

PRODUCTION AND CYCLING OF CALCIUM CARBONATE IN A SHELF-EDGE REEF SYSTEM (ST. CROIX, U.S. VIRGIN ISLANDS): APPLICATIONS TO THE NATURE OF REEF SYSTEMS IN THE FOSSIL RECORD¹

DENNIS K. HUBBARD, ARNOLD I. MILLER² AND DAVID SCATURO³

*West Indies Laboratory
Fairleigh Dickinson University
Teague Bay, St. Croix
U.S. Virgin Islands 00820*

ABSTRACT: Geologic reefs are the end-products of not only constructive processes that produce calcium carbonate, but also of destructive processes (e.g., bioerosion and wave action) that reduce solid substrate to sediment, and of physical processes that rework the reef fabric and transport sediment. A study was conducted at Cane Bay on the island of St. Croix, U.S. Virgin Islands to quantify the suite of processes that have influenced Holocene reef development. Data on carbonate production, reef accretion, bioerosion, and sediment transport were used to construct a detailed "carbonate budget" and to apply the findings of this study to the character of reefs observed in the fossil record.

Total carbonate production on the reef ranged from 0 to 5.78 kg/m² per year, with a reef-wide average of 1.21 kg/m² per year (1.13 by corals; 0.02 by coralline algae; 0.06 by primarily molluscs, forams and echinoderms). Based on 7 cores, only 0.91 kg/m² per year of this have been retained within the reef interior. The remaining 0.24 kg/m² per year of sediment, along with the 0.06 kg/m² per year contributed directly by molluscs, etc., are deposited within reef channels and are probably flushed from the reef by major storms. Of the material recovered in the cores, 58% was either loose sediment and rubble or open void space. Much of the recognizable coral material was demonstrably reworked and out of place.

Accretion rates across the shelf generally increased with water depth, as a result of active slumping along the steepening reef face over the past 2,000–3,000 years. The importance of detrital material in the reef fabric and the major role played by secondary processes that constantly rework the substrate have resulted in a reef whose interior is more of a "garbage pile" than an in-place assemblage of corals cemented together into a rigid "framework."

The physical similarities between the detrital fabric of the reef at Cane Bay and those found in many ancient deposits imply that the general processes operating along the Cane Bay shelf have persisted during much of the evolution of ancient reefs. It is proposed that our modern models overemphasize the importance of in-place framework as a criterion for an "ecologic reef."

INTRODUCTION

While Robert Ginsburg has eloquently likened reef evolution to a long-running play with changing players but a constant plot, others have expressed frustration at using modern reefs to interpret their ancient counterparts. Inherent in these discussions is the idea that through the evolutionary process, not only have reef biotas changed, but depositional patterns have been so profoundly altered that a uniformitarian approach to ancient reef systems has limited application.

Specifically, the lack of recognizable, *in-place* framework in many ancient deposits is contrary to our perception of the interiors of most modern reefs; true "reefs" (i.e., boundstones, framestones) must necessarily contain a significant and recognizable element of in-place and interlocking material. The Ecologic Reefs of Dunham (1970), Organic Framework Reefs of Wilson (1975) and Encrusted Skeletal Buildups of Heckel (1974) all share this distinction, with anything less being relegated to some other "reef-related" category. And again, in an excellent recent text (Fagerstrom 1987) and a thematic volume of Palaios dedicated to reefs through time (Stanley and Fagerstrom 1988), the importance of in-place framework is repeatedly underscored.

This emphasis on the role of framework is understandable when swimming over the magnificent architecture of any modern reef. Most of the first descriptions of modern reefs were biological in nature, and geologists borrowed heavily from the findings of those studies. The models that emerged extrapolated the high diversity and rapid carbonate production of present-day corals to the interior of the accreting reef.

Since the introduction of the submersible rock drill by Macintyre (1975), a number of papers have detailed the lithologies and accretionary histories of reefs in a variety of settings (Great Barrier Reef: Davies and Kinsey 1977; Hopley 1977; Hopley et al. 1978; Davies and Marshall 1979; Davies and Hopley 1983; Central Pacific: Montaggioni 1988; Caribbean: Adey and Burke 1976; Macintyre and Glynn 1976; Adey 1977, 1978; Halley et al. 1977; Macintyre et al. 1977; Lighty et al. 1978; Macintyre et al. 1985). These studies have provided much insight into processes occurring on Holocene reefs, but their concentration on shallow reef crests characterized by rapidly growing corals has reinforced the idea that the interiors of most modern reefs are dominated by coral framework left essentially in place. Discussions have focused on constructional processes, downplaying others that are also important in producing the fabric of both modern reefs and their fossil counterparts. Drilling logs, necessarily simplified for publication, have presented what in many cases is an overstatement of the importance of in-place framework.

The geometric structures of modern reefs not only are the by-products of various carbonate-producing organ-

¹ Manuscript received 26 August 1988; revised 10 October 1989.

² Present address: Department of Geology ML-13, University of Cincinnati, Cincinnati, Ohio 45221.

³ Present address: Coastal Science and Engineering, Inc., Columbia, South Carolina 29205.

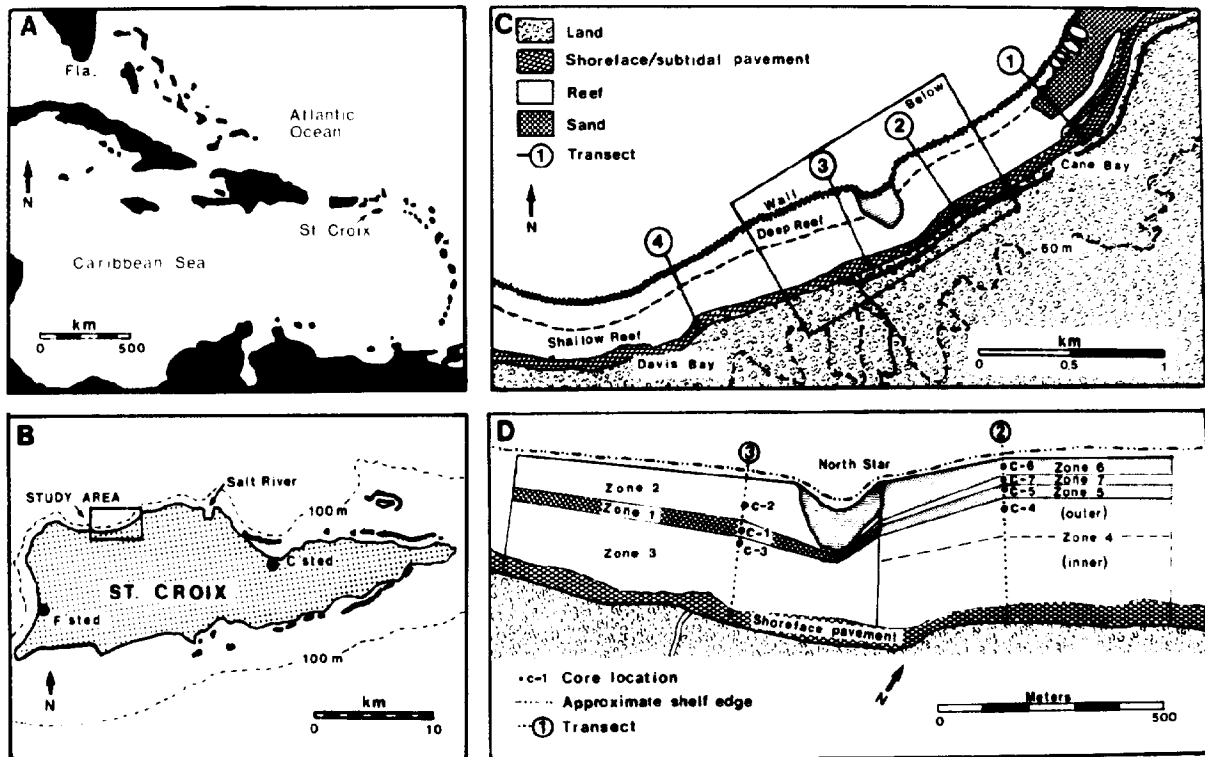


FIG. 1.—Maps showing the locations of St. Croix (A), Cane Bay (B) and the transects along which data were collected for the carbonate-budget calculations (C, D). The budget calculations are based on data collected from transects 2 and 3 only where core data are available.

isms (for a review, see Chave et al. 1972) but are also the end result of physical, chemical and biological processes involved in the degradation and transport of reef carbonate (Rutzler 1975; Moore and Shedd 1977; Stearn and Scoffin 1977; Warne 1977; Zankl and Multer 1977; Davies 1983; Hutchings 1986; Kiene 1988).

Early attempts to integrate these processes into a single budget are described in Neumann and Land (1975), Chave et al. (1972), Stearn and Scoffin (1977), Smith and Kinsey (1978) and Land (1979). A recurring problem in computing past "reef budgets" has been a lack of data systematically collected within a single area. While the paper of Land (1979) represents a landmark in the series of "budget papers," it self-admittedly suffered from its reliance on data collected from a variety of reef areas. The work of Hubbard et al. (1981) and Sadd (1984) at Cane Bay lacked information on either the spatial variability or geological history of the area.

Building on these earlier works, the present study attempted to address the major elements of the carbonate budget for a single reef system, primarily utilizing data collected from within the immediate area. The present-day surface of the insular shelf is compared to the reef interior as revealed in cores. The resulting "carbonate budget" addresses not only the processes of initial carbonate production but also the biological degradation of the reef surface and the redistribution of the resulting sediments within and around the reef. This approach has identified the importance of secondary depositional pro-

cesses in restructuring the reef interior into a package that more closely resembles ancient reef deposits dominated by detrital fabrics than it does the surface of present-day reefs. The authors hope that these observations will provide a useful framework within which modern reefs can be recognized as reasonable models for their fossil counterparts.

STUDY AREA

Cane Bay is located along the northwestern corner of St. Croix, in the U.S. Virgin Islands (Fig. 1A, B). The area is a broadly crescentic stretch of coastline partially protected along its eastern reach by a modest projection of land. The narrow insular shelf (< 300 m) slopes gradually seaward (ca. 5 degrees) to the shelf edge. At depths ranging from -25 to -80 m, the gradual slope gives way to a near-vertical face which decreases in declivity en route to oceanic depths of -4,500 to -5,000 m. The average slope between -80 and -5,000 m exceeds 20 degrees (Burton 1982), and is vertical over most of its upper 2,000 m.

Along most of Cane Bay, the reef extends essentially unbroken from near shore to the shelf edge (Fig. 1C). East of transect 1, the reef is much less continuous and is divided into several shore-parallel bands. A large re-entrant into the shelf between transects 2 and 3 (Fig. 1C, D) may represent a major slump in the steep reef face.

The reef surface is covered by a variety of corals (Fig.

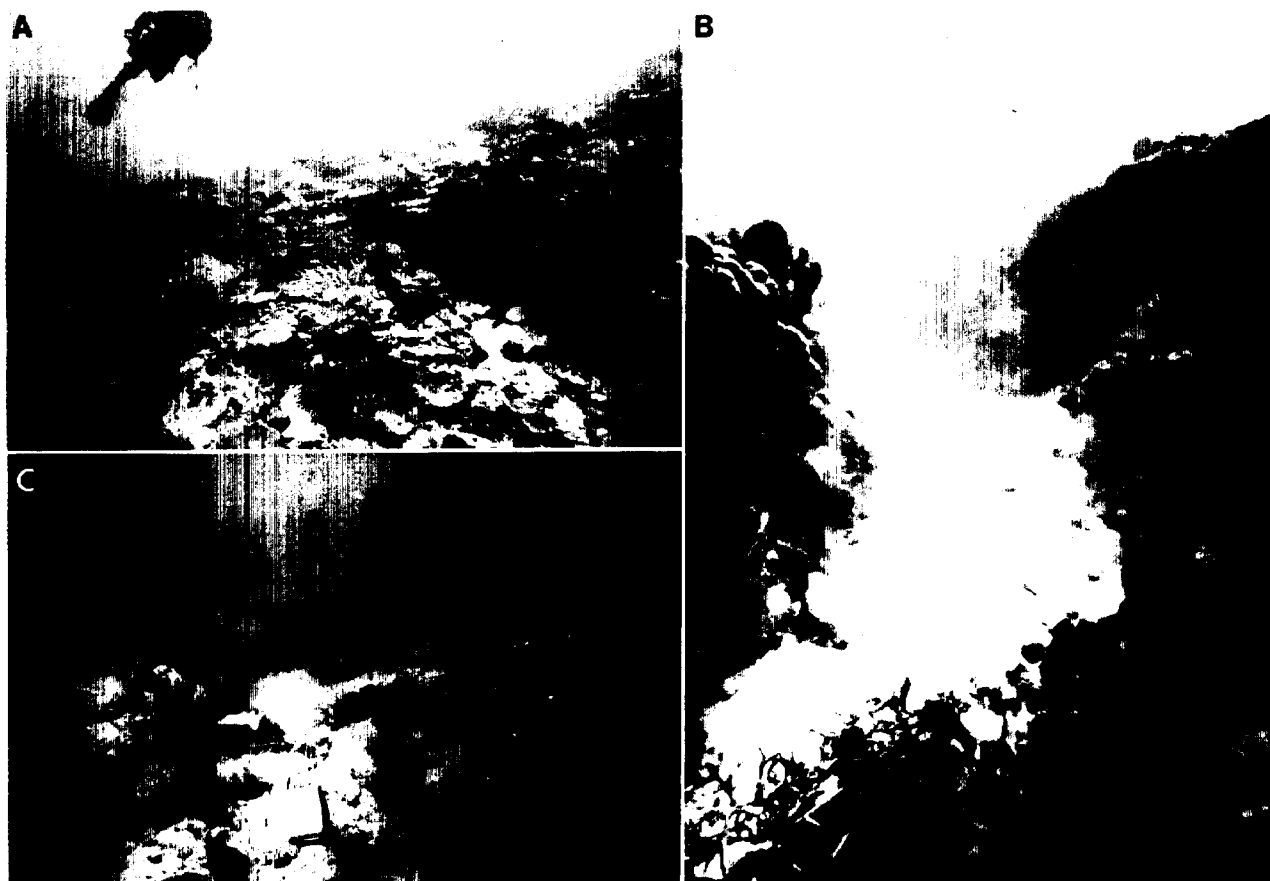


FIG. 2.—Photographs illustrating the reef character at Cane Bay. A. The reef top near the shelf edge is dominated by *Montastrea annularis*, *Porites* sp. and *Agaricia* sp. Water depth is approximately 20 m at this site, and many of the corals have a flattened morphology. B. Typical sand channel traversing the reef at a depth of 15–20 m; width is approximately 1.5 m. C. Wider sand channel near the shelf edge at a depth of 20–30 m; width is 4–5 m (note diver in background for scale). A sediment trap used to measure transport over the shelf edge can be seen in the foreground (arrow).

2A) that reach abundances over 50%. In the mid-shelf region (depth = -10 to -20 m), the reef is dissected by channels that are similar to spur-and-groove topography described in the literature and are oriented roughly normal to the shoreline (Fig. 2B). Toward the shelf edge, the channels increase in size (Fig. 2C), probably in response to the greater volume of sediment passing through them. These channels serve as short-term repositories for biologically generated sediments that are eventually exported through them, primarily by wave and current action.

The dominant carbonate-producing organisms on the reef are species of the scleractinean coral genera *Montastrea*, *Agaricia*, and *Porites*, along with a variety of crustose coralline algae. *M. annularis* and *P. astreoides* demonstrate polymorphic changes with depth, ranging from hemispherical colonies in shallower water to platy ones near the shelf break. *Acropora palmata* and *A. cervicornis* are rare both on the present reef surface and within its interior. Notably absent is the alga *Halimeda*, so common on many Caribbean reefs. For additional details, the reader is referred to Hubbard et al. (1981), Sadd (1984) and Hubbard (1989).

METHODS

The budget discussed below can be characterized by the formula:

$$P_g - P_n = SED, \quad [1]$$

where

P_g = gross carbonate production
 P_n = net carbonate production
 SED = sediment not incorporated within the reef fabric

Gross production refers to the amount of calcium carbonate produced by the organisms inhabiting the reef. These include primarily corals and coralline algae, along with less-important molluscs, forams, echinoderms, serpulids and bryozoans. The carbonate remaining within the reef (net production) is comprised in part by the recognizable remains of corals and coralline algae and in part by sediment resulting from their biological, physical and chemical breakdown. The remainder consists of mostly bioeroded sediment that is stored within reef channels to be removed by physical processes. Net on-

TABLE 1.—Summary of carbonate budget calculations

Parameter	Method	Rate*		
Gross Prod (P_g)	see Table 4	1.15 (0.66) by corals and algae		
Net Prod (P_n)	see Table 8**	0.91 (0.51)		
<u>Sediments introduced into channels:</u>				
–Bioerosion (SED)	$P_g - P_n$	= 0.25 (0.16)		
–Cor algae (SED _{ca})	(SED _i) × (ABN _{ca})***	= 0.02 (0.01)		
–Dir contr (SED _d)	(SED _i) × (ABN _d)***	= 0.06 (0.04)		
Total seds (SED _i)	(SED)/(ABN)	= 0.33 (0.21)		
<u>Sediment transport:</u>				
A. Total shelf area		= 412,200 m ²		
B. Total shelf length		= 1,440 m		
C. Area of channels		= 103,050 m ² (A/4)		
D. Total channel width		= 360 m (B/4)		
E. Total sediment prod		= 123,600 kg/yr (0.30 × A)		
Fair-weather (335 days)		= 65 kg/m per yr		
Storm-related (30 days)		= 1,130 kg/m per yr		
	$(65)(335) + (1,130)(30)$	= 153 kg/m per yr (Annual Avg)		
	365			
Total sediment export		= 55,100 kg/yr (153 × D)		
<u>Sediment Balance:</u>				
	(Sediment—in kg/year)			
	Sand	Mud	Total	% Sand
Into channels	92,700	30,900	123,600	75†
Exported	55,100	28,900	84,000	
Remaining	37,600	2,000	39,600	95‡
<u>Sediment accumulation:</u>				
Mass	(39,600 kg/yr)/(103,050)		= 0.38 kg/m ² per year	
Equivalent accretion			= 0.30 m/1,000 yr	

* Rate expressed in kg/m² per year and (m/1,000 yr).

** P_n [m/1,000 yr] = $\frac{\text{rec. in dated interval} + (\text{seds in dated interval} \times 0.67)}{\text{maximum age}}$

P_n [kg/m² per year] = P_n [m/1,000 yr] × 1.80.

*** ABN = abundance based on sediment thin sections (percent/100).

† 75% of sediment produced by bioerosion is sand (Eq. 4).

