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DESERT ROCK POOLS IN INTERMITTENT STREAMS OF
CAPITOL REEF NATIONAL PARK, UTAH

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CHEMICAL AND BIOLOGICAL CHARACTERISTICS OF DESERT ROCK POOLS IN INTERMITTENT STREAMS OF CAPITOL REEF NATIONAL PARK, UTAH

Jill S. Baron¹, Toben LaFrancois², and Boris C. Kondratieff²

ABSTRACT.—Chemical variability and biological communities of rock pools found in small desert drainage basins of Capitol Reef National Park were characterized over 8 mon in 1994. Neither flooding, drying, nor the presence or absence of surrounding vegetated wetlands had a great effect on chemical composition, which was very dilute and fluctuated somewhat in response to rain events. Neither flooding nor drying affected the composition of biological communities in the pools. Summer storms affected only a few drainages at a time, and only a few study pools of significant volume dried completely during the hot, dry summer. This suggests that only a portion of the Waterpocket Fold aquatic community is ever disturbed at a time, leaving undisturbed areas as a source of recovery. Pools bordered by vegetated wetlands always supported greater numbers of species throughout the year than those bordered only by bedrock, but the same taxa were found in both vegetated and bedrock pools. The rock pool fauna in Capitol Reef National Park appear to be resilient to climatic variability.

Key words: desert rock pools, aquatic invertebrates, aquatic chemistry, disturbance, Capitol Reef National Park, Utah.

Aquatic environments in the arid Colorado Plateau are extremely important resources for the maintenance of desert ecosystems. Many aquatic resources are ephemeral, characterized by spatial and temporal discontinuities in flow (Grimm and Fisher 1992). Ephemeral streams may flow after storms and snowmelt, but surface water rapidly becomes confined to pools as the running water evaporates or is transpired (Poff and Ward 1989).

The Waterpocket Fold is a 62 × 1.25-km (100 × 2-mi) ridge of exposed Navajo sandstone that runs the length of Capitol Reef National Park, Utah (Fig. 1). The Waterpocket Fold contains many small drainages cut laterally across its width due to water erosion. These small drainages represent an extreme example of ephemeral streams. Cut directly into sandstone bedrock, these drainages function as streams only a few days each year. Stream flow occurs during and immediately after rain or snowmelt. Between precipitation events, water resides in rock pools, many of which are large enough that they rarely dry out. Pools are of 2 morphologies: those cut directly into sandstone with no surrounding vegetation, and those with riparian vegetation borders. Sandy alluvial deposits that support vegetation also allow groundwater storage. Vegetation surrounding

these pools grades from obligate wetland species such as *Typha latifolia* (cattail), *Salix* spp. (willows), *Phragmites australis* (reed), and *Carex* spp. (sedges) to upland species common in surrounding desert shrub, pinyon-juniper, and slickrock communities (Spence and Henderson 1993). Spence and Henderson (1993) found an increase in the number and abundance of nonnative species associated with pools where cattle grazing had previously occurred, suggesting that these systems are vulnerable to such disturbance.

Limited information has been collected on desert rock pools along the Waterpocket Fold in Capitol Reef National Park. Previous investigations have addressed questions regarding the role of disturbance by flooding on aquatic organisms (Haefner and Lindahl 1988, 1991). Similar systems of the Colorado Plateau have received more attention, including a chemical characterization of rock pools in northern Arizona (Van Haverbeke 1990), biological characterizations of temporary pools near Moab, Utah (Dodson 1987), and ecosystem-scale studies in Sycamore Creek, Arizona (Gray and Fisher 1981, Fisher et al. 1982, Grimm and Fisher 1992). We conducted a 6-mon intensive study to assess the status of physical and biological resources as the essential 1st step in managing

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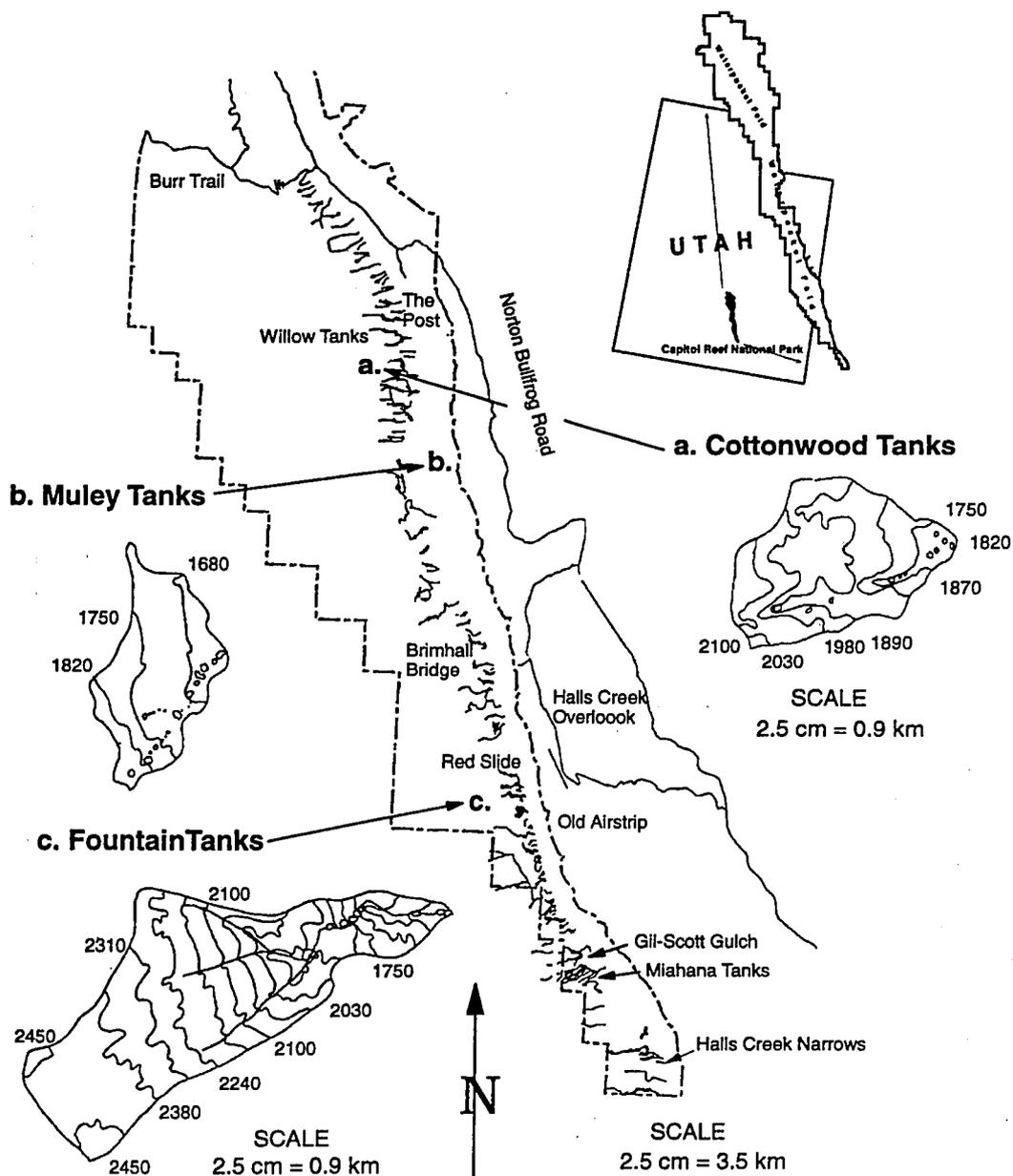


