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Front Cover: Rice Bay Formation, looking southwest along Grotto Beach. Photograph by
Sandy Voegeli.

Back Cover: Dr. John Milliman, The College of William and Mary. Keynote Speaker for
the 13th Symposium. Photograph by Sandy Voegeli.

FAUNAL AND GEOCHEMICAL VARIABILITY OF OSTRACODE FAUNAS FROM SALINE PONDS ON SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

We examined ostracode faunas from eleven lakes ranging from normal marine to hypersaline conditions on San Salvador Island, Bahamas to determine: 1) if lakes of higher salinity have different diversities than less saline lakes, 2) if there is a correlation between species distribution and water chemistry, 3) if genders of the same species have the same or different partitioning ratios, and 4) if species within the same lake have similar Mg and Sr partitioning ratios.

Water and ostracode samples were collected from all eleven lakes. Water temperature, pH, alkalinity, conductivity, and salinity were measured in the field with hand held meters. Over 600 right valves were counted from each lake and statistically analyzed to determine faunal distribution. Three species--*Cyprideis americana*, *Hemicyprideis setipunctata* and *Perissocytheridea bicelliforma* were geochemically analyzed for major trace elements, including Mg and Sr, using ICP-MS.

Species distribution and alpha diversity appears to be correlated to lake chemistry, primarily salinity, with peak diversity occurring at the calcite branchpoint. Surprisingly, dissimilar faunas occur in adjacent lakes with similar chemistries. Lakes that were similar in chemistry were sometimes geographically separated by distance or by a significant barrier. This similarity indicates that dispersal of ostracodes may not necessarily be as frequent and widespread as previously thought.

While species distribution appears to correlate with lake water chemistry, the partitioning ratios for Mg and Sr show different trends with respect to lake water salinity. For all valves measured, K_d [Mg] increases with salinity while K_d [Sr] shows a strong negative correlation. In addition, *P. bicelliforma* appears to have a wider variance of Mg and Sr partitioning ratios indicating a possible 'species effect.' There are also slight differences seen between males and females of *C. americana*. These minor differences in trace element uptake may be due to differences in average valve mass, as *P. bicelliforma*'s relatively small size as well as the smaller size of the female *C. americana*, suggest that these valves might have weaker calcification that might contribute to these differences. Whatever the cause, the differences, although slight, reinforce the necessity of using a single species for trace element and isotope analyses when analyzing cores or comparing water bodies.

INTRODUCTION

San Salvador Island (SSI)

San Salvador Island (SSI), Bahamas is a small island (~153 km^2) with multiple inland lakes having varying water chemistries (Davis and Johnson, 1989) and depositional histories (Figure 1). During Pleistocene sea-level high stands, deposits of dune, beach and sub-tidal carbonates accumulated across the San Salvador platform (Carew and Mylroie, 1995).

Many of the inland lakes occur between these ancient dune deposits or as karst features in the Pleistocene-Holocene carbonate bedrock (Bain, 1991; Teeter, 1985). These lakes vary dramatically in size, chemistry, and faunal composition (Table 1); most are not closed systems but are connected via conduits to each other and the ocean realm.

Prior studies have focused on reconstructing the depositional histories of some of these lakes including, Salt Pond, Little Lake, Watling's Blue Hole and Storr's Lake (Crotty, 1982; Sanger and Teeter, 1982; Sanger, 1983; Thalman, 1983; Corwin, 1985; Florentino, 1985; Nutt, 1985; Teeter, 1985; Zaleha, 1987; Teeter and Quick, 1990; Beltz, 1992; Cronin, 1994; and Shamberger, 1998). In most cases, the ostracodes from these lakes can be divided into faunal associations based on salinities and can be used as proxies for paleoenvironmental change (Sanger and Teeter, 1982; Teeter, 1985; Teeter and Quick, 1990; and Park and Beltz, 1998).

Modern Salinities and Sedimentation

Modern lakes on SSI vary in salinity due to factors such as the degree of development of the marine conduit system, the presence of local fresh groundwater lenses, the size of the lake and its elevation relative to sea level, as well as rainfall. Ponds and blue holes that have unimpeded connections to the open ocean exhibit normal-marine salinities and tidal change, although the

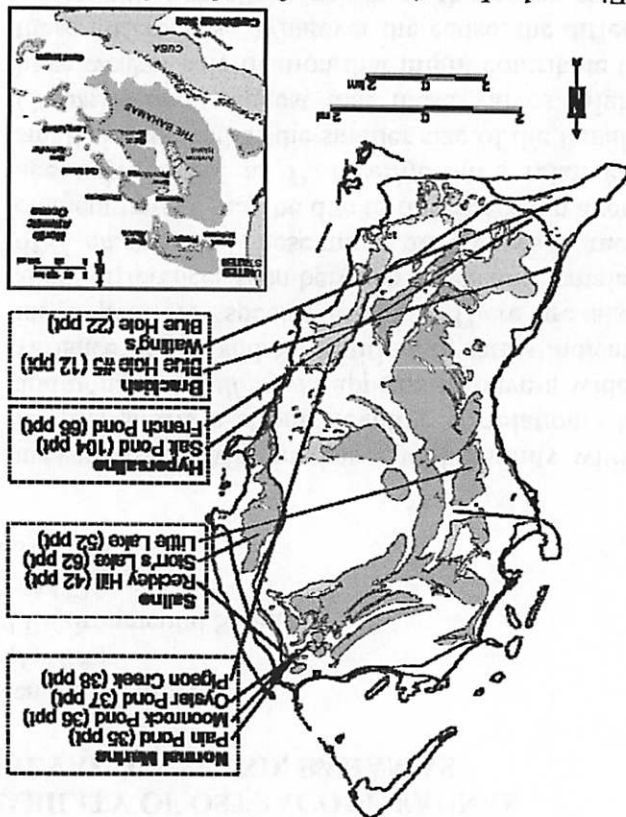Figure 1. Location map of ponds under study on San Salvador Island. Average salinity noted.

