PROCEEDINGS OF THE 16th SYMPOSIUM ON THE GEOLOGY OF THE BAHAMAS AND OTHER CARBONATE REGIONS

Edited by
Bosiljka Glumac and Michael Savarese

Gerace Research Centre
San Salvador, Bahamas

2016

Cover photo: San Salvador coastline photo by Erin Rothfus.

Press: A & A Printing

ISBN 978-0-935909-15-9

PALEOSALINITY RECORDS FROM THREE LAKES ON SAN SALVADOR ISLAND, BAHAMAS INFERRED FROM PRESERVED OSTRACODE ASSEMBLAGES

Andrew V. Michelson[a,b,*] and Lisa E. Park Boush[a,c]

[a] Department of Geology and Environmental Science, University of Akron, Akron, Ohio 44325-4101
[b] Present address: Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois 60637
[c] Present address: Center for Integrative Geosciences, University of Connecticut, Storrs, Connecticut 06269-1045

ABSTRACT. Quantitative records of past environments are needed to understand natural variability in ecosystems and their responses to climate change. Changing ostracode assemblages through time can produce such records since ostracode species are often sensitive to changes in their local environments. Before they can be used to indicate past environments, it is necessary to understand how distributions of assemblages change across the modern landscape. Thirty-two lakes on San Salvador Island, Bahamas were sampled for ostracodes and nineteen physio-chemical variables that may influence their distribution. Multivariate fuzzy set ordination indicated that change in ostracode assemblages was significantly and independently correlated with: electrical conductivity, dissolved oxygen, and alkalinity. A transfer function was then created to reconstruct past conductivity since changing conductivity of lakes on San Salvador has been linked to changes in climate and sea-level fluctuations. A 2-component weighted-averaging partial least squares model performed best as a transfer function for conductivity with an apparent r^2 of 0.76 and an r^2 of 0.69 between observed and predicted conductivity, as assessed by leave-one-out cross validation. The resulting transfer function was then applied to three San Salvador Island sediment cores from which ostracode paleoassemblages were sampled. The late Holocene paleoconductivity records show that changes in conductivity of lakes on San Salvador are broadly synchronous and that lakes respond to regional climate changes. In particular, variation in the strength of El Niño corresponds to changes in conductivity with times of strong El Niño events recorded as arid periods and times without strong El Niño events recorded as more humid periods. These results demonstrate that changing ostracode assemblages through time provide a reliable means to reconstruct past conductivity of lakes on San Salvador Island and that variation in the strength of El Niño events influences the aridity of the climate in the Bahamas.

[*]Corresponding author. E-mail: andymichelson@uchicago.edu

INTRODUCTION

Sediments from coastal lakes are important archives of local and regional environmental changes. Many of these lakes sit at the interface between the terrestrial and marine environments and can record sea-level changes and changes in the aridity of the local and regional climate (Teeter, 1995; Peros et al., 2007). Thus, records from these lakes can provide background information on natural environmental variability (Dietl and Flessa, 2011), insight into how global or regional climate changes affect local ecosystems (Edlund and Stoermer, 2000), and critical information that can help archaeologists interpret records of past human habitation (Berman and Gnivecki, 1995).

There are few such records of late Quaternary changes in sea-level and climate from the Caribbean because of the paucity of sites for paleolimnological investigation (Higuera-Gundy et al., 1999). Yet, this region is critically important for controlling climate since changing patterns of aridity control the strength of the North Atlantic Deep Water formation (NADW), greatly affecting the climate of the North Atlantic and the globe (Schmidt et al., 2004). This study provides paleolimnological records from three coastal lakes on San Salvador Island, Bahamas using changing ostracode assemblages through the mid-late Holocene.

Microfossil assemblages are important archives which can yield information on changes in ecosystems over long time scales. Organism-based calibration datasets, coupled with precise age control, have the potential to produce detailed, high-resolution records of past environments. Transfer functions based on these calibration datasets can provide high-resolution, quantitative records of past environments (Saros, 2009; Sayer et al., 2010). Transfer functions are regression models in which preserved assemblages of microfossils are used to predict one environmental variable of interest (Saros, 2009). They proceed by understanding the nature and strength of the association between modern assemblages and the abiotic environment. If a correlation of sufficient strength and paleolimnological interest is found, then a model can be created to predict that variable from preserved assemblages (Mischke et al., 2007). These models have the potential to be of significant use to environmental managers or policy makers. For instance, Mischke et al. (2010a) produced quantitative records of conductivity from individual lakes in the Middle East that can be related to changing precipitation/evaporation regimes in the past and can thus aid in evaluating the historical risk of water shortages at fine temporal and spatial scales.

This study utilizes Ostracoda (Phylum Arthropoda) from lakes and blue holes on San Salvador Island, Bahamas to produce quantitative records of past conductivity. Electrical conductivity measures the ability of water in these lakes to conduct electrical current. Because this is determined by the presence of ions dissolved in the lake water, salinity and electrical conductivity in these lakes measure the same variable and thus are perfectly correlated. Ostracodes are a class of bivalved microcrustaceans that live in all manner of aquatic habitats from the deep ocean to ephemeral ponds (Horne et al., 2002). Most non-marine species live as benthic organisms and are sensitive to changes in the abiotic environment such as salinity, water depth, temperature, or dissolved oxygen concentration (Frenzel and Boomer, 2005). Their low-Mg calcite shells commonly range from 0.5-2mm in size, can be preserved as fossils, and long have been used as biological proxies for environmental variables, especially salinity (Frenzel and Boomer, 2005). Each individual secretes 8-9 molted shells over its lifetime with the adult stage containing definitive characteristics that typically allow for species-level identification (Holmes, 2008). These organisms have already been used in transfer functions in lake sediments to reconstruct conductivity (Mezquita et al., 2005; Mischke et al., 2007; Mischke et al., 2010a), water depth (Mourguiart and Carbonel, 1994; Mourguiart et al., 1998; Alin and Cohen, 2003; Mischke et al., 2010b), and temperature (Mezquita et al., 2005; Viehberg, 2006).

San Salvador is a small (163 km^2) carbonate island with many interior lakes located within the Bahamian archipelago in the northern hemisphere-southwest Atlantic (Davis and Johnson, 1989). During times of elevated sea-level throughout the Pleistocene, dune sediments were deposited across the San Salvador platform. Many lakes occur on the island today between these ancient dunes, as cutoff-lagoons once open to the ocean, or as karst dissolution features in the carbonate bedrock (Bain, 1991; Teeter, 1995; Park and Trubee, 2008). The salinities of these lakes are controlled by basin geomorphology, degree of connection to the ocean, precipitation-evaporation balance, and climate (Teeter, 1995; Park et al., 2009). Lake sediments on the island are capable of preserving paleocommunities of ostracodes in sufficient abundance to be used in a transfer function (Teeter, 1995; Park et al., 2009).

