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Physical and chemical characteristics of ephemeral pond habitats in the Maracaibo basin and Llanos region of Venezuela

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Abstract

Physical and chemical variables of ephemeral rainwater pond habitats in the Maracaibo basin and Llanos region of Venezuela were investigated to assess environmental qefeatures important for future studies of the physiological ecology and bioenergetics of annual killifish. Dissolved oxygen, temperature, pH, Eh, and conductivity measurements were made in the field at each collection site. Water and filter samples were collected and analyzed for trace metals, cations, anions, and osmolality. Physical and chemical characteristics of rainwater ponds are highly variable both temporally and spatially. Large diurnal fluctuations occur in temperature and dissolved oxygen. Dissolved oxygen content, temperature, pH and conductivity values exhibit a high degree of interpool variation. All pools sampled have a high amount of suspended solids consistent with high turbidity. Pool sediments appear to be anoxic as indicated by measurement of Eh. Llanos region pools are dominated by calcium as the major cation, while Maracaibo basin pools are dominated by sodium as the major cation. Maracaibo pools can be further separated into two distinct regions, inland savanna and coastal desert, based on ionic composition. Annual killifish inhabiting ephemeral ponds may be exposed to extremes in dissolved oxygen concentration, temperature and pH values during adult, juvenile, and embryonic stages.

Introduction

Ephemeral rainwater pools offer a unique freshwater habitat to those organisms that can survive and persist in a highly variable and unpredictable environment. Although temporary pond habitats are common on most continents, they are most prevalent and ecologically important in arid and semi-arid regions where permanent water sources may be absent or rare (reviewed by Williams, 1985). Data describing the physical and biological conditions organisms encounter in ephemeral rainwater habitats of South America are largely unavailable. Characterization of these habitats is essential to understanding the physiology and ecology of the organisms that exploit them.

A number of invertebrate groups including aquatic insects, crustaceans, gastropods, and nematodes are quite successful at inhabiting temporary aquatic habitats (Williams, 1985; Hammer & Appleton, 1991; Hand, 1991). In contrast to the large number of invertebrates that regularly inhabit these waters, there are very few vertebrates that can persist in ephemeral ponds; fish are thought to be especially under-represented (Williams, 1985). Annual killifish (Cyprinodontiformes, Rivulidae) are an exception to this generalization. Members of this group have developed a life history strategy similar to many invertebrates that rely on drought-tolerant, diapause embryos to survive through the dry season (Wourms, 1972a, 1972c). Annual killifish have been reared by hobbyists for many years, and many aspects of their natural history and development are appreciated scientifically (Nico and Thomerson, 1989; Peters, 1963; Thomerson and Taphorn, 1992a, 1992b; Wourms 1972a, 1972b, 1972c). However, the physiological ecology of these species is still poorly understood, especially for early life history stages.

Ephemeral ponds inhabited by annual killifish were sampled to characterize the physical and chemical conditions experienced by these fish during the rainy season. This study reports the results of laboratory water chemistry analyses and field measurements of several chemical and physical properties of ephemeral rainwater pools in the Llanos region and Maracaibo basin of Venezuela.

Materials and methods

Water sampling and fish collection took place in June of 1995 in the high Llanos and Maracaibo basin in Venezuela. The locations for all sampling sites are identified on the map in Figure 1. The majority of sampling effort was concentrated in the Maracaibo basin, the primary habitat of *Austrofundulus limnaeus* Schultz 1949 in Venezuela. Fish were caught primarily using dip nets. Multiple, and often exhaustive, passes through each pool were made to assure the identification of all species present in each pool. For a few of the larger pools, a small beach seine was used in addition to dip nets.

Field measurements

Dissolved oxygen (D.O.) measurements were taken with a dissolved oxygen meter (Orion Research, Boston, MA) equipped with a gold/silver dissolved oxygen probe. The probe was calibrated twice daily using water saturated air. Measurements were recorded in percent saturation and later converted to concentration in mg O_2 l^{-1} using osmolality and barometric pressure data collected in the field. Water temperature was determined using the thermometer supplied with the D.O. probe. Air temperature and barometric pressure measurements were recorded with a digital barometer/thermometer (Fisher Scientific). Continuous measurements of water temperature for a period of seven days were obtained for two ponds using dataloggers (Onset Computer Corp., Pocasset, MA) set to a sampling interval of 144 s. pH measurements were taken using a portable pH/ISE meter and a Ag/AgCl triode pH electrode in temperature compensation mode(Orion Research). The meter was calibrated each morning using standards of pH 4, 7 and 10. Eh was measured using a pH/ISE meter equipped with a platinum calomel electrode (Orion Research). Sediment Eh was measured by inserting the probe approximately 1 cm into the sediments and waiting for a stable reading (usually 2–3 min.). Conductivity was determined using a digital conductivity meter (VWR Scientific). The meter was calibrated once a week using a standard solution of 100 μS. D.O., pH and conductivity probes were inserted directly into the pool and gently stirred until a constant reading was obtained.

Water sample collection

All bottles (Nalgene, high density polyethylene plastic) were acid washed in 1 N ultrapure nitric acid, rinsed and dried. Whatman GF/F Filters (nominal pore size 0.7 μm) were ashed, preweighed and stored in individual plastic bags until use.

Water samples were collected, preserved and analyzed according to Clesceri et al. (1989). Samples were taken from the center of each pond using a 500 ml plastic beaker. Pool water was immediately filtered through the GF/F filters using a Nalgene plastic filter apparatus and a hand vacuum pump. Filters were sealed in plastic bags for analysis of total suspended solids (TSS). For metal and trace metal analysis, a sub-sample of 50 ml was acidified with 0.5 ml of concentrated ultrapure nitric acid to yield a pH ≤ 2.0. A 25 ml sub-sample of filtered water was stored without preservation for analysis of chloride, sulfate and total osmolality. Another 100 ml of filtrate was acidified with 1 ml of concentrated sulfuric acid to yield a pH ≤ 2.0 for determination of nitrate and total dissolved nitrogen (TDN). All samples and filters were stored as collected until analysis and were refrigerated as often as possible. Some samples were not refrigerated for a number of days post-collection due to a lack of proper facilities in remote areas.

