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THE INFLUENCE OF ENVIRONMENTAL GRADIENTS ON MOLLUSCAN DIVERSITY, COMMUNITY STRUCTURE, BODY SIZE, AND PREDATION IN A CARBONATE TIDAL CREEK, SAN SALVADOR (THE BAHAMAS)

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ABSTRACT. The ecosystem at Pigeon Creek in San Salvador, the Bahamas, provides a unique opportunity for the analysis of complex modern biological processes and how they operate within spatial and chemical gradients in order to assess the stratigraphic scale of the incipient fossil record. This study considers the influence of environmental factors upon molluscan diversity, body size, and predator-prey interactions in order to assess the role that gradients may play at a single horizon. Samples were collected from 26 different localities within a carbonate intertidal creek, Pigeon Creek. Molluscan samples were identified to species level, measured for specimen length and width, presence of a drill hole, and drill diameter, and ordinated using canonical correspondence analyses (CCA). The CCA ordination determined salinity to be the strongest influence of environmental gradients measured for both gastropod and bivalve distributions. Our results show that both molluscan diversity and median body size decrease as salinity concentrations move from marine to elevated salinity conditions. Predatory drilling frequency is not significantly influenced by salinity; however, there is a strong correspondence between predator and prey body size at marine to intermediate salinities, a relationship which dissipates at elevated salinities. This study reinforces the idea that small scale local environmental gradients can strongly influence biotic communities and that spatial and environmental variation must be considered in order to properly interpret temporal trends in the fossil record, even at sub-parasequence scales.

Keywords: Caribbean, community analysis, predator-prey interactions, substrate, salinity

INTRODUCTION

Environmental gradients are characterized by gradual and co-varying changes in physical, chemical, and biological variables, and they can strongly influence the composition and function of ecosystems (Whittaker, 1956; Brown, 1995; Heino, 2001; Patzkowsky and Holland, 2012). While ecologists can readily study these processes and their effects on biota in modern settings, paleoecologists are constrained to inferring circumstances that may have influenced ancient community structures in the fossil record. Paleontological studies have often determined environmental constraints on fossil distributions, a process readily performed through multivariate ordinations of taxon abundance or occurrence data (Springer and Bambach, 1985; Olszewski and Patzkowsky, 2001). As such, gradient analysis has been used for correlation (Miller and others, 2001; Scarponi and others, 2014), testing the sequence stratigraphic model (Scarponi and others, 2013), sequence stratigraphic interpretation in homogenous lithologies (Holland and others, 2001), the reconstruction of bathymetric trends through sea level cycles (Webber, 2002; Scarponi and Kowalewski, 2004; Scarponi and others, 2014; Wittmer and others, 2014), investigating ecosystem stability and evolution through geologic time (Holland and Patzkowsky, 2004; Holland and Patzkowsky, 2009; Ayoub-Hannaa and others, 2013; Kowalewski and others, 2015), quantifying the influence of eustatic cycles on biotic interactions (Huntley and Scarponi, 2012;

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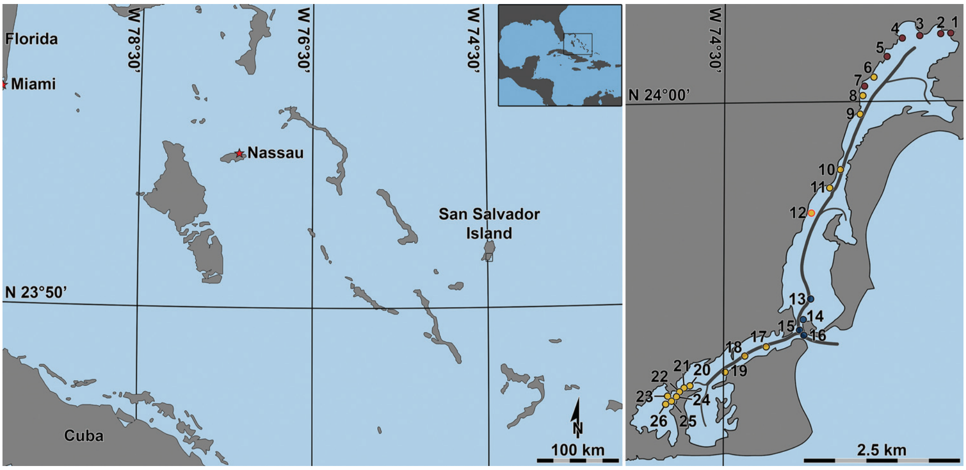

Fig. 1. Location of San Salvador in the Bahamas (left image). Major cities noted by red stars. Map of Pigeon Creek on San Salvador (from rectangle in left image), indicating the 26 sample localities color coded for salinity score (blue=<37ppt, yellow=37–42ppt, and red=42ppt) right image.

Huntley and others, 2014; Smrecak and Brett, 2014; Huntley and Scarponi, 2015), and investigating the relationship between taphonomy and fidelity (Tomašových and Kidwell, 2009a; Tomašových and Kidwell, 2009b). These studies validate the importance of understanding the associated complexities when using modern trends to interpret the fossil record. The inherent stratigraphic, taphonomic, and biological biases imposed by the fossil record must be considered for meaningful interpretations of paleoecological gradients. Most paleontological studies have investigated gradients at the regional scale, but here we investigate the relationship between environmental gradients and the macrobenthos at the local scale, effectively equivalent to Waltherian facies within a parasequence, forming in the incipient fossil record. Specifically, we investigate the influence of environmental gradients upon molluscan diversity, community structure, body size, and predator-prey interactions within a spatially restricted carbonate tidal creek, Pigeon Creek, San Salvador, the Bahamas.

MATERIALS AND METHODS

Study Site and Sampling

The island of San Salvador is located on the eastern margin of the Bahamas within the sub-tropical region of the western Atlantic Ocean (fig. 1). San Salvador was formed on an isolated carbonate platform during the Pleistocene, and, due to intense karst processes, is currently littered with lakes, ponds, and one tidal creek located on the southeast margin, Pigeon Creek. Pigeon Creek is an intertidal setting characterized by large spatial variation in salinity and spatio-temporal variation in temperature on both daily and seasonal scales (fig. 1). Pigeon Creek is 13 km long and, at its widest, one km across. The tidal channel diverges into two arms forming northern and southern channels, each of which reach a maximum depth of three meters. The substrates vary between coarse carbonate sand in the channel and fine sand with intermittent sea grass beds and shrimp mounds along the margins. The shrimp mounds are composed of coarse carbonate sediments with discontinuous organic detritus formed by burrowing callianassid shrimp (Jarochowska, 2012). The shallow northern and southwestern reaches of the creek experience increased temperature and salinity. Hydrodynamics vary based upon wind speed and tidal cycle but remained fairly strong in the channel

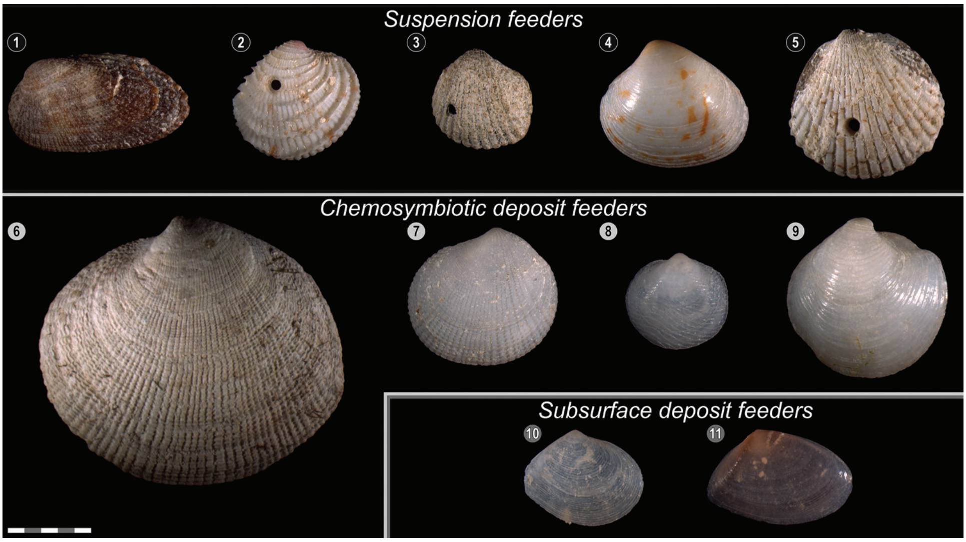

Fig. 2. Bivalve species analyzed in the CCA. Suspension feeders: 1. *Brachidontes exustus* 2. *Chione* sp. 3. *Ctenocardia guppyi* 4. *Transennella* sp. 5. *Tucetona pectinata*. Chemosymbiotic deposit feeders: 6. *Codakia orbicularis* 7. *Ctena* sp. 8. *Divalinga quadrinsulcata* 9. *Lucina pensylvanica*. Subsurface deposit feeders: 10. *Angulus merus* 11. *Angulus sybariticus*.

proper. Near the inlet, maximum water velocities of 25 m/minute were measured by Mitchell (1987). The community structure of Pigeon Creek is complex, with abundant benthic marine organisms including bivalves, gastropods, crustaceans, anemones, polychaetes, and echinoderms, specifically the keystone genus *Diadema*.

Data were collected in July 2015. Surface bulk samples of death assemblages from the uppermost one cm of sediment from approximately 3 m^2 were collected at 26 locations along a transect of the western perimeter of Pigeon Creek (fig. 1). All samples were taken from sites with a water depth of < 1 m. Samples were rinsed through a 5 mm sieve. Salinity and temperature measurements were taken at each locality using a YSI Model 30 Salinity/Conductivity/Temperature meter and categorized as low ($<$ 37 ppt), intermediate (37–42 ppt), and high ($>$ 42 ppt). Sediment type was categorized as either fine-grained carbonate sand (1), coarse-grained carbonate sand (2), or callianassid shrimp mounds (3). Whole specimens and uniquely identifiable fragments (gastropod apex or bivalve umbo) were counted and identified, when possible, to the species level (Redfern, 2013). All individuals from each sample site were photographed aperture or exterior side up and drill hole side up (when applicable) with a Nikon D3300 digital camera. Shell length, width, and drill hole diameter (when applicable) were measured from scaled photographs using ImageJ freeware (figs. 2 and 3). We measured outer drill hole diameter for bivalves (fig. 4) and inner drill hole diameter for gastropods (fig. 5) as the strong curvature and ornamentation of gastropods made the outer drill hole irregular in outline and unreliable as an index of size.

Quantitative Analyses

Taxa with fewer than 3 occurrences and samples with fewer than 20 individuals were not considered in multivariate ordinations and subsequent analyses in order to minimize the undue influence of rare taxa and small samples. The temperature, salinity, substrate type, and molluscan abundance data were subjected to three

