area, and outer

outlet community -- in 1874 S. I. Smith described a "smooth-backed" Hyaella from Colorado as H. inermis; the original H. azteca (named first, Amphitoe aztecus by Saussure in 1858) had mid-dorsal projections on the first two pleonites (abdominal segments). More than 75 years ago H. inermis was synonymized with H. azteca. The so-called H. azteca of Montezuma Well is the inermis type, but what is it really? It is fair to assume that there is a great more variety in the H. azteca complex than we have suspected. In Arizona, where the populations are very much set apart there might be several reproductively isolated species, or there might be evidence, at least, of incipient species formation. A research program for an advanced student (or his/her professor) could be based on an exploration of this problem. First, the animals are easily maintained in the laboratory and cross-breeding experiments could be performed simply, although Montezuma Well specimens are notoriously difficult when compared with others. Second, there are some remarkable populations of Hyaella to compare and test. The animals from Fossil Springs, Yavapai Co., quiet waters in Oak Creek Canyon, Coconino Co., and Monkey Spring, Santa Cruz Co. come to mind immediately. There are many others.

Looking for evidence of speciation and naming new species do not warrant scorn. They are not anachronistic activities. Allozyme genetics via electrophoresis, karyotyping, scanning electron microscopy, and RNA-DNA sequence mapping are modern techniques that might elucidate specific differences among southwestern Hyaella demes.

Years ago a geneticist experienced in karyotyping offered to help me if I would provide amphipod males from Montezuma Well. Unfortunately,

the males I supplied were infected with acanthocephalan eggs which led to them being mistaken for females, and very little work was done with them. One prepared and stained slide, however, showed that the chromosomes are numerous, but certainly possible to count and differentiate. The cooperative geneticist had very little time for me because of other commitments, and I accept the blame for the fiasco! Out of it came the belief on my part, however, that chromosome studies of Arizona hyalellids is feasible. In addition, some preliminary work on starch-gel electrophoresis done by Dr. David I. Rasmussen at ASU revealed excellent patterns in Hyalella. The chances are very good that molecular differences among amphipod populations can be revealed by this method.

A recent paper on a European amphipod, Gammarus fossarum by Anne-marie Goedmakers (1980) suggests another exciting possibility. She found what are best described as microgeographic races in the river Slack on the French Channel Coast. There was not a single large population in a 10-mile stretch of the river, but rather, a number of isolated populations which did not interbreed. Some of the differences were seasonal variation in mean size, percentage of ovigerous females at different times, number of eggs per female, and general reproductive rate. Now some questions arise about the amphipods referred to as H. azteca that are found outside the Well in the upper reaches of the ditch. We have assumed that individuals are commonly swept out from the swallet region where this amphipod congregates. This may be an erroneous idea because we never tested it by setting nets to catch nocturnally drifting animals. Perhaps the founders of the outer outlet population reached that site long ago, and there has been very little subsequent recruitment. The

genetic distance between the two populations could be determined as a research project. The results might be provocative, underscoring the segregation that exists between the Well and the ditch populations. Another problem that has engaged our fancy only: why doesn't the Hyalrella in the ditch range farther downstream than it does?

Laboratory experiments showed that Hyalrella consumes oxygen at a greater rate than Erpobdella. On a wet-weight basis this excess is about 300%. On a dry-weight basis the amphipod rate is not quite 2 times (1.88) that of the leeches. Hyalrella groups converted to dry-weight for comparison consumed $54 \text{ g O}_2/\text{m}^3$ for each gram per day at 20°C . The amphipods weigh less than the leeches, but because of their residual exoskeletons only 76.5% of the wet weight is lost as water. An average dry Hyalrella (we used a few adults for these data) has a mass of 1.24 mg. Thus, it usually would take a population of 800 or so to be equivalent to a gram of dry material.

At this time it would be worth pointing out again that the work in energetics among the plants and animals of Montezuma Well should be founded on ash-free dry weight (AFDW). Moreover, some work should be performed to quantify the differences between formalin-wet weight and the wet weight of unpreserved organisms. Formalin-killed leeches may differ more from their original live weight than do insects and amphipod crustaceans.

