J Paleolimnol
https://doi.org/10.1007/s10933-019-00072-6

ORIGINAL PAPER

Historical seagrass abundance of Florida Bay, USA, based on a foraminiferal proxy

Laurel S. Collins · Jie Cheng · Lee-Ann C. Hayek · James W. Fourqurean · Martin A. Buzas

Received: 10 January 2018 / Accepted: 5 February 2019

Abstract A foraminiferal proxy for seagrass abundance was developed, tested and used to construct a record of seagrass variability for Florida Bay, USA, since its initial flooding ~ 3800 cal years BP. Of 76 species recorded in the Bay, 13 seagrass-associated foraminifera were identified based on previously observed occurrences in seagrass beds of the region. Species that occurred more in seagrass beds than in other sediments were designated seagrass-associated foraminifera (SAF). SAF from six cores taken in four areas were tested against a large, well-studied seagrass die-off that began in 1987. SAF percentages of total foraminiferal assemblages declined in 1986 (^{210}Pb age, ± 2 years) with no recovery as of 2001 (the youngest core age), and discriminant analysis showed that SAF assemblages in 1970–1985 and 1986–2001 differed significantly. Results agree with observations of the decline in seagrass coverage, supporting SAF as a seagrass proxy for investigating earlier assemblages preserved in the cores. After anthropogenic influence began ~ 1880, the largest overall decreases in SAF percentages occurred in 1934–1940 (^{210}Pb ages, ± 5 years), possibly from decreased salinities due to three intense hurricanes that hit South Florida, and in

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10933-019-00072-6) contains supplementary material, which is available to authorized users.

L. S. Collins (✉) · J. Cheng
Department of Earth and Environment, Florida International University, Miami, FL 33199, USA
e-mail: collinsl@fiu.edu

L.-A. C. Hayek
National Museum of Natural History, Smithsonian Institution, Mathematics and Statistics, MRC-121, P.O. Box 7012, Washington, DC 20013-7012, USA
e-mail: hayekl@si.edu

L. S. Collins · J. W. Fourqurean
Department of Biological Sciences, Florida International University, Miami, FL 33199, USA
e-mail: fourqure@fiu.edu

J. W. Fourqurean
Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA

M. A. Buzas
Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA
e-mail: buzasm@si.edu

L. S. Collins
Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Republic of Panama

Published online: 28 March 2019

1987–2002 during the seagrass die-off. SAF assemblages in the oldest core record were significantly different over the four intervals of (1) initial flooding ~ 3800 cal years BP, (2) pristine conditions until ~ 1880 when agriculture and canal construction began, (3) anthropogenic and climatic influences 1880–1986, and (4) the 1987–2002 seagrass die-off. Historically, SAF assemblages indicate that this die-off resulted in extremely low coverage (comparable to inundation and development of the benthic ecosystem > 2500 cal years BP), probably a result of cumulative anthropogenic disturbance combined with natural events. This is the first study using foraminifera as a proxy to reconstruct the seagrass history of an area. The research introduced a new approach for developing a seagrass proxy: we identified species that are more abundant in seagrass beds than in other sediments, and tested them together as a proxy against a previously documented seagrass die-off.

Keywords Benthic foraminifera · Everglades · Florida Bay · Seagrass · Paleoecology · ^{210}Pb

Introduction

In coastal areas, seagrass abundance is an indicator of ecosystem health (Purvaja et al. 2018), which is altered by natural events such as hurricanes and droughts, and by anthropogenic causes such as agriculture and increased runoff, and storage and periodic release of freshwater. Seagrasses contribute to productivity and the carbon budget, stabilize seafloor sediments, and provide critical habitat for invertebrates and fisheries taxa (Orth et al. 2006). Because seagrasses are sensitive to light availability, salinity variation, and eutrophication, indicators of seagrass coverage can be used as a measure of water clarity and quality (Dennison et al. 1993). Historical accounts of water quality are useful as a calibration for assessing ongoing changes in coastal waters, where about 29% of the known areal extent of seagrass has disappeared since 1879 (Waycott et al. 2009).

Current efforts to restore Everglades National Park and the surrounding tropical wetlands of South Florida to an approximately original state have been guided by investigations of the natural range of ecosystem variability. Paleoenvironmental studies such as this one can assess long-term environmental variability. Beginning in the 1990s, Florida Bay, at the southern tip of the Florida peninsula, was studied with several environmental proxies (Wardlaw 2001). Florida Bay contains one of the world's largest seagrass beds of about 1800 km^2 (Zieman et al. 1989) and drains the Everglades. Herein we construct a record of seagrass coverage for Florida Bay with foraminifera from cores taken at four sites (Fig. 1).