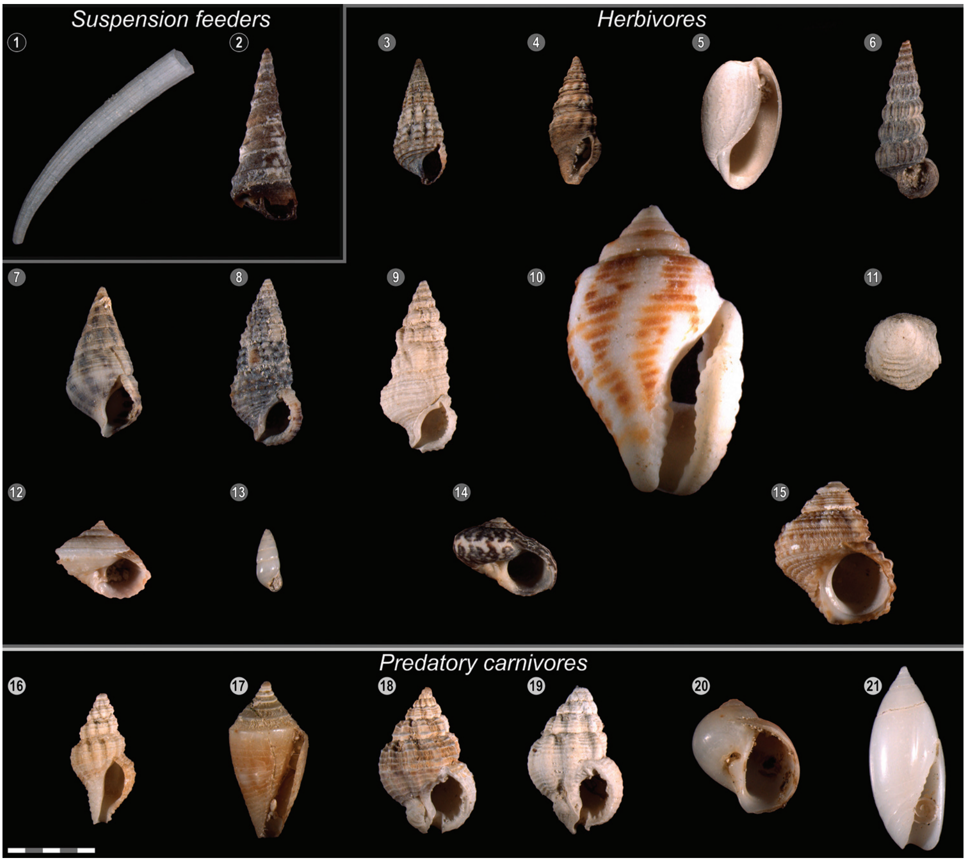

Fig. 3. Gastropod (and scaphopod) species analyzed in the CCA. Suspension feeders: 1. *Antalis* sp. 2. *Vermicularia spirata.* Herbivores: 3. *Batillaria minima* 4. *Bittium oryza* 5. *Bulla occidentalis* 6. *Cerithidea costata* 7. *Cerithium litteratum* 8. *Cerithium lutosum* 9. *Cerithium* sp. 10. *Columbella mercatoria* 11. *Hipponix antiquatus* 12. *Modulus modulus* 13. *Rissonia* sp. 14. *Tegula fasciata* 15. *Turbo castanea.* Predatory carnivores: 16. *Bailya parva* 17. *Conus flavescens* 18. *Nassarius albus* 19. *Nassarius ambiguus* 20. *Naticarius canrena* 21. *Olivella exilis.*

Canonical Correspondence Analyses (CCA; bivalves and gastropods separately and then combined), a common tool used to assess the influence of environmental gradients on the paleoecological distribution of taxa within the dataset using PAST v. 2.17c (Hammer and others, 2001; Holland, 2005). Water depth was not considered as it was uniform across sampled localities. Species richness, standardized richness (rarefaction analysis; bivalves: n=50; gastropods: n=38), Shannon index, and evenness metrics were calculated for each sample. Individual body size was calculated as the log2-transformed geometric mean of length and width. The relationships between body size of pooled and individual taxa and environmental variables (CC1 scores) were tested via ANOVA and Bonferroni-corrected Mann-Whitney *U* tests. Drilling frequency (DF) was calculated at the sample level for individual species. Drilling frequency for gastropods was calculated as the number of drilled shells divided by the total number of shells within a sample and for the bivalves as the number of drilled valves divided by half the total number of valves. ANOVA and Bonferroni-corrected Mann-Whitney *U* tests comparing DF binned by CCA scores were calculated (with a minimum of five taxon occurrences per bin) in order to test the influence of the environmental

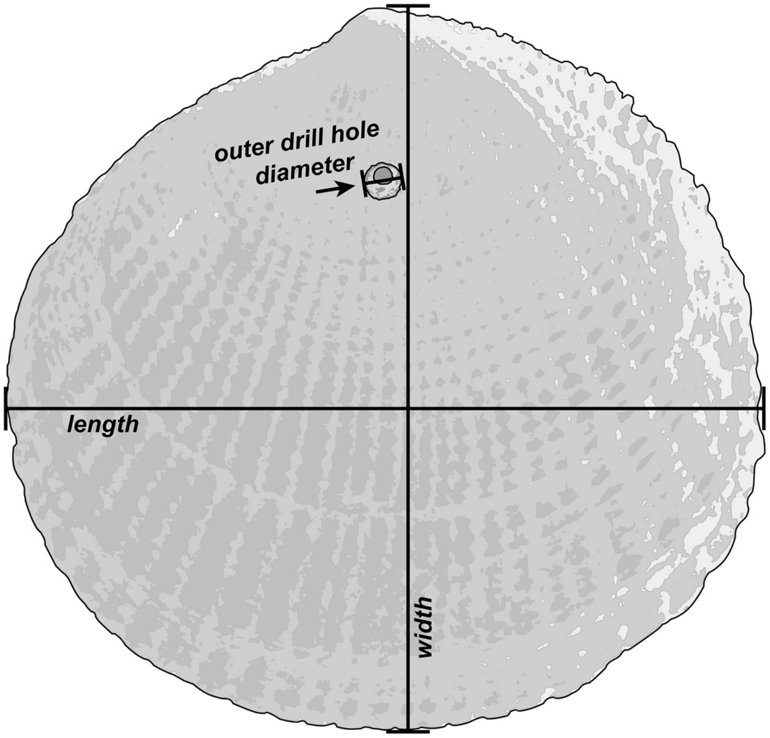

Fig. 4. Bivalve measurements including length, width, and outer drill hole diameter.

gradient on predator prey interactions. The influence of environmental gradient on the size selectivity of drilling predators was assessed by pooling body size data of drilled and non-drilled specimens of the most abundant gastropod taxon, *Cerithium* sp., and the most abundant bivalve taxon, *Ctena* sp., into CCA bins. Body sizes were compared between drilled and non-drilled specimens within each bin using Kruskal–Wallis and Kolmogorov–Smirnov tests. Each CC1 bin had a minimum sample size of 15 individuals. Pearson correlation coefficients between log2-transformed drill hole diameter and prey body size were calculated for *Cerithium* sp. from each CC1 bin. All statistical analyses were conducted in PAST v. 2.17c (Hammer and others, 2001), RStudio v.0.99.467 (R Core Team, 2015), and SAS v. 9.4 (SAS Institute, 1985). An $\alpha = 0.05$ is assumed for all analyses unless otherwise stated.

RESULTS

General Environmental and Ecological Survey

Recorded salinity concentrations were lowest at the mouth of the creek and increased towards the outermost regions of the channel arms (table 1). Water temperature primarily correlated with water depth, with lower temperatures measured at the mouth that increased toward the distal margins (table 1). Salinity and temperature measurements were collected in the morning hours, reflecting spatial variation between summer sampling locations, but do not capture any within location variation through time. A total of 3,425 uniquely identified bivalves from 16 taxa, 3,262 uniquely identified gastropods from 49 taxa, and 29 specimens of the scaphopod *Antalis* sp. were recovered from the 26 sampled localities. Scaphopods are benthic univalves that share

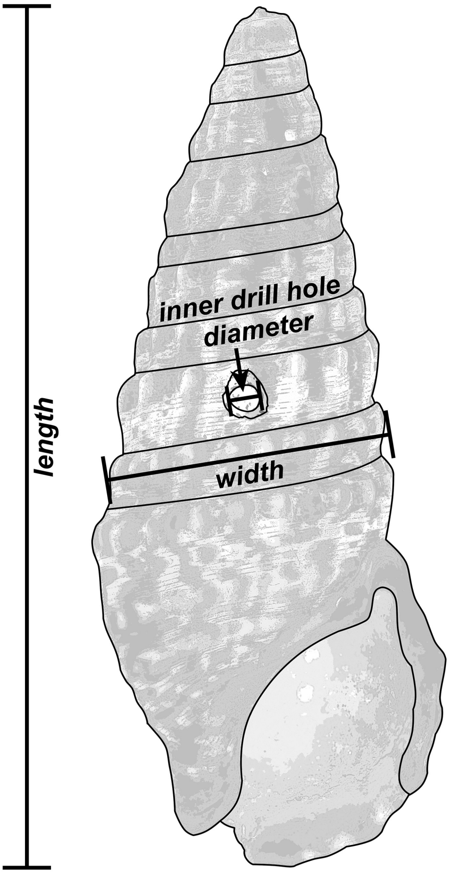

Fig. 5. Gastropod measurements including length (apex to aperture), width (widest portion of first whorl), and inner drill hole diameter.

similar feeding and life modes to the gastropods in this study and were therefore included with gastropods in further analyses. Removing *Antalis* sp. from the gastropod matrix did not appreciably affect the results of the CCA. The removal of rare taxa (fewer than 3 occurrences or 20 individuals) resulted in the loss of 0.005 percent of bivalve individuals (five taxa) and 0.0215 percent of gastropod individuals (29 taxa).

Canonical Correspondence Analysis

Site 12, with fewer than 20 bivalve and 20 gastropod individuals, was removed from consideration from all CCAs and subsequent analyses. These criteria resulted in data matrices of 3,220 gastropod individuals (21 taxa; table 2A) and 3,407 bivalve individuals (11 taxa; table 2B), greater than 99 percent of the total data by individual count, subjected to CCA ordinations.

Combined CCA.—CC1 of the combined gastropod and bivalve abundance matrices explained 80.7 percent of the variation in the data and displayed a strong positive correlation with salinity and a weak, negative correlation with temperature and sediment type (fig. 6). CC2 explained 19.3 percent of the variation and is moderately, positively correlated with salinity, temperature and sediment type. Samples are moderately dispersed in the combined taxa CC space in comparison to the gastropod and bivalve-based CCA ordinations.

Table 1

Sample location information, Pigeon Creek, San Salvador

Location Number	Latitude	Longitude	Salinity Score$^{\alpha}$	Mean Salinity (ppt)	Temperature (°C)	Sediment Type$^{\beta}$
1	24°0’40.8”	-74°27’37.7166”	H	45.7	32.4	3
2	24°0’40.6”	-74°27’45.4566”	H	44.6	31.7	1
3	24°0’40.1”	-74°27’58.1904”	H	43.8	31.6	1
4	24°0’37.7”	-74°28’10.7796”	H	42.9	29.5	1
5	24°0’27.6”	-74°28’20.7444”	H	43.1	29.6	3
6	24°0’15.6”	-74°28’29.784”	I	41.7	29.4	3
7	24°0’9.2”	-74°28’35.5368”	H	42.6	28.8	2
8	24°0’3.7”	-74°28’36.696”	I	41.8	28.6	2
9	23°59’53.6”	-74°28’37.815”	I	38.7	28.5	2
10	23°59’21.8”	-74°28’51.4302”	I	37.7	27.9	1
11	23°59’13.0”	-74°28’56.6076”	I	37.1	32.0	2
12	23°58’57.4”	-74° 29' 6.3	-	37.7	32.8	-
13	23°58’11.8”	-74°29’8.1558”	L	36.3	29.4	2
14	23°57’55.9”	-74°29’12.9048”	L	36.8	29.6	2
15	23°57’52.1”	-74°29’15.5322”	L	36.7	29.6	2
16	23°57’49.7”	-74°29’12.9264”	L	36.8	31.2	2
17	23°57’43.2”	-74°29’35.7714”	I	37.7	31.4	1
18	23°57’38.1”	-74°29’48.2856”	I	38.1	31.6	1
19	23°57’30.0”	-74°29’58.4802”	I	38.7	31.8	1
20	23°57’23.9”	-74°30’20.7894”	I	40.1	32.6	3
21	23°57’22.8”	-74°30’23.9178”	I	40.4	32.5	3
22	23°57’21.6”	-74°30’24.843”	I	40.3	32.4	3
23	23°57’20.3”	-74°30’30.135”	I	39.9	32.2	3
24	23°57’20.2”	-74°30’26.931”	I	39.1	32.2	3
25	23°57’19.8”	-74°30’28.6668”	I	39.7	32.4	3
26	23°57’18.4”	-74°30’30.4056”	I	39.8	32.3	3

Note: Sample location 12 was excluded for low sample size.
$^{\alpha}$Salinity score L=<37ppt, I=37-42ppt, and H=>42ppt.
$^{\beta}$Sediment type 1: Fine sand; 2: Coarse sand; 3: Shrimp mound.

Gastropod CCA.—CC1 explains 88.1 percent of the variation demonstrating a strong positive correlation with salinity (fig. 7A). CC2 explains 11.9 percent of the variation and displays a slight negative correlation with sediment type. Samples are least dispersed in the CC space defined by gastropods.