In August, 1960, at noon our samples showed the Hyalrella in the open water were located between 2 and 8 meters; there were, on the average, 4,233 per m^3 in that 6-m stratum of the water column. There was a concentration, however, of 14,200 per m^3 between 4 and 5 m. (Capturing and estimating numbers of the leeches was/is much more

difficult. We can only say that divers have reported a layer of swimming leeches below the day-time stratum of amphipods.) The Hyaella in the 4-5 m stratum would have consumed about 39 to 40 g O_2/m^3 per hour. With evidence also of 129,400 nauplius larvae of cyclopoid copepods per cubic meter in the same stratum, and 421,600 individuals of all stages of these cyclopoids per m^3 concentrated in the 3-4 m stratum, it is no wonder that a pronounced subsurface oxygen minimum is a mid-day feature during the summers in Montezuma Well. When the animals move to the surface at night the lake's circulation destroys this unique example of a negative heterograde oxygen profile. I know of no other such case in the limnologic literature and it has hardly been touched on in the Montezuma Well research!

A recent paper by Blinn et al. (1982) has something to say about the stability of Hyaella densities during the past two decades. The authors state that the top meter of water contains from 25,000 - 32,000 Hyaella/ m^3 at night. If the amphipods that were sampled at noon, August 1960, had all moved to the surface that night, there would have been 25,400 per cubic meter in the 0-1 m layer.

Copepoda

Other crustaceans in the Well have been assigned names that long have prevailed in the literature. Perhaps the study of these should be performed by an expert, or by a person in a position to examine material in the U. S. National Museum or the National Museum of Canada. On the other hand, a serious Masters candidate could make himself an expert in a relatively short time. The two cyclopoid copepods in the plankton community of the Well are considered nearly cosmopolitan. The larger of

the two, Macrocyclus albidus (Jurine) was named from European material in 1820. It is considered to be one of the commonest copepods in North America. It may be carnivorous. The other species, probably herbivorous, is Tropocyclops prasinus mexicanus. This so-called subspecies was supposed to be "Limnetic in Mexican lakes, may occur in states bordering on Mexico." (Yeatman, 1959). When we find it in Lake Superior and the other Great Lakes, we can start to wonder how much we really know about it. The generally accepted universal distribution of some cyclopoid copepods conflicts with sharply with what is known about others. For example, Mesocyclops tenuis was described from Calabasas in southern Arizona (Marsh, 1910). It can be found now in ponds in south-central and southeastern Arizona and adjacent New Mexico. I know also of its occurrence near Fort Knox, Kentucky, but I have never taken it in the Phoenix area or anywhere else in central or northern Arizona. It seems to be very locally distributed when compared with Macrocyclus albidus. Also an often-cited reference (Price, 1958) tells of breeding experiments with members of Cyclops (Acanthocyclops) vernalis in Canadian lakes. Seven reproductively isolated populations were found in a splendid example of cryptic speciation. Something we call A. vernalis is common in Arizona waters. An unusual population apparently referable to this species lives in some experimental ponds at the Phoenix sewage facilities. The males mature more rapidly than the females and transfer spermatophores to immature females (copepodid V) rather than to adult females, copepodid stage VI (Foster, 1973). This is a most unusual situation and may represent a new species -- perhaps one of many in Arizona, possibly showing adaptation for existence in short-lived pools.

Therefore, it is natural to ask questions about the cyclopoids in Montezuma Well. Is Macrocyclops albidus in the pool at Quitobaquito Springs, Organ Pipe Cactus National Monument, the same thing as M. albidus in Montezuma Well? Sometime this may be answered. It would be less difficult to study the trophic relationships between M. albidus and T. prasinus mexicanus. Does the former prey on the latter? At what rate does it take the smaller prey species in laboratory containers? Is it as capable a predator in the dark as in the light? How do seasonal aspects of their life histories compare? Can the leech Erpobdella catch either species?

The Chara beds from 0-0.25 m depth, sometimes yield another copepod that should be studied at least taxonomically. This is an undescribed harpacticoid, probably referable to the genus Elaphoidella. Mildred S. Wilson (in litt., 1961) stated that it was "... very interesting -- and may be a new species of Elaphoidella which I already have in manuscript (spms. from Sask. and Alaska)."