‡ Approximate average from sieved sediments.

shore-offshore sediment exchange with beach sediments is minimal in this area (Hubbard et al. 1981) and is ignored in this budget.

Gross Production

The total amount of carbonate produced on the reef is a function of 1) the relative abundance of calcifying organisms, 2) the total surface area which these organisms occupy, and 3) the production rates of each organism. To evaluate these factors, three shore-normal transects were extended from near the beach to a water depth of 40 m (transects 1–3; Fig. 1C). The measurements described below were made at 10-m horizontal intervals along those transects. Cores were collected along two of the transects (CB-02 and 03; Fig. 1C, D). The third transect, along with one at the easternmost end of the embayment (transect 4; Sadd 1984) provide additional data for comparison. The methods described below are briefly summarized in Table 1.

Species Abundance.—At each of 46 stations, a 10-m chain with 1-cm links was draped over the bottom, conforming to the irregular surface of the substrate (Fig. 3A).

The number of links covering each bottom component (e.g., coral, sand) was noted, and the relative abundance of each component was determined by dividing the number of links covering it by the total number of links in the chain. The amount of irregular reef surface covered by any individual component was computed by multiplying its relative abundance (0–1.0) by the surface area of the reef.

Reef-Surface Area.—Because of the irregular character of the reef surface, each square meter of reef in plan view contains more than one square meter of surface area. An approximation of this roughness (Surface Area Correction Coefficient = SACC) was made by dividing the 10-m length of the survey chain (L) by the linear distance it spanned (D in Fig. 3A). A section of reef measuring one square meter in plan view will have a surface area, in m², equal to the SACC. The surface area occupied by any organism can be determined by multiplying its proportion (i.e., percent/100) by the SACC of the reef section within which it is contained.

Carbonate Production by Corals.—Over 150 coral colonies were collected at 3-m depth intervals along the P_g -transects between shore and a depth of –39 m. Samples

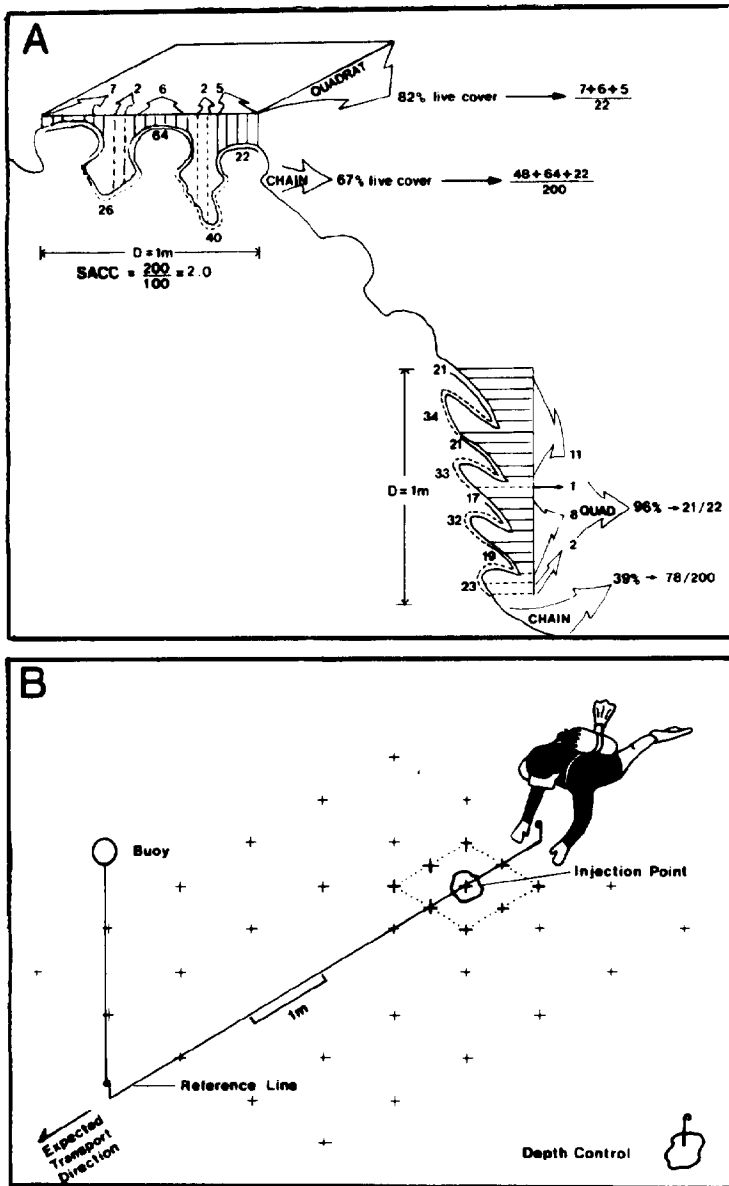


FIG. 3.—Diagrams illustrating the methods used to determine reef cover (A) and sediment-transport rate (B). Two examples are given in which percent cover determined by the chain method is compared to the same parameter determined by a quadrat. In the quadrat method, the dead substrate (dashed lines) on the undersides or edges of corals is typically obscured, yielding inflated estimates of live cover. The “roughness” of the reef surface (SACC) is determined by dividing the length of the survey chain (L) by the linear, plan distance surveyed (D). Sediment transport was measured by placing sediment, which had been dyed with fluorescent paint, on the bottom and allowing it to move naturally over some period of time. Samples were collected at the sites marked by x’s.

were slabbed and X-rayed to reveal density bands that have been shown by past studies (Knutson et al. 1972; Hudson et al. 1976) to represent annual growth increments. Linear-extension rate was measured along 5–10 growth axes of each sample. Bulk density was computed from measurements of volume and mass for cubes cut from each sample. These values were used to convert between linear extension and mass added per unit area. For a detailed discussion, see Hubbard and Scaturo (1985).

Along transect CB-02, samples of *Montastrea annularis*, *M. cavernosa*, *Agaricia agaricites*, *Siderastrea siderea*, *Diploria clivosa*, *Porites astreoides* and *Stephanocoenia* sp. were collected. At each depth, a ratio was computed between the growth rate of *M. annularis* and those of the other six species. Along transect CB-03, where only *M. annularis* was collected, this ratio was used to

approximate the growth rates for the other six corals (Table 2). This calculation assumes that all seven species react similarly to changing environmental conditions, and it may lead to errors in P_g values along transect CB-03. Given the dominance of *M. annularis* and the low degree of variability between transects, however, the resulting errors should be small. The remaining corals, which represented only a few percent of the total cover, were assigned a growth rate of another coral with a similar distribution and growth form (Table 3).

Production by *Acropora cervicornis* is based on data for St. Croix reported by Gladfelter (1984). She found that *A. cervicornis* extended axially at a rate of 10 cm/yr and laterally (i.e., radius) at 3 mm per year. Using a branch density of 33 tips per square meter measured on St. Croix, a density of 1,767 kg/m³, and applying Gladfelter’s rates

TABLE 2.—Growth rates measured for corals at Cane Bay (in mm/yr). Rates are given only for depths at which specific corals were found

Coral	Depth (m)												
	3	6	9	12	15	18	21	24	27	30	33	36	39
Transect CB-02:													
<i>M. ann</i>	8	6	6	3	2	2	2	2	2	2	2	2	2
<i>M. cav</i>	6	5	5	4	3	3	3	2	2	2	2	2	2
<i>Agaric</i>	—	2	2	2	2	2	2	2	1	1	1	1	1
<i>Millep*</i>	4	4	4	1	1	1	1	—	—	—	—	—	—
<i>P. ast</i>	3	3	3	3	3	—	—	—	—	—	—	—	—
<i>A. cer**</i>	3	3	3	3	—	—	—	—	—	—	—	—	—
<i>D. cli</i>	5	3	3	—	—	—	—	—	—	—	—	—	—
<i>D. lab</i>	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>S. sid</i>	3	3	—	—	—	—	2	—	—	—	—	—	—
Transect CB-03:													
<i>M. ann</i>	8	8	8	6	6	2	2	2	2	2	2	2	2
<i>M. cav</i>	6	6	7	—	—	—	—	3	3	1	1	1	1
<i>Agaric</i>	—	2	2	2	3	2	2	2	2	1	1	1	1
<i>Millep*</i>	4	4	4	—	—	—	—	—	—	—	—	—	—
<i>P. ast</i>	4	5	5	—	—	—	—	—	—	—	—	—	—
<i>A. cer**</i>	3	3	3	3	3	3	3	—	—	—	—	—	—
<i>D. cli</i>	—	5	5	5	6	6	3	3	3	—	—	—	—
<i>D. lab</i>	4	5	5	5	—	2	2	2	—	—	—	1	1
<i>S. sid</i>	4	3	3	4	4	—	—	—	—	—	2	—	—

* See text and Table 3.

** See discussion in text for calculation of these values.

to the formula for a cylinder, the production rate for *A. cervicornis* was computed to be 0.0003 m³/m² per year (0.53 kg/m² per year).

This value seems low when considering the high accretion rates reported for reefs dominated by this coral (e.g., 12 m/1,000 per year in some Caribbean reefs; Adey 1978). However, these high accretion rates are typically a function of either 1) the open, branching framework produced in an in-place reef, or 2) physical concentration of reef rubble derived from an area wider than that from which accretion rates were derived. At any rate, the lack of *A. cervicornis* in any of the cores, and its paucity on the reef surface, argue against its volumetric importance in the carbonate budget of this reef.

The same rate was used for *A. palmata*. This is likely an underestimation of production by this rapidly growing coral. However, it was found at only two sites on four transects, and it is preserved in the lowest section of only one core. Therefore, any error related to this would be negligible.

Gross production by each coral species is the product of the surface area it occupies and its individual rate of calcification. Total production at any one site was computed as the sum of the production rates for each coral and is reported in kg/m² per year and m³/m² per year. Values reported in m³/m² per year can be directly converted to accretion rate in m/yr (i.e., 1 m³/m² per year = 1 m/yr). A sample computation is provided in Table 4.

Gross Production by Coralline Algae.—No reliable data on calcification by these prolific organisms are available over the depth range examined at Cane Bay. Intense predation precludes direct measurement of growth. Rates obtained in areas where predators have been artificially removed are unreliable, as production is in part controlled by the intensity of herbivory (Adey and Vassar 1975; Steneck and Adey 1976).

The paucity of coralline algae in the cores despite their prominence on the reef surface likely implies that coralline growth has been roughly balanced by predation. Therefore, gross production by coralline algae and the

TABLE 3.—Presumed growth rates for corals (and *Millepora*) not directly measured in this study

Coral Measured	Other Corals Assigned Same Rate	Depth	Growth
<i>A. cervicornis</i>	<i>A. palmata</i>	0–10 m	0.37 cm/yr
<i>A. agaricites</i>	<i>Mycetophyllia</i> spp., <i>Helioseris</i> spp.	10–20 m	0.13 cm/yr
<i>D. clivosa</i>	<i>Meandrina</i> spp., <i>Colpophyllia</i> spp.	20–30 m	0.07 cm/yr
<i>M. annularis</i>	<i>Stephanocoenia</i> spp.	>30 m	0.00 cm/yr
<i>S. siderea</i>	<i>S. radians</i> , <i>Dichocoenia</i> spp.		
	<i>Millepora</i> :		
		1.40 × rate of <i>M. annularis</i>	
	<i>P. porites</i>	1.40 × rate of <i>M. annularis</i>	
	<i>M. decactis</i>		

TABLE 4.—Example of budget calculations at a single survey site

Coral	Growth [m/yr]	Cover %	Cor Cov [m ² /m ²]	Volume [m ³ /m ² per yr]	Density [kg/m ³]	Mass [kg/m ² per yr]	Accr [m/1,000 yr]
<i>Diploria</i>	0.0038	13.68	0.26	0.00099	1,628	1.61	0.99
<i>M. annularis</i>	0.0026	0.30	0.01	0.00003	1,808	0.05	0.03
<i>Agaricia</i>	0.0023	1.98	0.04	0.00009	1,757	0.16	0.09
Cor algae	—	58.97	1.11	<i>See sed. prod (methods)</i>			
Sand	0.0000	23.56	0.45	0.00000	—	0.00	0.00
Alcyonar	0.0000	1.51	0.03	0.00000	—	0.00	0.00
Total				0.00111		1.82	1.11
SACC = 1.89							

Sample calculation for *Diploria* using the above data:

Growth rate of *Diploria* = 0.0038 m/yr; on transect CB-03, this is derived from a ratio of 1.45:1.00 between the growth rates of *Diploria* and *M. annularis* ($0.0026 \times 1.45 = 0.0038$); on transect CB-02, it is measured directly.

Cor Cov = $(1.89)(13.68/100) = 0.26$.

Volume = Cor Cov \times Growth = $(0.26)(0.0038) = 0.00099$ m³/m² per yr.

Mass = Volume \times Density = $(0.00099)(1,628) = 1.61$ kg/m² per yr.

Accretion = Volume \times (1,000 yr/1,000 yr) = 0.99 m/1,000 yr.

amount of sediment produced by their breakdown must be nearly equal. The methods used to determine the bioerosion (and, therefore, gross production) of corallines are discussed below.

Net Production

Seven cores were recovered from transects CB-02 and CB-03 using a diver-operated drill similar to that described by Macintyre (1975). Core locations were chosen based on gross morphological character of the reef. The reef complex was subdivided into seven zones with a core in the center of each (Fig. 1D). The net-production rate for each zone was determined from the core within it.

Radiocarbon-age determinations were derived only from fresh samples of coral containing 100% aragonite (see Hubbard et al. 1985, 1986 for details). The rate of reef accretion, measured in m/1,000 yr, was computed by dividing the core interval to the last dated sample by its age. The reef surface, by definition, represents present time. It is important to remember that, in this paper, the term *accretion* refers only to the vertical change in the reef surface over time and implies nothing about the character of that surface at any instant or the continuity of processes responsible. The total carbonate preserved in each core (TC) was derived from the linear amount of solid core (coral, coralline algae and cemented sediment) recovered plus 67% of the intervals containing sand and rubble. The value of 67% is derived from a ratio between the bulk densities measured for coral (ca. 1,800 g/cc) and dry sand (ca. 1,200 g/cc). The total length derived in this manner was multiplied by 1,800 kg/m³ to yield an equivalent production rate in kg/m² per year.

Sediment Generation

Sediment found in the reef system comes from two sources. The first is bioerosion, which involves both mechanical and chemical removal of substrate. Workers have been successful in estimating bioerosion by single species over relatively small areas (e.g., Ogden 1977; Moore and Shedd 1977), but determining this for all species of bio-

eroders over an area as large as Cane Bay would be a Herculean task.

Land (1979) argued that the difference between what should be found in the reef based on the rate of gross production (P_g) and what is ultimately revealed by coring (P_n) is equal to the amount of sediment generated by bioerosion and exported from the reef (i.e., bioeroded sediment that is reincorporated within the reef remains as part of P_n). Because the dominant species found in the cores have a distribution similar to those on the present reef surface, it is likely that present conditions have persisted over the last 3,000–5,000 years and that the assumption of Land is reasonable at this site. Therefore, the overall amount of sediment generated by bioerosion and exported from the reef was estimated by subtracting the carbonate preserved in the cores (P_n) from the Gross Production (P_g). Total bioerosion was determined by adding in the amount of detrital sediment reincorporated into the reef fabric.

Of secondary importance is the direct contribution by accessory organisms (e.g., molluscs, benthic foraminifera) whose skeletons contribute directly to the sedimentary record without cycling through the reef (i.e., they must be added to both P_g and SED values based on coral data). To assess the importance of this, sediment samples were taken at 3-m depth intervals along transect CB-03. The relative abundance of each constituent was determined from 100-point counts of thin-sections at 40–100 \times magnification.

Total sediment production was computed using the formula:

$$SED_t = SED/ABN, \quad [2]$$

where:

SED_t = total sediment production, in kg/m² per year
 SED = sediment production from bioerosion ($P_g - P_n$, kg/m² per year)

ABN = proportion of bioeroded coral in the sediment

Production by Coralline Algae.—As discussed above, the growth of coralline algae is roughly balanced by bioerosion. Therefore, the rate of sediment generated by the

breakdown of corallines provides a close approximation of their rate of gross production. The abundance of coralline algal fragments in the sediment samples was multiplied by the rate of total sediment production (SED_t) to determine the amount of sediment produced by the degradation of these organisms. This value was also added to the rate of gross production by corals.

Sediment Export

Sediment not reincorporated into the reef moves into shore-normal channels and is eventually exported to the basin north of St. Croix. The long-term stability of the beaches in Cane Bay, and the confinement of the area on both ends by rocky promontories, infer a closed system with little net longshore flux. Therefore, nearly all sediment export from the system must occur over the shelf edge.

Sediment Traps.—Sediment traps were deployed below several major reef channels at the shelf edge (Fig. 2C) as well as along the deep-reef face between channels. The traps were attached to the vertical substrate by metal pins. Aluminum foil sealed the traps to the irregular substrate. Traps were collected at varying time intervals, depending on the severity of the sea state (i.e., experiments were left longer under calm conditions). Sediments were dried and weighed (with a correction for salt). Data include 9 measurements of offshelf transport.

Dyed Tracer.—Natural sediment was collected from each experimental site and impregnated with fluorescent paint thinned with Toluene. This caused no significant change in grain size (Hubbard et al. 1981), although small changes in bulk density likely occurred. Two to five kilograms of dyed sediment were placed in a shallow depression to match the existing bottom contour. The site was marked by a reference line suspended far enough above the substrate to avoid interference with the natural flow of water.

The dyed sediment was left for 11–73 days, depending on weather conditions. Just prior to sampling, the area was marked with a reference grid subdivided into 1-m segments (Fig. 3B). The grid squares closest to the injection site were divided into 0.5×0.5 -m segments. At each grid intersection a small piston core, 4 cm in diameter, was used to sample the upper 10 cm of sediment.

In the lab, preselected cores were examined under UV light to determine the depth into the sediment at which an abrupt diminution (usually to 0) in the tracer concentration could be seen. This was interpreted as the depth into the sediment over which transport had occurred. Uniform lengths of each core were dried, and the number of dyed grains in each were manually counted under UV light. Based on these counts, the new center of mass for the dyed sediment was determined using the method of moments. The distance between the original injection site and the new center of mass was divided by the time interval of the experiment to yield an advection rate in m/day. Multiplying the advection rate by the depth of reworking (usually 0.02–0.03 m), a unit width of 1 m, and 365 days/yr yielded a transport rate in m^3/yr per

linear width of channel (m^3/m per year). This was converted to kg/m per year using a sediment density of $1,200 kg/m^3$, determined from several samples of local carbonate sediment.

