

Sedimentary Petrology of a Declining Reef Ecosystem, Florida Reef Tract (U.S.A.)

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ABSTRACT

LIDZ, B.H. and HALLOCK, P., 2000. Sedimentary petrology of a declining reef ecosystem, Florida Reef Tract (U.S.A.). *Journal of Coastal Research*, 16(3), 675-697. West Palm Beach (Florida), ISSN 0749-0208.



Petrologic evaluation of biogenic sediments collected shelf-wide along the Florida reef tract in 1989 revealed three principal components: coral, the calcareous green alga *Halimeda*, and mollusc. The dominant grain was dependent in part upon local morphology that controlled composition and vitality of the biota. Either *Halimeda* or mollusc grains prevailed in sands off the upper Keys. In the middle and lower Keys, *Halimeda* grains prevailed nearshore and coral grains offshore. Comparison with similar analyses of samples collected in 1952 and 1963 indicates that, over 37 years, the relative abundance of molluscan grains more than doubled in the upper Keys and that of particulate coral tripled in the middle Keys. These changes can be interpreted in the context of physical and biological events that affected Florida Keys reefs over that period of time. In the 1970s, outbreaks of extremely cold water killed even representatives of the hardiest coral species. In the 1980s, black-band and white-band diseases decimated the major reef-building acroporid corals, and the pivotal herbivore, *Diadema antillarum*, disappeared. Although *Diadema* is a major coral bioeroder, the sea urchin is also essential to healthy reef growth. The increase in coral debris in the middle Keys may be related to Hurricane Donna in 1960, but it is also consistent with the prediction of accelerated bioerosion by boring organisms in response to increased plankton productivity. Plankton productivity is stimulated by nutrients from Florida Bay and by well-documented eutrophication of nearshore environments. In the upper Keys, where reefs are somewhat removed from bay and nearshore influence, a relative decrease in coral debris over the 37 years may reflect proliferation of algae and algae-grazing molluscs as well as suppressed rates of bioerosion in the absence of *Diadema*.

Human activities have substantially increased the natural flux of fixed nitrogen to coastal systems worldwide. Waters in the Florida Keys are no exception. Spatial and temporal trends in sediment constituents are compared to a previously published model that predicts the response of benthic biota to changes in nutrient supply. As adapted to interpret changes observed in reef-tract sediments, the model provides insights into the natural nutrient gradient along the Florida reef tract.

ADDITIONAL INDEX WORDS: *Bioerosion; biogenic carbonates; coral, Halimeda, and mollusc debris; coral reefs; Diadema antillarum; ecosystem alteration; effects of environmental change; geologic indicator; nitrification; quantification of reef health; regional geomorphology.*

INTRODUCTION

Geologic indicators of rapid environmental change provide a conceptual framework for assessing shifts in the biotic components of ecosystems (BERGER, 1998). The shifts may be due to natural processes or human activities. In a reef ecosystem, causes of change may be biotic, such as in community structure, or abiotic, either catastrophic (*e.g.*, hurricanes and winter storms) or slower and more pervasive (*e.g.*, coastal erosion and changes in sea level or in physical or chemical characteristics of the water). Anthropogenic hazards include air and water pollution, introduction of new pathogens, and damage by divers, anchors, or ship groundings. Each alters the ecosystem, and each has significant societal implications for outdoor recreation, fishery nurseries, and coastal-zone management. The application of geoinicators to the monitoring of ecosystem conditions, especially in long-term research, can

help scientists contribute more effectively to interdisciplinary efforts. Geoinicators may also help remind policy makers and the general public of the reality of natural change and the common difficulty of distinguishing it from human modification. As such, geoinicators can be applied to the concept of sustainability, which requires a capacity to assess current conditions and trends.

A method of assessment widely used in paleoenvironmental analyses of fossil reef systems yet not often applied in modern reef systems is sedimentary petrology. The general assumption here is that, if reef communities shut down, bioeroders will break the coral framework down, thereby producing a relative increase in coral grains in surrounding sediment. The more specific premises on which the study is based were proposed for Florida reefs by LIDZ *et al.* (1985). (a) Coral-sand production accelerates in direct proportion to the amount of weakened or dead-coral substrate available for bioerosion by grazing and boring organisms. (b) Particulate coral is the dominant grain in sands where reefs are

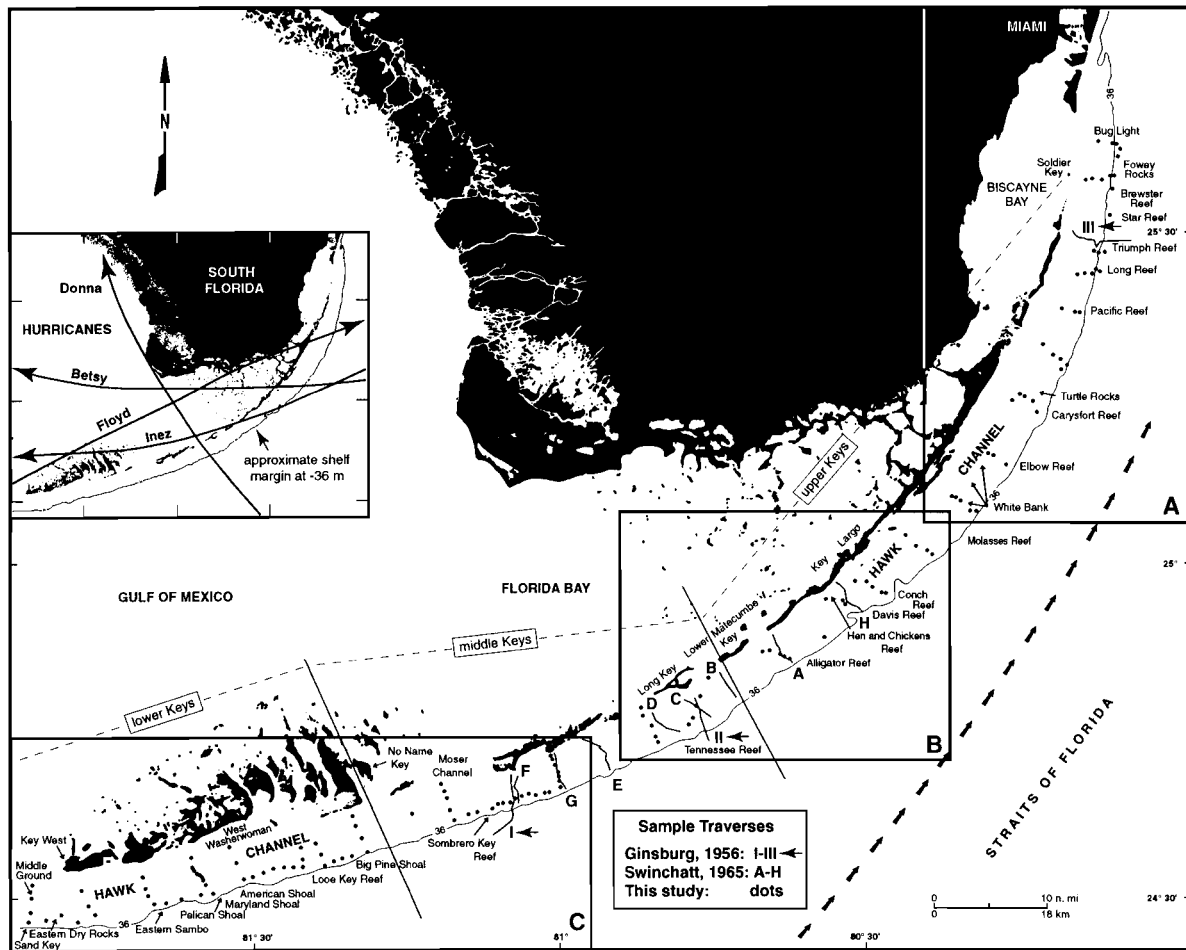


Figure 1. Index map of South Florida showing location of major geomorphologic features, reefs, and general area of sample traverses in three studies. Inset shows paths of major hurricanes in the area between 1952 and 1989. Study area extends from Bug Light off Miami/Biscayne Bay to Sand Key Reef off Key West and from the Keys seaward to the shelf break (36-m contour). Park and Sanctuary boundaries not shown. Note locations and widths of tidal passes in the middle Keys compared to those in the upper and lower Keys. Offshore arrows indicate northwestward Gulf Stream axis. Boxes A-C shown in Figure 2. Area sampled for this study measures roughly 600 nm².

declining or senescent (not actively accreting). Hence, (c) because observed modern coral growth, relative to Holocene coral growth, is less prevalent (*i.e.*, coral mortality has increased) opposite tidal passes than opposite protective islands, the coral-grain fraction of the sand should be greater off the passes. The variety of morphologies and reef conditions in the Florida Keys provides an ideal setting to test these hypotheses.

Three broad objectives are achieved by this study. (1) It provides the first Florida Keys-wide petrologic database. (2) It tests the hypothesis that differences in biotic communities, as observed in the field, are also visible in the sand and are thus preserved in the sedimentary record. (3) It demonstrates the concept that, as a geoinicator, the sedimentary record has potential in monitoring ecosystem conditions and the effectiveness of efforts to promote its sustainability. Implied in the second and third objectives is the use of sediments in a

reef system as an impartial petrologic tool to quantify reef vitality. This significant implication is supported by the regional sampling plan. The study was designed in part to show spatial influence of local geomorphologies on sediment composition and, to the degree possible given limited earlier data, to evaluate temporal trends of change. As such, the results are intended to provide a broad overview rather than to produce precise details of sediment distribution. The intent notwithstanding, we acknowledge certain factors that may be perceived as shortcomings.

Few historical data exist with which to make comparisons, and they are based on a limited number of samples from localized transects (GINSBURG, 1956; SWINCHATT, 1965; LIDZ *et al.*, 1985). Although samples collected for this study represent a much larger number and a significantly broader area (Figures 1, 2A-C), the realities of finite time and resources to cover some 600+ nm² necessitated sample numbers that

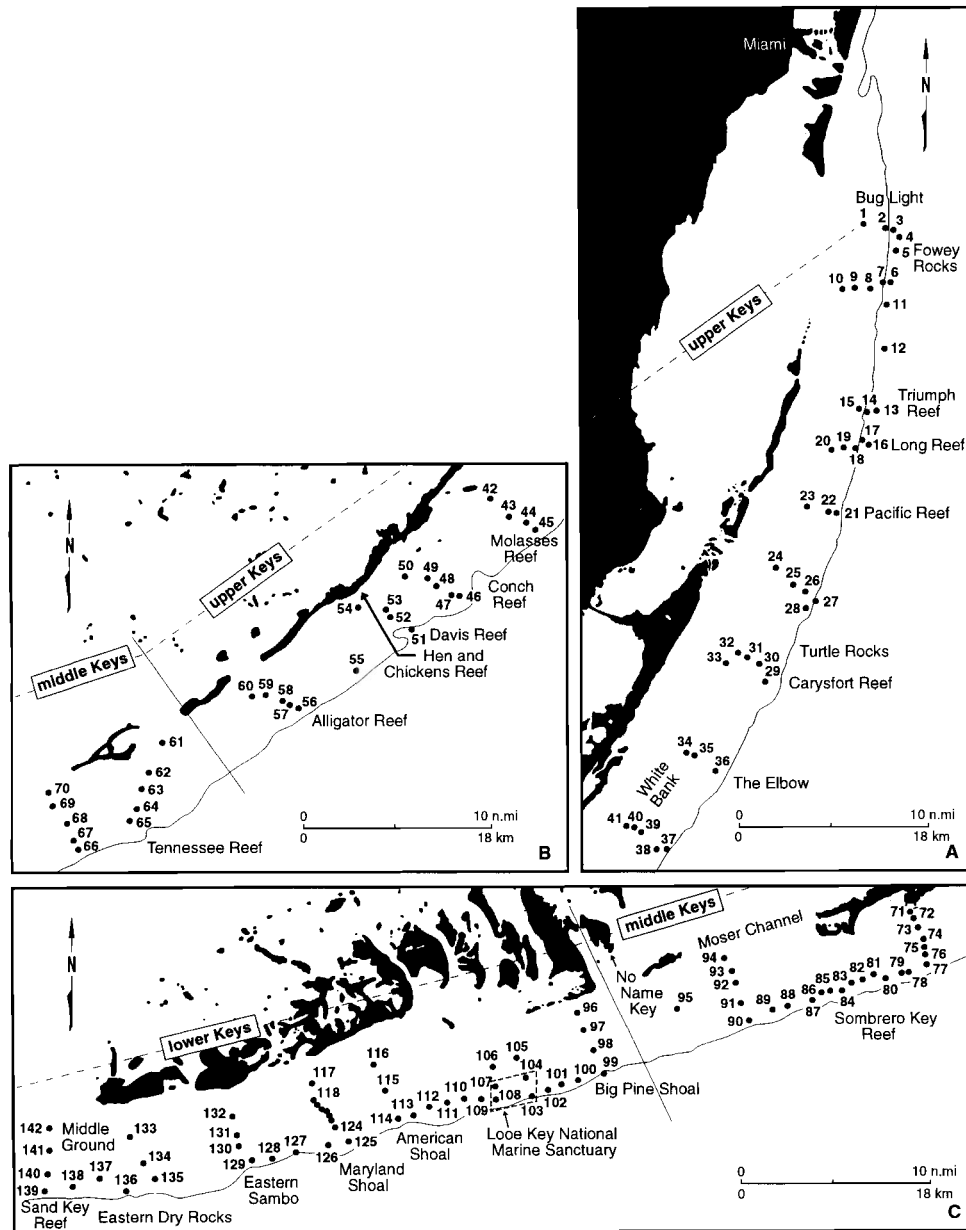


Figure 2. Enlarged boxes (A–C from Fig. 1) showing numbered 1989 sample sites. Note size of parallelogram representing Looe Key National Marine Sanctuary (dashed lines in C) relative to area of lower Keys shelf. Depths at sample-site plots, drawn from a navigational chart, are unreliable. True depths at each site (Appendix 1, column 3) were taken from shipboard fathometer.

are still low relative to the area of interest. Whereas several traverses paralleled areas sampled in the earlier studies, precise sites sampled previously could not be identified or reoccupied. Similarly, although the earlier studies and this one used surface sediments and grain counts from standard petrographic thin sections, sampling and sample preparation methods differed somewhat. We also recognize the inherent variability of biogenic carbonates. Areas of patchy reef development are prone to display substantial variations in bottom-sediment characteristics over short distances, likely

leading to different constituent-grain percentages at any given site relative to those at an adjacent site. Sand composition is also affected by local conditions, such as mechanical sorting related to water depth, currents, and presence or absence of grass beds. Nonetheless, where three (GINSBURG, 1956; SWINCHATT, 1965; this study) of the four studies traced similar traverses in the middle Keys, some interesting and consistent broad trends in dominant-grain distribution and changing grain percentages are indicated over recent decades (for sample years 1952, 1963, and 1989).

