

The effect of seasonal sea level changes on tropical intertidal foraminiferal assemblages of Trinidad (southeastern Caribbean Sea)

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Abstract

The foraminiferal communities of Caroni Swamp and Claxton Bay (W Trinidad, SE Caribbean Sea) were monitored monthly for two and one years, respectively, from March 2011 to July 2013. The foraminiferal assemblages of Caroni Swamp were previously examined in May 2006, when the assemblages occupied Zones I, II and III constrained by high, mid and lower elevations relative to the tidal frame. Q-mode cluster analyses of the total (live + dead) foraminiferal recovery from stations sampled at Caroni Swamp and Claxton Bay were performed in conjunction with that of stations sampled at Caroni Swamp in 2006, in separate analyses for each sample occasion. The stations that clustered in Zones I, II and III changed between sample occasions, which indicated species moved between stations and elevations of a sample site, and this often coincided with seasonal change. Seasonal flooding would cause the tidal range to extend landward during the wet season and regress during the dry season. Seasonal movement of foraminiferal assemblages cause dead tests to mix across zones. Therefore, the foraminiferal assemblages at Caroni Swamp and Claxton Bay did not show a clear vertical zonation that was fixed over time.

Keywords: foraminifera, intertidal, assemblages, tropical, seasonal, sea-level, flooding

INTRODUCTION

Intertidal foraminiferal communities are often described by separating the metacommunity (all stations) into zones (groups of stations populated by similar species) that are constrained by elevation (Scott & Medioli, 1978, 1980). The vertical distribution of foraminiferal species is tied to aerial exposure of the surface sediment between high and low tides, which influences the concentration of dissolved oxygen and salinity (Horton & Murray, 2006). Increased aerial exposure above mean high water results in increased dissolved oxygen and salinity (the latter being due to evaporation). Foraminiferal assemblages at higher elevations are almost exclusively agglutinated (Scott *et al.* 2001) while calcareous species inhabit lower elevations.

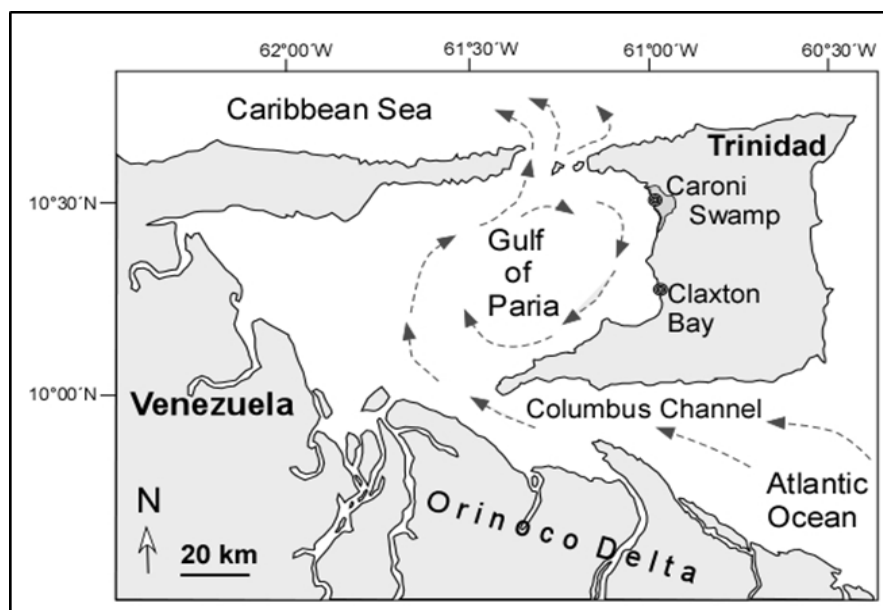
Fossil foraminiferal assemblages constrained by elevation relative to the tidal frame are used to reconstruct palaeo-sea levels (a few examples are Scott & Medioli, 1986; Scott & Leckie, 1990; Jennings *et al.* 1995; Hayward *et al.* 1999). Quiet coastal settings (such as marshes) are ideal settings to record foraminiferal assemblages deposited *in situ*, since reworking and displacement by gentle current and tidal action are here less likely to blur the signal (Hayward *et al.*

1999). However, this is not always the case (such as Barbosa *et al.* 2005) and the distribution of foraminiferal assemblages at several other marshes (de Rijk and Troelstra, 1997; Horton *et al.* 1999; Edwards *et al.* 2004; Patterson *et al.* 2004; Hansen & Knudsen, 2007) differs from the model proposed by Scott & Medioli (1978).

The vertical distributions of mangal-swamp foraminifera have been infrequently described (examples are Debenay *et al.* 2004; Barbosa *et al.* 2005; Woodroffe *et al.* 2005; Ghosh, 2012; Culver *et al.* 2013). Wilson *et al.* (2008) defined an assemblage scheme constrained by elevation at Caroni Swamp (NW Trinidad, SE Caribbean Sea) by sampling once in May 2006. In the north of Trinidad, sea-level is rising at a rate of 1 mm per year and four times that amount in the south (Miller, 2005). The Orinoco River (Venezuela) has an increased discharge rate of $7 \times 10^4 \text{ m}^3 \text{ s}^{-1}$ during the wet season (Hu *et al.* 2004). This causes sea level extremes within the Caribbean Sea, the largest being observed in the northwest of Trinidad (Torres & Tsimplis, 2004).

For this paper, the Caroni Swamp was monitored monthly from March 2011 to May 2013; and Claxton Bay (SW Trin-

Figure 1. Map of Trinidad showing mean ocean circulation patterns (adapted from van Andel & Postman, 1954 and Ibrahim, 2009).



idad) from July 2012 to July 2013. The impact of seasonal and long-term sea level change on the distribution of foraminiferal assemblages is examined in relation to the zones defined by Wilson *et al.* (2008). Zone I (> 0.22 m above mean sea level (AMSL)) was co-dominated by *Arenoparrella mexicana* and *Trochammina inflata*. Zone II (-0.45 m – 0.22 m AMSL) was co-dominated by an admixture of *Ammotium salsum*, *Miliammina fusca* and *Trochammina advena*. Zone III (below -0.49 m AMSL) was dominated by *Ammonia* sp. with lesser amounts of *T. advena*.