Water and filter analyses

Metal and cation concentrations were determined using inductively coupled plasma (ICP)/atomic emission spectrometry (Fisons Instruments, Dearborne, MI). Analyses were performed by the Laboratory for Environmental and Geological Sciences at the University of Colorado. Wavelengths were chosen to minimize inter-elemental interference while maximizing detection limits (see Appendix, Table 3 for a full list of wavelengths and analytes). Elements present in the highest concentrations (B, Ba, Ca, Fe, K, Mg, Mn, Na, Zn) were chosen for analysis based on a scan of the full suite of analytes on two randomly chosen samples (Appendix, Table 3).

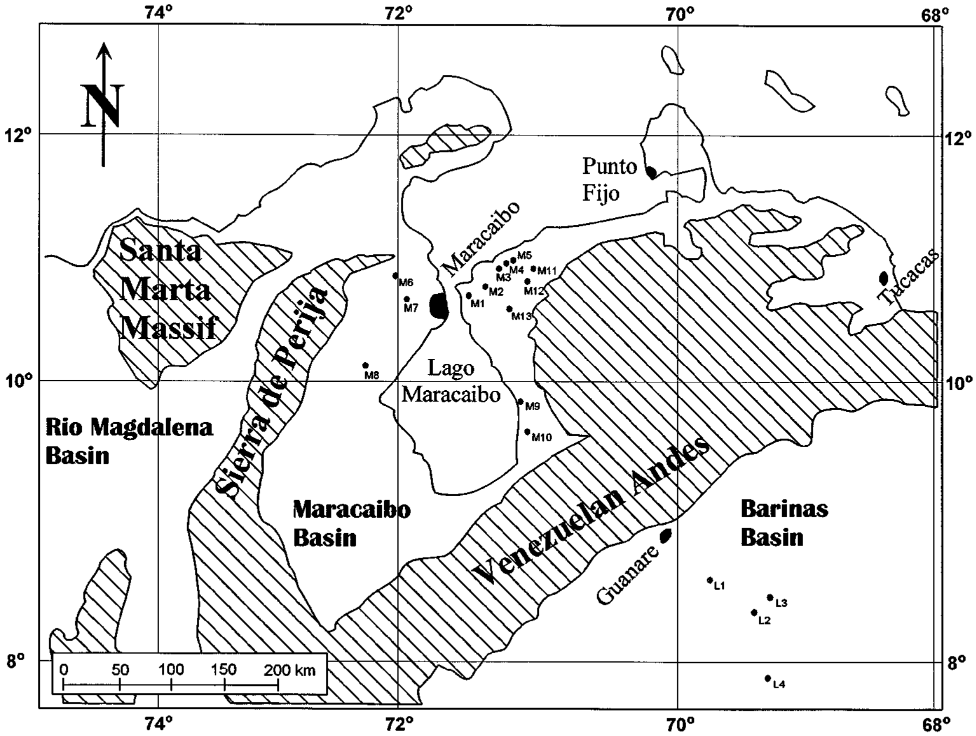

Figure 1. Map illustrating the collection sites in Venezuela. Sampling sites in the Llanos are denoted by L#, while Maracaibo basin sites are denoted by M#.

Sulfate and chloride ion concentrations were determined by anion exchange chromatography (Dionex, Sunnyvale, CA). Nitrate was quantified using a flow injection analyzer (Latchat, Milwaukee, WI). TDN was determined by oxidizing an aliquot of water with persulfate to convert all nitrogen species to nitrate followed by analysis for nitrate as above.

Osmolality was determined on non-preserved samples using a vapor pressure osmometer (Wescor, Logan, UT) calibrated with deionized water and a 100 mmol kg^{-1} H_2O standard. Each value is reported as the average of three determinations. The average coefficient of variation (CV) for triplicate determinations was 0.253.

Filters were dried to constant weight at 60 °C to determine TSS. The filters were then ashed at 460 °C for 3 h and reweighed to determine the organic contribution to TSS.

Cation data was plotted using trilinear plot analysis (e.g. Hamilton and Lewis, 1990). This graphing technique allows the ratios of major cations to be expressed as a single point on a triangular plot. Concentrations of major biologically active ions are expressed as a percentage of the total cation concentration in meq l^{-1}. When graphed in this manner, water samples can be compared to possible source waters. In addition, changes in cationic ratios can be visualized.

Results

The ephemeral ponds sampled in this study are all influenced to some extent by humans. Most of the ponds are roadside ditches or are in close proximity to a road. Many of the ponds are associated with culverts or concrete banks. The ponds are designated generally as roadside ditches or natural ponds, although there is a continuum between these two distinctions. Other prominent features that may influence the chemical and physical properties of the ponds are also listed (Table 1).

