Caribbean Journal of Science, Vol. 40, No. 3, 299-311, 2004
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Reef Morphology and Community Structure along a Fluvial Gradient, Rio Bueno, Jamaica.

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ABSTRACT.—**This study assessed the combined effects of natural riverine inputs and variation in wave energy upon the reef development and coral community structure in the small embayment of Rio Bueno, northern Jamaica. The embayment is subject to seasonally variable fluvial discharges of terrigenous sediment and freshwater. Water quality deteriorated with increasing proximity to the embayment head and river mouth, with sediment influx resulting in high turbidity levels and a reduced light environment within inner and central embayment areas. Sedimentation rates within the central embayment peaked at 43.2 mg cm^{-2} d^{-1} during this study. Coral communities were only present in the outer, clear water sites and central, moderately turbid sites, but were absent from the inner embayment areas which are adjacent to the river mouth. Mean (± 1 SD) hard coral cover was 11.6% (± 8.1), with a maximum of 42.9% along the reef flat in the medium-impacted zone. Within this zone, framework development was spatially and bathymetrically restricted. However, when compared with clear water sites, greater species richness, higher coral cover and a greater abundance of large, dome-shaped corals occurred. Common species included *Diploria strigosa*, *Porites astreoides* and *Siderastrea siderea*, which are suggested to be those most tolerant to sediment stress. At sites with coral framework (central and outer sites), algal cover was positively correlated with increasing distance from the head of the embayment, whilst coral cover was negatively correlated with increasing distance from the head, peaking in the central embayment.**

KEYWORDS.—**Coral reef zonation, fluvial inputs, Dornock river, sediment stress, nutrients, turbidity.**

INTRODUCTION

Whilst shallow marine environments on the northern coast of Jamaica have been comprehensively studied, most research has primarily focused on coral reef communities that are characteristic of clear, oligotrophic settings (Goreau 1959; Goreau 1968; Goreau and Land 1974; Liddell and Ohlhorst 1993; Andres and Witman 1995; Lapointe et al. 1997; Gayle and Woodley 1998; Vierros 2003) and lacking in fluvial sediment and freshwater inputs. Such reefs occur in environments which are widely perceived as having near optimal conditions with regards to salinity, temperature and light penetration (Ohlhorst 1980; Hubbard 1997) and are, consequently, characterised by 1) a predominance of organisms that produce calcium carbonate framework and sediment (Boss and Liddell 1987; Perry 1997), and 2) development of bathymetrically extensive reef framework structures (Liddell et al. 1984).

Whilst such environments have generally been regarded as being optimal (and often by inference the 'norm') for coral community development, in recent years there has been an increasing recognition of the diversity of coral communities occurring under less optimal conditions (e.g., settings subject to higher/lower salinity or temperature regimes, high sediment inputs or high turbidity levels, see Kleypas et al. 1999). Under these conditions, it is expected that very different types of coral communities and reef structures may develop (Perry and Larcombe 2003). These more marginal environmental conditions can both occur naturally or may be a response to humaninduced changes in the environment. Both scenarios apply in relation to sediment inputs, which may occur naturally in close proximity to river mouths, or can be associated with anthropogenic inputs such as dredging, construction, agriculture and forestry (Dodge and Vaisnys 1977; Marszalek 1981; Salvat 1987; Kent 2002; Linton et al. 2002). In recent decades the effects of elevated sedimentation rates on coral reefs has become increasingly common where land degradation and associated increases in terrigenous run-off has enhanced sediment yields (Rogers 1990; Linton et al. 2002). At such sites sedimentation has been widely regarded as a major limiting factor to reef growth (Hubbard 1986). Under these conditions, many studies have documented changes in coral community structure and in the extent of reef framework development (see Rogers 1990 for a review).

The Rio Bueno embayment on the north Jamaican coast is a site that receives significant inputs of fluvially-derived, terrigenous (clastic) sediment and freshwater from the Dornock River. The high-energy, open coast surf zone is also a prolific source of sediment generation, and carbonate clasts (e.g., sand and silt) are moved westwards along the coastline by local hydrodynamic processes that include longshore drift and local currents (JM personal observations). Consequently, natural inlets and embayments, such as Rio Bueno, break up the reef-fronted coastline and deep areas (ca. 30-200 m) act as traps and sediment sinks. As a result, environmental conditions differ from those that occur along much of the north Jamaican coast and in particular, from those areas that have received significant previous scientific attention (e.g., Discovery Bay).

This paper details a transitional coral reef system that has historically withstood and adapted to the natural sediment gradient found within Rio Bueno – a highly turbid, fluvially-influenced embayment. Whilst the coral reefs of Rio Bueno have been subject to the same recent disturbances that have impacted most Jamaican reefs (e.g., hurricane damage, overfishing, loss of the keystone herbivorous urchin *Diadema*) and have undergone a consequent phase shift away from coral to algal dominance (Hughes et al. 1985; Done 1992; Woodley 1992; McCook 1999; Munro 2000; Haley and Solandt 2001), this site provides an interesting counterpoint to the more extensively studied, clear water reefs along the north Jamaican coast. Fluvial inputs, terrestrial runoff, and resource extraction are increasing worldwide (Wilkinson 2002), and the implications of this for near shore reefal development is still largely unknown. The Rio Bueno coral communities offer a greater insight into systems that develop under 'non-optimal' conditions, and a perspective on spatial variation in coral reef community development along a fluvial gradient.

MATERIALS AND METHODS

Study area

Rio Bueno is a small embayment (ca. 0.8 km wide) on the north coast of Jamaica (18°28′N, 077°27′W), 5 km west of the much studied Discovery Bay (see Fig. 1). Rio Bueno is thought to be a drowned river valley (Woodley and Robinson 1977) with relict topography producing a steep-sided embayment. The coastal zone is subjected to north easterly trade winds, which are modified by local sea and land breezes (Gayle and Woodley 1998). The wave regime is primarily generated by local wind conditions, which peak between 10:00 and 14:00 local time. This section of coastline has a mixed tidal regime (e.g., diurnal spring tides and low amplitude semi diurnal neaps), with a daily tidal range at Discovery Bay of 15 to 60 cm, with an annual range of 1 m (Gayle and Woodley 1998). Jamaica has a subtropical climate with two distinct wet (December to April, and May to November) and dry seasons (November to December and April to May) and it is common for rainfall to persist for a week or more during the wet seasons.

