

FOUR THOUSAND YEARS OF HABITAT CHANGE IN FLORIDA BAY, AS INDICATED BY BENTHIC FORAMINIFERA

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ABSTRACT

Analyses of 203 samples of benthic foraminifera in six cores from four sites in Florida Bay indicate habitat change over the last ~4000 years. Sample ages were determined for the last ~120 years with ²¹⁰Pb, and for up to ~4000 years at two sites with ¹⁴C. The largest habitat changes upcore were identified with stratigraphically constrained cluster analysis (CONISS), which evaluates the similarity of vertically adjacent samples. Paleoenvironmental interpretations of habitat changes were mostly based on varying proportions of two defined associations of environmental indicator taxa and changes in diversity. The timing of the interpreted environmental changes was compared to known natural and anthropogenic events to examine their correspondence and possible relationship.

The bay's initial flooding ~4000 YBP was indicated at the offshore Ninemile Bank by a very high proportion of an *Ammonia* association and very low proportion of a *Quinqueloculina* association, similar to modern nearshore assemblages in Trout Cove, the core site closest to the mainland. Construction of the Florida Keys railroad in 1907–1910 led to restricted exchange with the open ocean; foraminifera indicate a salinity decrease at that time, probably from the increased influence of runoff. Faunal changes since the 1920s in central Florida Bay signify increasingly saline (>32 psu) waters. Between 1928–1938, concurrent peaks in the *Ammonia* association at all sites suggest widespread freshening of the bay, which corresponds to an unusual succession of three powerful, wet hurricanes between 1926–1938. After flushing of the bay by hurricanes, a long-term result of decreased circulation caused by railroad construction was the increased retention of organic materials in the bay; more organic-rich conditions after 1932 are indicated at Ninemile Bank by a shift in infaunal *Bolivina* species to their highest abundance. In the central bay after 1962, the amplitude of changes in the *Ammonia* association and diversity was greater, probably related to larger salinity shifts caused by increases in water management in addition to natural events such as droughts. In the central bay in 1987, decreases in diversity, increases in infaunal taxa and decreases in epiphytic species clearly reflect a severe, bay-wide seagrass die-off and drought. Thus, changes in Florida Bay habitats can be related to both anthropogenic and natural causes. Despite any degradation of water quality in the past 50 years, foraminiferal diversity has increased at most sites.

INTRODUCTION

Distinguishing the roles of natural and human causes of coastal habitat change provides baseline data for current

rehabilitation efforts in the Everglades wetlands. Over the past hundred years, the wetlands and Florida Bay, which drains the wetlands and is a part of Everglades National Park, have been greatly impacted by agriculture and the construction of canals and roads. Florida Bay habitats have been changing since initial flooding ~4000 YBP, progressing from a freshwater, Everglades-like setting to a mangrove swamp, and finally to a shallow bay with a mean depth of 1–2 m (Davies and Cohen, 1989; Wanless and Tagett, 1989). Sedimentologic evidence indicates that with sea level rise, eastern Florida Bay was gradually inundated until ~1500 YBP, when it became fully marine (Wanless and Tagett, 1989). Significant anthropogenic impact on South Florida began around 1900, with agricultural and urban development accompanied by the construction of roads, railroads, and water-diversion and -retention structures. Natural events that have affected the water quality include droughts and hurricanes. We studied habitat changes in Florida Bay with an analysis of the 4000-year sedimentary record of benthic foraminiferal assemblages, which generally reflect changes in physical conditions such as salinity, substratum type, temperature, food, and shifts in the coastline in response to sea-level change.

The history of sea-level change in Florida Bay after its initial inundation is somewhat unclear. In much of the bay, the earliest coastline is marked by the boundary between an approximately 4000-year-old freshwater mangrove peat and the underlying indurated, marine limestone of the Florida carbonate platform (Gleason and Stone, 1994). Subsequently, sea level rose at an average of 4 cm/100 yr (Wanless and others, 1994), although the history of sea-level fluctuation is open to debate. Shepard (1963) suggested that sea level rose over the last 6000 years at a gradually decreasing rate, which is supported by studies of mangrove peat deposits (Scholl and others, 1969; Gleason and Stone, 1994) and coral reefs in southwest Florida (Robbin, 1984). Alternatively, Fairbridge (1974, 1976) proposed that four major regressions and transgressions over the past 6000 years included higher sea levels than at present. Fairbridge's proposal is supported by research on west-central Florida geology (Missimer, 1980), barrier island growth in southwestern Florida (Stapor and others, 1987, 1991), archeology of Florida's Gulf Coast (Walker and others, 1995), and rhizoliths of southeastern Florida (Froede, 2002). Biological proxies such as corals (Robbin, 1984; Toscano and Lundberg, 1998) and benthic foraminifera (Hill and others, 2003) that are associated with particular water depths have also been used to determine local sea-level changes in Florida.

Of the benthic foraminifera used to track sea-level change, marsh foraminifera are the most accurate because of their narrow environmental tolerances and short vertical ranges in the intertidal zone (e.g., Scott and Medioli, 1978; Hippensteel and others, 2000; Scott and others, 2001; Cann

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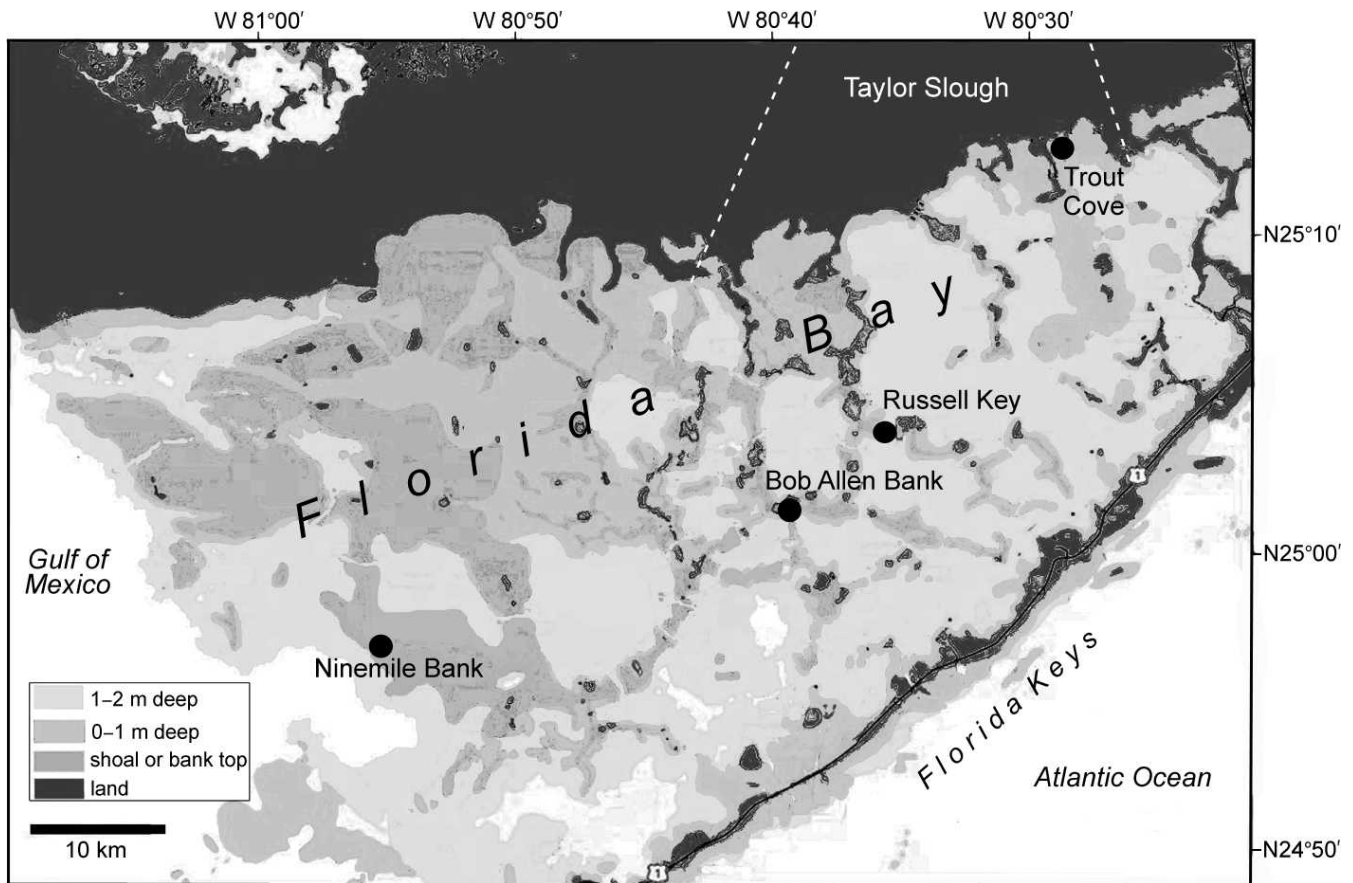