The bulk of the specimens Mrs. Wilson received from me were immature copepodids. They were collected in December; perhaps spring would have been a better sampling time for adults. Richard L. Watkins, at ASU, looms as one of the best local people to work up this harpacticoid. Mrs. Wilson is dead and no other North American workers have shown much interest in the freshwater harpacticoids. Watkins is an expert on the order and probably could work out its relationships and name it. Moreover, because there seems to be only one harpacticoid in the Well, the life cycle of Elaphoidella would make a good research project.

Ostracoda

Two other crustaceans in the shallow Chara beds have been specifically designated in the belief that cosmopolitanism prevails. Two representatives of the Ostracoda occur there. Neither is natatory. The larger is similar to Herpetocypris reptans named in the Old World in 1853. Its males are unknown and it is almost certainly hermaphroditic. (Is this the same species as the H. reptans reported from the pool at Quitobaquito Springs?) The other form is similar to Darwinula stevensoni, described originally from the other side of the Atlantic in 1889, and said to be the only species in the genus. This is an unusual form. It may be parthenogenic in North America because no males have been discovered from here. The young develop in a dorsal space within the valves of their mother where they can be seen moving about before being released. This seems to be unique to Darwinula.

The Chara beds are not extensive and may be a delicate habitat, but a study of this shallow community would be worthwhile. Oribatid mites (probably undescribed) and many stratomyid fly larvae are conspicuous there in addition to the three crustaceans discussed above. Of course, Erpobdella and Hyalella can be collected there also, but that can be said about every habitat in Montezuma Well.

INSECTA

There may be many taxonomic problems associated with the insects of the Well, but I would leave that to entomological specialists to determine. Robert L. Smith and Milton W. Sanderson are just two of the expert entomologists who have examined specimens since the 1965 Final

Report. The water scorpion (a Hemipteran, or true bug) was designated the common western Ranatra quadridentata when we sent examples to specialists in the early 1960s. Since that time John Polhemus studied this bug and found it to be a new species which he named R. montezuma, probably endemic (Polhemus, 1976).

Endemism may be a feature of the rather impoverished insect fauna of the Well. Just a review of the correspondence with Leonora K. Gloyd during 1960 and 1961 reveals some possibilities for further work. Despite the poorly preserved and surprisingly maimed naiad damselflies I sent her, and the paucity of adults in the material she examined, she spotted striking seasonal differences in the two species. They were assigned to the genera Enallagma and Telebasis, and Mrs. Gloyd even ventured guesses as to the correct species. But that was more than two decades ago. What has been added to the knowledge of odonatans since then, and has any student thought of concentrating on these two important members of the Well community? Enallagma is widespread and more than thirty species have been described. By contrast, Telebasis is represented by only two species restricted to the south and southwestern portions of North America. Each genus is said to be made up of predaceous naiads, typical of the odonatans.

Different types of problems exist with the insects, however. Why are there no notonectid or corixid bugs in the Well? Why do dragonfly eggs hatch and develop only in extremely rare cases (we found only one naiad in the 1960's despite the evidence of much oviposition there)? Why are chironomid fly larvae absent from the organic sediments in the deeps of the Well? Could these questions be answered with caged individuals subjected to the environmental factors (stresses?) of the water?

MOLLUSCA (Native)

Probably no section in the 1965 Final Report was taxonomically more erroneous than that dealing with the molluscs. Dr. Henry van der Schalie, of the Museum of Zoology at Ann Arbor, identified the snails for me, but in looking over the correspondence, I note that he expressed doubt about them and his determinations were tentative. I was responsible for assigning more certainty to the gastropods than was warranted. Subsequent work on the sediments of the Well (and particularly a study of the peat bed at the north side) by George L. Batchelder (1972, 1974 and pers. commun.) with taxonomic help by Dwight W. Taylor changed the picture.

The sphaeriid clam (now properly termed pisidiid clam) Pisidium can be designated more specifically. It probably is P. casertanum Poli, or close to that species. No live specimens have been taken, but its remains are distributed throughout cores from the sedge mat, and it was often found in dredge samples from the deeper regions of the lake. The snail Physa virgata Gould was also represented throughout the sedge mat cores, and presently lives in the Well and in other modern waters of northern Arizona. This is the snail Van der Schalie (in litt., 1962) said "...appears to be Physa ampullacea Gould. It is about as stunted as Physa can get! The Physa are a very poorly known group and need far more work than they are getting. The species names are circumspect."