Normal Marine
Pain Pond (35 ppt)
Moonrock Pond (36 ppt)
Oyster Pond (37 ppt)
Pigeon Creek (35 ppt)

Saline
Reckley Hill (42 ppt)
Storr's Lake (62 ppt)
Little Lake (52 ppt)

Hypersaline
Salt Pond (104 ppt)
French Pond (66 ppt)

Brackish
Blue Hole #5 (12 ppt)
Watling's Blue Hole (22 ppt)

Table 1. Pond and lake salinity, pH, conductivity, mean water temperature, area, alkalinity and number of ostracode species found.

Pond/Lake	Salinity Range (ppt)	Average Salinity (ppt)	pH	Conductivity (mS/cm)	Mean Water Temp (°C)	Max. Water Depth (m)	Lake Area km²	Total Alkalinity (meq)	No. Ostracode Species
Blue Hole #5	4-30	12	8.4	22.9	26.9	6	0.0004	3.54	4
French Pond	32-280	66	8.5	97.5	29.6	2	0.05	3.54	2
Little Lake	38-67	52	8.0	82.5	27.9	3	1.7	2.75	6
Moonrock Pond	na	36	8.0	55.7	30.1	1.5	0.06	3.15	6
Oyster Pond	34-38	37	8.0	59.9	27.4	2.5	0.07	3.15	10
Pain Pond	28-37	35	8.1	56.5	31.6	2	0.018	3.08	9
Pigeon Creek	35-45	35	8.1	66.7	23.9	2	4.4	2.36	19
Reckley Hill Pond	36-59	42	8.6	66.6	30.0	0.5	0.12	4.46	5
Salt Pond	59-356	104	8.6	140.3	37.8	0.5	0.05	3.80	3
Storr's Lake	60-76	62	8.4	95.4	26.0	1.1	3.2	3.34	3
Watling's Blue Hole	10-32	22	8.2	38.0	28.0	7	0.003	3.34	3

range is diminished and timing lags behind ocean tides. Water in ponds having poor interchange with the ocean have long residence times and higher salinities. Salt Pond, for example, can range in salinity from 60 to 300 ppt and has had gypsum and halite precipitating during its history (Furman et al., 1992; Shamberger, 1998). Cores taken from Salt Pond indicate that the pond went from a marine sub-tidal environment, to fresh-water conditions, followed by periods of saline intrusion and increasing salinity. These sediments also record several marked zones of presumed storm wash-over events that can be used to better understand frequency and intensity of tropical storms in the past 2,000 years (Park et al. this volume).

SSI Ostracoda

Ostracodes as Paleoenvironmental Indicators. Ostracodes are bivalved microcrustaceans that range in size from 500 µm to 2 mm. They are common in all aquatic environments and their low-Mg calcite carapaces are readily preserved in the geologic record. Biogenic fractionation of ostracode calcite with respect to the host waters makes them important indicators of salinity and temperature (Chivas et al., 1983; De Deckker et al., 1988; Holmes et al., 1992; Xia et al., 1997; De Deckker et al., 1998; Wansard et al., 1998; and Curry, 1999).

Prior studies on the relationship between water chemistry and ostracode diversity and distribution have been conducted on various lakes on the island, including Salt Pond and Little Lake (Sanger and Teeter, 1982; Teeter, 1985; Teeter and Quick, 1990). These studies indicate that each lake has a different associated fauna that most likely reflects water chemistry.

In this study, we examined the variability of the ostracode faunas in eleven lakes on the island, documenting and determining their chemical affinities as well as faunal distribution and ecology. Specifically, we addressed several questions: 1) do lakes of higher salinity have significantly different species richness than less saline

lakes? 2) is there a correlation between ostracode species distribution and lake water chemistry? 3) do different species within the same lake have the same uptake ratios? 4) do males and females of the same species have different uptake ratios of Sr and Mg?

METHODS

Field Sampling

Water and sediment samples were collected from each of the eleven lakes in this study. Measurements of pH, alkalinity, salinity, and temperature were done in the field using hand held meters. Alkalinity was measured using standard titration techniques (0.01639 N H_2SO_4 added to 25 ml H_2O to pH 4.5).

One liter of water was collected in each lake 10 cm above the sediment-water interface, in two sterile, acid-washed and MilliQ® water-rinsed 500 ml plastic bottles and capped underwater. The samples were refrigerated until analyzed.

Approximately 500 ml of sediment was collected as grab samples from the upper two centimeters of the lake-bottom sediment. These were wet-sieved in -2 Ø (2000 µm), 2.0 Ø (250 µm, and 3.0 Ø (125 µm) sieves within twenty-four hours of collection and allowed to air dry. Only live individuals at the time of collection were chosen for geochemical analysis.

Six hundred right valves were picked from each lake. Whether they were recently alive was not necessarily considered for this part of the analysis; the specimens used for geochemical analysis were included in diversity counts. In several samples (French Pond, Oyster Pond, Pain Pond, Reckley Hill Pond, and Salt Pond), there were not 600 adult right valves present in the volume of sediment collected, so all adult right ostracode valves were picked that were available. However, rarefaction analyses indicate that all rare species in these samples were adequately sampled with the number of valves counted, and a statistically robust sample was obtained.