Herbivorous and suspension feeding taxa are distributed across the range of CC1 scores. Predatory gastropods occupy a large range along the CC1 axis, however these taxa are skewed towards lower CC1 scores (fig. 7A). The most abundant taxa (*Cerithium* sp., *Cerithium litteratum,* and *Modulus modulus)* tend to plot with intermediate CC1 scores while the second most abundant taxon, *Cerithium lutosum,* plotted at the high end of the CC1 axis (fig. 7A). On the CC2 axis herbivores plot throughout the full range of CC2 scores. Other feeding groups are more restricted with predators found to be skewed toward positive CC2 values, while suspension feeders are restricted to just two taxa. Although taxa representing both life modes were collected, there does not

TABLE 2A

Total abundance of gastropod taxa by sample location used in the ordination

Location Number	***Cerithium* sp.**	***Cerithium lutosum***	***Modulus modulus***	***Bulla occidentalis***	***Cerithium litteratum***	***Naticarius canrena***	***Batillaria minima***	***Nassarius ambiguus***	***Antalis* sp.**	***Hipponix antiquatus***	***Bailya parva***	***Tegula fasciata***	***Nassarius albus***	***Vermiculria spirata***	***Olivella exilis***	***Columbella mercatoria***	***Rissoina* sp.**	***Conus flavescens***	***Cerithidea costata***	***Turbo castanea***	***Bittium oryza***
1	72	24	8	10	0	1	0	7	8	0	0	0	0	0	0	0	0	0	1	0	0
2	45	67	0	5	0	0	0	3	3	0	0	0	1	0	0	0	0	0	0	0	1
3	41	14	5	7	0	1	0	0	4	0	0	0	4	0	0	0	0	0	0	0	0
4	93	233	22	7	0	2	17	8	9	0	0	0	0	0	0	0	0	0	3	0	0
5	15	107	10	0	0	1	18	0	3	0	0	0	2	0	0	0	0	0	0	0	0
6	31	0	5	10	6	0	0	2	0	22	5	0	2	0	0	0	0	0	0	0	0
7	30	3	14	3	11	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
8	12	1	10	3	3	0	0	1	0	0	2	0	1	2	0	0	1	0	1	0	0
9	30	4	17	1	8	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0
10	53	0	35	6	17	2	0	1	0	0	2	0	1	1	0	0	0	0	0	0	0
11	26	0	5	7	10	1	0	2	1	0	1	0	3	0	0	0	0	0	1	0	0
12	6	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	15	10	1	2	7	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
14	16	0	3	3	10	8	0	0	0	3	0	9	2	0	6	1	0	3	0	2	0
15	32	2	1	2	7	3	0	1	0	0	1	3	0	0	1	2	0	1	0	1	0
16	4	0	1	7	4	0	0	0	0	3	0	7	0	0	8	11	0	4	0	2	0
17	29	0	11	4	10	1	0	0	1	0	0	2	1	4	0	0	0	0	0	0	0
18	43	0	36	6	4	2	0	1	0	0	2	0	1	0	0	0	0	0	0	0	0
19	67	2	15	3	1	0	0	0	0	0	0	1	3	0	0	0	1	0	0	0	0
20	207	21	59	7	3	3	0	1	0	0	3	0	0	5	0	0	3	0	0	0	0
21	169	2	41	7	1	3	0	2	0	0	0	0	0	1	0	0	0	1	0	0	1
22	29	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	114	18	34	13	0	2	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0
24	131	13	40	4	0	2	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
25	77	5	29	3	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
26	252	22	59	18	3	1	0	1	0	0	3	0	0	0	0	0	4	0	0	0	0

Table 2B

Total abundance of bivalve taxa by sample location used in the ordination

Location Number	***Angulus merus***	***Angulus sybariticus***	***Brachidontes exustus***	***Chione sp.***	***Codakia orbicularis***	***Ctena sp.***	***Ctenocardia guppyi***	***Divalinga quadrinsulca***	***Lucina pensylvanica***	***Transennella sp.***	***Tucetona pectinata***
1	31	5	0	17	0	118	100	0	0	29	0
2	6	2	24	6	0	21	7	0	0	7	0
3	14	0	22	0	1	38	0	0	0	6	0
4	35	5	27	7	0	137	28	2	2	9	1
5	16	0	52	23	0	47	2	3	7	3	0
6	28	8	32	3	0	89	0	1	7	6	1
7	17	1	6	1	0	106	1	1	1	2	1
8	4	0	4	0	3	89	0	0	3	5	0
9	17	1	2	1	0	87	0	0	4	3	0
10	3	0	2	1	0	294	1	2	15	5	0
11	1	0	0	1	0	88	0	0	16	1	0
12	4	0	1	3	0	4	0	5	1	0	0
13	7	1	1	0	0	1	0	56	23	0	0
14	5	1	4	14	2	3	2	46	31	3	0
15	0	0	0	0	4	0	0	6	43	1	0
16	1	3	4	7	0	10	3	32	64	4	0
17	2	1	15	6	1	145	1	1	31	1	0
18	0	0	2	1	0	95	0	1	29	1	0
19	1	0	0	0	0	70	1	0	8	0	0
20	1	0	0	0	1	154	32	1	10	0	3
21	0	0	0	4	0	66	25	0	33	0	0
22	1	0	0	3	0	69	11	1	24	1	0
23	0	0	0	3	0	48	6	0	0	0	0
24	1	0	0	1	0	120	17	0	7	1	2
25	1	0	1	1	0	37	9	0	1	0	0
26	2	0	0	1	0	81	5	1	1	0	0

appear to be any systematic relationship between in-/epi-faunality and position in the CCA space.

Bivalve CCA.—CC1 explains 83.6 percent of the variation and is strongly, positively correlated with salinity (fig. 8A). CC2 explained 16.3 percent of the variation and is related to sediment type. As with the gastropod CCA, temperature explained little variation in the data. Samples are most widely dispersed in the CC space defined by bivalves in comparison to the gastropod and combined CCA ordinations.

Bivalves with chemosymbionts all report negative CC1 values. The lucinids *Lucina pensylvanica* and *Divalinga quadrisulcata* have the lowest CC1 values of any bivalve taxon; whereas the lucinids *Codakia orbicularis* and *Ctena* sp. display intermediate CC1 value. The suspension feeding taxa typically have positive CC1 values (the venerid *Transennella* sp. and the mytilid *Brachidontes exustus*) or positive CC2 values (the glycymerid *Tucetona pectinata*, the cardiid *Ctenocardia guppyi*, and the venerid *Chione* sp.). The subsurface deposit feeders all plot with high CC1 values (the tellinids *Angulus merus* and *Angulus sybariticus*) (fig. 8A). Similar to gastropods, both infaunal and epifaunal bivalves were collected and show no systematic difference in position in the CCA space.

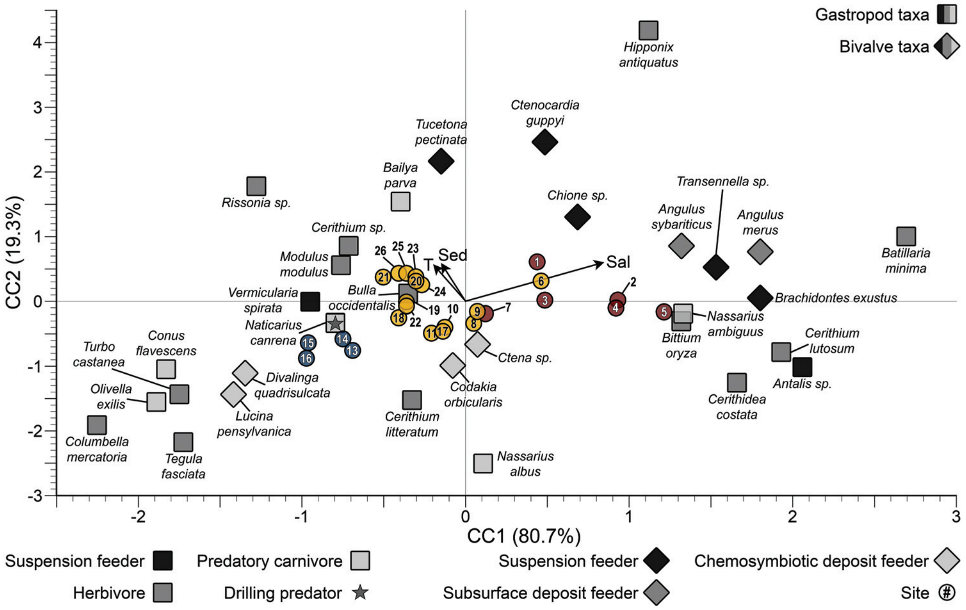

Fig. 6. Mollusk CCA. Sample sites color coded for salinity score (blue=<37ppt, yellow=37–42ppt, and red=42ppt), and molluscan species categorized by class and feeding mode. The loadings plot of the environmental variables correspond to their respective correlation coefficients.

The remainder of tests conducted in this study use CC1 scores to analyze the potential influence of the observed salinity gradient on diversity, body size, and predator-prey interactions, as salinity describes the most variation between/among the taxa and sampling sites in the CCA ordination. For clarity, salinity values have been categorized as low (< 37 ppt), intermediate (37–42 ppt), and high (> 42 ppt). CC1 bins were constructed at 0.5 unit intervals with a minimum of 15 species occurrences per bin between the values of −2.0 to 3.0 which represent increments along the salinity-driven environmental gradient.

Diversity

Gastropod diversity.—Species richness values for individual locations tend to increase as CC1 sample scores decrease (fig. 7C). As richness is often correlated with sample size, rarefaction analyses were conducted for each site in order to obtain comparable estimates of richness. Due to the shape of its rarefaction curve (fig. 7B), site 12 (n=14) was interpreted to be under-sampled and was removed from consideration in the ordination. Therefore, rarefied estimates of richness were calculated at n=38, the sample size of the second smallest sample (site 13). The rarefied data display a similar relationship to CC1 scores as the raw richness values, only muted, and will be referred to using the aforementioned salinity terms (low, intermediate, and high). The highest values for evenness are similarly found at sites with low CC1 values for sites 14, 16, and 22 where evenness values then drop off and taper with intermediate CC1 scores. Two smaller peaks in evenness are reported at sites 8 and 6, after which evenness values taper off again as CC1 scores continue to increase to high values. The Shannon diversity index follows similar trends with sites 16, 14, and 15 which report the highest diversity values at the lowest CC1 scores. Similar to the raw species count, the Shannon index value is uncharacteristically low at site 22 with the remaining scores oscillating between 0.89 and 1.83 (fig. 7C).

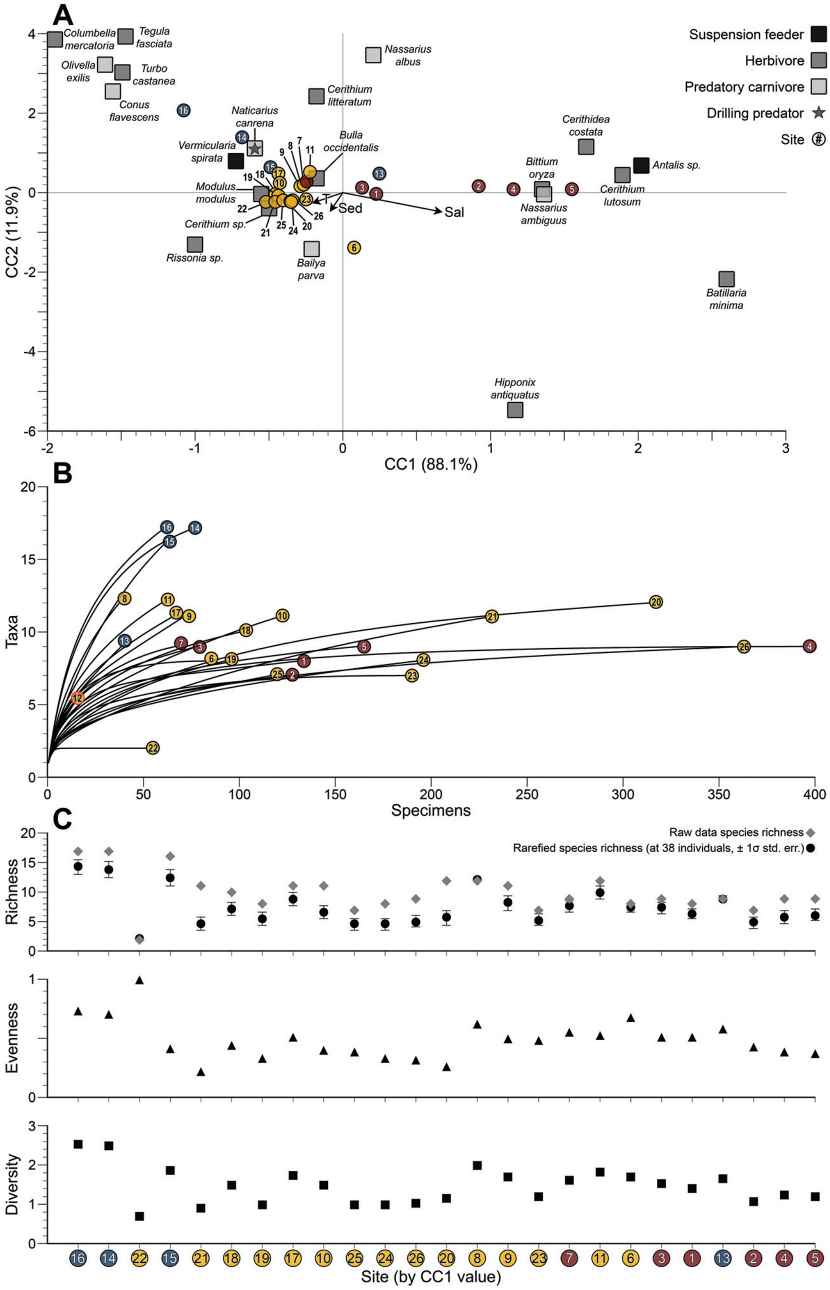

Fig. 7. Gastropod CCA. Sample sites color coded for salinity score (blue=<37ppt, yellow=37–42ppt, and red=42ppt), and gastropod species categorized by feeding mode (A). Rarefaction analysis (B) and diversity measurements (C), including species richness of both the raw data and rarefied species (gastropods: n=38), evenness, and Shannon index, compared to sample sites by CC1 value.