The snail reported as Amnicola integra (Say) is probably an undescribed species of Fontelicella. Members of this genus are found in springs throughout the Southwest; (there are still many unnamed species). Batchelder found fossil remains of this snail only in the middle section (100-110 cm) of a core from the sedge mat. There was another prosobranch

snail, Somatogyrus, similar to S. subglosus (Say), according to van der Schalie. Batchelder says nothing about this form as a relic in his cores. These small operculate snails were confusing to us, who were not experts, but they were extremely abundant in the bottom communities during the early 1960s. They were found from 0-8 m beneath the weeds, and below the open water to 17 m, the maximum depth. Some November collections from 13.3 m depth contained 24,710 individuals per square meter.

Since the 1965 Final Report, I found some lymnaeid snails in the Well, probably members of a species of Fossaria. Batchelder reported two species of this genus in cores from the sedge mat. He also found the semiterrestrial Vertigo ovata and shells representing a species of Succinea.

INTRODUCED SPECIES

Montezuma Well is, in a sense, an island. Somehow species are introduced there and flourish or perhaps become extinct. In the summer of 1974 an alien turtle was first spotted in the Well. It looked like a "dimestore" pet that had been set free. I do not know what taxonomic determinations have been applied to the species, but others have been reported since then (same species?). It should be removed, if possible, for the native Kinosternon might prove a unique population, and competition with the introduced species (plural?) could harm it. On the other hand, the introduced form might become extinct in the manner typical of many island immigrants.

Other introduced forms that were abundant in the early 1960s would be worth investigating now. At the southeast edge of the Well, in the grass near the cave, three species of exotic terrestrial isopods flourished. Originally, these were from Europe. How they arrived at the bottom of the depression is a question. Have they survived or did

they become extinct? Have other species arrived in the intervening years? There was an unusually numerous concentration of Armadillidium vulgare, Porcellio laevis, and Porcellionides pruinosus.

In the grass at a small promontary beneath the shade of a huge cottonwood tree (since removed) we suffered the effects of another introduced organism -- the dread "chigger" of the southeast. We always included powdered sulfur in our supplies when planning a trip to the Well in the early 1960s!

A phenomenon we could never explain is roughly analogous to the arrival of organisms at island sites. They may survive a while and then, inexplicably, go extinct; later the chance arrival of other members of the same species may initiate another population. This fits something we noted in the case of the cliff swallow, Petrochelidon. In 1960 we observed 28 old nests of these swallows plastered against a rock face at the southwestern side of the depression. We never saw cliff swallows at the Well, however, and as the years passed the nests eroded and became progressively less discernible. Suddenly in the late 1970s the swallows appeared again and built nests on the cliffs that bound the Well. It is tempting to relate this to island theory, but the reason for the long absence (probably more than 20 years) and reappearance of the birds may be related to other factors -- the availability of a mud supply for their nests, perhaps. Whatever, the reason for this sequence of events, the swallows would make an interesting study. Similarly, the Great Horned Owls (Bubo) appeared in the 1970s and began to nest annually in a small cave at the north cliff bounding the Well. They were not present during the 1960s.

Corbicula fluminea^{*/}

The arrival of Corbicula in Arizona was probably unnoticed for a few years before Dundee and Dundee (1958) spotted it in a Phoenix canal. By that time it had probably reached the Mississippi valley, for that was 20 years after it was first discovered in North America, in the Columbia River in Washington. It may well have been established in Arizona waters by the late 1940s, but no damage was reported until sometime in the 1960s when it fouled sprinkler systems on Phoenix golf courses. Denton Belk and Jerry Landye may have been the first to note the species in the vicinity of Montezuma Well; they found clams in the effluent ditch at the picnic grounds before March 1975. How it got there remains a mystery.