FIGURE 1. The four core sites in Florida Bay (black points). Dashed white lines delineate the approximate boundaries of Taylor Slough. Adapted from Everglades Park Map, U.S. National Park Service.

and others, 2002; Horton and others, 2003, 2005; Barbosa and others, 2005; Woodroffe and others, 2005). Most of the common, agglutinated, temperate salt-marsh taxa such as *Ammotium*, *Miliammina*, *Trochammina*, *Arenoparrella*, and *Tipotrocha* (Saunders, 1958; Benda and Puri, 1960; Brewster-Wingard and Ishman, 1999; Sen Gupta, 1999; Scott and others, 2001) also occur in mangrove swamps, the tropical-subtropical ecological equivalent of salt marshes examined in this study. However, calcareous perforate genera such as *Ammonia* and *Elphidium* may constitute up to 80% of the total population in the mangrove swamps (Rose and Lidz, 1977; Lidz and Rose, 1989), which in Florida Bay range in salinity from medians of 7 in the inner mangrove fringe to 15 in the outer fringe (Boyer and Fourqurean, 1997). In mangroves, larger calcareous imperforate foraminifera such as soritids are sparse or completely absent, and only small numbers (usually <10%) of the miliolids *Quinqueloculina*, *Miliolinella*, and *Triloculina* are occasionally present (Lidz and Rose, 1989), probably in response to the lower salinities. There is often a remarkable similarity among mangrove foraminiferal assemblages from different longitudes (Sen Gupta, 1999), so we also considered the ecology of foraminifera from other warm-temperate to tropical mangrove swamps and salt marshes (Scott and others, 1990; Halfar and Ingle, 2003; Barbosa and others, 2005; Vance and others, 2006). Shallow (<12 m)

subtidal assemblages away from fringing mangroves have higher proportions of calcareous imperforate species, which are generally epifaunal and prefer salinities of 32–65 psu (Murray, 1991). In this study, we track an intertidal mangrove association of foraminiferal taxa (*Ammonia* association) and a calcareous imperforate association (*Quinqueloculina* association) that are defined by species distributions described in the literature. Multiple cores from two of the four studied sites provided control for inter-site variability.

METHODS

CORING SITES AND SAMPLING

Eight sediment cores from near Bob Allen Bank, Nine-mile Bank, Trout Cove, and Russell Key (Fig. 1, Table 1) were collected by Collins and others on a U.S. Geological Survey barge with a mounted derrick and PVC piston device (Sansone and others, 1994). At each site, two cores ~100 m apart were collected from the sides of accreting banks, which because of their slow accumulation of sediments are less likely than open basins to include periods of low or no sedimentation. To sample a wide range of environments, we chose sites that historically have had different sources of freshwater runoff and water exchange. Trout Cove, at the mouth of Trout Creek, is closest to the

TABLE 1. Localities, water depths, and lengths of cores.

Site and core #	Latitude (N)	Longitude (W)	Water depth (cm)	Core length (cm)
Bob Allen Bank				
#122	25°01.670'	80°40.871'	48	200
#124	25°01.731'	80°40.795'	48	194
Russell Key				
#125	25°03.871'	80°37.501'	46	170
#127	25°03.851'	80°37.371'	46	170
Ninemile Bank				
#134	24°57.128'	80°53.607'	37	244
Trout Cove				
#1211	25°12.582'	80°31.932'	47	96

mainland and receives the largest amount of freshwater, which is delivered by canals transecting the natural Taylor Slough (Fig. 1). Bob Allen Bank, near the center of the Bay, is subject to large inter- and intra-annual variations in salinity, which may cause fluctuations in vegetative cover. At this site, previous geological studies (Brewster-Wingard and Ishman, 1999; Halley and Roulier, 1999; Orem and others, 1999) documented a relatively continuous (radiometrically dated) record of sedimentation over 20 years, and anthropogenic alterations of water flow did not significantly influence salinity (Nuttle and others, 2000). Russell Key is more proximal to the Everglades mainland than Bob Allen Bank and has accreted in a southerly direction (Wanless and Tagett, 1989). Ninemile Bank is farthest from the mainland and Florida Keys, and exchanges water primarily with the Gulf of Mexico.

The PVC piston core penetrated an average of 1.5 m of greenish-gray, calcareous mud containing little organic matter before it reached the limestone substratum (Table 1). Two sites, Bob Allen Bank and Ninemile Bank, contained mangrove peat at the base, which represents the shallowest facies (Enos, 1989). All cores were x-rayed before sampling for the foraminiferal analysis, except those from Ninemile Bank. The paucity of laminations and beds visible in the x-radiographs suggests bioturbation: 1) the Trout Cove core showed almost no bedding; 2) the Bob Allen Bank cores had little bedding; 3) and the Russell Key cores had slightly more bedding and some lamination within 1 m of their base. The cores were sliced completely into 2-cm-thick slabs. We analyzed six of the eight cores, including two each from Bob Allen Bank and Russell Key in the central bay and one each from Ninemile Bank and Trout Cove. We focused more effort on the central bay record because it should reflect more average bay conditions than the other two sites, based on its greater distance from mainland runoff and the Gulf of Mexico (Fig. 1).

PREPARATION AND IDENTIFICATION OF BENTHIC FORAMINIFERA

Two-hundred-three sediment samples were disaggregated by soaking in water, then washed through a 63- μ m sieve. Organic material was very sparse in the samples, which were predominantly mud, including those that consisted of peat mixed with mud near the base of the Bob Allen Bank and Ninemile Bank cores. The residues from each washed

sample were split successively until a split was estimated to contain at least 300 benthic foraminifera, as that minimum number is generally sufficient to accurately represent species' proportions; Murray, 1991) For each sample split, foraminifera were picked onto micropaleontological slides, sorted by species, and the number of specimens per species was counted.

Species identifications were based primarily on taxonomic studies of tropical and subtropical western North Atlantic foraminifera (e.g., Wantland, 1967; Bock and others, 1971; Rose and Lidz, 1977; Buzas and Severin, 1982; Javaux and Scott, 2003). Questionable identifications were checked against type specimens in the Cushman Collection at the U.S. National Museum of Natural History. Appendix 1 is the taxonomic list of species, and Appendix 2 presents the numbers of each species in the 203 samples.

