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Letter

Evidence for the southward migration of mud banks in Florida Bay

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ABSTRACT

The latticework of shallow polygonal mud banks encircling deeper ponds is a key morphological characteristic of Florida Bay. Composed of lime mud produced largely by calcareous algae and epibionts, these banks limit water exchange between the interior Bay and ocean waters from both the Gulf of Mexico and the Atlantic. They also influence salinity and benthic habitat distribution. It has been proposed that the position of mud banks may be dynamic, migrating southwards with time, but no long-term study has examined the spatial arrangement of banks within Florida Bay over sufficiently long timescales to ascertain movement. Using time-separated bathymetry surveys and aerial photography datasets spanning a period of many decades, this study establishes that indeed the bank positions are temporally dynamic. The work was conducted using geographic information systems (GIS), with all data referenced to the position of relatively stable islands. The analysis reveals a southward migration trend (headings ranging from 280° to 240°) with rates averaging 1.27 m/year. For the first time in Florida Bay, the migration and vector of movement for mud banks have been documented. Despite the southward movement, mud bank morphology remained consistent. It is speculated that strong winter winds out of the north/northeast provide the mechanism for such migration.

The southward migration of fine-grained, biogenic mud banks in Florida Bay demonstrates how change-detection remote sensing can be used to audit a geological process operating at time-scales of centuries. Though the available data may be unusually rich for Florida Bay, the study shows how the dynamics of other coastal systems may be accessed using a comparable work-flow. Similarly, the results here have implications for the geologic record and reevaluating paleo-landscapes where mudrock shoals have been identified.

1. Introduction

Located at the southern limit of the Florida mainland, Florida Bay is a shallow, roughly triangular body of water that covers an area of approximately 1550 km^2 The Bay is a low-energy environment — tidal range is limited to 17 cm (Holmquist et al., 1989). The weak water circulation occurring in the Bay interior (Lee et al., 2006) is controlled primarily by wind-driven currents (Fourqurean and Robblee, 1999). Despite the relatively calm winds throughout the year, strong winter winds (November through February) have the capacity to move large volumes of water out of the Bay through tidal passes. The passes, or breaks in between the islands of the Florida Keys, are the sole locations of direct water exchange between the Bay and the Atlantic Ocean (Lee and Smith, 2002).

Mud banks of Florida Bay consist primarily of biogenic carbonate lime mud originating from local calcium-carbonate producers (Stockman et al., 1967; Nelson and Ginsburg, 1986; Frankovich and Zieman, 1994). The most important of these producers are epiphytic organisms located directly on the seagrass blades of the common *Thalassia testudinum*. Frankovich and Zieman (1994) found the coralline red algae *Melobesia membranacea* and *Fosliella farinosa* and the serpulid worm *Spirorbis* sp., all of which grow on the blades of *T. testudinum*, to be the main suppliers of carbonate mud within Florida Bay. The calcareous algae *Penicillus* is also a contributor to the mud within Florida Bay (Stockman et al., 1967). The production of calcium carbonate mud is estimated at 118 g/m^2/year for seagrass-associated epibionts (Nelson and Ginsburg, 1986) and 3 g/m^2/year for algae (Stockman et al., 1967). Non-skeletal precipitation of aragonite has also contributed to the lime mud budget of Florida Bay (Smith, 1940; Cloud, 1962).

The morphology of Florida Bay is characterized by a network of anastomosing mud banks. With a generally flat, plateau-like surface, the mud banks of Florida Bay are shallow enough to limit flushing and water circulation from both the Gulf of Mexico and the Atlantic Ocean into the interior of the Bay (Perkins, 1977; Pitts, 1998; Smith, 2000). While the mechanism behind mud bank formation in Florida Bay is still debated, the current theory is that the banks formed along low-lying rill valleys that experienced saltwater encroachment before the rest of the Florida shelf at the last transgression; these lower areas were then colonized by mangroves that acted as current

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baffles, further increasing the deposition of biogenic sediment and subsequent bank growth (Hoffmeister, 1974).