In the New River, Virginia, the invasion rates have been carefully studied and it has moved upstream at the mean rate of 9 miles per year (Rodgers et al., 1977). The corbiculids have a planktonic larval stage (the veliger), which would not seem to be able to move upstream unaided. Although ciliated it is virtually a non-swimmer. The adult clams, however, can pass through the intestinal tracts of ducks in viable condition (Clench, 1970), and the role of humans in the spread of Corbicula is probably great. There is good evidence that it was carried upstream from the Phoenix region to Roosevelt Lake by fishermen (Rinne, 1974).

The clam usually shows dramatic increases in population density once it arrives at a suitable area. It is a monoecious species, thereby

^{*/} It has been variously designated as C. laena, C. manilensis and C. fluminea. At present the last name is being used most frequently.

increasing the probability of fertilization occurring. Fertilization takes place within reproductive ducts, and soon the embryos become lodged in the inner gills which serve as marsupia where the veligers develop. When released the ciliated veligers become planktonic, although they are virtually non-swimming. The veliger needs no fish host as do the native unionacean mussels. They spend a short time as planktotrophic organisms as the "foot" develops and they attach as pediveliger larvae, adhering by means of a sticky patch near the apex of the foot. A wide range of sediment types, temperature, and chemical conditions are suitable for colonization. Shell formation begins and is completed (in populations that have been studied elsewhere) at a length of about 0.9 mm. Within a year the shell is about 8 times this length and the animal is sexually mature.

Each individual may produce "several thousand offspring each year". In the New River, there seem to be two spawning periods during the warmer months of the year. At Montezuma Well the water temperature varies far less and, therefore, there may be more annual reproductive activity. (Hyaellas have been observed in the precopula embrace in the Well very close to the winter solstice, Dec. 27, 1960).

Corbicula has been subjected to many tests to assay its tolerance to various chemical and physical factors. Its populations drop rapidly when water temperatures approach 2°C (ca. 35.6° F) and temperatures of 36°C (ca. 96.8°F) or slightly higher seem to be lethal under laboratory conditions (Cherry et al., 1980). Water temperatures of 35° (95°F) in streams warmed by the effluent from cooling power-generating stations seem to have no adverse effects. The water in the Montezuma Well

outflow ditch has a yearly range at the most from 17 - 27° C (62.6 - 80.6°F), ideal for the Asian clam.

Corbicula is remarkably resistant to biocides, heavy metals (copper and zinc, for example) and chlorine. It escapes the effects of unfavorable environmental factors by ceasing to siphon, closing its valves, and burrowing in the sediments. Gaping, induced by sudden high temperature or prolonged exposure to toxic concentrations of metals, sometimes signals the proximity of death. EPA regulations for exposure time and dosages are surpassed by the treatments with copper, zinc, potassium, and chlorine that kill Corbicula (Cherry et al., 1980).

Potassium is particularly efficacious in inducing the gaping response. In an artificial stream environment 100 mg/liter of potassium for 48 hours brings about gaping in 50% of the population. Following this, chlorine application is especially effective. This would be dangerous and impractical in the Montezuma ditch. About 2,124.5 kg of KCl would have to be used, distributed continuously, in the ditch for two days to match this (there are only 5.4 gK/m³ in the water). The addition of potassium to bring the ion concentration up to 100 mg/liter would make the sodium/potassium ratio 0.5 by weight. Na/K ratios less than 10 in concentrated water are lethal to many freshwater animals. Even before chlorine were added to kill the gaping clams, much harm might have been done to other organisms in the ditch.

To my knowledge the effects of free CO₂ and carbonic acid have not been tested on the clam. A question that remains to be answered is whether the upstream distribution of Corbicula in the Montezuma ditch is limited by the increasing CO₂ tensions or to the current, which would