Maracaibo basin ponds differ from Llanos ponds in their degree of isolation from permanent water sources. While many Llanos pools may become very large, flood into other pools, or be joined with flooding rivers, the Maracaibo pools are typically isolat-

Table 1. Field Variables

Pools	D.O.	D.O.	pH	Eh,S	pE,S	T, H_2O	T, Air	Date	Time	Location	Classification	Species
Llanos												
L1	2.5[a]	0.206[b]	6.00	–[c]	–	26.8[d]	28.5[d]	6/4	11:05	08°53′44N, 069°29′34W	Roadside Ditch[e]	*A.t.;P.z.;R.m.*[f]
L2	45.0	3.59	6.25	–	–	27.3	29.5	6/4	13:40	08°56′00N, 069°27′38W	Natural	*A.t.;P.z.;R.m.*
L3	82.0	6.65	6.34	–	–	25.8	–	6/4	15:00	08°43′29N, 069°06′39W	Roadside Ditch	*A.t.;P.h.;P.z.*
L4	72.0	5.84	6.53	–	–	26.1	24.0	6/4	17:00	08°32′12N, 069°13′24W	Natural	*A.t.;R.m.*
Maracaibo												
M1	4.0	0.321	6.20	–130.0	–2.19	27.1	28.5	6/7	10:00	10°46′20N, 071°25′59W	Natural	*R.h.*
M2	73.0	5.65	6.26	–110.4	–1.84	29.4	34.5	6/7	12:05	10°47′29N, 071°21′07W	Natural	*A.l.;R.h.*
M3	256.0	17.9	6.23	–222.5	–3.65	34.5	39.0	6/7	15:00	10°52′08N, 071°18′49W	Roadside Ditch. *cul.*	*A.l.;R.h.*
M4	105.0	7.99	8.10	–190.0	–3.16	30.2	38.5	6/7	15:55	10°53′17N, 071°17′57W	Roadside Ditch. *cul.*	*A.l.*
M5	160.0	11.8	9.07	–	–	32.3	31.5	6/7	16:30	10°53′15N, 071°18′00W	Roadside Ditch. *cul.*	*A.l.*
M6	13.0	1.02	7.10	–203.3	–3.41	28.2	34.5	6/8	12:37	11°05′49N, 072°01′58W	Roadside Ditch. *con.*	*A.l.;R.p.*
M7	2.0	0.157	6.32	32.0	0.537	27.7	30.5	6/8	18:20	10°48′51N, 071°52′16W	Roadside Ditch, *cul.*	*A.l.*
M8	155.0	11.3	5.48	–72.8	–1.20	32.2	33.5	6/9	18:00	10°06′36N, 072°109′17W	Roadside Ditch	*A.l.;R.p.*
M9	4.0	0.315	6.20	–63.5	–1.06	28.4	32.5	6/11	13:00	09°56′48N, 071°05′36W	Natural	*A.l.;R.p.*
M10	47.0	3.16	5.82	–37.5	–0.610	37.0	34.5	6/11	16:20	09°45′48N, 071°05′36W	Natural, *oil field*	*A.l.;R.p.*
M11	163.0	12.4	8.55	–59.5	–0.992	29.7	34.5	6/14	11:00	10°55′02N, 071°02′14W	Roadside Ditch	*A.l.;R.h.*
M12	38.0	2.89	6.93	–81.0	–1.35	30.2	38.0	6/14	12:10	10°54′34N, 071°02′19W	Roadside Ditch	*A.l.;R.h.*
M13	165.0	11.2	7.23	–136.3	–2.22	37.0	36.5	6/14	14:15	10°43′47N, 071°13′46W	Roadside Ditch	*A.l.;R.p.*

[a] Dissolved oxygen,% saturation
[b] Dissolved oxygen, mg l^{-1}
[c] Eh of pool sediments, mV
[d] Temperatures reported in °C
[e] Classification: *con.* = concrete near or in pond, *cul.* = steel culvert in or near pond, *oil field* = oil wells near pond
[f] Species: *A.l.* = *Austrofundulus limnaeus; A.t.* = *Austrofundulus transilis; P.h.* = *Pterolebias hoignei; P.z.* = *Pterolebias zonatus; R.h.* = *Rachovia hummelinki; R.m.* = *Rachovia maculipinnis; R.p.* = *Rachovia pyropunctata*

ed and are rarely flooded or connected with permanent water sources (Nico and Thomerson, 1989). Most ponds inhabited by annual killifish will dry annually (Nico and Thomerson, 1989; T. Hrbek, unpublished observations). Pools in the Maracaibo basin fill with water during the short rainy season (mid-May to August; T. Hrbek, unpublished observations). Rain events are unpredictable on both spatial and temporal scales (J. Thomerson, pers. comm.), and many Maracaibo basin pools will experience multiple fillings in a single rainy season, each inundation lasting for a few weeks (T. Hrbek, unpublished observations). Sampled ponds were small with surface areas ranging from less than 3 m^2 to over 200 m^2. While larger pools were nearly a meter deep, many of the smaller pools were less than 10 cm deep.

Rainwater ponds are warm and experience high diel variations in temperature. Temperatures ranged from 25.8–27.3 °C in the Llanos pools and 26.0–37.5 °C in the Maracaibo basin pools (Table 1). Temperatures were recorded for two pools in the coastal desert during a diurnal cycle (Figure 2). These data illustrate an increase in temperature during the day until late afternoon and then a subsequent decrease at night. Temperature data collected over a period of seven days illustrate the same trends in pools M2 and M3 in the Maracaibo basin (Figure 3). The largest fluctuation in recorded temperature was 11.5 °C, (26–37.5 °C) in pool M3 over a 6.5 hour period. In addition, large differences are seen in the amplitude of temperature cycles between large and small pools (Figure 3).