Mud bank architecture varies between the northeast and southwest of Florida Bay. The latter is characterized by very broad mud banks which tend to have flanks that slope gradually. It is speculated that the larger mud banks in southwestern Florida Bay, the constructional zone of Tagett et al. (1989), gain such size due to their proximity to the carbonate production grounds of the Gulf shelf (Enos and Perkins, 1979). In the northeast destructional zone (Tagett et al., 1989; Wanless and Tagett, 1989), the narrow and irregular-shaped mud banks have distinct morphological and sedimentary characteristics along their windward and leeward flanks. Windward margins in the northeast tend to have a steeper gradient than the gently sloping leeward edge (Fig. 1). This differentiation is speculated to be a result of wave action associated with strong winds. The narrow banks in this region intercept strong winds and associated waves from the north during the winter months. Conversely, those banks in the southwestern area of the Bay receive a wind dissipated by islands, mud banks to the northeast, and a decreased fetch resulting from larger, broader banks (Enos and Perkins, 1979; Enos, 1989). As a result, distinct windward and leeward slopes are formed in the northeast. The windward side of banks tends to be slightly steeper and is characterized by coarse, skeletal sediment (Ginsburg, 1956; Enos and Perkins, 1979). Leeward margins slope more gradually and are associated with finer lime mud. These leeward edges are often colonized by dense beds of turtle grass (*T. testudinum*). The locations and densities of seagrass beds on leeward margins represent a stabilizing potential speculated to limit mud bank migration (Ginsburg and Lowenstam, 1958; Prager and Halley, 1999). These differences between the banks in the northeast and the southwest create a physical and biological gradient along the same axis (Schomer and Drew, 1982).

The mud banks of Florida Bay are discrete geologic structures, defined here as a configuration that will persist into the rock record, but may not be recognizable due to their subtle relief. Despite this, the architecture of these structures is such that they could conceivably be mobile. Although theories have been put forth regarding the possibility of bank movement (Enos and Perkins, 1979; Wanless and Tagett, 1989), previous attempts at examining mud bank position over time have not provided clear conclusions (Enos and Perkins, 1979; Wanless, 1981). It is the goal of this study to compare mud bank locations in Florida Bay from 1890 to 1990 using remote sensing and GIS.

2. Materials and methods

High-resolution bathymetric datasets from 1890 and 1990, coupled with satellite (Landsat 7 EMT+ and IKONOS) and aerial imagery, were used to compare mud bank positions in Florida Bay over the last century (Fig. 2). Bathymetric data (from 1890 and 1990) were provided by the United States Geological Survey (USGS). Both datasets were soundings acquired from vessels. The 1890 soundings were obtained using hand lines, while the soundings acquired in 1990 were made using sonar and are more densely packed and digitally archived. Georeferencing of the 1890 bathymetric dataset involved utilizing >100 control points, including inlets in the Florida Keys, National Geodetic Survey control points, navigation channels, and the southern coast of the Florida mainland. For quality assurance the 1890 dataset was superimposed on high-resolution aerial imagery from 2004. This check was performed to determine the geographic positioning accuracy of the georeferenced century-old dataset. Coastline transects from 1890 lined up correctly with islands colonized by terrestrial plants from contemporary topographic maps, allowing for a justified comparison between bathymetric datasets. These islands were used as a georeferencing tool across datasets under the assumption that terrestrially colonized islands, as compared to the mud banks, were static over the time period in question, an assumption supported by Enos (1989). The 1990 bathymetric soundings were geo-positioned at the time of acquisition and therefore did not require further georectification. The root mean square (RMS) error in lateral position between the 1890 and 1990 bathymetry data was calculated to be 1.5 m.