STUDY AREA

The Gulf of Paria is a shallow (~ 37 m; Neale, 2004), semi-enclosed embayment that separates Trinidad from Venezuela (Figure 1). Caroni Swamp and Claxton Bay, located on the west coast of Trinidad, open to the Gulf of Paria. Salinity in the Gulf of Paria is consistently lower than that of Tropical Atlantic Surface Water (Corredor & Morrel, 2001) due to freshwater input from the Orinoco River (NE Venezuela). The Guiana Current, a northwest-flowing branch of the Atlantic South Equatorial Current along the northern coast of South America, directs the Orinoco plume through the Gulf of Paria, where net flow is south to north at approximately 1 m s^{-1} (Neale, 2004). Trinidad is characterised by a monsoonal climate, with a dry season from January to May and wet season from June to December (Figure 2). During the wet season, salinity variations generated by the Orinoco plume and local fluvial runoff set up density circulation currents near the coastline. Current speeds are faster during the wet season as a result of increased fluvial output of the Orinoco River and the Caroni River, the latter being the largest river of Trinidad and enters the Gulf of Paria through

the Caroni Swamp.

Rainfall data were collected by the Trinidad and Tobago Meteorological Services (Figure 2), located at the Piarco International Airport, ~ 13.5 km east of Caroni Swamp and ~ 27.5 km northeast of Claxton Bay. Student's *t*-test was used to identify a significant difference ($p < 0.05$) between the average rainfall of wet and dry seasons for each year. There was a significant difference between the average rainfall recorded between the wet and dry seasons of 2011 ($p = 0.03$) and 2013 ($p = 0.02$), but not 2012 ($p = 0.25$). The latest La Niña event of 2011 – 2012 caused the late wet and dry seasons to be wetter than normal, and the following early wet season to be drier than normal. As such, La Niña in 2011–2012 may explain the lack of significant difference in average rainfall between dry and wet seasons in 2012.

Caroni Swamp ($10^{\circ}27'38''\text{N}$, $61^{\circ}14'55''\text{W}$; Fig. 3) is a micro-tidal wetland reserve with semi-diurnal tides. Bacon (1974) estimated the mangrove coverage to be 60 km^2 and a spring tidal range of ~ 1.2 m. However, the mangrove coverage has since expanded to 96.5 km^2 (Juman & Ramsewak 2011) and the spring tidal range is also likely to have increased according to the elevations of sample stations recorded here (Table 2). Claxton Bay ($10^{\circ}21'0''\text{N}$, $61^{\circ}38'0''\text{W}$; Fig. 4) is an industrial area located 35 km south of the Caroni Swamp. The Claxton Bay coastline, where it has not been cleared for infrastructure and ports, is fringed by mangrove forest. The coastline has semidiurnal tides with a micro-tidal range of $\sim 1\text{m}$ (Ibrahim, 2009).

At both Caroni Swamp and Claxton Bay, *Rhizophora mangal* dominates, with the sparse *Laguncularia racemosa* and

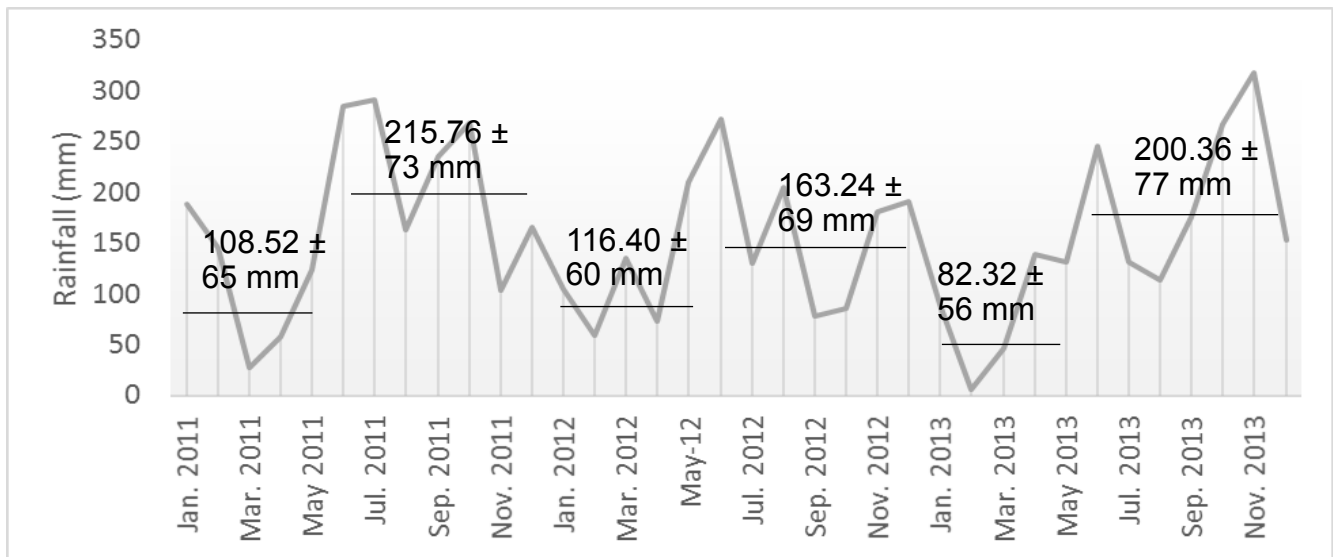


Figure 2. The average monthly rainfall (mm) and seasonal variations recorded by the Trinidad and Tobago Meteorological Services at Piarco International Airport (Trinidad) from January 2011 to December 2013.