The Dornock River head rises from the largest karst resurgence on Jamaica. From the headwaters the Dornock river flows in a northerly direction for approximately 16 kilometres, winding down through a

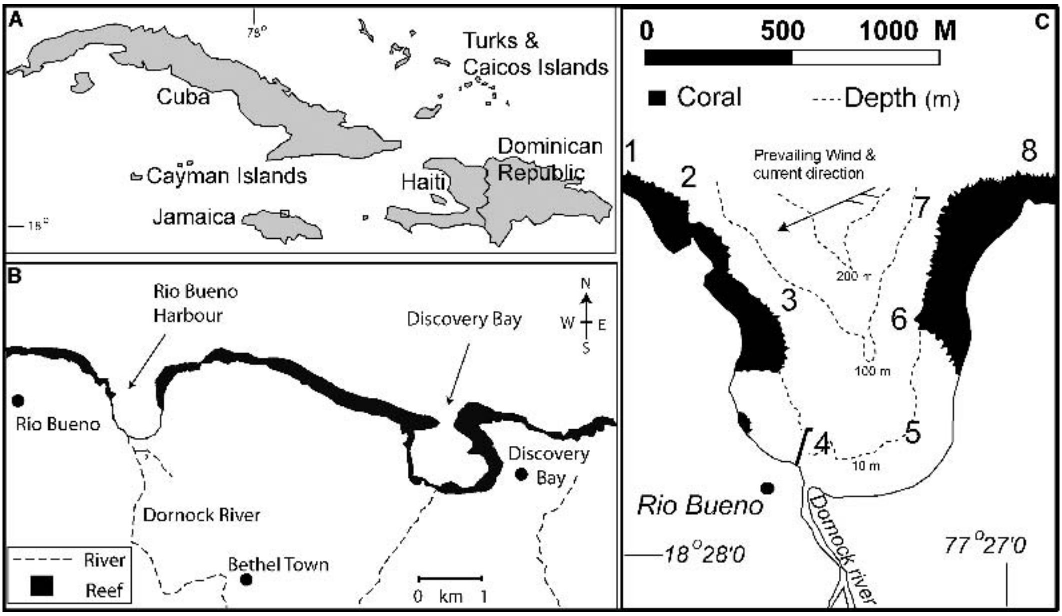

FIG. 1. Map showing (A) the location of the study area in the Caribbean, (B) the position of Rio Bueno, approximately 5 km west of Discovery Bay in the centre of the north coast, and (C) Rio Bueno showing the reef areas surveyed in this study.

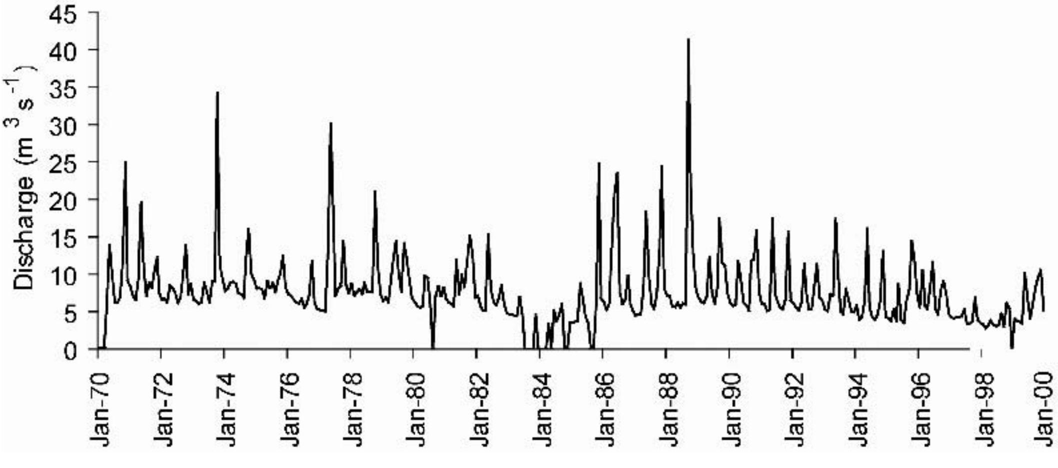

FIG. 2. The Dornock River, mean monthly discharge rates, 1970-1999.(Data source: The Water Resources Authority, Jamaica)

mountainous, predominantly rural landscape, through agricultural lands, into Rio Bueno town and finally into the Rio Bueno embayment. The river is prone to seasonal pulses of high river discharge and suspended sediments (Gayle and Woodley 1998; WRA 2001-2002). Consequently, surface waters (ca. 0-3 m) of the Rio Bueno embayment can fluctuate between marine and brackish salinity levels. Following heavy rainfall, a highly turbid freshwater plume often extends in a north-westerly direction from the river mouth across the embayment and may persist for weeks. This plume was characterised by brackish water salinities (10-25), high levels of suspended sediment, and reduced water clarity with consequent reductions in light penetration with depth. In addition to fluvial inputs, the embayment was subjected to complete mangrove clearance (E. Brown pers. com.) and selective seagrass clearance (JM pers. observations). Study sites were established at eight marine sites varying in proximity to the river mouth (see Fig. 1 C.) Within the embayment, the eight sites were defined as inner, central and outer zones situated at 50 to 400 m, 500 to 700 m, and 900 to 1500 m respectively, from the river mouth. Inner and central zones are located within the sheltered, deep embayment, and consequently are protected from prevailing trade winds, and characterised by low wave energy. Outer sites are situated on the open coast and subjected to high energy, wave-driven processes.