To corroborate the bathymetric datasets, archive aerial photography acquired by the National Geodetic Survey in 1935 over the area of the Bob Allen Keys (Fig. 2), was quantitatively compared to high-resolution IKONOS imagery acquired for the same area in 2004. These time-separated image sets were then stacked in GIS and, as for the bathymetry data, mutually registered by lining up islands common to both archives. Mud bank locations were then outlined manually. This was accomplished by importing the image sets into GIS software and delineating the outlines of each mud bank. These tracings, while maintaining georectification, were then layered over the same location from the opposing dataset. This resulted in a single image showing the outline of the same mud bank, which was then used to ascertain if the bank had shifted, and the direction of movement, between 1935 and 2004.

In order to examine changes in mud bank location over the last century using the bathymetric datasets, specific locations were isolated that contained a high density of depth soundings from each dataset (1890 and 1990). To find these zones, the bathymetric readings were superimposed onto a Landsat 7 EMT+ satellite image acquired in 2010. Areas were identified where the time-separated depth soundings were geographically located within 1.5 m of each other. This criterion of overlap was satisfied for 10 mud banks, all of which were located in central and eastern Florida Bay. Neither of the two bathymetry datasets contained soundings across the top of the mud banks since in both 1890 and 1990, water depths were too shallow to navigate by boat. Therefore, depth soundings from the windward and leeward bank-slopes were compared in order to determine changes in morphology and positioning through time.

To compare differences in bathymetry for the 10 locations, the 1890 and 1990 soundings were gridded to a raster with a 4-m pixel size. In order to create a 'difference' image, the 1890 layer was subtracted from the 1990.

To estimate movement, bathymetric sampling transects run perpendicular and parallel to mud bank orientation were superimposed on aerial imagery to compare current bank positioning with the available 1890 bathymetric dataset. Migration rate and direction were estimated by hand-digitizing the mud bank boundary in GIS. This exercise delivered two bathymetric contours, one from each dataset. Comparison of the contours produced an estimate of the direction of migration for each bank. Migration was also assessed by comparing the location of equivalent depths between 1890 and 1990 along the windward and leeward margin of each bank. These two methods for estimating bank migration were then averaged to get an overall value for change in mud bank position from 1890 to 1990.

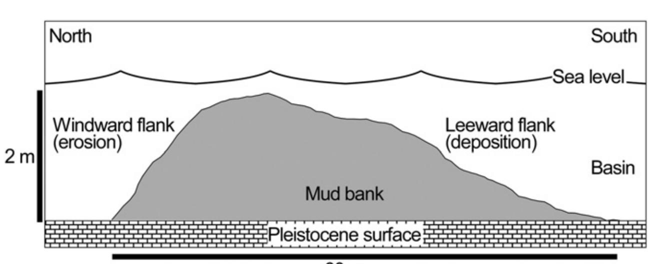

Fig. 1. Cross section schematic of an idealized Florida Bay mud bank.

3. Results

Analysis of mud bank morphology and positioning between 1890 and 1990 revealed a southward movement, with a heading between 280° and 240° (Fig. 3). Although individual mud bank migration