Geochemical Analyses

The three species most commonly found, *C. americana*, *H. setipunctata*, and *P. bicelliforma*, were analyzed by Inductively Coupled Plasma-Source Mass Spectrometer (ICP-MS) for trace elements. Male and female *C. americana* were analyzed separately to determine if gender affects the ostracode's uptake of trace elements. In many organisms, male and female physiology tends to be significantly different. *Cyprideis americana* specimens were chosen to address this question because they are easily differentiated by gender. Thus, for all geochemical analyses, two *C. americana* valves were used, one valve per analysis for *H. setipunctata*, and two to three valves for *P. bicelliforma* (*sensu* Chivas et al., 1983). The number of valves varied, so that the mass of each sample analyzed was greater than 0.001 mg. Masses were measured on a Mettler Toledo® MX5 microbalance. Valves were cleaned with a 000 camel's hair brush and visually inspected with a binocular microscope. Cleaned ostracodes were placed in a bath of 100% reagent grade bleach for twenty-four hours for optimal cleaning without degradation. Samples were removed and rinsed three times with triple distilled (i.e. MilliQ®) water. To ensure cleanliness, a final visual inspection of the cleaned ostracodes was made with a binocular microscope at 40 x magnification.

Analyses of both the dissolved ostracode valves and water samples were performed on a Perkin-Elmer® Elan 6000 ICP-MS using a nickel sampler and skimmer cones. New Tygon or Teflon tubing was used. All plasticware was cold acid leached and soaked in MilliQ® water (18.2 megaOhm) prior to use. Standards were prepared fresh from certified standards from SPEX Corp. All standards and blanks were matrix-matched to the samples using the control acid blank prepared at the time of the dissolution. The external standards were prepared so as to bracket the approximate known concentrations of the given analytes. For calcium ratio samples, the standard cross-flow nebulizer paired with a Scott® double-pass spray chamber was used. Operating conditions were optimized to minimize oxide production. Dwell times were set at 10 ms with each analysis consisting of 350 sweeps per reading, one reading per replicate and ten replicates per analysis. Individual isotopes of the elements of interest were chosen to minimize isobaric overlap and maximize natural abundance. Data files were reprocessed using the Elan software and imported into a Microsoft Excel spreadsheet.

Quantitative Analyses

Alpha diversity was measured by rarefaction and Shannon Diversity Indices. Cluster analyses were also conducted to quantify the similarity according to distance and similarity measures. K_d values for Mg and Sr for the three species analyzed for each lake were calculated using the method outlined by Holmes and Chivas (2002). The data from Pigeon Creek were not used to calculate the K_d values because Pigeon Creek is a tidal estuary, and unlike all the other lakes, is connected by a major channel to the ocean. It was expected that the chemistry of Pigeon Creek would be too greatly influenced by oceanic waters to be a useful comparison.

RESULTS

Chemical Analyses

Lakes were sampled July. They varied significantly with respect to water chemistry. Average salinities in these lakes range from 23.5 to 225.5 ppt (Table 1). Measured pH values ranged from 8.0 to 8.6. Field measurements of salinity ranged from 12 ppt to 104 ppt. Mean temperatures varied between 23.9 to 31.6 °C. Mg/Ca ratios of the water ranged from 3.44 to 6.02; and water Sr/Ca ratios ranged from 0.01 to 0.07. Chloride concentrations in the water varied from 381 to 1963 mM with major cations being dominated by Na (1270-9870 mM), Mg (68-308 mM), Ca (8-62 mM) and K (1-20 mM). The Mg and Sr content of the water was used to determine ostracode K_d values.

Faunal Analyses

Alpha diversity (i.e. species richness for individual lakes) (N=11) plotted versus measured salinity (ppt) indicates that hypersaline lakes (e.g. Salt Pond, French Pond, Storr's Lake and Reckley Hill Pond) contain fewer species than lakes that are less saline (Figure 2). The lakes with lower salinities had a greater variance in species richness than the hypersaline lakes (Figure 2). Lakes with measured salinities from 35-52 ppt had species richness values that ranged from 5 to 19. However, lakes with salinities greater than 100 ppt had species richness values of 4 or lower (Figure 2). This is similar to Smith (1993), who found that at 350-450 μS/cm there was the maximum species richness, which declined after 750 μS/cm.
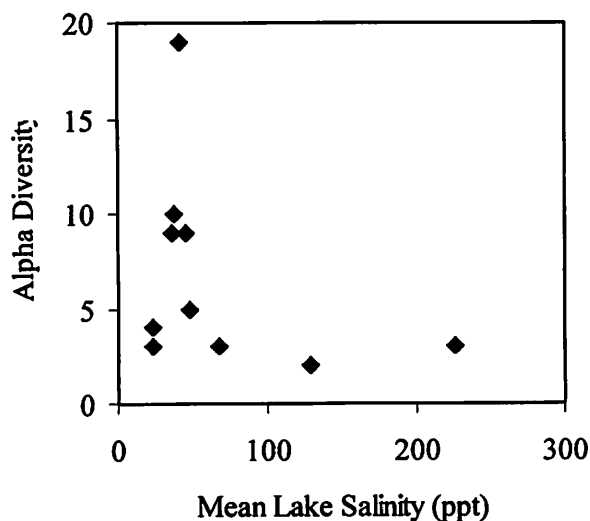

Figure 2. Scatter plot of mean host water salinity versus alpha diversity of all lakes in study. Mean lake water salinity (ppt) on x-axis; alpha diversity of each lake on y-axis. $R^2 = 0.14$.