Because seagrasses are rarely preserved in the sedimentary record, we use a proxy based on benthic foraminifera that have a strong association with seagrass beds, termed seagrass-associated foraminifera (SAF). The tests of foraminifera are well-preserved in the sedimentary record and are found in abundance in the Florida Bay cores. Cheng et al. (2012) studied whole assemblages of a total of 76 foraminiferal taxa from these cores and related them primarily to natural and anthropogenic changes in salinity, as did other studies (Brewster-Wingard and Ishman 1999; Wachnicka et al. 2013).

This study had three parts. (1) We first tested the SAF proxy against a large, well-documented 1987–2002 seagrass die-off to assess its validity. (2) Changes in SAF taxa and SAF percentages of total foraminiferal assemblages were then examined at the decadal scale over the last 120 years, comparing their timing to historical events such as the initiation of agriculture and the timing of hurricanes. (3) Finally, at the millenial scale, we analyzed levels of SAF during initial flooding of the Bay ~ 3800 cal years BP, and pre-and post-human intervals.

This is the first study using foraminifera as a proxy to reconstruct a regional seagrass history. Previous research on historical seagrass abundance was based in Australian ecosystems using geochemical proxies (Macreadie et al. 2012; Serrano et al. 2016), and in the western Atlantic using fossil sirenians (Vélez-Juarbe 2014).

Methods

Core sites, collection and sampling

Collins, Fourqurean and others collected sediment cores in 2002 from Trout Cove (offshore of Trout Creek and Taylor Slough), off Russell Key, Bob Allen Bank and Ninemile Bank (Fig. 1, Table 1). The areas

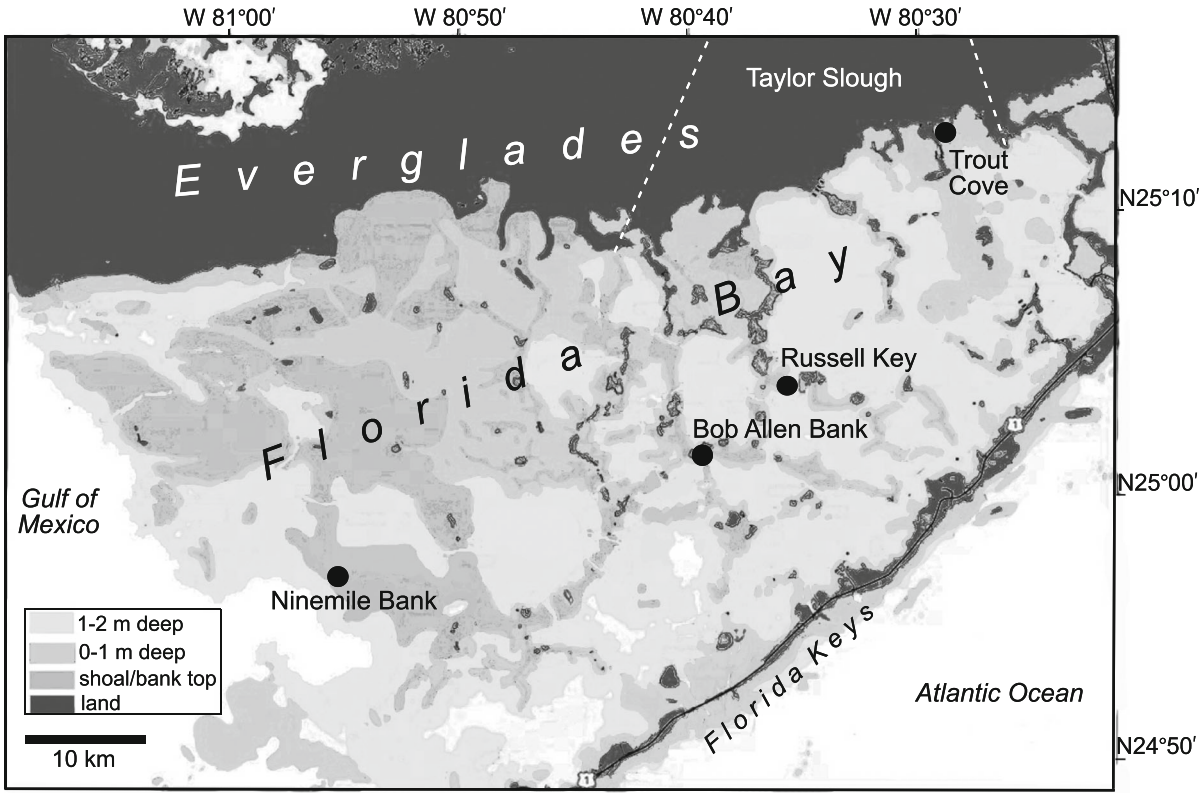

Fig. 1 Coring sites (filled circles) in Florida Bay, showing bathymetry of small basins separated by mud banks and mangrove islands. Ninemile Bank has the most water exchange with the Gulf of Mexico. Bob Allen Bank and Russell Key, central Bay, are most influenced by runoff from the Florida Keys, islands and Everglades, and input from the Atlantic and Gulf of Mexico. Trout Cove, at the mouth of Trout Creek and Taylor Slough, receives the most runoff from the Everglades. Modified from Cheng et al. (2012)

Table 1 Core localities, water depths and lengths

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

(described in detail by Wachnicka et al. 2013) reflect differences in sources of freshwater runoff and external water exchange. Sites with accreting banks were selected to maximize continuity of the sedimentary record (Holmes et al. 2001). At Russell Key and Bob Allen Bank, two cores per site were extracted about 100 m apart to study within-area variability in the central bay, furthest from runoff and the Gulf of Mexico. One core per site was analyzed from

Ninemile Bank at the edge of the Gulf of Mexico, and from Trout Cove at the mouth of Trout Creek.