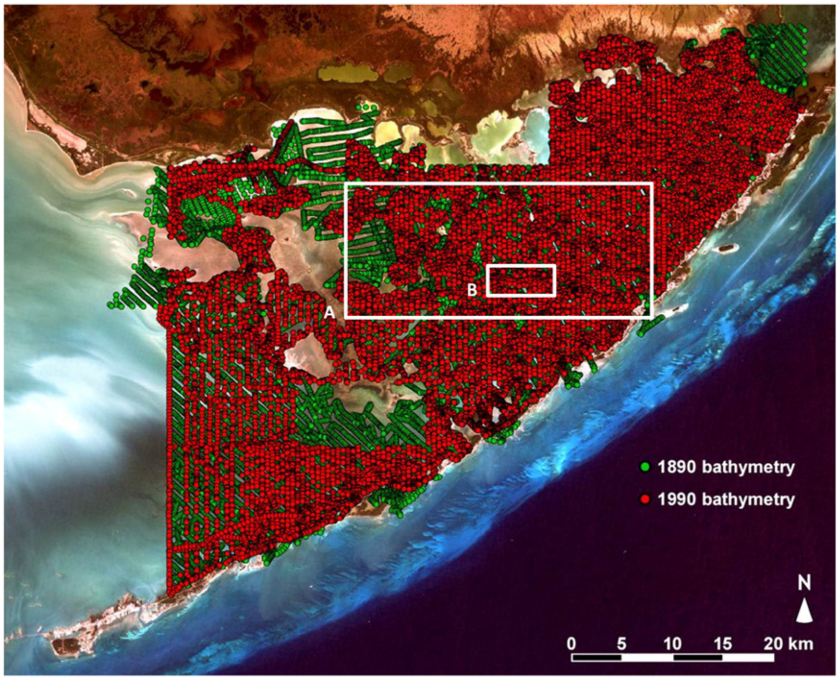

Fig. 2. Satellite imagery of Florida Bay with locations of bathymetric soundings from 1890 and 1990. (A) Location of bathymetry study site. (B) Location of aerial imagery study site (B).

rates varied, the overall direction appears to be consistent across all banks examined.

This migration is evident by the change in depths between 1890 and 1990 on the windward–leeward margins of each mud bank. The data suggest that deepening has consistently occurred on the windward (northern) margin while the leeward has shallowed. We interpret this pattern as arising from bank movement in a southerly direction (Fig. 4). Wanless and Tagett (1989) likewise determined that lateral accretion on the leeward margin, combined with erosion on the windward edge of a mud bank should be taken as proof of migration. Bathymetric transects along bank margins show obvious changes between 1890 and 1990 depths. Changes in average depths along each margin are significant (t-test, $p > .001$, $n = 20$, each bank margin was treated as a point). We interpret these spatial changes as evidence of migration for the ten considered mud banks on a time scale of 100 years.

Estimates for rates of migration based on bathymetric analysis vary from 0.95 to 1.53 m/year (mean: 1.27 m/year, SD: 0.19, $n = 10$). The differences among calculated migration estimates seem to correspond to specific areas along each mud bank. Transect depths along the sides of each southward concave mud bank (four out of the ten sampled) consistently yielded smaller changes during the last century than those taken at the southern apex of the bank. Such differences in migration rates were interpreted to be associated with strong wave action caused by winter winds out of the north (Prager and Halley, 1999). The southern apex of each mud bank intercepts waves from this direction. We speculate that the concavity of the bank works to amplify and concentrate the wave action at the southern terminus. Side margins (spits) experience a diminished effect due a lesser angle of concavity. The reduction in surface area open to the wind along spits results in less sediment transport. Our data suggest that spits are less mobile when they form along a north–south axis relative to the mud bank. Such an orientation would diminish the distance along the bank that is subjected to wave energy. This is in agreement with Enos (1989) who found the