There is a peak in alpha diversity at thirty-eight ppt (Figure 2). The apex in alpha diversity in a specific salinity range suggests that ostracodes live most effectively in that range of salinities. The highest alpha diversity is from Pigeon Creek, which is a tidal estuary and not an enclosed lake as are the other lakes in this study and may have higher alpha diversity for reasons other than optimal salinity. However, other lakes with

relatively similar salinities also showed higher alpha diversities, suggesting that salinity may play a significant role.

A rarefaction plot for all lakes shows that for all lakes except Pigeon Creek, the slope levels off at thirty to forty individuals (Figure 3). The alpha diversity of Pigeon Creek, which has the greatest diversity of all lakes sampled in this study, begins to level off at one hundred individuals. Since our sample counts were one hundred
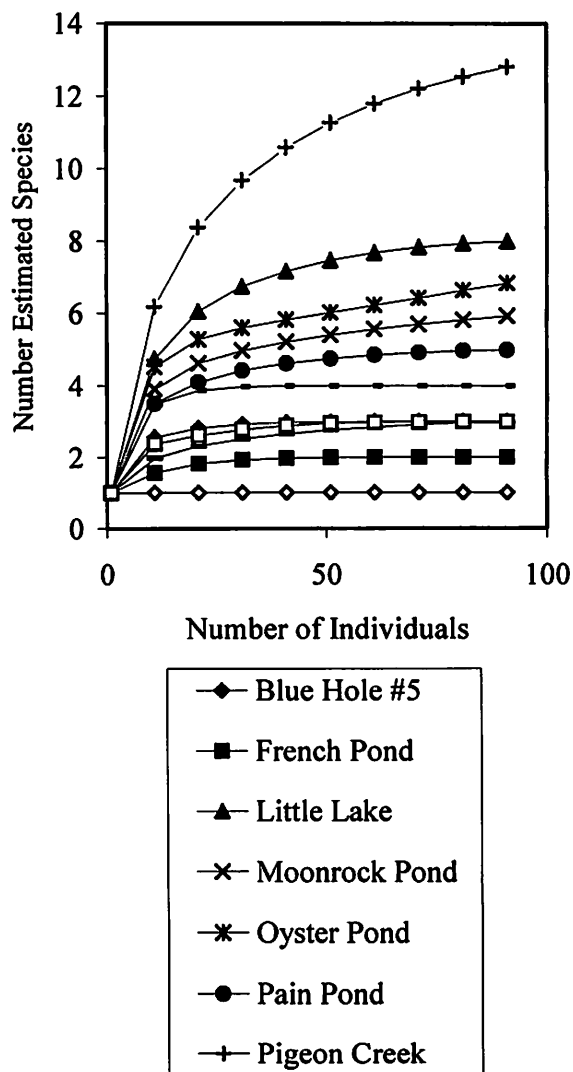

Figure 3. Rarefaction plot of number of individuals sampled versus number of estimated species for each lake in study. Number of individuals sampled on x-axis; estimated number of species on y-axis.

fifty per sample and approximately six hundred valves per lake, except for Salt Pond, French Pond, Pain Pond and Reckley Hill, which had 29, 239, 316 and 471 individuals counted respectively, our sampling method was effective in all cases since the rarefaction plot leveled off at a lower number of individuals than was collected.

Shannon Diversity Indices were calculated based on Shannon H' Log base 10, Shannon Hmax Log base 10, and Shannon J'. Pigeon Creek has the highest diversity index at 0.991, while Storr's Lake has the lowest at 0.027. Salt and French Pond have low indices at 0.111 and 0.213, respectively. Little Lake, and Moonrock, Oyster, Pain, and Reckley Hill Pond all have values between 0.55 and 0.73. The two "blue holes" have indices of approximately 0.4.

Detrended Correspondence Analyses of the fauna show similarity between lakes with similar salinities (Figure 4). For example, French and Salt Pond are plotted very close together and have similar species and water chemistries. Blue Hole #5 and Watling's Blue Hole also plot near one another as does Pain and Reckley Hill Ponds. Pigeon Creek and Storr's Lake are the least similar, despite being extremely close geographically. Little Lake and Oyster Pond also plot close to one another, despite having a great geographical distance between them.
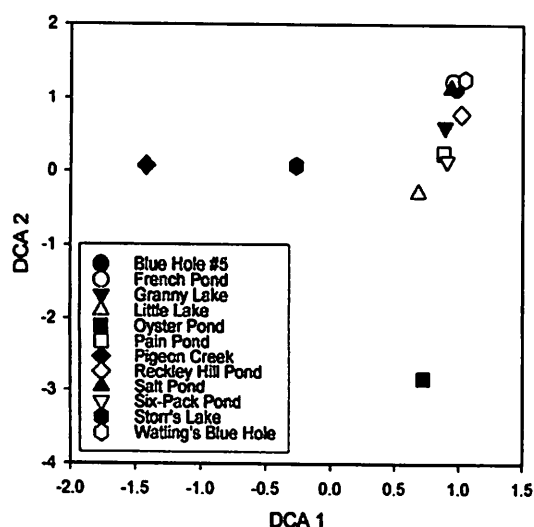
These trends and associations are corroborated by the Bray-Curtis cluster analysis showing the similarity of lake faunas in two-dimensional space (Figure 5). In this diagram, Salt and French Pond are clustered to themselves, with weak linkage to the other ponds or lakes. The two blue holes are also clustered together and linked to Pain and Reckley Hill Ponds. While the blue holes are close in proximity to each another and Pain and Reckley Hill Ponds are close in proximity to one another, neither grouping is in close geographical proximity to the other (Figure 1). Moonrock Pond, which is located in the northern part of the island in a group of karst-formed lakes that includes Oyster, Pain, and Reckley Hill Ponds is only weakly linked to those other ponds' faunas and shares the most faunal similarity with Pigeon Creek and Storr's Lake (Figure 5).
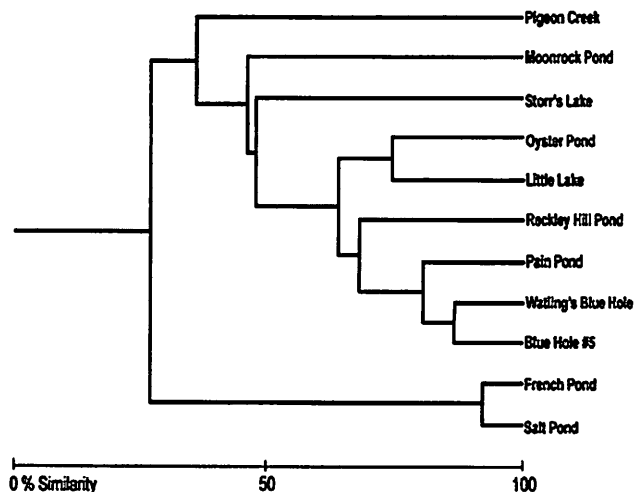