Five measurements were taken at three sites near the shelf edge. Using the data from these same traps and tracer experiments, Hubbard et al. (1981, 1982) and Sadd (1984) computed transport rates different from those reported here. They used various sediment densities drawn from the literature, however, while this paper uses data from local sediments.

RESULTS

Distribution of Organisms

Coral abundance increases steadily toward the shelf edge (Fig. 4), with the highest cover (51.2% and 36.6% along transects CB-02 and CB-03, respectively) occurring either near the shelf break or along the reef front. Algal cover follows a trend similar to that for coral (Fig. 4), with total cover by algae remaining consistently higher. In the inshore zone, coral generally comprises less than 10% of the substrate. Species diversity is low, and the bottom is often devoid of all but a few algal turfs and scattered patches of coralline algae. Beyond that, to a depth of -8 to -10 m, *Montastrea annularis* dominates, its abundance ranging from 5 to 30%. Along the outer shelf margin, *Agaricia* sp., *M. annularis* and *M. cavernosa* (and *Porites* sp. on transect CB-03) are the codominant species. *Agaricia* sp. assumes sole dominance along the steeply sloping reef front.

The higher coral cover near the shelf edge is related to two factors: 1) high levels of terrigenous sedimentation during intense rains discourage corals closer to shore, and 2) sediment shed by corals near the shelf edge is more easily removed from the reef. The latter is facilitated by the energetic circulation typically occurring at this abrupt interface (Roberts et al. 1977) and by steep slopes and proximity to a site of deeper-water deposition.

At first glance, coral abundance appears low compared to other areas. This is in large part due to methodology, however. Species abundance is typically estimated or measured using a quadrat, which overestimates the importance of irregular coral colonies and obscures underlying flat surfaces (Fig. 3A). The chain method described above gives a more accurate, but usually lower, estimate of the surface area occupied by living coral.

Gross Production (P_g)

Production by Corals.—In general, growth rates for *M. annularis* fall into two groups (Table 2). Shallower than -9 m, growth rates vary between 6 and 9 mm/yr. Deeper than -15 m, they range from 1 to 2 mm/yr. An abrupt drop in growth rate occurs at intermediate depths, and is discussed in Hubbard and Scaturo (1985).

Over most of the gently sloping shelf, water depth is less than 15 m. Because *M. annularis* comprises such a great portion of the reef fauna (Fig. 4) and coral-growth

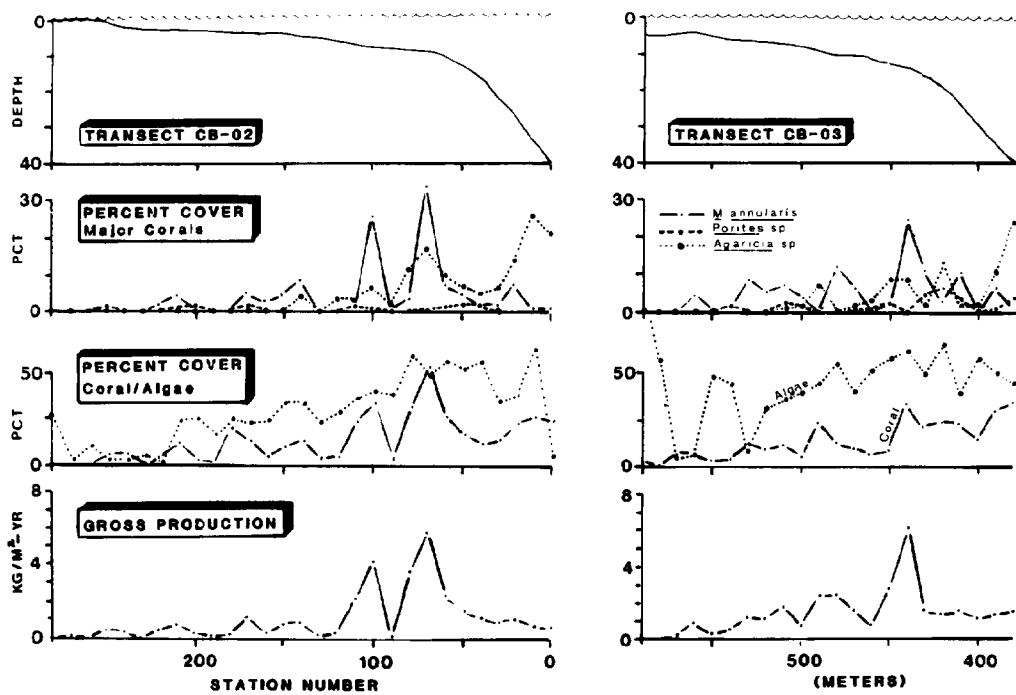


FIG. 4.—Summary of reef character along the two transects used in the carbonate-budget calculations. The most important corals are *M. annularis*, *Porites* sp. and *Agaricia* sp. In general, coral cover increases toward the shelf edge where stresses related to terrestrial sedimentation are reduced and water circulation is more vigorous. Total cover by algae (turfs plus corallines) and gross-carbonate production follow similar trends. The “saw-toothed” character of the productivity curves reflects the transects encountering sand channels as they cross the shelf.

TABLE 5.—Summary of survey data from Cane Bay. This is an abbreviated form of the spreadsheet data explained in Table 4

Transect CB-02					Transect CB-03						
Station	Water Depth	Coral Cover	SACC	Gross Production Rate		Station	Water Depth	Coral Cover	SACC	Gross Production Rate	
				[kg/m ² per year]	[m/1,000 yr]					[kg/m ² per year]	[m/1,000 yr]
000	39.6	22.9	1.22	0.58	0.33	380	39.6	36.6	2.00	1.41	0.81
010	35.1	26.0	1.37	0.71	0.41	390	35.1	31.5	1.82	1.35	0.76
020	27.5	21.2	1.74	0.91	0.52	400	30.2	16.0	1.56	1.07	0.65
030	22.6	14.4	1.92	0.89	0.48	410	24.4	22.6	1.67	1.56	0.91
040	16.5	11.0	2.62	1.01	0.58	420	19.8	22.9	1.72	1.30	0.74
050	12.8	17.7	1.85	1.41	0.81	430	16.8	21.3	1.49	1.53	0.85
060	10.7	25.6	1.96	2.20	1.26	440	14.3	34.9	2.00	5.78	3.23
070	9.2	51.2	2.04	5.78	3.43	450	13.4	9.4	1.48	2.82	1.60
080	8.8	30.3	2.38	3.47	2.02	460	11.0	7.4	1.39	0.81	0.45
090	8.3	2.3	2.38	0.14	0.08	470	10.7	10.0	1.61	1.66	0.92
100	7.9	33.7	1.95	4.04	2.42	480	10.4	12.5	1.44	2.38	1.33
110	7.6	22.7	1.68	2.03	1.19	490	9.1	23.5	1.61	2.32	1.27
120	6.7	4.5	1.38	0.22	0.12	500	7.9	6.7	1.33	0.82	0.47
130	6.1	2.3	1.30	0.10	0.06	510	7.3	11.6	1.32	1.81	1.02
140	5.5	11.3	1.30	0.96	0.57	520	6.7	8.9	1.34	1.04	0.60
150	4.6	9.5	1.15	0.80	0.47	530	7.0	12.0	1.14	1.11	0.67
160	4.4	3.4	1.14	0.30	0.18	540	6.3	4.2	1.15	0.24	0.14
170	4.3	11.5	1.37	1.10	0.62	550	5.9	3.8	1.37	0.45	0.27
180	4.3	20.0	1.44	0.21	0.12	560	4.9	6.6	1.22	0.93	0.52
190	4.3	0.0	1.11	0.00	0.00	570	4.6	7.1	1.43	0.09	0.05
200	3.7	1.7	1.12	0.16	0.10	580	5.2	0.0	1.18	0.00	0.00
210	3.4	10.5	1.20	0.71	0.41	590	5.0	1.7	1.25	0.23	0.13
220	3.1	4.5	1.11	0.42	0.26						
230	2.7	0.0	1.00	0.00	0.00						
240	2.7	4.7	1.03	0.35	0.22						
250	1.8	4.5	1.06	0.43	0.26						
260	1.5	0.0	1.13	0.00	0.00						
270	1.5	0.0	1.08	0.00	0.00						
280	0.9	0.00	1.30	0.00	0.00						

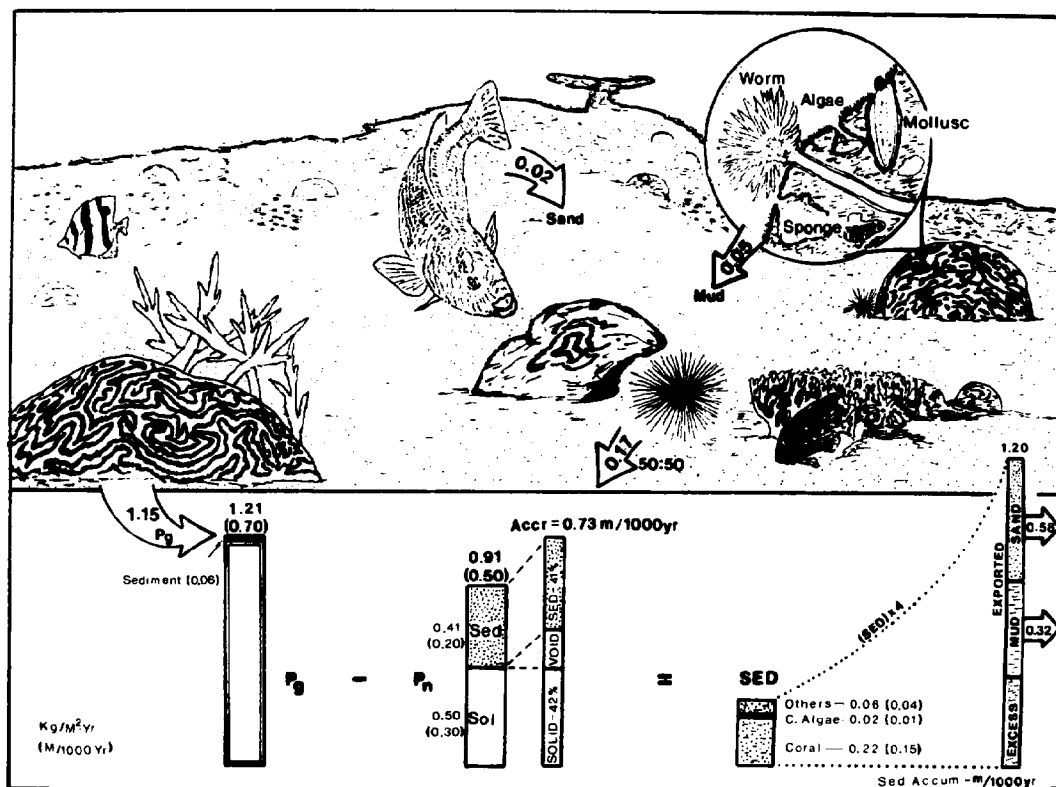


FIG. 5.—Summary of rates computed for the carbonate budget at Cane Bay. Of the 1.21 kg/m² per year of carbonate produced annually within the reef, nearly 60% is reduced to sediment by bioerosion, primarily by urchins (0.17), as well as grazing fish (0.02), boring sponges, molluscs, worms and endolithic algae (0.05). Over half of the sediment produced is reincorporated within the reef interior. The remaining detritus moves into the sand channels that dissect the reef surface and is eventually exported from the reef and over the shelf break. Within the reef “framework,” 58% is comprised of either sediment or open void space, with much of the remaining coral having been demonstrably moved from its original site of deposition. Values are reported in kg/m² per year and m/1,000 yr (parentheses).

rate remains high, carbonate production is more dependent upon total reef cover than on water depth. Gross production of carbonate is, therefore, highest (5.78 kg/m² per year on both transects) near the shelf edge where coral abundances are greatest (Fig. 4). Gross production by corals at individual survey sites ranged between 0 and 5.78 kg/m² per year (0–4.07 m/1,000 yr; Fig. 4; Table 5). Values for the eight shelf segments ranged from 0.49 to 3.13 kg/m² per year (0.28–1.84 m/1,000 yr; Table 6). The average rate for the entire shelf (weighted by the area of

each zone) is 1.13 kg/m² per year, or 0.65 m/1,000 yr (Table 6; Fig. 5).

Production by Coralline Algae.—While coralline algae cover a large portion of the substrate, the much slower growth rates of corallines relegating them to a secondary role as carbonate producers. They comprised only 6.8% of the reef-derived sediments found within the sand channels. Using formula [2], gross production by coralline algae was estimated to be 0.02 kg/m² per year. This corresponds to a growth rate of about 0.03 mm/yr, two orders

TABLE 6.—Production Data from the Cane Bay Shelf. Zones are shown in Figure 1

Zone	Area[m ²]	Gross Production*		Net Prod		Gross - Net		P _g /P _n
		[m]	[kg]	[m]	[kg]	[m]	[kg]	
CB-1	26,000	0.90 (0.91)	1.62 (1.64)	0.79	1.42	0.11	0.19	0.88
CB-2	58,800	1.19 (1.21)	2.10 (2.13)	1.02	1.83	0.17	0.27	0.86
CB-3	121,100	0.47 (0.50)	0.82 (0.87)	0.12	0.21	0.35	0.61	0.26
CB-40	41,900	0.98 (1.00)	1.67 (1.69)	0.78	1.40	0.20	0.27	0.84
CB-41	104,800	0.28 (0.28)	0.49 (0.50)	0.22	0.41	0.06	0.09	0.84
CB-5	19,300	1.84 (1.93)	3.13 (3.28)	0.72	1.30	1.11	1.83	0.42
CB-6	30,200	0.43 (0.35)	0.77 (0.62)	1.06	1.90	-0.63	-1.13	2.47
CB-7	9,900	0.58 (0.53)	1.01 (0.91)	1.26	2.27	-0.68	-1.26	2.35
Average		0.65 (0.66)	1.13 (1.15)**	0.50	0.91	0.16	0.25	

* The values in parentheses reflect the added gross production due to coralline algae.

** Adding 0.06 kg/m² per yr by direct contributors increases this to 1.21.

Note: [m] = [m/1,000 yr]; [kg] = [kg/m² per yr].

TABLE 7.—Carbonate-budget summary based on a gross production by coralline algae set at 10% that of *M. annularis* at each site. Values are reported in kg/m² per year. This ignores the 0.06 kg/m² per year of sediment from direct contributors

Zone	P _g (gross)		P _n (net)	P _g - P _n	
	T-6*	max†		T-6*	max†
CB-01	1.64	2.59	1.42	0.22	1.17
CB-02	2.13	2.54	1.83	0.30	0.71
CB-03	0.87	1.41	0.21	0.66	1.20
CB-040	1.69	2.34	1.40	0.29	0.94
CB-04I	0.50	0.59	0.41	0.09	0.18
CB-05	3.28	3.89	1.30	1.98	2.59
CB-06	0.62	0.92	1.90	-1.28	-0.98
CB-07	0.91	1.49	2.27	-1.36	-0.78
Average	1.15	1.61	0.91	0.27	0.70
Sediment from direct contributors				0.03	0.19
Total sediment in channels				0.30	0.89
Sediment stored in reef				0.41	0.41
Total sediment production				0.71	1.30

Sediment budget based on max values (compare to Fig. 9):

(0.89 kg/m² per yr)(412,000 m²) = 366,900 kg/yr.

Of this, 275,100 kg (75%) is sand; 91,800 kg is mud.

55,100 kg of sand is exported annually; 80,200 kg of mud.

The remaining 231,600 kg of sediment confined to the channels would result in an accretion rate of 1.87 m/1,000 yr (i.e., greater than the rate of reef accretion), and storm export would be required to "balance the budget."

* T-6 values are from Table 6.

† Max values are based on: 1) carbonate production by coralline algae = *M. annularis* × 0.10, and 2) all algal cover censused was coralline algae (i.e., no algal turfs).

of magnitude below the growth capability of *Lithophyllum congestum* under ideal conditions (i.e., in shallow water along exposed, high-energy shores). More analogous to Cane Bay, however, the growth rates of transplanted colonies on St. Croix dropped to zero at water depths below -1.20 m (see Steneck and Adey 1976, their fig. 11). This likely reflects both an increase in grazing and reduced calcification.

Total Production by Corals and Coralline Algae.—Together, corals and coralline algae produce 1.15 kg/m² per year of carbonate (0.66 m/1,000 yr; Fig. 5). This value is lower than those reported from other Caribbean reefs. Stearn and Scoffin (1977) calculated a rate of 8.9 kg/m² per year for a shallow fringing reef in Barbados. Land (1979) reported a rate of 5.2 kg/m² per year for a Jamaican reef in a setting more similar to Cane Bay, but with greater cover by fast-growing *Acropora* species and *Halimeda*.

This difference may partially be due to an underestimation on our part of the growth rates for coralline algae. Stearn and Scoffin (1977) reported a production rate for corallines an order of magnitude below that of corals. Our rate is roughly two orders of magnitude below that of the resident corals. If we assume the order-of-magnitude drop reported by Stearn and Scoffin (1977), then gross production rises to 1.61 kg/m² per year (Table 7). We feel that this higher rate is less reasonable, however, as it would require some mechanism to remove coralline algal fragments selectively from the Cane Bay sediments. Both coral and coralline algae generally break down into grains of similar size and density, precluding physical segregation. Furthermore, both are easily identified in thin section. While a slightly higher rate of coralline production cannot be totally discounted, it seems unlikely, and the potential impact of this on the budget is small.

Net Production

Core Description.—Core logs are provided in Figure 6; core statistics are summarized in Table 8. Recovery of solid material ranged from 11% in core CB-06 to 54% in core CB-05. Recovery averaged 41%. Drilling notes indicate that the remainder of the cores consisted of 40% sediment and 19% open voids. The poorest core recovery occurred along the steep reef face, where rubble dominated the accretionary fabric. Whether the void spaces within the reef remain open through time or are eventually filled by sediment and cement, more than half of the reef fabric will reflect a detrital origin. Furthermore,

TABLE 8.—Summary of core data. Cores are located in Figure 1

Core	Max Age (a)	Length (m)		Recov*		Void (m)	Seds (m)	Accr (a/b) (m/1,000 yr)
		Total	Last (b)	(m)	(%)			
CB-1	2,210	3.26	1.95	1.69	52	0.57	1.00	0.88
CB-2	2,530	4.10	4.10	1.69	41	1.09	1.32	1.62
CB-3	5,360	2.21	0.78	1.00	45	0.20	1.01	0.15
CB-40	5,580	8.39	5.79	2.28	27	0.42	5.69	1.04
CB-4I	—	—	—	—	—	—	—	0.30**
CB-5	3,250	3.82	3.82	2.05	54	1.33	0.44	1.18
CB-6	1,760	7.44	2.82	0.81	11	1.09	5.54	1.60
CB-7	1,100	1.87	1.87	0.40	21	0.00	1.47	1.70
Average					41			0.73 (0.92)†

Total = length of entire core

Last = length to deepest dated sample

* "Recovery," "void" and "sediments" are lengths over the entire core; "Accretion" is based on the interval between the reef surface and the deepest dated sample.

