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Seasonal variation and diurnal fluctuations in ephemeral desert pools

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Abstract

The physical variables which directly affect organisms inhabiting desert ephemeral pools were examined in four pools in southeastern Utah. During the day, pools were hyperoxic (240 torr) and hypocapnic (0.07 torr) while pH and temperature increased (7.5–9.0 & 17-35 °C respectively). Conversely, predawn pool measurements were hypoxic (40 torr) and hypercapnic (3 torr). While TA increased throughout the season (from 0.4 to 1.43 meq l^{-1}), due largely to increased bicarbonate concentration (from 0.5 to 1.4 mmol l^{-1}), water osmolarity remained relatively constant. These desert ephemeral systems represent unique environmental habitats where organisms experience both diurnal and seasonal changes in numerous physical variables over short time frames.

Introduction

Organisms inhabiting small water volumes face extremely variable environmental conditions. These habitats are greatly influenced by both environmental and life processes. When both plant and animal populations are present, photosynthetic and metabolic processes can cause large diurnal oscillations in oxygen and carbon dioxide, due partly to the low diffusive coefficients from water to air. Truchot and Duhamel-Jouve (1980) measured increases in oxygen to over 400 torr during the day and up to 3 torr increases in carbon dioxide during the night for intertidal rock pools. In addition, small bodies of water may undergo large and rapid fluctuations in temperature and increases in osmotic variables dependent on pool size and climactic conditions (see Williams 1985 for a review).

Williams (1985) pointed out that in spite of the relative ubiquity of temporary waters, little is known about the functional dynamics of these systems. This seems especially true for desert ephemeral pools where rapid changes, both diurnally and seasonally (from initial pool filling to final evaporation), may be important. For example, few studies have examined carbon dioxide fluctuations in ephemeral systems. Numerous workers have examined changes in pH but only one study (Truchot & Duhamel-Jouve, 1980) reported diurnal fluctuations in carbon dioxide for intertidal rock pools. Diurnal and seasonal changes in carbon dioxide in other ephemeral waters, especially freshwater systems in arid regions which typically have low buffer properties, are still largely unknown.

Desert ephemeral pools, such as those found in southwestern North America, fill during the summer months and last for only short periods due to high rates of evaporation (Horne, 1967). These pools often contain large numbers of organisms (Horne, 1971). Dodson (1987) found 23 taxa of macroinvertebrates and amphibians in 50 desert pools in Utah between July and October. These organisms must be able to tolerate desiccation and/or utilize rapid growth strategies to allow for completion of reproduction or metamorphosis before pool water disappears (Wiggins *et al.*, 1980). Thus, desert ephemeral pools represent a unique situation where organisms must develop and reproduce in compressed time frames while experiencing large and rapid diurnal fluctuations in numerous physical variables.

The present work aims to describe both the diurnal and seasonal changes of oxygen, carbon dioxide, temperature and osmotic concentrations in desert freshwater ephemeral pools in south-eastern Utah. These variables were chosen based on their critical effects on numerous physiological processes of the organisms inhabiting these environments.

Materials and methods

Four desert ephemeral pools near Moab Utah were studied during the period from July to August. Initial pool filling occurred on July 12 with a second filling event on July 25, day 12 of the study (Table 1). Pools were located in depressions on the tops of sandstone formations. Thus, pool linings were essentially sandstone with about 2–4 cm layer of sediment covering the bottom. Pools were chosen based on their relative isolation from human disturbance and on the abundance of macroinvertebrates.

Sampling

Measurements were made from initial pool filling to final evaporation. Daily sampling and measurements started before sunrise and continued through the day until one hour after sunset to determine maximum and minimum values of variables that are dependent on sun angle. Titration alkalinity was only determined on three pools and only on one pool for every sampling period due to limited amount of time and number of replicates needed for accurate readings. Maximum pool depth and surface area were recorded for each pool throughout the season. Two milliliter water samples were sealed in glass vials and stored frozen until they could be transported back to the laboratory for measurements of osmotic pressure. Titration alkalinity was determined from 10 ml water samples directly after sampling.