Fig. 1. Map showing location of Capitol Reef National Park and enlargements of the 3 study drainages where both chemical and biological analyses were conducted: (a) Cottonwood Tanks, (b) Muley Tanks, and (c) Fountain Tanks. Contour lines on enlargements are in meters.

natural resources (Stohlgren et al. 1995). This study complemented a larger survey of 460 rock pools in 80 major drainages (Berghoff 1994). We explored temporal and spatial variability of pools to answer several questions: How variable is pool chemistry and ecology

over time and space? Does the presence of surrounding vegetation influence water quality, pool volume, or ecology? How important are flooding and drought as disturbances to both water quality and aquatic invertebrate community composition?

SITE DESCRIPTION

The Waterpocket Fold, also known as Capitol Reef, is a north-south trending monocline of Navajo Sandstone that extends approximately 112 km north from Lake Powell in southern Utah (Fig. 1). The Waterpocket Fold is specifically named for the more than 460 waterpockets, or rock pools, that have been carved by water and scouring action in the many small west-east drainages cut into the sandstone. Drainages are typically <2 km long and are made up of a series of pools connected with a drainage depression that conducts water during and after precipitation events. Because there is no upwelling of groundwater in the Navajo Sandstone (Kimball 1988), precipitation is the only source of new water to these drainages. Rock pools range in volume from a few liters to >1000 m³. Some vegetated wetlands adjacent to pools can have sediment depths up to 2 m.

Mean annual precipitation ranges from 183 mm at Fruita (Capitol Reef NP headquarters) in the north to 140 mm near Lake Powell. The maximum mean July temperature is 33°C, while the minimum mean January temperature is -8°C (Spence and Henderson 1993, National Oceanic and Atmospheric Administration 1994).

METHODS

Studies were centered on 5 drainages in the southern part of Capitol Reef National Park: Cottonwood, Muley, Fountain, and Miahna Tanks, and Gil-Scott Gulch (Fig. 1). Each drainage supported pools with and without surrounding vegetation, from which we selected 2 pools with and 2 pools without vegetation for in-depth study. Those with surrounding vegetation were classified as either palustrine emergent or palustrine scrub-shrub wetlands (Cowardin et al. 1992). Bedrock-bordered pools were classified as lacustrine littoral (Cowardin et al. 1992). Drainages ranged from broad and open at Muley Tanks to long and narrow at Cottonwood. The headwaters of Cottonwood Tanks originate in a narrow slot canyon. We made an attempt to select drainages along a broad length of the Waterpocket Fold. To test the results of flooding, we chose pools from among larger, more permanent water bodies so that they would have water in them when July and August storms were expected. In spite of this selection objective, some pools dried out.

Precipitation and Pool Volume

We placed rain gages near the top and bottom of each drainage and monitored them weekly. Each gage was a funnel that drained to a coiled tygon tube connected to a plastic liter bottle. There were slight differences in the amounts collected by each pair of gages, but since we were unable to determine whether differences were due to precipitation variability or to gage catch efficiency, we used the gage that reported the greatest total precipitation for the summer to represent rain for each drainage. Past experience has suggested it is very difficult to overcollect precipitation in harsh environments, so the maximum amount recorded is more likely to represent actual rainfall than is a statistical average of 2 gages (Baron 1992). The volume of intensively studied rock pools was measured weekly by geometrical approximation using an algebraic formula for a half ellipse, and the depth of water was measured with a meter tape.

Chemical Analyses

Samples were collected approximately every other week from 1 pool with surrounding vegetation and 1 pool without surrounding vegetated wetlands in Cottonwood, Muley, and Fountain Tanks between March and August 1994. We collected 23 samples from Cottonwood Tanks (13 from vegetated and 10 from unvegetated pools), 22 from Muley Tanks (11 from each pool type), and 21 from Fountain Tanks (11 from vegetated and 10 from unvegetated pools). Water samples were collected in 125-mL high-density polyethylene (HDPE) bottles that had been acid-washed in 10% HCl solution, rinsed, and stored full of deionized water prior to sampling for pH and specific conductance. Samples collected for major ion analyses were stored in 250-mL HDPE bottles that had also been acid-washed with the same procedures. Because samples could not be refrigerated immediately, major ion samples were preserved with 0.5 mL chloroform (Keene et al. 1986). Samples were filtered in the field with a Nalgene hand pump through Whatman GF/C filters into baked dark-colored borosilicate glass bottles for analysis of dissolved organic carbon. Water temperature was recorded at the time of sampling.

Specific conductivity and pH of water samples were determined weekly using a conductivity (Amber Science Inc. Model 604) and pH

meter (Beckman Model 21). For summary statistics pH was converted to H^+ concentrations, averaged, and then reconverted to pH. Because pH values can vary diurnally according to algal photosynthetic activity and we did not standardize sample collection times to account for this, pH values should be viewed as approximate, rather than absolute. Preserved samples were analyzed for major ions within 3–4 mon after sample collection. Aliquots were filtered (Whatman GF/C filters) for cation analyses. Major ions were analyzed with ion chromatography, and alkalinity was analyzed with a Gran titration at the USFS Rocky Mountain Forest and Range Experiment Station in Fort Collins, Colorado (O'Deen et al. 1994). Dissolved organic carbon (DOC) was analyzed by the USGS Water Resources Division in Boulder, Colorado (Oceanography International Model 700 carbon analyzer). Quality of the chemical analyses was assessed by calculating the ion percent difference (IPD) between positively and negatively charged ions. This is an important component of being able to interpret results with confidence. All but 2 of the samples met 15% cutoff criteria for acceptable IPD at ionic strengths of greater than 200 $\mu\text{eq/L}$; these 2 data samples were discarded (Stensland and Bowersox 1984, O'Deen et al. 1994). Eight DOC samples were collected in duplicate; they compared within 10% over a range of 3–32 mg C/L.