Coral-Reef Ecosystems

Community structure varies among reef ecosystems because of differences in biogeographic and environmental settings, geologic histories, and ecosystem functions (DONE *et al.*, 1966), yet all reef systems have at least one common entity. Each is characterized by carbonate sands derived from skeletal breakdown of indigenous organisms (see ENOS, 1977, for discussion). Each thus provides an interpretable signature of those biota specific to a given reef system. Any significant variations in primary biota should be evident as changing percentages of constituent biogenic grains from one site to another or over time scales of years to decades.

Worldwide, as many as 60% of reef ecosystems may be seriously threatened by human activities (BRYANT *et al.*, 1998). Reef-building corals, in particular, are disappearing and are being replaced by biota that cannot construct reef framework (authors in D'ELIA *et al.*, 1991, and GINSBURG and GLYNN, 1994; WILKINSON, 1993; LITTLER and LITTLER, 1994). Reefs of the Caribbean (HUBBARD *et al.*, 1990; EDMUNDS, 1991) and Florida (DUSTAN and HALAS, 1987; PORTER and MEIER, 1992) are no exception. Although Florida's coral reefs are somewhat enhanced where land barriers exist, field observations indicate that ecosystem vitality has declined Keys-wide.

In the western Atlantic and Caribbean region, which includes the Florida reef tract, the primary sediment constituents are fragmented plates of calcified codiacean green algae (*Halimeda* spp.), along with coral and molluscan debris. GINSBURG (1956) and SWINCHATT (1965) were the first to examine sand composition relative to shelf-margin environments along limited parts of the Florida shelf (Figure 1). Their data for sample years 1952 and 1963 along a few traverses mainly off islands in the middle and upper Keys showed that the dominant grain sources were *Halimeda* at 70% of 79 sites and coral at 14% of those sites. However, within the Looe Key National Marine Sanctuary (LKS), located on the outer shelf opposite narrow tidal passes between the lower Keys (Figure 2C), LIDZ *et al.* (1985) found that in 1983 coral was the primary source of grains at 49% of 96 sites and *Halimeda* at only 13% of those sites. Compared to reefs off Key Largo, coral growth in the LKS has diminished, and most *Acropora palmata*, which once formed large, thriving spur-and-groove systems there, is no longer living (*e.g.*, SHINN *et al.*, 1989).

Surface sediments collected shelf-wide in 1989 provide the first broad petrologic database for the area seaward of the Florida Keys, between Fowey Rocks off Miami and Sand Key off Key West. In order to test one of the hypotheses of LIDZ *et al.* (1985), that coral grains should be most common off tidal passes, sampling strategy was based on regional morphologies: opposite the keys, opposite tidal passes, and along outer-bank reefs paralleling the shelf margin (Figures 1, 2A–C). The northernmost traverse extended seaward to the margin from a navigational marker southeast of Miami known locally as Bug Light (25°37'23"N, 80°07'07"W). The southernmost extended landward from Sand Key Reef, southwest of Key West (24°27'25"N, 81°52'37"W).

Physiographic and Sedimentologic Setting

Located several kilometers inland of the shelf break (Figure 1), the Florida Keys form an island chain flanked by Florida and Biscayne Bays to the north, the reef tract to the south, and numerous intra-island tidal passes of various widths and depths. The passes link turbid, nutrient-enriched lagoonal waters from the bays and the Gulf of Mexico with clear, nutrient-poor oceanic waters on the reefs. Where present, the keys offer protection from these waters to offshore coral reefs (HOFFMEISTER, 1974; SZMANT and FORRESTER, 1996). The part of the reef tract investigated in this study includes areas protected by the Biscayne National Park, John Pennekamp Coral Reef State Park, Key Largo National Marine Sanctuary, and the Looe Key Sanctuary, all of which lie within the eastern part of the Florida Keys National Marine Sanctuary.

In general topographic terms, the shelf seaward of the keys is sandier and several meters shallower to the northeast than southwest (LIDZ and SHINN, 1991). The inner shelf off Elliott Key and north Key Largo is dotted with thousands of circular patch reefs (MARSZALEK *et al.*, 1977). Throughout the keys, the outer shelf is rimmed with discontinuous linear reefs. The shelf substrate and island chain are constructed of porous limestone. The upper and middle Keys are lumped by orientation (NE-SW) but are distinct in their tidal-pass width. Composed of an ~125 ka (HOFFMEISTER *et al.*, 1967) arcuate complex of coalesced patch reefs, the upper and middle Keys extend ~175 km from Soldier Key near Miami southwest to No Name Key (HOFFMEISTER, 1974). The coalesced patch reefs comprise the Key Largo Limestone (SANFORD, 1909) or the Key Largo unit of the Miami Limestone (HOFFMEISTER *et al.*, 1967). The middle Keys include Lower Matecumbe to No Name Key and contain the widest, deepest tidal passes. The lower Keys are composed of cemented oolitic tidal-bar sands (Miami Limestone) of the same age as the Key Largo Limestone and are separated by numerous narrow, shallow tidal passes. The tidal-bar facies are oriented nearly normal (NW-SE) to the reef arc and extend ~130 km from No Name Key to Boca Grande Key in the Gulf of Mexico. Modern reefs are most luxuriant and abundant off Key Largo (upper Keys), least developed and sparse off the middle Keys, and moderately well developed in the immediate vicinity of the lower Keys (GINSBURG and SHINN, 1964; SHINN *et al.*, 1989). Between the Marquesas Keys, due west of Key West, and the Dry Tortugas farther west in the Gulf of Mexico, no rock-island barriers exist, north-south tidal currents are strong (SHINN *et al.*, 1990), and sparse reefs are dead or no longer actively accreting.

Sediments of the modern reef tract began forming about 6 ka when sea level was ~5.7 m lower than at present and inner-shelf bedrock lows began to flood (LIDZ and SHINN, 1991). In Florida (GINSBURG, 1956) and elsewhere (*e.g.*, HOBOLT, 1957), carbonate sands are produced *in situ*. The general similarity between the distribution of living sediment-producing organisms in the reef tract and their fragmentary remains in the sediments implies that there is no major transportation of sand-size sediment from one area to another. Even intense wind and wave actions of winter or tropical

storms and hurricanes simply mix but do not remove sands from the general area of their origin (BALL *et al.*, 1967). This factor, comparative stability of the sediments, is important to the type of grain that is dominant relative to the type (open or protected) of local morphology and to application of the sedimentary record as a potential geoinicator of changes in the reefs.

METHODS

A brief discussion of methods used in the earlier studies is in order to evaluate potential statistical bias in comparison of the data sets. GINSBURG (1956) collected sediment using a Peterson dredge sampler. Samples were oven-dried and divided into two sub-samples, one for grain-size analyses, the other for petrographic analyses. Samples with appreciable amounts of fines were disaggregated by soaking in 20% hydrogen peroxide for 2 days and wet-sieved through a 62- μ screen. The screen residue was washed, dried, and dry-sieved into size grades. A representative sub-sample of the fraction >1/8 mm was impregnated with a styrene plastic under a vacuum and thin sections were made. Grains were identified and point counted along traverses using a grid 1 mm by 1 mm. Areal percentages (volume estimation) of the constituent grains were estimated following the method of CHAYES (1949).

SWINCHATT (1965) collected samples by diving and scooping the top 2 to 3 cm of sediment into a glass jar. Samples were dried, split with a Jones micro-splitter for grain-size and petrographic analyses, and soaked in 5% sodium hypochlorite solution (household bleach) for 2 days to destroy aggregates formed during drying. A sub-sample was wet-sieved through a 62- μ screen, the residue dried and impregnated with plastic and thin sections prepared. Grains >1/16 mm were identified and point counted in thin section.

For our study in 1989, sediment samples consisting of approximately 227 g were collected at 142 sites using a spring-loaded grab sampler operated by an onboard electric-powered winch. No grain-size analyses were conducted. Each sample was washed in fresh water, oven-dried, mixed to obtain an homogenous aliquot, poured into ice-cube trays, and impregnated with polyester resin. Standard thin sections were prepared and point counted under a petrographic microscope to determine biotic origin and composition. Point-count traverses were run from slide top to bottom in order to minimize bias of settling or sorting that might have occurred during preparation. Distance between traverses was not measured, but position of each traverse was selected where maximum counts could be achieved. Grains were identified and counted every 0.5 mm. If a thin section contained voids or exceptionally large grains relative to surrounding matrix, the large grains, although crossed by more than one traverse, were tallied only once. In some cases, very fine-grained muddy sands hindered identification of many grains that fell beneath the cross hairs. Total point count was 37,150 grains with a maximum of 342 and minimum of 113 (very coarse) grains per slide (Appendix 1). Grain-count percentages were estimated with a probable error at the $\pm 95.4\%$ confidence level following the technique of GALEHOUSE (1971).

Ten types of grain were identified following the carbonate petrography manual of SCHOLLE (1978). Percentages (Appendix 1) were averaged by area (upper, middle, and lower Keys; Figure 3A–C). The percent of samples in which a particular grain type is dominant was also determined. Averaged percentages for the primary grains in this and the previous studies (Appendix 2A–D) were mapped by sample year to show temporal trends. Percentages were plotted by sample site on mylar overlays matching the index map to show spatial distribution of each dominant grain and relative composition within each grain category. Numbers were contoured by hand to show trends relative to regional morphologies and to healthy and senescent reefs as observed in the field. Seven types of grains identified (echinoids, byrozoans, coralline algae, benthic and planktic foraminifera, pellets, and quartz) provided percentages too low to be useful. Quartz grains, which can be common in upper Keys sands, were tallied for trend evaluation; there was none. Traditional sieving for grain-size distribution, a procedure normally conducted in siliclastic studies, was not attempted. Such analyses are considered of questionable value in studies of skeletal carbonate sands (SWINCHATT, 1965).

Comparisons between our data and those of the previous studies were performed in three ways. Because the 1952 data are very limited, simple, non-rigorous grain-percentage comparisons are presented. For limited areas that were sampled more intensively in 1952 (GINSBURG, 1956) or 1963 (SWINCHATT, 1965), grain-distribution percentages were mapped for comparison. Finally, to compare the data set of SWINCHATT (1965) with our data set for the corresponding area, sample data were grouped regionally into six categories (open shelf and shelf margin, for the upper, middle, and lower Keys). Each category was examined by multi-factor analysis of variance using a general linear model and arcsine transformation, which is appropriate for proportional data (ZAR, 1984).

RESULTS

Of 142 samples collected in 1989 and examined for this study, 139 contained sufficient sand-size grains for analysis. *Halimeda*, mollusc, or coral grains were dominant in 131 samples. Of the remaining 11, quartz dominated one, fecal pellets of sediment-ingesting organisms dominated seven, and three were too fine-grained to analyze. Off the upper Keys, *Halimeda* and mollusc grains outnumbered coral at all but three sites, but both abruptly and distinctly became eclipsed by coral off the middle and lower Keys. Grains of minor components seldom exceeded 15% in all samples.

Halimeda grains prevailed in 48% of 58 upper Keys samples, composing, on average, 32% of constituent grains in the area (Figure 3A–C). *Halimeda* debris was dominant in 34% of 35 middle Keys samples, averaging 26% of those constituent grains, and in 26% of 46 lower Keys samples, averaging 23% of the sediment. Molluscan particles were prevalent in 36% of upper Keys samples, 6% of the middle Keys samples, and in none from the lower Keys. The average molluscan contribution ranged from 28% in the upper Keys to 18% in the middle Keys to 23% in the lower Keys. Keys-wide, the most

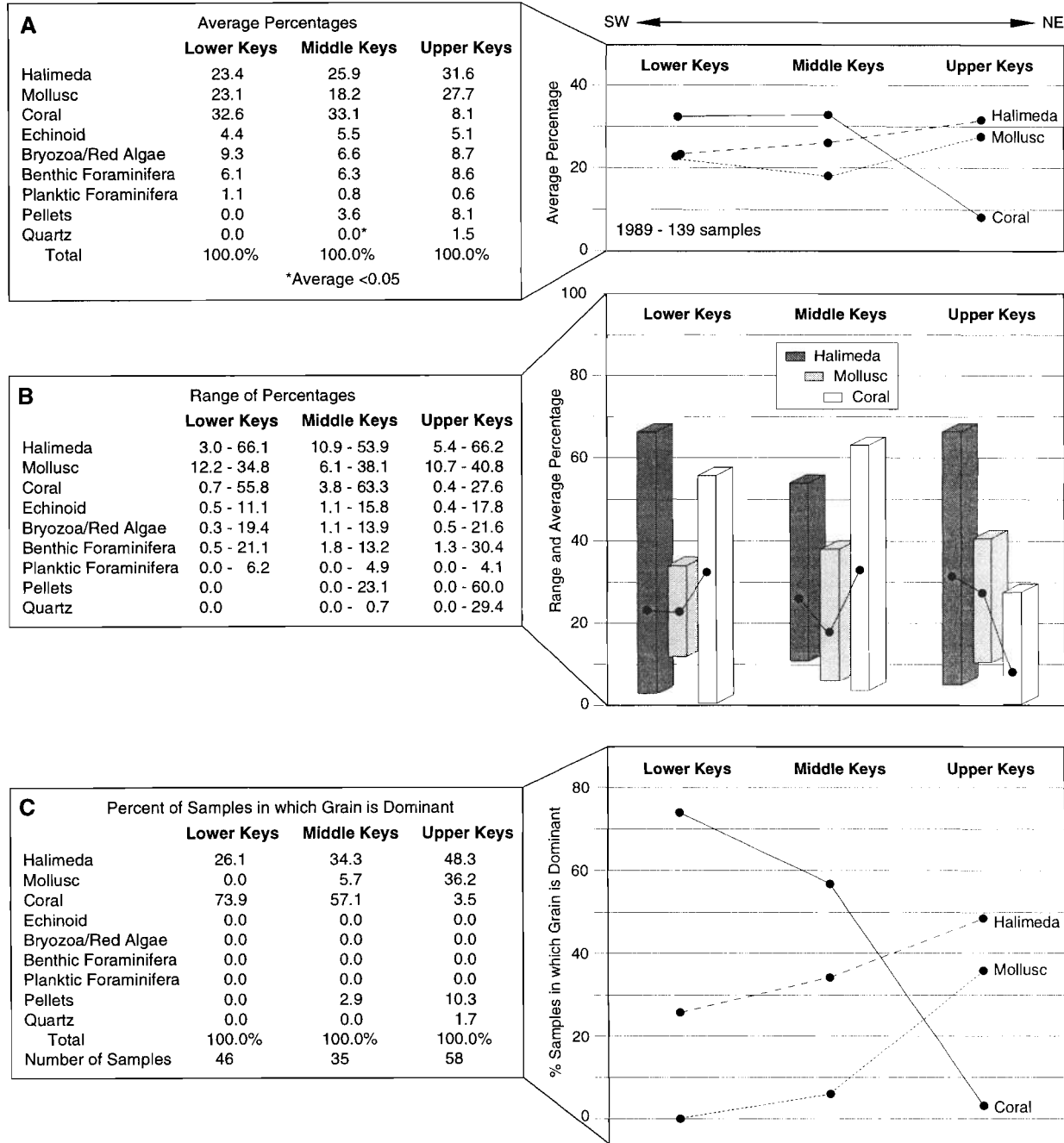


Figure 3. Tabular and graphic summary of 1989 Keys-wide petrologic data. (A) Averaged grain percentages (from Appendix 1) by upper, middle, and lower Keys areas with those for primary grains graphed. (B) Range and average of percentages by area. (C) Percentage of samples by area in which a particular grain is dominant.

conspicuous differences in sediment composition were observed in the coral averages. Coral was the primary source of grains in only 4% of upper Keys samples, but it was dominant in 57% of middle Keys samples and in 74% of lower Keys samples. The average contribution by coral debris was 8% in the upper Keys and 33% in the middle and lower Keys. Percentage ranges for each grain type show that *Halimeda*

exhibited substantial local variability (3% to 66% of an individual sample) throughout the Keys, whereas the molluscan component was more stable but variable nonetheless (6% to 41%). The range of coral-grain percentages was fairly low (28% maximum) in the upper Keys but varied widely in the lower and middle Keys (from 1% to 63%). All coral-grain values >20% in the upper Keys were found near Davis and Al-

ligator Reefs and appear to reflect a transition in dominant-grain type between upper and middle Keys sands.