Measurements

pH was measured using a portable pH/ISE meter (290A, Orion Research, Boston, MA, USA) with a Ag/AgCl triode pH electrode (91-57BN, Orion) The instrument was calibrated daily with three precision buffers and measurements made while continuously stirring the sample. Oxygen tension was measured using a portable oxygen meter with a dissolved oxygen probe (840, Orion) calibrated daily. The probe was continually moved at about 15 cm s^{-1} to assure flow across the membrane for accurate readings. Titration alkalinity (TA) was determined by Gran titration as described by Mackereth *et al.* (1987). 0.02N certified sulfuric acid solution (Fisher #SA218-1) was titrated from a micro-buret into a 15 ml narrow neck sampling bottle while continuously stirring the sample with a portable magnetic stirrer. Osmotic pressures were determined using a vapor pressure osmometer (5500, Wescor, Logan, Utah, USA) on frozen subsamples.

Water P_{CO_2}, concentrations of bicarbonate (HCO_3^-) and total CO_2 (C_{CO_2}) were calculated indirectly from pH and TA as described by Truchot & Duhamel-Jouve (1980) and Mackereth *et al.* (1989). From pH and TA values, CO_2 quantities were calculated from dissociation constants pK_1, PK_2 and the ionization of water expressed as pK_w. Values for dissociation constants applicable for dilute solutions were taken from Mackereth *et al.* (1989).

Pool volumes were calculated by fitting shape of pool bottoms to a parabolic curve based on maximum pool depths and radius, and then integrating for change in depth. Pool radii were determined by averaging three measurements of diameter. Volume calculations probably underestimate actual pool volumes due to the small amount of sediment covering pool bottom and irregularities in sandstone depressions.

Statistics

Values presented are means ± S.E.M. unless otherwise noted. Changes in pool volume are based on least square regression analysis where r^2's were greater than 0.89.

Results

Changes in pool volumes for the four pools are shown in Fig. 1. Rates of water loss for the four pools studied, based on least square regression analysis, are shown in Table 1. While inflow into these systems during filling events is due mainly to run-off, outflow may result from evaporation and possibly leeching and leaking from cracks in the sandstone. Calculations of rates of evaporation in this circumstance are inaccurate due to large and rapid changes in wind and temperature. Therefore, change in volume was used to indicate differences in water loss between pools and was not partitioned into evaporation and ground water effects.

Diurnal fluctuations

Average diurnal fluctuations during days 21 and 22, approximately halfway through field season, for the four pools are presented in Fig. 2. Temperature, pH

Table 1. Maximum and minimum values for four desert ephemeral pools

	Pool #1	Pool #2	Pool #3	Pool #4
Initial filling				
07-12 to 07-23				
Max. Depth (cm)	15.2	14.1	17.8	14.0
Max. Radius (cm)	244	130	149	148
Temp. (°C)	16.6–34.3	16.2–34.6	16.3–34.6	16.1–34.7
pH	6.69–9.21	7.09–9.35	7.02–9.16	7.15–9.60
Oxygen (torr)	50–229	45–235	49–234	30–244
Change in Volume (m^3/day)	0.069	0.020	0.037	0.033
Second filling				
07-25 to 08-18				
Max. Depth (cm)	35.5	24.5	35.5	22.9
Max. Radius (cm)	274	141	164	152
Temp. (°C)	15.9–33.4	16.0–33.1	16.3–31.8	16.2–33.6
pH	6.78–8.99	6.76–8.95	6.70–9.15	6.76–9.14
Oxygen (torr)	63–234	26–252	52–238	37–245
Change in Volume (m^3/day)	0.069	0.022	0.023	0.034