Figure 5. Bray-Curtis Cluster Analysis of lakes in study. Each lake shown on right side of dendrogram. Percent similarity on bottom.

Valve Chemistry

Mg/Ca and Sr/Ca ratios of the three ostracode species (*Cyprideis americana, Hemicyprideis setipunctata,* and *Perissocytheridea bicelliforma*) were calculated and plotted as a function of Mg/Ca and Sr/Ca ratios of the host water. Mg/Ca ratios for *C. americana* (male and female) and *H. setipunctata* had similar ranges (0.0131 to

Figure 4. Detrended Correspondence Analyses Plot for lakes in study. Axis 1 plotted versus Axis 2. Axes are functions of faunal populations.

0.0375), while ratios for *P. bicelliforma* were slightly higher from 0.0241 to 0.0397. There is a positive trend in Mg/Ca ratios for *C. americana* and *H. setipunctata* as the Mg/Ca ratios of the water increased. However, there was a slight negative trend between Mg/Ca ratios of the host water and Mg/Ca ratios of the carapace with *P. bicelliforma*.
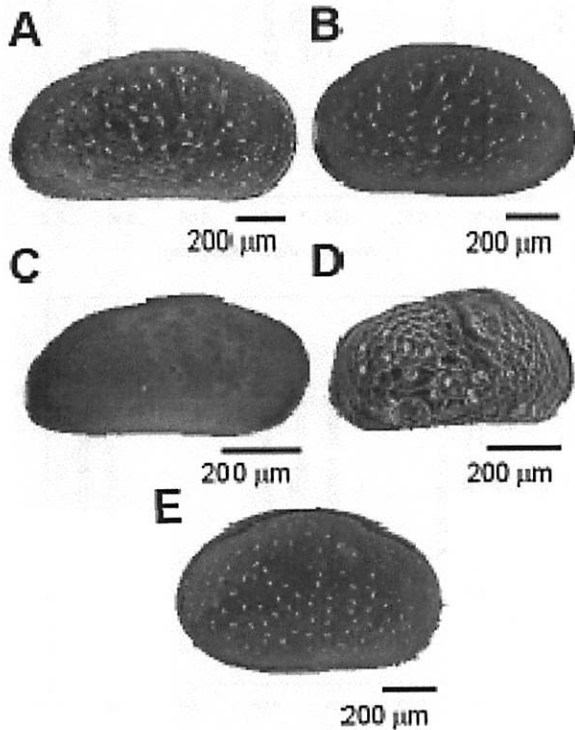

Figure 6. Scanning electron microscope images of the ostracodes used in the geochemical analyses in this study. A) Cyprideis americana *(male); B)* Cyprideis americana *(female); C)* Dolerocypria inopinata; *D)* Perissocytheridea bicelliforma; *E)* Hemicytheridea setipunctata. *All scale bars are 200 microns as indicated.*

The Sr/Ca ratios show a slightly different pattern. While all three species appear to have similar ranges (0.0034 to 0.0087), the lighter of the three, *P. bicelliforma* has a much wider range (0.0039 to 0.0085) than does *H. setipunctata* (0.0034 to 0.0059). This could be due to the fact that the latter species can be analyzed with a single valve, while the lighter species requires two to three valves per sample. Like the Mg/Ca ratios,

there is a positive trend between the Sr/Ca of the valves and water for *C. americana* and *H. setipunctata* but a slight negative trend for *P. bicelliforma*.