Dissolved oxygen and pH values showed a high degree of variation among ponds. Dissolved oxygen concentrations ranged from 0.206–6.65 mg O_2 l^{-1} (2.5–82% saturation) for the Llanos collection sites (Table 1). The Maracaibo basin sites ranged from 0.157–17.9 mg O_2 l^{-1} (2–256% sat.). Dissolved oxygen concentrations were recorded for two pools (M4 and M5) in the coastal desert area northeast of Lake Maracaibo (Quisiro area) from 10:00 AM to 5:30 PM on June 10, 1995 (Figure 4). These data indicate that oxygen levels increase during the day until mid to late afternoon when the dissolved oxygen levels begin to decline. Some pools, however, showed low dissolved oxygen levels even at mid-day, when elevated dissolved oxygen levels would be predicted. pH values ranged from 6.0–6.53 in the Llanos collection sites and 5.48–9.07 in the Maracaibo basin (Table 1). Mea-

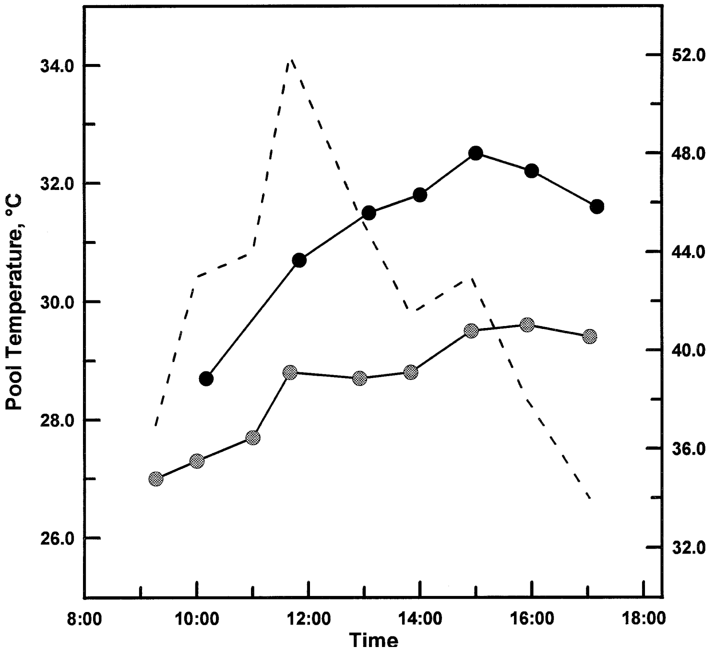

Figure 2. Water temperature vs. time of day for pools M4 (○) and M5 (●) from the coastal desert area near Quisiro, Maracaibo basin. Air temperature is indicated by the dashed line.

surement of pH during a diurnal cycle indicates that pH increases from the morning hours until the late afternoon when it plateaus or starts to decline (Figure 5).

Llanos and inland Maracaibo pools appear to be typically dilute and soft waters. A noted exception to this generalization are the coastal desert pools near Quisiro (M1–M5), which appear to be more concentrated. Conductivity (range, 27–110 μS), osmolality (range, 4.70–9.71 mOsm kg^{-1} H_2O) and calculated hardness (range, 16.63–57.95 mg l^{-1} $CaCO_3$) are all indicative of soft, dilute water in the Llanos pools (Table 2). The Maracaibo basin inland pools follow a similar trend with conductivity, osmolality and hardness ranges of 23–152 μS, 0.023–0.252 mOsm kg^{-1} H_2O, and 8.54–88.55 mg l^{-1} $CaCO_3$ respectively. Quisiro pools had the highest conductivity values ranging from 57–2,350 μS with correspondingly high osmolalities and hardness values (2.82–29.5 mOsm kg^{-1} H_2O and 14.52–342.9 mg l^{-1} $CaCO_3$ respectively). The wide range of values for these variables observed in the Quisiro area is the result of including pools M1 and M2 in the grouping. Pool M2 is a large semi-permanent pool and may be subject to different water chemistry than smaller ponds. Pool M1 is believed to have recently filled when the collection took place. This assumption is supported by the collection of only small fish larvae. While these two ponds are much more dilute than the other coastal desert ponds, they share similar ratios of biologically active cations.

A summary of the metals and ion composition data is presented in Table 2. Cation analysis indicates that the Llanos pools are dominated by Ca and K, while Na and Mg are found in lower concentrations (Table 2, Figure 6). Calcium and potassium values ranged from 4.12–13.0 mg l^{-1} and 5.68–17.1 mg l^{-1}, respectively, while sodium and magnesium concentrations were 2.16–6.38 mg l^{-1} and 1.54–6.19 mg l^{-1}. Sulfate is the dominant anion in this area and ranged from 0.479 to 8.15 mg l^{-1}, followed by chloride (2.55–6.86 mg l^{-1}), and nitrate (0.124–4.96 mg l^{-1}).

The Maracaibo basin has a characteristically different cationic composition compared to Llanos pools (Table 2, Figure 6). Two distinct areas of the Maracaibo basin, coastal desert and inland savanna, are distinguishable based on the cation and anion compositions. The coastal desert near Quisiro (M3–5), east of Lake Maracaibo, contains pools dominated by Na and Mg (155–331 mg l^{-1} and 45.2–59.2 mg l^{-1}, respectively), while Ca (27.1–39.7 mg l^{-1}) and K (3.20–9.58 mg l^{-1}) are found in lower concentrations. Chloride is the dominant anion (215–683 mg l^{-1}), followed by sulfate (42.2–210 mg l^{-1}) and then nitrate (0–1.24 mg