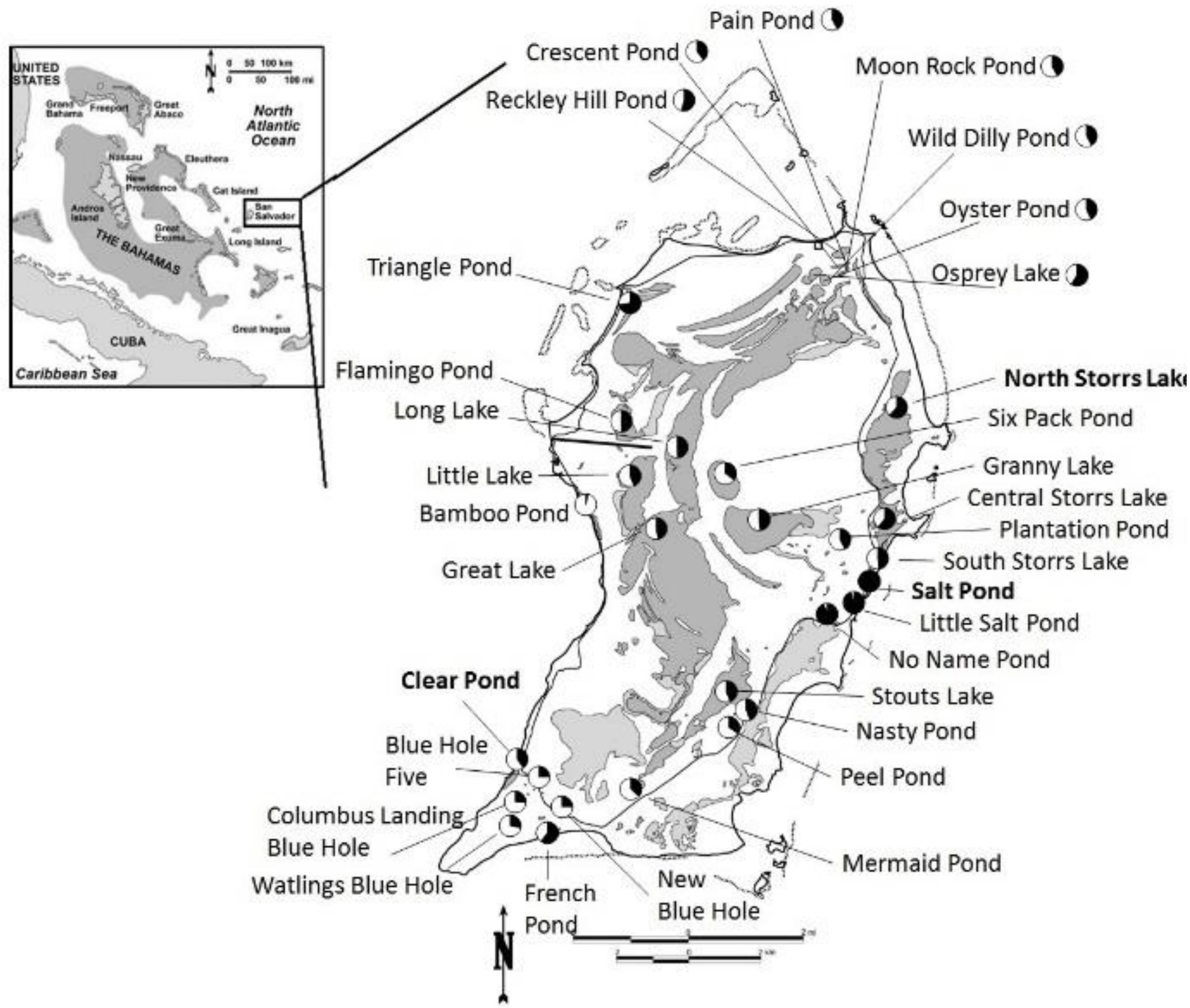

*Figure 1. San Salvador Island, Bahamas. Each pie chart indicates a lake sampled for ostracode assemblages and environmental variables, pie charts represent electrical conductivity, scaled according to the highest conductivity sample, Salt Pond (electrical conductivity: 124.7 mS/cm). Pie charts labeled in **bold** were also cored for sedimentary archives.*

The Bahamas receive airborne dust from North Africa which forms the major sources of aluminosilicates on the islands (Muhs et al., 1990; Foos, 1990). Strong El Niño events cause more of this African dust to be deposited across the Bahamas (Prospero and Lamb, 2003; Evan et al., 2006). These strong El Niño events are also associated with less tropical cyclone activity in the Atlantic since high wind shear in the tropical Atlantic acts to disrupt cyclone formation (Gray, 1984). Hurricanes hitting San Salvador lower the salinity of lakes on the island through input of freshwater in rainfall (Park et al., 2009). Therefore, we hypothesize that times of strong El Niño events, indicated by increased African dust deposition, would raise the salinity of lakes on San Salvador through less hurricane activity.

METHODS

Field and Laboratory Methods

In June 2008, March 2009, and June 2009 we collected surface sediment, water samples, and measured field limnological data from 32 lakes on

San Salvador Island (Figure 1). We sampled as many accessible lakes as possible and chose a location to sample in lakes randomly. Surface sediments were collected by sweeping a net with attached jar across the sediment-water interface, recovering the upper 1-2 cm of sediment. All samples were collected within the littoral margin, approximately 10 m from the shore. In a separate study, live/dead collections were made along two transects extending 19 m into each lake. Except for one lake, Watling's Blue Hole, live/dead agreement in rank-abundance and taxonomic composition was extremely high (Michelson and Park, 2013). Likewise, little or no variability was found along transects in these lakes (Michelson and Park, 2013). Thus, the one ostracode death assemblage per lake we used in this study was determined to represent "modern" assemblages, typical of the lakes from which they were sampled.

Five lake environmental variables were measured in the field with an YSI 556 field meter, including conductivity (± 0.5%), salinity (± 1%), total dissolved solids (± 4 g/L), dissolved oxygen (± 2%), and water temperature (± 0.15°C). Alkalinity was determined in the field using a Hach methyl orange and phenolphthalein (total) acidity digital titration kit (± 0.1 mg/L as $CaCO_3$). Water depth at each site was measured to the nearest cm. Latitude and longitude as well as lake area were determined using the San Salvador GIS database (Robinson and Davis 1999) and a hand-held GPS unit.

Sediments were sieved using 125 µm (φ-size 3) and 63 µm (φ-size 4) sieves with deionized water. Upon drying, ostracodes were picked using a dissecting microscope. In all cases, at least 400 ostracodes were picked from each sample and all adults were identified to species level. All samples included in this analysis contained more juveniles than adults indicating that the assemblage accumulated where the ostracodes lived and were not transported from another location (Park et al., 2003; Mischke et al., 2007).

Water samples were analyzed for the concentration of major cations using a Perkin Elmer Analysis 700 atomic absorption (AA) spectrometer at the University of Akron. Water samples were analyzed for chloride and sulfate anions using a Dionex DX-120 ion chromatograph. All major ions concentrations were expressed as mg/L. Sediment grain size was determined with a Malvern 2000 Mastersizer at Kent State University. Sediment samples were sieved to < 1 mm before grain size distribution was determined.

Numerical Methods

Species were retained in the dataset if they were found in at least three lakes or their abundance exceeded 30% of total adult ostracodes in any one lake. All species abundances were expressed as percent of total adult ostracodes.

We conducted non-metric multidimensional scaling (NMDS) on the Bray-Curtis dissimilarity matrix as an exploratory method to understand the relationship between species and environment in the dataset. NMDS is an unconstrained ordination technique in that variation in assemblages is displayed according to biotic data only. That variation was then correlated to measured environmental variables. NMDS was done in PAST (Hammer and Harper, 2005).

We then carried out forward multidimensional fuzzy set ordination (MFSO) (Roberts, 2009) using the R package MFO (Roberts, 2008) in order to directly relate environmental variables to variation in ostracode assemblages by reducing the environmental dataset to only those variables that significantly and uniquely correlate to ostracode β-diversity. These variables then became candidate variables to model in the transfer function. NMDS displays all variation in assemblages, whereas MFSO focuses only on that variation in assemblages that can be correlated to measured environmental variables. MFSO was chosen as the preferred method for directly relating environmental variables to change in assemblages since it tests the strength and significance of each individual environmental variable in the dataset. The effect size and significance of each variable in correlating to change in assemblages was then assessed. The single variable with the highest effect size was then retained in the model. The residuals were used to test for correlation with other environmental variables. In this way, MFSO eliminates model selection problems caused by correlations among measured environmental variables. All remaining environmental variables were tested for effect size and significance. The process stopped when no other environmental variables significantly correlated to the residuals (Roberts, 2008; 2009).

Taxon optima (niche position) and tolerances (niche breath) were calculated for all taxa using Gaussian logistic regression (GLR) in R. Methods in ter Braak and Looman (1986) were used to convert the regression coefficients from GLR into estimates of taxon optima and tolerance.

The program C2 (Juggins, 2003) was also used to construct the transfer function through weighted averaging partial least squares regression (WA-PLS). Low root-mean-square-error of prediction (RMSEP), a low maximum bias (ter Braak and Juggins, 1993), and a high coefficient of determination (r^2) between observed and predicted values, estimated by leave-one-out cross-validation (Birks, 1995), as well as the smallest number of 'useful' partial-least-squares components, all contributed to the selection of the minimum adequate WA-PLS model. We assessed the predictive ability of the transfer function model by the correlation between the measured and inferred conductivity and the apparent root mean squared error (RMSE) of prediction and the equivalent jackknifed values. Jackknifing is used to predict the conductivity of each sample using only the other samples in the dataset. It proceeds by leaving one lake out of the dataset and then using all 31 other lakes in the dataset to create a model to predict the left out lake's conductivity from its ostracode assemblage only. It is thus a method to assess the predictive ability of the model without collecting independent data.