sweep the veliger larvae downstream. Perhaps clams have been introduced upstream or to the Well, but have not survived. Or the pediveliger is vulnerable to high CO_2 . An excellent opportunity for experimentation exists here: clams contained by wire cages could be suspended at various places in the stream. The environmental factors changing as one moves from the picnic grounds upward toward the outer outlet are increasing: hydrogen ion concentration; suspended chlorophyll and presumably other particulate matter from the Well; and free CO_2 . An approach from supersaturation of calcite to equilibrium conditions also occurs. Although the water is supersaturated with calcite at the picnic grounds the conspicuous precipitation of CaCO_3 occurs during the next 15 minutes' flow, reaching about 500 m below. The free CO_2 at the picnic grounds varies during the day, the greatest amounts occurring just before dawn. From 76-83% of the gaseous CO_2 found in the water at the outer outlet disappears by the time it has flowed to the picnic grounds. The exact CO_2 can be approximated by the pH of the water, using the graph presented by Cole and Batchelder (1969: Fig. 1). The pH at the picnic grounds is in the neighborhood of 7.5; it is usually below 7.0 and maybe^{1#} as low as 6.0 at the outer outlet, about 1,000 m upstream.

The presence of chlorophyll in the water indicates sestonic matter in the ditch. This particulate matter is the nutritional source for Corbicula, classified functionally as a suspension feeder or a filtering collector, feeding on a variety of particle sizes. Collections from the outer outlet imply a loss of about 125 g of chlorophyll each day. About 40% of this arrives at the picnic ground segment of the ditch. Surely some zooplankters and protozoans accompany the pigmented algal

cells, and they must diminish downstream also, settling out and being intercepted by filter feeders such as the sessile, colonial ciliate, Carchesium, conspicuous in the ditch at the mouth of the outer outlet. Nutritional conditions should improve for caged and suspended experimental Corbicula clams as they are moved upstream toward the Well, even as the carbon dioxide tensions increase and stress is imposed (possibly).

At this point, it would be profitable to point out again that moving certain confined animals upstream would show their tolerances to, and the limitation caused by, free CO_2 . Of course, temperature shock and pH effects should be controlled before the animals are placed in the reach of the ditch that is being tested. It might be advisable to test the effect of CO_2 and bicarbonate, on native fishes so that an escape would not be disastrous, in the rare chance that they can survive conditions now thought to be lethal. Cyprinodon macularius, or Poeciliopsis occidentalis are two possibilities. A third would be the beautiful and endangered Cyprinodon elegans, a Texas species breeding in flowing water. Members of the Desert Fishes Council might vigorously oppose such a suggestion, and certainly that knowledgeable group should be consulted before anything is done with fish experimentation or introduction in the Montezuma Well-ditch system. Similarly, the downstream tolerance of the outer outlet community...Batrachospermum, Fissidens, Hyaella azteca(?), and Carchesium is fraught with interest and loaded with research opportunities.

The harm that the exotic Corbicula can do in the effluent ditch or in the Well proper is difficult to predict. There may be a nuisance created by shells piling up and clogging the ditch. There seem to be no

native bivalves that might be replaced by Corbicula, as has occurred in some river systems that had a native clam fauna. Valves of Pisidium casertanum have been identified from the Well sediments, but live individuals are either absent or extremely scarce. Filter-feeders of different systematic affinities might be affected by competition from Corbicula, but this is, also, speculation. Clogging of pipes and weakening concrete mixtures are two harmful acts that Corbicula populations have done elsewhere. There seems to be no threat of such events in the Well system.

On the plus side, Corbicula might serve as food for turtles, muskrats, and raccoons. These animals probably wouldn't control or eliminate the clam. The only method of eliminating this alien safely is probably by hand picking. Its resistance to biocides is so great that much harm would be done to other forms if, for example, chlorine were added to the ditch.

CONCLUDING REMARKS

Most of the foregoing material has been biological, for there are a great many questions to be addressed in that field and a large portion of the Well-system's uniqueness is owed to its biota. Some limnologists are prone to an ecosystem approach, and place, therefore, little emphasis on individual organisms. Primary productivity and respiration rates in some of the predominant animals provide data that contribute to understanding the ecosystem. Our estimates during 1960-62 disclosed a P/R (the ratio of gross photosynthesis to total respiration) ratio of approximately 1.0. This was done without ascertaining exactly what

organisms were contributing to P and R. The ratio, close to unity, showed Montezuma Well to be an ecosystem in dynamic equilibrium. Its photosynthesis is nearly matched by respiration. The slight excess of production could be stored in the sediments or lost down stream. Our work should be repeated by modern researchers and a complete balance sheet (of P vs. R) attempted. We can say now that the peat deposit in the Well (at the north shore) represents excess primary productivity. It accumulated at the mean rate of about 2 cm every 100 years (Batchelder, 1974). The organic sediments in the deeps of the Well may have been stored at a lower rate.