AGE DETERMINATIONS

Ages for the cores were determined with ^{210}Pb in their upper parts and ^{14}C in the lower parts. Age models were calculated for each core using the ^{210}Pb radiometric method, which is well developed for dating sediments of the last 150 years (Goldberg, 1963; Appleby and Oldfield, 1992), including those of Florida Bay (Robbins and others, 2000; Holmes and others, 2001). Samples were analyzed for ^{210}Pb activity every 2 cm in each core by alpha spectrometry according to the methods of Flynn (1968) using a secular equilibrium model (Holmes and others, 2001) at the U.S. Geological Survey, St. Petersburg, Florida. Supported ^{210}Pb activity was determined by continuing measurements until the activity became constant with depth, and excess ^{210}Pb activity was calculated by subtracting the supported ^{210}Pb activity from the total ^{210}Pb activity. In these age models, the atmospheric ^{210}Pb flux and sediment accumulation rate were assumed to be constant, and any variability in ^{210}Pb concentrations except for decay was averaged by sedimentological processes.

The limitations of ^{210}Pb dating preclude precise inter-site comparisons of interannual trends, especially during the late 19th to early 20th centuries, when the precision of ^{210}Pb dating is diminished. In general, the age error is about ± 2 years for samples deposited in the last 20 years, and about ± 5 years for older samples down to the level at which values are constant. In this project, we focus on the 1880–2001 period, although results from lower levels (some of

TABLE 2. Radiocarbon dates for Bob Allen Bank, Trout Cove, and Ninemile Bank cores obtained from Beta Analytic Laboratory, Miami. Ages were corrected for $^{13}\text{C}/^{12}\text{C}$, and global and local geographic reservoir effects (Talma and Vogel, 1993) prior to calibration ($^{13}\text{C}/^{12}\text{C} = 1.6$; local reservoir effect = -5 ± 20 ; global reservoir effect = -200 to 500). The database of Marine 98 (Stuiver and others, 1998) was used for calibration. The two-sigma age range is calculated for a 95% probability, recommended for interpretation.

Site	Depth (cm)	Material analyzed	Measured radiocarbon age (YBP)	Conventional radiocarbon age (YBP)	Two-sigma age range (cal. YBP)
Bob Allen Bank	58–60	<i>Brachiodontes</i> (mussel) valve	210 \pm 40	630 \pm 40	360–240
Trout Cove	56–58	3 0.5-cm-thick bivalves	250 \pm 40	630 \pm 40	360–240
	88–90	1.3-cm high-spired gastropod	1270 \pm 40	1640 \pm 40	1280–1130
Ninemile Bank	120–122	<i>Brachiodontes</i>	2340 \pm 40	2750 \pm 40	2660–2340
	152–154	<i>Brachiodontes</i>	2800 \pm 40	3210 \pm 40	3150–2920
	178–180	3 0.5-cm bivalves, <i>Brachiodontes</i> fragment	3030 \pm 40	3400 \pm 40	3360–3200
	20–210	1 0.5-cm broken gastropod	3210 \pm 40	3590 \pm 40	3580–3390
	228–230	2 gastropod fragments: topshell & olive shell	3320 \pm 40	3720 \pm 40	3800–3530

which have ^{14}C ages) are presented to show the historical range of variability.

Ages of samples from Ninemile Bank and Trout Cove that were outside the limit of ^{210}Pb dating were measured by the Beta Analytic Radiocarbon Dating Laboratory, Miami. The longest core, from Ninemile Bank, was chosen because its oldest (deepest), mangrove peat samples recorded the initial flooding of the bay. Samples from the shortest core, from Trout Cove close to the mainland, were dated to determine their similarity to earlier, presumably shallower water samples from Ninemile Bank. Radiocarbon ages were analyzed by synthesizing sample carbon to benzene (92% C), measuring for ^{14}C content in one of 53 scintillation spectrometers, and then calculating age. Marine carbonate samples were corrected for $^{13}\text{C}/^{12}\text{C}$, and for global and local geographic reservoir effects (Stuiver and others, 1998). The radiocarbon calibrations were calculated using the 1998 calibration database (Talma and Vogel, 1993; Stuiver and others, 1998). Following standard practice, calibrated radiocarbon ages (Table 2) are presented in years before present (YBP).

DATA ANALYSIS

Two types of cluster analysis and the index Fisher's α (Fisher and others, 1943) were used to analyze the similarity and diversity of the benthic foraminiferal assemblages, respectively. Counts of species with more than 1% abundance in any sample were transformed from percentage data using the relationship $2 \arcsin p^{1/2}$, where p = percentage (Buzas, 1970). The CONISS (CONstrained Incremental Sum of Squares) program for stratigraphically constrained cluster analysis (Grimm, 1987) was run on the assemblages of each core to investigate the similarity of vertically contiguous samples, and to plot relative abundances of taxa. CONISS is primarily a multivariate method for quantitative definition of stratigraphic zones, traditionally used in pollen analyses. As opposed to standard, unconstrained cluster analysis (below), only stratigraphically adjacent clusters are considered for merging so that larger, consecutive habitat changes can be identified.

Standard cluster analysis, a multivariate procedure for detecting natural groupings in data, was performed with SYSTAT (Wilkinson and others, 2004). Results are presented from Ward's method (Milligan, 1980) for

calculating the distance between two clusters, although five other methods achieved similar results. The assemblages from the offshore Ninemile Bank and coastal Trout Cove cores were analyzed to investigate their degree of similarity through time since the initial flooding of the bay.

Fisher's α was used to measure the species diversity of the benthic foraminiferal assemblages. Diversity within a particular area is commonly used to aid interpretations of environmental conditions (e.g., Murray, 1991; Jain and Collins, 2007) in general, more stressful conditions result in lower diversities.

RESULTS

Seventy-six benthic foraminiferal species (26 of which were figured by Cheng, 2010), ranging from 25–36 taxa/sample, were identified from 203 sediment samples collected from the six Florida Bay cores. Foraminiferal assemblages were dominated by calcareous forms, with agglutinated species constituting <1% of most samples. Soritidae such as *Archaias angulatus* (Fichtel and Moll), *Articulina mucronata* (d'Orbigny), *Peneroplis proteus* d'Orbigny and *Spiroculina eximia* Cushman occurred at low frequencies. Common hyaline species included *Ammonia tepida* (Cushman) gr., *Rosalina floridana* (Cushman), *Elphidium galvestonense* Kornfeld, *E. poeyanum* (d'Orbigny), *E. mexicanum* Kornfeld and *Haynesina depressula* (Walker and Jacob). The most common miliolids were *Heterillina cribrostoma* (Heron-Allen and Earland), *Triloculina fitterei* Acosta, *T. rotunda* d'Orbigny, *Biloculina eburnea* (d'Orbigny), *Quinqueloculina akneriana* d'Orbigny, *Q. bosciiana* d'Orbigny, *Q. polygona* d'Orbigny, *Q. poeyana* d'Orbigny, *Q. subpoeyana* Cushman and *Pateoris dilatata* (d'Orbigny).

The two main associations of species (Table 3) recognized in these shallow habitats are: 1) an *Ammonia tepida* gr. association (referred to as the *Ammonia* association) related to coastal mangrove settings with a 0–20 salinity range, and including *A. tepida* gr., *E. galvestonense*, *E. poeyanum* and *H. depressula*; and 2) a *Quinqueloculina* spp. association present in deeper marine environments with relatively higher salinities ranging 32–65 that includes *Quinqueloculina* spp., *Triloculina* spp., *P. proteus* and *A. angulatus* (Phleger, 1966; Lidz and Rose, 1989; Murray, 1991; Brewster-Wingard and Ishman 1999; Ishman 2001).

TABLE 3. The two environmentally defined foraminiferal associations and their habitats, as compiled from the literature.