Methods of Sediment Core Extraction

In order to use the resulting model to produce records of past environments, three sediment cores were extracted from lakes on San Salvador and assessed for ostracode assemblages. One 61 cm core was extracted from Salt Pond (Metzger, 2007), one 1.23 m core was extracted from Clear Pond (Dalman, 2009), and one 1.62 m core was extracted from the north basin of Storrs Lake (Figure 1). Using three cores allows us to determine whether changes in conductivity are synchronous across lakes on the island and to relate changes in conductivity of individual lakes to sea-level and/or changing climate (Teeter, 1995).

Salt Pond is a small (0.043 km^2 in surface area), shallow, hypersaline salina that can experience large fluctuations in salinity within a year and has substantial microbial mat growth (Park et al., 2009). The water depth and salinity of this lake may be exceptionally sensitive to changes in regional climate since it lacks a direct conduit to the ocean and sits very near sea-level. Clear Pond is larger than Salt Pond (0.117 km^2 in surface area), also shallow and its salinity is marine due to the presence of an ebb- and-flow spring on its eastern shore (Dalman, 2009). Clear Pond was previously a lagoon with a surficial connection to the ocean, but today it is isolated from the ocean by mid-Holocene eolianite dunes to the north and unlithified dunes to the south (Park, 2012). Storrs Lake is a larger (3.2 km^2), also shallow, hypersaline lake that, like Clear Pond, was once an oceanic lagoon (Park, 2012). The core used in this study was taken from the northern basin of Storrs Lake, the largest of its three basins.

All three cores were extracted by push-coring technique, were collected in 2 inch diameter black acrylonitrile-butadiene-styrene (ABS) tubing, and split and stored in the University of Akron's refrigeration facility. The cores were sampled at 1 cm intervals for ostracode assemblages. In each interval, 1 cm^3 of sediment was taken from the core and dissolved in water at 80°C. These sampled were then put through two

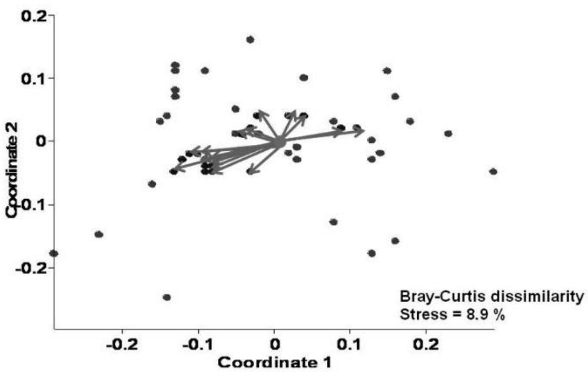

Figure 2. First 2-dimensions of a 3-dimensional non-metric multidimensional scaling plot of all 32 ostracode assemblages collected on the Bray-Curtis dissimilarity matrix. The correlations of both axes and all 19 environmental variables measured are overlain as arrow.

cycles of freezing and thawing to break up the sediment. Finally, all subfossil adult ostracodes in the sample were identified to species using a dissecting microscope and all valves were expressed as percentages of the total valves in the assemblage. The program C2 (Juggins, 2003) was used to convert these assemblages in records of past conductivity using the transfer function model created. Spectral analysis was run on these results to test for cyclicity in changes in conductivity from individual San Salvador lakes using the program PAST (Hammer and Harper, 2005).

To contextualize the ostracode-derived conductivity records for the three cores by providing records of the depositional environments, percent organic matter by weight and percent carbonate content by weight were determined for each core by loss-on-ignition (LOI) analysis (Heiri et al., 2001). 1 cm^3 of sediment from each core was extracted and subjected to three heat treatments to remove water content (105°C), organic content (550°C), and carbonate content (1000°C). Water content was removed by placing the samples in a drying oven for twenty-four hours, organic matter and carbonate matter were removed in a furnace by heating at four hours each. Samples were weighed after each heat treatment to note mass lost through each process. Organic matter and carbonate content were expressed as percentages of the dry sediment weight (Metzger, 2007; Sipahioglu, 2008; Dalman, 2009).

Sediment grain size was also analyzed to contextualize the records of past conductivity. Sediment grain size was determined with a Malvern 2000 Mastersizer at Kent State University by sampling 1 cm^3 of sediment continuously through the Salt and Clear Pond cores at 1 cm intervals (Metzger, 2007; Dalman, 2009). The North Storrs core was sampled at 2 cm intervals for grain size analysis using 1 cm^3 of sediment (Sipahioglu, 2008). Grain size was expressed as percent sand (62.5µm-2mm) of the sample by volume.

Records of potassium (K) were produced by x-ray fluorescence of the Clear Pond and North Storrs cores at the University of Minnesota, Duluth using an ITRAX x-ray fluorescence core scanner. Potassium was chosen as the proxy for African dust since it is present in the airborne dust (Prospero and Carlson, 1972; Foos, 1990) and the dust is the only source of aluminosilicate deposition in the Bahamas (Foos, 1990; Muhs et al., 1990). Both cores were scanned at 0.02 cm intervals.

Organic matter in the form of allochthonous leaves was collected at 25 cm depth in the Salt Pond core, at 20 cm, 49.5 cm, and 79 cm depth in the Clear Pond core, and 1.2 m in the North Storrs core and sent to Beta Analytic laboratories to determine their AMS radiocarbon ages. These dates were then calendar-year calibrated using CALIB online (http://calib.qub.ac.uk/calib/).

RESULTS

Lakes in this study are alkaline (pH 7.2-8.7) and have a wide range of conductivity (4.94-152.2 mS/cm).

Results of non-metric multidimensional scaling (NMDS) show the first two dimensions of three-dimensional NMDS ordinations overlain with measured environmental variables (Figure 2). No

Model type	WA-PLS
No. of PLS components	2
Apparent	
$r^2_{apparent}$	0.76
RMSE	12.24
Ave. bias	-0.0007294
Max. bias	25.25
Cross-validation jack-kniffing	
$r^2_{jack\text{-}knifed}$	0.68
RMSEP	14.47
Ave. bias	-0.06
Max. bias	28.11

Table 1. Performance of apparent and cross-validated statistics of the conductivity transfer function. WA-PLS weighted averaging partial least squares regression, RMSE(P) root mean square error (of prediction).

single environmental variable, out of the nineteen measured, shows a high correlation with the first two NMDS (akin to loadings of a Principle Components Analysis). Additionally, many environmental variables show a high degree of pairwise correlation with each other.

MFSO revealed three variables that significantly and uniquely correlate with change in ostracode assemblages: electrical conductivity, dissolved oxygen, and alkalinity, although the effect size of alkalinity is quite low. The constrained ordination with these three variables correlate strongly with the Bray-Curtis dissimilarity of the ostracode assemblages (r=0.826). Conductivity is highly correlated with concentrations of major ions; concentrations of Sr and Mn correlate with change in ostracode assemblages almost as well as conductivity. Individually, these three environmental variables have stronger effect size than other single- variable MFSO.

Gaussian logistic regression of each species niche over the conductivity gradient with the regression coefficients converted to species' optimum and tolerance according to ter Braak and Looman (1986) reveals that most species have niche positions tightly clustered in the range of marine salinity (Figure 3). Exceptions include *Physocypria denticulata* and *Hemicyprideis setipunctata* whose niches are in the brackish range and *Aurila floridana* whose niche is positioned in slightly saline conductivity. The niche breadths', however, are widely divergent. Three species have noticeably broad niches (*Cyprideis americana*, *Perissocytheridea bicelliforma*, and *Hemicyprideis setipunctata*), while other species have narrower niches. A few species display patterns of decreasing abundances away from their optima, but many species have similar abundances in marine conductivity (Figure 3).