** P_g(0.84)

† 0.73 = rate assuming accretion (P_n) along inner shelf is P_g(0.84).

0.92 = rate based on accretion of 1.04 m/1,000 yr for all of zone 4.

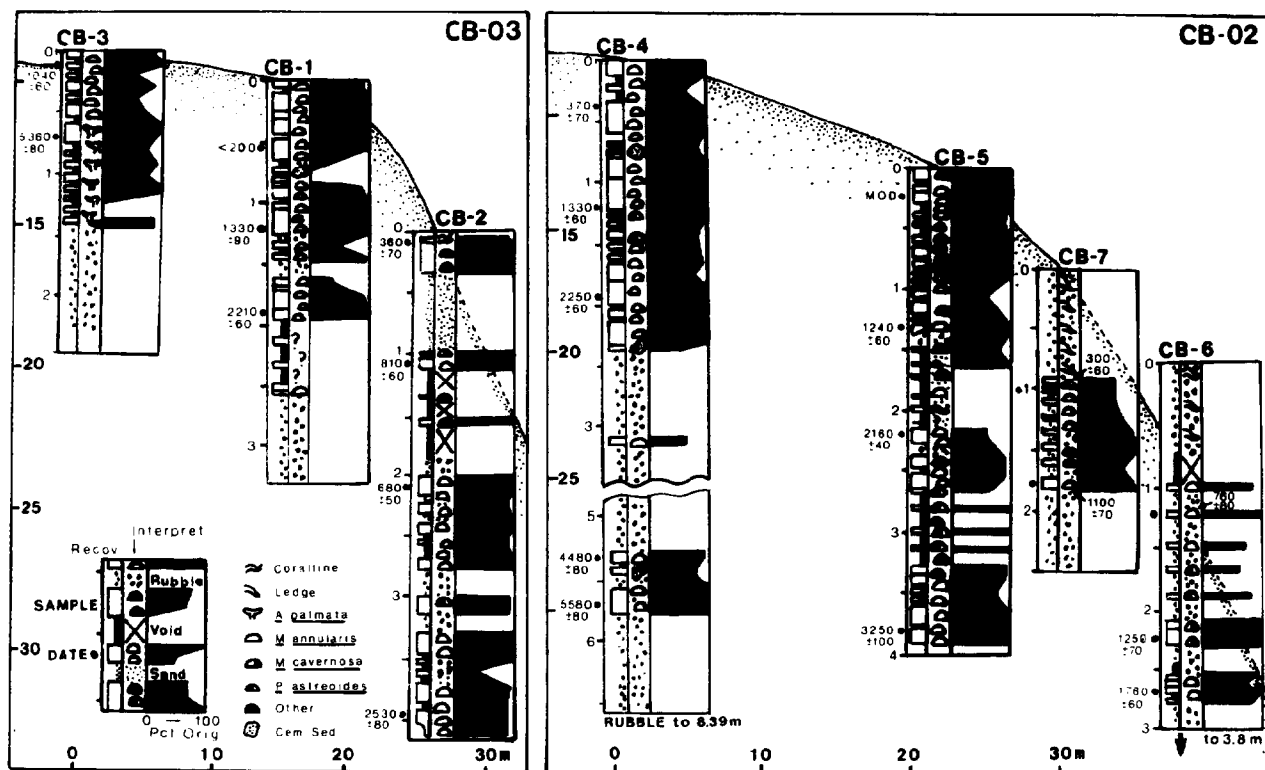


FIG. 6.—Core logs for the seven Cane Bay cores used in the budget calculations. In the intervals occupied by coral, much of the original carbonate remains unmodified, although not demonstrably in place. Note the lack of order in the upper three dates from core CB-2, reflecting physical reworking. The left side of each column shows the actual position of samples recovered, the center is an interpretation, and the right portion is a graph of the percent of original coral left in each sample.

many of the recognizable “framework” corals are not in growth position.

Densities of boring infauna are low compared to those reported by Hubbard et al. (1985, 1986) for nearby Salt River submarine canyon. The dominant infauna include the boring sponge *Cliona*, along with subordinate numbers of worms and molluscs (Fig. 7A, B). There is no apparent pattern to the degree of reworking with water depth, but coral recovery improves decidedly in the upper two meters of the cores from the shelf top. With the exception of cores CB-02 and CB-05, the reef is dominated by loose rubble near the base of the recovered section.

The ubiquitous submarine cements reported in other modern reef environments (Land and Goreau 1970; James and Ginsburg 1979) are conspicuous in their absence. This is particularly surprising given the likelihood of active water circulation through this exposed margin. Where found, secondary cements are limited to quantitatively insignificant whiskery needles on the interiors of coral calices (Fig. 7C) and detrital infills bound by Mg-calcite(?) cement (Fig. 7D).

Patterns of Net Production (Accretion).—Average accretion rates range from 0.15–1.70 m/1,000 yr, with the highest values near the shelf margin (Table 8). Accretion averaged 0.92 m/1,000 yr (Fig. 5). Recognizable coral represents less than 40% of this, with much of the accretionary fabric dominated by water- or sediment-filled voids. Net production at Cane Bay averages 0.91 kg/m²

per year. This corresponds to a volume of 0.50 m³ with a density of 1,800 kg/m³.

Because core CB-04 is from the more productive outer part of Reef Zone 4 (P_g generally ranged from 1 to 5 kg/m² per year), it is unlikely that the accretion rate from this core applies to the less-productive ($P_g < 1$ kg/m² per year) inner shelf as well. The net-production rate derived from core CB-04 was applied only to the outer zone from which it was recovered. In three of the five shelf-top cores, the ratio of P_n/P_g fell between 0.84 and 0.88 (Table 6). In the other two cores, ratios were lower, reflecting poorer preservation of the carbonate produced on the reef surface. A net production rate for the inner section of Zone 4 was approximated by multiplying its gross-production rate (0.49 kg/m² per year) by 0.84, the ratio of P_n/P_g derived from core CB-04 and the gross production figures from the outer portion of Zone 4.

The consistency of the P_n/P_g ratios along the shelf top supports the validity of this approach. Keeping in mind the lower ratios in two of the cores (CB-03 and CB-05; Table 6), the possibility that we have slightly overestimated net production along the inner shelf should be kept in mind throughout the discussion below.

Sediment Generation

The difference between gross and net production is 0.24 kg/m² per year (Fig. 5). Of that, 0.02 kg/m² per year is derived from the breakdown of coralline algae. Molluscs,

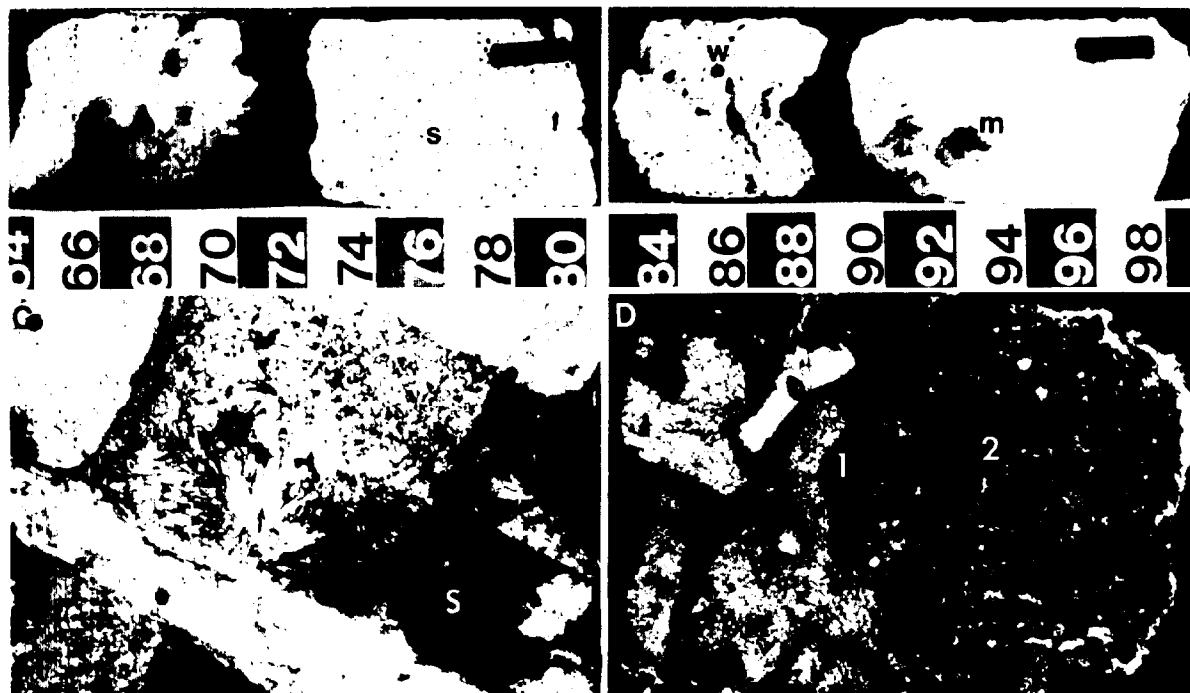


FIG. 7.—Photographs of core slabs (A and B) and thin sections (C and D) from the Cane Bay cores. The left-hand slabs in the upper photos are comprised of coral fragments cemented together in a sedimentary matrix. The primary borers include clionid sponges (s), worms (w) and molluscs (m). Scale graduations are 2 cm. The most common cements are radiating bundles of aragonite (arrow in C; field of view = 1 mm horizontally) and cemented sediment (S), generally of detrital origin. Detrital infills are often multi-generational. Inside the 1.5-mm boring shown in D, the older detrital fill (1) is darker than the younger and less-cemented fill (2).

forams and echinoderms comprise 21% of the reef sediments, and account for an additional 0.06 kg/m² per year.

In addition to the 0.30 kg/m² of sediment stored in the channels annually, another 0.41 kg/m² is reincorporated into the reef interior. This brings the total rate of sediment production in the reef system up to 0.71 kg/m² per year. This is 59% of the 1.21 kg/m² per year of the total carbonate initially produced in the reef and is greater than the 0.50 kg/m² per year of solid material remaining in the reef fabric. These rates ignore dissolution, which is a mechanism used by some bioeroders to excavate. The amount of carbonate lost to the water column by this mechanism, relative to the sediment generated, is negligible, however.

Sediment Export

Sediment-transport data are summarized in Table 9. The traps deployed at the shelf break (Traps 1 and 2) provided consistent rates for both fair weather (avg = 112 kg/m per year) and storm conditions (745 kg/m per year). The deeper-water trap (T-4; depth = 49 m) measured a fair-weather transport rate of 35 kg/m per year. The tracer experiments from the lower (tracer-10) and upper (tracer-8) reaches of two shelf-edge channels gave values of 17 kg/m per year and 1,514 kg/m per year during fair weather and storms, respectively.

The values used in the budget calculations (fair weather = 65; storm = 1,130 kg/m per year) are averages of results from the two methods. Assuming 30 days of stormy

weather each year, the average transport rate through the sand channels is 153 kg/m per year. This value is based on the formula:

$$SED_e = \frac{(30 \text{ days}) (R_s) + (335 \text{ days}) (R_f)}{365 \text{ days}}, \quad [3]$$

where:

SED_e = annual sediment-export rate

R_s = export rate during storms

R_f = export rate during fair weather

Reasonable changes in the number of stormy days per year make little difference in the value for total annual export.

Based on numerous diver observations and bottom surveys, it is estimated that the channels occupy roughly 25% of the 1,440-m shelf margin. Therefore, total sediment export over the shelf edge at Cane Bay is approximately 55,100 kg/yr (1,440 m × 0.25 × 153 kg/m per year).

DISCUSSION

Reef Development at Cane Bay

The cores were taken primarily to determine the net rate of carbonate production over the past few thousand years, and they did not reach the underlying Pleistocene surface. While control by antecedent topography cannot be addressed, the cores still provide useful information

TABLE 9.—Sediment transport at Cane Bay. Rates are expressed as kg of sediment passing through each linear meter of channel width per day and year

Exper	Duration (day)	Weather	Transport Rate	
			(kg/m-day)	(kg/m-yr)
Trap-1	49	calm	0.194	71
	63	calm	0.199	73
	32	5st; 27c*	0.480	175
	5	storm**	2.000	733
Trap-2	49	calm	0.497	181
	63	calm	0.325	119
	32	5st; 27c*	0.668	244
	5	storm**	2.075	757
Trap-4	11	calm	0.095	35
Trap Ave	(T-1,2)	CALM	0.306	112
		STORM	2.041	745
Tracer-10 (d = 24 m)	10	calm	0.023	8
	73	5st; 68c*	0.346	126
	5	storm**	4.728	1,726
Tracer-08 (d = 18 m)	11	calm	0.066	24
	73	5st; 68c*	0.306	112
	5	storm**	3.570	1,303
Tracer-05 (d = 15 m)	11	calm	0.108	40
Tracer Ave	(T8, 10)	CALM	0.044	17
		STORM	4.150	1,514
Grand averages (tracer and traps):				
Calm			0.176	65
Storm			3.095	1,130

* "5st; 27c" refers to a 32 day period during which 5 days were stormy (wave height = 5 m; period = 6 seconds) and 27 were calm.

** Storm rates were computed using the following formula:

$$\text{Storm Rate} = \frac{[(\text{Avg})(\text{Dt})] - [(\text{Rf})(\text{Df})]}{\text{Ds}}$$

where:

Avg = Average transport rate over experiment duration
 Dt = Duration of experiment (either 32 or 73 days)
 Rf = Transport rate during fair weather ("calm" for same site)
 Df = Duration of fair-weather conditions (27 or 68 days)
 Ds = Duration of stormy weather (5 days)

Assuming 30 days of stormy weather per year:

$$\frac{(30 \text{ days})(1,130) + (335 \text{ days})(65)}{365 \text{ days}} = 153 \text{ kg/m per yr}$$

Based on sand channels occupying 25% of the 1,440-m shelf edge:

$$(1,440 \text{ m}) \times (0.25) \times (153) = 55,080 \text{ kg/yr (total sediment export)}$$

about the development of the reef at Cane Bay. All but two of the cores (CB-02 and CB-05) bottomed in Holocene reef rubble. The rubble consists of broken and reworked reef fragments, probably derived from upslope. These may be the earliest Holocene deposits on the shelf. All subsequent reef development occurred on top of this loose substrate that was probably mobile at least during heavy seas.

Accretion is not a continuous process but rather is characterized by episodes of coral growth separated by intervals of sediment or open void. As the positions of live coral shift through time (cover = 20–50%), any given location on the reef will alternately accrete by coral growth and remain static or be reduced by bioerosion during intervening periods. While the positions of the major sand

channels have probably persisted over the past few thousand years, cover on the intervening reef tops has continuously shifted. For the most part, the character of the reef cores probably reflects this style of alternating production and destruction at individual sites, rather than a widespread interruption of reef accretion.

Reef Accretion on the Shelf Top.—The first reefs seen in the cores colonized the shelf prior to 5,000 YBP (Fig. 8). Along the western transect (CB-03), *Acropora palmata* grew in 5–10 m of water. A recent, undated core located 50 m landward of core CB-03 indicates that this fringing reef extended closer to shore at that time. To the east (transect CB-02), a reef dominated by *Montastrea annularis* formed in shallower water, but further from shore. Today, the more-protected eastern end of Cane Bay receives higher levels of terrestrial sedimentation. If this was also true in the past, it would probably have deterred the development of *A. palmata*, which has no effective means of sediment removal.

Along both transects, there is a hiatus in the shelf-top cores separating these initial reefs from an overlying one dominated by *M. annularis* and other head corals. Along the eastern transect, the earlier reef was buried by rubble, probably from an upslope reef. Despite the fact that no rubble interval was encountered to the west, the possible impact of a shallower reef cannot be discounted. Recolonization probably occurred around 1,100 YBP.

Such breaks in reef development are not isolated occurrences peculiar to this area. Adey et al. (1977) described a similar hiatus on eastern St. Croix between 9,000 and 7,000 YBP and related it to turbidity from a Pleistocene soil horizon being reworked by rising sea level. Hallock and Schlager (1986) noted that high nutrient levels generally accompany terrestrial sedimentation and can likewise be detrimental to reef development. For a more detailed discussion of the problems surrounding the "drowning" of ancient reefs, the reader is referred to Schlager (1981).

Other Caribbean shelf margins have been the sites of Holocene reefs that flourished soon after the reef flooded, only to be left behind by the subsequent sea-level rise (e.g., Belize: Macintyre et al. 1982; southern Puerto Rico: Hubbard and Morelock, unpubl. data). As at Cane Bay, the rise of sea level alone was apparently insufficient to outpace the reefs inhabited by corals capable of rapid growth.

In the Devonian reefs of Canada (Viau 1983; Muir et al. 1985) and Australia (Playford 1980; Hall 1984; Hurley 1986) the abandonment of deeper reefs and the subsequent colonization of shallower, more-landward sites (i.e., backstepping) have been similarly noted. While these latter examples from the rock record have typically been attributed to a rapid rise in sea level, the numerous Holocene examples from the Caribbean demonstrate that the story may not be that simple. A more thorough understanding of the processes that trigger reef development and demise on a large scale still remains an illusive objective.