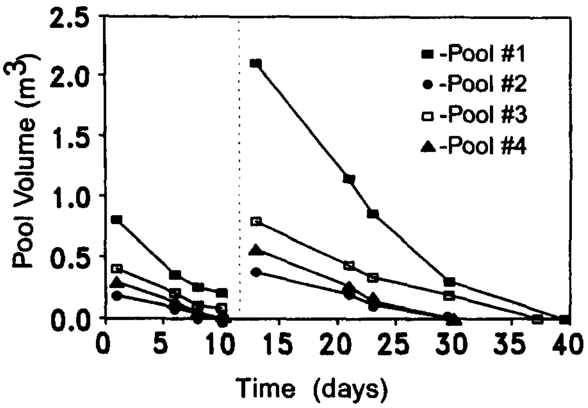

Fig. 1. Daily changes in pool volume (m^3) for the four study pools. The dashed line represents a second filling event which occurred at day 12 of the study period.

and oxygen all increased from sunrise to approximately 16:00 hrs, when pools no longer received direct sunlight (Fig. 2). P_{co2} decreased during the same period and then increased during the night, to maximum recorded predawn values. Measurements during the night were not made.

Titration alkalinity remained constant throughout the day and increased slightly during the night (Fig. 2). Truchot and Duhamel-Jouve (1980) also reported increases in TA during the night for rock pools, which they attributed to CO_2 accumulation, but they also reported consistent decreases in TA during the day.

Seasonal fluctuations

The range of measured values for temperature, pH and oxygen are presented in Table 1. Although the pools differed in size, there was very little variation in extreme values between pools.

Pool osmolarity was constant during the study period (Fig. 3). Overall, changes in osmotic pressure for the four pools averaged less than 10 mOsmol. This corresponds to previous suggestions that evaporation would not significantly increase total salt content of freshwater ephemeral pools due to low initial salt concentrations (Horne, 1967; Williams, 1985). Therefore, large fluctuations in salinity do not appear to be an important component in these systems.

In contrast, TA continually increased as pool volume decreased (Fig. 3). Concentrations of bicarbonate and total C_{o2}, calculated from TA for pool #1 (Fig. 4), also increased throughout the season. However, the increases in bicarbonate, less than 1.5 mmol l^{-1}, were not detectable from osmotic measurements. Other workers have reported seasonal increases in conductiv-

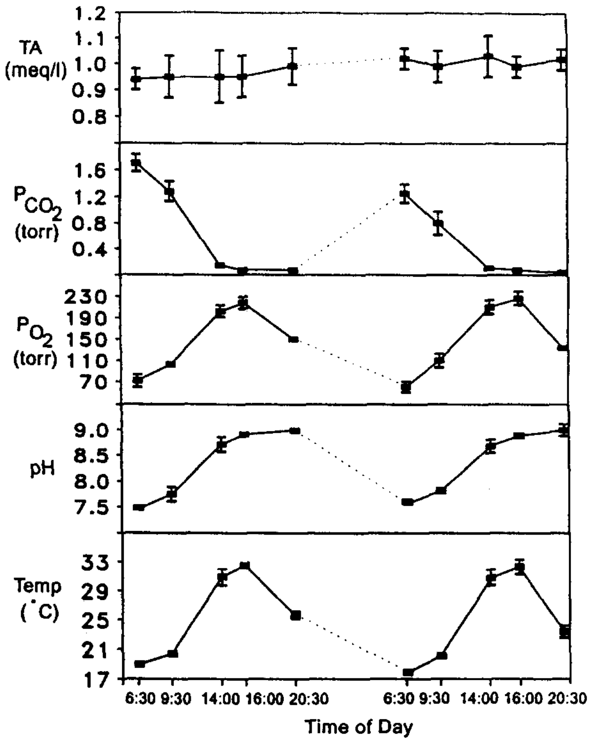

Fig. 2. Diurnal fluctuations of titration alkalinity (TA), carbon dioxide partial pressure (P_{co2}), oxygen partial pressure (P_{o2}), pH, and temperature (Temp) for a 38 hr period for the four study pools. Values are for days 21 and 22, approximately halfway through the second filling period. Values presented are means ± S.E.M.