A 2-component weighted-averaging partial least squares model performed best as a transfer function for conductivity (Table 1, Figure 4). This model performs well with an apparent r^2 of 0.76 and an r^2 of 0.69 between observed and predicted conductivity, as assessed by leave-one-out cross validation (Table 1; Figure 4A). There is no systematic relationship between the residuals of the full model and the observed conductivity, although lakes in the middle of the sampled gradient tended to overestimate the conductivity of lower-conductivity lakes and underestimate higher-conductivity lakes (Figure 4B).

Sampling across the conductivity gradient is not even. Bamboo pond, the sample with the lowest conductivity, is noticeable; it is a high leverage point, but not a highly influential point. Even though it is the only sample from the very low end of conductivity, its species composition is on-trend with the remainder of the dataset. Most of the samples fall in the mid-range of conductivity and

Core	Depth (cm)	Radiocarbon date, calibrated to calendar years before present (ybp)
Salt Pond	25	1300 ± 40 ybp
Clear Pond	20	1250 ± 40 ybp
	49.5	1850 ± 40 ybp
	79	3350 ± 40 ybp
North Storrs	120	3870 ± 40 ybp

Table 2. Results of radiocarbon dating of all three cores.

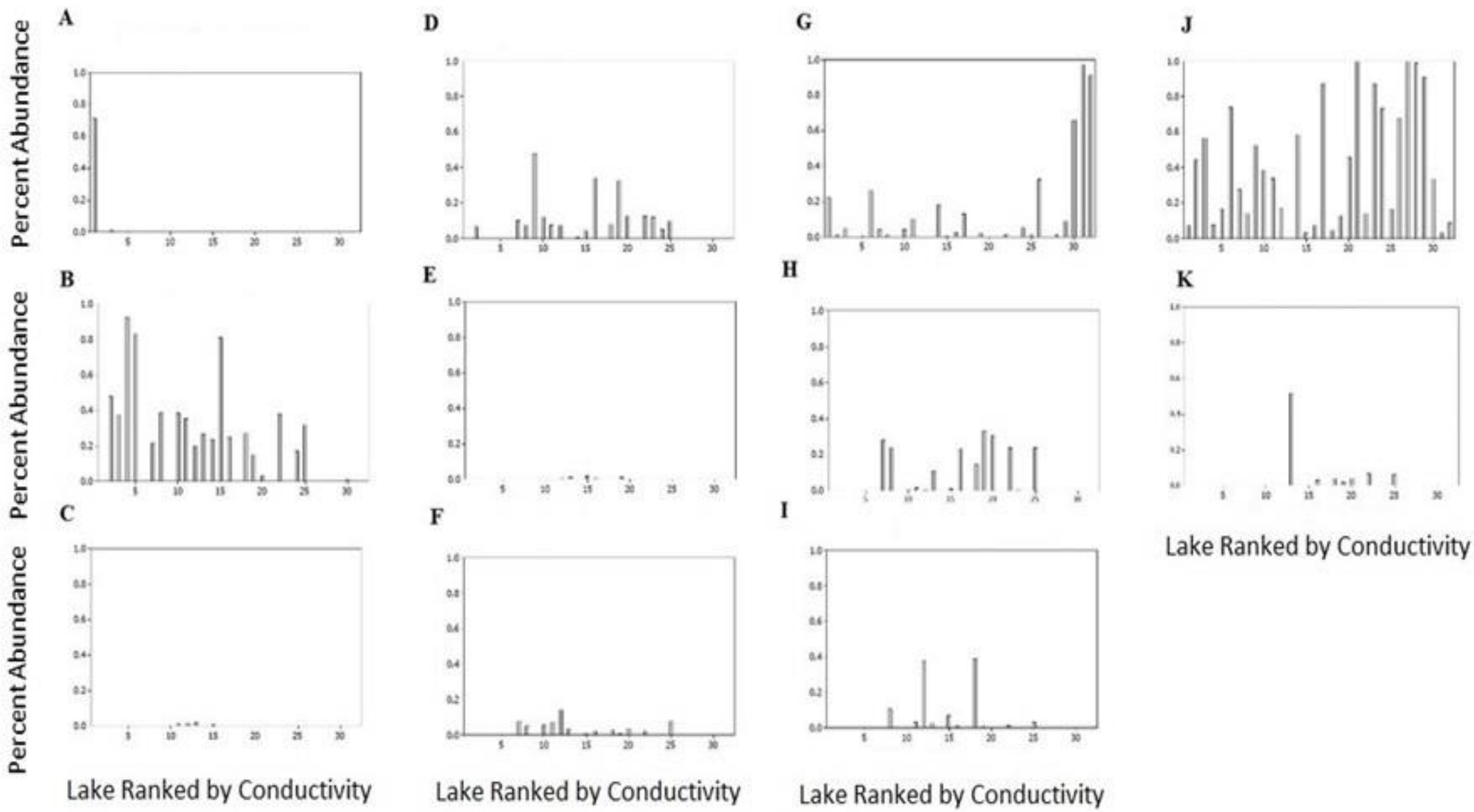

Figure 3. Raw abundances of all species: A) Physocypria denticulata, *B)* Hemicyprideis setipunctata, *C)* Cytherella arostrata, *D)* Dolerocypris inopinata, *E)* Paranesidea harpago, *F)* Reticulocythereis multicarinata, *G)* Perissocytheridea bicelliforma, *H)* Xestoleberis curassavica, *I)* Loxochoncha pursubrhomboidea, *J)* Cyprideis americana, *K)* Aurila floridana. *Lakes are arranged along the abscissa according to measured conductivity. Species are arranged from bottom to top in increasing order of their conductivity optima as assessed by Gaussian logistic regression according to the methods of ter Braak and Looman (1986). Key to lake number: 1-Bamboo Pond, 2-Blue Hole Five, 3-New Blue Hole, 4-Columbus Landing Blue Hole, 5-Watlings Blue Hole, 6-Peel Pond, 7-Six Pack Pond, 8-Mermaid Pond, 9-Crescent Pond, 10-Clear Pond, 11-Pain Pond, 12-Wild Dilly Pond, 13-Moon Rock Pond, 14-Plantation Pond, 15-Oyster Pond, 16-Little Lake, 17-Nasty Pond, 18-Stouts Lake, 19-Great Lake, 20-Granny Lake, 21-South Storrs Lake, 22-Long Lake, 23-Flamingo Pond, 24-Reckley Hill Pond, 25-Osprey Lake, 26-French Pond, 27-Central Storrs Lake, 28-North Storrs Lake, 29-Triangle Pond, 30-No Name Pond, 31-Little Sale Pond, 32-Salt Pond.*

display lowering residuals with increasing conductivity (Figure 4B). Three samples fall on the highest end of the conductivity gradient and their residuals display no systematic relationship with observed conductivity.

Based on one radiocarbon date in the Salt Pond core, a sedimentation rate of 0.019 cm/yr was calculated (Table 2). Also based on one radiocarbon date for the North Storrs core, a sedimentation rate of 0.031 cm/yr was calculated (Table 2). Based on three dates, a linear sedimentation rate of 0.024 cm/yr was calculated for the Clear Pond core (Table 2).

According to their age models, the Salt Pond core extends to 3146 ybp, the Clear Pond core extends to 5133 ybp, while the longest North Storrs core extends to 5208 ybp (Figure 5). All three cores show large fluctuations in conductivity throughout the mid-late Holocene that are for the most part synchronous, while Clear Pond is the only core to show a secular trend towards lower conductivity (Figure 5).

In all three cores, percent organic matter and percent carbonate content vary inversely with each other, but peaks in these records do not seem to correspond with changes in the records of conductivity as determined by ostracode assemblages (Figure 5). Changes in percent sand by volume do correspond to changes in conductivity through time with peaks in the sand record coeval with times of lowered conductivity (Figure 5). This relationship can be seen in the Salt Pond core from 500 to 800 years before present (Figure 5A) and in the Clear Pond core for over the most recent approximately 500 years (Figure 5B) when noticeable dips in conductivity coincides with prominent peaks in the cores' percent sand.