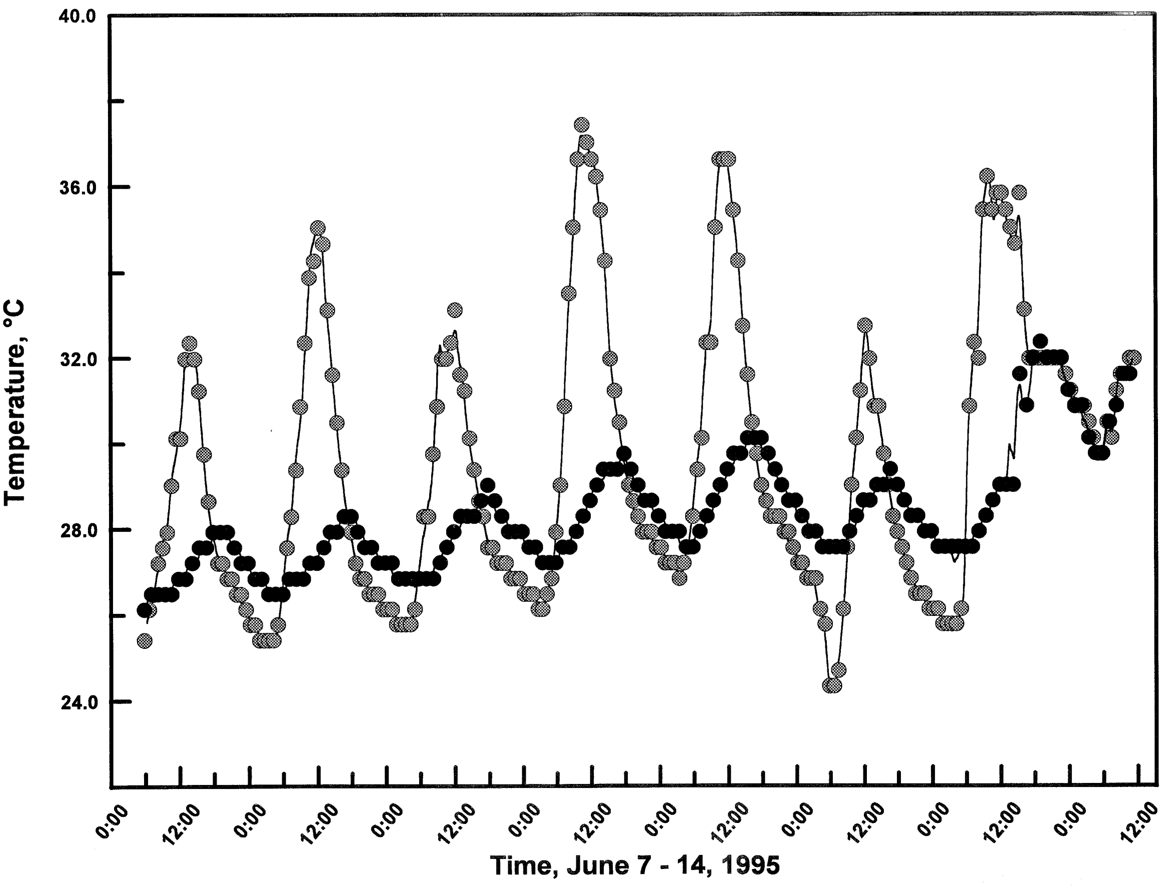

Figure 3. Water temperature vs. time of day for a large, semi-permanent pool M2 (●) and a small ephemeral pool M3 (○) over a 7 day sampling period. Symbols are spaced every 20 data points (48 min) while the sampling interval was actually every 144 s.

l^{-1}). Collection sites M1 and M2 are near the Quisiro area, and show similar patterns for cations and anions although the overall osmolality of the ponds is much lower than the other ponds in this area. Inland savanna areas in the Maracaibo basin (M6–13) are dominated by Ca and K (1.72–27.3 mg l^{-1} and 2.46–24.0 mg l^{-1}, respectively) and had overall lower metals concentrations during this sampling. The inland areas of the Maracaibo basin are also characterized by chloride as the dominant anion (2.3–34.2 mg l^{-1}), then sulfate (0.191–7.42 mg l^{-1}) and last nitrate (0–7.38 mg l^{-1}). Although there are marked differences among total concentrations of cations in the desert pools versus the inland savanna pools, these comparisons may not be meaningful due to differences in evaporation state, local weather patterns and the age of the pool at the time of sampling. Elevated levels of K in many Llanos and inland Maracaibo pools may be the result of cattle grazing in or near the ponds (Mathews et al., 1994).

Most pools appeared to have a large amount of suspended mud and clay particulates that gave the water a rich tan or brown color. High turbidity was especially evident in the Maracaibo basin, specifically the Quisiro area. The qualitatively high degree of turbidity in these ponds is illustrated indirectly by relatively high values of TSS (Table 2). Values in the Maracaibo basin ranged from 4.60 mg l^{-1} to 199.1 mg l^{-1} with the Quisiro area having a higher average value (136.3 mg l^{-1}) than the inland Maracaibo regions (37.41 mg l^{-1}). The Quisiro area pools averaged about 15.8% suspended organics while the inland pools averaged a 38% contribution from organics. Levels of TSS and the organic contribution to TSS are similar in the Llanos and inland Maracaibo pools.

The sediments of rainwater pools in the Maracaibo basin appear to be anoxic. Sediment Eh values ranged