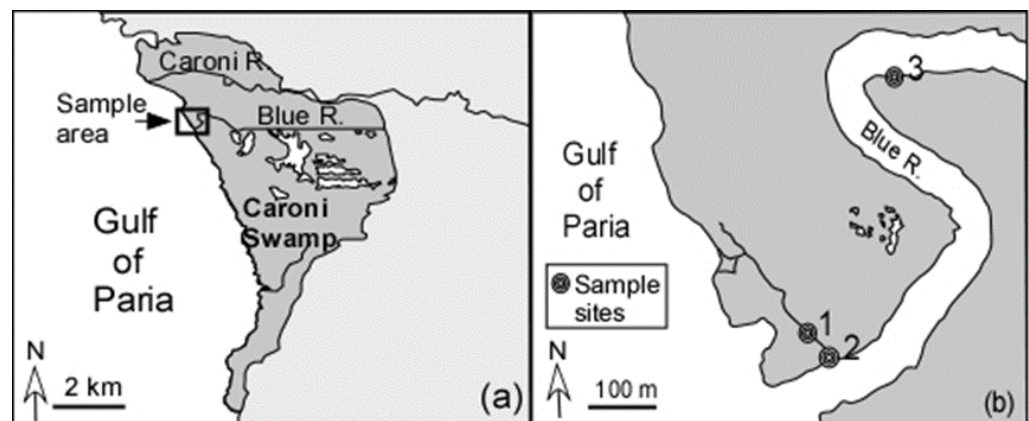
Avicennia germinans at the highest elevations. Sample sites 1 and 2 at Caroni Swamp are located 50 m apart along a north-south trending tributary to the Blue River (also referred to as the Cunupia River), and in close proximity to the sample sites of Wilson *et al.* (2008). The third site at Caroni Swamp is located ~ 1 km landward of sample site 2, on the southern bank of the Blue River. At Claxton Bay, one site was sampled (Figure 4b) where the coastline could be accessed at the mouth of a rivulet and approximately 100 m south of a shipping dock from which cement is loaded.

METHODS

The foraminiferal communities were monitored monthly at Caroni Swamp from March 2011 to May 2013 (27 sample occasions) and Claxton Bay from July 2012 to July 2013

(13 sample occasions). At each sample site, stations were placed at high (A), mid (B) and lower (C) elevations. The elevation of stations was determined by using GPS, rod and level (refer to Tables 2 and 5). At site 3 of Caroni Swamp and site 1 of Claxton Bay, the highest high water mark was not discernible. This was identified at other sites by a wash of mangal leaf litter. At these sites, station A was placed at the furthest inland access point. Four replicate sediment samples (1 cm x 75 cm²) were collected at each station to overcome errors caused by the patchy spatial distribution of foraminiferans in the sediment (Buzas *et al.* 2002). More than the usual 50 cm³ of sediment (Schönfeld *et al.* 2012) was collected because foraminiferal populations at Caroni Swamp were previously determined to be sparse (Wilson *et al.* 2008). It was continued at Claxton Bay for consistency.

Figure 3: Caroni Swamp (NW Trinidad) sample area (a) and sample sites (b).



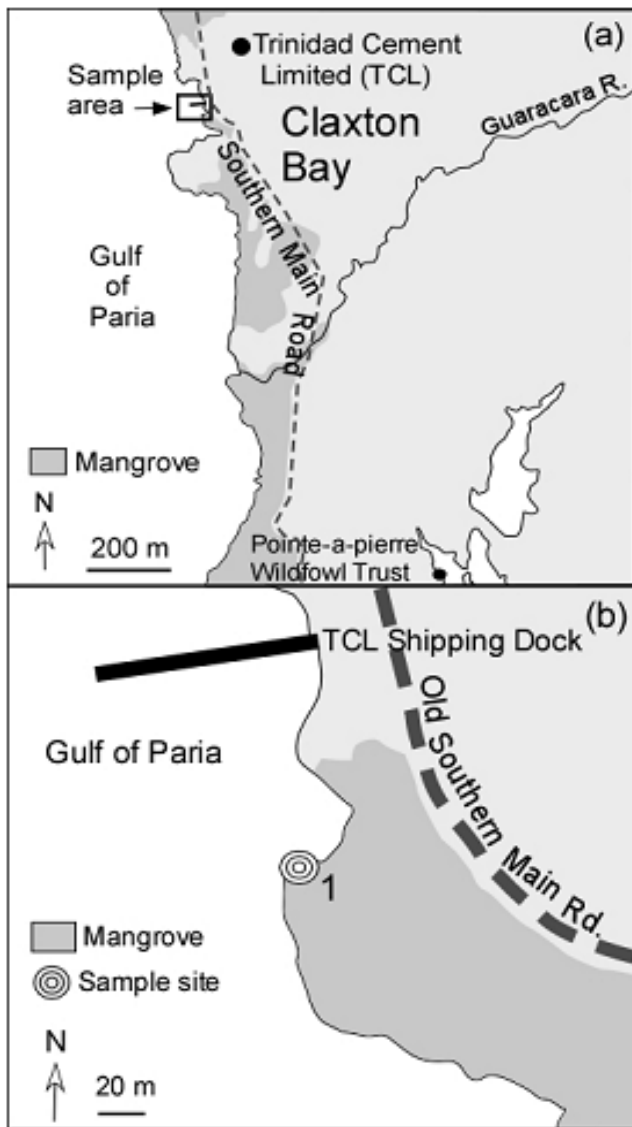


Figure 4. Claxton Bay (SW Trinidad) sample area (a) and sample sites (b).

A solution of rose Bengal and 70% isopropyl alcohol was added to each sediment sample in the field and left to soak for 15 days, which stained the cytoplasm of living specimens at the time of collection (Walton, 1952). Each 75 cm³ of sediment was washed through sieve sizes 2000 µm and 63 µm. The barren > 2000 µm fraction was discarded on every sample occasion. All specimens were picked wet and counted from the 63 – 2000 µm fraction. Sediment samples collected at Claxton Bay were split using a wet microsplitter into 1/16 aliquots and the number of specimens from each aliquot was multiplied by 16 to average the foraminiferal density in 75 cm³ of sediment. The taxonomy followed Todd & Brönnimann (1957).