Environmental data: methods

The extent of fluvial impacts and anthropogenic stress was determined by qualitative observations (notes on observed fishing activity, seagrass clearance, etc.) and by a series of environmental measurements, including salinity, temperature, sedimentation rates, water clarity and light attenuation. All measurements were repeated from April to September 2001 for each site with the exception of sediment trap data, which was only taken at three of the eight sites from April to September 2001 (sites 3, 6 and 8) and at four sites June to August 2002 (sites 2, 3, 6 and 8).

Salinity and temperature were measured using a Horiba^{Tm} probe. At each site salinity was recorded on 19 occasions at the following depths: 0.1, 0.5, 1.0, 2.5, 5.0 and 10 m. Water clarity was estimated using standard Secchi disk extinction measurements on 19 separate occasions. Light attenuation was measured using a Licor^{Tm} light metre probe. At each site, the percentage surface light attenuation was calculated for 0.5, 1.0, 2.5, 5, 10, 15, 20, 25 and 30 m depths in the water column; these measurements were taken on 13 separate occasions.

Gross sedimentation rates (the flux in downward sediment) were measured using sediment traps. Three replicate traps were deployed 0.5 m above the substrate at a depth of 10 m at each site. Each sediment trap had 5.5 cm diameter and 19.1 cm tall. These dimensions were chosen to limit sediment resuspension out of the trap (Bloesch and Burns 1980). The traps were attached to PVC poles that were secured to the substrate and anchored with concrete blocks. Sediment traps were collected bi-weekly if under water visibility allowed, if not as soon as underwater visibility permitted. The maximum time a trap was deployed for was 3 weeks. Sediment trap data also reflects the effects of local sediment re-suspension within the embayment, which is principally determined by temporally and spatially-variable wave energy.

Habitat mapping and benthic community surveys were conducted using a linear intercept method (Huston 1985b). A weighted 10 m tape measure was draped along a depth contour on the reef (conforming to all surface irregularities), and each substrate type and species recorded and measured along the transect at 1 cm intervals. Three replicate transects were conducted at each of the eight sites at set depth intervals (2, 5, 10, 15, 20, 25 m) and data was combined to give a mean percentage benthic cover for each site and depth.

Statistical analysis of data was conducted using the statistical package SPSS (version 11) for Windows. Pearson's correlation (r) was used to examine trends in environmental data across the fluvial gradient. The Shannon-Wiener index (Krebs 1989), using Ln, (H') was used to describe variation in hard coral diversity, and hierarchical cluster analysis was performed in order to designate zones of fluvial disturbance.

RESULTS

Environmental Parameters

Surface salinities (0.15 m) varied with proximity to the river mouth. Readings varied from 23.6 at inner sites 4 and 5, which are closest to the river mouth, to 35 at outer site 8. Normal marine salinities (35.0 – 36.0) were recorded at all sites at depths equal to, or greater than, 2.5 m. Water temperature at the study sites was relatively uniform with depth with the exception of sites 4 and 5 which showed reduced water temperature in the upper 1 m (Table 1).

Light attenuation decreased exponentially with depth, for example at a depth of 30 m light levels dropped to 4.1, 3.4 and 8.2% of surface light at sites 3, 4, and 8, respectively, as illustrated in Figure 3. If the percentage light reduction with depth is considered at all sites, there was a strong positive correlation between increasing proximity to the river mouth and higher levels of light attenuation (e.g., at a depth of 15 m: $r = 0.881$, $n = 8$, $P = 0.004$). Water clarity (Secchi disk readings) ranged from a minimum of 0.03 m at site 5 to a maximum of 35.0 m at site 1. Sites 1, 2, and 8 had the greatest mean water clarity 19.0, 17.7 and 19.7 m respectively (Fig. 4). Water clarity increased significantly with increasing distance from the river mouth ($r = 0.922$, $n = 8$, $P = 0.01$).

Sedimentation rates among sites varied from 1.6 mg cm^{-2} d^{-1} at site 8 to 43.2 mg cm^{-2} d^{-1} at site 6 during the sampling periods (Fig. 5). Poor underwater visibility at inner sites 4 and 5 prevented regular collection of sediment traps. However, sedimentation rates were recorded at central and outer sites. Central sites 3 and 6 (Fig. 1) had significantly higher sedimentation rates during both sampling periods. Interestingly there was both intra and inter-site variation. The intra site variation between years may be explained by the smaller sampling period during 2002. Sediment inputs into the system increased after periods of rainfall, and sampling during 2002 was initiated following a period of heavy rainfall. Consequently mean sedimentation rates are considerably higher during these events. Neither of these sampling seasons took place during the hurricane seasons and it is anticipated that during this season sedimentation associated with heavy rainfall and high energy events would peak at greater rates than those recorded during this study.

To classify the effects on marine environmental parameters of the freshwater from the Dornock River entering the Bay, a cluster analysis was performed. All sites were grouped based on their similarity in relation to the range of water quality variables (i.e., mean water clarity, surface salinity and surface temperature, surface = 0.5 m) at each site. Using furthest neighbour, squared Euclidean distance (variables standardised) the sites formed three distinct clusters (Fig. 6). Outer sites 1, 8 and 2 formed group 1; inner sites 3 and 6 were also linked with outer site 7 forming group 2; and sites 4 and 5 were clearly split from the other sites forming group 3.

Geomorphology and community composition

Benthic cover at each site is shown in Figure 7 for a depth range of 2 to 25 m at all 8 sites, Figure 8 illustrates schematic cross sections for the outer sites (1, 2, 7, and 8) and Figure 9 shows the inner (sites 4 and 5)

TABLE 1. Mean temperature and salinity data (±1 standard deviation) April to September 2001, n = 12. The top figure gives Salinity, whilst the bottom figures in italics are temperature °C.