Reef Accretion at the Shelf Break.—Near the shelf edge (cores 1 and 5), accretion has been relatively continuous

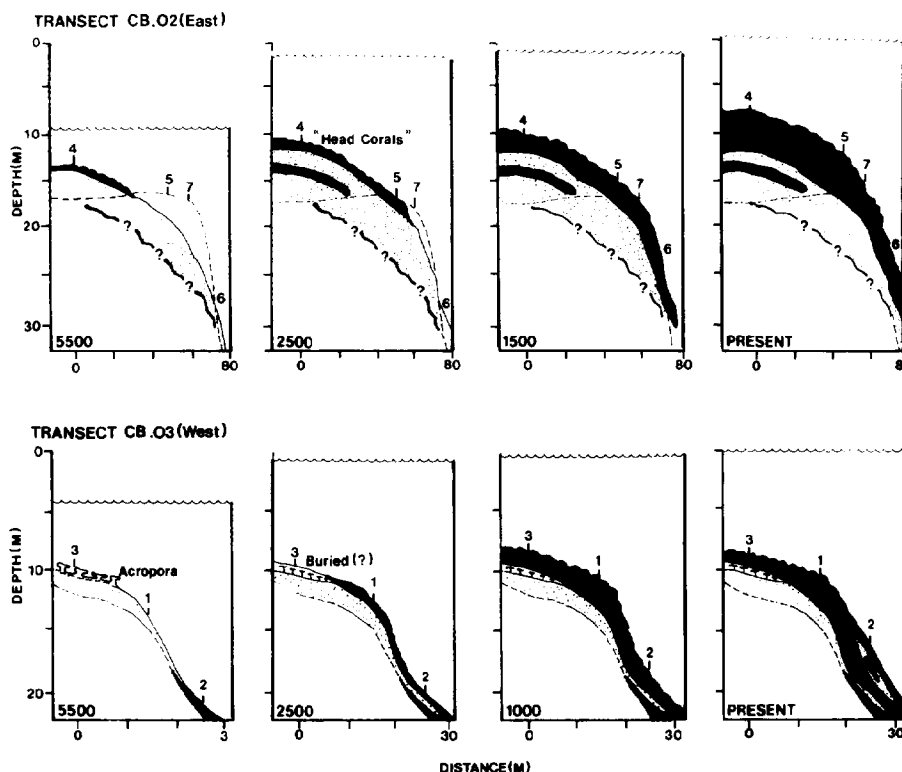


FIG. 8.—Accretionary history revealed by the Cane Bay cores. Along the eastern transect (CB-02), a reef dominated by head corals colonized a rubble substrate at about 5,500 YBP (years before present). To the west (transect CB-03) an *A. palmata* reef formed at about the same time, possibly in an area of less sedimentation. Along both transects, an interruption in coral preservation occurs. The numerous interruptions throughout the upper sections of the cores cannot be correlated from core to core and are interpreted as a gradual shifting of the sites of coral growth along the reef surface rather than area-wide interruptions of reef development. The dashed lines represent the extent of core recovery.

over the past 2,000–3,000 years. Coral diversity is greatest in these cores, as is the case on the present-day shelf margin. The cores are dominated by 10–20 cm segments of well-preserved corals separated by decimeter-scale voids and sediment-filled intervals.

The alternation between active “framework” and sediment may explain the generally good preservation of the corals in these cores. The surfaces of the samples show evidence of encrustation and bioerosion, the latter usually extending only a short distance into the coral. This could reflect short intervals of coral growth interrupted by rapid burial and a longer period of non-production as coral growth temporarily shifted to another site on the reef surface. It is difficult to discern the extent to which grazers might have eroded back the coral surfaces before burial ultimately occurred.

Along the reef front, cores from the steep slope reflect processes of slumping and rapid sedimentation. Intervals of recovered coral are typically smaller than in the shelf-top cores, although preservation is still good within the corals that do occur. Sediment-filled intervals are much more common. In core CB-02, the radiocarbon dates do not follow an orderly progression, likely reflecting a largely allochthonous deposit. Similar processes dominate the steep reef margin at Salt River submarine canyon to the east (Hubbard et al. 1986). The highest overall accretion rates from anywhere in the reef occur here and actually

exceed the rates of gross production on the reef front in some instances. The secondary reworking of the reef combined with the importance of bioeroded sediment reincorporated in the reef interior has resulted in the deposition of an active reef core that would be difficult to distinguish from what has been typically interpreted as a detrital facies in the past.

Balancing the Budget

An average of 1.21 kg/m² of carbonate (1.13 by corals; 0.02 by corallines; 0.06 by direct sediment contributors) are produced annually in water depths less than –40 m (Fig. 5). Of this, 0.65 kg/m² per year is reduced to sediment by bioerosion. Another 0.06 kg/m² per year of sediment is added directly by molluscs, echinoderms, foraminifers and others.

Roughly half (0.41 kg/m² per year) of the total sediment is reincorporated within the interior of the accreting reef (Fig. 9). Volumetrically, this occupies as much space as preserved coral (see “Accr” column in Fig. 5). The remaining 0.30 kg/m² per year of sediment makes its way into the channels that regularly traverse the reef. Based on a total reef area of 412,200 m², this translates into 123,600 kg of sediment (Fig. 9). Confining this material to the channels, which occupy roughly one quarter of the reef, the resulting sediment-accumulation rate of approx-

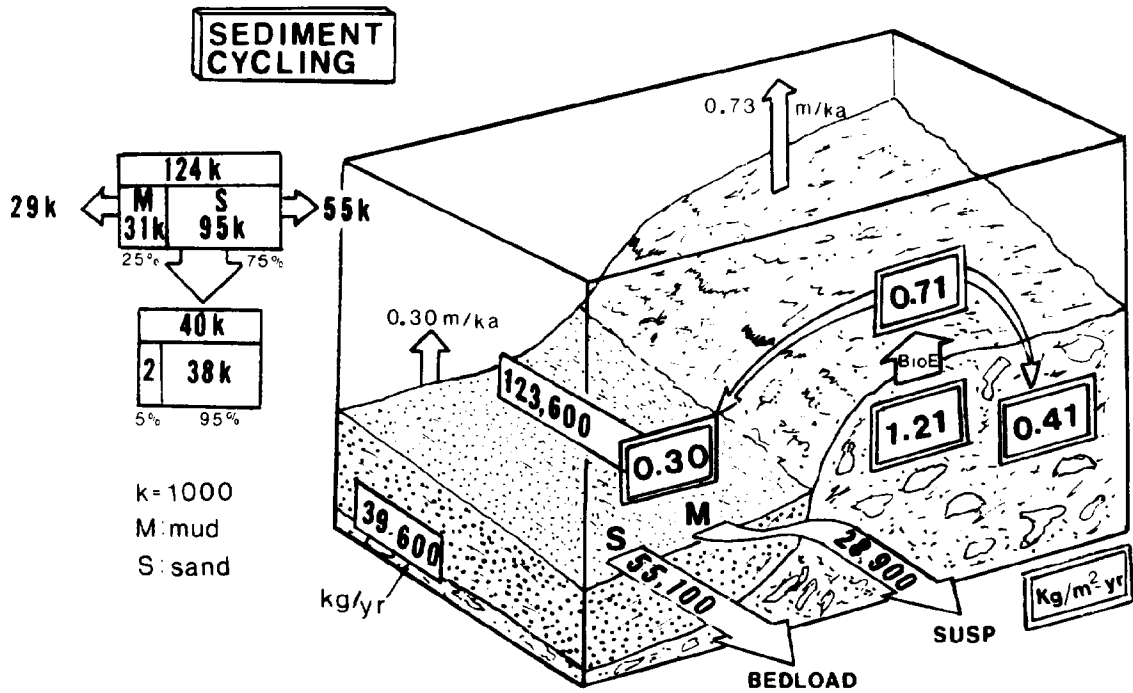


FIG. 9.—Diagram summarizing the cycling of detrital sediment through the reef at Cane Bay. Gross-production is 1.21 kg/m² per year. Of the 0.71 kg/m² of sediment generated annually by bioerosion (BioE), 0.41 kg/m² is reincorporated in the reef interior. The remaining 0.30 kg/m² per year translates into 123,600 kg/yr of sediment spread over the 412,200 m² of reef at Cane Bay. Of this, 75% is sand and 25% is mud. Each year, 28,900 kg of sediment are exported in suspension and 55,100 kg are exported as bedload, leaving 39,600 kg of excess sediment (95% sand) to be stored in the reef channels (Column at left). Spread over the 103,000 m² of channel area in the reef, this translates into a sediment-accumulation rate of 0.30 m/1,000 yr.

imately 1.20 m/1,000 yr (Fig. 5) would exceed that of reef accretion.

Land (1979) argued that sediment production in any reef system must be roughly balanced by its removal. This is not entirely true, however, as the volume of detrital sediment must only be reduced to the point that the reef can accrete faster than the sediment can accumulate. "Balancing the budget," therefore, hinges on the ability of physical, biological and gravitational processes to remove that amount of sediment from the reef.

The annual sediment-export rate at Cane Bay was determined to be 55,100 kg/yr. This value reflects only bedload transport, however. Although suspended-sediment levels can easily be measured, translating this into an accurate rate of sediment export in the water column is

impossible. Sediment-laden water is recycled over the shelf many times, and simply multiplying suspended load by current velocity would give an exaggerated picture of sediment export. A reasonable estimate can be made based on several more easily measured parameters.

Ogden (1977) measured bioerosion by urchins (4.60 kg/m² per year) and parrotfish (0.49 kg/m² per year) on eastern St. Croix. He also concluded that urchins produce roughly equal parts of sand and mud, while parrotfish generate only sand. In the same area, Moore and Shedd (1977) measured a bioerosion rate of 1.25 kg/m² per year (mostly mud) by the burrowing sponge *Cliona*, which is probably responsible for 90% of all bioerosion by boring organisms (MacGeachy 1977). While the total rate of bioerosion measured at Cane Bay is lower than on eastern St. Croix, the relative contribution by the various organisms is likely to be reasonably similar. Using the above information, it was estimated that 75% of the bioeroded sediment will be sand (Table 10).

Based on this, the 123,600 kg of sediment introduced into the channels annually would consist of 92,700 kg (75%) of sand and 30,900 kg (25%) of mud. Present-day sediments found in the channels contain approximately 5% mud. If 55,100 kg of sand is removed annually, then 28,900 kg of mud would have to be winnowed away to end up with sediment containing 5% mud (Fig. 9). Confined to the 103,050 square meters of sandy substrate at Cane Bay (reef area × 0.25), the remaining 39,600 kg of sediment would accumulate at a rate of 0.30 m/1,000 yr

TABLE 10.—Sediment production by bioerosion

Organism	kg/m ² per year	% sand	% BioE	Source
(a) urchins	4.60	100	71 (a/e)	Ogden 1977
(b) parrotfish	0.49	50	8 (b/e)	Ogden 1977
(c) <i>Cliona</i>	1.25	0	—	Moore and Shedd 1977
(d) all borers	1.39*	0	21 (d/e)	computed
(e) (a) + (b) + (d)	6.48			

* 1.39 = (1.25)(0.90), after estimates of MacGeachy (1977).

75% sand = $\frac{(71)(100) + (8)(50) + (21)(0)}{100}$

($0.38 \text{ kg/m}^2 \text{ per year} \div 1,200 \text{ kg/m}^3$). This is roughly half of the 0.73 m/1,000 yr rate of reef accretion (Fig. 5).

Thus, sediment production is offset in two ways. Roughly half of the detritus is reincorporated within the accreting reef interior. The remainder is stored in the channels that serve both as short-term repositories for excess sediment and as the ultimate conduits for its removal. Based on the above calculations, the volume of sediment that is removed, primarily by physical reworking, is sufficient to allow the accreting reef to keep ahead of the accumulation of detrital sediment in the channels.

If we use a higher rate of gross production, based on a greater contribution by coralline algae (Table 7), then the rate of excess-sediment accumulation in the channels increases to 1.87 m/1,000 yr . This is greater than the rate of reef accretion and would require some process not addressed by our measurements to remove the additional sediment. One possibility is the passage of major hurricanes as initially proposed by Sadd (1984) and Hubbard (1986a). Observations do exist that indirectly support this idea. Along the southern margin of Little Bahama Bank, Hubbard et al. (1974) reported accelerated sediment transport during storm passage. They related this to bottom-hugging, offshore flows that were generated as water was piled up against the shoreface of Grand Bahama Island by storm waves. During a moderate storm in 1978, downcanyon currents generated by 5-m waves removed a volume of sediment from Salt River submarine canyon that had been deposited there over a 5–10 year period (Hubbard 1986b). It also moved the 60-ton "Hydrolab" underwater laboratory located in the canyon. In 1980, Hurricane Allen passed north of Jamaica, flushing most of the sediment from the channels at the shelf edge in 30–50 m of water (Woodley et al. 1981). While shallower reef environments were devastated, deeper areas surrounding the channels were left essentially untouched.

We still feel that the actual gross-production rate falls closer to $1.21 \text{ kg/m}^2 \text{ per year}$, meaning that the budget essentially "balances." However, with a differential of only 0.42 m/1,000 yr between the rates of reef accretion (0.72 m/1,000 yr) and sediment accumulation (0.30 m/1,000 yr), the relief in the present reef channels is greater than would be expected based on our budget numbers. This implies an influence by storm-related export even if it is not required to "balance the budget." In other areas, where normal transport processes cannot remove sufficient volumes of sediment, storm-induced transport likely tips the balance in favor of the reef.

Carbonate Cycling in the Reef Environment

Two assumptions lie at the heart of most modern reef models: 1) the existence of abundant corals on the reef surface will be reflected in a significant "framework" component in the reef interior (e.g., see the discussion of Shaver et al. 1976 on "Silurian Buildups as Ecologic (Organic-Framework) Reefs"; also, the recent Palaios volume edited by Stanley and Fagerstrom 1988), and 2) the pattern of decreasing growth rates by corals with depth

will be mimicked by patterns of accretion in the reefs on which they live (e.g., see Kinsey 1982).

The Role of Framework.—Sediment and remaining voids constitute 59% of the reef at Cane Bay. Furthermore, much of the remaining "framework" has been displaced from its original position. The result is a reef fabric dominated by detritus with only a portion of the remaining coral left demonstrably in place. At nearby Salt River submarine canyon, the recovery of recognizable coral is even poorer, and detrital sediment plays a much greater role in reef deposition (Hubbard et al. 1985, 1986). It is likely that a critical examination of core data from other areas would lead to the conclusion that modern reefs characterized by true boundstones or framestones are in the minority.

In this regard, the character of many ancient reefs should come as no real surprise. The alternating episodes of sedimentation and coral colonization described by Hubbard et al. (1986) on the eastern margin of Salt River submarine canyon (Fig. 10A, B) have produced a reef fabric very similar to the Devonian stromatoporoid reefs described by Mountjoy and Geldsetzer (1981) in the Canadian Rockies (Fig. 10C–E).

While coral abundance at Cane Bay is higher than at Salt River, the patchy pattern of coral cover is still reflected in an interior fabric of loosely connected corals "floating" in a matrix of internal sediment and voids. Recognizable corals are an important part of the preserved record, but a tightly packed network of interlocked or largely in-place corals is difficult to demonstrate. We suspect that this is a more widespread situation than the present literature reflects. In this regard, present usage of the term "framework" is troublesome. While we do not wish to add to the already burdensome proliferation of jargon, the present concept of "framework" is so entrenched that simply changing our use of the term as it stands would meet with little success. We, therefore, suggest using *in-place* and *detrital* framework to differentiate between fabrics containing recognizable biological material and those dominated by demonstrably in-place, undisturbed colonies. Certainly our definition of reefs in ancient settings must be expanded to recognize that the interiors of what we would all agree are card-carrying modern reefs often possess little of the in-place fabric that we require to identify their ancient counterparts.

Taphonomic Factors.—Considering the syndepositional processes that degrade and rework modern reefs, it seems more appropriate to puzzle over ancient examples where framework is well-preserved rather than trying to explain away the places where it is not. In reefs producing algal boundstones (e.g., Fig. 11A, B), their massive character results from slow accretion that produces a structure capable of resisting breakage from the high waves that protect the algae from grazers. But how did branching corals such as those preserved in the upper Triassic reefs of southern Germany and Austria (Fig. 11C, D) survive, seemingly unaltered by post-depositional degradation?

One possibility is the syndepositional binding of reef framework by soft-bodied or coralline algae. At Myrmidon Reef, in the Great Barrier Reef, corallines have

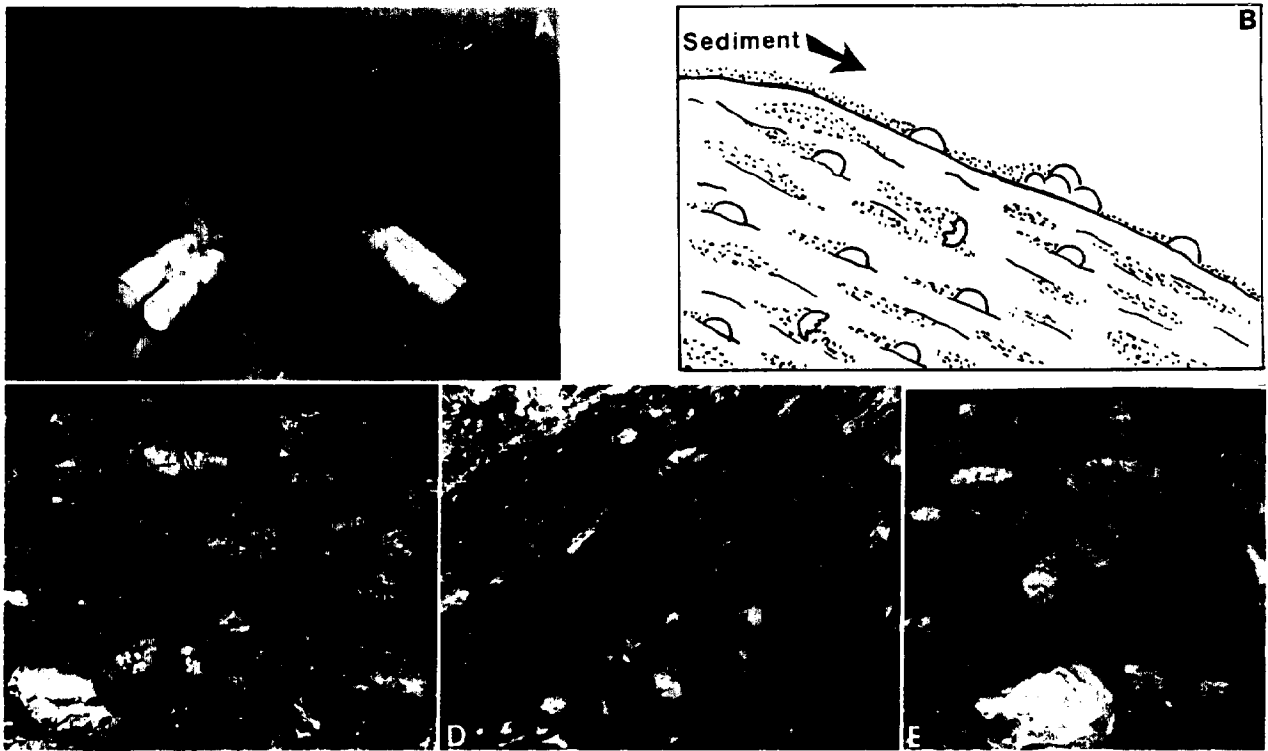


FIG. 10.—Photographs and sketch illustrating the character of modern and fossil reefs in a deeper-water (ca. 15–30 m) setting. A. Photograph of the east slope of Salt River submarine canyon on the north shore of St. Croix (Fig. 1B). B. Internal fabric of the east slope of Salt River submarine canyon as interpreted from drill cores and diver observations. Preservation of original coral material in this environment is probably the result of rapid burial. C. Outcrop photograph of a Devonian stromatoporoid reef northwest of Calgary (“Big Hill” section of Mountjoy and Geldsetzer 1981). Much of the material in this section appears out of place but still within deposits that are biohermal in nature (i.e., in the “reef”). The large stromatoporoid at the lower left is about 20 cm across. D and E. Photos from the Grassi Lakes outcrops from the same area. Much more of the stromatoporoid material in D appears in place and is part of a well-developed bioherm clearly visible in outcrop. The environment of deposition envisioned for these areas is very similar to that of eastern Salt River or parts of Cane Bay, where sites of scattered coral growth shift rapidly, leaving a fabric dominated by widely spaced corals in a matrix of cemented, detrital sediment. The scale in the lower part of D is 15 cm long. The large stromatoporoid near the bottom of C is approximately 20 cm across.

bound an *Acropora* framework together, apparently in place (Davies and Hopley 1983; Fig. 11E), and may provide a modern analogue to well-preserved branching corals occurring near Adnet. The algal overgrowths provide both added rigidity as well as protection from bioerosion. On St. Croix, this mechanism is responsible for maintaining pinnacle-like *A. palmata* reefs north of St. Croix (Fig. 11F). These “haystacks” stand as resistant structures rising 10–15 m above the surrounding bottom and are dominated in their internal structure by large branches of broken coral bound together by coralline algae (Fig. 11G).