Mean ostracode valve mass was determined for the three species and plotted versus the $K_d[Mg]$ and $K_d[Sr]$ of those species, as calculated using the following equation:

$$K_D[M]_T = \frac{M/Ca_{valve}}{M/Ca_{water}}$$

Where M=Mg or Sr, T=temperature (°C), and M/Ca are molar ratios. K_d is the trace element uptake coefficient for a given element at a given temperature (Chivas et al., 2002).
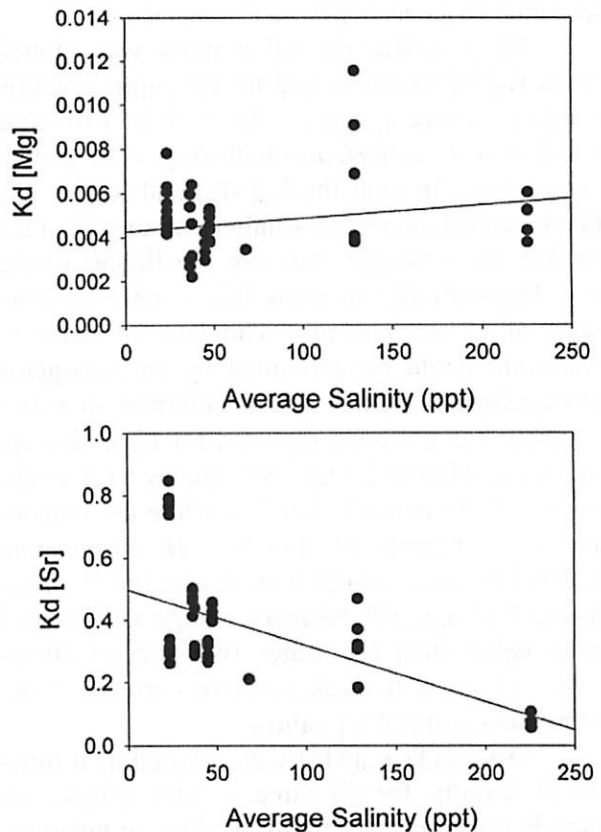

Figure 7. Scatter plots of mean water salinity versus $K_d[Mg]$ and $K_d[Sr]$ for ostracode valves of male and female Cyprideis americana, *as well as* Hemicyprideis setipunctata *and* Perissocytheridea bicelliforma.

Perissocytheridea bicelliforma is the lightest species (mean mass 0.004 mg); *H. setipunctata* is the heaviest (mean mass 0.110 mg). *Cyprideis americana* (both male and female) had a total mean value of 0.051 mg. There is a difference in mass between the males and females of *C. americana* of 0.002 mg. The 0.002 mg difference measured within the valves is within the resolution of the microbalance (+/- 0.001 mg). While there is a slight but not statistically significant overall negative trend (R^2= 0.018) between ostracode sample mass and K_d ratios for Mg, *P. bicelliforma* is statistically different (*p*=0.95) than either *C. americana* or *H. setipunctata*. This could be the case because *P. bicelliforma* is significantly lighter than the other two species. The K_d values for *C. americana* and *H. setipunctata* are most similar, yet their masses are very different, with *H. setipunctata* being more than twice as heavy as *C. americana*.

Mean ostracode valve mass was plotted versus K_d[Sr] as calculated by the same equation as above. There appears to be a slight difference in K_d[Sr] in *C. americana* with respect to gender (Figure 3B). In both the K_d[Mg] and K_d[Sr], the male *C. americana* has a smaller variance than the females, even though they are the lighter of the two. Interestingly, in some lakes, there were no males of *C. americana*. The lack of male *C. americana* could be explained by parthenogenic reproduction, which is not uncommon in ostracodes but has not been reported for *Cyprideis* sp. (Smith and Horne, 2002). The males have a narrower K_d[Sr] range (0.21-0.77), while the females have a wider range (0.11-0.79). *H. setipunctata* (0.18-0.79) has a similar wide range, but *P. bicelliforma* has a much narrower range and overall lower value than the other two species (0.06-0.43). There is a weak positive correlation between mass and K_d[Sr] values.

Ostracode K_d[Mg] were plotted as a function of salinity for all three species (Figure 6). There is no significant trend, positive or negative, between K_d[Mg] and salinity. While Teeter and Quick (1990) reported a negative trend and De Deckker et al. (1999), on a different species of *Cyprideis* from Australian lakes, reported a posi-

tive correlation, our data do not suggest any relationship between K_d[Mg] and salinity. In some of
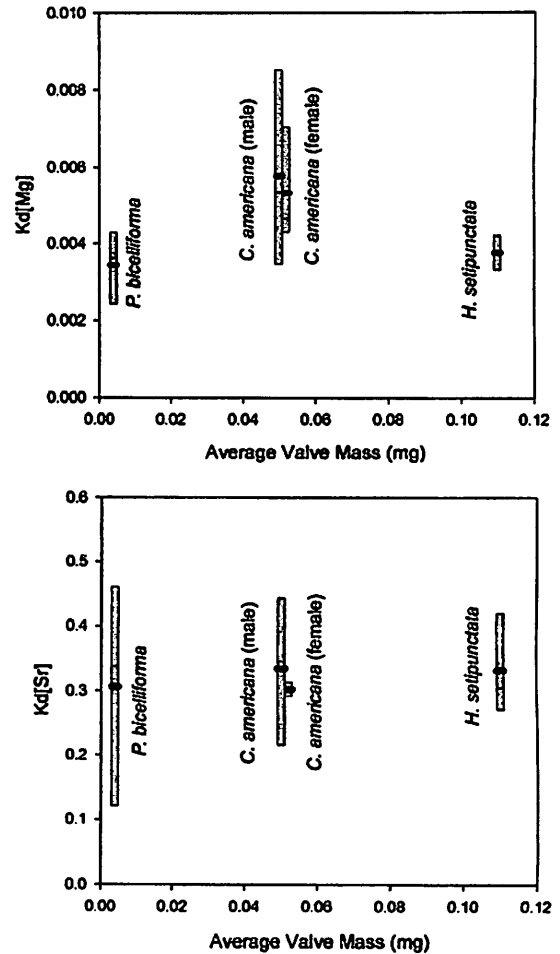

Figure 8. K_d[Mg] and K_d[Sr] vs average mass.

these lakes, dolomite may be forming and has been shown to form, which may account for this trend, as the Mg gets taken up in this process (Bain, 1991).