Depth (m)	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
0.15	34.4 ± 1.9	33.7 ± 3.0	30.3 ± 6.8	23.6 ± 8.7	23.6 ± 8.1	30.3 ± 8.7	32.8 ± 7.1	35.0 ± 1.0
	28.3 ± 0.6	*28.3 ± 0.7*	*28.2 ± 0.7*	*27.5 ± 0.8*	*27.4 ± 0.7*	*28.2 ± 1.0*	*28.3 ± 0.7*	*28.3 ± 0.7*
0.5	34.6 ± 2.0	34.2 ± 2.6	31.4 ± 7.0	30.4 ± 7.5	29.8 ± 6.2	33.8 ± 3.4	33.7 ± 5.0	35.1 ± 1.0
	28.3 ± 0.6	*28.3 ± 0.6*	*28.4 ± 0.7*	*28.1 ± 0.9*	*28.0 ± 0.7*	*28.4 ± 0.8*	*28.4 ± 0.6*	*28.2 ± 0.7*
1.0	34.6 ± 2.0	34.7 ± 1.6	34.7 ± 1.2	33.8 ± 3.0	35.1 ± 1.2	35.1 ± 1.3	35.2 ± 1.1	35.1 ± 1.0
	28.3 ± 0.6	*28.3 ± 0.6*	*28.4 ± 0.7*	*28.4 ± 0.6*	*28.5 ± 0.7*	*28.4 ± 0.6*	*28.4 ± 0.6*	*28.2 ± 0.7*
2.5	35.2 ± 1.2	35.3 ± 1.0	35.4 ± 0.9	35.3 ± 1.0	35.1 ± 1.7	35.3 ± 1.0	35.3 ± 1.0	35.3 ± 1.0
	28.2 ± 0.6	*28.3 ± 0.6*	*28.3 ± 0.7*	*28.4 ± 0.7*	*28.3 ± 0.7*	*28.3 ± 0.6*	*28.3 ± 0.6*	*28.2 ± 0.7*
5.0	35.4 ± 1.0	35.4 ± 1.0	35.5 ± 1.0	35.4 ± 1.0	35.4 ± 1.1	35.4 ± 1.0	35.7 ± 1.1	35.3 ± 1.0
	28.2 ± 0.6	*28.2 ± 0.6*	*28.2 ± 0.7*	*28.2 ± 0.7*	*28.2 ± 0.7*	*28.2 ± 0.7*	*28.3 ± 0.6*	*28.2 ± 0.7*
10.0	35.5 ± 1.0	35.4 ± 1.0	35.5 ± 1.0	35.4 ± 1.1	35.5 ± 1.0	35.5 ± 1.0	35.4 ± 1.0	35.4 ± 1.0
	28.1 ± 0.7	*28.1 ± 0.7*	*28.2 ± 0.7*	*28.2 ± 0.7*	*28.1 ± 0.7*	*28.1 ± 0.7*	*28.1 ± 0.8*	*28.2 ± 0.7*

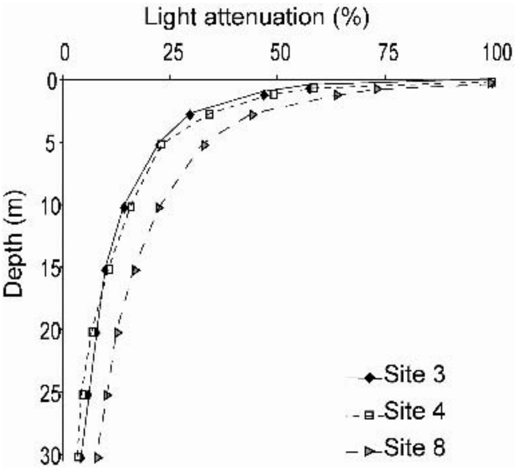

FIG. 3. Mean light attenuation at sites 3, 4 and 8 through the water column, April to Sept. 2001, n = 13.

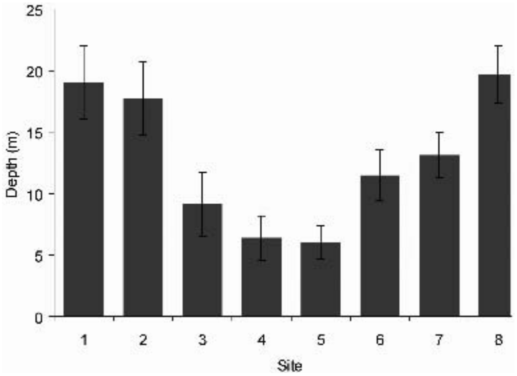

FIG. 4. Mean water clarity (m) (± 1 Standard Error), April to September 2001, n=13.

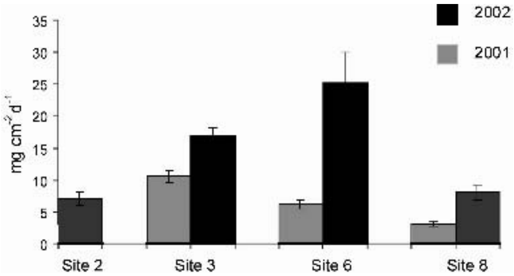

FIG. 5. Mean sedimentation rates (± 1 Standard Error), April to September 2001 and June to August 2002, n=9, with the exception of site 8, 2001 and site 2, 2002 where n = 11 and 6 respectively.

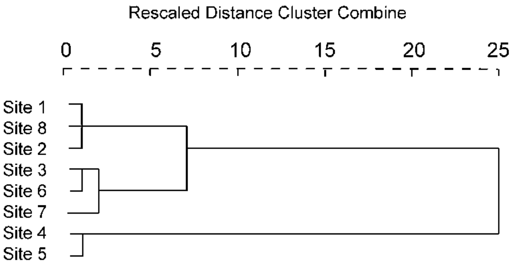

FIG. 6. Cluster analysis - water clarity, salinity and temperature, (furthest neighbour, squared euclidean, standardised variables).

and central sites (sites 3 and 6). These cross sectional profiles highlight the reef structure and geomorphology at each site as described below.

Inner sites 4 and 5 were characterised by open, gently sloping fluvial silts down to a depth of 9 to 12 m. The silty slope then drops away sharply down to 40 m (diver observations did not exceed this depth). There was minimal benthic cover (< 1%) at these sites (0-30 m), the dominant species being the seagrass *Halophila baillonis* (Fig. 9).