Comparisons of mean chemical characteristics between the 3 drainages were made using a Student-Newman-Keuls test for studentized range. The studentized range is the difference between the largest and smallest treatment means divided by an estimate of the standard error of each single treatment mean. Separation of the means in the rank order influences the size of the difference required for significance (Ferguson 1981).

Comparison of the chemistry of pools adjacent to vegetated wetlands with pools surrounded by sandstone was done with a Wilcoxon matched pairs signed-rank test. Because the test assumes independence between the 2 groups being compared, we used a reduced data set. Connection of the pools during flooding events invalidates the assumption of independence. No vegetated versus unvegetated comparisons were run for Cottonwood drainage, since rain events caused observed flow

between the Cottonwood pools through July and August. Pools in Muley drainage were separated all summer, as no rain event was strong enough to cause spillage from the top pools. Pools in Fountain drainage overflowed only once, in late July. Chemical analyses after the flooding event in Fountain were excluded from the analysis.

Biological Analyses

We sampled aquatic fauna from macrozooplankton to vertebrates weekly from 4 pools in each drainage March through August 1994. Additional collections were made in September 1993 and January, February, and September 1994. Macrofauna were defined as any animals larger than the mesh size (1 mm^2) of a standard dip-net. Based upon previous laboratory identifications, we field identified organisms to the lowest practical taxon, usually species, and noted their life history stage (juvenile or adult). Bottle-trap and light-trap collections were used for specific identification of adult insects. A voucher collection of the invertebrate samples has been deposited in the C.P. Gillette Museum of Arthropod Diversity at Colorado State University.

Semi-quantitative measures of abundance were recorded as a rank based upon 3 standard dip-net sweeps of each pool. The sweeps were taken from different sides of the pool and the samples were combined in a single white pan. Organisms were placed into taxa and ranked 0 (no individuals), 1 (1–10 individuals), 2 (11–50 individuals), or 3 (51+ individuals). Three additional sweeps were then taken to insure consistent monitoring of rare species, and any taxa found that were not present in the first 3 sweeps were given an abundance rank of 1. Organisms were returned to the pool after enumeration and identification.

Common methods for quantitatively sampling the pools were field tested in February and March 1994. These were found to be unreliable and destructive. In such small systems it was important to sample nondestructively to avoid affecting pool communities through direct removal of pool organisms. Both a 30-micron plankton tow and standard Ekman dredge produced variance as large as population means. The rock pool organisms do not, however, fit other characteristics expected of a Poisson distribution that would exhibit this variance (Bhattacharyya and Johnson 1977). Rock pool

communities cannot be assumed to be independent of each other, but are affected by the previous community. Standard sampling methods also were subject to other problems, such as not accounting for patchiness of pool organisms and escape tactics by most adult beetles and hemipterans. The portable box method (Dodson 1987) of quantification, which was found suitable only for shallow pools of <1.2 m, was ineffective for quantifying the more abundant benthos such as chironomid larvae.

Cluster analysis and a transformed Pearson correlation matrix using 22 species were used to examine the biological structure of rock pool communities. Species chosen included all species present on a given sampling day and represent the major functional groups as well as the most abundant pool fauna. Pearson correlation coefficients among each species' abundance for a given period were transformed into a distance measure, and the data were then treated as distances in a cluster analysis to determine whether or not groups of organisms could be considered nonrandomly associated. Groups of species that appeared together as clusters between zero and 0.3 were considered nonrandom associations. This analysis was performed 3 times, using data from the weeks of 15 March, 10 June, and 14 July.

The effect of disturbance, defined as flooding, on the number of species present and ratio of juvenile to adult life history stages was evaluated with *t* tests. The effect of pool volume and temperature on biological parameters was examined with Pearson correlation coefficients.

RESULTS

Hydrology

The summer of 1994 was unusually dry, even for Capitol Reef National Park. Total precipitation at Cottonwood, Muley, and Fountain Tanks was 66.1, 27.2, and 31.0 mm, respectively (Fig. 2). According to the 38-yr record analyzed by Spence and Henderson (1993), 1/3 of the annual precipitation, 46–60 mm, usually falls as thunderstorms in July and August (Julian dates 182–243). In 1994 the July and August combined precipitation was 22.7, 5.0, and 31.9 mm at Cottonwood, Muley, and Fountain Tanks, respectively.

Volumes of the 6 intensively studied pools with vegetation increased with rain events, although only 5 events over the entire sampling

period caused flooding, defined as overflow from the pools. Maximum measured volumes ranged from 325 to 800 m³ for pools bordered by vegetation and 50 to 635 m³ for pools bordered by bedrock. Minimum volumes of 0–150 m³ were measured for pools bordered by vegetation and 5–150 m³ for pools bordered by bedrock. Major flash floods did not occur during the study period, although flooding was observed in Cottonwood and Fountain Tanks, but not in Muley Tanks. Normalized pool volume values (against maximum measured volume) with time showed that pool volumes covaried with rain events for pools with and without surrounding vegetation (Fig. 2). There appeared to be less variation in volume of pools with surrounding vegetation and soils, presumably because of the effects of evapotranspiration and soil water storage.

Pool water temperatures warmed over the summer from March to mid-April lows (4–18°C) to highs (32–35°C) in June, July, and August (Fig. 3). After mid-April most pool waters had temperatures in the 22–25°C range, regardless of location, exposure, or whether they were bordered by vegetated wetlands or bedrock. Pools were sampled at different times of day. Temperatures indicated in Figure 3 should be interpreted as within a range of measured temperatures for any given week because of wide diurnal variability.

Chemical Characterization

The waters of the rock pools we sampled were dilute, with specific conductivities <200 µS/cm and pH values near 7.0. The ionic ratio of calcium to alkalinity in the pools was similar to that measured from groundwater wells of the Navajo Sandstone (calcium:alkalinity of 0.4 in the pools compared with 0.3 reported from well samples by Kimball 1988), although the pools were far more dilute. Ratios of calcium:silica (>20) and calcium:sulfate (>8) did not compare well to those in groundwater (calcium:silica <5, calcium:sulfate <2). While silica can be consumed by diatoms, it is more likely that mineralogical variation in the bedrock and far less water residence time in the pools account for the different chemistries between groundwater and surface water.