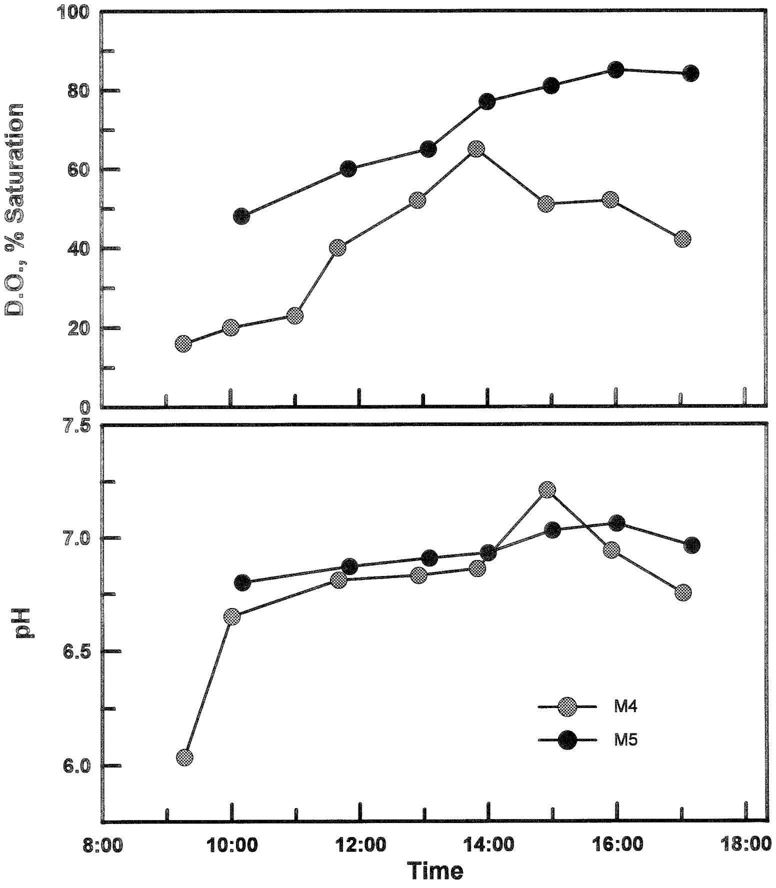

Figure 4. Dissolved oxygen concentration and pH vs. time of day for pools M4 (○) and M5 (●) from the coastal desert area near Quisiro, Maracaibo basin. Both these pools were exposed to direct sunlight and are approximately similar in size and depth.

from 32.0 to −222.5 mV (Table 1). These values correspond to pE values ranging from 0.537 to –3.65. pE values in this range are considered anoxic.

Fish collection

Collections of annual killifish reported here agree with previous species distributions reported by Lilyestrom and Taphorn (1982). Species of fish collected at each site are summarized in Table 1. *Austrofundulus limnaeus* is distributed on both the east and west sides of Lake Maracaibo. The distribution of *A. limnaeus* appears to be broken by the swamps of Rio Catatumbo in the southern portion of the Maracaibo basin. *Rachovia pyropunctata* were collected primarily in the inland pools of the basin and were also absent in the swamps of Rio Catatumbo. *R. hummelinki* were only collected in the coastal desert areas on the eastern shore of Lake Maracaibo in the states of Zulia and Falcon. The number of pools sampled in the Llanos region is small and does not cover a sufficient area to warrant an analysis of fish distributions.

Discussion

Rainwater pools in Venezuela show a high degree of variation in many important physical and chemical properties. Pools investigated during the early portion of the rainy season can generally be described as small, shallow, and turbid pools. The characteristics of ponds appear to fluctuate during the diurnal cycle in a manner similar to previous studies of small pond habitats (Bamforth, 1962; Scholnick, 1994). Based upon the high degree of inter-pool and temporal variation in variables such as dissolved oxygen concentration, temperature, pH, and ionic composition we predict that annual killifish can tolerate a wide range