	<i>Ammonia tepida</i> gr. Association	<i>Quinqueloculina</i> spp. Association
Taxa	<i>Ammonia tepida</i> gr. <i>Elphidium galvestonense</i> <i>Elphidium poeyanum</i> <i>Haynesina depressula</i>	<i>Quinqueloculina</i> spp. <i>Triloculina</i> spp. <i>Peneroplis proteus</i> <i>Archaias angulatus</i>
Substratum	Calcareous sands and silts	Turtle grass (<i>Thalassia testudinum</i>), carbonate sand, mud, fine quartz sand
Habitat	Intertidal mangrove swamps, brackish, <20 psu	< 12 m water depth, normal marine to hypersaline, 32–65 psu

To avoid misidentification, we designate the *A. tepida* specimens as a taxonomic group. Analysis of foraminiferal DNA (Hayward and others, 2004) shows apparent misidentification of other species of similar morphology. The Florida Bay specimens of *A. tepida* gr. compare well with the *A. tepida* lectotype and paralectotypes from Puerto Rico (Hayward and others, 2003) and with (unpublished) individuals from the Indian River, eastern South Florida. However, our specimens also agree with the morphology of molecular type T11 from Cuba of Hayward and others (2004, pls. 2–4), which were distinguished from other taxa of Cuba and Puerto Rico with similar morphologies.

We used stratigraphically constrained cluster analysis on the total assemblages in each of the six cores to identify the largest changes, which are the cut points between the clusters. To interpret possible habitat changes at these points we compared the relative abundances of the *Ammonia* and *Quinqueloculina* associations, together with diversity (Fisher's α). Below, patterns of change in the benthic foraminifera are summarized for the four sites.

Bob Allen Bank Cores #122 and #124

The constrained cluster analyses (Figs. 2A–B) and proportions of the *Ammonia* and *Quinqueloculina* associations (Figs. 3, 4) have similar trends in the two cores, which are described together chronologically. Core #124 had its largest change, separating clusters 1 and 2, in ~1590–1710 (Fig. 2B) when the *Ammonia* association was highest (Fig. 3) and *Quinqueloculina* association near-lowest (Fig. 4). Subsequently, until ~1880 (core #124), the *Ammonia* association declined to its lowest values. Around 1907–1910 in both cores, assemblages changed greatly as shown by dashed lines that distinguish major clusters (1a vs. 1b for #122, 2a vs. 2b for #124); the *Ammonia* association reached highs of ~50% and the *Quinqueloculina* association fell to its lowest values of <20%. After 1910 in both cores, the *Quinqueloculina* association gradually rose to ~50%, and the *Ammonia* association in 1932–1934 dropped to lower levels of ~20%. In core #122, the drop in the *Ammonia* association helps separate clusters 1 (pre-1934) and 2 (post-1942), and pre- vs. post-1990 assemblages are further distinguished in clusters 2a and 2b, respectively.

Forty-five species were identified in 18 samples from core #122 and 29 samples from core #124. Before ~1880, there were larger fluctuations to higher levels of diversity (Fisher's α , Fig. 5) than afterwards. From 1889 on, Fisher's α in core #124 fluctuated around 5–6 and in core #122 around 6–7 (increasing to 7–8 in 1977–1987), with mostly parallel trends in the cores after 1940. The large faunal change and crash in the *Ammonia* association around 1932–

1934 corresponded to a change in diversity only in core #124 as a decrease in α from 7 to 4.

Russell Key Cores #125 and #127

The two Russell Key cores (Figs. 2C–D) show similar patterns of faunal change and proportions of the *Ammonia* association that are synchronous within age error. In core #125, percentages of the *Ammonia* association were moderate (~20–30%) in the late 1800's and succeeded by lower levels of <20% until rising to their highest peak (42%) in 1928, the time of greatest faunal change as shown by the cut point between clusters 1 and 2 (Fig. 2C). Core #127, which begins at 1918, also had lower levels of the *Ammonia* association (~10%) until a peak in 1938, when the largest faunal change occurred (between clusters 1 and 2, Fig. 2D). The next large faunal change detected in core #125 is between 1964–1967 (division of clusters 2a and 2b, Fig. 2C) and in core #127 between 1955–1962 (division of clusters 2a' and 2a'', Fig. 2D). Both assemblage changes are synchronous between cores within age error and correspond to doubling of proportions of the *Ammonia* association (Fig. 3), which fluctuated with larger amplitude from that point on. The proportion of the *Quinqueloculina* association generally decreased when the *Ammonia* association increased.

Fifty-one species were identified in each core from 37 samples of core #125 and 24 samples of core #127. Diversity in both cores as measured by Fisher's α generally increased from ~4 in 1911 (#125)/1918 (#127) to 6–7 in ~1960. After a dip lasting until ~1970, α increased to high levels ($\alpha = 10$ in core #127) until ~1975, after which it varied between ~5–8 with no general trend. There is no clear correspondence between changes in diversity (Fig. 5) and the magnitude of changes in either the whole fauna (Figs. 2C–D) or the proportions of the ecological associations (Figs. 3–4).

Trout Cove Core #1211

Core #1211 generally contains higher proportions of the *Ammonia* association (~50–90%, Fig. 3) and lower proportions of the *Quinqueloculina* association (~10–25%, Fig. 4) than the other cores have. The largest faunal change, separating clusters 1 and 2 at 70–76 cm (Fig. 2E), occurred around 1141–809 YBP (by linear interpolation between ^{14}C ages; Table 2), when the mean *Ammonia* association dropped from 76% for cluster 1 to 66% for cluster 2, and the mean *Quinqueloculina* association increased from 13% to 17%. The next-largest faunal change occurred between 1880–1891.