Within the central region (Sites 3 and 6; Fig. 9) of the embayment, reef framework development occurred in shallow water (< 2 m) and resulted in the development of a wide (ca. 130 m), shallow reef flat that extends towards the centre of the bay. At site 3, on the western side of the bay, the reef flat leads to a drop-off which forms a vertical wall extending to a maximum depth of 26 m at the most northern point of this site. At the base of this wall there was a steep silt covered depositional apron. Site 6 (Fig. 9) is located in the central eastern portion of the bay. In comparison to site 3, it was a more rugged site sloping off steeply until about 12 m, where the substrate becomes silty with patches of seagrass *Halophila baillonis.* At approximately 14 m the coral framework grows vertically down continuing to depths of 30 m+ and was interspersed with channels of silt. Much of the coral framework was covered in a fine layer of silt. At the base of the wall was a steep, silt-covered apron.

The relative percentage abundance of the dominant hard coral species is shown in

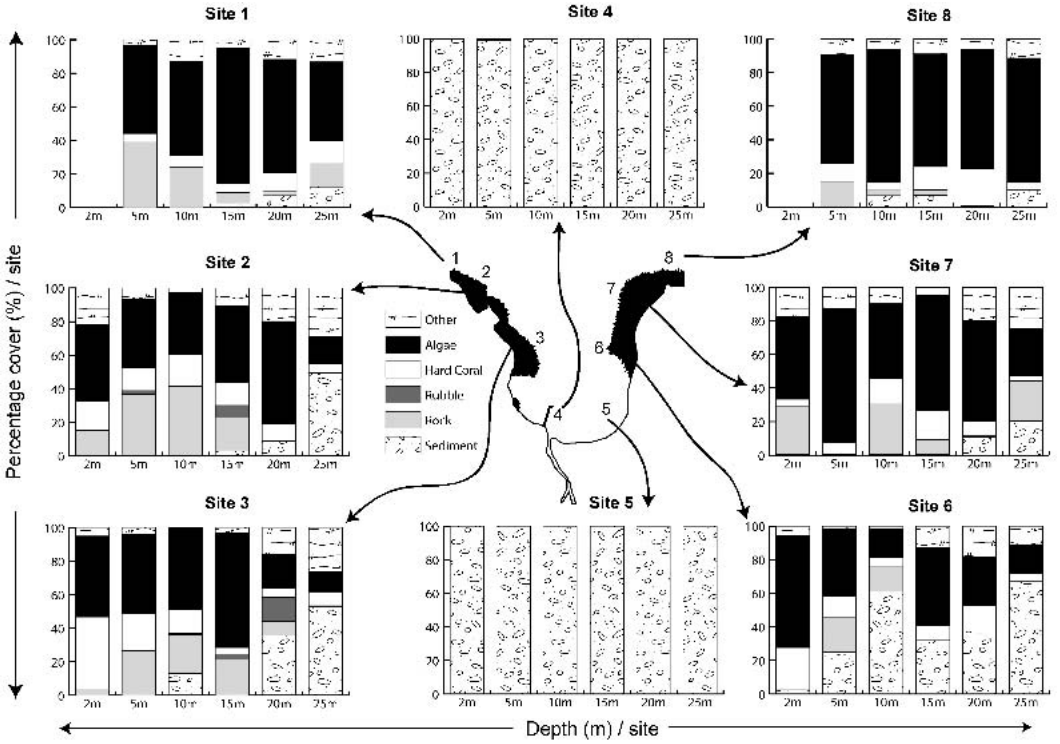

FIG. 7. Mean community composition at different depths at the eight sites in Rio Bueno.

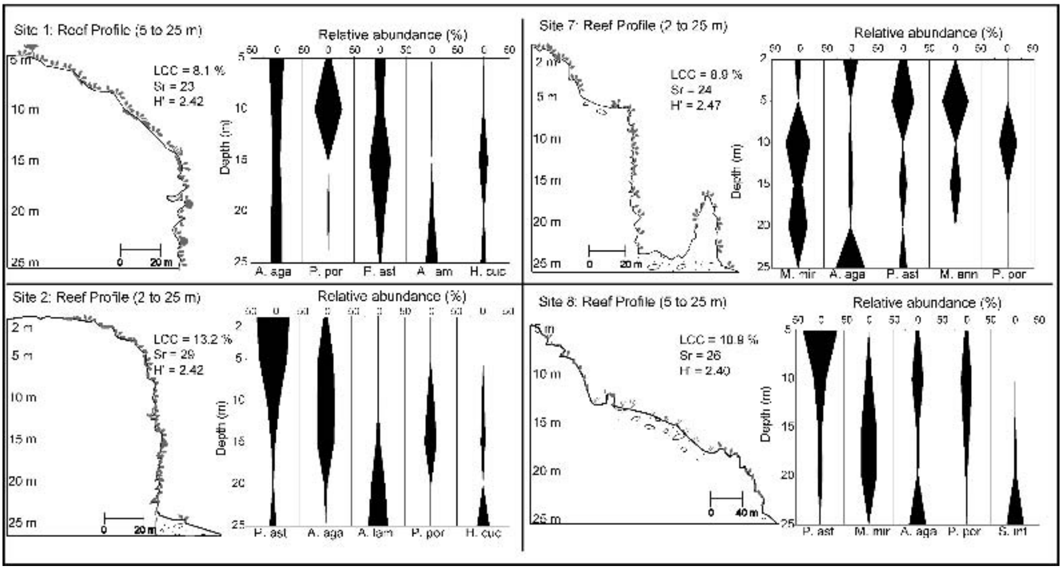

FIG. 8. Schematic cross sections detailing geomorphology, structure and dominant coral species found at outer sites (sites 1, 2, 7, and 8) sites down to a depth of 25 m. LCC = live coral cover, Sr = species richness, H' = Shannon-Wiener species diversity. (A. aga = *Agaricia agaricites*, A. lam = *Agaricia lamarcki*, H. cuc = *Helioceris cucullata*, M. ann = *Montastrea annularis*, M. mir = *Madracis mirabilis*, P .ast = *Porites astreoides*, P. por = *Porites porites*, S. int = *Stephanocoenia intersepts*).