DISCUSSION AND INTERPRETATIONS

Spatial Compositional Trends: Keys-wide, 1989

In 1989, sediments off the upper Keys consisted primarily of fragmented *Halimeda* plates and molluscan shells with *Halimeda*-dominant sands covering the larger area (Figure 4A). *Halimeda* was the principal grain along much of the outer shelf-margin rim, as was also the case along the margin off St. Thomas (USVI) in the 1980s (KINDINGER *et al.*, 1983). Coral debris became dominant along the outer shelf only opposite the first major tidal pass south of Key Largo. Molluscan grains were prevalent in an isolated patch in Hawk Channel south of Long Key and were otherwise subordinate to *Halimeda* and coral particles throughout the middle and lower Keys. *Halimeda* sands lined the middle and lower Keys inner shelf, and coral-rich grains characterized sands of the outer-bank reefs.

Broad trends in distribution of constituent-grain percentages were also observed. For *Halimeda*, elevated percentages were found in bands across the upper Keys shelf but were present only along the inner shelf to the southwest (Figure 4B). Keys-wide, grains of *Halimeda* generally decreased offshore and southwestward. The highest percentages (>50%) were found in patches west of White Bank, Alligator Reef, and northwest of American and Maryland Shoals. The lowest percentages (<10%) were found along a narrow band in Hawk Channel north of Alligator Reef and at the shelf margin at Sand Key and Eastern Dry Rocks Reefs, southwest of Key West.

Without coral as a dominant component on the upper Keys shelf, mollusc to *Halimeda* ratios were nearly reciprocal. Mollusc percentages (Figure 4C) thus showed a trend grossly similar to that of *Halimeda*. Whether the percentages are related more to variations in algal abundance than to mollusc zonation (*e.g.*, KINDINGER *et al.*, 1983) is not known. Sand "belts" with a variable but moderately high molluscan content alternated across the upper Keys shelf, in contrast to the steady, albeit local, offshore decrease in mollusc grains previously reported at Triumph Reef (GINSBURG, 1956). In fact, in 1989, Triumph Reef and the margin north of Turtle Rocks had the highest percentages of mollusc grains (30% to >40%). Our data for the middle and lower Keys showed a seaward and southwestward decrease in mollusc grains. Sands with the lowest mollusc-grain content (<10%) were found just north of Sombrero Key.

Percentages for coral grains show a reciprocal relation with the combined percentages of *Halimeda* and molluscan debris (compare Figures 4A and D). In 1989, essentially the entire shelf northeast of Conch Reef harbored sediments containing only minor percentages of coral grains (<10%). Off the middle and lower Keys, however, sands with very high coral fractions (in places exceeding 60%) occupied the outer shelf, with lower percentages (generally 10% to >20%) spanning the inner shelf where *Halimeda* was the principal grain. Keys-wide, coral-grain percentages showed a substantial and progressive seaward and southwestward increase.

Temporal Compositional Trends: Middle Keys, 1952–1989

Distribution of the dominant grains and their concentrations in the middle Keys in 1952 (GINSBURG, 1956) and 1963 (SWINCHATT, 1965) showed different trends from those in 1989 (Figures 4A–D). Both earlier data sets (Figure 5A–D) showed that *Halimeda* was the most abundant constituent in shelf-margin sands and that mollusc grains decreased steadily from the inner shelf to beyond the shelf break. Both also showed that coral grains peaked at the shelf break and that substantial differences occurred only in coral and mollusc grains between the inner shelf and outer-shelf margin. Maps were not prepared for the 1983 lower Keys data because the time between studies was short (6 years), the area of Looe Key Sanctuary relative to that of the lower Keys shelf is very small (Figure 2C), and LKS sands were dominated by coral in both years (LIDZ *et al.*, 1985, and this study).

The 1963 (Figure 5A–D) and 1989 (Fig. 4A–D) data sets display locations where a particular type of grain remained dominant over the 26-year period, despite nearby passage of Hurricanes Betsy (1965), Inez (1966), and Floyd (1987) (inset, Figure 1). These data sets indicate that notable changes occurred in proportions of molluscan and coral grains. Both data sets, averaged by lower, middle, and upper Keys area by sample year (Figure 6A, Table 1), also show compositional trends through time. (1) Keys-wide, *Halimeda* grains are common throughout, but become distinctly subordinate to coral grains in offshore sediments of the lower and middle Keys. (2) Relative abundances of molluscan grains remain comparatively unchanged in the lower and middle Keys but increase substantially in offshore samples from the upper Keys. (3) Proportions of coral grains appear to have declined in the upper Keys but have increased substantially in the middle and lower Keys. Multi-factor analysis of variance (*e.g.*, ZAR, 1984) demonstrated the statistical significance of these trends (Table 2). In most cases, differences were significant temporally (*i.e.*, between 1963 and 1989), with distance offshore (*i.e.*, open shelf *versus* shelf margin), and regionally (*i.e.*, upper, middle, and lower Keys). *Halimeda* samples provided the only exception, showing no significant differences between open-shelf and shelf-margin sediments.

Storms, Diseases, and Nutrients: Deciphering the Trends

Comparison of constituent-grain distributions for 1963 and 1989 showed that proportions of coral debris had changed the most. The question is, why? Factors influencing coral-grain production and distribution must include both biological processes that yield the coral debris and physical processes that can also produce it and may disperse it. Hurricane activity is the major physical process that could, theoretically, alter constituent-grain composition over an area as large as the middle Keys. Rates of production of coral debris depend both on availability and type of bioerodable coral substrate and on rates of bioerosion, which vary with bioerosional agents. Can regional differences along the reef tract provide insight into the overall trends in sediment constituents throughout the Keys? Do events or changes in reef communities over the 37-

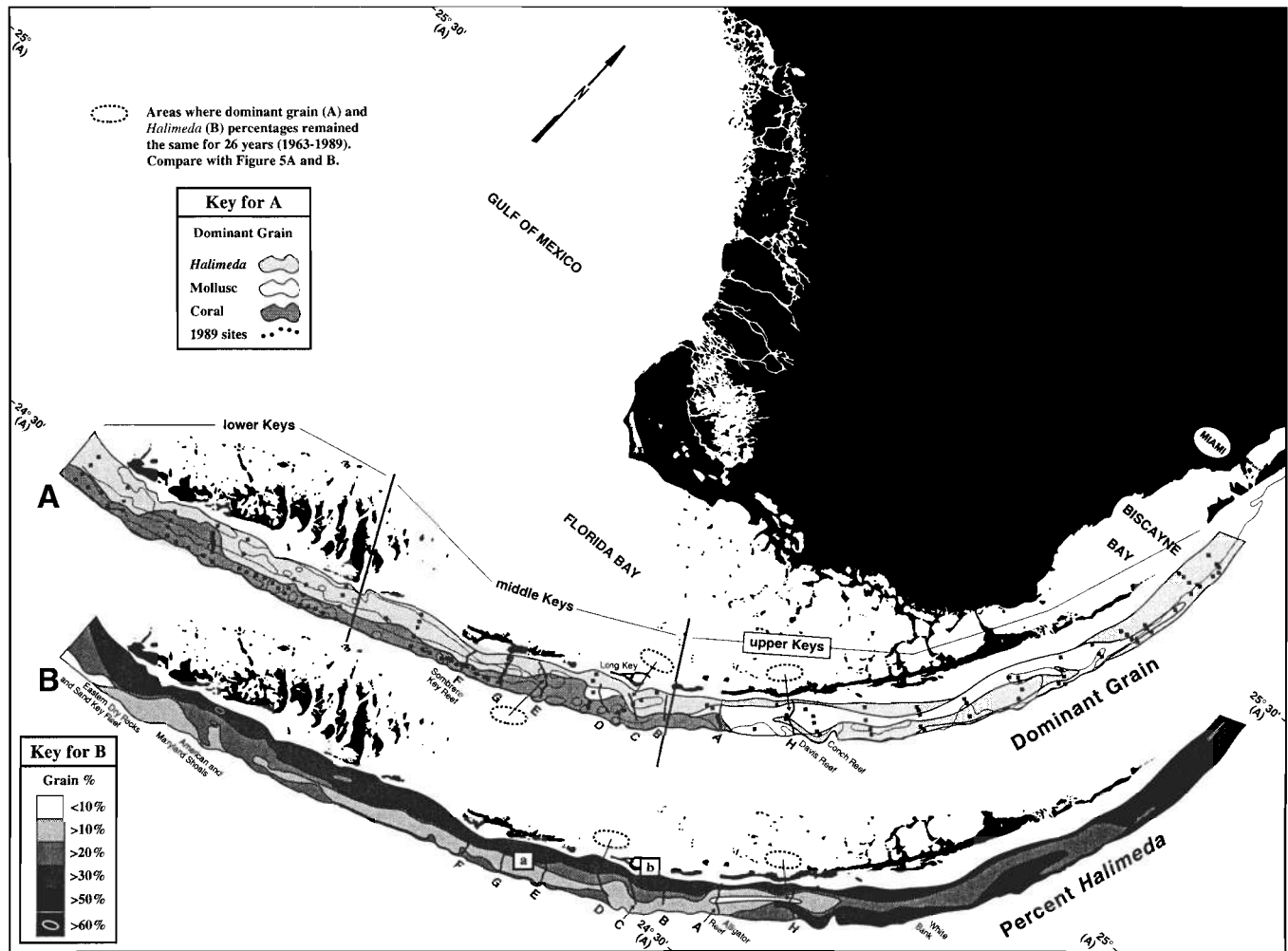


Figure 4. (A) Contour maps showing Keys-wide distribution of primary grains in 1989. Traverses of SWINCHATT (1965) labeled A–H. Dots indicate 1989 sample sites. (B–D) Primary-grain percentages. Boxed letters (a–e) correspond to 37-year trends in changing composition summarized in Figure 5. (E) Generalized locations of healthy, declining, and senescent reefs based on field observations. Compare with type of dominant grain and grain percentages in area of Conch, Davis, Tennessee, and Sombrero Key Reefs in 1952 and 1963 (Fig. 5A–D). Correlation of observed reef vitality (E) with coral-grain concentrations (F) as a proposed method to quantify areas of healthy, declining, and senescent reefs. Parallel lines align areas of different reef vitalities with coral-grain percentages in those areas. Latitude relative to (A) and (F).

year period provide clues to explain the changes in sediment constituents?

Storms

One of the most notable facts regarding hurricane activity in the Florida Keys over the decades encompassing the sample years is the relative lack of major storms (NEUMANN *et al.*, 1988). The most powerful hurricane to impact the area between sample years 1952 and 1989 was Hurricane Donna, a Category 4 storm that bore sustained winds of 140 mph with gusts to 180. Donna slammed into the middle Keys in 1960 on a north-northwest track perpendicular to the margin (inset, Figure 1). Wind-driven waves and surf as high as 4.5 m north of the eye pounded the outer reefs, displacing boulder-size rubble and moving great amounts of grass-free sand

~45 m landward onto grass-covered sand, yet effects on general distribution of sediments behind the outer reefs was limited (BALL *et al.*, 1967). The dominant-grain maps for 1952 and 1963 (Fig. 5A) indicate landward movement of coral-rich sands, but the percentage change in the middle Keys coral-debris component between those years is negligible (+5%, Figure 6A). In contrast, paths of Hurricanes Betsy, Inez, and Floyd between 1965 and 1987 were more distant and tangential to the middle Keys, with Betsy and Inez tracking west and Floyd northeast. None of those storms should have moved middle Keys outer-reef sands landward, yet a 17% increase (Figure 6A; >20 percentage points, Table 1) in the coral-debris average occurred between 1963 and 1989. Although mechanical effects of breakage by increased turbulence and current and wave action may fragment large coral

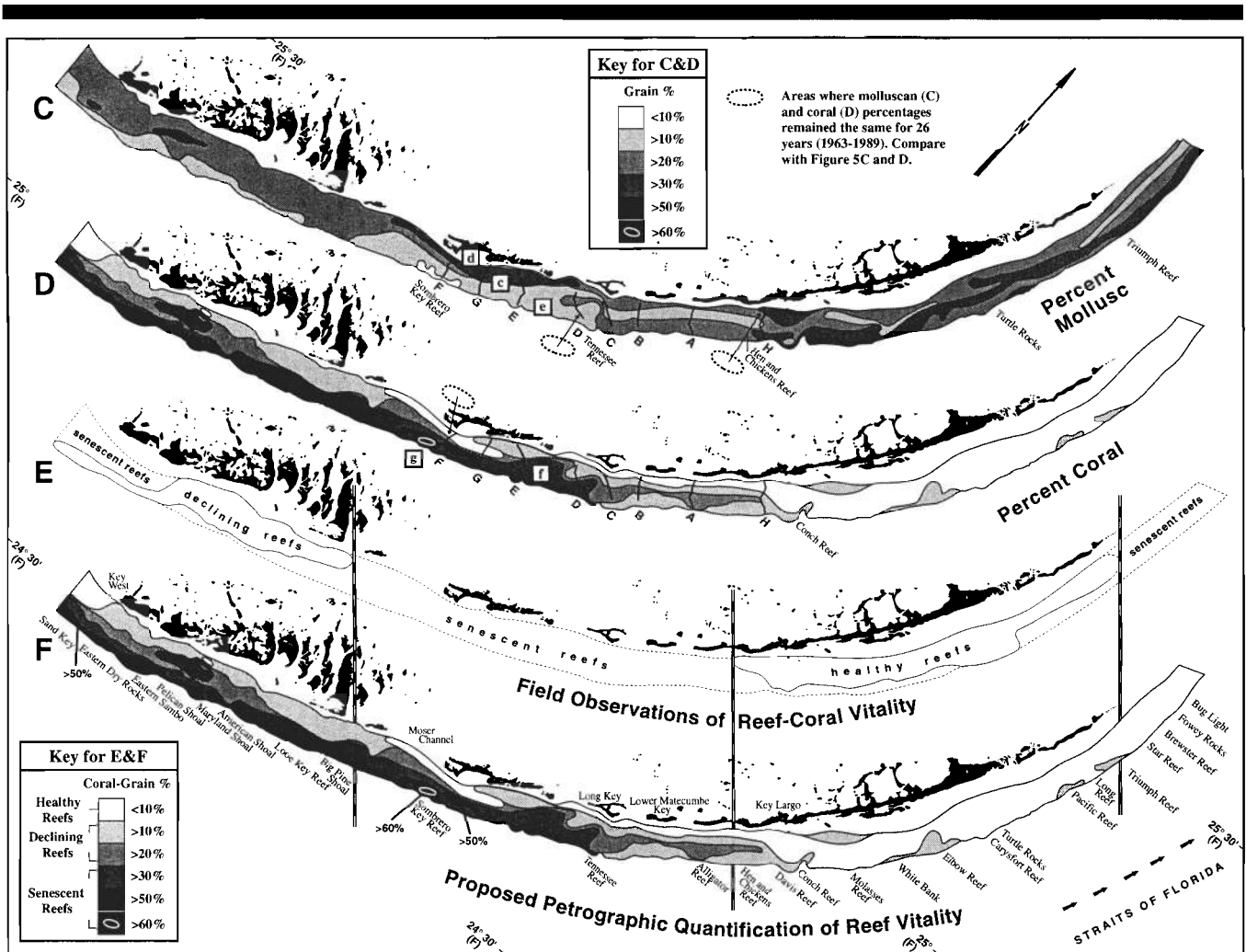


Figure 4. Continued.

heads or break large fragments from the reef framework, producing smaller grains in the process, such breakage is limited to the outer reefs and the area immediately behind them (SWINCHATT, 1965). The only other alternative for coral breakdown elsewhere on the shelf is through biological action.