Phosphate, an essential and often limiting nutrient, was never measured in concentrations above detection limits. Nitrate concentrations

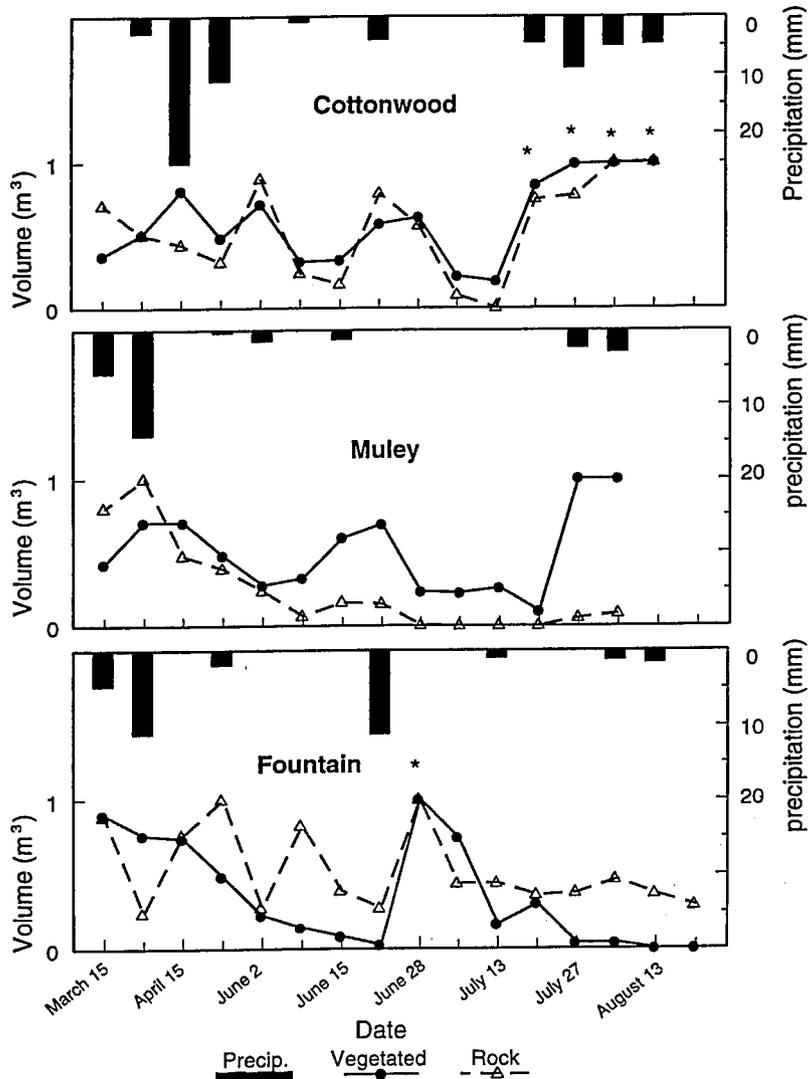


Fig. 2. Precipitation (bars) and normalized (against maximum measured volume) pool volumes (lines) for Cottonwood, Muley, and Fountain Tanks drainages during the period of study, March–August 1994. Rain events that caused flooding are marked with an asterisk. Flooding was defined as overflow from one pool to another.

were also low, while ammonium was present in somewhat higher concentrations.

Alkalinity and conductivity were similar in concentration to those reported by Fisher and Grimm (1983) for an ephemeral desert stream, and conductivity was similar to that reported by Van Haverbeke (1990) for ephemeral rock pools. Nitrate was somewhat lower in concentration in the study pools than reported for the ephemeral stream in Arizona (Fisher and Grimm 1983). Nitrate concentrations of 4.8–6.5 $\mu\text{mol/L}$ were much lower than those measured

in summer wet precipitation from the 2 nearest National Atmospheric Deposition Program sites, Green River and Bryce Canyon, Utah. Summer volume-weighted mean nitrate concentrations at these 2 sites were 29.1 $\mu\text{mol/L}$ and 43.4 $\mu\text{mol/L}$, respectively (NADP/NTN 1996).

Sulfate concentrations in Cottonwood and Muley Tanks (21.9 $\mu\text{mol/L}$ and 27.1 $\mu\text{mol/L}$, respectively) were similar to sulfate measured in precipitation (10.7 $\mu\text{mol/L}$ at Bryce Canyon, 25.1 $\mu\text{mol/L}$ at Green River). Sulfate was

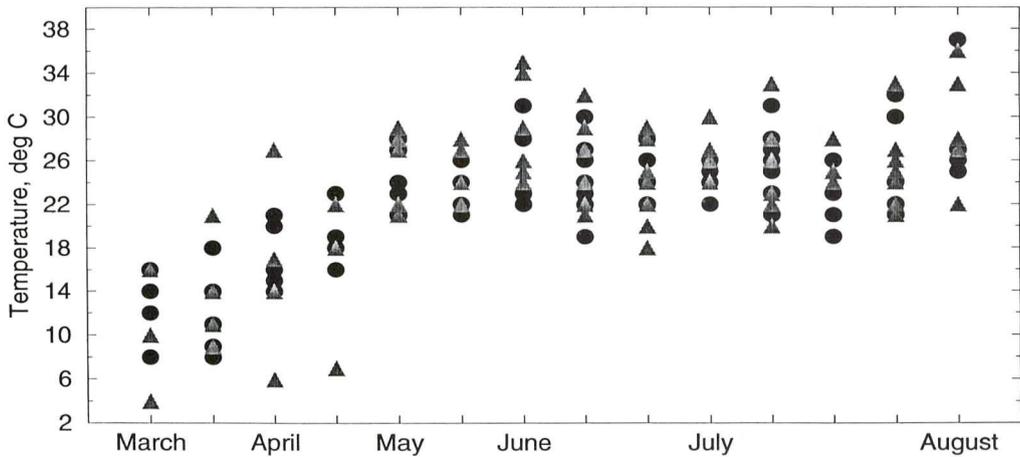


Fig. 3. Pool temperatures ($^{\circ}\text{C}$) during the study period. Circles represent temperatures of pools with vegetated wetlands; triangles are pools surrounded by bedrock.

higher in Fountain Tanks, with a mean concentration of $38.5 \mu\text{mol/L}$. Fountain Tanks is the southernmost set of pools for which we analyzed chemical composition and closest to regional industrial centers that are dominant sources of sulfur oxides in the region (Eatough et al. 1996). Although it is possible that higher sulfate values in Fountain Tanks are due to deposition, and that deposition certainly contributes to the solute load of the pools, it is more likely that a slight change in bedrock mineralogy is the source of solutes. The highest concentrations of alkalinity, Ca^{2+} , Na^{+} , Mg^{2+} , and Cl^{-} , of all pools sampled were found in Fountain Tanks, and this suggests the difference in water quality is due to different bedrock composition rather than deposition.