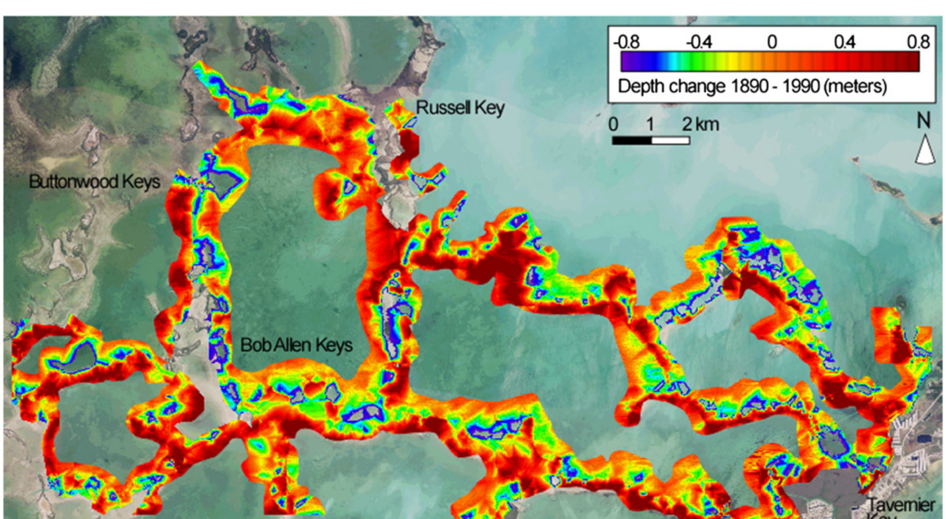

Fig. 3. Aerial imagery of central Florida Bay overlain with color-mapped changes in depth from 1890 to 1990.

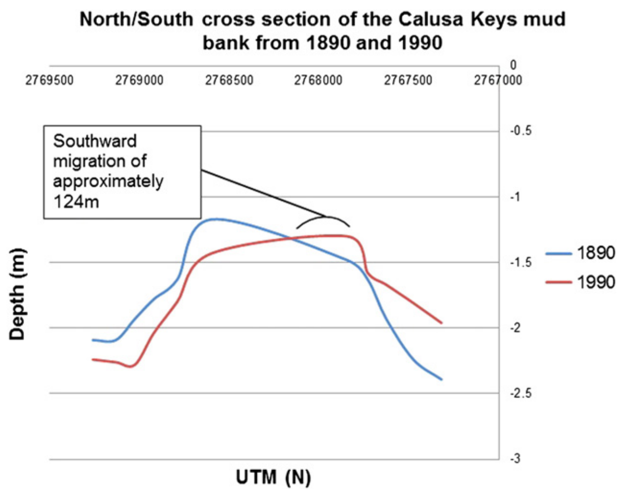

Fig. 4. Cross section of a Calusa Keys mud bank from 1890 and 1990 with estimate of migration distance.

most extensive areas of erosion to be normal to the fronts of refracted waves. Nevertheless, while the distance migrated may have varied, all banks revealed a consistent pattern of erosion on the windward margin and deposition on the leeward slope.

A comparison of aerial imagery from 1935 and 2004 corroborates the bathymetric datasets (Fig. 5). Estimates of migration rate based on the aerial images from the Bob Allen Keys average 0.84 m/year (RMS: 3.02 m, SD: 0.28, $n = 26$, assessments were made at 100 m intervals along the length of the two traced banks as well as around the basin). This value is similar to an average of 1.27 m/year as estimated from the 1890 and 1990 bathymetric data. Direction of migration varied more among the aerial images (headings ranged between 220° and 130°) than delivered by our bathymetric analyses. We attribute the greater variation to arise from the challenge of precisely delineating mud banks whose boundaries are often vague in the archive aerial photographs. Since the analysis of the aerial imagery was based on the manual delineation of bank boundaries, we deem estimates of migration to be of lower accuracy than derived from the bathymetric datasets.

4. Discussion

The data presented in this paper are not sufficient to provide a precise measurement of the distance that the mud banks in Florida Bay have migrated over the last century. Rather, the data and findings are intended to show that these banks are dynamic in nature. The lack of definitive mud bank boundaries precludes the calculation of exact values of migration. Taking this into account, and utilizing bathymetric datasets and aerial imagery, a comparison of similar depths across each dataset allowed for an estimation of migration under the assumption that banks have maintained their shape from 1890 to 1990. This assumption is supported by recent and archival aerial imagery. Although we are aware that the two bathymetric datasets each have their own level of spatial inaccuracy, and that these vagaries will carry over into the subsequent analysis, we deem the comparison to be sufficiently robust to support the conclusions drawn.