Classical (hierarchical) Q-mode cluster analysis of the total (live + dead) foraminiferal densities (N_t) was performed in

PAST 3.0 (Hammer & Harper, 2001). The Pearson's product moment correlation coefficient (termed Correlation in PAST 3.0) and the unweighted pair-group average method of linkage was used. The N_t of replicate samples collected at each of the stations were summed. Those stations where $N_t < 50$ specimens and taxa with a recovery < 2% of the total recovery were omitted.

In separate analyses, N_t of stations recorded at Caroni Swamp and Claxton Bay for each sample occasion was clustered with N_t of stations recorded in May 2006 by Wilson *et al.* (2008). The foraminiferal assemblages of the zones produced at Caroni Swamp in May 2012 and Claxton Bay in May 2013, were examined in more detail since the comparable zones of Wilson *et al.* (2008) were produced for May 2006. Diversity was measured using species richness (S), the Shannon index (H' ; Equation 1) and the equitability index (E ; Equation 2). For details of H' and E see Magurran (1988, 2004) and Hayek & Buzas (1997).

$$H' = - \sum p_i \cdot \ln p_i \quad (1)$$

$$E = \frac{e^{H'}}{S} \quad (2)$$

A linear trend in values of N_t , S , H' and E were examined using the correlation coefficient of the line of best fit (R). Stationary population dynamics have values of R that fluctuate around 0 (Raffalovich, 1994). If there is a long-term increasing or decreasing trend, values of R approach ± 1 . If $R > \pm 0.5$, population dynamics displayed a long-term increasing or decreasing trend over the sample period. Significant differences between the mean ($\bar{x}$) of N_t , S , H' or E values from successive periods were detected using the student t-test with a 95% confidence interval ($\alpha = 0.05$). Where p was ≤ 0.05 , the two data sets had significantly different means. The standard deviation (σ) of the means reflects the degree of variability or spread of data points around the mean.

RESULTS

Caroni Swamp

The N_t of the Caroni Swamp foraminiferal metacommunity (all 9 stations) from March 2011 to May 2013 ($\bar{x} = 2447$ and $\sigma = 2518$ specimens / 300 cm³ of sediment) had a long-term increasing trend ($R = 0.59$; Figure 5a). The N_t of the first year, March 2011 to 2012, ($\bar{x} = 597$ and $\sigma = 419$ specimens / 300 cm³ of sediment) was significantly lower ($p = 0.00$) than that of the second year, April 2012 to May 2013 ($\bar{x} =$

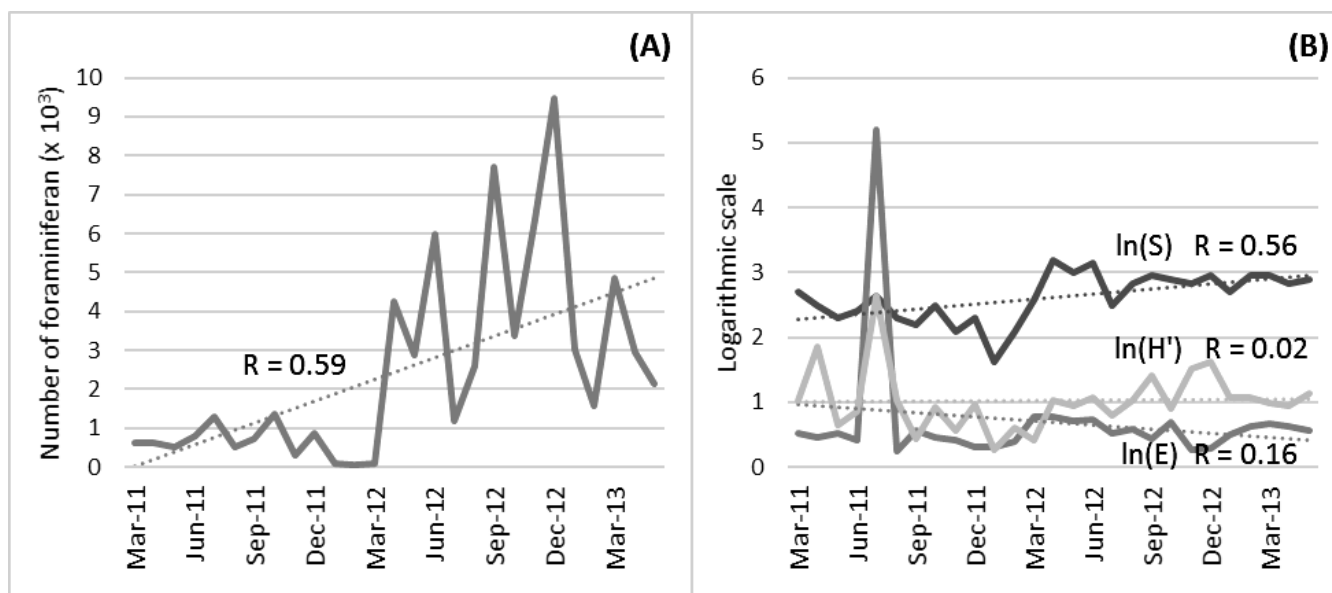


Figure 5: The Caroni Swamp foraminiferal metacommunity (a) total density, N_t (specimens / 2700 cm³ of sediment) and (b) diversity measured by species richness (S), Shannon diversity index (H') and the equitability index (E).