Fountain Tanks solutes were 2–3 times more concentrated than either Cottonwood or Muley Tanks (Table 1), except for the major plant nutrients potassium, nitrate, and phosphate. The mean pH of Fountain Tanks (7.6) was slightly higher than the pH of Cottonwood and Muley Tanks (7.0 and 7.3), and the difference was significant between Cottonwood and Fountain Tanks, but not between Fountain and Muley Tanks ($P = 0.01$). Similarly, chloride concentrations were slightly higher for Fountain Tanks, but significantly different only between Fountain and Cottonwood Tanks ($P = 0.03$). Ammonium was lower and less variable in Fountain Tanks than the other 2 drainages. Concentrations of all solutes in Cottonwood and Muley Tanks were not significantly different from each

other, with the exception of dissolved organic carbon (DOC). DOC was significantly higher (10.6 mg C/L), and more variable, in Muley Tanks than in either of the other 2 drainages ($P = 0.01$). Concentrations of DOC averaged 6.3 and 4.3 for Cottonwood and Fountain Tanks, respectively.

There was no discernible seasonal pattern to solute concentrations with time over the summer (Fig. 4). Alkalinity and calcium became more concentrated in vegetated pools of Fountain Tanks during the summer, but a similar pattern did not occur in the unvegetated Fountain Tank pools, nor in pools of either of the other drainages. Dissolved organic carbon at Muley Tanks reached concentrations as high as 13.2 mg C/L , possibly because a small rainstorm flushed organic material into pools from the surrounding watershed. Ammonium and nitrate concentrations were highly variable through time, ranging from below detection limits to $>80 \mu\text{eq NH}_4/\text{L}$ and $28 \mu\text{eq NO}_3/\text{L}$. There was no significant difference in concentrations within each drainage between pools surrounded by rock or vegetation. A plot of conductance versus normalized pool volume, using all pools, exhibits a negative relationship (Fig. 5). Drying accounted for only 0.29% of the change in measured conductance for the entire data set, but there was variability by drainage. In Fountain Tanks 68% of conductance variability was explained by pool drying, while 30% and 27% were explainable for Muley and Cottonwood Tanks, respectively.

TABLE 1. Mean concentrations (and standard deviations) of major ions from 3 drainages of Capitol Reef National Park, Utah. Means with the same letter are not significantly different. Solutes are reported as $\mu\text{mol/L}$ unless otherwise indicated.

Analyte	Cottonwood Tanks		Muley Tanks		Fountain Tanks	
	Mean (s)	Sig.	Mean (s)	Sig.	Mean (s)	Sig.
pH	7.0 (0.4)	A	7.3 (0.9)	A	7.6 (0.5)	B/A
Conductivity, $\mu\text{S/cm}$	52.5 (34.3)	A	62.1 (41.5)	A	114.8 (49.5)	B
Calcium	192.1 (157.2)	A	217.1 (152.2)	A	524.0 (279.4)	B
Magnesium	57.6 (41.2)	A	65.8 (49.4)	A	135.8 (61.7)	B
Sodium	17.4 (13.1)	A	17.4 (17.4)	A	34.8 (13.1)	B
Potassium	32.25 (23.0)	A	43.5 (38.4)	A	28.1 (15.3)	A
Ammonium	22.2 (33.3)	A	33.3 (44.4)	A	5.5 (11.1)	B
Chloride	16.9 (11.3)	A	19.7 (22.6)	A	31.0 (11.3)	B/A
Nitrate	4.8 (12.9)	A	4.8 (9.7)	A	6.5 (8.1)	A
Sulfate	21.9 (13.5)	A	27.1 (3.1)	A	38.5 (15.6)	B
Phosphate	below detection	A	below detection	A	below detection	A
Alkalinity	502.8 (436.0)	A	555.3 (458.4)	A	1226.8 (729.8)	B
Silica	13.3 (1.7)	A	8.3 (1.7)	A	23.3 (18.3)	B
DOC, mg C/L	6.3 (2.6)	A	10.6 (9.5)	B	4.3 (1.7)	A

Biological Characterization

In all pools sampled, 59 separate macroinvertebrate and vertebrate taxa were found (Table 2). These included fathead minnows (*Pimephales promelas* Rafinesque) in the lowest Miahana pool that terminates close to Hall's Creek, a stream in which this species is common. Anurans were represented by the spadefoot toad (*Scaphiopus intermontanus* Cope), canyon treefrog (*Hyla arenicolor* Cope), and 2 other toads, *Bufo woodhousei* Girard and *Bufo punctatus* Baird and Girard. The fairy shrimp (*Streptocephalus texanus* Packard) occurred in all pools. A snail, *Physella* sp., was observed in all drainages. The remainder of the taxa were arthropods, present in both larval and adult forms.

Larvae of the caddisfly *Limnephilus taloga* Ross were common throughout the winter and spring months, and larval activity was observed even under ice in January. The mayfly *Calibaetis pictus* (Eaton) was found as nymphs throughout spring, summer, and fall.

Aquatic beetles were well represented in all pools. The diverse assemblage included predaceous dytiscid diving beetles ranging in size from the minute *Liodessus affinis* (Say) to the larger *Dysticus* sp. Common hydrophilid water scavenger beetles included *Berosus punctatissimus* (LeConte) and *Tropisternus ellipticus* LeConte. These water scavenger beetles are

predaceous as larvae but collector-gatherers as adults (Merritt and Cummins 1996).

Water bugs, Notonectidae and Corixidae, were common throughout the year. The crawling water bug family Naucoridae was also found in late summer. The neuston complex consisted of water striders *Aquarius remigis* (Say) and *Microvelia torquata* Champion, and the whirligig beetle *Gyrinus plicifer* LeConte. Dipterans were represented by a single species of tabanid, various common chironomids, and a few mosquito species. Dragonflies and damselflies were common, including *Aeshna* spp. and *Sympetrum obtrusum* (Hagen) (Table 2).

Most species in the pools are also common in other aquatic habitats of the Colorado Plateau. Small groups of predators dominate the communities, whose species all appear to be either extremely vagile in dispersal and colonization attributes or adapted to hydrologically fluctuating habitats, such as the anurans (Figs. 6a-c). Associations changed through the sampling period, primarily due to life history phenologies. Sixty-two percent of species found in the pools were predators, and each cluster was primarily composed of species considered predaceous. Thirty-four percent of the species were herbivorous collector/gatherers and scrapers, while the remainder were collector/filter feeders.

The proportion of juveniles in rock pools decreased throughout spring and summer (Fig.