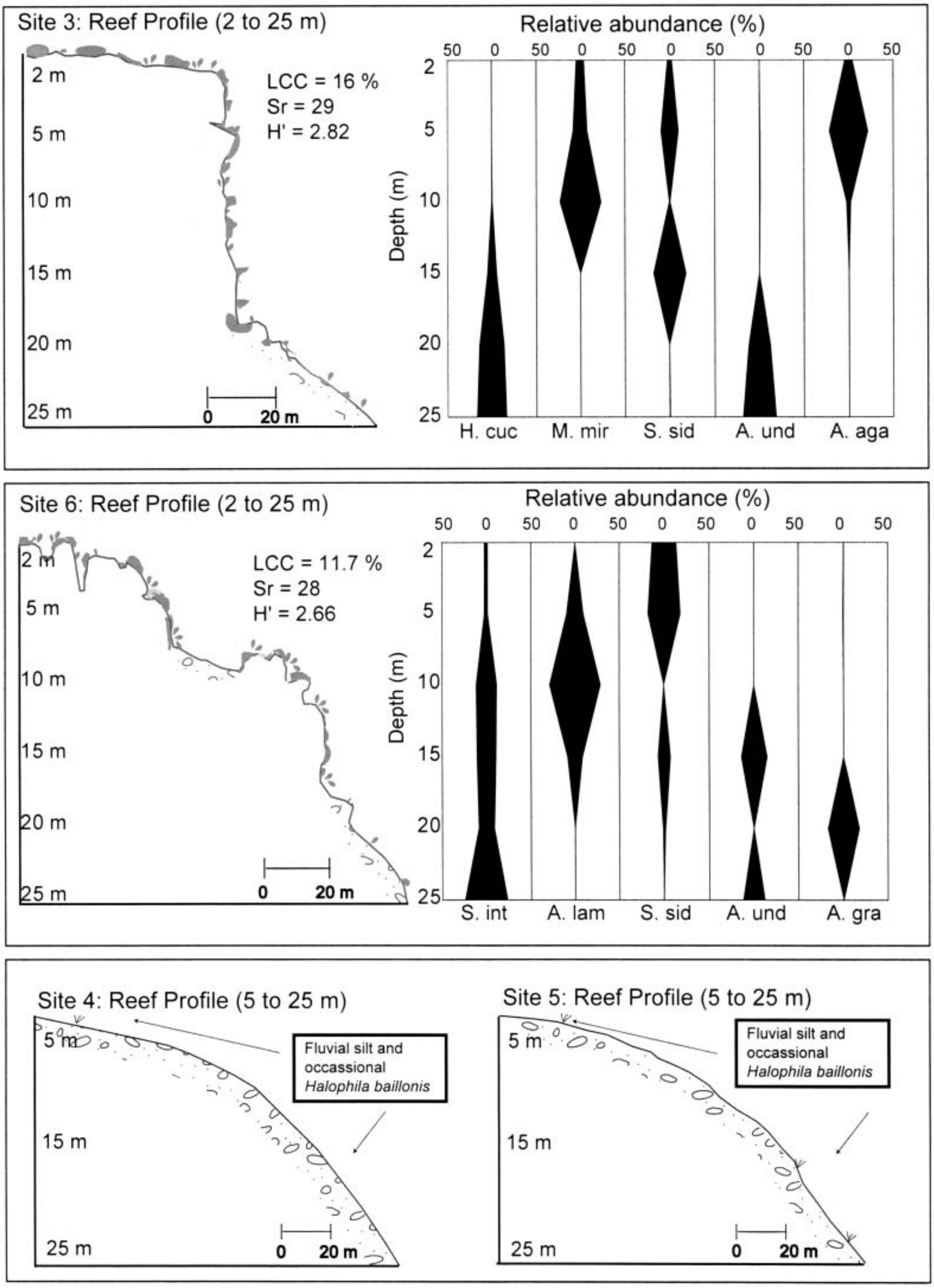

FIG. 9. Schematic cross sections detailing geomorphology, structure and dominant coral species found at inner (site 4 and 5) and central (site 3 and 6) sites down to a depth of 25 m. LCC = live coral cover, Sr = species richness, H′ = Shannon-Wiener species diversity. (A. aga = *Agaricia agaricites*, A. gra = *Agaricia grahame*, A. lam = *Agaricia lamarcki*, A. und = *Agaricia undata*, H. cuc = *Helioceris cucullata*, M. mir = *Madracis mirabilis*, S. int = *Stephanocoenia intersepts*, S. sid = *Siderastrea siderea*).

Figure 9 for the central embayment. Sites 3 and 6 had the greatest hard coral species diversity of all the sites (Shannon-Wiener species diversity H′ = 2.82 and 2.66 respectively), whilst at depths of 2–14.9 m the coral community at site 3 was dominated by *Madracis mirabilis, Agaricia agaricites, Diploria strigosa,* and *Montastrea annularis*. At greater depths, 15-25 m, plate-like colonies of *Agaricia spp., Helioceris cucullata,* and *Porites spp.*, were dominant. The dominant coral species at site 6 between 2–14.9 m were *Siderastrea siderea* and *Montastrea faveolata.* At greater depths (15-25 m) *Stephanocoenia intersepts* and *Agaricia spp.* dominate. Coral cover was greatest along the 2 m transects ranging from 42.9% at site 3 to 24% at site 6. These central sites were dominated by algae (i.e., macro algae and turf). However, the mean algal cover from 2 to 25 m at sites 3 and 6 was 40.8% and 36.0%, respectively. The dominant macro algal species were *Halimeda spp.*, and *Dictyota spp.* at both sites.