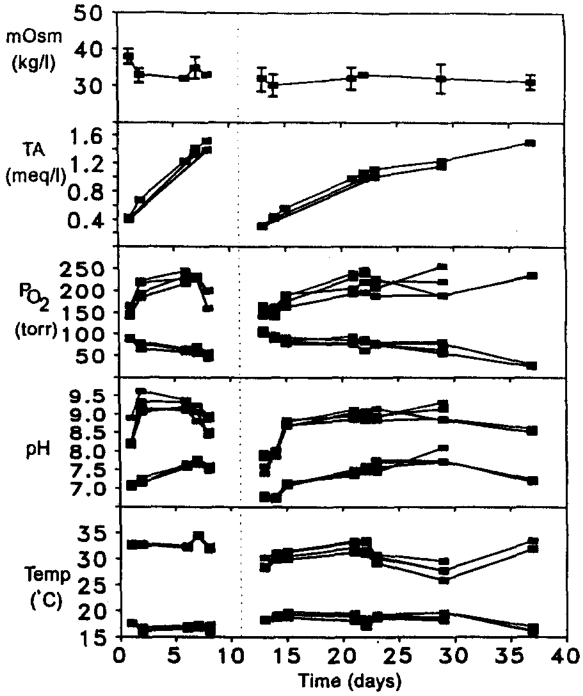

Fig. 3. Daily minimum and maximum values for oxygen partial pressure (P_{o2}), pH, and temperature (Temp) for the study season, data was pooled for the four study pools. Pool osmolality (mOsm) was sampled only once per day and are presented as means ± S.E.M for the four pools. Titration alkalinity (TA) did not vary throughout the day and is therefore presented for 9:30 readings only. Dashed line represents a second filling event which occurred at day 12 of the study period.

ity in freshwater ephemeral pools in Africa (Hamer & Appleton, 1991).

Pre-dawn hypercapnia did not increase during the season (Fig. 4) for pool #1. This was somewhat unexpected considering the large decrease in volume and probable increases in pool biomass.

Discussion

While this study did not specifically address population dynamics, several pertinent observations on the biota were noted. No vascular plants were observed in any of the study pools. Thus, algae (majority of which appeared to be filamentous) and phytoplankton appeared to be solely responsible for photosynthetic production of oxygen while numerous macroinvertebrates and amphibian tadpoles, in addition to the photosynthetic organisms, contributed to oxygen consumption and CO_2 production. Between 20 and 50 *Bufo punctatus*, Baird & Girard (red spotted toad) tadpoles were observed in each of the four study pools. While

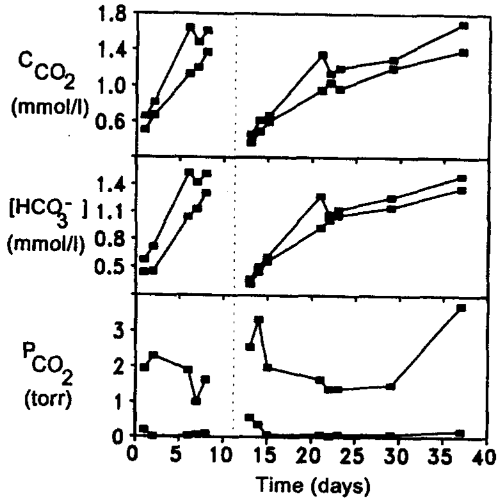

Fig. 4. Daily minimum and maximum values for total carbon dioxide (C_{co2}) concentration of bicarbonate (HCO_3^-), and partial pressure of carbon dioxide (P_{co2}) for the study season for pool #1. Dashed line represents a second filling event which occurred at day 12 of the study period.

hatching occurred within 24 hrs of initial pool filling, none of the tadpoles completed metamorphosis before the end of the season. Why larval development rates do not correspond to permanency of these pools, as Zweifel (1968) reported for this species, is unclear. *Triops longicaudatus*, LeConte (tadpole shrimp) appeared to be the top predator in the pools: they were the largest organisms inhabiting the study pools (over 2 grams wet weight by the end of the season), although they were present in relatively low numbers (less than 30 per study pool). *T. longicaudatus* preyed, or attempted to prey, on almost all pool inhabitants (see Dodson 1987 for complete list of animal assemblages for pools of the area).