Spectral analysis reveals cyclical changes in conductivity in only the records from Salt Pond with cycles of 140-year frequency. Only the Clear Pond core exhibited secular changes in the form of long-term freshening over the time recorded in these records. The detrended records of these cores show changes in lake conductivity related to

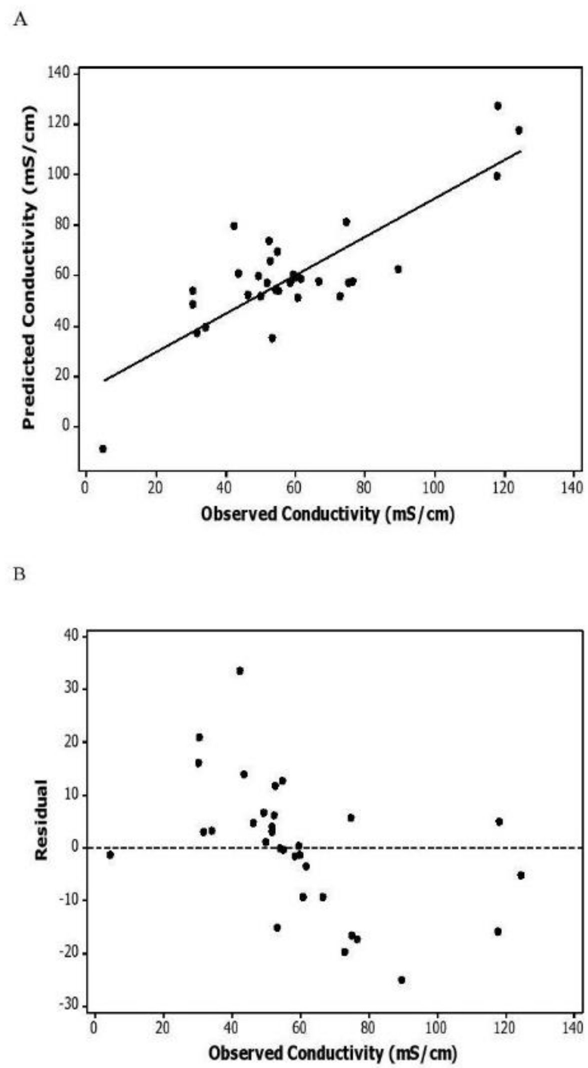

Figure 4. A: Relationship between measured and inferred conductivity using a two-component weighted averaging partial least squares (WA-PLS) regression and calibration model. B: residuals against measured conductivity.

climate (Figure 6). This is simply the deviation from the mean conductivity over the entire record of the core for Salt Pond and North Storrs, while the long-term freshening trend has been eliminated from the record of Clear Pond by simple linear regression over time. Plotting these detrended records allows for the identification of times of aridity and humidity that may be related to regional or global climate changes.

Records of potassium from Clear Pond and North Storrs show good correspondence to the first

6,000 years of an independently-derived record of El Niño strength (Moy et al., 2002): times of increased potassium deposition are coincident with strong El Niño events (Figure 7). The ostracode-derived record of conductivity from these lakes also shows a positive correlation with the potassium record, peaks in the potassium record correspond to times of elevated conductivity in these lakes (Figure 7).

DISCUSSION

Conductivity Records from San Salvador Lakes

Changes in conductivity in lakes on San Salvador caused by climate changes have been broadly synchronous across the late Holocene (Figure 6). Clear Pond, however is the only lake to show a secular trend, only Salt Pond shows cyclical changes, and the utility of the Storrs Lake cores is limited by the paucity of assemblages recovered (Figure 5). Since the majority of the sections in the Storrs Lake core from which no adult ostracodes were recovered were associated with evaporite minerals (principally gypsum and halite), these times may represent lower lake levels and thus periods of aridity. Further and more extensive coring of Storrs Lake is needed to more fully understand its depositional history.

Deposition of allochthonous sand in these lakes is due to infrequent large storms which lower the salinity of these lakes by contributing a large amount of fresh water in the form of precipitation and alter their species composition (Park et al., 2009). Furthermore, large storms may contribute marine water which is of a lower salinity than the water of these hypersaline lakes (Park et al., 2009). This decrease in salinity following tropical cyclones is observed in modern lakes (Park, unpublished data). Therefore, times of increased sand input should be linked to a drop in the conductivity of the lakes as determined by ostracode assemblages. This pattern is evident in Salt Pond as most sand peaks in the Salt Pond record correspond to times of lower conductivity

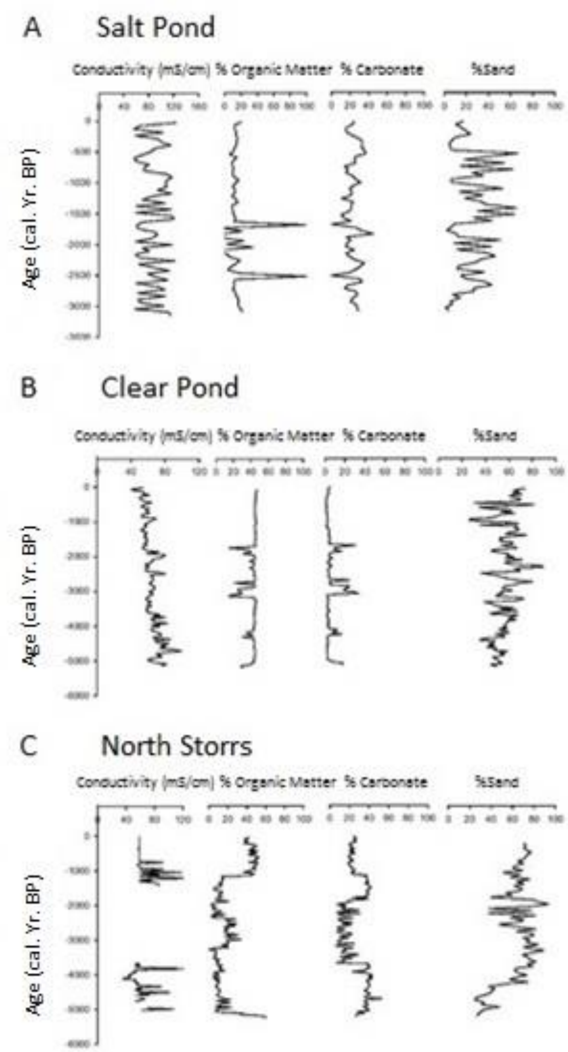

Figure 5. Results of ostracode-based transfer function for conductivity as applied to the three cores from this study plotted according to the age models derived for Salt Pond (A), Clear Pond (B), and North Storrs (C). Also plotted for each core are percent organic matter and percent carbonate content by weight and percent sand by volume. Gaps in the North Storrs core represent depths at which no adult ostracode valves were recovered.

(Figure 5A). This relationship is inconsistent through the Clear Pond record (Figure 5B), but some periods, such as the most recent 500 years and at approximately 2000 years before present show decreased conductivity and peaks in the percent sand. This relationship is weakest in North Storrs Lake (Figure 5C). The weaker relationship