Framework preservation can also be facilitated by burial. In the Steinplatte region of Austria, branching colonies of *Thecosmilia* occurred along the landward side of a platform facing the paleo-Tethys Sea (Zankl et al. 1987). Preservation of the fragile branching corals in this reef (Fig. 11C) is probably the result of the protected nature of this environment and the rapid burial of the reef by grainstones and packstones derived from the platform.

The fact that any framework-dominated reefs can be found in the rock record at all argues against evolutionary factors precluding framework preservation at any one

point in the past. Hallock (1988) discussed nutrients as a control of framework preservation in modern and ancient reefs. She proposed that under conditions of increasing nutrient availability, bioerosion would increase and framework would gradually be replaced by more detrital fabrics. Even under ideal (i.e., lower nutrient) conditions, however, framework constitutes less than half of the depositional fabric of the reef in her model.

Natural processes that discriminated against preservation of framework in the past probably continue in the present. In this regard, corals occurring along the deeper reef front or in the backreef have the greatest potential for preservation. The dominance of detrital sediment in these environments is consistent with the nature of many “framework-poor” reefs found in the rock record. Also, the greater opportunity for rapid burial and protection from bioerosion increases the probability for preservation, albeit *not* in the form of in-place, interlocking framework. A critical re-examination of the role played by taphonomy and the types of environments that would favor preservation is warranted.

Temporal Variability.—As discussed above, there can be serious problems with trying to extrapolate present-

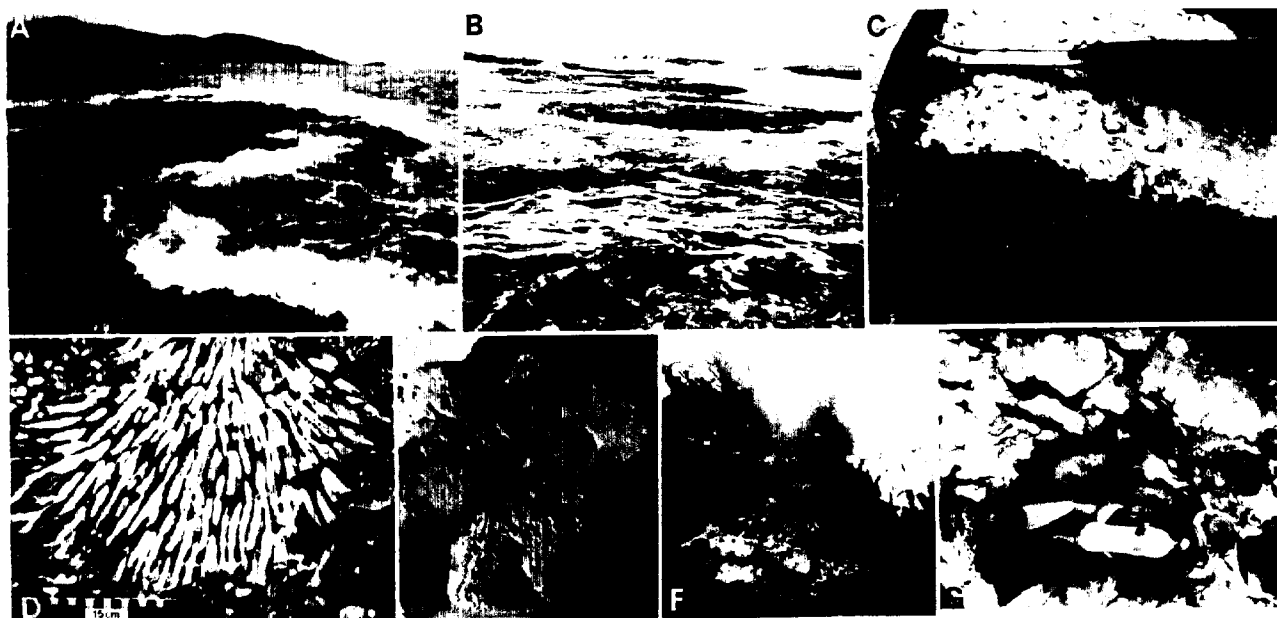


FIG. 11. — A. Photograph of Robin Bay algal ridge located on the south shore of St. Croix. The ridge-top is dominated by *Lithophyllum congestum* and *Porolithon pachydermum* which form an encrusting cap over an interior of broken and in-place *Acropora palmata*. B. Photograph of a Pacific algal ridge on the southwestern shore of Tikehau atoll in the Tuamotu Archipelago. The waves in the background are approximately 2 m high. The gaps in the seaward lip are scoured surge channels described as spur-and-groove by early researchers in the Pacific. C. Photograph of the Triassic coral *Thecosmilia* sp. from the Steinplatte region of Austria. The excellent preservation of this thicket-like coral occurs over an area of several acres in what has been interpreted as a backreef environment similar to that found off Belize today (Heinrich Zankl, pers. comm.). D. Well-preserved colony of *Thecosmilia* from the Adnet region of Austria. This is part of a group of patch reefs located on the platform top seaward of the area discussed in 11C. Note how the colony has remained intact despite its having been overturned. A yellow rind over the coral (not visible in black and white) may reflect algal binding. E. In-place (?) coral bound by coralline algae. Core slab from Myrmidon Reef in the Great Barrier Reef courtesy of Peter Davies and the Bureau of Mineral Resources in Canberra, Australia. F and G. Underwater photographs of an *A. palmata* reef north of St. Croix. This pinnacle-like reef (15–20 m high; 30–50 m across) has accreted almost entirely by the breakage and cementation of *A. palmata* fragments.

day conditions from the present reef surface into its interior. Recent developments in the Caribbean have forced us to question our perceptions of what is “normal” on modern reefs and, therefore, applicable to the ancient record. A recent survey by Bythell et al. (1989) has shown a dramatic community shift over the past decade at Buck Island, just north of St. Croix. This has resulted from a near-total die-off of *Acropora palmata* and *A. cervicornis* related to a regional outbreak of “white-band disease.” While the present-day coral community at Cane Bay appears similar to that recorded in the cores, using the surficial character of other reefs to model their interiors should be done with caution. In the same vein, the long-spined sea urchin, *Diadema antillarum*, is presumed to have played an important role in the generation of sediment at Cane Bay throughout its depositional history. In 1981, this once ubiquitous urchin was all but removed from Caribbean reefs by an undetermined cause. The similarities between the progression of the mortality and known current patterns in the region may suggest a water-borne pathogen. Initially, one might surmise that the removal of this important bioeroder would shift the budget toward net accretion. However, since the die-off, the competitive balance between corals and fleshy algae has shifted toward the latter (Carpenter 1985). Thus, while the rate of bioerosion is lower (other herbivores do not appear to be filling

the void left by *Diadema*), initial carbonate production is also lower as fleshy algae are occupying space needed for the settlement of coral larvae.

Depositional Patterns. — Even with recent core studies, our focus on constructional processes has fostered the idea that the patterns of reef deposition necessarily mimic trends in calcification on the reef surface. The data from Cane Bay show that within the photic zone neither gross production nor reef accretion need follow a simple depth gradient (Fig. 12). On the shelf top, net production increased in a seaward direction. Maximum accretion rates occurred in the three deepest cores (2, 6 and 7), in some instances exceeding the amount of carbonate the present reef community is capable of producing at those depths.

Accelerated accretion in the deeper cores reflects the importance of sedimentary processes that rework the reef interior independent of water depth or the ability of individual corals on the reef surface to produce calcium carbonate. During the past 2,000 years, the rate of accretion on the reef face has gradually increased (core 2; Fig. 13), while aggradation on the shelf top has slowed (core 3; Fig. 13). This was largely the result of slumping from the upper reef margin as the steepening slope became progressively more unstable. The result is a pattern of deposition controlled as much by secondary processes of reworking as by initial patterns of calcification. At nearby

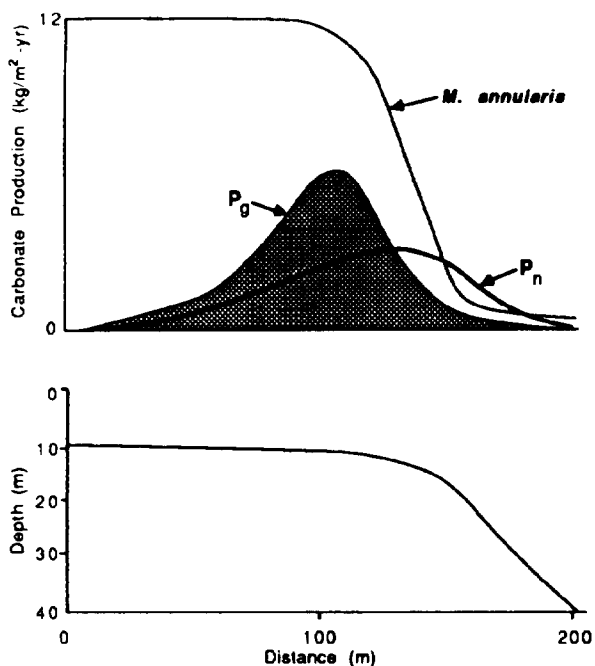


FIG. 12.—Diagram summarizing carbonate production along a depth gradient at Cane Bay. The data are approximate averages from the two transects discussed in the text. The growth rate of *M. annularis*, the dominant coral in the area, is much higher than the actual gross production across the shelf. P_g peaks near the shelf edge as a result of the greater coral cover in this area. P_n is below P_g along the upper shelf, but actually exceeds P_g along the outer slope. Along the steep reef face, P_n can actually exceed the ability of present-day corals (with 100% cover) to produce carbonate. This is a result of allochthonous material from above being piled up in this area.

Salt River, these processes are largely responsible for at least 26 m of lateral accretion in water depths of -30 m (Hubbard et al. 1986). While the patterns seen at Cane Bay and Salt River do not represent universal models, and biological processes certainly cannot be ignored, the importance of secondary reworking and the ability of deeper reef environments to contribute significantly to

the depositional record should be kept in mind when examining any ancient reef sequence. In this regard, it is suggested that the grossly misleading term “reef growth,” which emphasized only in-place, biological production, be abandoned in favor of the more generic term “reef accretion.”

Carbonate Production in Ancient Systems

Reefs.—It is not likely that unequivocal data on growth rates of fossil corals or other reef-building organisms will be found. Nevertheless, available information does suggest that the success of these faunas in the past was at least in part due to their ability to produce calcium carbonate at rates approaching those measured on modern reefs.

Present-day corals rely in large part on the photosynthetic activity of symbiotic algae to support the metabolism required to sustain high rates of calcification (Goreau 1959; Pearse and Muscatine 1971; Vandermeulen et al. 1972; Oliver et al. 1983). This has likely been the case since the Triassic (Stanley and Swart 1984; Stanley 1988). It has further been proposed that the large rudists that dominated Cretaceous reefs owed their size and their success to the presence of zooxanthellae (Kauffman and Johnson 1988) similar to those found in the giant Pacific mollusc *Tridacna* (for a review, see Cowen 1983).

In many fossil corals, it is possible to discern regular density patterns that closely resemble annual bands seen in modern corals (Fig. 14A). If the density bands in Oligocene colonies of *Porites panamensis* from Puerto Rico (Fig. 14B) do represent annual growth increments, then they record coral-growth rates similar to those of their counterparts on modern reefs. In western New York state, density bands in Silurian colonies of *Favocites* (Fig. 14C) imply a similarly high rate of gross production. Growth bands described by Runcorn (cited in Shinn 1981) and Wells (1966) imply elevated rates of calcification in corals as far back as the Devonian.

Throughout much of the past, organisms responsible

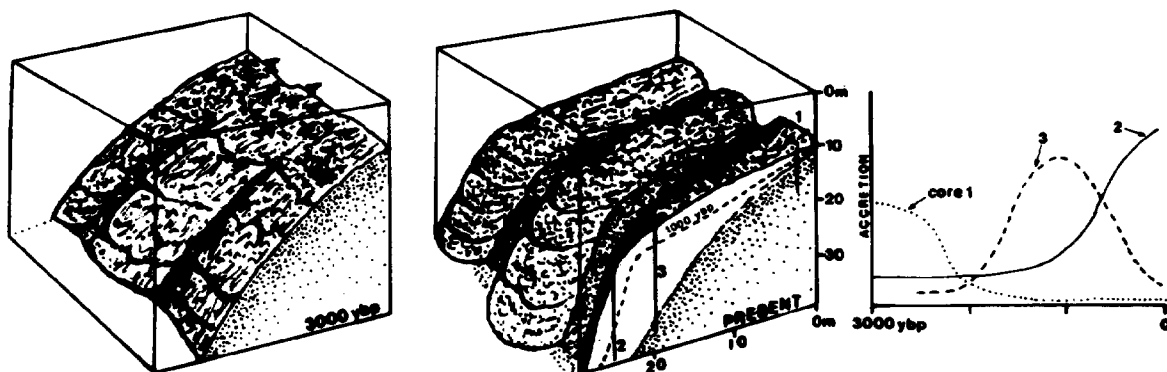


FIG. 13.—Block diagrams illustrating the accretionary history of the reef at Cane Bay. At 3,000 YBP, the shelf edge was occupied by a reef with a lower slope than that presently existing. Mixed head corals and *A. palmata* dominated the shallower areas of the reef. The present reef is the result of accretionary patterns that have gradually steepened the shelf margin. By 1,000 YBP, the reef had probably reached its present configuration (see the 1,000 YBP time line in the “present” block diagram). At this point, the greatest rates of accretion occurred in the deeper-water cores (first CB-3, later CB-2; see accretion curves at right), related to slumping of the steepening reef face.

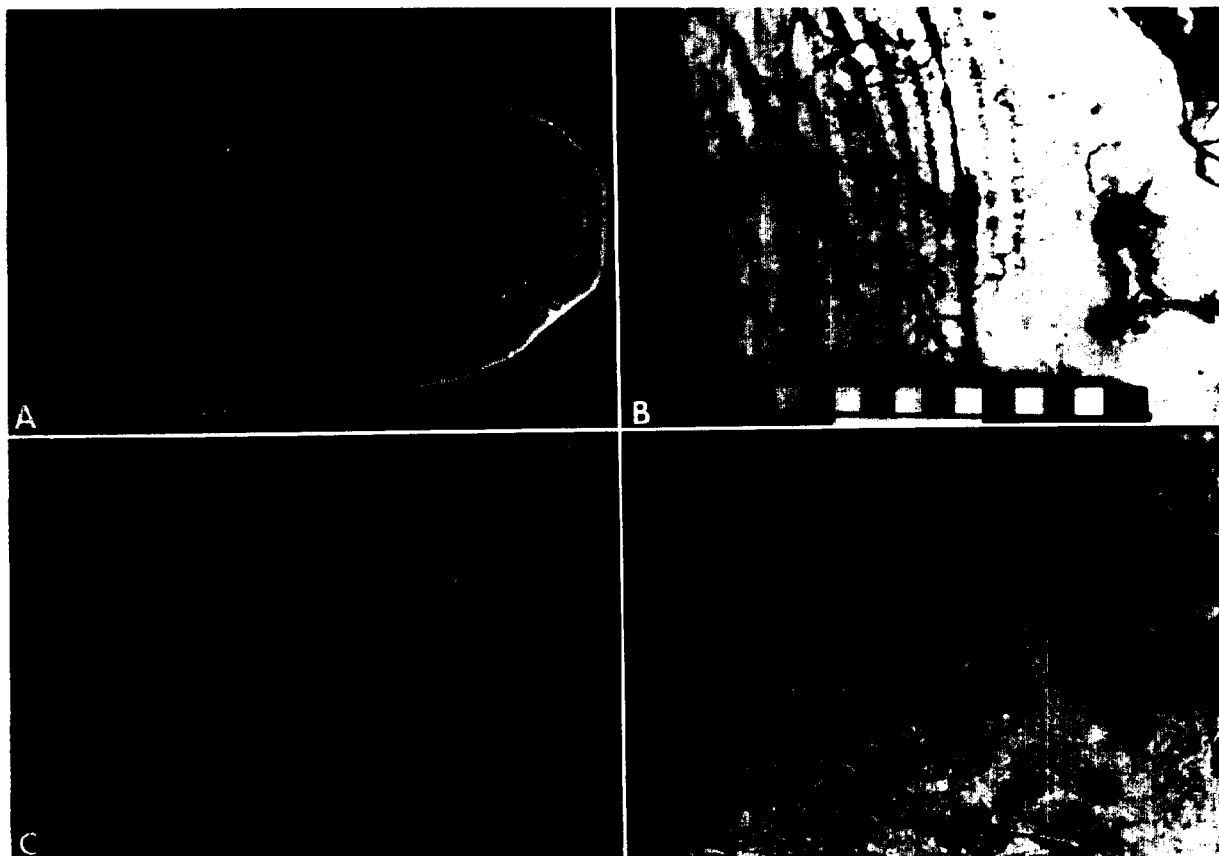


FIG. 14.—Photographs of modern and ancient reef corals. All photos are reproduced at approximately the same scale. Scale in B is 15 cm. A. X-radiograph of a modern *Montastrea annularis* from the shallow reef at Cane Bay. The dark bands are annual occurrences that have been used to calibrate the growth rates of this and many other modern reef corals. B. Oligocene *Porites panamensis* from near Guayanilla on the south coast of Puerto Rico. Diagenesis and mineralization have highlighted the annual growth bands. The inferred growth rate of approximately 8 mm/yr is similar to that for many modern corals at Cane Bay. C. Silurian *Favosites* (coral) from the Crane St. quarry in Lockport, NY. The original density bands have again been preserved by diagenesis. D. Bioeroded (?) and encrusted colony of Oligocene *Porites panamensis* from near Guayanilla, Puerto Rico.

for the destruction of reef fabric have also persisted (Steneck 1983). The earliest grazing organisms appear to have evolved by mid-Cambrian time, but these were incapable of excavating into carbonate substrates (Fig. 15). Echinoids were important by Triassic time, with grazing fish probably becoming important as bioeroders in the Tertiary. Figure 14 (C and D) contains ample evidence of boring, grazing and encrustation.