Although corals can be devastated on a grand scale during storms, recovery is rapid. Because scattering of live fragments by Hurricane Donna was widespread and many pieces became growth sites of new colonies, there was virtually no sign of destruction in the middle Keys within 1 year after the storm, even to the experienced eye (SHINN, 1976). Reef recovery from other weather phenomena, however, is less rapid, allowing time for breakdown of freshly killed coral. Recovery from death by chilling, for example, requires settlement of imported planktic coral larvae and a substrate suitable for larval attachment (SHINN, 1976). Resettlement is subject to the effects of currents, the distance from larval sources, predators, pollution, and competition for substrate. Unusually severe winter cold fronts impacted coral commu-

nities Keys-wide in 1970 (HUDSON *et al.*, 1976) and again in 1977 (PORTER *et al.*, 1982; ROBERTS *et al.*, 1982) when it snowed in Miami. Reefs opposite major tidal passes in the middle Keys and in exposed locations in the lower Keys were particularly vulnerable. Both events killed not only the more temperature-sensitive branching corals (*Acropora* spp.), but also the much harder head corals including *Montastrea annularis* as far inshore as at Hen and Chickens Reef (Figure 2B; HUDSON *et al.*, 1976; HUDSON, 1981). These events may well have contributed to increased bioerosional rates between 1963 and 1989.

Sediment Sources and Diseases

Halimeda and molluscan grains are produced in both sandy and hardbottom environments throughout the Keys. Production of coral debris occurs mostly in hardbottom settings, where bioerodable substrate can include fossil coral, recently killed coral, and the skeleton underlying live coral. Therefore, the amount of bioerodable substrate in an area depends upon

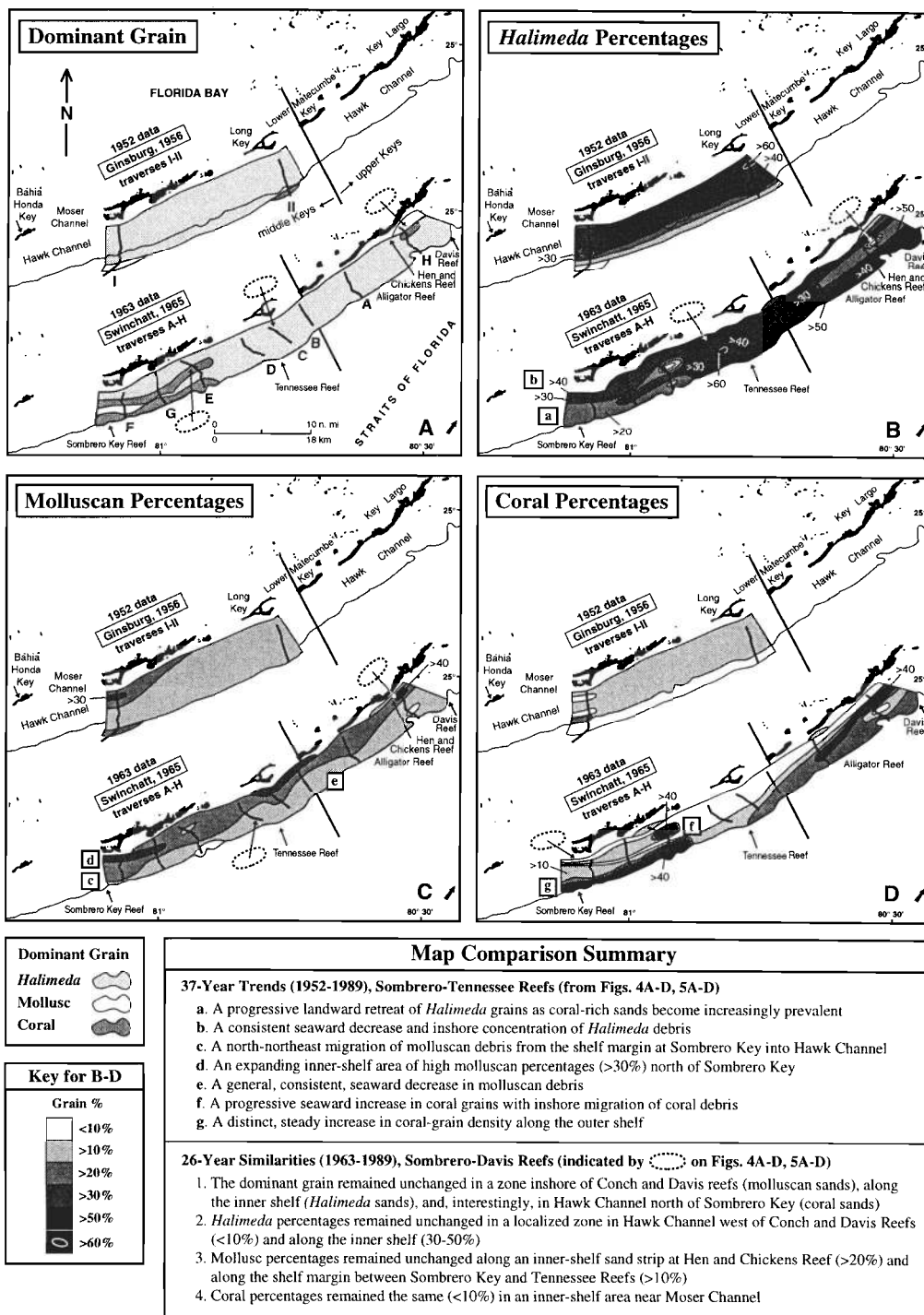


Figure 5. (A-D) Contour maps showing spatial and temporal trends in coral-grain percentages between Sombrero Key and Tennessee Reefs (~18 km, GINSBURG, 1956) and Sombrero Key and Davis Reefs (~35 km, SWINCHATT, 1965) in the middle Keys over periods of 37 and 26 years, respectively (compare with Fig. 4A-D). The 1952 maps, based on sparse samples (16 sites along two traverses), cannot be compared closely to the later maps but are useful for a sense of sediment composition in the area in 1952. The 1963 maps, more detailed and covering a broader area, are more comparable to those for 1989.

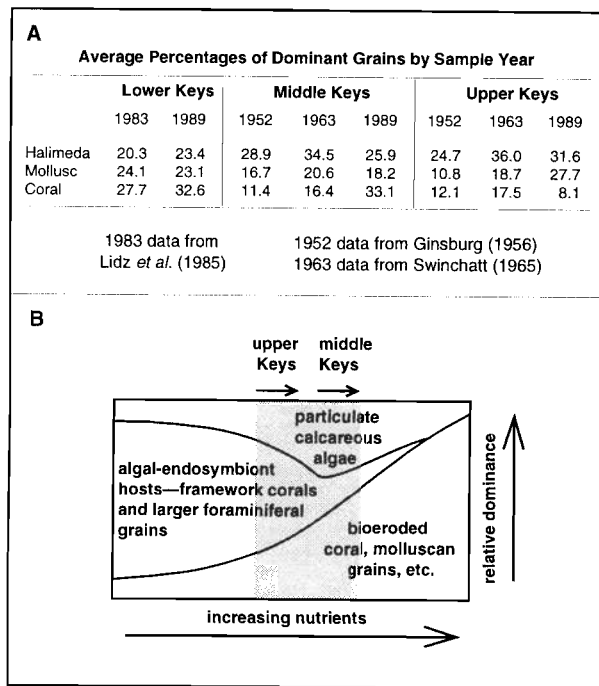


Figure 6. (A) Summary of all available petrologic data averaged by sample year for upper, middle, and lower Keys. Note data sources. (B) Conceptual model predicting effects of nutrification on biogenic sedimentary components in a reef ecosystem (adapted from HALLOCK *et al.*, 1988). Shaded area represents present conditions in the Florida Keys. Arrows show postulated shifts in upper and middle Keys bioerosional components (*i.e.*, changes in benthic communities) between 1963 and 1989.

the amount of skeletal material that is exposed and accessible to bioeroders. Although there is no reason to suspect that the area of fossil-coral hardbottom has varied significantly over the time frame studied, the area of freshly dead coral has undoubtedly increased. Historically and as recently as in the 1960s, species of *Acropora* were the principal reef-building corals in Florida (*e.g.*, SHINN, 1963; SHINN *et al.*, 1981) and the Caribbean (ARONSON and PRECHT, 1997). In the 1970s and 1980s, however, acroporids throughout these regions were decimated by white-band disease (GLADFELTER, 1982). At approximately the same time, black-band disease became common (RÜTZLER *et al.*, 1983), killing or damaging massive species such as *Montastrea annularis* and *Colpophylia natans*. Even though individual Florida reefs appear to have quite individual characteristics (ARONSON and MURDOCH, 1997), the loss of acroporids and other corals has likely affected most reefs to some degree. A hypothesis of LIDZ *et al.* (1985), that coral-sand production should accelerate in direct proportion to the amount of weakened or dead-coral substrate available, may in part be true. However, factors other than the quantity of accessible fossil- and dead-coral substrate must be considered to explain why proportions of coral grains have decreased in the upper Keys and increased in the middle Keys (Figure 6A). Activities of bioeroding species are also likely mechanisms.

Bioeroders and Nutrients

Three major categories of bioeroding organisms exist whose populations, activities, and food sources must be considered in estimating relative rates of bioerosion. Herbivores such as *Diadema antillarum* remove scraps of dead coral as they feed upon attached algae. GLYNN (1988) estimated that sea urchins have bioeroded eastern tropical Pacific reefs, whose corals were mostly killed by the 1983 El Niño/Southern Oscillation Event, at rates of 3–36 kg CaCO₃ m⁻² yr⁻¹. Various species of fish bioerode reefs by biting off bits of either live coral or attached algae and excreting coral sand (*e.g.*, SCOFFIN *et al.*, 1980; GLYNN, 1997). The third group of bioeroders consists of numerous boring organisms, such as endolithic algae, fungi, barnacles, lithophagid bivalves and other molluscs, and boring sponges (HUDSON, 1977; GLYNN, 1997). NEUMANN (1966) estimated bioerosion rates by clionid sponges during infestation at 23 kg CaCO₃ m⁻² yr⁻¹, though long-term rates are probably on the order of 7 kg CaCO₃ m⁻² yr⁻¹ (RÜTZLER, 1975). The high bioerosion rates of the Panama and Galapagos reefs studied by GLYNN (1988) were augmented by internal excavation by clionid sponges and lithophagid bivalves at rates of about 7 kg CaCO₃ m⁻² yr⁻¹. An important comparison is that production rates of even thriving coral reefs seldom exceed 10 kg CaCO₃ m⁻² yr⁻¹ (*e.g.*, KINSEY, 1985).

In 1983 in Florida and throughout the Caribbean, an unknown plague decimated populations of *Diadema antillarum* (LESSIOS *et al.*, 1984; LESSIOS, 1988). They have not reappeared. Without this important check to maintain biotic equilibrium, the balance has swung to favor algae and grazing molluscs (CARPENTER, 1985). In Jamaica, the combination of loss of *Diadema* (HUGHES, 1994), destructive hurricanes, and anthropogenic nutrification (LAPOINTE *et al.*, 1997) has resulted in profound changes in hardbottom communities. In the early 1980s, Jamaican communities consisted of more than 50% live-coral cover; in the early 1990s, they exhibited 90% algal cover and less than 5% live-coral cover (HUGHES, 1994). Similar extreme changes have occurred in hardbottom communities of the upper Keys, where percentages of live-coral cover had dropped into the single digits in quadrats surveyed between 1996 and 1997 (EPA, 1998). Other examples include changing conditions at Carysfort Reef, where branching framework-building acroporids that were thriving in the 1960s are now dead (E.A. SHINN, *pers. commun.*, 1998), and at Grecian Rocks, where both branching and head corals have been replaced by soft corals and algae (Figure 7A, B). In cases where algal overgrowth of reefs has occurred but bioerosional rates by fish and boring organisms have not increased significantly, the proportions of particulate *Halimeda* and grazing molluscs should increase relative to coral grains. Stable bioerosional rates may explain the increase in *Halimeda* and mollusc grains observed in our data from the upper Keys sediments. Unfortunately, this scenario does not explain why proportions of coral grains are now so much higher in the middle and lower Keys reefs, and why, at least in the middle Keys, proportions of coral grains have increased sharply since the 1950s.

Numerous researchers have concluded that rates of bio-

1963 (Swinchatt, 1965) 1989 This Study	Year 1963			Year 1989		
	<i>Halimeda</i> debris	Mollusc debris	Coral debris	<i>Halimeda</i> debris	Mollusc debris	Coral debris
UpKeys/Open Shelf Average	26%	26%	14%	27%	26%	6%
StanDev	12%	11%	15%	15%	7%	6%
Number	8	8	8	22	22	22
UpKeys/Shelf Margin Average	49%	11%	24%	35%*	29%*	10%*
StanDev	7%	2%	8%	11%	8%	7%
Number	7	7	7	36	36	36
MidKeys/Open Shelf Average	42%	23%	8%	31%*	22%	22%*
StanDev	8%	6%	3%	13%	7%	16%
Number	12	12	12	20	20	20
MidKeys/Shelf Margin Average	41%	13%	20%	18%**	13%	49%**
StanDev	8%	2%	3%	3%	4%	11%
Number	4	4	4	14	14	14
LowKeys/Open Shelf Average	32%	24%	16%	28%	26%	24%
StanDev	13%	6%	14%	13%	4%	13%
Number	13	13	13	24	24	24
LowKeys/Shelf Margin Average	26%	16%	28%	19%	20%	42%*
StanDev	8%	5%	13%	6%	5%	8%
Number	9	9	9	22	22	22

Table 1. Comparison of means and standard deviations of Swinchatt's (1965) petrographic data from samples collected in 1963 with analogous data from samples collected in 1989. Changes of >10 percentage points are asterisked (*); changes of >20 percentage points are noted by double asterisk (**). Statistical analyses show same results as percentages of point-counted grains. Open shelf = samples landward of Hawk Channel; shelf margin = samples seaward of Hawk Channel.