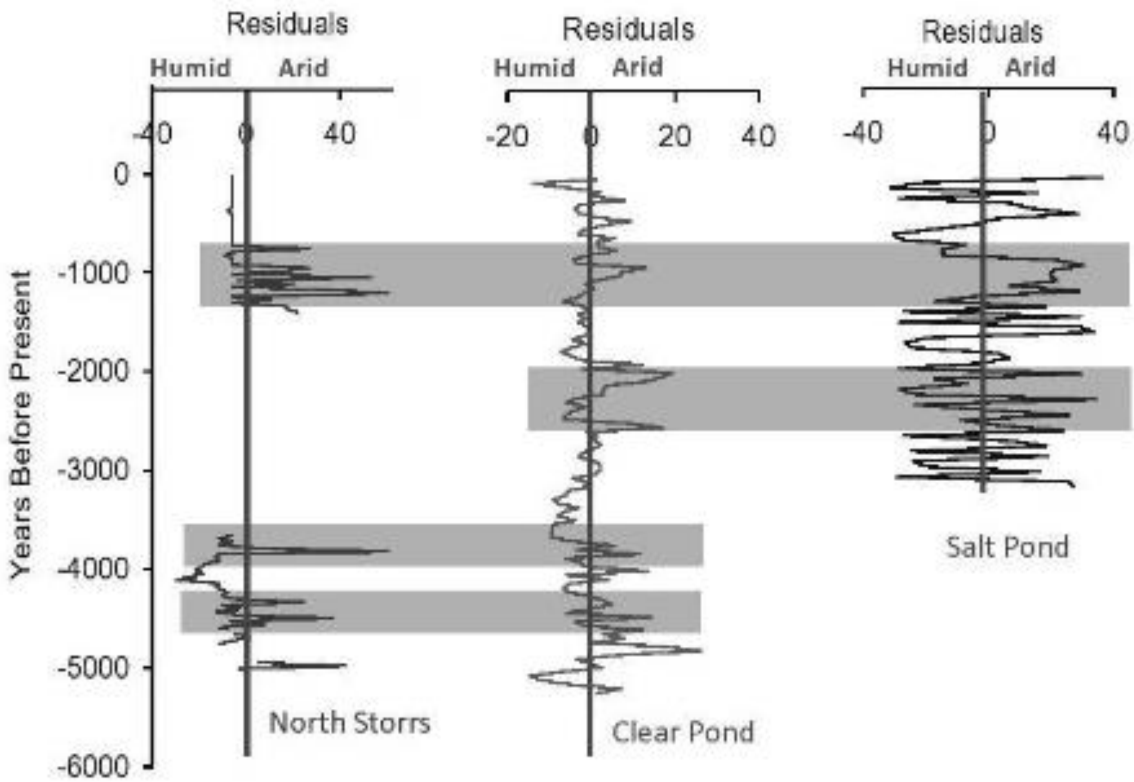

Figure 6. Detrended results of ostracode-based transfer function for conductivity as applied to the three cores from this study plotted according to the age models derived for each core. Arid periods are represented as positive residuals, while moist periods are represented as negative residuals. Gaps in the North Storrs record represent depths at which no adult ostracode valves were recovered. Grey bars represent times of synchronous arid periods recorded in all three lakes.

between peaks in the sand record and lowered conductivity in Clear Pond and North Storrs reflects the different degrees of time-averaging in the allochthonous sand records and autochthonous ostracode assemblages. The sand records are highly-pulsed whereas the ostracode records likely accrue more evenly through time. The lack of correspondence between the sedimentary records of organic matter and carbonate with the ostracode-derived records of conductivity probably again reflects this differential degree of time averaging. The weakest relationship between peaks in the sand content of the cores and changes in conductivity is seen in North Storrs Lake because this core was taken furthest from the ocean, so sand deposition when hurricanes overwash the dune would only make its way to this position with the largest storms.

Clear Pond's long-term freshening trend may be caused by the gradual rise in sea-level for the Caribbean basin (Lidz and Shinn, 1991). Before 3400 ybp, Clear Pond was a lagoon with a surficial connection to the ocean, similar to Pigeon Creek on San Salvador today (Dalman, 2009). At 3400 years before present Clear Pond closed to the ocean through dune progradation, but seawater continued to flow to the pond through an ebb-and-flow spring on its eastern shore (Dalman, 2009; Park, 2012). A rising sea-level may have lessened the impact of this seawater on the pond's water budget through a rising fresh groundwater lens (Carew and Mylroie, 1994), thus causing the observed freshening trend represented in this core. While variation in this long-term freshening trend is related to short-term climate fluctuations, these fluctuations are not as high in magnitude nor as regular as in Salt Pond (Figure 6).

In addition to it being the only lake exhibiting cyclical changes in conductivity, Salt Pond also shows the largest changes in conductivity. Due to its nature as a closed basin (Metzger, 2007), Salt Pond may thus most conclusively capture changes in the precipitation/ evaporation balance of the area. The 140 year cycles of conductivity recorded in the core are harder to explain. Since precipitation in this region is strongly influenced by hurricanes with much of the annual precipitation falling during the hurricane season (Park et al., 2009), these cycles may be related to changing magnitudes of El Niño events. Times of strong El Niño result in high wind shear across the Atlantic, inhibiting hurricane formation (Gray, 1984), thus these cycles in the strength of El Niños. Times of strong El Niño events would produce less precipitation, raising conductivity and times without strong El Niño events would be associated with more frequent hurricane impacts, resulting in lowered conductivity.

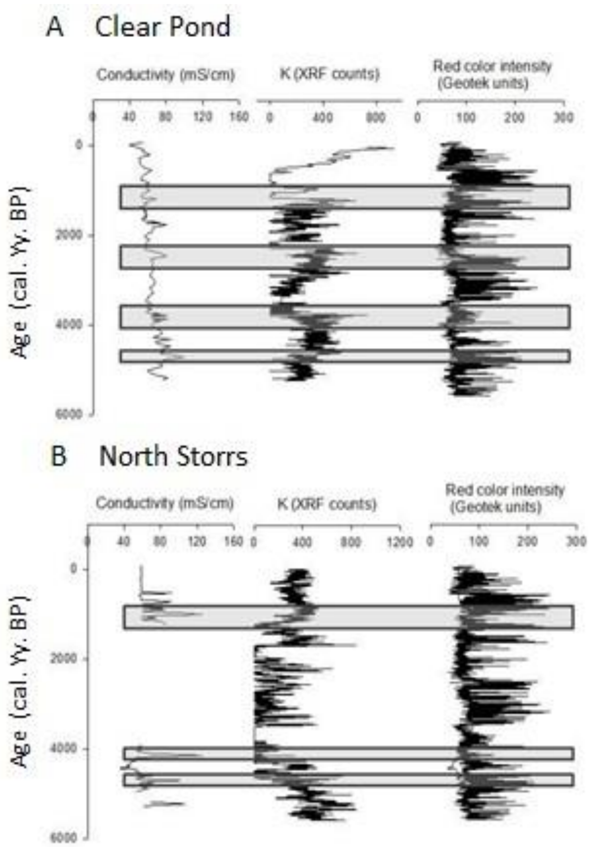

Figure 7. Results of ostracode-based transfer function for conductivity from Clear Pond (A) and North Storrs (B) compared to the XRF-derived record of K for each core and El Niño proxy reconstruction from Laguna Pallcacocha Ecuador (Moy et al., 2002). Peaks in red color intensity represent allochthonous material washed into the lake during strong El Niño events. Grey bars represent times of correspondence between high salinity, high potassium, and high red color intensity.

This relationship between strong El Niño events and increased conductivity is also seen in the Clear Pond and North Storrs cores. The potassium records from these cores show good correspondence with an independently-derived record of El Niño strength (Moy et al., 2002) indicating that it should faithfully record times of strong El Niño events when more dust is blown from Africa and deposited in the Bahamas (Prospero and Lamb, 2003; Evan et al., 2006). Many of these times of strong El Niño events correspond to times of increased conductivity in Clear Pond and North Storrs and times of decreased El Niño events correspond to times of decreased conductivity (Figure 7). Thus, the variation in hurricane activity in the Atlantic, driven by changes in El Niño/ Southern Oscillation (ENSO) cycle, controls much of the variation in the salinity of lakes on San Salvador Island, Bahamas.

Performance of Transfer Function

Compared to other published ostracode-based inference models for conductivity (Mezquita et al., 2005; Mishchke et al., 2007; Mishke et al., 2010), our transfer function performs comparably as assessed by the coefficient of determination between measured and inferred conductivity (0.69). This is surprising given that this transfer function has a lower sample size than other studies. This transfer function does, however, have noticeably higher average and maximum bias (Table 1). This measure of performance would probably improve with a higher sample size. Nevertheless, the ostracode assemblages of San Salvador Island, Bahamas do indeed show a strong relationship to conductivity and this study demonstrates their effectiveness as proxy indicators in tropical environments.

One lake (Bamboo) had higher leverage due to its position in brackish salinity. Nonetheless, it contained an assemblage consistent with those of other lakes. Two generalist species (*Cyprideis americana* and *Perissocytheridea bicelliforma*) were found in low abundances in this lake, but Bamboo Lake was dominated by *Physocypria denticulata* which was found in low abundance in only one other lake. This resulted in *Physocypria denticulata* having much lower conductivity optima than all other species as assessed by Gaussian logistic regression according to ter Braak and Looman (1986). This species may be evolutionarily unique in comparison with all other species sampled in this dataset. Park and Beltz (1998) concluded that ostracode species recovered from non-marine samples in the Caribbean must have invaded from the marine realm since many species reached highest abundances in lakes of marine salinity. *Physocypria denticulata* provides a counter example to this general pattern. It may have exhibited more rapid evolution than other taxa to colonize and dominate brackish lakes or may have invaded via a different route than other species.