An interesting question concerns the changing balance of constructive and destructive processes in reefs through time. Has reef evolution been driven to any degree by competition between organisms that create framework and those that destroy it? Hallock (1988) proposed nutrient levels as a possible mediator of carbonate production and bioerosion. Has the rough balance between production and degradation remained essentially constant through time, or have major changes in reef character been triggered by an imbalance in this relationship? If so, are the calcifying organisms responding to grazing pressure, as discussed by Steneck (1983), or is the grazing community responding to changing resources (i.e., food availability and substrate complexity)? In this latter vein,

Wilson (1987) cited an increased availability of crevices as an important control in the radiation of nestling and other cryptic faunas in cobble-dominated habitats during the Mesozoic. A much closer examination of evolutionary patterns in reef-related organisms could likely shed considerable light on such questions.

Triassic Platforms of Northern Italy.—Spectacular examples of upper Triassic carbonate platforms occur in the Alps of northern Italy (Bosellini 1984; Gaetani et al. 1981). Throughout the Late Triassic, carbonate production atop these banks effected progradation over large distances (Bosellini and Rossi 1974). In Ladinian time, the 800-m thick Catinaccio platform prograded 6 km over a 4 my period (Bosellini 1984, 1987). Assuming 20% porosity, this reflects a net production rate of approximately 1 kg/m² per year over the surface of the expanding platform. The adjacent Latemar platform is approximately 3 km in diameter and the same thickness. A net-production rate of approximately 0.5 kg/m² per year would be required to form this platform during the 4 million years of Ladinian time.

The nearby Sella platform (Carnian in age) likely ex-

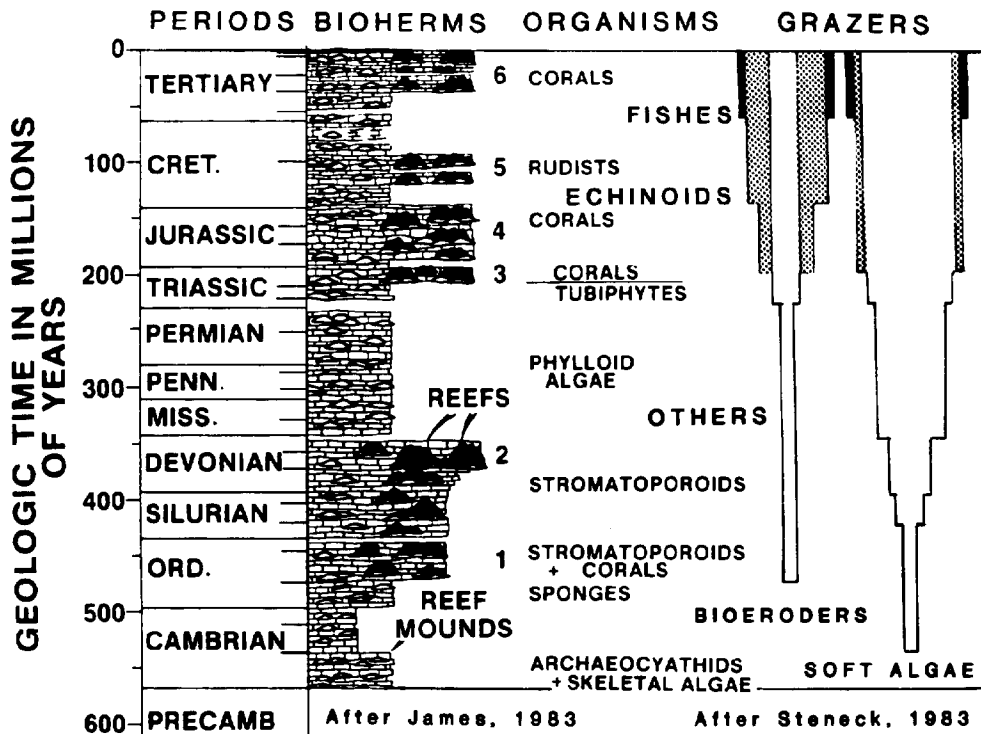


FIG. 15.—Evolutionary trends in reef character (left; after James 1983) and organisms that have grazed on soft algae or bioeroded reef substrate (right and center, respectively; after Steneck 1983). The appearance of stromatoporoid and coral reefs of the mid-Ordovician correspond to the appearance of grazers that could bioerode solid substrate. The shift from corals in the Triassic to rudists in the mid-Cretaceous and back to corals in the Tertiary corresponds quite well with the radiation of bioeroding grazers since Triassic time, and particularly urchins in the Cretaceous and fishes in the Tertiary.

panded from a Ladinian nucleus approximately 2 km in diameter (Bosellini 1987). Its final diameter was approximately 7.5 km. A net-production rate of 0.22 kg/m² per year could have produced the 400-m thick platform in the 9 million years of Carnian time. This platform is overlain, however, by the shallow-water deposits of the Durenstein and Raibl Formations, each attaining thicknesses equalling that of the platform sediments. Thus, it is likely that the Sella platform exposed in northern Italy was deposited in only 3–4 m.y., implying net-production rates more on the order of 0.4–0.6 kg/m² per year.

Neumann and Land (1975) measured carbonate production and export on southern Little Bahama Bank. Their data imply a net production of 3.8 kg/m² per year, a gross-production rate of 15.2 kg/m² per year, and a net export of 11.6 kg/m² per year of sediment. If we apply their ratio of P_g/P_n derived from this area (ca. 4.0) to the platforms exposed in northern Italy, then 1.6–4.0 kg/m² per year becomes a reasonable estimate of gross production on these Triassic banks.

Silurian Reefs of the Michigan Basin.—Since the earliest descriptions of the Silurian reefs of the north-central U.S. (Bretz 1939; Lowenstam 1950; Ingels 1963), there has been considerable discussion over the paleoenvironment of the pinnacle reefs of the Michigan basin in southern Illinois and Indiana. Some authors (Shaver and Sunderman 1982; Mikulic and Klussendorf 1985; Berger and Weiss 1986) argue for shallower-water features dominat-

ed by deposition at or above wave base. They suggest that the deposits on the platform flanks are largely detrital and were derived from a platform tracking rising sea level. Another school (Pray 1976; McGovney 1978) has proposed an environment in much deeper water, perhaps greater than 1,000 m. Among their evidence is the geometry of the platform. Pray (1976) argued that carbonate production from what was likely a small platform top would have been insufficient to maintain a feature of the magnitude preserved in the Thornton quarry in central Illinois.

Both the reconstruction of Ingels (1963) and the cross-section of Shaver (1976) show a platform with a top 700–1,000 m across. If we assume a geometry similar to those shown schematically in Figure 16 to represent the climax stage of Thornton Reef, then a net-production rate of only 1 kg/m² per year on the bank top (depth set at –10 m) down to a water depth of –30 m could have produced the preserved platform in 435,000 years. Using Neumann and Land's (1975) overproduction ratio of 4:1, this would infer a gross-production rate of 4 kg/m² per year. Pray (1976) argued for a much smaller platform top. However, if the marginal slopes were greater than 20 degrees, as he proposes, then an even wider platform top than used in this example would be required to satisfy geometric constraints. Even if we do assume a smaller platform top only 100 m across, the Thornton complex could have been deposited in 5 million years, which is not unrea-

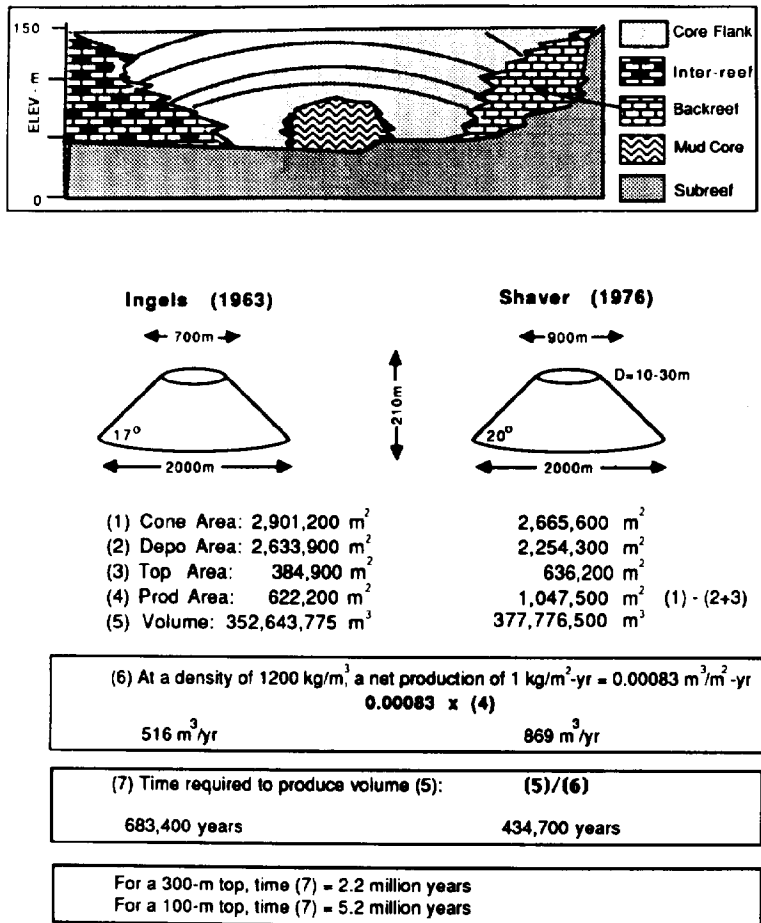


FIG. 16.—Summary of carbonate-production calculations for Thornton Reef located southwest of Chicago, Illinois. The morphological character of the reef in outcrop and subsurface is given in the two insets. Assuming the geometries of Ingels (1963) and Shaver (1976), a net-production rate of 1.0 kg/m² per year could have produced this reef mound in only 430,000–680,000 years. Even assuming a much smaller bank top, as proposed by Pray (1976) and McGovney (1978), this “pinnacle” could have been produced in 2–5 million years, within the proposed timing constraints of reefs in this region. Calculations are based on the assumption that production was confined between depths of –10 (top of bank) and –30 m.

sonable given the 5–10 million-year time interval within which this reef is stratigraphically confined.

Based on growth data from modern crinoids (Oji 1987, pers. comm.), rates of carbonate production by these organisms alone likely exceeded those used in this example. Adding to this the production by corals and stromatoporooids, a small shallow-water platform remaining at or near sea level could have easily provided the volume of sediment required to maintain the structure exposed in the Thornton quarry. This is consistent with interpretations that the sedimentological and ecologic gradients seen in the outcrop reflect a platform accreting through wave base, accompanied by a progressive increase in water depth at its base (Berger and Weiss 1986).

SUMMARY AND CONCLUSIONS

The study at Cane Bay has demonstrated the potential importance of detrital material in modern reefs. The sen-

timents expressed in this paper parallel those offered much earlier by Newell (1971):

... a persistent misconception remains that organic reefs are mainly composed of a wave-resistant framework of rigidly cemented *in-situ* skeletons of corals and algae.

The same patterns of production and degradation that can be recognized in modern reefs have probably been important in the deposition of reef systems throughout most of their evolution. Furthermore, the lack of framework in many ancient reefs likely reflects taphonomic processes that can be demonstrated in present-day carbonate systems.

Although there have been numerous evolutionary changes in reef-associated carbonate producers throughout the Phanerozoic, it is likely that most of the physical and chemical processes involved in both the formation of reefs and the export of reef sediments have existed throughout this interval of time. Thus, a more thorough understanding of carbonate production and transport,

along with a more critical look at the interiors of modern reef systems, would almost certainly improve our understanding of carbonate cycling in ancient reefs as well. We must first come to grips with the idea that our models of modern reef deposition are likely flawed. Our focus on primarily constructional processes that are readily observable on the surface of shallow-water reef environments has left us with unrealistic expectations about the character of their interiors. Furthermore, our models are based on very limited examples from a select few geographical areas and are generally confined to the shallowest portions of the reef. And finally, our oft-used approach of comparing only physical attributes, be they real or perceived, of modern reefs and their ancient counterparts have met with repeated frustration. The depositional patterns in modern or ancient reefs are *not* the universal models we seek, but rather are the signatures of *processes* which constitute the common denominator between the present and the past. The replacement of old assumptions with new data can hopefully give fresh insight into modern reef dynamics and provide the start of a more realistic model to apply to the fossil record.

From the above data we offer the following conclusions:

- 1) Approximately 1.21 kg/m² per year of carbonate are produced by organisms on the fringing reef at Cane Bay. Of this, 1.13 kg are produced by corals, 0.02 by corallines, and 0.06 by organisms that contribute directly to the sedimentary record.
- 2) Of that, 0.91 kg/m² per year is retained within the reef fabric; 45% of that is detrital sediment.
- 3) Bioerosion generates 0.65 kg/m² per year of sediment; 0.41 kg/m² per year is reincorporated within the reef. The remaining 0.24 kg, plus the 0.06 kg derived primarily from the death and breakdown of molluscs, forams and echinoderms, is deposited in channels that cross the reef.
- 4) Sediment-export rates along the shelf edge average 65 kg/m per year during fair weather and 1,130 kg/m² per year during annual storms (avg = 153 kg/m² per year). This is sufficient to prevent excess sediment from deterring reef development.
- 5) Coral cover and carbonate production are greatest near the shelf break. Neither follows a simple depth-related pattern. Reef accretion reflects secondary processes of degradation and reworking as much as initial patterns of calcification.
- 6) Accretion of the Cane Bay shelf averaged 0.73 m/1,000 yr over the past 3,000–5,000 yr. Less than half of the present reef interior is recognizable as coral, with 40% being occupied by sand and rubble, and 19% remaining as open voids. This pattern of deposition is much more consistent with what is found in the fossil record than are models based on the dominance of in-place framework.
- 7) The rates of production measured in modern reefs do not appear significantly different from those characterizing many ancient carbonate systems. Furthermore, examples of reef "framework" can be found in the ancient, implying that their occurrence has been limited not by critical differences in the growth habit

of fossil organisms, but rather by preservational controls that continue in present-day reefs. If the patterns seen at Cane Bay are applicable on even a regional scale, then fossil reefs dominated by detritus should come as no surprise, and our models of modern reefs warrant re-examination.

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REFERENCES

- ADEY, W. H., 1977, Shallow water Holocene bioherms of the Caribbean Sea and West Indies: Proc. Third Intl. Coral Reef Symp., v. 2, p. xxi-xxiv.
- , 1978, Coral reef morphogenesis: a multidimensional model: Science, v. 202, p. 831–857.
- ADEY, W. H., AND BURKE, R., 1976, Holocene bioherms of the eastern Caribbean: Geol. Soc. Am. Bull., v. 87, p. 95–109.
- ADEY, W. H., AND VASSAR, J. M., 1975, Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales): Phycologia, v. 14, p. 55–69.
- ADEY, W. H., MACINTYRE, I. G., STUCKENRATH, R., AND DILL, R. F., 1977, Relict barrier reef system off St. Croix: its implications with respect to late Cenozoic coral reef development in the western Atlantic: Proc. Third Intl. Coral Reef Symp., v. 2, p. 15–23.
- BOSELLINI, A., 1984, Progradation geometries of carbonate platforms: examples from the Triassic of the Dolomites, Northern Italy: Sedimentology, v. 31, p. 1–24.
- , 1987, Progradation geometry and dynamics of Triassic carbonate platforms (Dolomites, Northern Italy), in Zankl, H., Wilson, J. L., and Bosellini, A., eds., Outcrop Models for Seismic Stratigraphy, Field Guide for ERICO Field Trip Through the Triassic Alps of Southern Europe, August, 1987, p. 43–79.
- BOSELLINI, A., AND ROSSI, D., 1974, Triassic carbonate buildups of the Dolomites, Northern Italy, in Laporte, L. F., ed., Reefs in Time and Space: SEPM Spec. Pub. 18, p. 209–233.
- BERGER, K. J., AND WEISS, M. P., 1986, Deep and shallow water processes of an early Paleozoic reef: Abstracts SEPM Annual Midyear Meeting, Raleigh, N.C., p. 9.