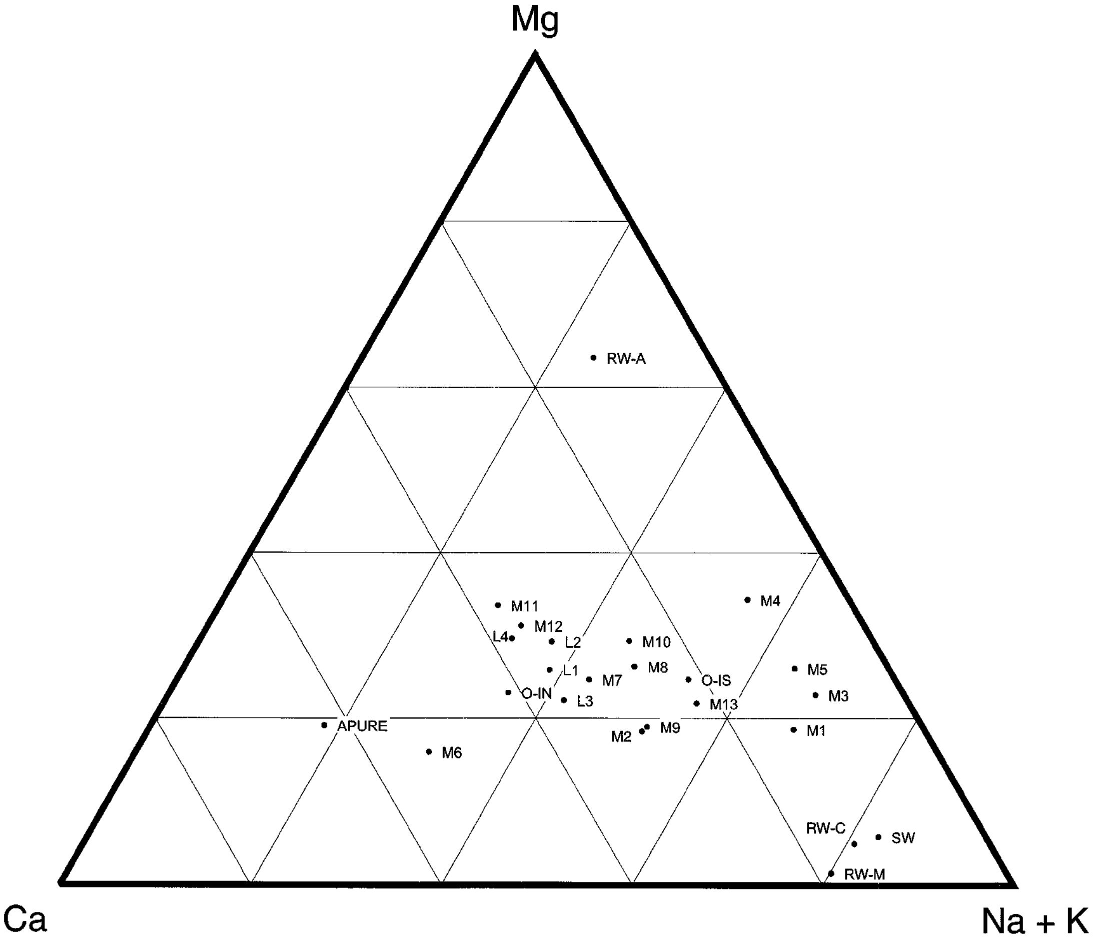

Figure 5. Trilinear cation plot of calcium, magnesium, and sodium plus potassium concentrations. Values are expressed as a percentage of the total cation concentration in meq l^{-1}. Llanos pools are denoted by L#, while Maracaibo basin pools are denoted by M#. Rainwater from the western Maracaibo basin, RW-M (Morales et al., 1995), the Apure River drainage, RW-A, the Caura River drainage, RW-C (Hamilton & Lewis, 1990) as well as seawater, SW (Thurman, 1988) and Apure River water, APURE (discharge weighted mean, Lewis et al., 1995) are provided for comparison and as possible source waters for the investigated pools. Mean values for several Orinoco River floodplain pools (Hamilton & Lewis, 1990) are also included to illustrate changes in ionic composition related to the isolation and subsequent evaporation of seasonal freshwater pools (O-IN, pools at inundation, O-IS, pools after several months of isolation and evaporation).

of environmental variables which are known to affect physiological processes.

Temperature was a highly variable parameter in the shallow rainwater pools. Maracaibo basin pools showed a considerable amount of interpool variation (range, 27.1 °C to 37 °C). Diurnal temperature fluctuations for individual ponds were similar in magnitude to the interpool variation; pool M3 near Quisiro changed from 26 °C to 37.5 °C in 6.5 h, equivalent to 1.74 °C h^{-1} (Figures 2 and 3). Although thermal stratification was not investigated in this study, other authors have reported microstratification in shallow ephemeral waters (reviewed by Williams, 1985). Differences between surface and bottom temperatures in small ponds may be significant and persist on a diurnal basis. Cooler water temperatures were evident near the bottom of some of the larger pools (e.g. M2). Williams (1985) indicates that organisms may use these cooler bottom water temperatures as refugia from high surface water temperatures. While fish were often caught in the deeper, possibly cooler waters, sometimes specimens were only caught around the shallow margins of the pools were temperature should be the most extreme.

Dissolved oxygen concentrations ranged from 2.0–256% saturation. Early morning values of D.O. were low and afternoon values were high and often super-

Table 2. Chemical Composition

Pools	Ca	K	Mg	Na	Ba	B	Fe	Mn	Zn	Cl	SO_4	NO_3	TDN	TSS	TSO	H	Cond.	Osm
Llanos																		
L1	8.98[a]	8.10[a]	3.95[a]	6.38[a]	0.390[a]	0.051[a]	6.73[a]	0.328[a]	0.056[a]	2.55[a]	0.479[a]	0.124[a]	19.3[b]	11.46[c]	36.50[d]	38.69[e]	27[f]	5.01[g]
L2	8.42	12.9	4.43	3.04	0.220	0.045	0.393	0.371	0.035	6.62	7.73	0.186	5.46	8.50	11.40	39.27	110	6.58
L3	4.12	5.68	1.54	2.16	0.393	0.053	0.188	0.035	0.045	2.88	2.88	1.55	8.06	630.8	67.80	16.63	470	4.70
L4	13.0	17.1	6.19	2.90	0.355	0.091	0.210	0.004	0.046	6.86	8.15	4.96	17.2	73.86	16.25	57.95	910	9.71
Maracaibo																		
M1	5.80	16.0	4.81	23.5	0.417	0.279	2.85	0.487	0.079	34.2	5.49	0.186	15.4	–	–	34.29	216	3.45
M2	3.59	5.88	1.35	3.73	0.449	0.092	1.44	0.176	0.061	8.16	1.44	1.24	6.76	100.5	25.20	14.52	57	2.82
M3	39.7	3.92	59.2	331	0.469	0.239	0.052	0.004	0.005	683.	42.2	1.24	8.68	155.0	28.20	342.9	2,350	29.5
M4	27.1	9.58	52.9	155	0.366	0.235	0.021	0.234	0.008	215.	115.	0.434	10.7	199.1	38.20	285.5	1,220	19.1
M5	28.4	3.20	45.2	209	0.198	0.162	0.169	0.021	0.005	308.	210.	0.000	8.06	90.60	17.00	257.0	1,510	21.0
M6	27.3	20.5	4.95	6.02	0.330	0.126	2.37	0.342	0.043	18.2	1.49	1.67	18.0	4.60	14.60	88.55	252	6.58
M7	7.92	7.45	3.69	7.86	0.786	0.129	0.398	0.087	0.100	10.1	6.38	0.000	3.91	–	–	34.97	118	4.39
M8	1.72	2.46	1.03	2.06	0.548	0.075	2.59	0.020	0.099	2.30	0.259	1.05	4.77	33.00	26.80	8.54	23	4.70
M9	5.28	15.8	2.10	1.62	0.331	0.077	2.46	0.056	0.058	4.39	0.692	0.310	15.0	21.40	15.20	21.83	91	8.46
M10	5.61	11.6	3.90	4.54	0.481	0.062	4.04	0.059	0.081	12.5	7.42	0.062	11.1	44.00	16.10	30.07	95	4.39
M11	12.3	5.31	6.75	7.99	0.343	0.133	0.264	0.014	0.006	11.7	0.939	0.062	50.3	45.20	17.30	58.51	152	2.82
M12	6.79	4.23	3.57	4.65	0.318	0.080	1.79	0.061	0.043	7.43	1.44	0.496	9.98	82.80	13.80	31.66	80	2.82
M13	7.21	24.0	4.28	6.63	0.305	0.067	2.73	0.105	0.031	16.6	0.191	7.38	11.3	30.90	16.60	35.63	150	5.64

[a] mg l^{-1}
[b] TDN (total dissolved nitrogen), mg l^{-1} NO_3^- equivalents
[c] TSS. (total suspended solids), mg l^{-1}
[d] TSO. (total suspended organics), mg l^{-1}
[e] Hardness, mg l^{-1} $CaCO_3$, calculated from the following equation: $H = (2.497 \bullet Ca) + (4.118 \bullet Mg)$
[f] Conductivity, μS
[g] Osmolality, mOsm kg^{-1} H_2O

saturated (Figure 4 and Table 1). For example, oxygen concentration in pond M4 changed from 16% to 65% saturation over 5 h. Daily fluctuations similar to the ones observed in this study have been described by other authors and may be attributed to high levels of oxygen production via photosynthesis during the mid-day sun (Bamforth, 1962; Scholnick, 1994). Although most pools appeared to follow this pattern, pools M7 and M9 are exceptions. These pools were only 2% and 4% saturated with oxygen in the early evening or afternoon, respectively, times when high dissolved oxygen concentrations are expected.