4170 and $\sigma = 2427$ specimens / 300 cm³ of sediment). Over the entire sample period, mean $S = 14$ ($\sigma = 5$), $H' = 1.59$ ($\sigma = 0.47$), $E = 0.40$ ($\sigma = 0.16$) and species with recovery $\geq 2\%$ varied from 4 to 11 species. Only values of S had a long-term increasing trend ($R = 0.56$; Figure 5b) and S of the first year ($x = 11$ and $\sigma = 3$ species) was significantly less ($p = 0.00$) than that of the second year ($x = 18$ and $\sigma = 3$ species). Values of H' and E were consistent over the sample period ($R = 0.02$ and 0.16 , respectively; Figure 5b). In the first year, the metacommunity was dominated in varying proportions by *Ammonia* sp. on most occasions, and less frequently by either *Trochammina advena*, *Miliammina fusca*, *Ammotium salsum*, *Trochammina laevigata*, *Trochammina inflata* or *Lagena* sp. In the second year, either *Ammonia* sp., *A. salsum* or *T. advena* were dominant on most occasions and less frequently *M. fusca*, *T. inflata* and *A. mexicana* dominated the metacommunity in varying proportions. Species which comprised $< 2\%$ of the recovery on rare occasions (≤ 8 months), were *Textularia gramen*, *T. earlandi*, *Gaudryina exilis*, *Involutina minima*, *Glomospira gordialis*, *Ammobaculites exiguus*, *Discorbis* sp., *Triloculina trigonula* and *Lagena* sp.

The $N_t < 50$ specimens at all stations sampled on January, February and March 2012 and cluster analyses of these months were omitted. From March 2011 to 2012, mostly stations 1A and 1B were clustered in Zone I; stations 2B, 3A and 3B in Zone II; and stations 1C, 2C and 3C in Zone III. In August 2011 stations 2B and 2C shifted into Zones I and II, respectively, and station 3C shifted into Zone II in October 2011. Thereafter, stations frequently moved be-

tween zones. Mostly stations 1A and 1B clustered in Zone I (except in October, November 2012 and May 2013). Stations 2A, 2B, 3A and 3B often clustered in Zone II (except in November, December 2012 and May 2013). Zone III commonly comprised stations 1C, 2C and 3C (except in December 2012 and May 2013). The shifts in stations between zones mostly coincided with the end of the wet season (October to December) or dry season (May).

Caroni Swamp assemblages (May 2012)

The Caroni Swamp metacommunity in May 2012 had $N_t = 2869$ specimens / 2700 cm³ of sediment ($x = 319$ and $\sigma = 235$ specimens / 300 cm³ of sediment; Table 2). All stations had $N_t > 50$ specimens, so no station was omitted from cluster analysis. Values of S and H' were low, and ranged from 14 to 7 and 1.86 to 1.08, respectively, between stations (Table 2). Species diversity did not increase or decrease according to the elevations of stations, but fluctuations were random. For example, the stations with the highest (2A) and lowest (1C) elevations had approximately equal values of H' (~ 1.4) and stations 1A (0.66 m AMSL) and 3C (-0.12 m AMSL) both had values of $S = 11$ (Table 2).

Eight species of the Caroni Swamp metacommunity had recovery $\geq 2\%$ (Table 2 and 3), of which *Ammotium salsum*, *Arenoparrella mexicana* and *T. advena* were abundant (Table 3). The lowest values of E (Table 2) were recorded at stations 1A and 1C, where *A. mexicana* strongly dominated with fewer *T. inflata* (Table 3). Stations 1B, 2B and 3C had values of $E \sim 0.4$ (Table 2) where, the number of abundant species ranged from 2 to 4 and $p_i \leq 54\%$ for each. Stations

Table 1: Cluster analysis of Caroni Swamp from March 2011 to May 2013 in relation to the assemblage scheme of Wilson et al. (2008).

SO	Clusters of stations		
	Zone I	Zone II	Zone III
Mar-11	-	2B & 3B	1C & 3C
Apr-11	1A	2B & 3A	1C & 3C
May-11	1A	2B	2C & 1C
Jun-11	-	2B, 3A & 3B	1C, 2C & 3C
Jul-11	1A & 1B	2B & 3A	2C & 1C
Aug-11	1A, 1B & 2B	2C	-
Sep-11	1B	2B, 3A & 3B	-
Oct-11	2A	2B, 2C, 3A, 3B & 3C	1C
Nov-11	-	3A	3B & 3C
Dec-11	-	3A	3B & 3C
Jan-12	-	-	-
Feb-12	-	-	-
Mar-12	-	-	-
Apr-12	1C	1A, 1B, 2A, 2B, 2C, 3A, 3B & 3C	-
May-12	1A, 1B, 1C & 2A	2B, 2C, 3A, 3B, & 3C	-
Jun-12	1A, 1B & 1C	2A, 2B, 3A, 3B, & 3C	-
Jul-12	1B	2A, 2B & 3C	-
Aug-12	1A, 1B, 1C & 2A	3B & 3A	-
Sep-12	1B	2A, 2B, 3A, 3B, & 3C	1C & 2C
Oct-12	1A	2C, 3A, 3B & 3C	1B, 1C & 2B
Nov-12	-	1A	1B, 1C, 2B, 2C, 3A, 3B & 3C
Dec-12	-	2A & 2B	1C, 2C, 3C & 3B
Jan-13	-	2A, 2B, 3A & 3B	1A, 2C & 3C
Feb-13	1A	2A, 2B, 3A & 3B	1C, 2C & 3C
Mar-13	1A	2A, 2B & 3B	2C & 3C
Apr-13	1A & 1B	2B, 3A & 3B	2C & 3C
May-13	1A, 2A & 2B	1B & 3A	1C, 2C, 3B & 3C

Table 2: Caroni Swamp metacommunity (May 2012). Only species with $p_i \geq 2\%$ are listed.

Caroni Swamp	Metacommunity			Stations								
	Total	Mean	p_i	1A	1B	1C	2A	2B	2C	3A	3B	3C
Elevation (m, AMSL)	-	-	-	0.66	0.45	-0.18	1.49	0.20	-0.06	-0.14	-0.10	-0.12
Nt	2869	319	-	447	193	418	63	750	447	79	57	415
Species richness, S	21	10.11	-	11	11	14	7	13	9	7	8	11
Species diversity, H'	2.05	1.53	-	1.08	1.54	1.35	1.39	1.73	1.86	1.63	1.61	1.57
Equitability index, E	0.37	0.50	-	0.27	0.42	0.28	0.58	0.43	0.72	0.73	0.63	0.44
<i>Ammonia</i> sp.	110	12	0.04	0	1	11	0	31	44	0	0	23
<i>Ammonium salsum</i>	797	89	0.28	9	38	31	8	282	165	16	24	224
<i>Arenoparrella Mexicana</i>	652	72	0.23	294	66	265	5	9	8	0	2	3
<i>Lagena</i> sp.	258	29	0.09	3	1	5	0	168	45	28	1	7
<i>Miliammina fusca</i>	137	15	0.05	5	1	6	1	29	56	14	3	22
<i>Triloculina trigonula</i>	262	29	0.09	3	0	2	0	120	73	14	11	39
<i>Trochammina advena</i>	312	35	0.11	45	19	39	22	84	29	1	12	61
<i>Trochammina inflata</i>	215	24	0.07	83	57	45	25	5	0	0	0	0

each. Stations 2A, 2C, 3A and 3B had the highest values of E that ranged from 0.58 to 0.73 (Table 2), and were characterised by 3 to 4 abundant species with $p_i \leq 42\%$ for each (Table 3).