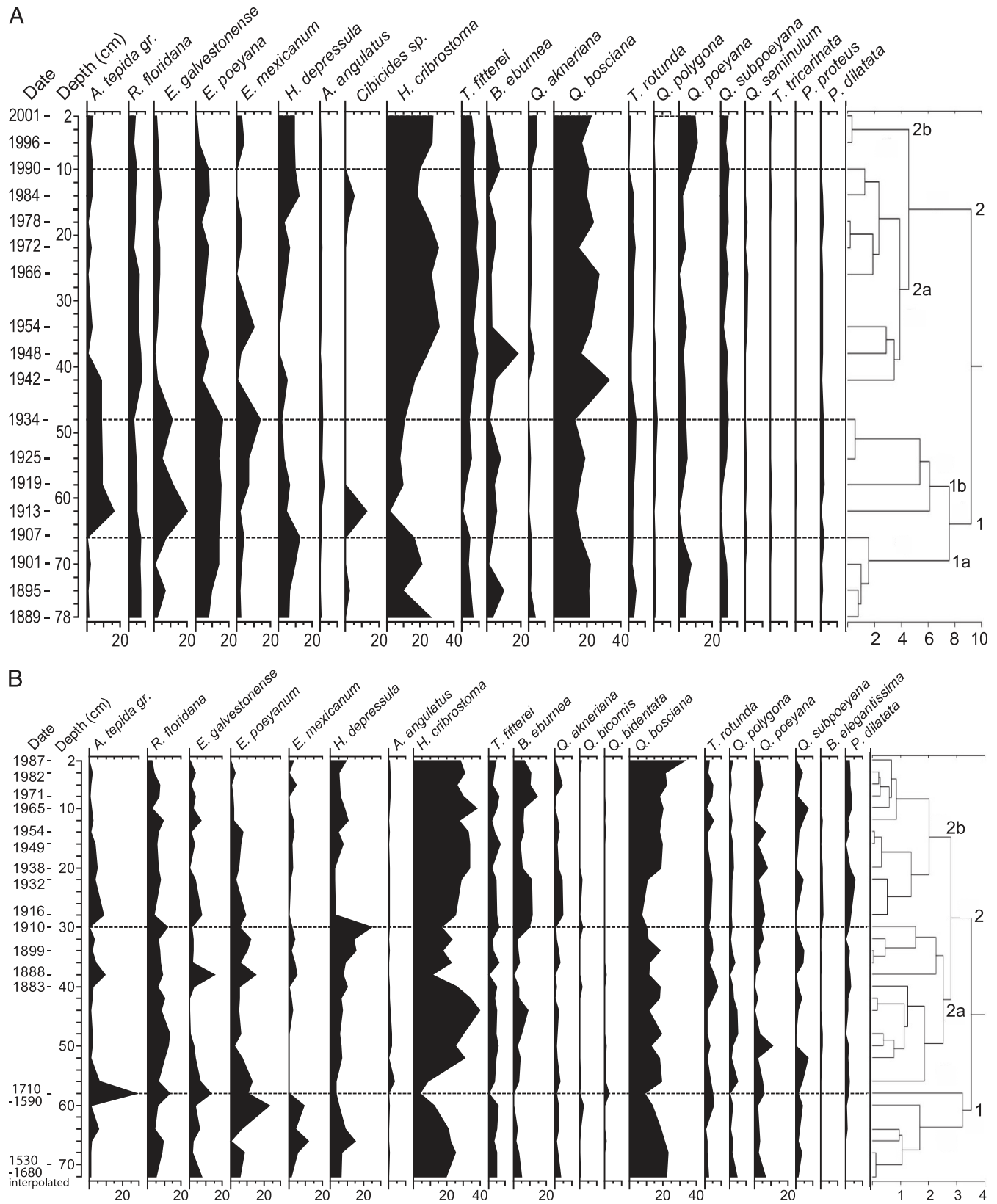


FIGURE 2. Curves of percentages of common benthic foraminifera, and constrained cluster analyses (units are total sum of squares) of all taxa including those not shown by curves. A. Bob Allen Bank core #122, B. Bob Allen Bank core #124, C. Russell Key core #125, D. Russell Key core #127, E. Trout Cove core #1211, and F. Ninemile Bank core #134. Dates are ages of the identified assemblages, except for ^{210}Pb ages of part F, which are shown at decadal intervals.

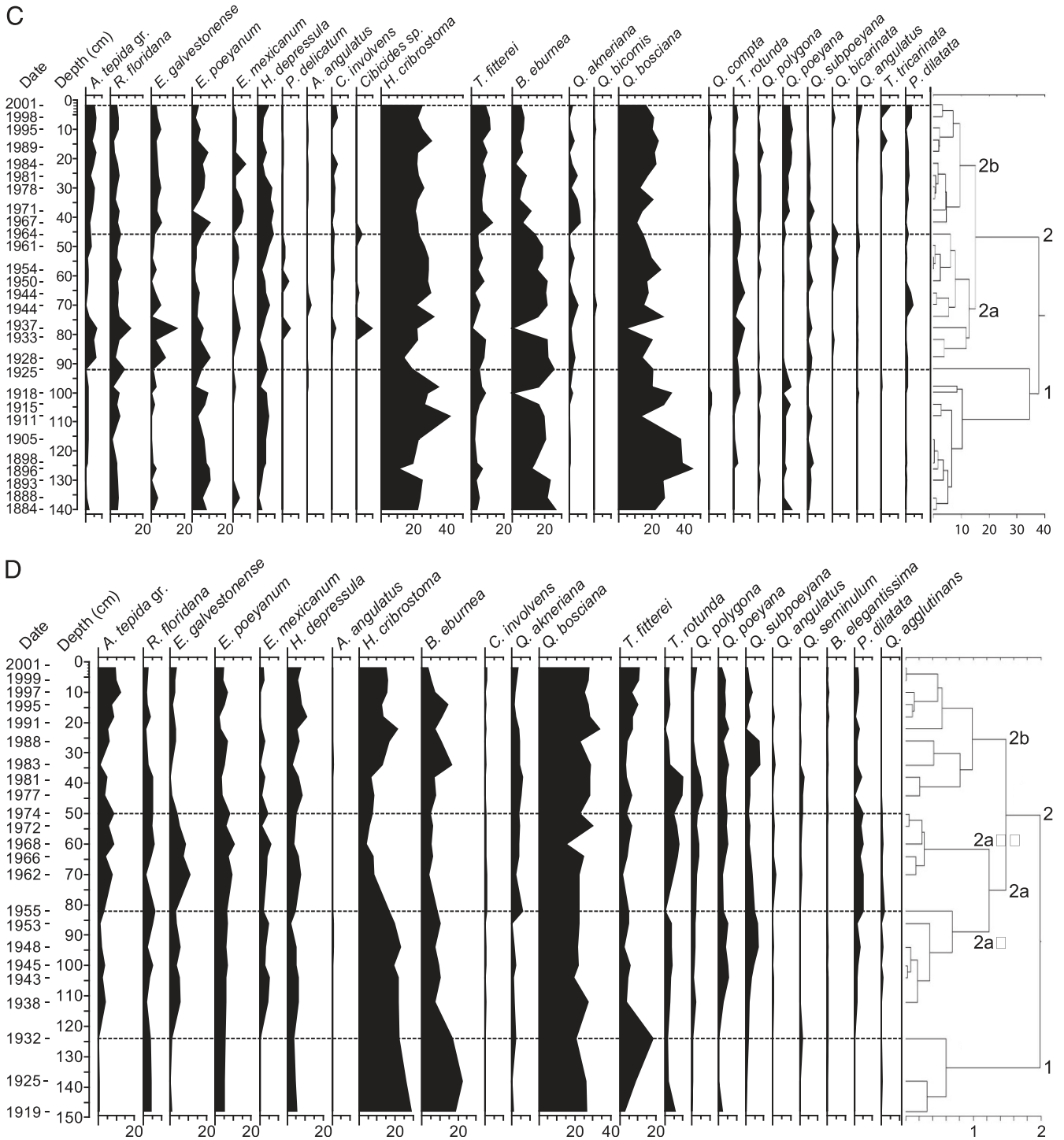


FIGURE 2. Continued.

Forty-five benthic foraminiferal species were identified from core #1211. Fisher's α for the assemblages ranged 4–7 (Fig. 5). The largest sustained trend after 1880 was an increase from ~5 in 1950–1980 to 7 in 1984–1994.

Ninemile Bank Core #134

The *Ammonia* association dominates the two mangrove peat assemblages (85% mean; Fig. 3) at the base of the core,

where *A. tepida* gr. and *Elphidium* spp. compose almost 80% of the fauna, although *Haynesina depressula* (part of this association; Table 3) averages only 7% (cluster 1a, Fig. 2F). During the years spanned by cluster 1b, ~3665–3280 YBP (^{14}C range midpoints; Table 2, 230–178 cm), the *Ammonia* association dropped to a mean of 27% (Fig. 3), the *Quinqueloculina* association rose from a mean of 4% in the basal peats to 22%, and the quinqueloculinid *Heterillina cribrostoma* (ecology unknown) dominated at up to 45%.