The mechanism of bank migration is theorized to be directly related to strong northern winds and the associated wave action (Roberts et al., 1982). This corresponds to the findings that the majority of the mud banks in Florida Bay are being eroded along their northern margin (Enos and Perkins, 1979; Davies, 1980; Quinn, 1983). Although the winds are mainly out of the east/southeast throughout the year (National Data Buoy Center, 2010), during the winter months, winds in excess of 10 m/s are thought to have adequate strength to initiate southerly sediment transport. Evidence for this assumption is provided by Prager and Halley (1999) who showed a wind speed of ~10 m/s to be sufficient to produce wide spread sediment suspension in Florida Bay.

The postulation that the mud banks of Florida Bay are mobile has already been put forth (Wanless and Tagett, 1989) and has been shown in other locations. Froidefond et al. (2004) documented an extensive mud suspension over siliciclastic mud flats off the coast of French Guiana. Using *in-situ* data and SPOT (Système Probatoire d'Observation de la Terre) satellite imagery archives, the authors revealed a gradual northwestward migration of large mud banks close to shore. Estimates of yearly bank migration off the coast of French Guiana varied greatly among locations studied. Between 1991 and 2002 rates ranged from 200 to 2500 m/year (Froidefond et al., 2004), with variability attributed to changes in wind intensity, different orientation between tailing and leading edges of mud banks, sparsely vegetated flats and local environmental parameters such as coastline orientation (Perkins, 1977). While these velocities are multiple orders of magnitude greater than those that we report for Florida Bay (~1 m/year), it is important to note that the coast of French Guiana is a high-energy system. Open to the Atlantic Ocean, the coastline is susceptible to strong wind and wave action as well as the North Equatorial Current. The winds in Florida Bay are considerably weaker as compared to the trade winds of French Guiana and therefore bank migration distances between these two locations should be expected to differ. Nevertheless, from the work

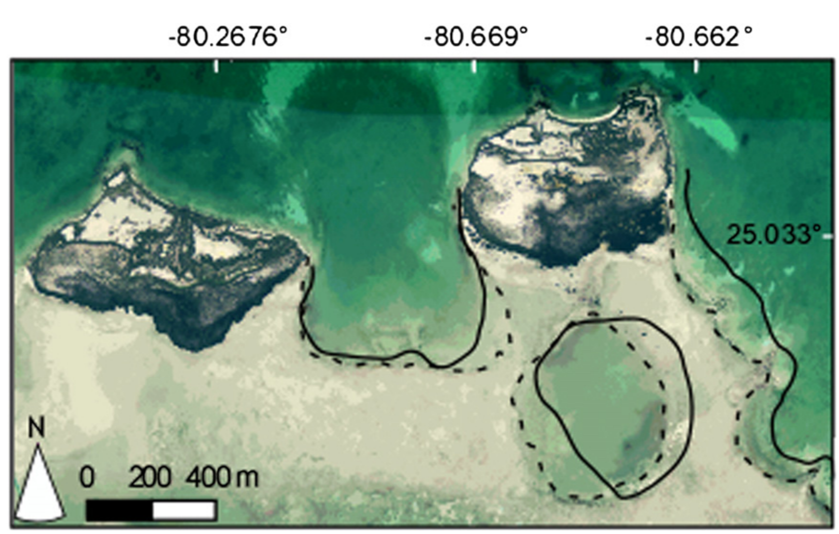

Fig. 5. Bob Allen Keys mud Bank tracings from 2004 (dashed line) and 1935 (solid line) superimposed on aerial imagery from 2004.

of Froidefond et al. (2004) and Gardel and Gratiot (2005) it is seen that mud banks can and do migrate under favorable wind conditions.

It is worthwhile to mention that Florida Bay lies within the hurricane belt. Despite the strong winds associated with such events it has been shown that the influence of hurricanes over sedimentation and mud bank morphology is negligible (Ball et al., 1967; Perkins and Enos, 1968; Prager and Halley, 1999). Only 9 major hurricanes have affected Florida Bay in the past 100 years (NOAA National Hurricane Center, 2011). Therefore these severe storms represent an anomalous, short duration change to normal wind patterns. On the century time scale of this study it is assumed that changes to bank morphology as a result of hurricane action would eventually be corrected as traditional wind patterns return.