Analysis of Variance Results between 1963 and 1989 Data Sets							
Source	Degrees of Freedom	<i>Halimeda</i> F Value	<i>Halimeda</i> Probability	Mollusc F Value	Mollusc Probability	Coral F Value	Coral Probability
Year	1	18.2	<0.01	14.3	<0.01	6.1	0.015
Location	2	9.8	<0.01	17.0	<0.01	70.2	<0.01
Year*Location	2	3.1	0.049	10.3	<0.01	30.3	<0.01
Distance	1	0.02	0.67	33.2	<0.01	74.9	<0.01
Year*Distance	1	3.2	0.075	16.0	<0.01	0.1	0.76
Location*Distance	2	19.1	<0.01	8.0	<0.01	6.8	<0.01
Year*Location*Distance	2	0.57	0.57	6.8	<0.01	1.8	0.17

Table 2. Results of multifactor analysis of variance (general linear model using arcsine transformation of proportional data presented in Table 1). Differences between years and location (lower, middle, or upper Keys) are significant ($P < 0.05$) in all cases; differences between locations (open shelf versus shelf margin) are significant for molluscan and coral debris but not for *Halimeda* grains and thus show same results as percentages of point-counted grains.

rosion are a function of abundances of bioeroders and of their food supplies (e.g., GLYNN, 1997). Certainly, bioerosional rates of the eastern tropical Pacific reefs (GLYNN, 1988) were accelerated by increased recruitment of urchins to an algae-dominant environment that evolved after widespread coral mortality. HIGHSMITH (1980) noted that abundances of lithophagid bivalves in coral heads in museum collections corresponded to the amount of plankton productivity in the region from which they were collected. HALLOCK (1988) and

EDINGER and RISK (1994) derived similar conclusions regarding the correlation between food supply and abundances of plankton-feeding boring organisms.

Is it possible that the increase in proportions of coral grains in middle Keys sands between 1963 and 1989 might be a function of both increased dead-coral substrate and higher rates of bioerosion? Boring bivalves and sponges should benefit from plankton-enriched water carried offshore from the vicinity of inhabited keys and Florida Bay.

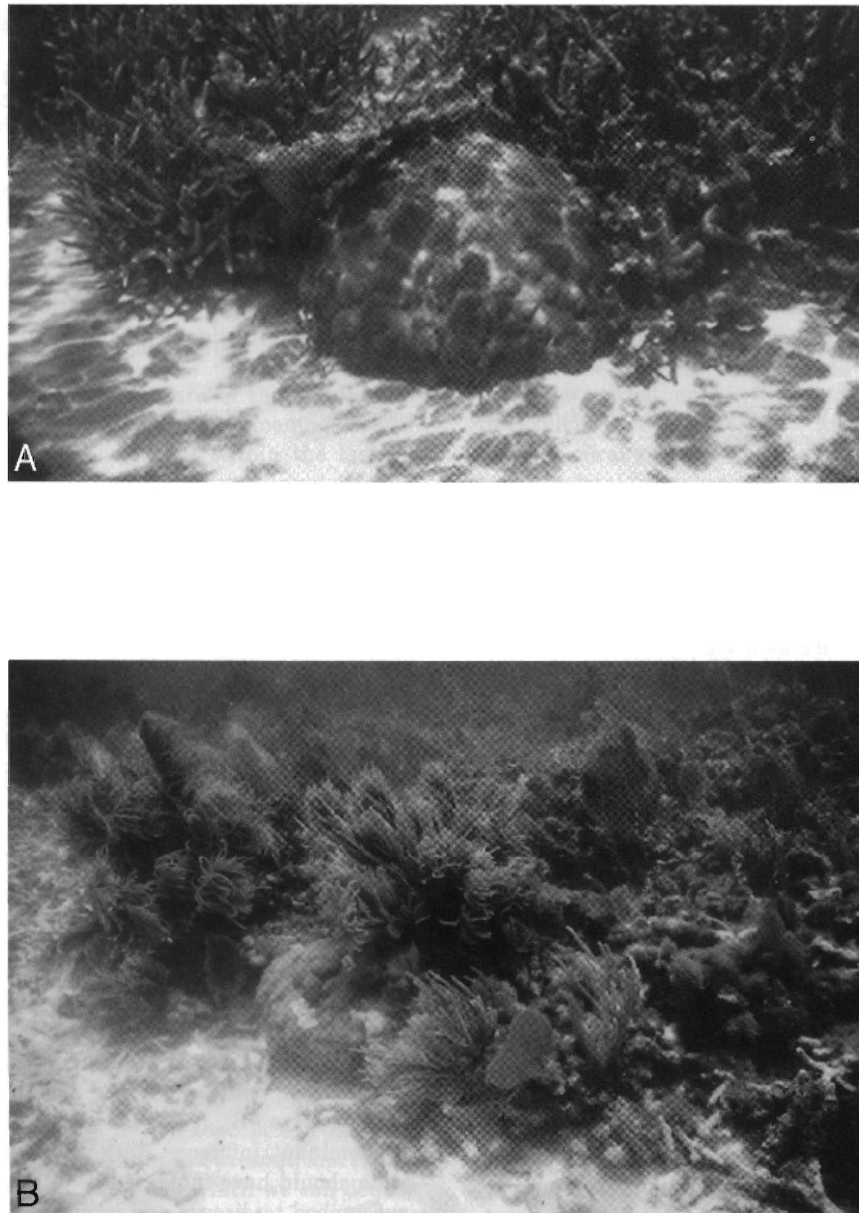


Figure 7. (A) A healthy stand of corals at Grecian Rocks in the upper Keys in 1971. Head coral (*Montastrea annularis*) and blade of elkhorn coral (*Acropora palmata*) are surrounded by sticks of staghorn coral (*A. cervicornis*). This particular stand of corals has been monitored and photographed since 1965. (B) Same stand of corals in 1998. Note patches of white-band disease on head coral, rubble of dead elkhorn at immediate left, and broken sticks of dead staghorn. Sea whips, sea fans, and algae have replaced the coral-framework builders. Photographs courtesy of E. A. Shinn.

There is evidence for nutrient infiltration to nearshore waters (LAPOINTE *et al.*, 1990; SHINN *et al.*, 1993, 1994). SZMANT and FORRESTER (1996) have reported plumes of discolored Florida Bay water flowing seaward to offshore reefs through the passes on either side of Long Key. The discolored water contains elevated levels of nutrients and chlorophyll. Aerial photographs exist that show similar brown plumes drifting offshore from the sewage outfall off Key West (B.E. LAPOINTE, *pers. commun.*, 1999). It would

appear quite likely, therefore, that the high coral-grain percentages in the middle Keys are influenced by geographic location relative to tidal passes and thus by direct communication between deleterious nearshore and bay waters and the offshore reefs. These findings establish the link between tidal passes, declining reefs, and coral-dominant sands proposed by LIDZ *et al.* (1985). In the Keys, declining or senescent reefs and the highest coral-grain percentages occur together and are located opposite tidal passes.

Environmental Conditions	Effects	Authors
Nutrient-poor water Nutrient-enriched water Increased nutrient supply	Reef ecosystems flourish Reef ecosystems succumb Subtropical/tropical benthic communities change from coral/algae-dominant to algae/sponge-dominant	MARGALEF, 1968; FALKOWSKI et al., 1993 SMITH et al., 1981; HALLOCK and SCHLAGER, 1986 BIRKELAND, 1987, 1997; TRIFFLEMAN et al., 1992
Annual terrestrial nitrogen flux into aquatic systems has increased Annual fixed-nitrogen flux to terrestrial ecosystems is double pre-anthropogenic levels		BARBER, 1988 VITOUSEK et al., 1997a,b
Saharan dust, the source of iron- and clay-rich soils on isolated Caribbean islands, is hypothesized to be the common forcing factor Oceanic N-fixation is iron-regulated, whether iron source is eolian, tectonic, sedimentary, or anthropogenic	Episodic benthic algal blooms and cyanobacterial infestations	SHINN, 1988; RAWLS et al., 1988; HAYES et al., 1988 BARBER, 1988
Saharan dust is believed to be the effective agent for infiltration of <i>Aspergillus</i> (soil fungus) spores in Caribbean and Florida reefs One billion tons of air-borne Saharan dust are carried into the Caribbean each year	Sea fans infected with <i>Aspergillus</i>	PROSPERO and NEES, 1986; MUHS et al., 1990; SMITH et al., 1996 D'ALMEIDA, 1986

Table 3. Variable nutrification conditions and their documented effects on corals in general.

The Sedimentary Signature as a Geoinicator and Its Implications

The shelf-wide sedimentary signature can be examined in the context of a model (HALLOCK *et al.*, 1988) that predicts changes in benthic community structure with increasing nutrient flux into the environment. Although we recognize the unresolved controversy over whether nutrification is a factor in the decline of Florida Keys reefs, there are well-known facts (Table 3) regarding the effects of nutrification on corals in general. The natural variety of nutrient sources to Florida's reefs ranges from the Florida Current and African dust to the Everglades, Florida and Biscayne Bays, and groundwater flow (*e.g.*, HALLOCK *et al.*, 1993). Human activities have contributed nutrients to these natural sources and have also added purely anthropogenic sources, such as air pollution and farm fertilizers (*e.g.*, FANNING, 1989; BRYANT *et al.*, 1998), offshore sewage outfalls, and direct delivery that injects detergents and both human and boat effluents into the system. Although this discussion is not intended to prove or disprove the nutrification argument, we must consider it unrealistic to assume that coastal waters of Florida are immune to the biological consequences of increasing anthropogenic-nutrient influx. Our point is to show the striking relation between what the petrologic data indicate and what the nutrient-flux model (HALLOCK *et al.*, 1988) predicts relative to the sedimentary record.

Considering the natural variety of nutrient sources, Florida's reef communities were never at the very low-nutrient end of the gradient (BIRKELAND, 1987, 1997; HALLOCK, 1988). For example, even prior to the 1960s and relative to populations found on many Indo-Pacific reefs (HALLOCK, 1981; HALLOCK, 1988), larger foraminifera were never dominant sediment constituents in Florida (ROSE and LIDZ, 1977). The nutrient-flux model, as adapted to constituent sedimentary grains (Figure 6B), predicts that under very low-nutrient flux (*i.e.*, "oceanic" conditions of BIRKELAND, 1997),

shells of larger foraminifera and grains of *Halimeda* should dominate sediments because rates of reef-framework accretion would be high and framework degradation would be minimal. As nutrients increase in regions closer to continental influence (*e.g.*, BIRKELAND, 1997), such as the Florida Keys, the larger-foraminiferal and reef-framework component should decline, while contributions by algae and grazing gastropods should increase. The coral-grain component should also increase as food supplies for grazing urchins and boring bioeroders increase.

Examining the sedimentary record of the Keys in the context of the adapted nutrient-flux model reveals both insights and unknowns. Sediment patterns in the 1950s and 1960s indicate conditions near the mid-range of the model, with those in the upper Keys falling within the left part of the shaded area and those in the middle Keys somewhat to the right (Figure 6B). If nutrification had been a consistent and predominant influence Keys-wide, then coral grains Keys-wide should have increased in relative abundance as corals succumbed to disease and provided more substrate for bioerosion. However, the die-off of *Diadema* urchins in 1983 interjected an additional complicating factor. The relative decline in coral grains in the upper Keys indicates that either rates of bioerosion have declined or the coral fraction has been diluted by high productivity and rapid turnover of *Halimeda* and molluscan populations, possibly both. The decline in coral grains supports observations by SZMANT and FORRESTER (1996) that nutrient levels in upper Keys waters are not elevated. Anthropogenic-nutrient flux to upper Keys reefs between the 1960s and late 1980s was apparently insufficient to stimulate an increase in coral bioerosion in the absence of *Diadema*.

On the other hand, the coral-grain component increased substantially in the middle Keys, indicating that rates of bioerosion of dead coral by other members of the benthic community more than compensated for both the loss of *Diadema*

and the increased habitats for *Halimeda* and grazing molluscs. In the middle Keys, wide tidal passes allow Florida Bay and nearshore waters to reach and impact the outer reefs on a regular basis (e.g., SZMANT and FORRESTER, 1996; ARONSON and MURDOCH, 1997). Sediments there were predominantly of *Halimeda* origin in 1952 and 1963 (Figure 5A). By 1989, the dominant grain had become coral (Fig. 4A). Whereas plankton- and nutrient-enriched bay and inshore waters have probably provided additional food for filter-feeding bivalve and sponge bioeroders, these waters have also caused stressed conditions for coral survival. Those corals compromised or killed by the cold fronts of 1970 and 1977, and by diseases in the 1980s, have clearly supplied increased substrate for attack.

Judging by the bioerosional signature in the middle and lower Keys sediments relative to well-documented loss of reef-framework builders in those areas within the last 40 years, comparative abundances of biogenic grains appear to be excellent geoindicators of reef health. In this case, the increasing proportions of coral grains attest to deteriorating reef health. Sediments of Jamaican reefs (PRECHT and ARONSON, 1997) and along the flanks of Channel Cay on the Belizean Barrier Reef (ARONSON and PRECHT, 1997) contain similar evidence of widespread coral mortality. The Belizean record shows a biotic transition from ~70% staghorn coverage (*Acropora cervicornis*) in the late 1980s, and as far back as at least the past 3,800 years, to 0% staghorn in 1995 and an opportunistic ~56% coverage by species of the lettuce coral *Agaricia*. White-band disease had killed the staghorn that had survived for thousands of years. Even though we may not understand precisely which factors (abiotic, anthropogenic, or both) are responsible for changing the reef-system environment, we cannot deny that conditions have declined in recent years. Any such change in its environment and consequently in its biota is preserved in ecosystem sands. This most recent change will be as well.

The fact that so much about a reef ecosystem can be observed in the sedimentary signature has impressive implications. As a reliable geoindicator, the sedimentary record provides the capacity required by the concept of ecosystem sustainability to assess and monitor past, present, and future changes in community structure, from which we can deduce trends in health of the biota and thus that of the ecosystem as a whole. Comparative sedimentary petrology can be quite an effective tool for ecologists, sedimentologists, and Sanctuary managers and policy-makers to evaluate effects of physical and chemical changes in the reef environment and the effectiveness of efforts to promote its sustainability. Unfortunately, effects of natural forces, such as cold-temperature outbreaks or sedimentation due to coastal erosion or rising sea level, will limit the degree to which long-term sustainability can be achieved.