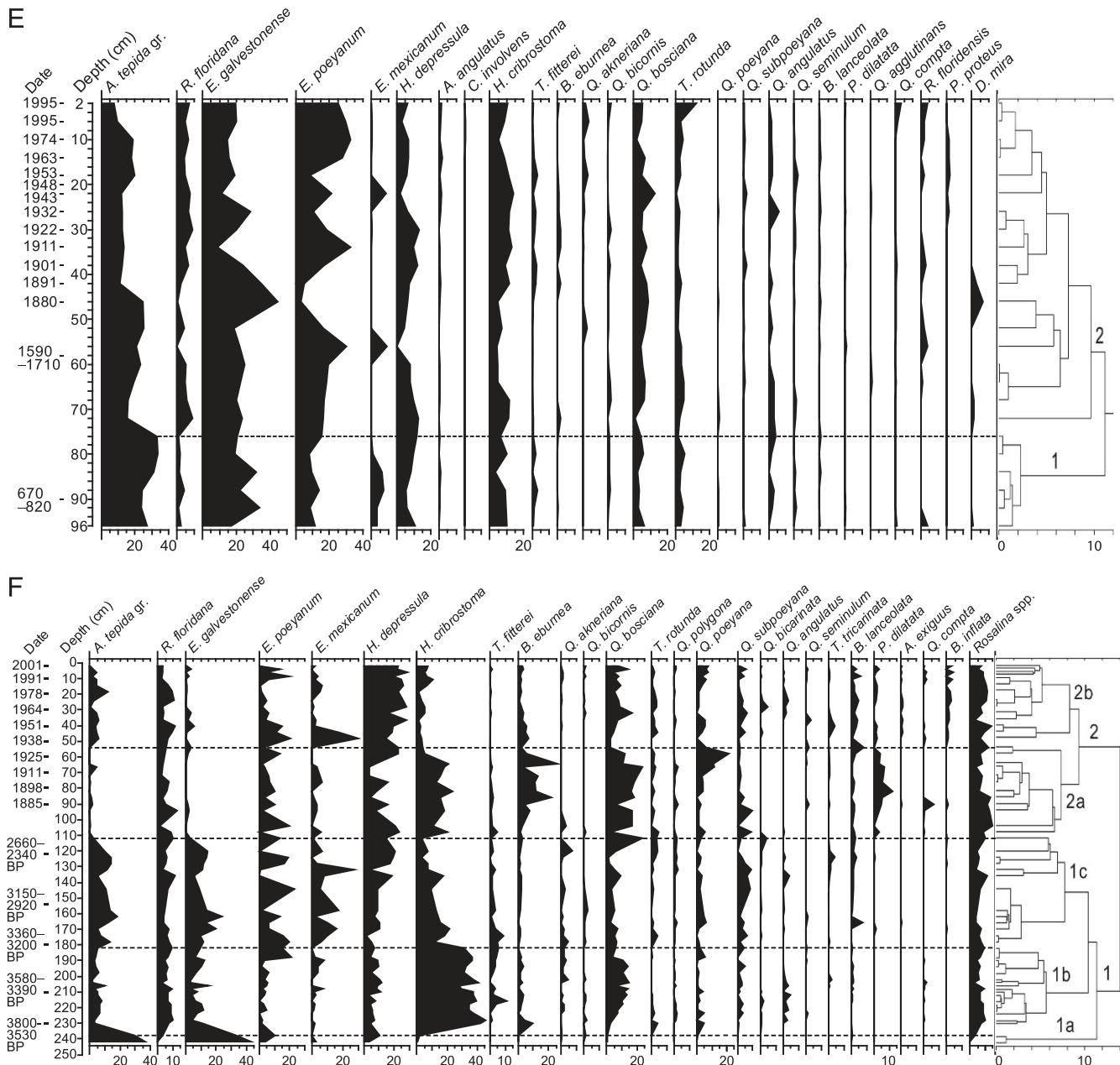


FIGURE 2. Continued.

From ~3280 (178 cm) to ~2300 YBP (110 cm, extrapolated from the highest ^{14}C age using the mean sediment accumulation rate of underlying sediments), which is the timespan of cluster 1c, the *Ammonia* association occurred at higher percentages, averaging 52% (Fig. 3). The largest faunal change (cluster 1–2 boundary, Fig. 2F) was marked by decreasing percentages of most species in the *Ammonia* association (Fig. 3), which averaged 26% of the cluster 2a fauna.

Within the last 120 years (dated with ^{210}Pb), the largest assemblage change occurred between 1932–1940 (cluster 2a–2b boundary), during which the *Ammonia* association (especially *H. depressula*, Fig. 2F) rose to its highest proportion of 71%, while the *Quinqueloculina* association fell to its lowest point of 7%. After 1940, mean percentages

of the *Ammonia* association (38%) and *Quinqueloculina* association (24%) were relatively moderate.

Forty-eight benthic foraminiferal species were identified from the 58 studied samples of the Ninemile Bank core. Diversity (Fisher's α) was lowest at ~4000 YBP in the two basal samples containing mangrove peat fragments (Fig. 6), then rose to fluctuate at ~5–8 until between 1966–1972, after which it increased again to between 8.5–11.5. The large 1909–1951 dip in the Fisher's α curve (Figs. 5, 6) reached the lowest diversity (excluding the basal samples) of 4 in 1927. The diversity dip spans the time of a large pulse of the *Ammonia* association that peaked in 1940.

A stratigraphically unconstrained cluster analysis (Fig. 7) investigated the similarity of assemblages from the mangrove-peat-containing samples at the base of the Ninemile

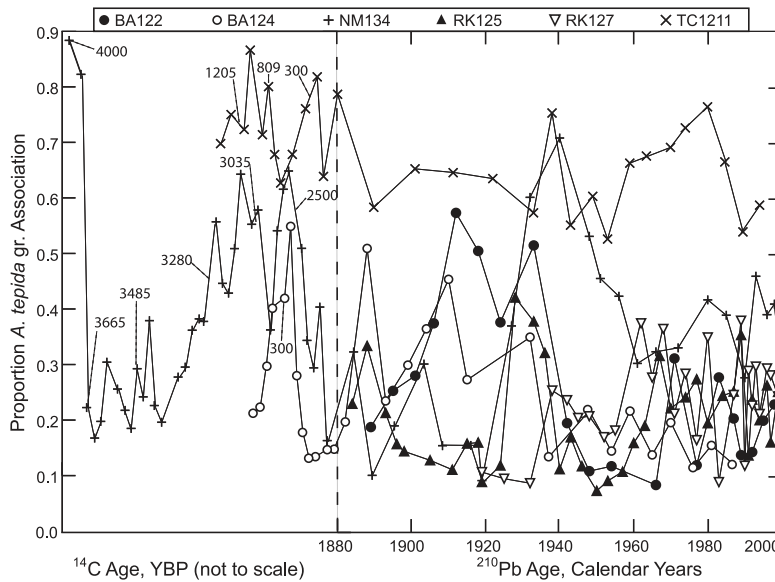


FIGURE 3. Proportion of the *Ammonia tepida* gr. association (Table 3) in the core samples. Ages after 1880 were determined from the ²¹⁰Pb method. Ages before 1880 are midpoints of radiocarbon age ranges.

core and assemblages of the Trout Cove core taken next to the mainland. The analysis clearly differentiates the two sites' assemblages, except that Trout Cove cluster 1 includes the bottom two peat-containing samples of the Ninemile Bank core as well as the 160–162 cm sample.

DISCUSSION

All benthic foraminiferal assemblages of Florida Bay from the past 4000 years are of relatively low diversity (Fig. 5, Fisher's $\alpha < 12$) when compared to coastal lagoons of the Caribbean (e.g., Collins, 1999, mean of $\alpha = 20$) and Gulf of Mexico (Murray, 2006, < 14), but are consistent with other Florida bays and lagoons (e.g., Biscayne Bay; Carnahan, 2005, $\alpha < 11$). The low diversities reflect the relatively unstable conditions characterized by a large annual variability in freshwater input, seasonal rainfall,

salinity, nutrients, pH, and turbidity (Rudnick and others, 1999; Wardlaw, 2001; Kelble and others, 2007). The bay has also experienced longer-term changes from extreme natural events such as droughts, and anthropogenic causes including construction of canals and water retention areas that cut off freshwater flow through the Everglades.

Trout Cove assemblages differed substantially from the others except for those of Ninemile Bank's basal mangrove peats (Fig. 7), deposited during the initial marine flooding. All Trout Cove assemblages had low percentages of the *Quinqueloculina* association (Fig. 4) and domination by the *Ammonia* association (Fig. 3), which is typical of intertidal mangrove swamps.