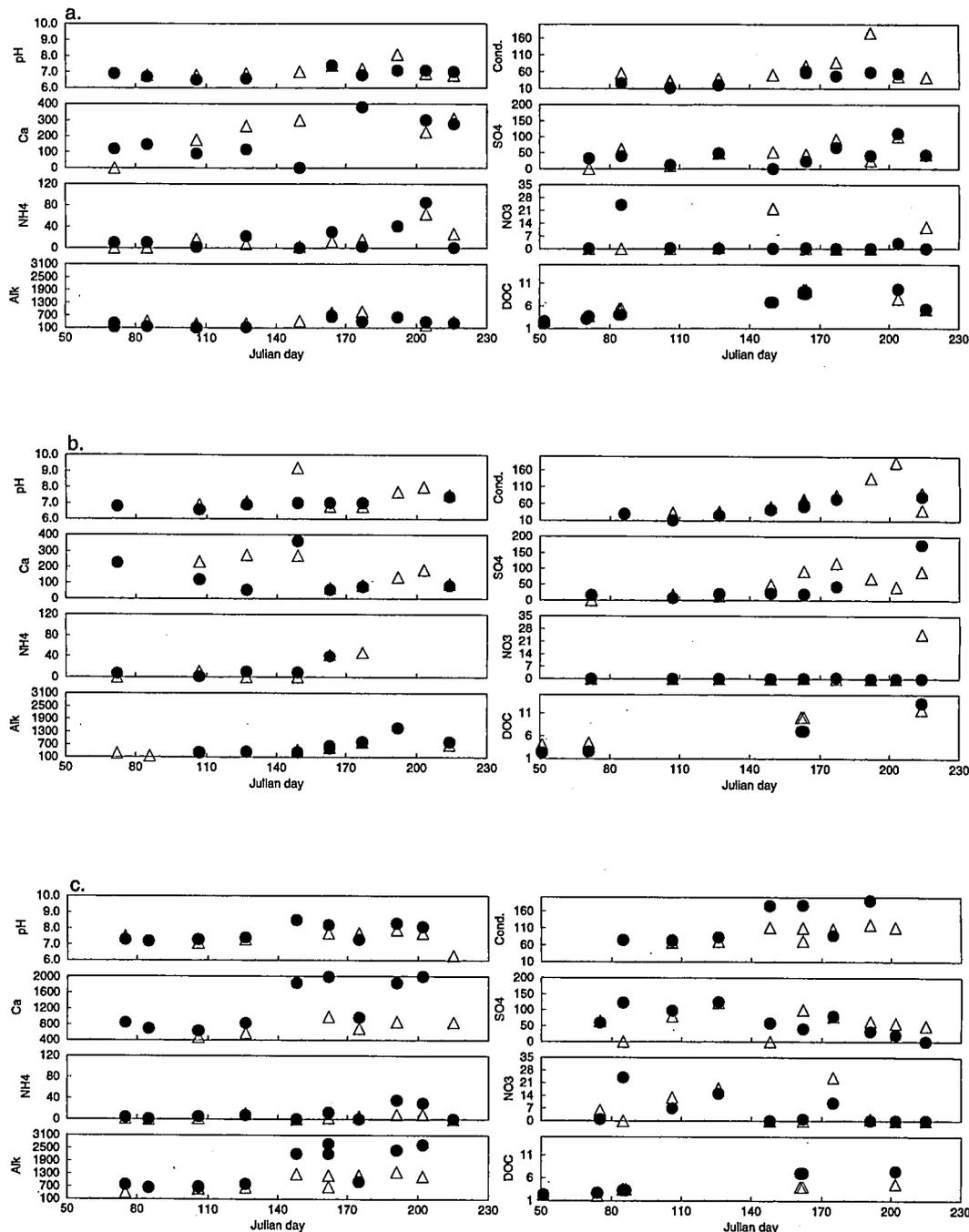


Fig. 4. Chemical dynamics of selected solutes over time in (a) Cottonwood Tanks, (b) Muley Tanks, and (c) Fountain Tanks. Solid circles represent pools with surrounding vegetation; open triangles are from unvegetated pools. Values for calcium (Ca), sulfate (SO₄), ammonium (NH₄), nitrate (NO₃), and alkalinity (Alk) are in µeq/L. Note difference in scale for Ca for Fountain Tanks. Specific conductance (Cond.) values are in µS/cm², and dissolved organic carbon (DOC) values are in mg C/L. Julian days are numbered days of year since day 1 on January 1.

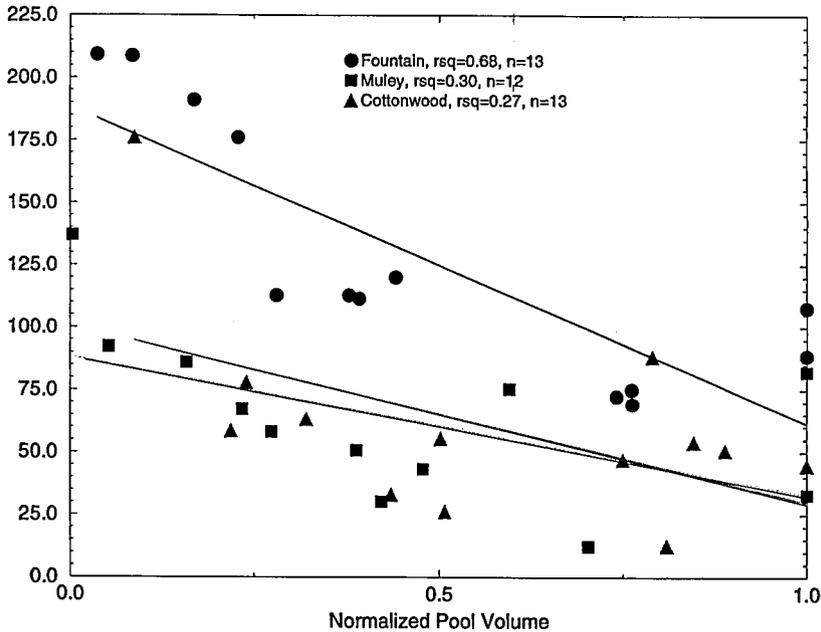


Fig. 5. Relationship of specific conductance ($\mu\text{S}/\text{cm}^2$) with normalized pool volume. Volume was normalized by dividing weekly volumes by the maximum pool volume measured during the study period.

7a), but there was no difference in the proportion of juvenile versus adult stages between pools with vegetation versus those surrounded by rock ($P = 0.586$). There were more species in pools that were components of vegetated wetlands (mean = 10.5, $s = 4.4$, $n = 116$) than pools situated in bedrock only (mean = 7.2, $s = 3.2$, $n = 116$), although numbers of species declined in both types of pools from spring through summer (Fig. 7b). Neither pool volume ($P = 0.54$) nor temperature ($P = 0.74$) affected the number of species present.