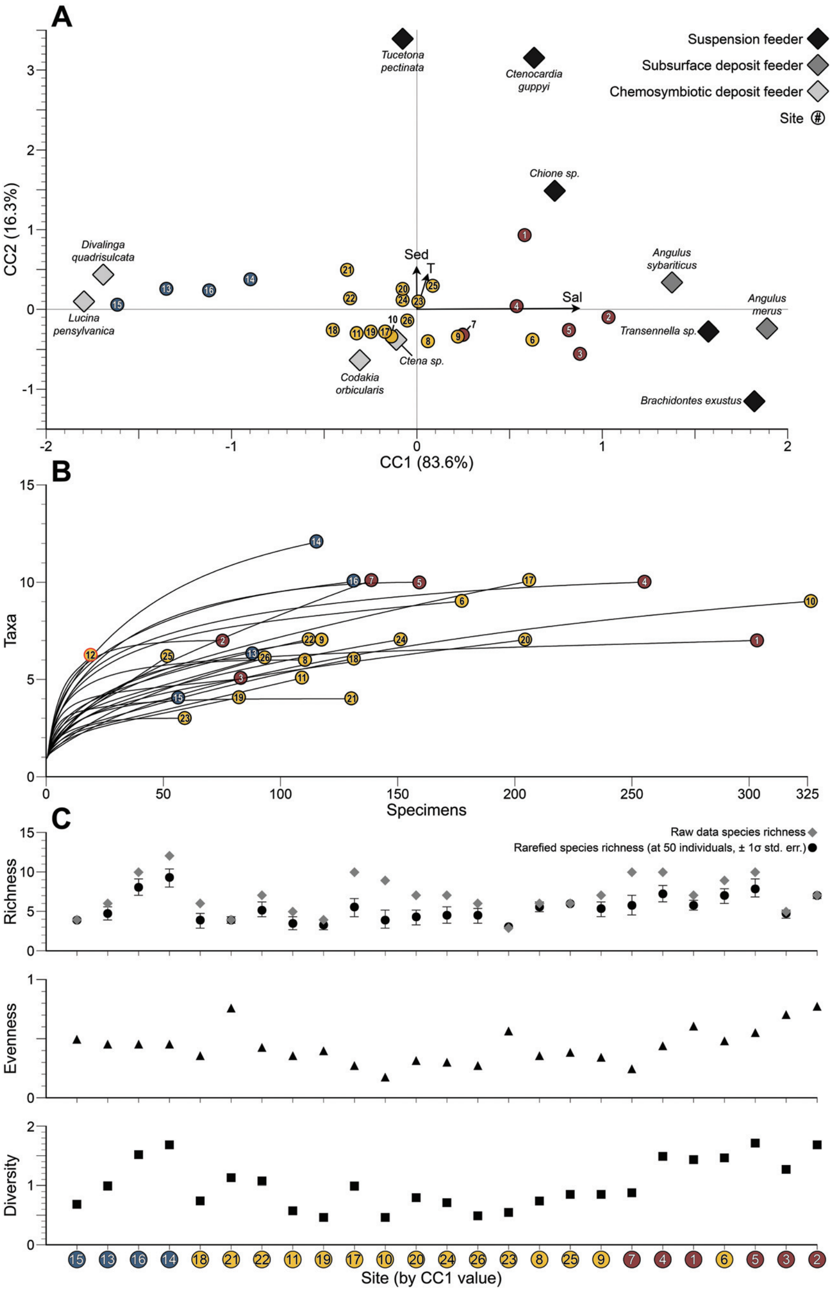

Fig. 8. Bivalve CCA of sample sites color coded for salinity score (blue=<37ppt, yellow=37–42ppt, and red=>42ppt) and bivalve species categorized by feeding mode (A). Rarefaction analysis (B). Diversity measurements (C) included species richness of both the raw data and rarefied species (bivalves: n=50), evenness, and Shannon index compared to sample sites by CC1 value.

Bivalve diversity.—Species richness for bivalve samples generally display peak richness values among low, intermediate, and high salinity samples. Rarefied estimates of bivalve richness were calculated at n=50, the sample size of the second smallest sample (site 25), as site 12 was removed from the CCA and further analyses (fig. 8B). The rarefied data display similar, though muted, peaks at low and high salinities, though the peak at intermediate salinity is notably absent (fig. 8C). Similarly, Shannon diversity values peak among low and high salinity samples, the latter being more apparent than that found in richness values. Bivalve sample evenness values are largely consistent across the salinity gradient with an interquartile range of 0.33 to 0.52 and displaying individual peak values (sites 21, 23, and 1) and individual low values (sites 10 and 7) (fig. 8C).

Body Size

Gastropod body size.—Median body size values of all gastropod individuals (pooled taxa) from each sample are greatest at low CC1 values and decrease with increasing salinity (fig. 9A). The ANOVA indicates a statistically significant difference in mean body size across CC1 bins (*p*=1.6E-68) (table 3A). Similarly, the Bonferroni-corrected pairwise Mann-Whitney tests resulted in statistically significant differences in median body sizes within CC1 bins for all comparisons (table 3A). Considering a single taxon that spans the CC1 axis, *Cerithium* sp., there is stasis in body size across the CC1 salinity gradient until reaching high CC1 values where there is a significant decrease in body size (fig. 9B). The ANOVA indicates a statistically significant difference in mean body size across CC1 bins (*p*=1.7E-15), however the Bonferroni-corrected pairwise Mann-Whitney tests displayed significant differences only among comparisons with high CC1 value samples (table 4A).

Bivalve body size.—When comparing body size of all bivalve taxa across the CC1 gradient, the mean and median body sizes are greatest at locations with low CC1 values, typically near the mouth of the creek (fig. 10A). Statistically significant differences are found for both the ANOVA test in mean body size (*p*=2.9E-127) and pairwise Bonferroni-corrected Mann-Whitney tests in median body size among CC1 bins (table 3B). The most abundant and widespread bivalve taxon, *Ctena* sp., demonstrated significant shifts in mean and median body size values (ANOVA *p*=6.2E-25; (fig. 10B; table 4B), though these do not seem to systematically co-vary with the salinity gradient.

Predator-Prey Interactions

Drilling predation on gastropods.—A total of 839 gastropods were found with drill holes (table 5A). An ANOVA of drilling frequency values of *Cerithium* sp., *Cerithium lutosum, Cerithium litteratum,* and *Modulus modulus* suggests a hint of a negative relationship, though not statistically significant (*p*=0.078), between predation intensity and CC1 bins (fig. 11). The influence of environmental gradient on the size selectivity of drilling predators was assessed by pooling body size data into CC1 bins and comparing the body size of drilled and non-drilled specimens of *Cerithium* sp. (fig. 13A) with a minimum of five individuals per sampling site and a minimum of 15 individuals per CC1 bin. Median body size values for drilled specimens in bin 2 (-0.5–0) are significantly lower than that of non-drilled valves (Kruskal–Wallis *p*=0.0013, Kolmogorov–Smirnov *p*=0.000016). A similar pattern is found in bin 4 (0.5–1.0), where drilled gastropods are on average smaller than their non-drilled counterparts (Kolmogorov–Smirnov *p*=0.015). The remainder of the data showed no significant difference in drilled vs. non-drilled body size among CC1 bins. Additionally, linear regression models using Pearson's r of drill hole diameter and prey body size were calculated for *Cerithium* sp. from each CC1 bin (fig. 13B). Significant positive correlations are reported in bins 1 (r=0.55, *p*=0.0057), 2 (r=0.35, *p*=1.1E-13), and 3 (r=0.46, *p*=0.00016), but not in bins 4 and 5.

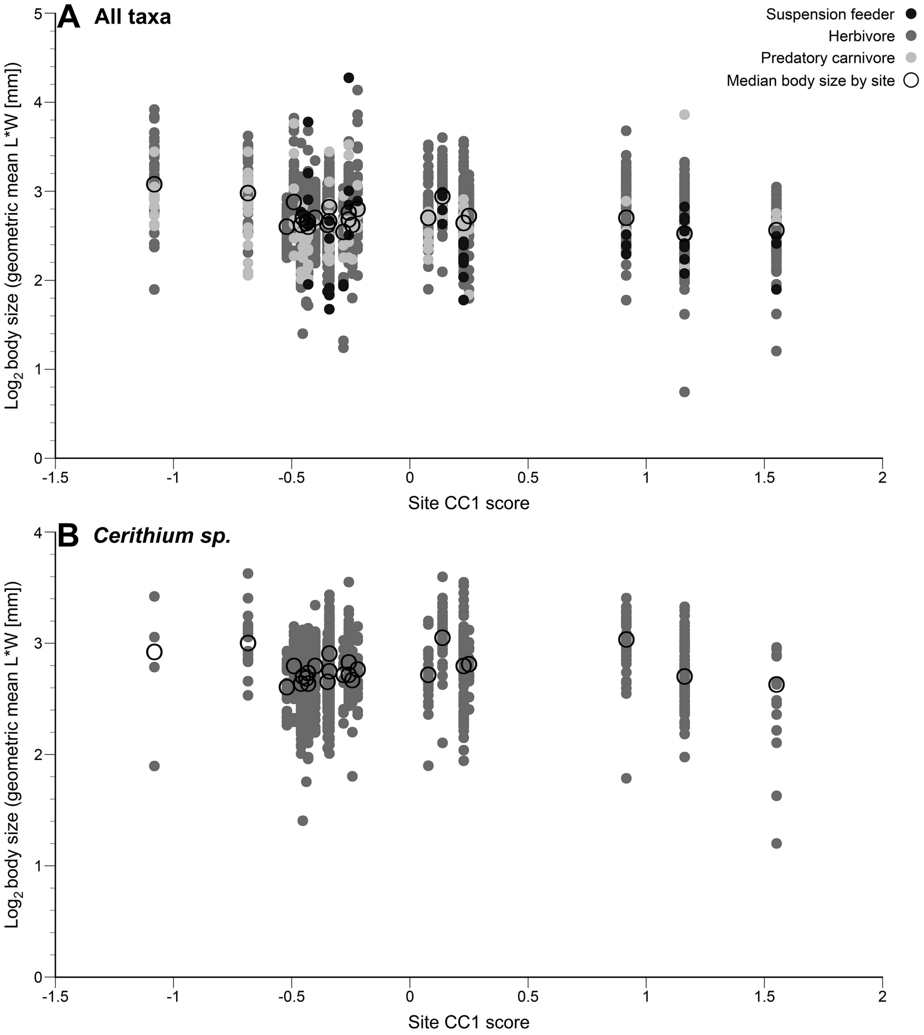

Fig. 9. Individual gastropod body size was calculated as the log2-transformed geometric mean of length and width for all taxa (A) and *Cerithium* sp. (B) plotted against the CC1 scores produced by the gastropod CCA plot.