The outer embayment sites are illustrated in Figure 8 highlighting the dominant hard corals and their relative percentage abundance. At sites 1 and 8 reef framework was limited to depths of 4 m or more. Sites 1 and 2 are located on the western outer margins of the embayment on a submarine precipice. These sites extend from the shoreline as a reef flat for approximately 20 to 40 m at site 2 and approximately 90 m at site 1. The reef flat slopes downwards gradually to a depth of about 6 m. At greater depths (7–30 m), the sites slope down steeply as a spur and groove zone followed by a vertical drop-off. This wall extends down to 200 m+ (Liddell and Ohlhorst 1993). Coral assemblages at site 2 were dominated by *P. astreoides* and *A. agaricites* from 5 to 14.9 m, and then from 15 to 25 m by *A. lamarcki* and *A. agaricites* (Fig. 8). At site 1, the dominant coral species from 5 to 14.9 m were *Porites porites* and *P. astreoides*. At greater depths (15–25 m) *P. astreoides and Agaricia spp.* dominated. Shannon-Wiener hard coral species diversity ranged at the outer sites from H′= 2.47 at site 7 to H′= 2.40 at site 8. Algal communities dominated sites 1 and 2 from the shallows to depths of 25 m (Fig. 7). The dominant macro algae at these sites were *Halimeda spp.*, and *Dictyota spp.*

Outer sites 7 and 8 (Fig. 8) are located on the north eastern side of the bay. Site 7 slopes downward sharply to depths of 7-10 m, a sand patch stretches out westwards, horizontally, for 10-15 m, and then a wall of coral framework drops vertically to 29-32 m. At the base of the wall sediment slopes dominate. The coral community was dominated by *Madracis mirabilis* and *P. astreoides* from 2-14.9 m. At depths greater than this (15-25 m) *M. mirabilis, Montastrea spp.* and *Agaricia spp.* dominate. Algae accounts for 55.1% of the benthic cover from 2 to 25 m. Macro algae were dominated by *Halimeda spp.*, and *Dictyota spp.*

Site 8 (Fig. 8), is located in the outer, eastern embayment and is furthest away from the river mouth. The coral framework here forms restricted buttresses, which slope down sharply from 4 to 15 m. At this depth, sand and seagrass dominated, (*Thalassia testudinum* and *Syringodium filiforme),* and a gradual slope stretches for a distance of 80-100 m interspersed by occasional patches of rock and coral framework. At a depth of 20 m coral framework occurred sloping down steeply to depths of 27 m + which, at the base, gives way to a gently sloping sand profile (10–15 °). The dominant coral species from 2-14.9 m was *P. astreoides.* At greater depths (15-25 m) *M. mirabilis* dominated. Algae accounted for 71.5% of the benthic cover from 5 to 25 m. Dominant macro algal communities were *Dictyota spp.*, and *Lobophora variegata.*

To summarise, only central and outer sites (sites 1, 2, 3, 6, 7 and 8) contained carbonate framework, whilst the greatest coral cover and species diversity was observed at shallow, turbid water, central sites (sites 3 and 6).

DISCUSSION

This study found that coral communities and reefal framework only occurred at central and outer sites. At these framework producing sites, benthic community structure changed with increasing proximity to the head of the embayment and the mouth of the Dornock River, the following patterns were noted at central and outer sites: 1) an overall increase in coral cover and species diversity; 2) a shift in coral morphologies to dome-shaped and platy forms; and 3) spatially and bathymetrically restricted reefal development. Other studies in turbid environments found both increases and decreases in coral diversity (Cortes and Risk 1985; Van Woesik and Done 1997), shifts in coral morphologies to encrusting and plate-like forms with increased turbidity (Van Woesik and Done 1997), and thinner, shallower, restricted reefs supporting deeper water species than those outside the turbid region (Hallock and Schlager 1986; Acevedo and Morelock 1988; Kleypas 1996; Perry 2003).

It is widely known that high turbidity and low salinity levels can act as limiting factors on reef development in the vicinity of river mouths (Hubbard 1997). However, the extent to which reef development is inhibited is highly site specific and dependant upon factors such as the magnitude and frequency of fluvial discharge events, and the influence of nearshore processes on sediment deposition, resuspension and accumulation (Larcombe and Woolfe 1999) as is the case in Rio Bueno. At sites subject to increased fluvial discharge it is often impossible to determine if changes in community structure are due to sediment particles or freshwater inputs. However, in Rio Bueno freshwater impacts were limited to the surface of the water column (ca. 2.5 m or less), which may indicate that salinity changes are unlikely responsible for the observed differences in benthic community structure. Instead, such changes may be attributed to high levels of turbidity, reduced light penetration, sedimentation, surface topography, substrate type and the local hydrodynamic regime. The complete lack of reefal growth at the inner sites in Rio Bueno may be attributed primarily to the close proximity of the river mouth and the associated fluvial inputs, the effects of which are further compounded by the swamping of this zone with longshore sediment transport from the east. High sedimentation rates have resulted in limited available hard substrate for coral recruitment, and chronic turbidity in a reduced light environment. This area was consequently composed of silt and isolated patches of seagrass.

Central areas of the Rio Bueno embayment are very different in character. Sites are characterised by a broad, shallow, turbid reef flat dominated by large, dome-shaped coral colonies. The reef crest then plunges downwards forming vertical walls. Coral colonies on the wall are dominated by platy corals (e.g., *H. cucullata* and *Agaricia spp*.). Coral cover and species richness peaks on the reef flat and then decreases with depth down the wall. This contrasts with more typical clear water settings where coral diversity would normally peak in the middle depths around 15–30 m (Huston 1985b). At the time of this study, coral cover on clear water Jamaican reefs was 2-20% (Linton et al. 2002). Central sites in Rio Bueno had very prolific coral cover on the reef crest (24 to 42%) however, reefal development was limited to 30 m or less, and reef zones were compressed into this depth range. This has also been noted in other studies whereby high turbidity results in reduced light penetration and consequent spatial and bathymetric restrictions of reef development (Hallock and Schlager 1986; Acevedo and Morelock 1988; Kleypas 1996; Perry 2003).