The four central bay cores from Bob Allen Bank and Russell Key, farthest from mainland and Gulf of Mexico influences, contain proportionately more *Quinqueloculina* association than does the Trout Cove core, reflecting the

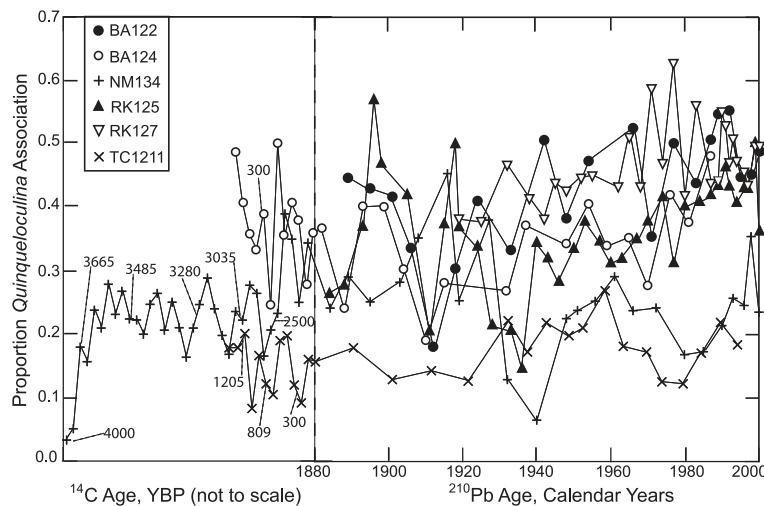


FIGURE 4. Proportion of the *Quinqueloculina* spp. association (Table 3) in the core samples. Ages after 1880 were determined from the ²¹⁰Pb method. Ages before 1880 are midpoints of radiocarbon age ranges.

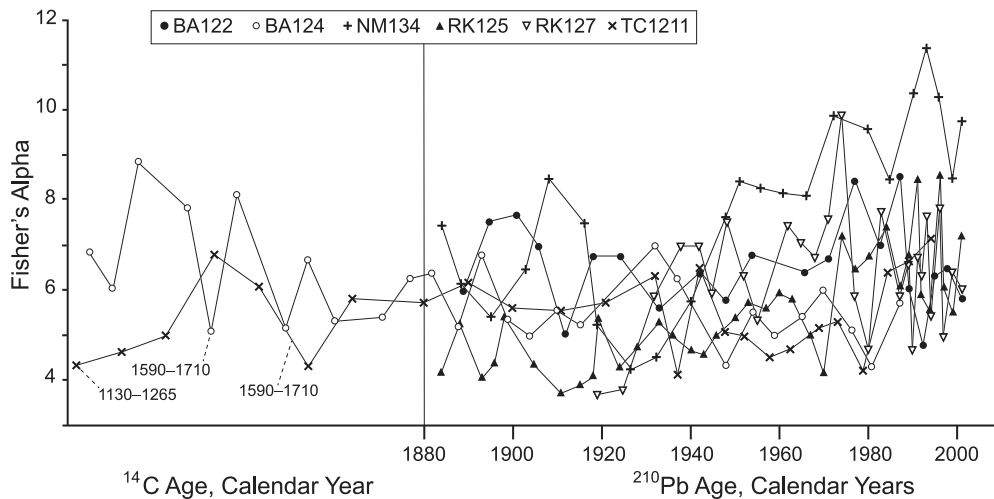


FIGURE 5. Fisher's α from the six cores from Bob Allen Bank, Russell Key, Ninemile Bank, and Trout Cove. Symbols as in Figures 3 and 4.

deeper, normal marine setting over the last 120 years. At both Bob Allen Bank sites, a large peak in the *Ammonia* association 1907–1910 was coincident with a reduction in the *Quinqueloculina* association at those sites and Russell Key. These trends suggest a salinity decrease, also interpreted from foraminifera (but not mollusks) in a study by Brewster-Wingard and Ishman (1999). In two of three central bay cores, diversity decreased 1900–1910 (Fig. 5), possibly in relation to this change. A potential cause for salinity change during this period was the 1905–1912 construction of the railroad from the mainland through the Florida Keys, which restricted inflow from the Atlantic Ocean. A small yet significant increase in the $\delta^{18}\text{O}$ of a Florida Bay coral skeleton at this time (Swart and others, 1996) could reflect a slight increase in salinity; however, input of Everglades water, which has undergone considerable evaporation, can also cause increasing $\delta^{18}\text{O}$ in the bay (Swart and others, 1996). Additional influence by mainland runoff, coincident with increased rainfall or increased restriction of Atlantic waters, may have caused a salinity decrease.

In the central bay since the 1920s, increasing proportions of the *Quinqueloculina* association in three cores (and in the fourth after 1940) indicate higher salinity (>32), which agrees with interpretations of stable-isotope values of a reef

coral (Swart and others, 1996) and foraminifera (Brewster-Wingard and Ishman, 1999). The post-1920s pattern of increasing salinity contradicts Russell Key microfossil data that indicate decreasing salinity after 1958 (Wardlaw, 2001), illustrating the need for analysis of multiple cores per site and multiple sites in coastal waters with highly variant conditions. Most previous studies have suggested that a long-term increase in salinity began with more restricted inflow from dumping fill between the Florida Keys for railroad construction 1905–1912, followed by decreased runoff due to canal construction in the Everglades (1907–1929).

In the central bay after 1962, the amplitude of variation in both the *Ammonia* association (Fig. 3) and diversity (Fig. 5) was much greater, probably because of larger shifts in salinity caused by water management practices. Previous studies of salinity proxies (Brewster-Wingard and others, 1998; Brewster-Wingard and Ishman, 1999) noted a similar increase in variation after ~1940. Possible reasons for this difference in the perceived onset of larger salinity shifts include the greater number of faunal groups and additional geochemistry of the previous studies, our greater number of studied cores, and natural variation in conditions across the bay. By the early 1960s the larger salinity swings corresponded to increased freshwater management such as

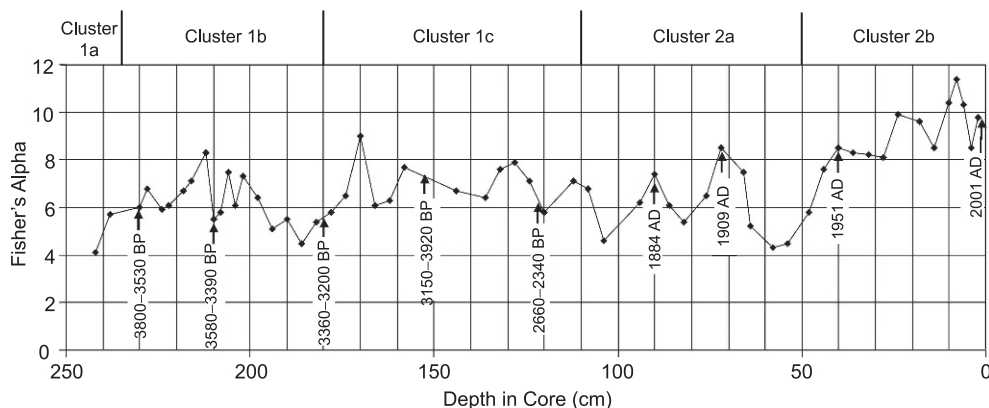


FIGURE 6. Fisher's α from Ninemile Bank, last ~4000 years. Clusters as in Figure 2F.

plunged and remained relatively low at all sites except brackish Trout Cove.

After the hurricanes' flushing of the bay, the long-term result of reduced circulation caused by construction of the Florida Keys railroad was apparently an increased retention of organic materials in the bay. After 1932, a shift at Ninemile Bank to the highest abundances of typically infaunal *Bolivina* taxa (*B. inflata* and *B. lanceolata*, Fig. 2F) indicates more organic-rich conditions (Sen Gupta, 1999; Ishman, 2001; Scott and others, 2001). After 1948, more eutrophic conditions in connection with more restricted circulation were indicated by $\delta^{13}\text{C}$ values of a Florida Bay reef coral (Swart and others, 1996, 1999).