Drilling predation on bivalves.—A total of 272 bivalves were found with drill holes (table 5B). An ANOVA of pooled drilling frequency values of *Ctenocardia guppyi, Angulus merus, Ctena* sp. and *Lucina pensylvanica* suggested no significant difference in mean taxon occurrence drilling frequencies across the salinity gradient (fig. 12). Gradient influence on size selectivity was assessed by pooling bivalve body size data into CC1 bins comparing the body size of drilled and non-drilled specimens of *Ctena* sp. (fig. 14A) with a minimum of five individuals per sampling site and a minimum of 15 individuals per CC1 bin. Both the Kruskal–Wallis and Kolmogorov–Smirnov tests indicated non-significant differences in body size within the salinity gradient bins. Linear regression models using Pearson's r of drill hole diameter and prey body size were calculated for *Ctena* sp. from each CC1 bin (fig. 14B). Significant positive

Table 3A

Summary statistics, one way ANOVA, and Kruskal-Wallis tests for body size of all gastropod taxa sorted by CC1 bin

	B	**C**	**D**	**E**	**F**	**G**	**H**
CC1 Bin	**(-1.5 to -1)**	**(-1 to -0.5)**	**(-0.5 to 0)**	**(0 to 0.5)**	**(0.5 to 1)**	**(1 to 1.5)**	**(1.5 to 2)**
Summary Statistics							
N	51	118	2048	316	125	393	156
Min (cm)	0.55	0.61	0.31	0.27	0.51	0.17	0.31
Max (cm)	1.17	1.07	1.26	1.06	1.1	1.16	0.89
Mean (cm)	0.92	0.82	0.79	0.79	0.80	0.73	0.73
Median (cm)	0.92	0.81	0.79	0.80	0.8	0.73	0.75
Variance	0.01	0.01	0.007	0.01	0.009	0.006	0.007
ANOVA	F = 58.14		*p*(same) = 1.586E-68				
Kruskal-Wallis	*Bonferroni Corrected*						
B (-1.5 to -1)	-	-	-	-	-	-	-
C (-1 to -0.5)	7.99E-06	-	-	-	-	-	-
D (-0.5 to 0)	7.83E-15	0.006402	-	-	-	-	-
E (0 to 0.5)	4.27E-10	1	0.1869	-	-	-	-
F (0.5 to 1)	6.42E-08	1	1	1	-	-	-
G (1 to 1.5)	1.90E-20	1.18E-18	1.97E-38	3.62E-22	2.84E-13	-	-
H (1.5 to 2.0)	1.17E-17	4.16E-12	3.13E-13	1.39E-11	3.52E-08	1	-

correlations are reported in bins 2 ($r=0.34$, $p=0.0008$) and 3 ($r=0.56$, $p=0.016$), but not in bin 4.

DISCUSSION

Ordination

This study utilized CCA ordinations to assess the influence of environmental gradients on the distribution of molluscan taxa throughout Pigeon Creek. As measured here, the salinity values, while admittedly lacking information on annual or longer term temporal variability, are broadly consistent with the salinity gradient reported by Mitchell (1987). This suggests consistent salinity values in this environment over the last 30 years. The combined gastropod and bivalve CC1 explains 80.7 percent of the variation in the data and displays a strong positive correlation with salinity and a weak, negative correlation with temperature and sediment type (fig. 6). Low CC1 values are indicative of typical open marine salinities and those with high CC1 values correspond to elevated salinities. CC2 accounts for 19.3 percent of the variation with a moderate, positive correlation with salinity, temperature and, sediment type, however the combination of these factors appears to only weakly influence taxon and sample distribution in the CC-defined space. While biotic patchiness can cause apparent high-frequency variation in ordination sample scores (Holland, 2005; Webber, 2005), we posit that our results accurately indicate an ecosystem structured along a salinity gradient due to large sample sizes, the removal of rare taxa, and consistency of ordinations across taxonomic groups. The influence of time-averaging is likely relatively low in Pigeon Creek. Despite a probable deep mixing zone brought

Table 3B

Summary statistics, one way ANOVA, and Kruskal-Wallis tests for body size of all bivalve taxa sorted by CC1 bin

CC1 Bin	A (-2 to -1.5)	B (-1.5 to -1)	C (-1 to -0.5)	D (-0.5 to 0)	E (0 to 0.5)	F (0.5 to 1)	G (1 to 1.5)
Summary Statistics							
N	54	217	111	1523	467	962	73
Min (cm)	2.77	2.3	2.45	1.11	1.03	1.51	1.79
Max (cm)	5.48	4.57	5.56	5.99	5.91	4.78	4.81
Mean (cm)	4.20	3.29	3.82	2.79	2.72	2.90	2.99
Median (cm)	4.31	3.27	3.74	2.77	2.69	2.87	2.80
Variance	0.34	0.20	0.39	0.17	0.23	0.20	0.55
ANOVA	F = 197.7		p(same) = 1.02E-216				
Kruskal-Wallis	*Bonferroni Corrected*						
A (-2 to -1.5)	-	-	-	-	-	-	-
B (-1.5 to -1)	8.51E-17	-	-	-	-	-	-
C (-1 to -0.5)	0.000484	3.17E-13	-	-	-	-	-
D (-0.5 to 0)	7.27E-30	7.17E-50	6.89E-50	-	-	-	-
E (0 to 0.5)	4.43E-28	1.73E-47	3.23E-45	0.000531	-	-	-
F (0.5 to 1)	5.43E-27	1.02E-26	4.60E-41	8.23E-10	9.31E-15	-	-
G (1 to 1.5)	5.60E-12	0.0002	1.48E-10	1	1	1	-

about by extensive bioturbation, the current tidal creek sediments are no older than 3,000 years (Curran and Williams, 1997; Curran and Martin, 2003).

When considering the gastropod CCA, the CC1 axis explains 88.1 percent of the variation, the most found among the three ordinations (fig. 7). Similar to the combined CCA, low CC1 values correspond to marine salinity conditions and high CC1 values indicate elevated to hypersaline conditions. The position of samples in the ordination space corresponds closely to the salinity gradient and in their approximate position relative to the mouth of Pigeon Creek. Herbivorous and suspension feeding gastropods are dispersed across the CC1 axis, indicating that salinity had no clear influence on the distribution of these taxa based on their feeding behaviors. Conversely, predatory gastropods, though occupying a relatively large range of the CC1 axis, are concentrated at low to intermediate values, indicating predatory gastropods are seemingly more restricted from living in and efficiently feeding in areas of elevated salinity as compared to gastropods at lower trophic levels. Some of the most abundant taxa (*Cerithium* sp., *Cerithium litteratum*, and *Modulus modulus)* have intermediate CC1 values due to their high abundance in slightly elevated salinity conditions, however they can be found at nearly all sample sites (fig. 7A; table 2A). *Cerithium lutosum*, the second most abundant taxon, however, plots on the right on the CC1 axis, indicating that it is not deterred by higher salinities, perhaps occupying less competitive, higher stress habitats. The gastropod CC2 axis explains 11.93 percent of the variation and is slightly correlated with sediment type, which plays a very small role in the distribution of taxa and samples, but may be considered as a secondary ecological factor, related to water energy, influencing community structure. Locations with fine-grained carbonate sand tend to have low CC2 values (< -1), while coarse-grained samples are

Table 4A

Summary statistics, one way ANOVA, and Kruskal-Wallis tests for body size of Cerithium sp. sorted by CC1 bin

CC1 Bin	**B (-1 to -0.5)**	**C (-0.5 to 0)**	**D (0 to 0.5)**	**E (0.5 to 1)**	**F (1 to 1.5)**	**G (1.5 to 2)**
Summary Statistics						
N	45	1272	158	46	93	15
Min (cm)	0.66	0.389	0.545	0.518	0.569	0.317
Max (cm)	1.076	1.044	1.064	0.998	0.978	0.87
Mean (cm)	0.807	0.799954	0.828177	0.877196	0.793968	0.709533
Median (cm)	0.81	0.803	0.835	0.8935	0.789	0.762
Variance	0.008352	0.005558	0.009576	0.006506	0.006397	0.024063
ANOVA	F = 16.09	*p* (same) = 1.656E-15				
Kruskal-Wallis	*Bonferroni Corrected*					
B(-1to -0.5)	-	-	-	-	-	-
C(-0.5 to 0)	1	-	-	-	-	-
D(0 to 0.5)	1	0.000517	-	-	-	-
E(0.5 to 1.0)	0.000249	1.12E-10	0.004931	-	-	-
F(1.0 to 1.5)	1	1	0.0279	2.07E-07	-	-
G(1.5 to 2.0)	0.8713	0.2383	0.02128	0.000121	0.6771	-

represented by intermediate CC2 scores (-1–2), and samples associated with shrimp mounds tend to have high CC2 scores (> 2). Herbivorous taxa occupy the full range of the CC2 axis, demonstrating that these gastropods are not likely to be limited by substrate type. There are, however, a greater amount of herbivores that plot between intermediate and high CC2 values which may show that they prefer to feed near the organic rich substrates provided by the shrimp mounds, as these are often associated with seagrass beds. Other feeding groups are more restricted, with predators found in areas of intermediate to high CC2 values, while suspension feeders are only seen at intermediate CC2 values (fig. 7A). Predatory drilling gastropods such as the naticids, are often found in sandy substrates (Huelsken and others, 2008), which is reflected in the CC2 plot with *Naticarius canrena* plotting at an intermediate value. The suspension feeders only represent two of the 21 overall taxa in the ordination and therefore cannot be accurately assessed based on the limited data.

The CC1 axis of the bivalve ordination accounts for 83.6 percent of the variation and similarly indicates a strong, positive correlation with salinity as low CC1 values are representative of normal marine conditions and high CC1 values correspond to elevated salinities (fig. 8A). Moreover, taxa and samples in the bivalve ordination are more evenly distributed along CC1 than those in the gastropod and combined taxa ordinations. Samples in the gastropod ordination were more clustered at intermediate CC1 values and taxa were distributed along a trend intermediate between CC1 and CC2. Samples and taxa in the combined taxa ordination displayed a pattern intermediate between those found in the bivalve and gastropod ordinations. This disparity between ordinations indicates: 1) of the environmental variables measured, salinity is the primary influence on the occurrence of bivalve taxa; 2) the occurrence of gastropods is controlled primarily by salinity and secondarily by substrate type, thereby

Table 4B

Summary statistics, one way ANOVA, and Kruskal-Wallis tests for body size of Ctena sp. sorted by CC1 bin. Asterisk indicates that the bin had <10 individuals and was therefore not considered for body size analysis.

CC1 Bin	**B (-1 to -0.5)**	**C* (-0.5 to 0)**	**D (0 to 0.5)**	**E (0.5 to 1)**	**F (1 to 1.5)**	**G (1.5 to 2)**
Summary Statistics						
N	11	3	1182	367	429	21
Min (cm)	2.68	-	1.53	1.03	1.84	2.26
Max (cm)	3.82	-	3.88	3.85	3.68	3.49
Mean (cm)	2.99	-	2.76	2.68	2.92	2.71
Median (cm)	2.89	-	2.77	2.70	2.97	2.67
Variance	0.11	-	0.08	0.13	0.11	0.11
ANOVA	F = 33.42	*p* (same) = 5.01E-27				
Kruskal-Wallis	*Bonferroni Corrected*					
B(-1to -0.5)	-	-	-	-	-	-
C(-0.5 to 0)	0.3719	-	-	-	-	-
D(0 to 0.5)	0.08099	0.000986	-	-	-	-
E(0.5 to 1.0)	1	5.03E-19	1.04E-19	-	-	-
F(1.0 to 1.5)	0.2629	1	1	0.04298	-	-
G(1.5 to 2.0)	0	0.03719	0.008099	0.8477	0.02629	-

resulting in an increased significance of CC2 among gastropods relative to bivalves; and 3) the clustering of samples in the gastropod ordination is the result of strong taxonomic overlap at low to intermediate salinity values. These results highlight the importance of exploring the role of taxon selection in multivariate ordinations and gradient analysis as taxonomic groups may differ in their response to these gradients.

Diversity

The richness, evenness, and diversity values in Pigeon Creek were assessed for both gastropods and bivalves. Gastropod measurements of diversity were all highest at sites with marine conditions (fig. 7C). Rarefaction revealed under-sampling at locations of near marine conditions, likely due to a high proportion of singletons found in these areas of increased diversity. As reported by Redfern (2013), the Bahamas contains a high number of very rare species. The raw species richness values displayed the highest number of taxa from sites with low CC1 values nearing marine conditions, with richness oscillating as CC1 increases in concert with elevated salinity values. Raw species richness is highest at near marine salinities, likely due to lower halo-tolerance-related stressors on the gastropods. In contrast, site 22 is characterized by unusually low richness, reporting only two species. This site is found near the distal end of the southern channel and may reflect low richness as a result of other abiotic stressors, though neighboring samples contain higher richness values. The rarefied data follow a similar trend as the raw data (with, on average, 2.6 fewer taxa per site), suggesting that under-sampling is not a widespread problem with our dataset. As salinity increases in the more distal regions of Pigeon Creek, conditions become less hospitable and the richness, evenness, and diversity of gastropods decline.