Inter-pool pH values ranged from 5.48–9.07. pH also changed diurnally, based on data for two coastal desert ponds showing that changes of over 1 pH unit are possible in a 9 h period (Figure 5). Even larger fluctuations have been reported for ephemeral pools in North America (Scholnick, 1994) and may be possible in the ponds examined in this study.

Rainwater pools sampled in this study are characteristically composed of soft and dilute waters. Low values for osmolality, conductivity and hardness are consistent with this generalization. Pools in the coastal desert near Quisiro are a notable exception and are much more concentrated than other pools in the Maracaibo basin (Table 2). It is not known whether this is due to a direct oceanic influence, the composition of rainfall in the area, a subsequent concentration of ions due to evaporation, or a combination of these and other variables.

The cationic composition of ephemeral rainwater pools appears to be unique when compared to their rainwater sources (Figure 6). The Llanos pools are similar in ionic composition to floodplain pools of the Orinoco River as reported by Hamilton and Lewis (1990). Both of these habitats are dominated by Ca and therefore occupy the same area on a trilinear cation plot. Pools in the inland Maracaibo basin also show a similar pattern. Coastal desert pools (Quisiro area) have a unique composition with Na as the dominant cation. These pools occupy an area of the trilinear diagram distinct from all other pools and water sources. Hamilton and Lewis (1990) showed that ion ratios of isolated floodplain pools tend to change as the pools evaporate. This change moves the points from the left of center to the lower right corner of the trilinear cation plot.

The ratios of biologically active ions can be used as a rough indicator of evaporation in isolated rainwater pools (Cole 1968). Ratios of Na:K and Ca:Mg are reported by Cole (1968) to decrease during evaporative concentration due to differential precipitation of salts. While the Ca:Mg ratios for the Quisiro area are reduced compared to the other sampling sites, this pattern does not hold true for the Na:K ratio (data not shown). High levels of Na, causing the high Na:K ratios in contrast to the low Ca:Mg ratios, are probably a result of coastal influences which confound the more generalized patterns outlined by Cole (1968).

Although turbidity was not directly measured, the large amounts of TSS are consistent with the high turbidity observed. Based on the data reported by Hamilton and Lewis (1990), the TSS values for ponds in our study would correspond to Secchi depths of 0.05–0.7 m.

Flooded soils and pond sediments can often be depleted of oxygen soon after inundation (Sposito, 1989). The depletion of oxygen by microbial activity leads to a reduced redox state in flooded soils and an increase in electron availability. Thus, an Eh probe can be used to estimate the redox state of soils and sediments. These values can then be used to make qualitative inferences about the amount of oxygen in a soil solution that is available to organisms. Sposito (1989) indicates that pE values greater than 7 are considered oxic, values between +2 and +7 are suboxic, and values below +2 are anoxic (sediment pH of 7 is assumed for these values). Eh and pE values presented in this study (Table 1) indicate that sediments in the ephemeral rainwater pools can be generally classified as anoxic at a depth of 1 cm.

Data on the water chemistry and physical properties of the ephemeral ponds have been used to establish laboratory rearing conditions for *A. limnaeus*. Incubation media for embryos and the salt composition of aquarium water has been formulated to mimic the natural waters of this species during the early rainy season. Of the variables measured in this study, dissolved oxygen may have the greatest influence on physiological homeostasis in annual killifish. Dissolved oxygen levels not only change drastically on a diurnal basis, but may remain relatively low throughout the day in some ponds. Annual killifish embryos may be exposed to hypoxic or anoxic conditions frequently and chronically due to the anoxic nature of pond sediments. Preliminary data indicate that diapause embryos of *A. limnaeus* may have a very high tolerance for anoxia (over 15 days at 25 °C with no mortality). The effect of hypoxia and anoxia on the development, metabolism and occurrence of diapause in annual killifish embryos is currently under investigation in our laboratory.

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Appendix . Emissions wavelengths for analysis with the ICP/emissions spectrometer and a full suite of analytes for pools L4 and M9

Element	Wavelength, nm	Pool L4	Pool M9
Ag	328.068	ND[a]	ND[a]
Al	396.152	0.099	0.007
As	193.759	ND	0.005
B	249.678	0.091	0.077
Ba	455.403	0.356	0.325
Be	313.042	ND	ND
Ca	317.933	13.000	5.219
Cd	226.502	ND	ND
Co	228.616	ND	ND
Cr	267.716	ND	ND
Cu	324.754	0.013	0.012
Fe	259.940	0.210	2.460
K	766.491	16.530	17.362
Li	670.784	ND	ND
Mg	279.079	6.910	2.003
Mn	257.610	0.004	0.050
Mo	202.030	ND	ND
Na	589.592	3.370	2.025
Ni	231.604	ND	ND
Pb	220.353	ND	ND
Sb	217.581	ND	ND
Se	196.090	ND	ND
Si	288.158	6.248	1.499
Sr	407.771	0.061	0.040
Ti	336.121	ND	ND
Tl	190.864	ND	ND
V	292.402	ND	ND
Zn	213.856	0.051	0.060

[a] values in mg l^{-1}, ND indicates values below the detection limits