Mean sedimentation rates in the central embayment were high (i.e., greater than 10 mg cm^{-2} d^{-1}). Such figures have been widely linked with moderate to severe impacts on coral communities e.g., reductions in live coral cover, species richness and growth (Pastorok and Bilyard 1985; Rogers 1990). However, it is not unusual for sedimentation rates in many Caribbean reefal settings to exceed this threshold as was the case in central Rio Bueno, whereby sedimentation rates fluctuate between 3.2 and 43.2 mg cm^{-2} d^{-1} over the relatively short periods of time involved in this study. Despite this, a diverse, bathymetrically restricted, reefal community flourished. Long term studies under natural conditions have also documented fluctuating sedimentation rates in the wider Caribbean ranging from 0.3 to 37 mg cm^{-2} d^{-1} (Pastorok and Bilyard 1985). These studies highlight a general trend whereby increased sediment loads inhibit reefal development. Previous studies note how healthy coral communities may persist in areas of high sediment inputs, where build up was prevented by strong wave action (Pastorok and Bilyard 1985). However, the central embayment area, especially eastern site 6, is sheltered from the prevailing trade winds. The central site 3 (in the west) was where the most persistent turbidity occurred indicating that wave energy here was generally low. This promotes settlement of fine-grained material onto the surrounding benthos resulting in high sedimentation rates. During this period of study, it was observed that the majority of the benthic cover usually had a very fine layer of silt overlying it. The lack of wave-generated currents meant that silt removal must be undertaken by the coral polyp (e.g., mucous production and increased cilia activity).

The most common, and often larger, coral species in turbid sites are considered to be the sediment tolerant species (McClanahan and Obura 1997). Within central Rio Bueno the most abundant, and potentially sediment resistant, species found on these shallow reef crests were dome-shaped corals such as *Montastrea spp.*, *Diploria spp.* and rounded *Siderastrea spp.* Other studies have also recorded an increase in secondary, dome-shaped species in areas of high terrestrial sediment input (e.g., *Siderastrea siderea* and *Porites astreoides*) and concluded that these species were the most tolerant (Acevedo and Morelock 1988; Torres and Morelock 2002). These species then gave way to plate-like colonies e.g., *Agaricia spp.* and branched colonies e.g., *Madracis mirabilis* at depths as shallow as 5 m. Sediment rejection is known to be a function of both morphology and orientation (Rogers 1990). In Rio Bueno, the large dome-shaped corals and plate-like colonies exhibit morphologies that promote general sediment removal. Sediment particles naturally migrate downwards on a dome-shaped coral or on vertically orientated plate coral. Clasts are unable to adhere to thin, cylindrical, upward facing branches of *Madracis spp.* and this facilitates sediment removal. In addition to this, the platy corals may have morphologies adapted to low light levels that under clear water settings would be found at greater depths, which is also consistent with other turbid water studies (Cortes and Risk 1985; Kleypas 1996).

In contrast, the outer sites were characterised by clear waters, low sedimentation rates (less than 10 mg cm^{-2} d^{-1}), and increased wave energy levels. There was no evidence of bathymetric restriction in the sense that individual coral species appeared at comparable depths to those reported from clear water sites in other areas of Jamaica (Gayle and Woodley 1998; Linton et al. 2002; Perry 1997). Coral cover peaked at intermediate depths of 10 to 25 m and then dropped off as would be anticipated in clear water reefs (Huston 1985a). Coral cover ranged from 3 to 22% - falling within the typical range for Jamaican clear water reefs (Linton et al. 2002). At shallow depths (< 10 m) encrusting species e.g., *A. agaricites*, *Montastrea spp.* and small branching colonies of *P. porites* dominated; these colonies were able to withstand the high wave energy on the reef crest. The middle depths (10 to 25 m) were mixed but dominated by encrusting species (*P. astreoides*) and branching species (*M. mirabilis* and *P. porites*) which then gave way at greater depths to plate-like colonies, e.g., *Agaricia spp.* and encrusting forms (*Helioceris cucullata)* (20 m plus) which are typically considered deep water species. These zones resembled modern, clear water, Jamaican reefs (Gayle and Woodley 1998) all of which still lack an *Acropora* zone.

In conclusion, spatial variation in the water quality of Rio Bueno was determined by both riverine inputs and inter-site variability in wave energy. This environmental gradient has resulted in three distinct zones – inner, central and outer. 1) The inner embayment – a low energy, reduced light environment with apparently chronic sediment inputs, where no coral communities exist. 2) The central embayment – a medium energy, reduced light environment. High turbidity and sedimentation rates as compared with open coast conditions have resulted in reefal development that was both spatially and bathymetrically restricted.

However, unusually high coral cover occurs on the reef crest. Coral species that appear to be most sediment-tolerant were dome-shaped morphotypes of *D. strigosa, M. annularis, M. faveolata, P. astreoides, C. natans* and rounded colonies of *S. siderea*. Other coral species adapted to the reduced light by being positioned at shallower depths and orientated in order to enhance sediment rejection. 3) The outer, open coast sites which are minimally impacted by fluvial inputs and processes of sediment entrapment. Light penetration was good, wave energy high, and sedimentation rates low. Coral zonation reflects that of typical Jamaican clear water reefs.

Acknowledgements.—JM was funded by Manchester Metropolitan University and the Royal Geographic Society (with IBG) Slawson Award, UK. We would like to thank Dr Chris Harrod, Dr Rob Nunny and an anonymous reviewer for providing constructive comments. Thank you to all the staff and students at Discovery Bay Marine Laboratory and the many other people who helped with the logistics of this project. In particular Robert Stevenson, Dr Caroline Roberts, Dr Iain Macdonald, Dr Leandra Cho, Dr Anthony Greenway, Kayann Cambell, Tyrone Rose, Anthony Downes, Dalton Smilie, Evon Brown, Debbie-Ann Ramsey and Jahsen Levy. This is publication number 683 of the Discovery Bay Marine Laboratory.

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