Cluster analysis grouped stations 2A, 1A, 1B and 1C, with

with elevations between 1.487 and -0.176 m AMSL (Table 2), with stations of Zone I (Figure 6). Collectively these stations had $N_t = 1121$ specimens / 1200 cm^3 ($x = 280$ and $\sigma = 184$ specimens / 300 cm^3 of sediment), $S = 17$, $H' = 1.4$ and $E = 0.24$. The assemblage was dominated by *A. mexicana*, with fewer *T. inflata* and *T. advena* (Table 3). Stations

Table 3: Percentage proportional abundances of species with recovery $\geq 2\%$ at Caroni Swamp (May 2012).

Caroni Swamp / species with recovery $> 2\%$	Metacommunity	Zone I	Zone II	Stations								
				1A	1B	1C	2A	2B	2C	3A	3B	3C
<i>Ammonia</i> sp.	4%	1%	6%	0%	1%	3%	0%	4%	10%	0%	0%	6%
<i>Ammotium salsum</i>	28%	8%	41%	2%	20%	7%	13%	38%	37%	20%	42%	54%
<i>Arenoparrella mexicana</i>	23%	56%	1%	66%	34%	63%	8%	1%	2%	0%	4%	1%
<i>Lagena</i> sp.	9%	1%	14%	1%	1%	1%	0%	22%	10%	35%	2%	2%
<i>Miliammina fusca</i>	5%	1%	7%	1%	1%	1%	2%	4%	13%	18%	5%	5%
<i>Triloculina trigonula</i>	9%	0%	15%	1%	0%	0%	0%	16%	16%	18%	19%	9%
<i>Trochammina advena</i>	11%	11%	11%	10%	10%	9%	35%	11%	6%	1%	21%	15%
<i>Trochammina inflata</i>	7%	19%	0%	19%	30%	11%	40%	1%	0%	0%	0%	0%

2B, 2C, 3A, 3B and 3C, with elevations between 0.453 m and -0.140 m AMSL (Table 2), clustered with stations of Zone II (Figure 6). These five stations had $N_t = 1748$ specimens / 1500 cm³ of sediment ($x = 350$ and $\sigma = 288$ specimens / 300 cm³ of sediment), $S = 15$, $H' = 1.81$ and $E = 0.41$. *Ammotium salsum* dominated the assemblage with fewer *T. trigonula*, *Lagena* sp. and *T. advena* (Table 3).

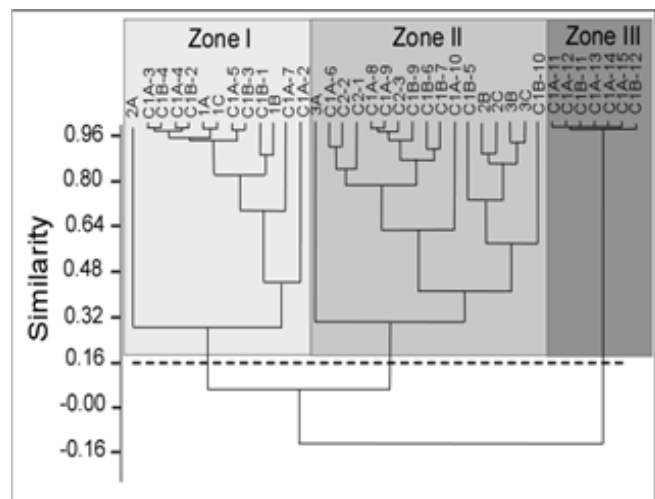
Claxton Bay

The Claxton Bay metacommunity had mean $N_t = 73266 \pm 25005$ specimens / 300 cm³ of which higher values were recorded for the wetter period from July to December ($x = 501840$ and $\sigma = 83640$ specimens / 300 cm³ of sediment) than the drier period from January to July 2013 ($x = 450624$ and $\sigma = 64375$ specimens / 300 cm³ of sediment). However, there was no long-term decreasing trend ($R = 0.44$) and mean N_t of the two periods did not differ significantly ($p =$

0.18). Over the entire sample period, the metacommunity had mean values of $S = 17$ ($\sigma = 2$), $H' = 1.29$ ($\sigma = 0.25$) and $E = 0.22$ ($\sigma = 0.05$). Only values of E had a long-term decreasing trend over the sample period ($R = 0.78$; Figure 7b) and significantly higher values ($p = 0.02$) were recorded in the wetter period ($x = 0.19 \pm 0.04$) than the drier period ($x = 0.24 \pm 0.04$). Dominance of *Trochammina advena* increased through the wet season from July (0%) to December (62%) and November 2012 (42%). During the dry season *Ammonia* sp. increased from January (21%) to April (41%) and May 2013 (35%).

Only in September 2012 the foraminiferal species at all stations differed and clustered separately to those of Caroni Swamp in May 2006 (Figure 4). Stations 1A and 1B shifted from Zone II in October and November 2012 to Zone III in December to February, which coincided with a change from

Figure 6: Cluster analysis of Caroni Swamp stations sampled in May 2012 with stations sampled in May 2006 by Wilson et al. (2008).