The movement of mud banks shown here has implications for reevaluating mudrock geobodies in the geologic record. Paleoenvironments in which sedimentary rocks were laid down should be reassessed. Although the presence of lime mud implies a low-energy environment existed at the time of deposition (Potter et al., 2005), the results shown here prove that if the correct conditions are met, these fine-grained structures are dynamic. We can speculate therefore that the classification of low-energy and high-energy systems based simply on the presence or absence of mudrock might not be as straight forward as once thought. Relating back to the study at hand, it can be conjectured that the interior landscape of Florida Bay, specifically the honey-comb network of mud banks, might have looked dramatically different than it appears today, all within the span of only several thousand years.

5. Conclusions

The migration of mud banks in Florida Bay provides evidence of the dynamic characteristics of fine-grained lime mud. Despite slight deviations in migration rates among the banks audited, the direction of migration is consistent as shown in our bathymetric and aerial datasets. The occurence of this geomorphological change, within such a relatively short time period, is surprising considering the low-energy environment characterizing Florida Bay. Previous research into the migration of mud banks has concentrated only on high energy environments (Froidefond et al., 2004; Gardel and Gratiot, 2005). Studies into mud bank suspension and migration in such areas as French Guiana are powered by oceanic currents (North Equatorial current) and wave energy. To the contrary, this study documents the migration of mud banks in a low-energy environment.

The findings of this study beg the question as to why there is not a 4 km band in northern Florida Bay denude of mud banks. If the process of bank migration described here has been on-going since the flooding of the Bay 4000 years ago, shouldn't the mud banks in this area have migrated southward? Although this study only looked at the spatial arrangement of banks in central and eastern Florida Bay the authors postulate that lime mud is continuously being consolidated into new banks in these northern areas. Nevertheless, further research into mud bank formation should be encouraged.