The effect of flooding on species numbers was not significant, either when comparing numbers of species within all pools before and after flood events ($P = 0.54$), or when rock-bordered pool species numbers were treated separately from those surrounded by vegetation ($P = 0.87$). Data were normalized by square root transformation. To eliminate the potential for autocorrelation, we did not use the 2 middle flooding events in Cottonwood drainage (see Fig. 2). The first and last storms were considered sufficiently separate events to satisfy conditions of independence.

A similar test was performed to examine the responses of pools to drying as a disturbance. Such disturbances were relatively infrequent

(compared with pools studied by Dodson 1987). Pre-drying numbers of species and juvenile-to-adult ratios were tested against post-drying parameters directly after the first filling event. Both variables were normalized with square root transformations. Neither was significantly different as a result of drying (species numbers, $P = 0.16$; life history stage ratio, $P = 0.49$).

DISCUSSION

Communities found before and after both flooding and drying events were very similar, suggesting that hydrologic extremes do not constitute much of a stress on community composition. Close spatial association of the rock pools and high numbers of predators in small systems buffered variations in the community structure expected to result from physical disturbance or competition (McLachlan 1985, Schneider and Frost 1996). Summer storms affected only a few drainages at a time, and only a few study pools of significant volume dried completely during the hot, dry summer. This suggests that only a portion of the Water-pocket Fold aquatic community is ever displaced at a time, leaving undisturbed areas as a

TABLE 2. Species list of macroinvertebrate and vertebrate rock pool species collected 11 September 1993 to 23 September 1994, and 25 October 1995 in Capitol Reef National Park, Utah.

VERTEBRATA
CYPRINIDAE

Pimephales promelas Rafinesque

Anura

Scaphiopus intermontanus (Cope)
Bufo punctatus Baird and Girard
Bufo woodhousei Girard
Hyla arenicolor Cope

GASTROPODA

Physella sp.

NEMATOMORPHA
ARTHROPODA
Class Anostraca

Streptocephalus texanus Packard

Class Conchostraca

Eulimnidia texana Packard

Class Nostostraca

Triops longicaudatus (LeConte)

Class Arachnida
Hydrachnida
Class Hexapoda
Collembola
ISOTOMIDAE
Ephemeroptera
BAETIDAE

Callibaetis pictus (Eaton)

Odonata
AESHNIDAE

Aeshna multicolor Hagen
Aeshna palmata Hagen
Anax junius (Drury)

LIBELLULIDAE

Sympetrum obtrusum (Hagen)
Libellula saturata (Uhler)

LESTIDAE

Archilestes grandis (Rambur)

COENAGRIONIDAE

Enallagma cyathigerum (Charpentier)
Argia sp.

Hemiptera
NOTONECTIDAE

Notonecta kirbyi Hungerford
Notonecta undulata Say
Buena margaritacea Torre-Bueno

NAUCORIDAE

Ambrysus mormon mormon Montandon

GERRIDAE

Aquarius remigis (Say)

VELIIDAE

Microvelia torquata Champion

CORIXIDAE

Graptocorixa abdominalis (Say)

BELOSTOMATIDAE

Lethocerus americanus (Leidy)

Trichoptera
LIMNEPHILIDAE

Limnephilus taloga Ross

Coleoptera
GYRINIDAE

Gyrinus plicifer LeConte

HYDROPHILIDAE

Hydrophilus triangularis Say
Tropisternus ellipticus (LeConte)
Hydrochara lineata (LeConte)
Berosus punctatissimus LeConte
Laccobius sp.

DYTISCIDAE

Agabus disintegratus (Crotch)
Agabus lugens LeConte
Agabus tristis Aube
Agabus semivittatus LeConte
Rhantus gutticollis (Say)
Laccophilus maculosus decipiens LeConte
Stictotarsus striatellus (LeConte)
Liodes affinis (Say)
Neoclypeodytes discretus (Sharp)
Hygrotus collatus (Fall)
Thermonectus marmoratus marmoratus
 (Hope)
Uvarus subtilis (LeConte)
Dytiscus sp.

HALIPLIDAE

Peltodytes callosus (LeConte)

Diptera
TABANIDAE

Tabanus sp.

CHIRONOMIDAE

Chironomus sp.
Polypedilum sp.
Phaenopsectra dyari (Townes)
Phaenopsectra sp.
Micropsectra sp.
Alotanypus sp.

CERATOPOGONIDAE

Bezzia sp.

CULICIDAE

Anopheles franciscanus McCracken
Culex tarsalis Coquillett
Culiseta inornata (Williston)
Culiseta sp.

source of recovery. Many of the species we found were well adapted for rapid recolonization of pools after disturbance, having highly mobile adult stages, terrestrial adult mating and dispersal stages, or animal- or wind-dispersed eggs. Recolonization can also come from survivors or eggs laid prior to disturbance (Cushing and Gaines 1989). Pools that were

components of vegetated wetlands supported greater numbers of species throughout the year, but none of these species occurred only in pools with vegetated wetlands. The lack of distinct species associations in the cluster analysis implies that all species occupied a similar ecological niche, which is likely the result of close ecological association, and proximity and