Despite human-induced environmental degradation of the last 100 years, foraminiferal diversity (Figs. 5, 6) increased at most sites. At Ninemile Bank over 4000 years, Fisher's α remained mostly between 4 and 8 until after 1950, when it increased to >11 . In the central bay, diversity increased at Russell Key sites from about 4 to 8, but at Bob Allen Bank it generally decreased over the last 400 years from about 8 to 6. At Trout Cove, values were highest in the last ten years. Clearly, anthropogenic environmental stressors were not great enough to have reduced foraminiferal diversity.

CONCLUSIONS

Benthic foraminifera preserved in Florida Bay sediments were used to trace the history of sea-level and salinity changes. The correspondence in time of ecological trends (in the *Ammonia* and *Quinqueloculina* associations) and the largest changes in species' proportions (shown by cluster analyses) to natural and anthropogenic environmental events was evaluated within the age error of the dating methods. Below, the larger habitat changes are summarized in relation to the series of environmental events.

1. About 4000 YBP at Ninemile Bank, the initial marine flooding of Florida Bay was recorded by very high proportions of the intertidal mangrove *Ammonia* association and very low proportions of the normal marine to hypersaline *Quinqueloculina* association. These basal assemblages are similar to those in modern Trout Cove next to the mainland and near mangroves with high freshwater input, supporting this placement of a ~4000-year-old shoreline.
2. Around 1907–1910, large changes in central-bay assemblages from Bob Allen Bank and Russell Key indicate decreased salinity, possibly from an increased influence of mainland runoff due to more restriction of open-ocean exchange caused by construction of the Florida Keys railroad.
3. Since the 1920s in central Florida Bay, salinity increased (>32), as shown at Bob Allen Bank and Russell Key by long-term increases in the proportions of the *Quinqueloculina* association. This trend coincides with, and is attributed to, decreased runoff due to 1907–1929 canal construction in the Everglades to manage water levels for agriculture.
4. Between 1928–1938 at all sites, concurrent peaks in the *Ammonia* association suggest freshening of the bay, possibly resulting from the unusual succession of three strong, relatively wet hurricanes that hit South Florida between 1926–1938.
5. After 1962 in the central bay, larger amplitude changes in the *Ammonia* association and diversity confirm a pattern of greater salinity shifts. Probable causes include water management practices (1960–1963 completion of water retention areas in the Everglades, 1965–1970 short-term plans for water management, and 1970–early 1980s plan for water delivery to Taylor Slough) in addition to natural events such as the 1960–1963 and 1971–1974 droughts.
6. Around 1987 in the central bay, decreases in diversity, increases in infaunal taxa, and decreases in epiphytic species reflect the large, bay-wide seagrass dieoff concurrent in part with drought (Zieman and others, 1999).
7. Fisher's α increased at most studied sites, indicating that any anthropogenic degradation of water quality has not negatively impacted benthic foraminiferal diversity.

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APPENDIX 1

Benthic foraminifera identified in this study.

- Ammobaculites exiguus* Cushman and Brönnimann, 1948
- Ammonia tepida* (Cushman) = *Rotalia beccarii* (Linnaeus) var. *tepida* Cushman, 1926.
- Archaias angulatus* (Fichtel and Moll) = *Nautilus angulatus* Fichtel and Moll, 1803.
- Articulina mucronata* (d'Orbigny) = *Vertebralina mucronata* d'Orbigny, 1839a.
- Biloculina eburnea* (d'Orbigny) = *Triloculina eburnea* d'Orbigny, 1839a.
- Biloculina globosa* (Bornemann) = *Fissurina globosa* Bornemann, 1855.
- Bolivina inflata* Heron-Allen and Earland, 1913
- Bolivina lanceolata* Parker, 1954
- Bulimina elegantissima* d'Orbigny, 1839b
- Cancris sagra* (d'Orbigny) = *Rotalina (Rotalina) sagra* d'Orbigny, 1839a.
- Clavulina tricarinata* d'Orbigny, 1839a

Cyclogyra involvens (Reuss) = *Operculina involvens* Reuss, 1850.
Discorbis mira Cushman, 1922
Elphidium galvestonense Kornfeld, 1931
Elphidium mexicanum Kornfeld = *E. incertum* (Williamson) var. *mexicanum* Kornfeld, 1931.
Elphidium poeyanum (d'Orbigny) = *Polystomella poeyanum* d'Orbigny, 1839a.
Elphidium sagrum (d'Orbigny) = *Polystomella sagrum* d'Orbigny, 1839a.
Fursenkoina pontoni (Cushman) = *Virgulina pontoni* Cushman, 1932.
Gaudryina exilis Cushman and Brönnimann, 1948
Haynesina depressula (Walker and Jacob) = *Nautilus depressula* Walker and Jacob, 1789.
Heterillina cribrostoma (Heron-Allen and Earland) = *Miliolina circularis* var. *cribrostoma* Heron-Allen and Earland, 1915.
Massilina protea Parker, 1953
Miliolinella fichteliana (d'Orbigny) = *Triloculina fichteliana* d'Orbigny, 1839a.
Miliolinella oblonga (Montagu) = *Vermiculum oblonga* Montagu, 1803.
Nonionella atlantica Cushman, 1947
Nonionina grateloupi d'Orbigny, 1839a
Pateoris dilatata (d'Orbigny) = *Quinqueloculina dilatata* d'Orbigny, 1839a.
Peneroplis proteus d'Orbigny, 1839a
Protelphidium delicatulum (Bermudez) = *Elphidium delicatulum* Bermúdez, 1949.
Pyrgo elongata (d'Orbigny) = *Biloculina elongata* d'Orbigny, 1826.
Pyrulina cylindroides (Roemer) = *Polymorphina cylindroides* Roemer, 1838.
Quinqueloculina agglutinans d'Orbigny, 1839a
Quinqueloculina akneriana d'Orbigny, 1846
Quinqueloculina angulatus (Williamson) = *Miliolina angulatus* Williamson, 1858.
Quinqueloculina bicarinata d'Orbigny, 1826
Quinqueloculina bicornis (Walker and Jacob) = *Serpula bicornis* Walker and Jacob, 1798.
Quinqueloculina bidentata d'Orbigny, 1839a
Quinqueloculina bosciiana d'Orbigny, 1839a
Quinqueloculina candeiana d'Orbigny, 1839a
Quinqueloculina compta Cushman, 1947
Quinqueloculina goesi d'Orbigny, 1839a
Quinqueloculina impressa Reuss, 1851
Quinqueloculina laevigata d'Orbigny, 1826
Quinqueloculina lamarckiana d'Orbigny, 1839a
Quinqueloculina planciana d'Orbigny, 1839a
Quinqueloculina poeyana d'Orbigny, 1839a
Quinqueloculina polygona d'Orbigny, 1839a
Quinqueloculina seminulum (Linnaeus) = *Serpula seminulum* Linnaeus, 1758.
Quinqueloculina striata Deshayes, 1833
Quinqueloculina subpoeyana Cushman, 1922
Quinqueloculina tenagos Parker 1962
Rosalina floridana (Cushman) = *Discorbis floridana* Cushman, 1922.
Rosalina floridensis (Cushman) = *Discorbis bertheloti* (d'Orbigny) var. *floridensis* Cushman, 1930.
Spirillina obconica Brady, 1879
Spirillina vivipara Ehrenberg, 1843
Spiroloculina communis Cushman and Todd, 1944
Spiroloculina eximia Cushman, 1922
Trifarina bella (Phleger and Parker) = *Angulogerina bella* Phleger and Parker, 1951.
Triloculina bassensis Parr, 1945
Triloculina bicarinata d'Orbigny, 1839a
Triloculina fiterrei Acosta, 1940
Triloculina gracilis d'Orbigny, 1839a
Triloculina linneiana d'Orbigny, 1839a
Triloculina rotunda d'Orbigny, 1826
Triloculina trigonula (Lamarck) = *Miliolites trigonula* Lamarck, 1804.

APPENDIX 2

All species in six cores from Florida Bay.

Counts of benthic foraminifera. This table can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2011001.