- BRETZ, J. H., 1939, Geology of the Chicago region: Illinois State Geological Survey Bull., v. 65, pt. 1, 118 p.
- BURTON, W. J., 1982, Seafloor environments North St. Croix Margin and Virgin Islands Trough: Report for Office of Naval Operations by Naval Ocean Research and Development Activity, NSTL Station, Miss., 82 p.
- BYTHELL, J., GLADFELTER, E. H., GLADFELTER, W. B., FRENCH, K., AND HILLIS, Z., 1989, Buck Island Reef National Monument—Change in modern reef-community structures since 1967, in Hubbard, D. K., ed., *Terrestrial Marine Geology of St. Croix, U.S. Virgin Islands*: Special Publication no. 8, St. Croix, West Indies Lab, p. 145–154.
- CARPENTER, R. C., 1985, Sea urchin mass mortality: effects on reef algal abundance, species composition and metabolism and other coral reef herbivores: *Proc. Fifth Intl. Coral Reef Symp.*, v. 4, p. 53–59.
- CHAVE, K. E., SMITH, S. V., AND ROY, K. J., 1972, Carbonate production by coral reefs: *Marine Geology*, v. 12, p. 123–140.
- COWEN, R., 1983, Algal symbiosis and its recognition in the fossil record, in Tevesz, M. S. J., and McCall, P. L., eds., *Biotic Interactions in Recent and Fossil Benthic Communities*, Topics in Geobiology, v. 3: New York, Plenum Press, p. 431–478.
- DAVIES, P. J., 1983, Reef growth, in Barnes, D. J., ed., *Perspectives on Coral Reefs*: Manuka, A.C.T., Australia, Brian Clouster Publisher, p. 69–106.
- DAVIES, P. J., AND HOPLEY, D., 1983, Growth facies and growth rates of Holocene reefs in the Great Barrier Reef: *BMR Jour. Australian Geol. and Geophys.*, v. 8, p. 237–252.
- DAVIES, P. J., AND KINSEY, D. W., 1977, Holocene reef growth—One Tree Island, Great Barrier Reef: *Marine Geology*, v. 24, p. 1–11.
- DAVIES, P. J., AND MARSHALL, J., 1979, Aspects of Holocene reef growth, substrate age and accretion rate: *Search*, v. 10, p. 276–279.
- DUNHAM, R. J., 1970, Stratigraphic reefs vs. ecologic reefs: *Am. Assoc. Petroleum Geologists Bull.*, v. 54, p. 1931–1932.
- FAGERSTROM, J. A., 1987, *The Evolution of Reef Communities*: New York, Wiley, 600 p.
- GAETANI, M., FOIS, E., JADOU, F., AND NICORA, A., 1981, Nature and evolution of Middle Triassic carbonate buildups in the Dolomites (Italy): *Marine Geology*, v. 44, p. 25–37.
- GLADFELTER, E. H., 1984, Skeletal development in *Acropora cervicornis* III: a comparison of monthly rates of linear extension and calcium carbonate accretion measured over a year: *Coral Reefs*, v. 3, p. 51–57.
- GOREAU, T. F., 1959, The physiology of skeleton formation in corals. A method for measuring the rate of calcium carbonate deposition under different conditions: *Biol. Bull.*, v. 116, p. 59–75.
- HALL, W. D. M., 1984, The stratigraphic and structural development of the Givetian-Frasnian reef complex, Limestone Billy Hills, Western Pillara Range, W. A., in Purcell, P. G., ed., *The Canning Basin*, W. A.: *Proc. GSA/PESA Canning Basin Symp.*, p. 215–222.
- HALLEY, R. B., SHINN, E. A., HUDSON, H., AND LIDZ, B., 1977, Recent and relict topography of BooBee patch reef, Belize: *Proc. Third Intl. Coral Reef Symp.*, v. 2, p. 29–35.
- HALLOCK, P., 1988, The role of nutrient availability in bioerosion: consequences to carbonate buildups: *Paleogeog., Paleoclim. Paleoecol.*, v. 63, p. 275–291.
- HALLOCK, P., AND SCHLAGER, W., 1986, Nutrient excess and the demise of coral reefs and carbonate platforms: *Palaos*, v. 1, p. 389–398.
- HECKEL, P. H., 1974, Carbonate buildups in the geologic record: a review, in Laporte, L. F., ed., *Reefs in Time and Space*: *SEPM Spec. Pub.* 18, p. 90–154.
- HOPLEY, D., 1977, The age of the outer ribbon reef surface, Great Barrier Reef, Australia: implications for hydro-isostatic models: *Proc. Third Intl. Coral Reef Symp.*, v. 2, p. 23–28.
- HOPLEY, D., MCLEAN, R. F., MARSHALL, J., AND SMITH, A. S., 1978, Holocene–Pleistocene boundary in a fringing reef: Hayman Island, North Queensland: *Search*, v. 9, p. 323–325.
- HUBBARD, D. K., 1986a, Carbonate cycling in a shelf-edge, Holocene reef system, St. Croix, USVI: Abstracts of the 12th Intl. Sed. Congr., Canberra, Australia, p. 145.
- , 1986b, Sedimentation as a control of reef development: *St. Croix, U.S.V.I.: Coral Reefs*, v. 5, p. 117–125.
- , ED., 1989, *Terrestrial and Marine Geology of St. Croix, U.S. Virgin Islands*: West Indies Laboratory Spec. Publ. No. 9, West Indies Laboratory, St. Croix, U.S.V.I., 225 p.
- HUBBARD, D. K., BURKE, R. B., AND GILL, I. P., 1985, Accretion in deep, shelf-edge reefs, St. Croix, U.S.V.I., in Crevello, P. D., and Harris, P. M., eds., *Deep-water Carbonates*: *SEPM Core Workshop*, v. 6, p. 491–527.
- HUBBARD, D. K., BURKE, R. B., AND GILL, I. P., 1986, Styles of reef accretion along a steep, shelf-edge reef, St. Croix, U.S. Virgin Islands: *Jour. Sed. Petrology*, v. 56, p. 848–861.
- HUBBARD, D. K., SADD, J. L., MILLER, A. I., GILL, I. P., AND DILL, R. F., 1981, The production, transportation and deposition of carbonate sediments on the insular shelf of St. Croix, U.S. Virgin Islands: *Tech. Rpt. No. MG-1*, West Indies Laboratory, St. Croix, USVI, 145 p.
- HUBBARD, D. K., SADD, J. L., AND ROBERTS, H. H., 1982, The role of physical processes in controlling sediment transport on the insular shelf of St. Croix, U.S.V.I.: *Proc. Third Intl. Coral Reef Symp.*, v. 1, p. 399–404.
- HUBBARD, D. K., AND SCATURO, D., 1985, Growth rates for seven scleractinian corals at Cane Bay, St. Croix, U.S.V.I.: *Bull. Mar. Sci.*, v. 36, p. 325–338.
- HUBBARD, D. K., WARD, L. G., FITZGERALD, D. M., AND HINE, A. C., 1974, Bank margin morphology and sedimentation, Lucaya, Grand Bahama Island: *Tech. Rpt. No. 7-CRD*, Dept. of Geology, Univ. of S. Carolina, 36 p.
- HUDSON, J. H., SHINN, E. A., HALLEY, R. B., AND LIDZ, B., 1976, Sclerochronology: a tool for interpreting past environments: *Geology*, v. 4, p. 361–364.
- HURLEY, N. F., 1986, Geology of the Oscar Range Devonian reef complex, Canning Basin, Western Australia: Abstracts 12th Intl. Sed. Congr., Canberra, Australia, p. 148.
- HUTCHINGS, P. A., 1986, Biological destruction of coral reefs: a review: *Coral Reefs*, v. 4, p. 239–252.
- INGELS, J. J. C., 1963, Geometry, paleontology and petrography of Thornton reef complex of northeastern Illinois: *Am. Assoc. Petroleum Geologists Bull.*, v. 47, p. 405–440.
- JAMES, N. P., 1983, Reef, in Scholle, P. A., Bebout, D. G., and Moore, C. H., eds., *Carbonate Depositional Environments*: *AAPG Memoir No. 33*, p. 345–462.
- JAMES, N. P., AND GINSBURG, R. N., 1979, The seaward margin of Belize barrier and atoll reefs: *IAS Spec. Pub. No. 3*, Oxford, Blackwell Scientific, 191 p.
- KAUFFMAN, E. G., AND JOHNSON, C., 1988, The morphological and ecological evolution of middle and upper Cretaceous reef-building rudists: *Palaos*, v. 3, p. 194–216.
- KIENE, W. E., 1988, A model of bioerosion on the Great Barrier Reef: *Proc. Sixth Intl. Coral Reef Symp.*, v. 3, p. 449–454.
- KINSEY, D. W., 1982, The Pacific/Atlantic reef growth controversy: *Proc. Fourth Intl. Coral Reef Symp.*, v. 1, p. 493–498.
- KNUTSON, D. W., BUDEMMEIER, R. W., AND SMITH, S. V., 1972, Coral chronometers: seasonal growth bands in coral reefs: *Science*, v. 177, p. 270–272.
- LAND, L. S., 1979, The fate of reef-derived sediment on the north Jamaican island slope: *Marine Geology*, v. 29, p. 55–71.
- LAND, L. S., AND GOREAU, T. F., 1970, Submarine lithification of Jamaican reefs: *Jour. Sed. Petrology*, v. 40, p. 457–462.
- LIGHTY, R. G., MACINTYRE, I. G., AND STUCKENRATH, R., 1978, Submerged early Holocene barrier reef, south-east Florida shelf: *Nature*, v. 275, p. 59–60.
- LOWENSTAM, H. A., 1950, Niagaran reefs of the Great Lakes area: *Jour. Geol.*, v. 58, p. 430–487.
- MACINTYRE, I. G., 1975, A diver operated hydraulic drill for coring submerged substrates: *Atoll Res. Bull.*, v. 185, p. 21–25.
- MACINTYRE, I. G., BURKE, R. B., AND STUCKENRATH, R., 1977, Thickest recorded Holocene reef section, Isla Perez hole, Alacran reef, Mexico: *Geology*, v. 5, p. 567–574.
- MACINTYRE, I. G., BURKE, R. B., AND STUCKENRATH, R., 1982, Core holes in the outer fore reef off Carrie Bow Cay, Belize: a key to the Holocene history of the Belizean barrier reef complex: *Proc. Fourth Intl. Coral Reef Symp.*, v. 2, p. 567–574.
- MACINTYRE, I. G., AND GLYNN, P. W., 1976, Evolution of modern Caribbean fringing reef, Galeta Point, Panama: *Am. Assoc. Petroleum Geologists Bull.*, v. 60, p. 1054–1072.
- MACINTYRE, I. G., MULTER, H. G., ZANKL, H., HUBBARD, D. K., WEISS, M., AND STUCKENRATH, R., 1985, Growth and depositional facies of

- a windward reef complex (Nonsuch Bay, Antigua, W.I.): Proc. Fifth Intl. Coral Reef Symp., v. 6, p. 605-610.
- MACGEACHY, J. K., 1977, Factors controlling sponge boring in Barbados reef corals: Proc. Third Intl. Coral Reef Symp., v. 2, p. 477-483.
- McGOVNEY, J. E. E., 1978, Deposition, Porosity Evolution, and Diagenesis of the Thornton Reef (Silurian) Northeastern Illinois [unpubl. Ph.D. diss.]: Univ. of Wisconsin, 447 p.
- MIKULIC, D. G., AND KLUSSENDORF, J., 1985, Classic Silurian reefs of the Chicago area: Field trip guide, 49th Annual Tri-State Geological Field Conference, 45 p.
- MONTAGGIONI, L. F., 1988, Holocene reef growth history in mid-plate high volcanic islands: Proc. Sixth Intl. Coral Reef Symp., Townsville, Australia, v. 3, p. 455-460.
- MOORE, C. H., AND SHEDD, W. W., 1977, Effective rates of sponge bioerosion as a function of carbonate production: Proc. Third Intl. Coral Reef Symp., v. 2, p. 499-506.
- MOUNTJOY, E., AND GELDSETZER, H. H. J., 1981, Devonian stratigraphy and sedimentation, southern Rocky Mountains, in Thompson, R. I., and Cook, D. G., eds., Field Guides to Geology and Mineral Deposits: Geol. Assoc. Canada Annual Meeting, p. 195-224.
- MUIR, I., WONG, P., AND WENDTE, J., 1985, Devonian Hare Indian-ramparts (Kee Scarp) evolution, Mackenzie Mountains and subsurface Norman Wells, NWT: basin fill and platform development, in Longman, M., Stanley, K., Lindsay, R., and Eby, D., eds., Rocky Mountain Carbonate Reservoirs—A Core Workshop: SEPM Core Workshop No. 7, p. 311-341.
- NEUMANN, A. C., AND LAND, L. S., 1975, Lime mud deposition and calcareous algae in the Bight of Abaco, Bahamas: Jour. Sed. Petrology, v. 45, p. 763-786.
- NEWELL, N. D., 1971, An outline history of tropical organic reefs: Am. Museum Novitates, no. 2465, New York, Am. Mus. Nat. History, 37 p.
- OGDEN, J. C., 1977, Carbonate sediment production by parrotfish and sea urchins on Caribbean reefs, in Frost, S. H., Weiss, M. P., and Saunders, J. B., eds., Reefs and Related Carbonates—Ecology and Sedimentology: Am. Assoc. Petroleum Geologists, Studies in Geology No. 4, p. 281-288.
- OJI, T., 1987, Natural history of the Isocrinidae (Post-Paleozoic stalked crinoids) from Japan [unpubl. Ph.D. diss.]: Univ. of Tokyo, 77 p.
- OLIVER, J. K., CHALKER, B. E., AND DUNLAP, W. C., 1983, Bathymetric adaptation of reef-building corals at Davies Reef, Great Barrier Reef, Australia, I. Long-term growth responses of *Acropora formosa*: Jour. Exp. Mar. Biol. Ecol., v. 73, p. 11-35.
- PEARSE, V. B., AND MUSCATINE, L., 1971, Role of symbiotic algae (zooxanthellae) in coral calcification: Biol. Bull., v. 141, p. 350-363.
- PLAYFORD, P. E., 1980, Devonian "Great Barrier Reef" of the Canning Basin, Western Australia: Am. Assoc. Petroleum Geologists Bull., v. 64, p. 814-840.
- PRAY, L. C., 1976, The Thornton Reef (Silurian), northeastern Illinois, 1976 revisitation, in Silurian Reefs, Interreef Facies, and Faunal Zones of Northern Indiana and Northeastern Illinois: North-Central Sec. Geol. Soc. Am. guidebook, 70 p.
- ROBERTS, H. H., MURRAY, S. P., AND SUHAYDA, J. N., 1977, Physical processes in a fore-reef environment: Proc. Third Intl. Coral Reef Symp., v. 2, p. 507-515.
- RUTZLER, K., 1975, The role of burrowing sponges in bioerosion: Oecologia (Berl.), v. 19, p. 203-216.
- SADD, J. L., 1984, Sediment transport and CaCO_3 budget on a fringing reef, Cane Bay, St. Croix, U.S. Virgin Islands: Bull. Mar. Sci., v. 35, p. 221-238.
- SCHLAGER, W., 1981, The paradox of drowned reefs and carbonate platforms: Geol. Soc. Am. Bull., v. 92, p. 197-211.
- SHAVER, R. H., 1976, Silurian reefs, interreef facies and faunal zones of northern Indiana and northeastern Illinois: Field Trip Guide, North-Central Sec. Geol. Soc. Am., 37 p.
- SHAVER, R. H., AULT, C. H., AUSICH, W. I., DROSTE, J. B., HOROWITZ, A. S., JAMES, W. C., OKLA, S. M., REXROAD, C. B., SUCHOMEL, D. M., AND WELCH, J. R., 1976, The search for a Silurian reef model: Great Lakes area: Special Report 15, Bloomington, Indiana Geological Survey, 36 p.
- SHAVER, R. H., AND SUNDERMAN, J. A., 1982, Silurian reefs at Delphi and Pipe Creek Jr. quarry, Indiana, with emphasis on the question of deep vs. shallow water: Field Trip Guide, North-Central Sec. Geol. Soc. Am., 39 p.
- SHINN, E. A., 1981, Time capsules in the sea: Sea Frontiers, v. 27, p. 364-374.
- SMITH, S., AND KINSEY, D. W., 1978, Calcification and organic carbon metabolism as indicated by carbon dioxide, in Stoddart, D. R., and Johannes, R. E., eds., Coral Reefs: Research Methods: Paris, UNESCO, Mono. on Oceanographic Methodology, No. 5, p. 469-484.
- STANLEY, G. D., 1988, The history of early mesozoic reef communities: a three-step process: Jour. Sed. Petrology, v. 3, p. 170-183.
- STANLEY, G. D., AND FAGERSTROM, J. A., eds., 1988, Ancient Reef Ecosystems Theme Issue: Palaios, v. 3, 256 p.
- STANLEY, G. D., AND SWART, P. K., 1984, A geochemical method for distinguishing zooxanthellate and non-zooxanthellate corals in the fossil record: Advances in Reef Science (Abstracts), Atlantic Reef Committee and Intl. Soc. for Reef Studies, Miami, Fla., p. 118-119.
- STEARNS, C. W., AND SCOFFIN, T. P., 1977, Carbonate budget of a fringing reef, Barbados: Proc. Third Intl. Coral Reef Symp., v. 2, p. 471-477.
- STENECK, R. S., 1983, Escalating herbivory and resulting adaptive trends in calcareous algal crusts: Paleobiology, v. 9, p. 44-61.
- STENECK, R. S., AND ADEY, W. H., 1976, The role of environment in control of morphology in *Lithophyllum congestum*, a Caribbean reef ridge builder: Botanica Marina, v. 19, p. 197-215.
- VANDERMEULEN, J. H., DAVIES, N., AND MUSCATINE, L., 1972, The effect of inhibitors of photosynthesis on zooxanthellae in corals and other marine invertebrates: Marine Biology, v. 16, p. 185-191.
- VIAU, C., 1983, Depositional sequences, facies and evolution of the upper Devonian Swan Hills buildup, central Alberta, Canada, in Harris, P., ed., Carbonate Buildups—A Core Workshop: SEPM Core Workshop No. 4, p. 113-143.
- WARME, J. E., 1977, Carbonate borers—their role in reef ecology and preservation, in Frost, S. H., Weiss, M. P., and Saunders, J. B., eds., Reefs and Related Carbonates—Ecology and Sedimentology: Am. Assoc. Petroleum Geologists, Studies in Geology No. 4, p. 261-280.
- WELLS, J. W., 1966, Paleontological evidence of the rate of the Earth's rotation, in Marsden, B. F., and Cameron, A. G. W., eds., The Earth-Moon System: New York, Plenum Press, p. 70-81.
- WILSON, J. L., 1975, Carbonate Facies in Geologic History: New York, Springer-Verlag, 471 p.
- WILSON, M. A., 1987, Ecological dynamics on pebbles, cobbles and boulders: Palaios, v. 2, p. 594-599.
- WOODLEY, J. D., CHORNESKY, E. A., CLIFFORD, P. A., JACKSON, J. B. C., KAUFMAN, L. S., KNOWLTON, N., LANG, J. C., PEARSON, M. P., PORTER, J. W., ROONEY, M. C., RYLLARSDAM, K. W., TUNNICLIFFE, V. J., WAHLE, V. J., WULFF, J. L., CURTIS, A. S. G., DALLMEYER, M. D., JUPP, B. P., KOEHL, M. A. R., NEIGEL, J., AND SIDES, E. M., 1981, Hurricane Allen's impact on Jamaican coral reefs: Science, v. 214, p. 749-755.
- ZANKL, H., AND MULTER, H. G., 1977, Origin of some internal fabrics in Holocene reef rocks, St. Croix, U.S. Virgin Islands: Proc. Third Intl. Coral Reef Symp., v. 2, p. 127-133.
- ZANKL, H., WILSON, J. L., AND BOSELLINI, A., 1987, Outcrop models for seismic stratigraphy: Field guide for ERICO field trip through the Triassic Alps of southern Europe, August, 1987, 79 p.