Examining K_d[Sr] versus salinity, there is a strong negative correlation between them (Figure 6). All three species have wider ranges at lower salinities (0.26 to 0.85), while in K_d[Mg], the higher values were found only in the *P. bicelliforma*.

Examining the male versus female Sr/Ca uptake ratios of *C. americana* suggests that male *C. americana* metabolize Sr differently than fe-

males (Figure 7). Statistically, the Sr/Ca ratios of *C. americana* are not the same between genders, as evidenced by t-test results ($p=0.95$), further suggesting that at least in some cases, the gender of the ostracode affects the calculated $K_d[Sr]$ for a given species. Despite this possible gender effect for Sr uptake, results of a t-test ($p=0.95$) on Mg/Ca ratios indicate that there is no significant difference between male and female *C. americana* for this ion. In both instances, more data would be useful to further test this relationship.

DISCUSSION

Results of this study indicate several important relationships regarding ostracode valve chemistry and host water as well as faunal affinities and distributions.

The lakes and ponds on San Salvador vary dramatically in size, chemistry, and faunal composition. Interestingly, some lakes that are the closest in geographic proximity have the greatest difference in fauna or in chemistry. This is similar to other invertebrates on the island and suggests that much of this distribution is based on chance. Other biotic factors, such as competing meiofauna or macrophytes may play a minor role, but similar biogeographic patterns also exist in ostracode faunas from the Great Plains of North America (A. Smith, personal communication) with little explanation other than random dispersal processes. Likewise, the lakes that are most similar in chemistry have differences in fauna. In general, lake formation and history on San Salvador is controlled by karst and geomorphic processes. The island's bedrock is dominated by marine and aeolian lithified carbonates, of both marine and aeolian origin. In addition, these lakes are not closed systems, but are connected via lake drains to each other and the ocean realm. The connection of the lakes to the ocean realm and to each other has an influence on ostracode shell chemistry as well as faunal distribution.

Faunal Distribution and Ecology

Alpha diversity is affected by lake salinity. Hypersaline lakes are less diverse than lakes with normal or average salinity. Less saline lakes have a greater variability with respect to species richness than hypersaline lakes. Data suggest that there is a "preferred" salinity for high alpha diversity, near marine salinities and the calcite branchpoint, even if the faunal populations are not similar for similar salinities. Lakes with extreme salinity ranges tend to be populated by a few cosmopolitan species that tolerate a wide range of salinities, while the faunal composition and distribution in lakes with lower salinities is most likely controlled by other factors, such as size, depth, substrate, longevity, basin history and biotic factors.

Rarefaction analyses indicate that species sampling was adequate to capture the diversity of each lake. In all cases, the sampling threshold was exceeded. This indicates that the underlying sampling was reflective of the ostracodes present in the lakes. The Shannon Diversity Indices calculated indicate that Pigeon Creek, which is a tidal estuary, was different from the rest of the lakes or ponds. This is not surprising because it is a well-documented bestiary for fish and mollusks (Godfrey et al., 1994).

Finally, the correspondence and cluster analyses were highly significant because not only did they corroborate one another, they indicated that 1) adjacent lakes are not necessarily similar in fauna, while lakes geographically separated by distance or barriers may be similar, and 2) lakes of similar chemistries did not always have similar faunas, yet the lakes with the most extreme salinities were the most similar in faunal composition. Interestingly, Salt Pond and French Pond, are not geographically close, therefore, their extreme conditions must be influencing the faunas. Cosmopolitan, euryhaline species (*P. bicelliforma* and *C. americana*) that can tolerate such hypersaline conditions populate these two lakes. The lack of clinal distribution of ostracodes within these lakes and ponds on such a small island (~153 km²) suggests that ostracode dispersal mechanisms remain enigmatic. The lake drains that connect these ponds and lakes to the marine cannot necessarily have that great an influence on species' presence or absence because then all lake and ponds would have similar or the same fauna. Likewise, the tra-

ditional explanation of dispersal via bird's feet may or may not have a role here. With such a small island and so many lakes and ponds, it would appear highly probable that they would have more similar faunas if birds were the predominant mechanism of dispersal. However, if birds were one of the primary mechanisms, then it would suggest that this type of dispersal event is rare in the ecological and evolutionary history of these organisms. Core studies have indicated presence of certain species and their disappearance due to environmental change (Sanger and Teeter, 1982). Whether or not this could explain the entire extant biogeographical distribution of these ostracodes is still not known. Further work, particularly with the fossil record via cores, is required to sufficiently address this question.

Geochemistry

The weak positive correlation between the Mg/Ca and Sr/Ca ratios of the host water and the resulting Mg/Ca and Sr/Ca ratios of the ostracodes that live in the water is consistent with other studies (Chivas et al., 1983; De Deckker et al., 1988; Holmes et al., 1992; Xia et al., 1997; De Deckker et al., 1998; Wansard et al., 1998). This is because the organism precipitates its valve from the contents of the host water, therefore relative concentrations of trace elements present in the host water will be reflected in the shell as it is being precipitated (Turpen and Angell, 1971).

The K_d uptake ratios for both Mg and Sr indicates that K_d is not necessarily dependent on ostracode valve mass (which is a function of valve thickness and density). However, *P. bicelliforma* may have a wider variance or higher K_d[Mg] and K_d[Sr] due to either its low mass or the fact that the measurements were made on more than one valve and thus averaged. These results are consistent with De Deckker et al. (1999) in that the partition coefficient appears to be species-dependent and K_d is most likely controlled by species and not mass. However, there are some concerns that *P. bicelliforma* is so weakly calcified as compared to the other two species in the geochemical analysis, that mass may still play a role, but only as a

function of varying physiological conditions of different species.