Proposed Petrologic Criteria for Quantifying Reef Vitality

No method yet exists to quantify reef vitality. One goal of this study was to provide a technique based on the sedimentary record. This study shows that in Florida, reef health (*i.e.*,

community structure) and constituent grains in surrounding sediment are complementary and vary with respect to local morphology. The least healthy reefs and the highest percentages of bioeroded coral grains occur together, and both are present off the widest tidal passes (Figure 4E, F). This basic knowledge and the site-by-site coral-grain percentages as they existed in 1989 in areas of divergent reef vitality provide an unbiased approach to quantifying reef health. (1) Where coral substrate is present yet coral grains form <10% of constituent components, reefs are healthiest. (2) Where coral grains comprise 10% to 29% of the sediment, reefs are declining. (3) Where coral grains constitute >30% of the sand, reef framework is rapidly deteriorating. Where coral-grain percentages are high, ample coral substrate is available for breakdown, whether it is fossil coral, recently killed coral, or the skeleton beneath live coral. In the middle and lower Keys in 1989, coral grains exceeded 50% and in some places 60% of all skeletal fragments along the margin (Figure 4F).

The 1989 sedimentologic data set provides a general Keys-wide petrologic database for monitoring broad changes in dominant biota and *post-mortem* sediment components through future comparative studies. Changes in the sedimentary record reflect biotic changes observed in the field and thus can be applied as a geoindicator to monitor changing reef communities. This database will also serve for contrast and integration with results of diver-oriented, live-coral quantification studies in progress by others (W.C. Jaap, *pers. commun.*, 1999).

CONCLUSIONS

This study provides the first shelf-wide petrologic record for Florida Keys surface sediments, as they existed in 1989. Dominant grains in upper Keys sands were derived from *Halimeda* plates or mollusc shells, with generally a <10% particulate-coral component. In the middle and lower Keys, the two most prevalent grain types demarcated the inner and outer shelf. Fragments of *Halimeda*, dominant nearshore, commonly comprised 30% to 40% of the sands. Coral debris, dominant offshore, usually formed 30% to 50% of the sands but attained proportions exceeding 60% at the margin.

Comparison of percentages of these grains in 1989 with analogous data collected in 1963 shows significant increases in upper Keys molluscan and middle Keys coral components and a relative decrease in the upper Keys coral fraction. The decrease in upper Keys coral grains suggests that, despite widespread coral loss to white-band, black-band, and other diseases, the 1983 disappearance of *Diadema antillarum* may have reduced the rate of coral degradation at approximately the same time that habitats for *Halimeda* and grazing gastropods increased. The sharp rise in the middle Keys coral component indicates that increased bioerosional rates by other organisms more than compensated for both the loss of *Diadema* and the habitat expansion for *Halimeda* and molluscs. In addition, the increased rates may reflect increased exposure of coral substrate (coral mortality) caused by severe cold fronts in the 1970s and rising occurrences of diseases in the 1980s. The changes observed in sediment constituents are consistent with a published model that predicts consequences

of increasing nutrification on the benthic community structure. The trends observed in the changing sedimentary record Keys-wide are consistent with field observations of a widespread decline in coral reefs and an ecosystem in jeopardy.

In Florida, coral-grain percentages are related to location (geomorphology) and rates of bioerosion. In general, coral percentages are highest off tidal passes, where reefs are exposed to nutrient-enriched waters, amounts of dead-coral substrate are greatest, and hence rates of bioerosion by plankton-feeding boring organisms are highest. Percentages are lowest off the upper Keys, where reefs are protected from such waters and therefore breakdown by borers is more limited. However, the obvious proliferation of algae and herbivorous molluscs in the upper Keys is a sign that the ecosystem there is also nonetheless changing. These patterns imply that the sedimentary signature in the Florida Keys involves interplay between physical and biological processes and landforms. The results are evidence that the composition of reef sediments is a reliable geoinicator of reef health and can be used to assess and monitor past, present, and future conditions and trends in the changing ecosystem.

ACKNOWLEDGMENTS

The senior author gratefully acknowledges the late Captain Roy Gaensslen, who skillfully navigated the *R/V Captain's Lady* around head corals in shallow waters during sampling. Jack L. Kindinger, Robert Montague, and Eugene A. Shinn assisted in the field; E.A. Shinn also provided anecdotal background information relating to coral-reef conditions over time. Robert G. Muller assisted in statistical analyses. The authors thank Robert N. Ginsburg and Alina M. Szmant for constructive comments and suggestions on an early version of the manuscript. Stephen P. Smith prepared Figure 1 and the composites for Figures 4 and 5.

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Appendix 1. Continued (A-D) Tabulation of 1989 data collected at 142 sites along 33 traverses in the upper (samples #1-60), middle (#61-95), and lower Keys (#96-142) showing general bottom description (not intended to be quantitative or all inclusive) by site, total grain count per thin section, and estimated percentage for identifiable grains. Bold lines separate data by area (upper, middle, and lower Keys). Dots next to grain counts indicate those samples counted twice for verification of low percentages. Boxed sample in upper Keys group indicate very fine-grained sediment. Lat./Long. Locations of sample sites (column 2) are true to latitude and longitude as converted from Loran C TDs. General sample site locations shown on index maps (Figs. 1, 2).

Transect and Sample Nos.	Lat/ Long.	Depth (m), Location, Bottom Description	Grain Count	Estimated percent constituent particles									A
				<i>Halimeda</i>	Mollusc	Coral	Echinoid	Bryozoa/ Red Algae	Benthic Forams	Planktic Forams	Pellets	Quartz	
1	89-1	25.37.23 80.07.07	279	26.5±5.3	19.4±4.7	5.7±2.8	2.2±1.8	5.7±2.8	2.9±2.0	0.3±0.7	7.9±3.2	29.4±5.5	
	89-2	25.37.16 80.05.45	245	32.6±6.0	31.4±5.9	8.2±3.5	5.7±3.0	13.9±4.4	4.1±2.5	---	---	4.1±2.5	
	89-3	25.37.10 80.05.19	242	43.4±6.4	30.2±5.9	9.5±3.8	2.5±2.0	9.0±3.7	5.4±2.9	---	---	---	
	89-4	25.36.29 80.04.59	229	43.7±6.6	32.3±6.2	3.5±2.4	6.6±3.3	10.0±4.0	2.6±2.1	---	---	1.3±1.5	
	89-5	25.36.03 80.05.12	234	42.7±6.5	33.3±6.2	4.3±2.7	0.4±0.8	17.2±4.9	1.3±1.5	0.4±0.8	---	0.4±0.8	
2	89-6	25.34.28 80.05.25	232	32.7±6.2	30.6±6.1	3.9±2.5	3.0±2.2	21.6±5.4	4.3±2.7	---	---	3.9±2.5	
	89-7	25.34.17 80.05.52	306	34.7±5.4	27.8±5.1	4.9±2.5	2.9±1.9	11.1±3.6	4.6±2.4	0.3±0.6	13.4±3.9	0.3±0.6	
	89-8	25.34.07 80.06.38											
	89-9	25.34.13 80.07.26	248	43.2±6.3	18.2±4.9	1.6±1.6	1.2±1.4	4.0±2.5	2.4±1.9	---	---	29.4±5.8	
	89-10	25.34.02 80.08.38	249	42.2±6.3	27.3±5.7	0.8±1.1	7.6±3.4	2.0±1.8	8.4±3.5	0.4±0.8	---	11.3±4.0	
3	89-11	25.33.27 80.05.38											
	89-12	25.31.02 80.05.48	246	33.7±6.0	35.8±6.1	4.9±2.8	5.7±3.0	17.1±4.8	2.0±1.8	---	---	0.8±1.1	
4	89-13	25.27.46 80.06.28	239	38.9±6.3	26.8±5.7	10.0±3.9	2.5±2.0	16.8±4.8	5.0±2.8	---	---	---	
	89-14	25.27.38 80.06.49	273	25.6±5.3	40.7±5.9	3.7±2.3	6.2±2.9	15.3±4.4	8.1±3.3	---	---	0.4±0.8	
	89-15	25.27.52 80.07.26	217	36.9±6.6	28.6±6.1	1.8±1.8	9.7±4.0	9.7±4.0	8.7±3.8	---	---	4.6±2.8	
5	89-16	25.26.01 80.06.55	244	45.5±6.4	26.2±5.6	6.6±3.2	1.2±1.4	16.8±4.8	3.7±2.4	---	---	---	
	89-17	25.26.08 80.07.03	274	26.3±5.3	28.5±5.5	15.7±4.4	5.1±2.7	10.9±3.8	13.1±4.1	---	---	0.4±0.8	
	89-18	25.25.53 80.07.30	265	36.2±5.9	37.0±5.9	4.1±2.4	9.1±3.5	5.3±2.8	6.0±2.9	2.3±1.8	---	0.5±1.0	
	89-19	25.25.54 80.08.10	287	39.7±5.8	18.8±4.6	5.2±2.6	12.5±3.9	5.0±2.6	16.7±4.4	1.7±1.5	---	0.4±0.8	
	89-20	25.25.58 80.09.00	256	43.3±6.2	23.8±5.3	7.0±3.2	6.6±3.1	3.9±2.4	15.2±4.5	0.2±0.6	---	---	
6	89-21	25.22.18 80.08.42	273	26.7±5.4	33.7±5.7	13.9±4.2	3.7±2.3	18.7±4.7	3.3±2.2	---	---	---	
	89-22	25.22.24 80.09.07	268	23.9±5.2	31.0±5.7	4.1±2.4	14.9±4.4	8.9±3.5	16.8±4.6	1.1±1.3	---	---	
	89-23	25.22.48 80.10.24	266	27.1±5.5	29.3±5.6	1.5±1.5	6.8±3.1	10.9±3.8	23.3±5.2	1.1±1.3	---	---	
	89-24	25.19.42 80.12.15	272	27.9±5.4	29.0±5.5	0.7±1.0	13.2±4.1	7.1±3.1	20.6±4.9	1.5±1.5	---	---	
7	89-25	25.18.45 80.11.05	244	33.2±6.0	32.4±6.0	2.9±2.2	5.3±2.9	4.5±2.7	11.1±4.0	1.6±1.6	8.2±3.5	0.8±1.1	
	89-26	25.18.03 80.10.19	213	23.0±5.8	20.1±5.5	3.5±2.6	3.3±2.4	0.5±1.0	6.1±3.3	0.5±1.0	41.3±6.7	1.4±1.6	
	89-27	25.17.21 80.10.06	265	34.0±5.8	37.4±5.9	6.4±3.0	1.1±1.3	9.8±3.7	4.9±2.7	0.4±0.8	6.0±2.9	---	
	89-28	25.17.07 80.10.43	277	27.4±5.4	40.8±5.9	8.3±3.3	2.2±1.8	8.3±3.3	8.3±3.3	1.1±1.3	3.6±2.2	---	
8	89-29	25.13.30 80.12.42	255	46.3±6.3	23.1±5.3	6.7±3.1	1.6±1.6	18.4±4.9	3.9±2.4	---	---	---	
	89-30	25.14.31 80.13.23	254	43.3±6.2	36.2±6.0	1.6±1.6	2.4±1.9	11.0±3.9	5.5±2.9	---	---	---	
	89-31	25.14.43 80.13.52	274	47.8±6.0	27.0±5.4	8.0±3.3	2.6±1.9	2.9±2.0	5.5±2.8	---	6.2±2.9	---	
	89-32	25.15.01 80.14.12	276	5.4±2.7	37.0±5.8	0.7±1.0	17.8±4.6	6.9±3.1	30.4±5.5	1.4±1.4	---	0.4±0.8	
	89-33	25.14.59 80.12.07	253	16.6±4.7	32.8±5.9	0.4±0.8	10.7±3.9	10.2±3.8	27.3±5.6	2.0±1.8	---	---	
9	89-34	25.09.45 80.17.39	218	13.8±4.7	15.6±4.9	2.8±2.2	2.8±2.2	4.6±2.8	4.1±2.7	---	60.0±6.6	0.5±1.0	
	89-35	25.09.45 80.17.08	275	25.5±5.3	36.4±5.8	14.9±4.3	2.9±2.0	7.6±3.2	9.8±3.6	---	2.9±2.0	---	
	89-36	25.08.46 80.15.51	273	22.7±5.1	21.6±5.0	18.3±4.7	1.8±1.6	17.6±4.6	16.5±4.5	1.5±1.5	---	---	
10	89-37	25.04.39 80.18.54	265	30.2±5.6	38.5±6.0	11.3±3.9	1.1±1.3	13.2±4.2	5.7±2.8	---	---	---	
	89-38	25.04.48 80.19.21	278	66.2±5.7	14.0±4.2	4.0±2.4	5.4±2.7	4.3±2.4	4.7±2.5	1.4±1.4	---	---	
	89-39	25.05.52 80.20.22	243	7.4±3.4	22.6±5.4	4.5±2.7	4.1±2.5	3.3±2.3	4.1±2.5	---	54.0±6.4	---	
	89-40	25.05.59 80.20.30	268	32.8±5.7	23.5±5.2	4.5±2.5	10.1±3.7	7.1±3.1	20.5±4.9	1.5±1.5	---	---	