No other lakes were noticeable outliers. Lakes in the mid-range of salinity, however, may exhibit the edge effect common to regression techniques that model species with unimodal responses to environmental gradients (Mischke et al., 2007) since lakes in the middle of the sampled gradient tended to overestimate the conductivity of lower-conductivity lakes and underestimate higher-conductivity lakes. However, this effect was not seen in the one lake on the very lowest end of the gradient and the three lakes on the highest end of the gradient.

Abiotic Factors Controlling Distribution of Ostracode Assemblages

The environmental variables identified as best able to explain the variation in ostracode assemblages were: conductivity, dissolved oxygen, and alkalinity. Conductivity has been commonly identified as correlated with ostracode assemblages in disparate environments (Mezquita et al., 2005; Mischke et al., 2007; Mischke et al., 2010a). Given that the ostracodes found in lacustrine environments on San Salvador may have invaded from the ocean, it is reasonable to assume that salinity would be a driver of ostracode diversity today since there are ample opportunities for diversification in lakes of divergent conductivity found today on San Salvador. The processes responsible for the formation of lakes on San Salvador lead to lakes of differing salinities and hydrologic conditions (Park et al., 2014).

Similarly, previous work (Delorme, 1969; Frenzel and Boomer, 2005) has identified dissolved oxygen as a potential driver of diversity in ostracode assemblages since some species may have differing oxygen requirements. While alkalinity explains a significant and unique proportion of the Bray-Curtis dissimilarity matrix of ostracode assemblages, this proportion is quite small. Like conductivity, the processes responsible for lake formation on San Salvador have led to lakes with different alkalinities, so this may also be an important factor in the evolutionary ecology of ostracodes inhabiting San Salvador lakes.

Representativeness of Samples

Dalman (2009) and Sipahioglu (2008) have demonstrated that some lakes exhibit substantial seasonal variability in salinity. Studies are needed to estimate variability in salinity across all lakes to see if this could affect ostracode assemblage distribution. This variation in salinity could then be imputed as an environmental variable to see if it significantly correlated with ostracode β-diversity. It is possible that certain species may be better adapted to this disturbance and may come to dominate shallow, smaller lakes, or those that lack a robust connection to the ocean. In that case, analyses that use a one-point sample of salinity would miss this potential driver of β-diversity on San Salvador Island.

Modeling of Species Niches across the Sampled Conductivity Gradient

This paper presents the first quantitative estimates of responses across a salinity gradient for many species of lake-dwelling ostracodes. In general, it accomplishes this with mixed results. In some species it produces a significant and biologically meaningful model, while it gives a misleading result in other cases. *P. bicelliforma*, for instance, is a generalist species found in many of the sampled lakes. However, a Gaussian logistic regression on these data produces a concave niche with increasing probability of being found in lakes on the extreme high and low ends of the sampled gradient. This is the opposite of theoretical unimodal gradients on which this analysis is based. More studies need to be done on the autecology of these species to produce more reasonable unidimensional models of individual species' niches because unimodal modeling of the niches of generalist species or species adapted to extreme environments may be inappropriate.

Limits of Quantitative Paleoenvironmental Reconstruction

Belyea (2007) has identified many potential problems with the transfer function method that could lead to spurious and unreliable results. In this dataset, many of those problems may be moot since neither abiotic factors sampled nor the Bray-Curtis dissimilarity matrix of ostracode assemblages are spatially autocorrelated. Thus spatial factors are unlikely to bias the results in this case. Additionally, MFSO avoids overfitting the relationship between ostracode assemblages and the measured environmental variables, since after a variable has entered the model, only the residuals are used to fit the model. In this way, the correlation of environmental variables themselves will not bias the ordination results. A more thorough understanding of potential problems in quantitative paleoenvironmental reconstruction using these data will be a subject of later work.

CONCLUSIONS

A transfer function for conductivity with reasonable predictive ability was developed using ostracodes on San Salvador Island, Bahamas, further demonstrating their ability to produce records of past environments. This model would be improved by further sampling of lakes and estimation of seasonal variation in conductivity in all lakes.

Changes in the conductivity of lakes on San Salvador were broadly synchronous and related to climate change, with times of increased conductivity corresponding to times of strong El Niño events when there are fewer hurricanes providing freshwater input to these lakes. Thus, variation in the strength of El Niño events exerts a strong influence on the aridity of the climate of the Bahamas.

ACKNOWLEDGMENTS

We would like to thank Dr. Donald T. Gerace, Chief Executive Officer, Tom Rothfus, Executive Director, and Erin Rothfus, Research Coordinator of the Gerace Research Center, San Salvador, Bahamas. We would also like to thank Mark Dalman, Sara Bright, Emily Frank, and Emily Woodward for providing field assistance and Tom Quick for providing laboratory assistance. Andrew V. Michelson received funding from the University of Akron geology and environmental science department, University of Akron program in integrated bioscience, University of Akron graduate student government, and the Gerace Research Centre. Lisa E. Park Boush received funding from the National Science Foundation (EAR 0851847). This work was done under Permit

G234 and G235 to Park Boush and was supported by the National Science Foundation as part of the author's Individual Research Plan.

REFERENCES

Alin, S.R., and Cohen, A.S., 2003, Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water-depth reconstruction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 199, p. 31-49.

Bain, R.J., 1991, Distribution of Pleistocene lithofacies in the interior of San Salvador Island, Bahamas and possible genetic models, *in* Bain, R.J., ed., Proceedings of the Fifth Symposium on the Geology of the Bahamas: Bahamian Field Station, Ft. Lauderdale, FL, p. 11-27.

Belyea, L.R., 2007, Revealing the Emperor's new clothes: niche-based palaeoenvironmental reconstruction in the light of recent ecological theory: The Holocene, v. 17, p. 683-688.

Berman, M.J., and Gnivecki, P.L., 1995, The colonization of the Bahama archipelago: A reappraisal: World Archaeology, v. 26, p. 421-441.

Birks, H.J.B., 1995, Quantitative palaeoenvironmental reconstructions, *in*: Maddy, D., and Brew, J.S., eds., Statistical Modelling of Quaternary Science Data, Quaternary Research Association Technical Guide, v. 5, p. 161–254.

Carew, J.L., and Mylroie, J.E., 1994, Geology and karst of San Salvador Island, Bahamas: A field trip guide, Bahamas Field Station: Fort Lauderdale, FL.

Dalman, M., 2009, Paleotempestology and depositional history of Clear Pond, San Salvador Island, Bahamas, Unpublished M.S. Thesis: University of Akron, Akron, OH, 160 pp.

Delorme, L.D., 1969, Ostracodes as Quaternary paleoecological indicators: Canadian Journal of Zoology, v. 6, p. 1471-1476.

Dietl, G.P., and Flessa, K.W., 2011, Conservation paleobiology: putting the dead to work: Trends in Ecology and Evolution, v. 26, p. 30-37.

Edlund, M.B., and Stoermer, E.F., 2000, A 200,000-year, high-resolution record of diatom productivity and community makeup from Lake Baikal shows high correspondence to marine oxygen-isotope record of climate change: Limnology and Oceanography, v. 45, p. 948-962.

Evan, A.T., Dunion, J., Foley, J.A., Heidinger, A.K., and Velden, C.S., 2006, New evidence for a relationship between Atlantic tropical cyclone activity and African dust outbreaks: Geophysical Research Letters, v. 33, p. L19813-L19817.

Foos, A.M., 1990, Aluminous lateritic soils, Eleuthera, Bahamas: A modern analog to carbonate paleosols: Journal of Sedimentary Petrology, v. 61, p. 340-348.

Frenzel, P., and Boomer, I., 2005, The use of ostracods from marginal marine, brackish waters as bioindicators of modern and Quaternary environmental change: Palaeogeography, Palaeocliamtology, Palaeoecology, v. 225, p. 68-92.