Conversely, bivalve species richness and diversity both display peaks at marine salinity and high salinity values and their feeding modes are more clearly delineated in

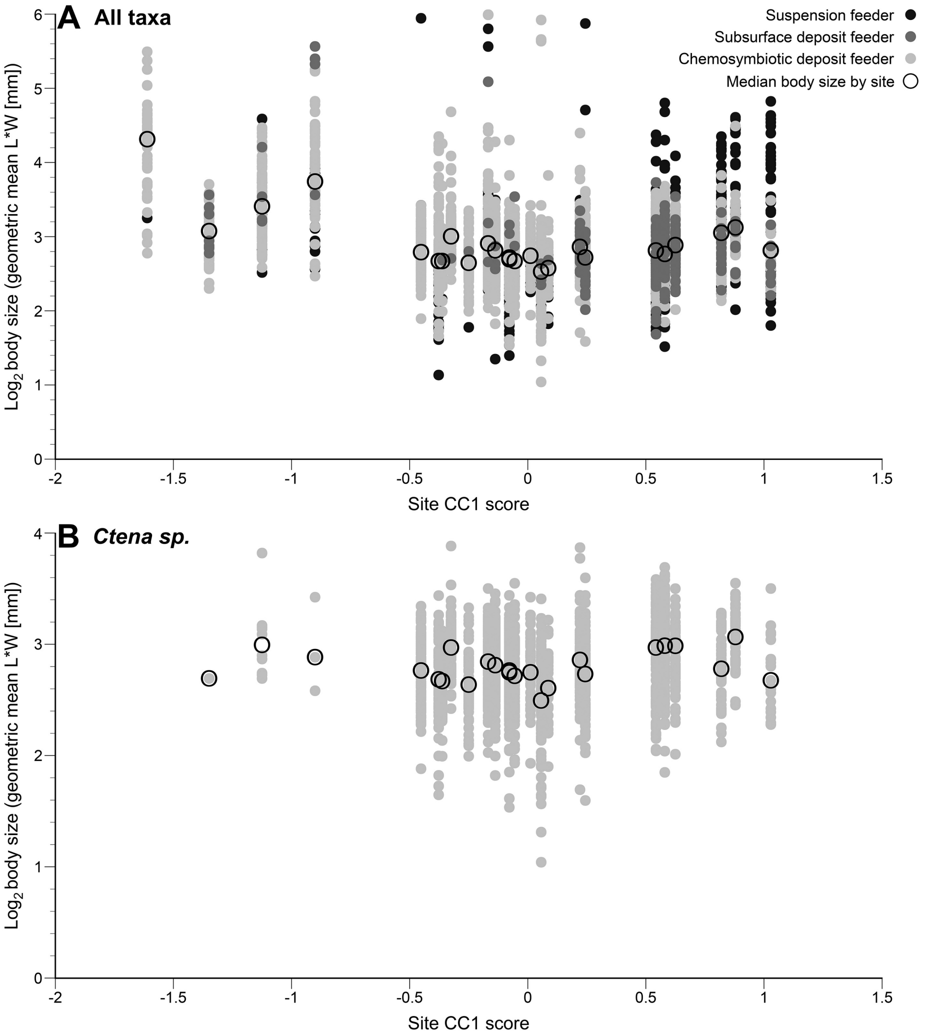

Fig. 10. Individual bivalve body size was calculated as the log2-transformed geometric mean of length and width for all taxa (A) and *Ctena* sp. (B) plotted against the CC1 scores produced by the bivalve CCA plot.

the ordination space than the gastropods (fig. 8C). Chemosymbiotic taxa (*D. quadrisulcata* and *L. pensylvanica*) dominate the marine salinity samples while deposit feeding taxa (*A. merus*, *A. sybariticus*, *Transennella* sp., and *B. exustus*) are predominant in elevated salinities. The chemosymbiotic *Ctena* sp., however, does not display salinity selectivity and is the most abundant taxon across the salinity gradient. Evenness values of bivalve samples fluctuate in a non-systematic manner relative to the salinity gradient. In general, there appears to be a group of bivalve taxa adapted to high salinity conditions, a group adapted to marine salinity conditions, and generalists that can tolerate the breadth of salinity variation in Pigeon Creek. The seemingly broader halo-tolerance of bivalves relative to gastropods helps explain the broad, and non-clustered, distribution of bivalve taxa within their CCA.

Table 5A

Total number of gastropod drilled taxa from each location. Periods represent a location with no observed drill holes.

Location Number	***Cerithium* sp.**	***Cerithium lutosum***	***Modulus modulus***	***Bulla occidentalis***	***Cerithium litteratum***	***Naticarius canrena***	***Batillaria minima***	***Nassarius ambiguus***	***Antalis* sp.**	***Hipponix antiquatus***	***Bailya parva***	***Tegula fasciata***	***Nassarius albus***	***Vermiculri a spirata***	***Olivella exilis***	***Columbella mercatoria***	***Rissoina* sp.**	***Conus flavescens***	***Cerithidea costata***	***Turbo castanea***	***Bittium oryza***
1	20	6	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	1	.	.
2	8	5	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
3	14	4	2	.	.	1	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.
4	22	47	2	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
5	1	16	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6	17	.	2	.	3	.	.	1	.	.	.	.	2	.	.	.	.	.	.	.	.
7	8	1	1	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8	6	.	2	.	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
9	7	1	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	24	.	8	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
11	12	.	2	1	4	1	.	1	.	.	.	.	3	.	.	.	.	.	1	.	.
12	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	10	6	.	.	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	6	.	2	.	4	2	.	.	.	.	.	3	2	.	1	.	.	.	.	.	.
15	29	1	.	.	6	.	.	1	.	.	1	1	.	.	.	1	.	.	.	.	.
16	4	.	.	.	2	.	.	.	.	.	.	4	.	.	1	.	.	1	.	.	.
17	4	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	20	.	5	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
19	28	1	4	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
20	73	11	14	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
21	69	.	16	.	.	1	.	2	.	.	.	.	.	1	.	.	.	.	.	.	.
22	18	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
23	27	3	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
24	40	8	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25	11	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
26	47	9	9	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.

Table 5B

Total number of bivalve drilled taxa from each location. Periods represent a location with no observed drill holes.

Location Number	***Angulus merus***	***Angulus sybariticus***	***Brachidontes exustus***	***Chione* sp.**	***Codakia orbicularis***	***Ctena* sp.**	***Ctenocardia guppyi***	***Divalinga quadrinsulcata***	***Lucina pensylvanica***	***Transennella* sp.**	***Tucetona pectinata***
1	1	.	.	1	.	3	11	.	.	2	.
2	1	1	.	.	.	1	1	.	.	.	.
3	2	.	.	.	1	.	.	.	.	.	.
4	3	1	1	1	.	9	2	.	.	.	.
5	3	.	2	6	.	4	.	.	.	.	.
6	4	.	.	.	.	6	.	.	.	1	1
7	4	.	.	.	.	4	.	.	.	1	.
8	.	.	.	.	.	4	.	.	1	1	.
9	1	.	.	.	.	5	.	.	.	1	.
10	.	.	1	1	.	19	.	.	.	1	.
11	.	.	.	.	.	5	.	.	1	.	.
12	.	.	.	1	.	.	.	.	.	.	.
13	.	.	.	.	.	.	.	3	3	.	.
14	1	1	1	2	.	1	.	4	1	.	1
15	.	.	.	.	.	.	.	.	4	.	.
16	1	.	.	.	.	1	.	5	6	1	.
17	1	1	.	1	.	17	.	.	2	1	.
18	.	.	.	.	.	9	.	1	4	.	.
19	.	.	.	.	.	2	.	.	.	.	.
20	.	.	.	.	.	8	7	.	.	.	.
21	.	.	.	1	.	11	10	.	.	.	.
22	.	.	.	.	.	9	4	.	.	1	.
23	.	.	.	1	.	2	.	.	.	.	.
24	.	.	.	.	.	13	3	.	.	.	.
25	.	.	.	.	.	3	1	.	.	.	.
26	.	.	.	.	.	2	1	.	.	.	.

Body Size

Median gastropod body size for pooled taxa is greatest at the low CC1 values, corresponding to near marine salinity conditions. Body size then gradually declines from the creek mouth toward the channel arms, before significantly dropping off at the highest salinity environments located in the most distal reaches of the creek (fig. 9A). The significant results from the ANOVA and pairwise Mann-Whitney tests allow us to reject the null hypothesis that there is no difference in body size central tendency across the salinity gradient for all taxa (table 3A). Median body size of *Cerithium* sp. exhibits stasis across much of the gradient and then decreases significantly across the most saline CC1 bins (fig. 9B). Salinity appears to influence gastropod body size hierarchically, both within and across taxa. These relationships between body size and salinity gradient are likely due to physiological stresses induced by elevated salinity concentrations, as organisms must have either a high tolerance to these conditions or the ability to regulate cationic concentrations internally (Shumway, 1996). We infer that these regulatory processes are energetically expensive and that, perhaps, the

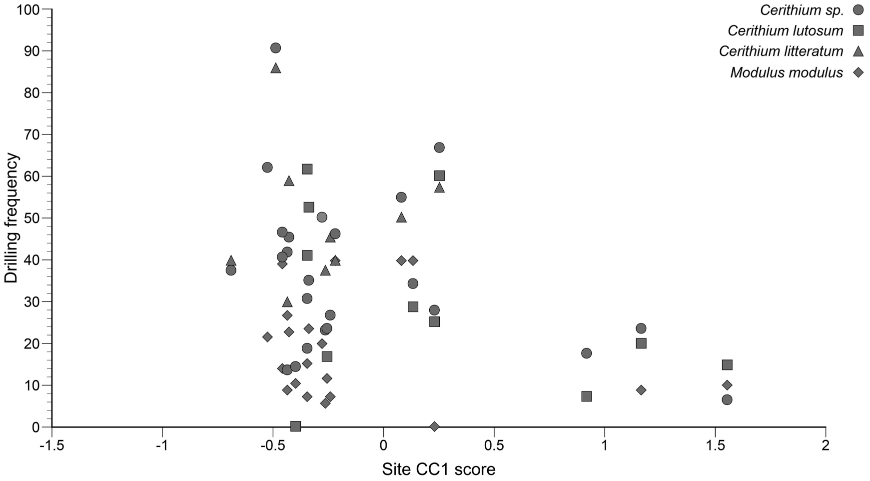

Fig. 11. Drilling frequency was calculated at each locality for the top four most abundant species (*Ceritium* sp., *Cerithium lutosum, Cerithium litteratum,* and *Modulus modulus*) as the number of drilled valves divided by the total number of valves within a sample plotted against the CC1 score produced by the gastropod CCA plot.

growth of some taxa may be limited due to energy costs being allocated to regulate physiological processes in high salinity environments.

Similarly, pooled bivalve taxa were largest in normal marine salinities and decreased in median size across the increasing salinity gradient (fig. 10A; table 3B). The widespread bivalve genus, *Ctena* sp., displayed significant variation in body size, however, size did not co-vary systematically with salinity (fig. 10B; table 4B). As seen with diversity and the multivariate ordinations, bivalves respond to the salinity gradient

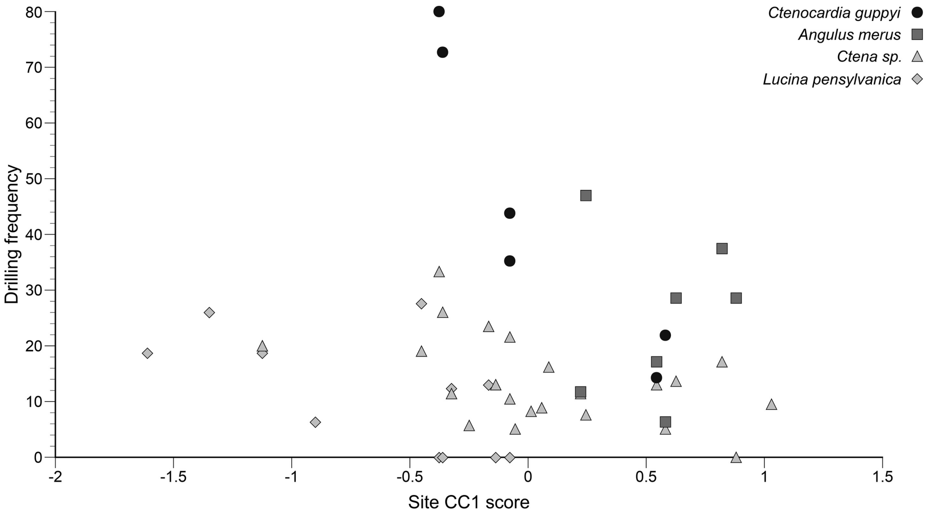

Fig. 12. Drilling frequency was calculated at each locality for the top four most abundant species (*Ctenocardia guppyi, Anulus merus, Ctena* sp., and *Lucina pensylvanica*) as the number of drilled valves divided by half the total number of valves plotted against the CC1 scores produced by the bivalve CCA plot.