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References

Ball, M.M., Shinn, E.A., Stockman, K.W., 1967. The geological effects of Hurricane Donna in south Florida. Journal of Geology 75, 583–597.
Cloud, P.E., 1962. Environment of calcium carbonate deposition west of Andros Island, Bahamas. US Geological Survey Prof. Paper, 350.
Davies, T.D., 1980. Peat formation in Florida Bay and its significane in interpreting the recent vegetational and geological history of the bay area. Ph.D. Thesis. Pennsylvania State University, p. 316.
Enos, P., 1989. Islands in the Bay — a key habitat of Florida Bay. Bulletin of Marine Science 44, 365–386.
Enos, P., Perkins, R.D., 1979. Evolution of Florida Bay from island stratigraphy. Geological Society of American Bulletin 90, 59–83.
Fourqurean, J.W., Robblee, M.B., 1999. Florida Bay: a history of recent ecological changes. Estuaries 22, 345–357.
Frankovich, T.A., Zieman, J.C., 1994. Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. Bulletin of Marine Science 54, 679–695.
Froidefond, J.M., Lahet, F., Hu, C., Doxaran, D., Guiral, D., Prost, M.T., Ternon, J.F., 2004. Mudflats and mud suspension observed from satellite data in French Guiana. Marine Geology 208, 153–168.
Gardel, A., Gratiot, N., 2005. A satellite image-based method for estimating rates of mud bank migration, French Guiana, south America. Journal of Coastal Research 21, 720–728.
Ginsburg, R.N., 1956. Environmental relationships of grain size and constituent particles in some South Florida carbonate sediments. Bulletin of the American Association of Petroleum Geologists 40, 2384–2427.
Ginsburg, R.N., Lowenstam, H.A., 1958. The influence of marine bottom communities on the depositional environment of sediments. Journal of Geology 66, 310–318.
Hoffmeister, J.E., 1974. Land from Sea: The Geologic Story of South Florida. University of Miami Press.
Holmquist, J.G., Powell, G.V., Sogard, S.M., 1989. Sediment, water level and water temperature characteristics of Florida Bay's grass-covered mud banks. Bulletin of Marine Science 44, 348–364.
Lee, T.N., Smith, N., 2002. Volume transport variability through the Florida keys tidal channels. Continental Shelf Research 22, 1361–1377.
Lee, T.N., Johns, E., Melo, N., Smith, R.H., Ortner, P., Smith, D., 2006. On Florida Bay hypersalinity and water exchange. Bulletin of Marine Science 79, 301–327.
National Data Buoy Center, 2010. http://www.ndbc.noaa.gov/station_page.php?station=lonf1.
Nelson, J.E., Ginsburg, R.N., 1986. Calcium carbonate production by epibionts on *Thalassia* in Florida Bay. Journal of Sedimentary Petrology 56, 622–628.
NOAA National Hurricane Center, 2011. R.-A.P. http://www.nhc.noaa.gov/pastall.shtml#tracks_us.
Perkins, R.D., 1977. Pleistocene depositional framework of south Florida. In: Enos, Paul, Perkins, R.D. (Eds.), *Quaternary* sedimentation in south Florida: Geological Society of America Memoir, 147, pp. 131–198.
Perkins, R.D., Enos, P., 1968. Hurricane Betsy in the Florida–Bahama area — geological effects and comparison with Hurricane Donna. Journal of Geology 76, 710–717.
Pitts, P.A., 1998. Tidal and long-term volume transport through Jewfish Creek, Florida Keys. Bulletin of Marine Science 63, 559–570.
Potter, P.E., Maynard, J.B., Depetris, P.J., 2005. Mud and Mudstones: Introduction and Overview, 1st Ed. Springer, Wurzberg, Germany.
Prager, E.J., Halley, R.B., 1999. The influence of seagrass on shell layers and Florida Bay mudbanks. Journal of Coastal Research 15, 1151–1162.
Quinn, T.M., 1983. Evolution of selected Holocene mangrove-finged islands of west-central Florida Bay. M.S. Thesis, Wichita State University, Wichita, Kansas.
Roberts, H.H., Rouse, L.J.J., Walker, N.D., Hudson, J.H., 1982. Cold-water stress in Florida Bay and northern Bahamas: a product of winter cold-air out breaks. Journal of Sedimentary Petrology 52, 145–155.
Schomer, N.S., Drew, R.D., 1982. An Ecological Characterization of the Lower Everglades, Florida Bay, and the Florida Keys. U.S. Fish and Wildlife Service, Office of Biological Services. FWS/OBS-82/58.1, 246 pp.
Smith, C.L., 1940. The Great Bahama Bank, I. General hydrographic and chemical factors; II. Calcium carbonate precipitation. Journal of Marine Research 3, 147–189.
Smith, N.P., 2000. Observations of shallow-water transport and shear in western Florida Bay. Journal of Physical Oceanography 30, 1802–1808.
Stockman, S.V., Ginsburg, R.N., Shinn, E.A., 1967. The production of lime mud algae in South Florida. Journal of Sedimentary Petrology 37, 633–648.
Tagett, M.G., Wanless, H.R., Cottrell, D.J., 1989. Gradients in carbonate mudbanks stratigraphy and dynamics, Florida Bay, South Florida. Soc. Econ. Paleontologists Mineralogists, Midyear Mtng. Abs., 108.
Wanless, H.R., 1981. Fining-upwards sedimentary sequences generated in seagrass beds. Journal of Sedimentary Petrology 51, 445–454.
Wanless, H.R., Tagett, M.G., 1989. Origin, growth and evolution of carbonate mudbanks in Florida Bay. Bulletin of Marine Science 44, 454–489.