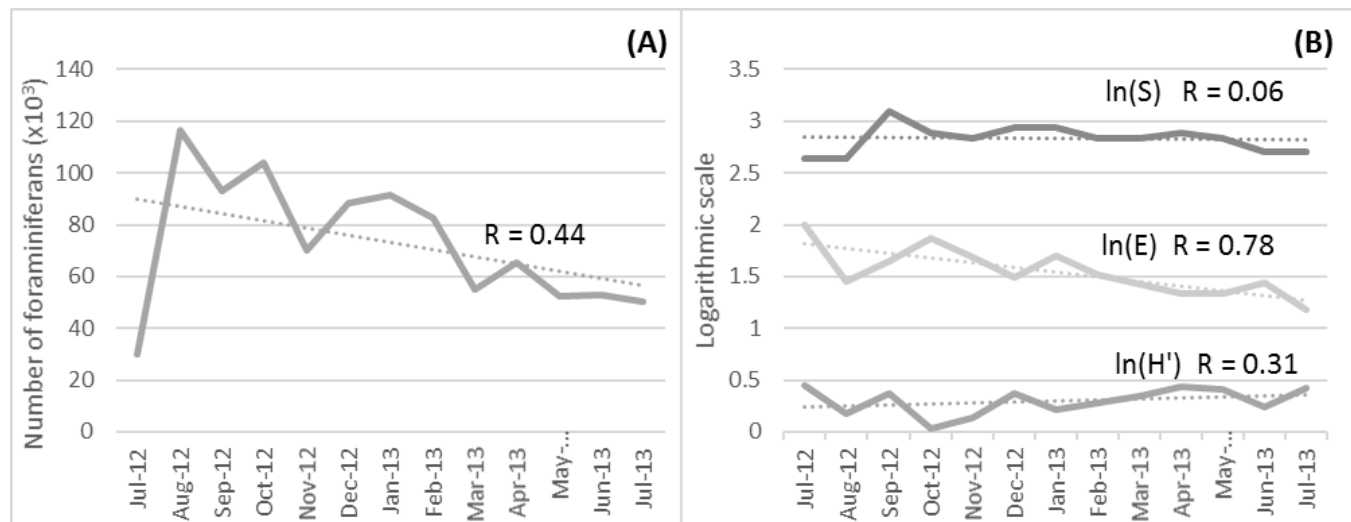


Figure 5: The Caroni Swamp foraminiferal metacommunity (a) total density, N_t (specimens / 2700 cm³ of sediment) and (b) diversity measured by species richness (S), Shannon diversity index (H') and the equitability index (E).

wet to dry conditions. Thereafter, station 1B shifted back into Zone II, until the start of the 2013 wet season when it shifted once more to Zone III.

Claxton Bay assemblage (May 2013)

The Claxton Bay metacommunity in May 2013 had $N_t = 50688$ specimens / 900 cm³ of sediment (Table 5). Species diversity did not correspond with elevation since H' of station 1B was greater than 1A, and S of station 1B was lower than stations 1A and 1C (Table 5). The highest value of E was recorded at station 1B (Table 5) where *T. advena* dominated with lesser *Ammonia* sp. and *A. salsum* (Table 6). Values of E were similar at stations 1A and 1C (Table 5) where *A. tepida* dominated with lesser *T. advena* and *Triloculina oblonga* was common at station 1A only (Table 6). Cluster analysis grouped stations 1A and 1C with the highest and lowest elevations (0.228 and -0.151 m AMSL, respectively)

spectively) in Zone III dominated by *Ammonia* sp. and lesser *T. advena* (Table 6). Station 1B (0.051 m AMSL) clustered with stations of Wilson et al. (2008) belonging to Zone II, dominated by *T. advena* and lesser *Ammonia* sp. and *A. salsum* (Table 6). No stations grouped in Zone I (Figure 8).

DISCUSSION

The vertical distribution of marsh foraminifera, as first described by Scott & Medioli (1978), is commonly divided into three assemblages constrained by elevation. The vertical distribution of the benthonic foraminiferal community at Caroni Swamp and Claxton Bay from March 2012 to July 2013 did not follow this pattern. The three assemblages formerly described by Wilson et al. (2008) were not always simultaneously represented at Caroni Swamp from March 2012 to May 2013. On 14 of 25 sample occasions (omitting

Table 4: Cluster analysis of Claxton Bay from July 2012 to 2013 in relation to the assemblage scheme of Wilson et al. (2008).

SO	Cluster of stations		
	Zone I	Zone II	Zone III
Jul-12	-	-	1A, 1B & 1C
Aug-12	-	1A & 1B	1C
Sep-12	-	-	-
Oct-12	-	1A, 1B & 1C	-
Nov-12	-	1A, 1B & 1C	-
Dec-12	-	-	1A, 1B & 1C
Jan-13	-	-	1A, 1B & 1C
Feb-13	-	-	1A, 1B & 1C
Mar-13	-	1B	1A & 1C
Apr-13	-	1B	1A & 1C
May-13	-	1B	1A & 1C
Jun-13	-	-	1A, 1B & 1C
Jul-13	-	-	1A, 1B & 1C

Table 5: Claxton Bay metacommunity (May 2012). Only species with $p_i \geq 2\%$ are listed.