Transect and Sample Nos.	Lat./ Long.	Depth (m), Location, Bottom Description	Grain Count	Estimated percent constituent particles								B	
				<i>Halimeda</i>	Mollusc	Coral	Echinoid	Bryozoa/ Red Algae	Benthic Forams	Planktic Forams	Pellets		
89-41 10	25.06.12 80.21.13	6.1, west edge Hawk Channel, dense grass, fine sands	271	54.2±6.1	21.0±5.0	0.4±0.8	3.4±2.2	3.7±2.3	17.3±4.6	---	---	---	
89-42 11	25.02.29 80.25.49	4.9, Hawk Channel near Molasses Reef, <i>Thalassia</i> & <i>Syringodium</i>	256	48.8±6.3	18.8±4.9	12.5±4.1	5.0±2.7	2.3±1.9	10.9±3.9	2.3±1.9	1.7±1.6	---	
89-43	25.01.32 80.24.48	8.2, Hawk Channel, grassy, fine sand w/ <i>Halimeda</i>	243	22.2±5.3	29.6±5.9	3.3±2.3	6.6±3.2	5.4±2.9	21.8±5.3	4.1±2.5	7.0±3.3	---	
89-44	25.01.07 80.23.55	6.4, backreef, sand halo around patch reef	262	37.4±6.0	34.7±5.9	7.3±3.2	1.6±1.6	3.4±2.2	5.7±2.9	---	9.9±3.7	---	
89-45	25.00.30 80.23.16	6.1, inside Molasses Reef, sand w/ sporadic hardbottom areas	245	36.7±6.2	32.7±6.0	7.8±3.4	2.4±2.0	13.5±4.4	3.7±2.4	---	3.2±2.3	---	
89-46 12	24.57.06 80.27.53	5.5, south end Conch Reef, very coarse, pristine <i>Halimeda</i> sand	253*	51.8±6.3	10.7±3.9	17.7±4.8	3.2±2.2	10.3±3.8	5.9±3.0	0.4±0.8	---	---	
89-47	24.57.11 80.28.16	4.9, backreef, sand pocket in rocky bottom	223	25.1±5.8	35.0±6.4	3.6±2.5	5.8±3.1	17.1±5.0	7.6±3.6	---	5.8±3.1	---	
89-48	24.57.42 80.29.06	5.5, backreef, uniformly spread sparse grass, pelletal sand	278	16.5±4.5	27.7±5.4	9.4±3.5	5.8±2.8	4.7±2.5	11.5±3.8	0.7±1.0	23.7±5.1	---	
89-49	24.58.18 80.29.25	6.4, Hawk Channel, sparse grass, pelletal sand	247	19.8±5.1	37.3±6.2	4.9±2.8	8.9±3.6	2.4±2.0	8.5±3.6	0.8±1.1	17.4±4.8	---	
89-50	24.58.31 80.30.31	4.6, Hawk Channel, sandier than same position to north (#89-42)	234	19.7±5.2	34.6±6.2	6.4±3.2	4.7±2.8	4.3±2.7	9.8±3.9	---	20.5±5.3	---	
89-51 13	24.55.33 80.30.21	6.1, Davis Reef, inshore Marker 14, sand hole in <i>Thalassia</i>	266	28.6±5.5	35.3±5.9	15.8±4.5	1.5±1.5	16.5±4.6	2.3±1.8	---	---	---	
89-52	24.55.28 80.31.57	6.4, Davis Reef, large sand ripples on bare-rock bottom	255	38.8±6.1	15.7±4.6	27.5±5.6	2.0±1.8	12.1±4.1	3.5±2.3	0.4±0.8	---	---	
89-53	24.55.31 80.32.01	5.2, mid-reef tract, fine pelletal sand w/ grass patches	245	8.2±3.5	19.6±5.1	13.9±4.4	4.9±2.8	4.1±2.5	3.6±2.4	1.6±1.6	44.1±6.3	---	
89-54	24.55.46 80.32.57	6.1, at Marker 40 south of Hen & Chickens Reef, grassy	303	31.4±5.3	21.8±4.7	6.9±2.9	4.9±2.5	3.3±2.1	5.3±2.6	1.0±1.1	25.4±5.0	---	
89-55 14	24.53.25 80.33.53	8.5, ~30 m inside outer-bank reef line, sand	290	28.2±5.3	29.0±5.3	14.5±4.1	2.4±1.8	10.7±3.6	10.0±3.5	0.7±1.0	4.5±2.4	---	
89-56 15	24.51.13 80.37.11	2.7, ~300 m inside Alligator Reef light, sand	236*	14.0±4.5	22.0±5.4	26.3±5.7	2.5±2.0	7.6±3.5	7.2±3.4	0.9±1.2	19.5±5.2	---	
89-57	24.51.39 80.37.52	4.0, backreef, sand	254*	16.9±4.7	25.2±5.5	27.6±5.6	4.7±2.7	6.7±3.1	5.5±2.9	0.8±1.1	12.6±4.2	---	
89-58	24.51.43 80.38.15	5.2, south edge Hawk Channel at Marker 43, pelletal, <i>Syringodium</i>	263	8.3±3.4	20.9±5.0	23.6±5.2	8.0±3.4	2.3±1.9	4.6±2.6	1.1±1.3	31.2±5.7	---	
89-59	24.52.14 80.39.15	4.9, Hawk Channel, dense grass, pelletal sand	254	16.1±4.6	16.9±4.7	11.8±4.1	7.9±3.4	2.8±2.1	5.9±3.0	1.2±1.4	37.4±6.1	---	
89-60	24.52.07 80.40.04	3.7, Hawk Channel, grass, fresh <i>Halimeda</i> sand	251	58.1±6.2	16.3±4.7	8.0±3.4	5.2±2.8	0.8±1.1	6.4±3.1	1.2±1.4	4.0±2.5	---	
89-61 16	24.49.07 80.45.36	4.0, Hawk Channel, fine sand, scattered grass beds	272	32.4±5.7	25.0±5.3	6.6±3.0	8.8±3.4	2.9±2.0	8.1±3.3	0.4±0.8	15.8±4.4	---	
89-62	24.48.09 80.46.11	6.7, Hawk Channel, <i>Thalassia</i> w/ <i>Halimeda</i>	275	37.4±5.8	20.0±4.8	18.2±4.7	4.0±2.4	1.1±1.3	5.4±2.7	2.2±1.8	11.3±3.8	0.4±0.8	
89-63	24.47.04 80.46.32	7.6, Hawk Channel, <i>Thalassia</i> , pelletal sand	278	27.3±5.3	14.4±4.2	16.5±4.5	4.7±2.5	2.2±1.8	9.3±3.5	1.1±1.3	24.5±5.2	---	
89-64	24.45.52 80.46.56	6.7, Hawk Channel, rippled sand	247	10.9±4.0	21.1±5.2	28.3±5.7	7.3±3.3	6.9±3.2	4.9±2.8	0.4±0.8	20.2±5.1	---	
89-65	24.45.21 80.47.09	7.0, inside Tennessee Reef, rippled sand on hardbottom	234	19.2±5.2	17.1±4.9	22.6±5.5	5.6±3.0	8.1±3.6	4.3±2.7	---	23.1±5.5	---	
89-66 17	24.43.42 80.50.23	9.8, backreef southwest of Tennessee Reef, grass	252	25.4±5.5	16.7±4.7	31.7±5.9	4.4±2.6	13.9±4.4	6.3±3.1	0.4±0.8	1.2±1.4	---	
89-67	24.44.19 80.50.37	7.3, backreef, sand	308	13.6±3.9	18.5±4.4	35.1±5.4	6.8±2.9	10.4±3.5	8.1±3.1	---	7.5±3.0	---	
89-68	24.45.23 80.51.09	7.0, Hawk Channel, fine pelletal sand	279*	24.7±5.2	27.6±5.4	10.4±3.7	9.0±3.4	8.6±3.4	6.8±3.0	1.1±1.2	11.1±3.8	0.7±1.0	
89-69	24.46.25 80.51.57	7.3, Hawk Channel, <i>Thalassia</i> & <i>Syringodium</i>	282	40.4±5.8	14.2±4.2	23.0±5.0	5.3±2.7	2.1±1.7	8.2±3.3	1.8±1.6	5.0±2.6	---	
89-70	24.46.57 80.52.03	5.5, Hawk Channel, <i>Halimeda</i> & <i>Thalassia</i> , very fine sand	306*	42.8±5.7	30.4±5.3	6.2±2.8	8.2±3.1	1.6±1.4	10.1±3.4	0.7±1.0	---	---	
89-71 18	24.42.47 81.01.00	4.3, north edge Hawk Channel, <i>Thalassia</i> , coarse sand	247*	53.9±6.3	17.0±4.8	12.9±4.3	5.7±3.0	4.0±2.5	5.7±3.0	0.8±1.1	---	---	
89-72	24.42.23 81.00.53	7.0, north edge Hawk Channel, <i>Thalassia</i> , coarse sand	277*	47.7±6.0	30.7±5.5	10.8±3.7	6.1±2.9	2.9±2.0	1.8±1.6	---	---	---	
89-73	24.41.55 81.00.37	10.1, inner reef tract, <i>Halimeda</i> skeletal sand lobe in trough	250*	47.2±6.3	30.8±5.8	8.8±3.6	5.6±2.9	3.2±2.2	4.4±2.6	---	---	---	
89-74	24.41.12 81.00.25	13.1, Hawk Channel, soft silky very fine sand	265	18.5±4.8	38.1±6.0	3.8±2.3	15.8±4.5	5.7±2.9	13.2±4.2	4.9±2.7	---	---	
89-75	24.40.54 81.00.18	8.2, Hawk Channel, <i>Thalassia</i> & <i>Syringodium</i>	251	17.9±4.8	17.1±4.7	31.5±5.9	8.4±3.5	9.5±3.7	7.6±3.3	2.4±1.9	5.6±2.9	---	
89-76	24.40.24 81.00.13	6.4, backreef, open area of coarse sand	271	14.4±4.3	10.3±3.7	53.1±6.1	2.6±1.9	10.7±3.8	6.3±3.0	0.4±0.8	2.2±1.8	---	
89-77	24.39.54 81.00.06	7.9, backreef, coarse <i>Halimeda</i> sand	276	18.1±4.6	11.2±3.8	55.4±6.0	2.6±1.9	6.9±3.1	5.4±2.7	0.4±0.8	---	---	
89-78 19	24.39.39 81.01.09	7.6, backreef along outer bank, barren, coarse-sand bottom	293	21.5±4.8	15.0±4.2	47.1±5.8	1.7±1.5	7.5±3.1	6.2±2.8	1.0±1.2	---	---	
89-79	24.39.39 81.01.29	8.2, backreef, reefy, very coarse sand	268	22.4±5.1	15.3±4.4	41.4±6.0	5.2±2.7	8.6±3.4	7.1±3.1	---	---	---	
89-80	24.39.18 81.02.33	7.6, backreef, reefy, very coarse sand w/ grass	297	20.5±4.7	8.8±3.3	49.8±5.8	2.7±1.9	12.5±3.8	5.4±2.6	0.3±0.6	---	---	

Appendix 1. Continued

Transect and Sample Nos.	Lat./ Long.	Depth (m), Location, Bottom Description	Grain Count	Estimated percent constituent particles									C
				<i>Halimeda</i>	Mollusc	Coral	Echinoid	Bryozoa/ Red Algae	Benthic Forams	Planktic Forams	Pellets	Quartz	
89-81	24.39.21	8.2, south edge Hawk Channel, coarse reefy sand, no grass	294	15.6±4.2	17.7±4.5	51.0±5.8	3.8±2.2	6.1±2.8	5.8±2.7	---	---	---	
19	81.03.13												
89-82	24.39.12	9.1, south edge Hawk Channel, very coarse sand	290	15.9±4.3	14.8±4.2	55.9±5.8	3.1±2.0	7.2±3.0	3.1±2.0	---	---	---	
	81.03.49												
89-83	24.38.54	7.0, south edge Hawk Channel, sand	310	21.0±4.6	12.6±3.8	49.0±5.7	2.9±1.9	8.7±3.2	5.5±2.6	0.3±0.6	---	---	
	81.04.23												
89-84	24.38.48	6.7, backreef off Moser Channel, very coarse reefy sand	274	17.9±4.6	13.1±4.1	53.6±6.0	1.1±1.3	9.5±3.5	4.4±2.5	0.4±0.8	---	---	
	81.05.00												
89-85	24.38.43	4.6, backreef, very coarse reefy sand	294	15.3±4.2	6.1±2.8	63.3±5.6	2.0±1.6	7.2±3.0	5.8±2.7	0.3±0.6	---	---	
	81.05.41												
89-86	24.38.17	6.4, backreef, reefy sand but w/ soritids (grass nearby?)	291	16.8±4.4	10.7±3.6	55.3±5.8	4.8±2.5	7.2±3.0	4.5±2.4	0.7±1.0	---	---	
	81.06.18												
89-87	24.38.06	3.1, inside Sombbrero light, grass, rocky, sand on top dead reef	342	19.6±4.3	7.9±2.9	61.1±5.3	1.8±1.4	7.3±2.8	2.0±1.5	0.3±0.6	---	---	
	81.06.47												
89-88	24.37.45	9.1, backreef, <i>Halimeda</i> w/ <i>Thalassia</i> , coarse sand	295	22.0±4.8	14.6±4.1	45.4±5.8	2.7±1.9	11.9±3.8	2.4±1.8	1.0±1.2	---	---	
	81.08.06												
89-89	24.37.39	10.1, backreef, reefy rocks, very coarse sand, sparse grass	264	16.3±4.5	12.1±4.0	53.4±6.1	4.2±2.5	7.2±3.2	6.8±3.1	---	---	---	
	81.09.06												
89-90	24.37.12	9.8, backreef, rocky w/ veneer of coarse sand	271	18.1±4.7	16.2±4.5	49.4±6.1	2.6±1.9	7.8±3.3	5.5±2.8	---	---	0.4±0.8	
	81.10.24												
89-91	24.38.00	9.1, Hawk Channel, thick grass bed (all species), muddy sand	332	17.5±4.2	11.8±3.5	41.6±5.4	8.4±3.0	9.3±3.2	9.3±3.2	2.1±1.6	---	---	
	81.10.57												
89-92	24.39.00	11.3, north edge Hawk Channel, <i>Halimeda</i> , grass	282	38.3±5.8	19.2±4.7	22.3±5.0	3.9±2.3	3.2±2.1	10.3±3.6	2.8±2.0	---	---	
	81.11.08												
89-93	24.39.36	9.1, north edge Hawk Channel, fine sand w/ grass	293	31.4±5.4	22.9±4.9	25.3±5.1	10.9±3.6	2.0±1.6	7.5±3.1	---	---	---	
	81.11.21												
89-94	24.40.27	5.8, Moser Channel seaward of 7-mile bridge, <i>Halimeda</i>	301	46.8±5.8	30.6±5.3	7.3±3.0	8.6±3.2	3.7±2.2	3.0±2.0	---	---	---	
	81.11.36												
89-95	24.36.37	9.1, north edge Hawk Channel, grass, fine sand, coarse grains	275	37.1±5.8	25.8±5.3	10.5±3.7	12.0±3.9	2.6±1.9	10.9±3.8	1.1±1.3	---	---	
	81.14.54												
21													
89-96	24.37.17	8.8, north edge Hawk Channel, <i>Thalassia</i> & <i>Syringodium</i>	288	49.7±5.9	23.3±5.0	15.3±4.2	3.4±2.1	1.7±1.5	5.9±2.8	0.7±1.0	---	---	
	81.20.41												
89-97	24.36.30	10.4, Hawk Channel, v. fine sand, <i>Syringodium</i> , no <i>Thalassia</i>	263	28.9±5.6	25.1±5.3	11.4±3.9	9.5±3.6	5.7±2.9	15.6±4.5	3.8±2.4	---	---	
	81.20.21												
89-98	24.35.24	12.8, Hawk Channel, fine sand	273	30.4±5.6	28.9±5.5	12.4±4.0	4.8±2.6	5.1±2.7	15.8±4.4	2.6±1.9	---	---	
	81.19.48												
89-99	24.34.12	7.6, east edge Big Pine Shoal, sand veneer on rocky bottom	306	17.6±4.4	26.8±5.1	31.4±5.3	5.5±2.6	10.8±3.5	5.9±2.7	2.0±1.6	---	---	
	81.19.15												
89-100	24.33.54	8.2, backreef, coarse reefy sand	260	27.3±5.5	20.0±5.0	30.8±5.7	3.8±2.4	13.1±4.2	4.6±2.6	0.4±0.8	---	---	
	81.20.42												
89-101	24.33.39	8.2, backreef, coarse reefy sand	296	24.3±5.0	17.9±4.5	36.5±5.6	4.1±2.3	12.2±3.8	4.7±2.5	0.3±0.6	---	---	
	81.21.24												
89-102	24.33.24	7.6, backreef, coarse reefy sand	248	25.0±5.5	12.9±4.3	45.6±6.3	4.0±2.5	10.1±3.8	2.4±1.9	---	---	---	
	81.22.24												
89-103	24.33.00	9.1, SE corner Looe Key Sanctuary (LKS), coarse sand	274	21.5±5.0	15.0±4.3	42.3±6.0	3.3±2.2	12.4±4.0	5.5±2.8	---	---	---	
	81.23.15												
89-104	24.34.07	12.8, south edge Hawk Channel, NE corner LKS, grass in fines	339	16.8±4.1	27.4±4.8	30.7±5.0	7.7±2.9	7.4±2.8	8.5±3.0	1.5±1.3	---	---	
	81.23.36												
89-105	24.35.06	11.0, north edge Hawk Channel, very fine sand	263	30.8±5.7	22.8±5.2	17.5±4.7	9.5±3.6	6.5±3.0	7.6±3.3	5.3±2.8	---	---	
	81.24.07												
89-106	24.34.35	11.9, north edge Hawk Channel, shell hash & <i>Halimeda</i> in fines	250	31.6±5.9	26.8±5.6	12.8±4.2	2.8±2.1	6.8±3.2	14.0±4.4	5.2±2.8	---	---	
	81.25.30												
89-107	24.33.32	9.1, NW corner LKS, fine skeletal sand, no mud	285	22.1±4.9	28.4±5.3	33.0±5.6	3.1±2.1	7.4±3.1	6.0±2.8	---	---	---	
	81.25.18												
89-108	24.32.45	11.9, outer reef tract, west center LKS, very coarse reefy sand	241	10.0±3.9	25.7±5.6	37.3±6.2	2.5±2.0	17.4±4.9	7.1±3.3	---	---	---	
	81.25.20												
89-109	24.32.57	8.8, backreef, coarse sand	287	17.1±4.4	25.4±5.1	38.0±5.7	3.5±2.2	6.6±2.9	8.7±3.3	0.7±1.0	---	---	
	81.26.21												
89-110	24.32.50	7.6, backreef, south edge Hawk Channel, sand near grass	266	26.7±5.4	27.8±5.5	30.1±5.6	4.9±2.7	7.5±3.2	3.0±2.1	---	---	---	
	81.27.20												
89-111	24.32.43	9.8, backreef, south edge Hawk Channel, coarse sand, grass	275	18.2±4.7	28.7±5.5	34.2±5.7	5.5±2.7	6.9±3.1	5.8±2.8	0.7±1.0	---	---	
	81.28.21												
89-112	24.32.21	7.0, backreef, south edge Hawk Channel, reefy, no grass	250	13.6±4.3	27.6±5.7	42.8±6.3	2.0±1.8	9.6±3.7	3.6±2.4	0.8±1.1	---	---	
	81.29.18												
89-113	24.32.03	7.6, north edge American Shoal, sand hole in bedrock low	286	22.0±4.9	12.2±3.9	49.0±5.9	1.8±1.6	9.1±3.4	5.6±2.7	0.3±0.7	---	---	
	81.30.17												
89-114	24.31.48	4.6, inside American Shoal light, very coarse reefy sand	241	25.3±5.6	15.4±4.7	38.6±6.3	3.7±2.4	12.0±4.2	3.7±2.4	1.3±1.5	---	---	
	81.31.09												
89-115	24.33.18	9.1, Hawk Channel, grass, fine sand	299	27.8±5.2	24.7±5.0	25.1±5.0	9.0±3.3	3.7±2.2	7.4±3.0	2.3±1.7	---	---	
	81.31.59												
89-116	24.34.57	6.1, north edge Hawk Channel, dense grass, very fine sand	246	39.4±6.2	21.6±5.3	15.9±4.7	9.3±3.7	4.5±2.6	6.9±3.2	2.4±2.0	---	---	
	81.32.31												
89-117	24.33.52	6.1, Hawk Channel, <i>Halimeda</i> bed w/ <i>Thalassia</i> & fines	292	66.1±5.5	24.0±5.0	0.7±1.0	5.5±2.7	0.3±0.6	2.7±1.9	0.7±1.0	---	---	
	81.36.16												
89-118	24.32.59	6.7, West Washerwoman Shoal, very, very coarse, <i>Halimeda</i>	201	3.0±2.4	34.8±6.7	48.3±7.0	0.5±1.0	12.9±4.7	0.5±1.0	---	---	---	
	81.36.06												
89-119	24.32.43	4.6, mid-reef tract, West Washerwoman Shoal, <i>Thalassia</i> , no live <i>Halimeda</i>	268	28.4±5.5	21.6±5.0	32.8±5.7	7.5±3.2	6.3±3.0	2.6±1.9	0.8±1.1	---	---	
	81.35.55												
89-120	24.32.35	2.7, mid-reef tract, West Washerwoman, reef sand & <i>Halimeda</i>	263	21.7±5.1	30.8±5.7	37.2±6.0	1.5±1.5	7.6±3.3	0.8±1.1	0.4±0.8	---	---	
	81.35.44												