Perhaps most surprising are the apparent differences in male versus female Sr/Ca uptake ratios of *C. americana* ($p=0.95$). However, these results are understandable because most organisms in the animal kingdom have significant physiological differences between males and females. This is a potentially significant concern for future applications of trace element geochemistry for palaeoenvironmental reconstruction, as it makes it necessary to discriminate between a species' gender. It is also significant that there is no difference between male and female *C. americana* uptake of Mg ($p=0.95$). In both instances, additional studies need to be done to determine if this trend is present in other species and in *C. americana* in other locations.

The lack of any significant trend in Mg/Ca (valve)/Mg/Ca (water) as salinity increases for all species, is not consistent with De Deckker et al. (1999) or Teeter and Quick (1990). De Deckker and others (1999) noted this discrepancy between their findings and Teeter and Quick (1990), suggesting that the differences between these two previous studies was because Teeter and Quick did not measure the Mg/Ca of the waters in which they collected their ostracodes. In addition, it was also suggested that Teeter and Quick's samples might have been time averaged due to molting at different times of the year or transport due to strong tides or affected by formalin treatment after collection. Finally, De Deckker et al. (1999) suggested that the differences could be due to certain ostracodes being collected from high salinities and therefore were poorly calcified.

While these are conceivable explanations, data presented in this study indicate that none of the reasons given by De Deckker et al. (1999) are necessarily valid for the San Salvador system and the discrepancy between their results and that of Teeter and Quick (1990) may be due to the fundamental differences in the systems under study. Specifically, our data were collected and analyzed similar to De Deckker et al. (1999), measuring the Mg/Ca of the host waters and not preserving the valves in formalin. Time-averaging due to the differences in molting times was negligible be-

cause the overall trends are consistent with one another and therefore all species would have to have the same time-averaging problem in every lake, which is highly improbable due to differences in lake-basin size and sedimentation patterns. In addition, geochemical analyses were performed on ostracodes collected while still living in the water. Tidal influence for ostracode transport is also considered to be negligible because lakes adjacent to one another do not share similar faunal assemblages. If tidal influence was prominent, then lakes linked closely via karsted conduits would be more likely to share similar faunas, especially if they shared similar salinities. This is clearly not the case on SSI. Indeed, ostracodes are not the only species that show this disjointed distributional pattern on the island; bivalves, gastropods and crustaceans all show similar disconnectedness (Godfrey et al., 1994).

In addition, the fact that *P. bicelliforma* is so light in mass and poorly calcified, and that *H. setipunctata* is so heavy, yet their K_d values overlap, indicates that stress due to high salinity causing poor calcification in the carapace is not the case in this carbonate-dominated, open lake system. Because the SSI lakes are perched upon limestone carbonate bedrock and connected to the marine realm via lake drains, carbonate availability is not a problem, nor is availability of Mg or Sr as trace elements. Therefore, the differences in these trends may simply be due to the differences in the systems under study. The lakes on San Salvador are being continuously "refreshed" and carbonate is always available from both the host waters and underlying bedrock. These findings in no way invalidate the findings of De Deckker et al., (1999), but instead, help further support their findings by explaining, as they indicate, the only documented case where their relationships did not hold.

The wider range of Sr/Ca (valve)/Sr/Ca (water) values at lower salinity values for *C. americana, H. setipunctata* and *P. bicelliforma* indicates that valves from higher salinities have lower Sr/Ca (valve)/Sr/Ca (water) values and lower salinity valves can have higher or lower values. It is not a linear relationship and is consistent with De Deckker et al. (1999). This is also important to note, because it is consistent with the Mg/Ca (valve)/Mg/Ca (water) trends. This suggests that Mg and Sr are correlated in this environment.

CONCLUSIONS

The ostracodes from the lakes sampled for geochemistry on SSI indicate that there may be a slight difference between uptake ratios between different species. However, this is not necessarily related to individual species mass, but to some other vital effect. Likewise there appears to be a difference in the male and female uptake ratios of Sr for *C. americana* but not for Mg. In addition, it appears that lakes with higher salinity have less alpha diversity and those species present are most likely cosmopolitan and adapted to wide environmental tolerances. Interestingly, some of these hypersaline lakes lack males in some species, suggesting parthenogenesis under these extreme conditions. Finally, there is not necessarily a correlation between ostracode species distribution and lake-water chemistry. In some cases, such as the hypersaline lakes, there is. However, in the less saline lakes, species distribution appears to be influenced and controlled by other factors. Thus, faunal analyses alone may not be enough to reconstruct palaeoenvironments. Corroborative geochemical data should also be used, when and where possible.

Thus, our study yields significant implications for palaeoclimatological, palaeoecological and palaeogeographical investigations. First, before choosing to use ostracodes as geochemical proxy indicators for palaeoclimatological reconstructions, one needs to choose the species that not only is the most abundant, but has a well-calcified carapace to limit the amount of variability that exists in the lighter species, such as *P. bicelliforma*. Second, looking at the palaeoecological changes within a single lake system may not give you a complete picture of the ostracode fauna within that region. Since ostracode faunas can differ dramatically from adjacent lakes with similar chemistries, examining more than one lake, in this geographical context, is essential for under-

standing the entire ostracode fauna on this island. In addition, the presence or absence of a specific species does not always correlate to geochemical conditions. It is clear from our analysis that *C. americana* would be the best species for palaeoclimatological and palaeoecological studies in the future.

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