Gray, W.M., 1984, Atlantic seasonal hurricane frequency. Part I: El Niño and 30 mb quasi-biennial oscillation influences: Monthly Weather Review, v. 112, p. 1649-1668.

Hammer, Ø., and Harper, D.A.T., 2005, Paleontological data analysis: Wiley-Blackwell, New York, NY.

Heiri, O., Lotter, A.F., and Lamcke, G., 2001, Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results: Journal of Paleolimnology, v. 25, p. 101-110.

Higuera-Gundy, A., Brenner, M., Hodell, D.A,, Curtis, J.H., Leyden, B.W., and Binford, M.W., 1999, A 10,300 ^{14}C yr record of climate and vegetation change from Haiti: Quaternary Research, v. 52, p. 159-170.

Holmes, J.A., 2008, Sample-size implications of the trace-element variability of ostracod shells: Geochemica Cosmochimica Acta, v. 72, p. 2934-2945.

Horne, D.J., Cohen, A., and Martens, K., 2002, Taxonomy, morphology and biology of Quaternary and living Ostracoda, *in*: Chivas, A., and Holmes, J., eds., The Ostracoda: applications in Quaternary research: American Geophysical Union, Washington, DC, v. 131, p. 5-36.

Juggins, S., 2003, C2: Software for Ecological and Palaeoecological Data Analysis and Visualisation: User Guide, Version 1-3: Newcastle University, Newcastle upon Tyne, UK.

Lidz, B.H., and Shinn, E.A., 1991, Paleoshorelines, reefs, and a rising sea: South Florida, USA: Journal of Coastal Research, v. 7, p. 203-229.

Metzger, T.J., 2007, Event deposition and faunal fluctuations after storm deposits: A multi-proxy sediment core analysis from Salt Pond, San Salvador Island, Bahamas, Unpublished Undergraduate Thesis: University of Akron, Akron, OH, 38 pp.

Mezquita, F., Roca, J.R., Reed, J.M., and Wansard, G., 2005, Quantifying species-environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: examples using Iberian data: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 225, p. 93-117.

Michelson, A.V., and Park, L.E., 2013, Taphonomic dynamics of lacustrine ostracodes on San Salvador Island, Bahamas: High fidelity and evidence of anthropogenic modification: Palaios, v. 28, p. 129-135.

Mischke, S., Almogi-Labin, A., Ortal, R., Rosenfeld, A., Schwab, M.J., Boomer, I., 2010a, Quantitative reconstruction of lake conductivity in the Quaternary of the Near East (Israel) using ostracods: Journal of Paleolimnology, v. 43, p. 667-688.

Mischke, S., Böβneck, U., Diekmann, B., Herzschuh, U., Jin, H., Kramer, A., Wünnemann, B., and Zhang, C., 2010b, Quantitative relationship between water-depth and sub-fossil ostracod assemblages in Lake Donggi Cona, Qinghai Province, China: Journal of Paleolimnology, v. 43, p. 589-608.

Mischke, S., Herzschuh, U., Massmann, G., and Zhang, C., 2007, An ostracod-conductivity transfer function for Tibetan lakes: Journal of Paleolimnology, v. 38, p. 509-524.

Mourguiart, P., and Carbonel, P., 1994, A quantitative method of palaeolake-level reconstruction using ostracode assemblages: an example from the Bolivian Altiplano: Hydrobiologia, v. 288, p. 183-193.

Mourguiart, P., Correge, T., Wirrmann, D., Argollo, J., Montenegro, M.E., Pourchet, M., and Carbonal, P., 1998, Holocene palaeohydrology of Lake Titicaca estimated from an ostracode-based transfer function: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 143, p. 51-72.

Moy, C.M., Seltzer, G.O., Rodbell, D.T., and Anderson, D.M., 2002, Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch: Nature, v. 420, p. 162-165.

Muhs, D.R., Bush, C.A., Stewart, K.C., Rowland, T.R., and Crittende, R.C., 1990, Geochemical evidence of Saharan dust parent material for soils developed on Quaternary limestones of Caribbean and Western Atlantic islands: Quaternary Research, v. 33, p. 157-177.

Park, L.E., 2012, Comparing two long-term hurricane frequency and intensity records from San Salvador Island, Bahamas: Journal of Coastal Research, v. 28, p. 891-902.

Park, L.E., and Beltz, J.F., 1998, Biogeography of Neogene tropical non-marine Caribbean ostracod faunas: GSA abstracts with programs, v. 30, p. 287.

Park, L.E., Cohen, A.S., Martens, K., and Bralek, R., 2003, The impact of taphonomic processes on interpreting paleoecological changes in large lake ecosystems: Ostracodes in Lakes Tanganyika and Malawi: Journal of Paleolimnology, v. 30, p. 127-138.

Park, L.E., Myrbo, A., and Michelson, A., 2014, A qualitative and quantitative model for climate-driven lake formation on carbonate platforms based on examples from the Bahamian archipelago: Carbonates and Evaporites, v. 29, p. 409-418.

Park, L.E., Siewers, F.D., Metzger, T., and Sipahioglu, S., 2009, After the hurricane hits: recovery and response to large storm events in a saline lake, San Salvador Island, Bahamas: Quaternary International, v. 195, p. 98-105.

Park, L.E., and Trubee, K.J., 2008, Faunal and geochemical variability of ostracodes faunas from saline ponds on San Salvador Island, Bahamas, *in*: Park, L.E., and Freile, D., eds., 13th Symposium on the Geology of the Bahamas and Other Carbonate Regions: San Salvador Island, Bahamas, p. 11-24.

Peros, M.C., Reinhardt, E.G., and Davis AM, 2007, A 6000-year record of ecological and hydrological changes from Laguna de le Leche, north coastal Cuba: Quaternary Research, v. 67, p. 69-82.

Prospero, J.M., and Carlson, T.N., 1972, Vertical and areal distribution of Saharan dust over the western equatorial North Atlantic Ocean: Journal of Geophysical Research, v. 77, p. 5255-5265.

Prospero, J.M., and Lamb, P.J., 2003, African droughts and dust transport to the Caribbean: Climate change implications: Science, v. 302, p. 1024-1027.

Roberts, D.W., 2008, Statistical analysis of multivariate fuzzy set ordinations: Ecology, v. 89, p. 1246-1260.

Roberts, D.W., 2009, Comparison of multivariate fuzzy set ordination with CCA and DB-RDA: Ecology, v. 90, p. 2622-2634.

Robinson, M.C., and Davis, R.L., 1999, Preliminary geographical information system analysis and maps of physical, hydrological, archaeological, and biological resources, San Salvador Island, Bahamas, *in*: Curran, H.A., and Mylroie, J.E., eds., Proceedings of the 9th Symposium on the Geology of the Bahamas and other Carbonate Regions: San Salvador Island, Bahamas, p.101- 110.

Saros, J.E., 2009, Integrating neo- and paleolimnological approaches to refine interpretations of environmental change: Journal of Paleolimnology, v. 41, p. 243-252.

Sayer, C.D., Davidson, T.A., Jones, J.I., and Langdon, P.G., 2010, Combining contemporary ecology and paleolimnology to understand shallow lake ecosystem change: Freshwater Biology, v. 55, p. 487-499.

Schmidt, M.W., Spero, H.J., and Lea, D.W., 2004, Links between salinity variation in the Caribbean and North Atlantic thermohaline circulation: Nature, v. 428, p.160-163.

Sipahioglu, S.M., 2008, Tracking storms through time: Event deposition and biologic response in Storr's Lake, San Salvador Island, Bahamas: Unpublished M.S. Thesis, University of Akron, Akron, OH, 179 pp.

Teeter, J.W., 1995, Holocene saline lake history, San Salvador Island, Bahamas: Geological Society of America Special Papers, v. 300, p. 117-124.

ter Braak, C.J.F., and Juggins, S., 1993, Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages: Hydrobiologia, v. 269/270, p. 485-502.

ter Braak, C.J.F., and Looman, C.W.N., 1986, Weighted averaging, logistic regression, and the Gaussian response model: Vegetatio, v. 65, p. 3-11.

Viehberg, F.A., 2006, Freshwater ostracod assemblages and their relationship to environmental variables in waters from northeast Germany: Hydrobiologia, v. 571, p. 213-224.