The desert ephemeral pools examined in this study have diurnal cycles that are similar to those reported for other temporary freshwater systems (see Williams, 1985; Dejours, 1975 for reviews). However, the hyperoxic and hypocapnic conditions measured during the day and the hypoxic and hypercapnic states during the night were not as severe as those reported for intertidal rockpools by Truchot and Duhamel-Jouve (1980).

The large surface areas, compared to water volumes (Table 1), and the rapid changes in volume recorded for the study pools appear to be important in limiting fluctuations in oxygen and carbon dioxide. A large surface area to water volume relationship should significantly enhance diffusion across the water air interface. This effect will be especially important when gas tension gradients between air and water are large. Similarly, decreases in pool volume should further increase surface area to volume differences and thus enhances diffusion later in the season. This surface area effect may be especially important to inhabitants of these environments by suppressing hypoxia and hypercapnia extremes during warm summer nights when metabolic rates are high. Another physical factor which may also be important in limiting oxygen extremes is the exponential change in gas solubility coefficients with changes in temperature.

Rapid changes in pool volumes (as high as 100% in 8 days) corresponded to relatively large changes in alkalinity (as high as 0.13 meq d^{-1}) while osmotic pressures remain constant (Figs 1 and 2). Increases in alkalinity in lakes is thought to be due to photosynthesis along with a number of biogeochemical reactions (Lerman & Stumm, 1989). In soft-water lakes increases in alkalinity are typically small (21–38 ueq l^{-1} yr; Psenner, 1988). Most of this increase is thought to be due to release of calcium and magnesium from sediments coupled with the reduction of sulfate, nitrate and iron (Adamec and Ondok, 1992; Psenner, 1988). Increases in alkalinity due to evaporation in lakes is generally assumed to be minimal due to the large water volume and effects of inflows or catchments (Psenner, 1988). The present work suggests that a very different situation occurs in desert ephemeral pools.

Data from the National Parks Service for desert ephemeral pools in South Eastern Utah for 1988–89, including the pools used in this study, show that the major ion constituents are Ca^{2+}, SO_4^{2-} and Fe^{2+}, 13.0, 11.4 and 1.76 mg l^{-1} respectively (unpublished means from National Parks Service Gran County 1988–1989). One hypothesis to describe changes in TA is that both large rates of photosynthesis combined with reduction of iron, sulfate and calcium from sediment and sandstone surfaces, may allow for the build up of total carbon dioxide, largely in the form of bicarbonate (Fig. 4). While this hypothesis was not directly tested, the end result is that pool buffer capacity increases throughout the season without changing osmotic variables.

Seasonal changes in oxygen levels (Fig. 3) probably result from both decreases in pool volume and increases in phytoplankton and algal biomass. Since photosynthesis and respiration are driving changes in pH, it is interesting that seasonal changes in oxygen did not coincide with changes in pH (Fig. 3). This may be a direct consequence of the increased bicarbonate recorded throughout the season. The daily changes in P_{co2} (about 3 torr) are small compared to the seasonal increases in total C_{o2} (greater than 1 mmol l^{-1}), the majority of which is bicarbonate (approximately 80%, Fig. 4).

The effect of seasonal and diurnal fluctuations on organisms inhabiting desert freshwater systems is still unknown. While many authors have suggested different adaptations to temporary water habitats (see Williams, 1985 for a review), the physiological effects have been largely ignored. Truchot (1986) found that fluctuations in oxygen and carbon dioxide in intertidal rock pools had opposing affects on the acid-base status of the shore crab *Carcinus maenas*. Other workers (De jours *et al.*, 1985) similarly showed that simultaneous changes in temperature and oxygen do not affect acid-base balance in *C. maenas*. Surprisingly, changes in acid-base status have been reported for crayfish from freshwater environments (Dejours & Armand, 1983) when simultaneous changes in temperature and oxygen were examined. Thus, it appears that there may be very different responses to multiple environmental fluctuations between freshwater and saline habitats. It has been suggested that differences in chloride concentration, which can greatly influence acid-base regulation in crustaceans (Wood & Rogan, 1986), may explain this discrepancy. Therefore, one would expect large disruptions in acid-base balance and other physiological processes resulting from the numerous environmental fluctuations reported in this study.

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