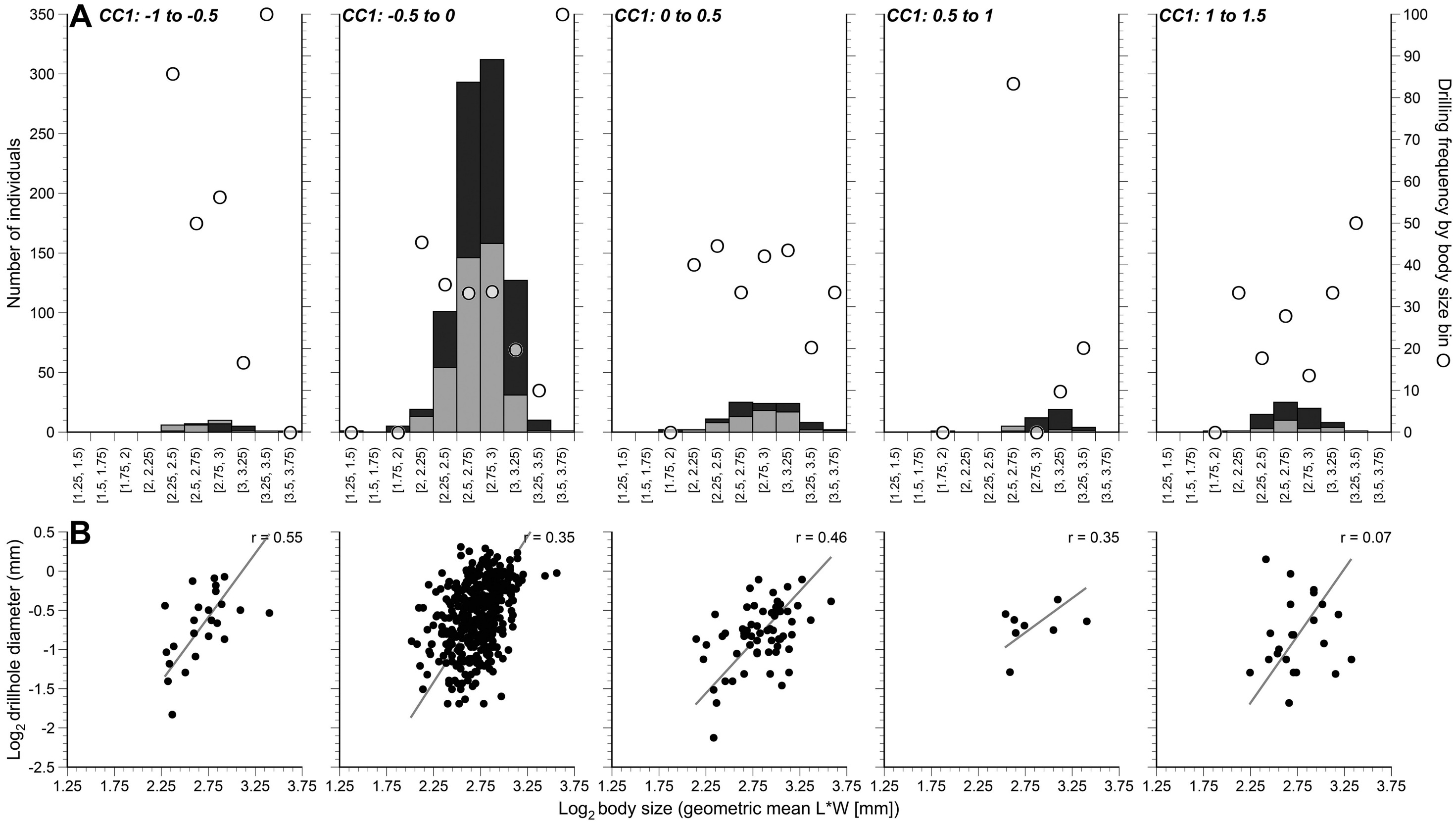

Fig. 13. The number of *Cerithium* sp. individuals for both drilled (light gray) and non-drilled (dark gray) body size data pooled into CCA bins based on the gastropod CCA with the drilling frequency calculated for each body size bin (A). Pearson correlation coefficients between log2-transformed drill hole diameter and log2-transformed prey body size were calculated for *Cerithium* sp. (B).

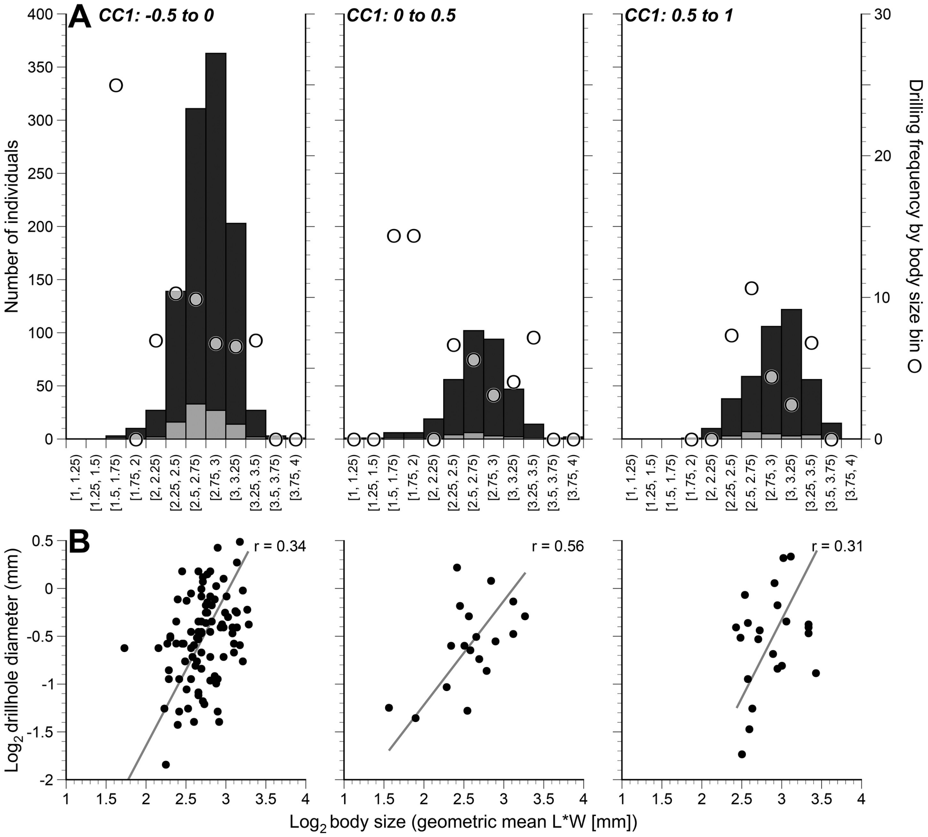

Fig. 14. The number of *Ctena* sp. individuals for both drilled (light gray) and non-drilled (dark gray) body size data pooled into CCA bins based on the bivalve CCA with the drilling frequency calculated for each body size bin (A). Pearson correlation coefficients between log2-transformed drill hole diameter and log2-transformed prey body size were calculated for *Ctena* sp. (B).

differently than gastropods. These results suggest that larger bivalve taxa are more likely to be found in normal marine salinities, but salinity does not influence body size within a single, wide spread taxon (unlike the gastropods).

Predator-Prey Interactions

No significant difference is present between drilling frequencies across the salinity gradient for the pooled individual species occurrence data of *Cerithium* sp., *Cerithium lutosum, Cerithium litteratum,* and *Modulus modulus* (fig. 11). A broad range of drilling frequency values are observed at intermediate salinities and then seemingly decrease with increasing salinity. As our test results are nearly significant (a relationship is possible, but not statistically demonstrated), we can only suggest that the "missing" elevated drilling frequency values are due to a sampling artifact, specifically at sites 2, 4, and 5, which have high CC1 values. The rarefaction curves for these specific sites, however, suggest adequate sampling of body fossils (fig. 7B), so it is likely that these samples are representative of predatory behaviors at these sites. These results demonstrate the patchy nature of predator-prey interactions, even along an environmental gradient. The influence of salinity on the size selectivity of drilling predators was assessed by comparing the body size of drilled and non-drilled specimens of *Cerithium* sp. within and among CC1 bins (fig. 13A). While bins 2 and 4 demonstrated significant differences in mean size between drilled and non-drilled valves, these differences were likely due to sample size biases. Bin 2 contains, by far, the greatest number of both drilled and non-drilled gastropods, as it encompasses the majority of both sites and individuals. Consequently, small differences in mean size are statistically, if not ecologically, significant. On the other hand, bin 4 only reports data collected from site 2. At this site, drilled gastropod body size data are skewed to smaller sizes in comparison to the larger non-drilled individuals. Therefore, it can be said that there is no significant systematic variation in predator selectivity of prey size across a salinity gradient. Additionally, size selectivity, as estimated by the correspondence between predator and prey body size, was assessed through the comparison of drill hole diameter and prey body size data for *Cerithium* sp. via linear regression models and Pearson's r from each CC1 bin (fig. 13B). Analyses in bins 1 to 3 resulted in significant positive correlations, indicative of smaller predators selecting smaller prey and larger predators selecting larger prey within marine to intermediate salinities. At elevated salinities, the results are nonsignificant, indicating that predators are less selective of their prey's size. It is possible that the random scattering of data, specifically in bin 5, is representative of random predatory attacks. As both predator and prey abundance are lowest and physiological stress is highest in elevated salinities, it is plausible that predators attack their prey at any size, preying upon that which is available.

Among the bivalve prey: 1) there was no significant variation in drilling frequency along the salinity gradient, 2) no significant difference in body size between drilled and non-drilled bivalves, and 3) a positive correlation between predator and prey body size that dissipates at elevated salinity. These results are similar to those of gastropod prey items, with the exception that the correspondence between predator body size and prey body size is lost in a lower salinity bin with bivalve prey than with gastropod prey. Again, it appears that salinity is only partially influencing the spatial trends in drilling predation, that being the loss of stereotypical size selectivity of predators at elevated salinities where drilling predators drill the prey items that are available, regardless of size. This loss of stereotypy is indicative of less efficient feeding as predators become unable to select optimally-sized prey in order to maximize predator-prey size ratios (Kitchell and others, 1981).