Appendix 1. Continued

Transect and Sample Nos.	Lat./ Long.	Depth (m), Location, Bottom Description	Grain Count	Estimated percent constituent particles									D Quartz
				<i>Halimeda</i>	Mollusc	Coral	Echinoid	Bryozoa/ Red Algae	Benthic Forams	Planktic Forams	Pellets		
89-121 28	24.32.27 81.35.30	8.5, mid-reef tract, shoal bed-rock low surrounded by hard-bottom, fines w/ coarse grains	293 ●	25.3±5.3	27.9±5.5	37.4±5.9	1.9±1.7	6.0±2.9	1.5±1.5	---	---	---	
89-122	24.32.18 81.35.21	3.4, mid-reef tract, coarse sand near patch reef, <i>Halimeda</i>	296	26.0±5.0	26.7±5.1	35.1±5.5	1.4±1.4	8.8±3.3	1.7±1.5	0.3±0.6	---	---	
89-123	24.31.55 81.35.06	11.9, Hawk Channel, very fine stiff mud	298	17.1±4.4	23.8±4.9	27.2±5.2	11.1±3.6	6.4±2.8	12.1±3.8	2.3±1.7	---	---	
89-124	24.31.18 81.34.59	4.6, backreef, large sand hole in grass bed, coarse sand	243	17.3±4.8	17.7±4.9	43.6±6.4	3.7±2.4	16.1±4.7	1.6±1.6	---	---	---	
89-125	24.30.42 81.34.05	4.3, Maryland Shoal, coarse reefy sand pocket	302	15.2±4.1	16.6±4.3	49.0±5.8	2.0±1.6	13.2±3.9	2.7±1.9	1.3±1.3	---	---	
89-126 29	24.30.28 81.35.21	8.5, outer reef tract, very, very coarse gravelly sand	239	21.8±5.3	18.4±5.0	51.5±6.5	0.8±1.2	6.3±3.1	1.2±1.4	---	---	---	
89-127	24.30.15 81.37.18	3.4, east edge Pelican Shoal, rocky, coarse sand w/ grass	271	15.5±4.4	24.3±5.2	41.0±6.0	3.3±2.2	11.1±3.8	4.8±2.6	---	---	---	
89-128	24.29.55 81.38.41	6.1, Eastern Sambo Reef, very coarse gravelly reefy sand	253	17.8±4.8	16.6±4.7	49.8±6.3	2.0±1.8	8.7±3.5	5.1±2.8	---	---	---	
89-129 30	24.29.45 81.39.48	4.6, ~900 m inside Eastern Sambo marker, reefy sand	298	14.8±4.1	19.8±4.6	53.0±5.8	2.7±1.9	7.7±3.1	2.0±1.6	---	---	---	
89-130	24.30.34 81.40.30	10.7, south edge Hawk Channel, very fine sand	241	19.1±5.1	18.7±5.0	22.0±5.3	9.5±3.8	11.6±4.1	16.2±4.7	2.9±2.2	---	---	
89-131	24.31.12 81.40.30	10.1, Hawk Channel, salt-and-pepper fines w/ shell hash	268	16.8±4.6	31.3±5.7	35.1±5.8	4.4±2.5	7.5±3.2	4.9±2.6	---	---	---	
89-132	24.32.03 81.40.54	9.5, north edge Hawk Channel, very fine stiff mud		no thin-section data available									
89-133 31	24.30.54 81.46.56	11.0, inner reef tract off Key West, grassy, fines	316	31.6±5.2	28.8±5.1	14.9±4.0	8.9±3.2	4.1±2.2	11.1±3.5	0.6±0.9	---	---	
89-134	24.29.45 81.46.11	11.9, Hawk Channel, grass	287	35.5±5.7	22.7±5.0	21.6±4.9	4.2±2.4	9.4±3.5	5.6±2.7	1.0±1.2	---	---	
89-135	24.28.49 81.45.29	14.9, backreef, <i>Syringodium</i>	304	17.7±4.4	25.0±5.0	31.3±5.3	6.3±2.8	10.2±3.5	7.9±3.1	1.6±1.4	---	---	
89-136 32	24.28.12 81.47.05	9.8, outer reef tract, reefy w/ sediment veneer, no grass	235	19.2±5.1	16.6±4.9	50.6±6.5	1.3±1.5	10.2±4.0	2.1±1.9	---	---	---	
89-137	24.28.31 81.48.57	10.1, backreef, reefy w/ coarse sand veneer, no grass	236	7.2±3.4	30.1±6.0	46.2±6.5	0.8±1.2	13.6±4.5	1.7±1.7	0.4±0.8	---	---	
89-138	24.28.07 81.50.09	4.6, Eastern Dry Rocks, coarse rippled sand w/ head coral inside hardbottom area	326	24.9±4.8	23.0±4.7	34.0±5.2	0.9±1.0	14.1±3.9	2.8±1.8	0.3±0.6	---	---	
89-139 33	24.27.25 81.52.37	3.7, inside Sand Key, very, very coarse sand on hardbottom	113	4.4±3.9	18.6±7.3	55.8±9.3	0.9±1.8	19.4±7.4	0.9±1.8	---	---	---	
89-140	24.27.47 81.52.37	7.0, north edge Sand Key, rippled sand in hole surrounded by grass & rocks	286 ●	24.1±5.1	17.8±4.5	40.6±5.8	3.2±2.1	9.1±3.4	5.2±2.6	---	---	---	
89-141	24.28.26 81.52.42	11.9, south edge Middle Ground, very fine sand	322	26.1±4.9	22.1±4.6	7.1±2.9	10.2±3.4	14.0±3.9	14.3±3.9	6.2±2.7	---	---	
89-142	24.29.02 81.52.32	10.7, north edge Middle Ground, very fine sand	251	33.5±6.0	18.7±4.9	4.4±2.6	5.2±2.8	15.1±4.5	21.1±5.2	2.0±1.8	---	---	

Total grain count = 37,150; maximum 342; minimum 113; mean 267. True depths taken from onboard fathometer. ● Sample counted twice for accuracy.

Appendix 1. Continued

A 1952 Data Averaged by Traverse (from Ginsburg, 1956)				
No. Samples	Grain	Av. %	Traverse	Reef (Area)
10	H	24.3%	I	Sombrero (middle Keys)
	M	18.9		
	C	11.2		
6	H	36.7%	II	Tennessee (middle Keys)
	M	13.0		
	C	11.8		
9	H	24.7%	III	Triumph (upper Keys)
	M	10.8		
	C	12.1		
Total: 25				

All 1952 Data Averaged by Area (from Ginsburg, 1956)				
9	H	24.7%	III	upper Keys
	M	10.8		
	C	12.1		
16	H	28.9%	I, II	middle Keys
	M	16.7		
	C	11.4		
Total: 25				

B 1963 Data Averaged by Traverse (from Swinchatt, 1965)				
No. Samples	Grain	Av. %	Traverse	Reef (Area)
8	H	40.8%	A*	Alligator (upper Keys)
	M	18.1		
	C	20.5		
5	H	38.2%	B	No. of Tennessee (middle Keys)
	M	20.9		
	C	11.6		
6	H	40.9%	C*	Tennessee (middle Keys)
	M	21.8		
	C	10.6		
5	H	45.6%	D*	So. of Tennessee (middle Keys)
	M	18.1		
	C	9.7		
9	H	26.2%	E	No. of Sombrero (middle Keys)
	M	18.6		
	C	22.0		
4	H	26.9%	F*	Sombrero (middle Keys)
	M	25.1		
	C	19.5		
9	H	33.6%	G	No. of Sombrero (middle Keys)
	M	20.9		
	C	19.4		
8	H	31.2%	H*	Davis (upper Keys)
	M	19.2		
	C	14.6		
Total: 54				

All 1963 Data Averaged by Area (from Swinchatt, 1965)				
16	H	36.0%	A, H	upper Keys
	M	18.7		
	C	17.5		
38	H	34.5%	B-G	middle Keys
	M	20.6		
	C	16.4		
Total: 54				

C 1989 Data Averaged by Middle and Upper Keys Traverses (this study)				
No. Samples	Sample #	Grain	Av. %	Reef (Area)
7	71-77	H	31.1%	Sombrero (middle Keys)
		M	22.2	
		C	25.2	
5	66-70	H	29.4%	So. of Tenn. (middle Keys)
		M	21.5	
		C	21.3	
5	61-65	H	25.4%	Tennessee (middle Keys)
		M	19.5	
		C	18.4	
5	56-60	H	22.7%	Alligator (upper Keys)
		M	20.3	
		C	19.5	
4	51-54	H	26.8%	Davis (upper Keys)
		M	23.1	
		C	16.0	
3	13-15	H	33.8%	Triumph (upper Keys)
		M	32.0	
		C	5.2	
Total: 29				

All 1989 Data Averaged by Area (this study)				
58		H	31.6%	upper Keys
		M	27.7	
		C	8.1	
35		H	25.9%	middle Keys
		M	18.2	
		C	33.1	
46		H	23.4%	lower Keys
		M	23.1	
		C	32.6	
Total: 139				

D 1983 Looe Key Sanctuary Data Averaged (from Lidz et al., 1985)			
Sample #	Grain	Av. %	Reef (Area)
2, 10-14, 42-44, 47-50, 70-71, 76	H	17.0%	lower Keys
	M	24.6	
	C	26.5	
Total: 16			

1989 Looe Key Sanctuary Data Averaged (this study)			
103-104, 107-108	H	17.6%	lower Keys
	M	24.2	
	C	35.8	
Total: 4			

All 1983 Looe Key Sanctuary Data Averaged (from Lidz et al., 1985)			
	H	20.3%	lower Keys
	M	24.1	
	C	27.7	
Total: 96			

Appendix 2. (A-D) Averaged percentages along local traverses by sample year, calculated from 1989 petrologic record and previous data of other authors. H = *Halimeda*; M = mollusc; C = coral.