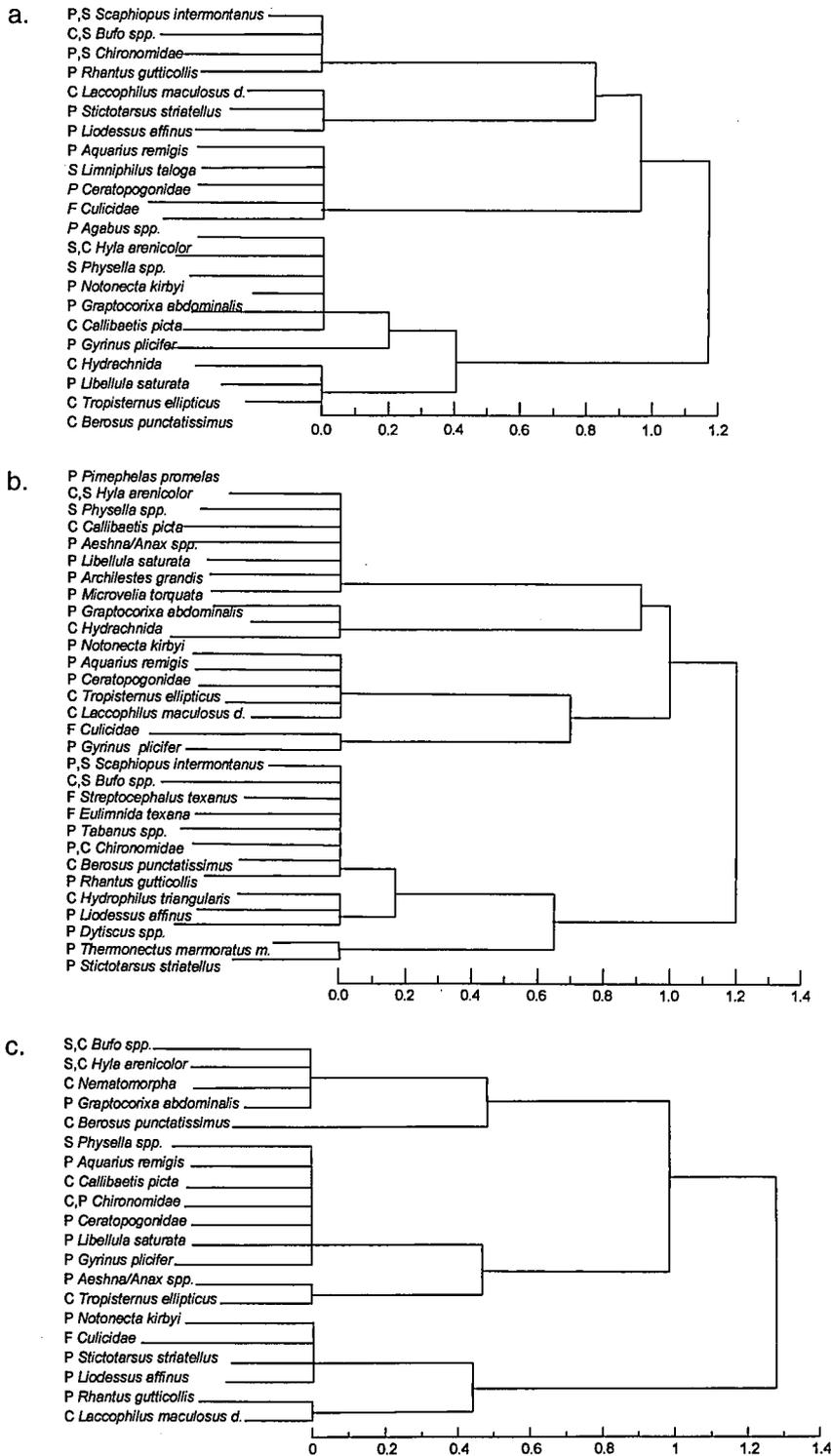


Fig. 6. Average linkage cluster analysis for aquatic species collected on (a) 15 March 1994, (b) 10 June 1994, and (c) 29 July 1994. Clusters are expressed as normalized root mean square distances. Species are annotated with functional feeding group after Merritt and Cummins 1996 as follows: P, predator; S, scraper; C, collector/gatherer; and F, filter feeder.

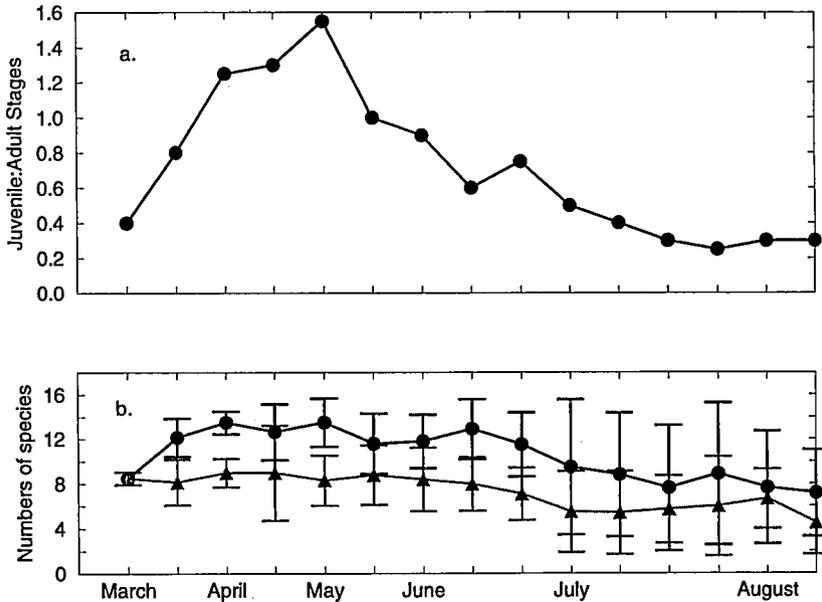


Fig. 7. Characteristics of aquatic organisms in Capitol Reef rock pools over time: (a) average ratio of juvenile to adult stages, and (b) species numbers. Circles are numbers in pools with vegetation, and triangles are numbers in pools surrounded by bedrock.

similarity of the rock pools. The alternative, which was not observed, would have shown persistent and distinct clusters of species.

The rapidity of recovery suggests these systems display great resilience, a conclusion also reached in a study of macroinvertebrate recovery after flash floods in Sycamore Creek, Arizona (Grimm and Fisher 1989). Flood events can introduce nutrients and detritus from precipitation and upstream as they wash debris and salts from upstream contributing areas (Creed et al. 1996). Grimm and Fisher (1989) hypothesize flood events are necessary to the maintenance of macroinvertebrate populations because they refresh the food supply for fast-growing organisms.

There was a chemical response to drying and flooding in the pools, although the strength of the response varied by solute and pool. It appears that nutrients and DOC increased after flood events, but salts became more concentrated with drying. Some chemical constituents, such as alkalinity, increased by an order of magnitude during the study period (concurrent with declining pool volume) but rapidly decreased after a rain event (Fig. 4). Pool chemistry was very dilute and was not significantly

influenced by the presence or absence of vegetated wetlands.

In summary, rock pools of Capitol Reef National Park are populated with a fauna well adapted to survival in an environment of hydrologic extremes. The dilute chemical concentrations we measured did not vary broadly enough to pose a salinity problem for aquatic organisms. The ability of communities to recover after floods and droughts is consistent with a hypothesis posed by Hynes (1970) and results found by others (summarized by Cushing and Gaines 1989), that streams with flashy hydrology should have less abundant and less varied fauna than others. Cushing and Gaines (1989) developed a classification scheme for colonization and recolonization characteristics of different stream types. Capitol Reef rock pools fit well under the classification for exorheic cold desert streams in that the many small streams of the Waterpocket Fold provide colonization sources for each other. The diversity of stream and drainage habitats offers many pathways for faunal recovery, including downstream drift, upstream migration, both surface and hyporheic refugia in wetlands surrounding some pools, as well as adult and egg survivors of disturbances.

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