CONCLUSIONS

To accurately interpret the fossil record, it is vital to understand the complexities associated with modern biological processes and how they operate within spatial and chemical gradients. In this study, we have investigated the influence of environmental factors upon molluscan diversity, body size, and predator-prey interactions within Pigeon Creek, San Salvador, The Bahamas, in order to assess the role that gradients may play at a smaller scale in the incipient fossil record. The CCA ordination delineated the influence of environmental gradients, primarily salinity and secondarily water energy and sediment type, on gastropod and bivalve distributions. The gastropod CCA essentially describes an ecotone of advancing saline conditions with a transition between areas of marine to intermediate salinities to regions of elevated salinity. Herbivorous and suspension feeders can be found throughout Pigeon Creek, while predatory gastropods are skewed towards low CC1 scores, indicating that drilling gastropods prefer less physiologically stressful environments. The bivalve CCA describes a similar salinity pattern; however, samples are more widely dispersed in the bivalve CC space in comparison to the gastropod and combined CCA ordinations. Bivalves with chemosymbionts tend to plot at lower salinity values while suspension feeders and subsurface deposit feeders typically plot at elevated salinity values. Molluscan diversity appears to be greater at marine salinities owing to generally favorable biotic conditions and fewer abiotic stressors. Median body size data for pooled gastropod and bivalve taxa (respectively) decreases as salinity concentrations increase along the gradient. This is presumably due to increased salinity, which has been shown to increase embryonic mortality and decrease developmental rate (Przeslawski, 2004), and thereby may constrain body growth as harsher conditions make feeding and energy allocation more difficult. The body size of the widely dispersed gastropod genus *Cerithium* sp. decreases at only the highest salinities while the common bivalve genus, *Ctena* sp., does not appear to show systematic co-variation of body size with the salinity gradient. Thus, salinity appears to influence body size distributions by both restricting the occurrence of large bodied taxa and, as in the case of *Cerithium* sp., by limiting the growth of taxa that are present. In general, drilling predation frequency is not significantly influenced by salinity, however, the correspondence between predator and prey body size, which is strong at marine to intermediate salinities, breaks down at elevated salinities for both gastropod and bivalve prey. While predatory gastropods still occupy regions of elevated salinity, their ability to select optimally sized prey in order to maximize the cost:benefit ratio becomes limited. These results, addressing a broad range of topics of interest to paleoecologists, indicate that local environmental gradients too can have a strong influence on biotic communities. These influences may create patchiness in the distribution of fauna which may reflect the biotic composition of a localized region rather than being representative of the true biotic signal over time (Bennington, 2003; Holland, 2005; Webber, 2005). Similar to the stratigraphic paleobiology paradigm that warns against a literal reading of temporal trends in the fossil record without proper consideration of sequence stratigraphic context, we reinforce the idea that local, geographically restricted gradients can introduce bias at the scales of beds, bedsets, and parasequences. At most, the sediments at Pigeon Creek represent two or three facies in the incipient fossil record, yet patterns of diversity, body size, and predation are notably variable at this small scale. An implication of this for paleontologists is that spatial and environmental variation, even at the scale of local outcrops displaying similar facies, can significantly influence temporal trends and that it is imperative to collect multiple samples from “time equivalent” strata to account for this variation. This potential bias is likely limited by time averaging such that 10^2 to 10^4 years of generations of organisms and perhaps some range of the gradient, though spatial mixing is generally limited, is incorporated into a single horizon (Kowalewski, 2009; Kidwell and Tomašových, 2013).

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REFERENCES

Ayoub-Hannaa, W., Huntley, J. W., and Fürsich, F. T., 2013, Significance of Detrended Correspondence Analysis (DCA) in palaeoecology and biostratigraphy: A case study from the upper Cretaceous of Egypt: Journal of African Earth Sciences, v. 80, p. 48–59, https://doi.org/10.1016/j.jafrearsci.2012.11.012

Bennington, J. B., 2003, Transcending patchiness in the comparative analysis of paleocommunities: A test case from the Upper Cretaceous of New Jersey: Palaios, v. 18, n. 1, p. 22–33, https://doi.org/10.1669/0883-1351(2003)018<0022:TPITCA>2.0.CO;2

Brown, J. J., 1995, Macroecology: Chicago, University of Chicago Press, 284 p.

Curran, H. A., and Martin, A. J., 2003, Complex decapod burrows and ecological relationships in modern and Pleistocene intertidal carbonate environments, San Salvador, Bahamas: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, n. 1–4, p. 229–245, https://doi.org/10.1016/S0031-0182(02)00687-9

Curran, H. A., and Williams, A. B., 1997, Ichnology of an intertidal carbonate sand flat: Pigeon Creek, San Salvador Island, Bahamas, *in* Carew, J. L., editor, Proceedings of the Eighth Symposium on the Geology of the Bahamas and Other Carbonate Regions: Bahamian Field Station, San Salvador, Bahamas, p. 33–46.

Hammer, Ø., Harper, D. A. T., and Ryan, P. D., 2001, PAST. Paleontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4, n. 1, 9 p., http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Heino, J., 2001, Regional gradient analysis of freshwater biota: Do similar biogeographic patterns exist among multiple taxonomic groups?: Journal of Biogeography, v. 28, n. 1, p. 69–76, https://doi.org/10.1046/j.1365-2699.2001.00538.x

Holland, S. M., 2005, The signatures of patches and gradients in ecological ordinations: Palaios, v. 20, n. 6, p. 573–580, https://doi.org/10.2110/palo.2004.p04-28

Holland, S. M., and Patzkowsky, M. E., 2004, Ecosystem structure and stability: Middle upper Ordovician of central Kentucky, USA: Palaios, v. 19, n. 4, p. 316–331, https://doi.org/10.1669/0883-1351(2004)019<0316:ESASMU>2.0.CO;2

——— 2009, The stratigraphic distribution of fossils in a tropical carbonate succession: Ordovician Bighorn Dolomite, Wyoming, USA: Palaios, v. 24, n. 5, p. 303–317, https://doi.org/10.2110/palo.2008.p08-095r

Holland, S. M., Miller, A. I., Meyer, D. L., and Dattilo, B. F., 2001, The detection and importance of subtle biofacies within a single lithofacies: The upper Ordovician Kope Formation of the Cincinnati, Ohio Region: Palaios, v. 16, n. 3, p. 205–217, https://doi.org/10.1669/0883-1351(2001)016<0205:TDAIOS>2.0.CO;2

Huelsken, T., Marek, C., Schreiber, S., Schmidt, I., and Hollmann, M., 2008, The Naticidae (Mollusca: Gastropoda) of Giglio Island (Tuscany, Italy): Shell characters, live animals, and a molecular analysis of egg masses: Zootaxa, v. 1770, p. 1–40.

Huntley, J. W., and Scarponi, D., 2012, Evolutionary and ecological implications of trematode parasitism of modern and fossil northern Adriatic bivalves: Paleobiology, v. 38, n. 1, p. 40–51, https://doi.org/10.1017/S0094837300000397

——— 2015, Geographic variation of parasitic and predatory traces on mollusks in the northern Adriatic Sea, Italy: Implications for the stratigraphic paleobiology of biotic interactions: Paleobiology, v. 41, n. 1, p. 134–153, https://doi.org/10.1017/pab.2014.9

Huntley, J. W., Fürsich, F. T., Alberti, M., Hethke, M., and Liu, C., 2014, A complete Holocene record of trematode–bivalve infection and implications for the response of parasitism to climate change: Proceedings of the National Academy of Sciences of the United States of America, v. 111, n. 51, p. 18150–18155. https://doi.org/10.1073/pnas.1416747111

Jarochowska, E., 2012, High-resolution microtaphofacies analysis of a carbonate tidal channel and tidally influenced lagoon, Pigeon Creek, San Salvador Island, Bahamas: Palaios, v. 27, n. 3, p. 151–170, https://doi.org/10.2110/palo.2011.p11-063r

Kidwell, S. M., and Tomašových, A., 2013, Implications of time-averaged death assemblages for ecology and conservation biology: Annual Review of Ecology, Evolution, and Systematics, v. 44, p. 539–563, https://doi.org/10.1146/annurev-ecolsys-110512-135838

Kitchell, J. A., Boggs, C. H., Kitchell, J. F., and Rice, J. A., 1981, Prey selection by naticid gastropods: Experimental tests and application to the fossil record: Paleobiology, v. 7, n. 4, p. 533–552, https://doi.org/10.1017/S0094837300025574

Kowalewski, M., 2009, The youngest fossil record and conservation biology: Holocene shells as eco-environmental recorders, *in* Dietl, G. P., and Flessa, K. W., editors, Conservation Paleobiology: Using the Past to Manage the Future: New Haven, Connecticut, Yale University Printing and Publishing Services, p. 1–23.

Kowalewski, M., Wittmer, J. M., Dexter, T. A., Amorosi, A., and Scarponi, D., 2015, Differential responses of marine communities to natural and anthropogenic changes: Proceedings of the Royal Society B (Biological Sciences), v. 282, p. 2014–2990, https://doi.org/10.1098/rspb.2014.2990

Miller, A. I., Holland, S. M., Meyer, D. L., and Dattilo, B. F., 2001, The use of faunal gradient analysis for intraregional correlation and assessment of changes in sea-floor topography in the type Cincinnatian: The Journal of Geology, v. 109, n. 5, p. 603–613, https://doi.org/10.1086/321965

Mitchell, S. W., 1987, Sedimentology of Pigeon Creek, San Salvador Island, Bahamas, *in* Curran, H. A., and Gerace, D. T., editors, Proceedings of the third symposium on the Geology of the Bahamas: Ft. Lauderdale, Florida, CCFL Bahamian Field Station, p. 215–230.

Olszewski, T. D., and Patzkowsky, M. E., 2001, Measuring recurrence of marine biotic gradients: A case study from the Pennsylvanian-Permian Midcontinent: Palaios, v. 16, n. 5, p. 444–460, https://doi.org/10.1669/0883-1351(2001)016<0444:MROMBG>2.0.CO;2

Patzkowsky, M. E., and Holland, S. M., 2012, Stratigraphic paleobiology: Understanding the distribution of fossil taxa in time and space: Chicago, Chicago University Press, 274 p., https://doi.org/10.7208/chicago/9780226649399.001.0001

Przeslawski, R., 2004, A review of the effects of environmental stress on embryonic development within intertidal gastropod egg masses: Molluscan Research v. 24, n. 1, p. 43–63, https://doi.org/10.1071/MR04001

R Core Team, 2015, R: A language and environment for statistical computing, R Foundation for Statistical Computing: Vienna, Austria, https://www.R-project.org/

Redfern, C., 2013, Bahamian seashells: 1161 species from Abaco, Bahamas: Bahamianseashells.com, Incorporated, 501 p.

SAS Institute, 1985, SAS user's guide: Statistics, v. 2: Cary, North Carolina, SAS Institute.

Scarponi, D., and Kowalewski, M., 2004, Stratigraphic paleoecology: Bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy: Geology, v. 32, n. 11, p. 989–992, https://doi.org/10.1130/G20808.1

Scarponi, D., Kaufman, D., Amorosi, A., and Kowalewski, M., 2013, Sequence stratigraphy and the resolution of the fossil record: Geology, v. 41, n. 2, p. 239–242, https://doi.org/10.1130/G33849.1

Scarponi, D., Huntley, J. W., Capraro, L., and Raffi, S., 2014, Stratigraphic paleoecology of the Valle di Manche Section (Crotone Basin, Italy): A Candidate GSSP of the Middle Pleistocene: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 402, p. 30–43, https://doi.org/10.1016/j.palaeo.2014.02.032

Shumway, S. E., 1996, Natural environmental factors, *in* Kennedy, V. S., Newell, R. I. E., and Eble, A. F., editors, The Easter Oyster: *Crassostrea virginica*: College Park, Maryland, Maryland Sea Grant College, p. 467–513.

Smrecak, T. A., and Brett, C. E., 2014, Establishing patterns in sclerobiont distribution in a Late Ordovician (Cincinnatian) depth gradient: Toward a sclerobiofacies model: Palaios, v. 29, n. 2, p. 74–85, https://doi.org/10.2110/palo.2012.128

Springer, D. A., and Bambach, R. K., 1985, Gradient versus cluster analysis of fossil assemblages: A comparison from the Ordovician of southwestern Virginia: Lethaia, v. 18, n. 3, p. 181–198, https://doi.org/10.1111/j.1502-3931.1985.tb00697.x

Tomašových, A., and Kidwell, S. M., 2009a, Fidelity of variation in species composition and diversity partitioning by death assemblages: Time-averaging transfers diversity from beta to alpha levels: Paleobiology, v. 35, n. 1, p. 94–118, https://doi.org/10.1666/08024.1

——— 2009b, Preservation of spatial and environmental gradients by death assemblages: Paleobiology, v. 35, n. 1, p. 119–145, https://doi.org/10.1666/07081.1

Webber, A. J., 2002, High-resolution faunal gradient analysis and an assessment of the causes of meter-scale cyclicity in the type Cincinnatian Series (Upper Ordovician): Palaios, v. 17, n. 6, p. 545–555, https://doi.org/10.1669/0883-1351(2002)017<0545:HRFGAA>2.0.CO;2

——— 2005, The effects of spatial patchiness on the stratigraphic signal of biotic composition (type Cincinnatian Series; Upper Ordovician): Palaios, v. 20, n. 1, p. 37–50, https://doi.org/10.2110/palo.2004.p04-15

Whittaker, R. H., 1956, Vegetation of the Great Smoky Mountains: Ecological Monographs, v. 26, n. 1, p. 1–80, https://doi.org/10.2307/1943577

Wittmer, J. M., Dexter, T. A., Scarponi, D., Amorosi, A., and Kowalewski, M., 2014, Quantitative bathymetric models for Late Quaternary transgressive-regressive cycles of the Po Plain, Italy: The Journal of Geology, v. 122, n. 6, p. 649–670, https://doi.org/10.1086/677901