This leads us to paleontology; much good work has been done in this discipline in the Verde Valley and in the Well itself (Batchelder 1972, 1974; Batchelder and Cole, 1978; Hevly, 1978) but it has not been drawn together yet, and there is much more to be done. Batchelder's (1972, 1974) seismic and resistivity studies showed an homogenous layer of material extending at least 13 m below the peaty sedge mat (which is about 11,000 years old). The longest cores of sediment obtained from the center of the Well are only 2 m; Batchelder's peat core was only 2.5 m.

Some problems at the Well are unusual for paleontologists and palynologists. Examination of fossil pollen grains, algal relics, and molluscan shells, in addition to assessing the vertical profile of total organic carbon, bring to light a unique feature of the Well. Many fossil fluctuations seem to be the result of an astatic shoreline that has little to do with climatic changes. Blocking of past inner outlets and the opening up of others led to the rise and fall of the water. Perhaps

the present scarcity of Scirpus and Typha fringing communities is the result of rising water level. One stratum from the lake sediments with an abundance of grass pollen relics suggests a time when the water streamed across a wet meadow and out through a now-blocked opening to Beaver Creek; no substantial pond seemed to exist then. Batchelder thinks the water has not risen substantially during the last 11,000 years because it would have destroyed the sedges that formed the peat bed, and he has found no evidence for such an interruption in the peat bed's growth. There seem to be, however, fine-grained lacustrine sediments rather high on the slopes west of the cave near the swallet. They have not been examined carefully.

Also accompanying the changes in fossil profiles are evidences of climatic change. Thus, Batchelder has distinguished pinyon pine from ponderosa pine pollen. These grains, blown in from the terrestrial environment have much to tell about climate; ponderosa pine in the Montezuma Well region was typical of the Pleistocene, or Pluvial time. The evidence for fluctuating water temperatures could be due to climatic shifts, or variations in the entering artesian water, possibly not related to climate. The abundant molluscan shells in Batchelder's sedge-mat core could be analyzed for $^{18}\text{O}/^{16}\text{O}$ ratios in their carbonates as an index to water temperatures of the past. Montezuma Well offers a complex mixture of problems for the paleontologist to solve.

Turning to a concluding example of the Well's singularity and its seemingly unlimited store of research problems, I address the physical chemist (perhaps he is a "pure" chemist, an engineer, or a geologist).

Except perhaps for a spring on Havasu Creek, there is no better example of concentrated calcium bicarbonate water in Arizona. Blue Springs in the gorge of the Little Colorado River, and Monkey Springs in Santa Cruz Co., are high in $\text{Ca}(\text{HCO}_3)_2$, but they are essentially sodium chloride and calcium sulfate waters, respectively. Fossil Springs, in Yavapai Co., is a good calcium bicarbonate water, but its ionic strength is surpassed by Montezuma Well. Moreover, the Well is more accessible than any of the other waters mentioned above.

All facets of carbonate solubility and equilibrium dynamics could be investigated in the Well. Minute, particulate calcite (not yet quantified) is suspended in the water, and especially in the ditch. These particles add a dimension to the common alkalinity titration (with standard acid) that most workers never experience. They create an unnatural gulf between hardness assays (with EDTA or similar complexing agents) and alkalinity tests.

The pH of calcite equilibrium is very low in the Well-system waters, being below 7.0 as opposed to the theoretic 8.3, the turning point of phenolphthalein indicators. The precipitation of CaCO_3 is delayed; the ditch water is oversaturated after 45 minutes' flow from the outer outlet; precipitation occurs in the next 15 minutes. Perhaps MgCO_3 suppresses and delays the precipitation as it does in sea water. Perhaps aragonite as well as calcite is deposited. They are both minerals of CaCO_3 , but are crystallized differently, and have different solubilities.

The Montezuma Well system is an unexcelled natural laboratory for chemistry, engineering, or geology students concerned with all aspects of CaCO_3 dynamics. Welcome! The biologists need you.

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