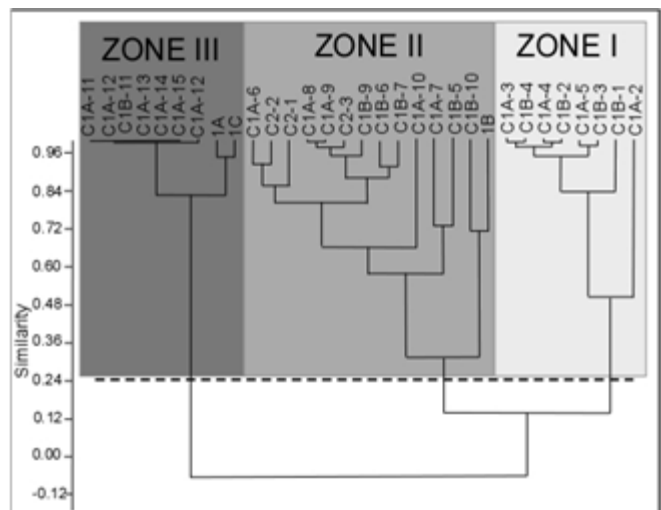
Claxton Bay	Metacommunity			Stations		
	Total	Mean	p_i	1A	1B	1C
Elevation (m, AMSL)	-	-	-	0.228	0.051	-0.151
N_t	50688	319	-	18288	17856	14544
Species richness, S	17	14	-	15	11	15
Species diversity, H'	1.50	1.36	-	1.39	1.45	1.23
Equitability index, E	0.26	0.29	-	0.27	0.39	0.23
<i>Ammonia</i> sp.	18576	6192	0.37	9088	2768	6720
<i>Ammotium salsum</i>	4288	1429	0.08	672	2144	1472
<i>Bolivina striatula</i>	1456	485	0.03	288	1104	64
<i>Elphidium excavatum</i>	1744	581	0.03	848	768	128
<i>Triloculina oblonga</i>	3088	1029	0.06	2240	608	240
<i>Trochammina advena</i>	21536	7179	0.42	5152	10464	5920

January – March 2012), either Zone I or III was not represented at Caroni Swamp. At Claxton Bay, Zone I was never represented because station 1A was placed at the furthest inland access point which most likely did not extend to the upper foraminiferal assemblage since the highest high water mark was not discernible. On 8 of 12 sample occasions (omitting September 2012), Zone II or III was not represented at Claxton Bay. At both locations, changes to the clusters of stations often coincided with seasonal change. The N_t recorded at Caroni Swamp had a long-term increasing trend, where significantly lower N_t was recorded from March 2011 to 2012 which may be attributed to less favorable conditions during the last La Niña event.

The abundant species at Caroni Swamp and Claxton Bay in May 2012 and 2013 were similar to that of Caroni Swamp in 2006, except *T. trigonula* and *Lagena* sp. were more abundant than *Ammonia* sp. at Caroni Swamp in May 2012. Cluster analysis of the foraminiferal metacommunity at the

Caroni Swamp in May 2012 grouped stations dominated by *A. mexicana* in zones I and *A. salsum* in zone II. At Claxton Bay in May 2013, stations dominated by *T. advena* were grouped in zone II and *Ammonia* sp. in Zone III. The zones were not constrained by the elevations of stations and the values of H' recorded at Caroni Swamp in 2012 did not correspond with elevation, although in 2006 a significant and negative correlation existed between H' and elevation (Wilson *et al.* 2008).

Seasonal floods and the influence of the Orinoco plume during the wet season are suggested to raise highest high water level at Caroni Swamp and Claxton Bay (Tsimplis & Woodworth, 1994). This may cause a landward shift of the assemblages. During the dry season, depressed tidal levels could cause a seaward shift of the assemblages. Landward or seaward shifts of the assemblages cause mixing of dead tests across zones and explain the high variability of clusters of stations between sample occasions. In May 2012 Zone I

Figure 8: Cluster analysis of Caroni Swamp stations sampled in May 2012 with stations sampled in May 2006 by Wilson *et al.* (2008).

included station 1C at -0.18 m below AMSL probably due to the seasonal mixing of assemblages. However, if this station were excluded, the lower limit of Zone I would be at station 1B (0.45 m above AMSL) which is higher than that recorded in May 2006 (0.22 m above AMSL). The lower limit of Zone II was extended by 0.57 m in May 2012 (-0.12 below AMSL) compared to May 2006 (0.45 m below AMSL). The extended vertical ranges of the zones and the approximate tidal range based on the elevation of stations recorded here could be attributed to long-term sea level rise (Miller, 2005).

Even in sheltered estuarine mangrove systems, reworking and displacement by gentle current and tidal action can result in foraminiferal assemblages that are not constrained by elevation (Barbosa *et al.* 2005). Extended tidal ranges by seasonal flooding, induced by fluvial hypopycnal plumes (Tsimplis & Woodworth, 1994; Hu *et al.* 2004), can cause reworking of dead foraminiferal tests and movement of live foraminiferans to favorable zones. Additionally, tropical environments have many different challenges for foraminiferal assemblages, including bioturbation (by crabs and gastropods), which disaggregates the surface sediment, increasing aeration at lower elevations (Woodroffe *et al.* 2004).

Scott & Medioli (1986) acknowledged species composition of foraminiferal assemblages may differ between areas, but the vertical extent of the assemblages was expected to be similar. More recently, the vertical extent of assemblages are considered to be highly variable between marshes (Edwards *et al.* 2004) and seasons (Horton *et al.* 1999), and not always are three assemblages represented (Horton, 1999; Patterson *et al.* 2004; Hansen and Knudsen, 2007) or a clear vertical zonation (de Rijk & Troelstra, 1997; Gehrels & van de Plassche, 1999). The global application of three distinct foraminiferal assemblages located in zones relative to tidal elevation, is not realistic if the unique characteristics of each marginal marine environment are considered.

CONCLUSIONS

The foraminiferal assemblages of Caroni Swamp and Claxton Bay monitored between March 2011 and June 2013 were not constrained by elevation, and the stations which defined assemblages varied between sample occasions. Shifts in the clusters of stations commonly coincided with seasonal change. Seasonal flooding, tidal currents, and bioturbation can separately or simultaneously cause lateral mixing of foraminiferal assemblages along the tidal gradient. As a result, the traditional assemblage scheme comprising of three zones constrained by elevation, is not applicable. Studies that use time series data sets of foraminiferal

counts are likely to find that the stations that cluster together in one month differ to subsequent months even when using the dead or total counts for cluster analysis. Choosing one assemblage scheme, which can be applied across all months, is difficult but necessary to illustrate temporal variability. It is recommended that analysis of the foraminiferal metacommunity is provided along with assemblages. For studies that aim to estimate palaeo-sea levels using vertical assemblages, it is necessary that assemblages be constrained by elevation, but this is not necessary for studies that aim to investigate species-level fluctuations over time.

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