The cores were collected on a U.S. Geological Survey barge with a mounted derrick and a PVC piston device, following the procedures of Sansone et al. (1994). The device was deployed through a central hole in the deck. The core barrel was pushed through an average of 1.5 m of greenish gray, calcareous mud to indurated Pleistocene limestone. To prevent sediment loss from the core barrel, the bottom was capped. The core barrels were raised with a winch. Cores were transported to the Key Largo Multi-Agency Science Center, Everglades National Park. All cores except the longer, Ninemile Bank core were x-rayed before being sliced into 2-cm-thick portions for analysis. The sediments were mostly bioturbated with little bedding visible by eye or x-radiograph.

Age determinations

Sample ages were determined with ^{210}Pb in their upper parts, and ^{14}C in the lower part of the Ninemile Bank core. An age model for each core was calculated using the ^{210}Pb radiometric method described previously for the Florida Bay cores (Wachnicka et al. 2013). The ^{210}Pb activity was measured in consecutive samples by alpha spectroscopy whereby ^{210}Pb and its decay product ^{210}Po are assumed to be in secular equilibrium. Supported ^{210}Pb activity was determined by continuing measurements until activity became constant with depth, while excess ^{210}Pb activity was computed by subtracting the supported ^{210}Pb activity from the total ^{210}Pb activity. Comparison of interannual trends was not possible due to the ^{210}Pb age error of approximately $\pm$ 2 years for samples deposited in the last 20 years and $\pm$ 5 years for older samples.

The longest (Ninemile Bank) core below supported ^{210}Pb activity was dated with ^{14}C. Five samples of mollusks were analyzed at Beta Analytic Radiocarbon Dating Laboratory, Miami by synthesizing sample carbon to benzene (92% C), measuring for ^{14}C content in one of 53 scintillation spectrometers, and then calculating age. The marine carbonate samples were corrected (Talma and Vogel 1993) for ^{13}C/^{12}C, and for global and local geographic reservoir effects; ^{13}C/^{12}C = 1.6; local reservoir effect = $-$ 5 $\pm$ 20; global reservoir effect = $-$ 200 to 500) prior to calibration with the Marine 98 database (Stuiver et al. 1998). Cheng et al. (2012) list the mollusks analyzed, measured radiocarbon ages, conventional radiocarbon ages and two-sigma age ranges. The ages of the 34 foraminiferal samples were interpolated using midpoints of the two-sigma age ranges (cal years BP) and assuming constant sediment accumulation rates between the ^{14}C ages.

Benthic foraminifera

Two hundred and three sediment samples were disaggregated by soaking in water and sieved to obtain specimens > 63 µm, which should include all adult and nearly all juvenile foraminifera. Dried residues were successively halved with a Gilson microsplitter to produce representative samples of > 300 specimens, generally sufficient to accurately represent species' proportions (Buzas 1990). Foraminifera were removed onto cardboard slides and identified mostly to the species level with taxonomic literature on the tropical to subtropical, western North Atlantic (Bock 1969; Bock et al. 1971; Rose and Lidz 1977; Wantland 1967; Buzas and Severin 1982). Questionable identifications were checked against type specimens in the Cushman Collection of Foraminifera, U.S. National Museum of Natural History, and The Catalogue of Foraminifera (Ellis and Messina, 1941–2009). Abundances of all identified foraminifera and their full taxonomic names were presented by Cheng et al. (2012).

Species were identified as seagrass-associated foraminifera (SAF) from their ecologies as compiled from literature of the region (Table 2). SAF taxa were those found more in seagrass beds than in other sediments. Variations in species' relative abundance distributions and the percentage of SAF throughout the cores were used to interpret fluctuations in seagrass abundance.

Data analysis

Discriminant analysis showed how well time intervals were distinguished by the relative abundances of SAF taxa, where the SAF species for which the locations differ most are more heavily weighted. Proportions of species in an assemblages were first transformed using the relationship arcsin $p^{1/2}$, where p is the percentage (Hayek and Buzas 1997). Fisher's classification function coefficients were used directly for classification. A separate set of classification function coefficients

Table 2 General ecology of predominantly seagrass-associated foraminifera preserved in the six cores

Species	Ecology	References
Articulina mucronata (d'Orbigny)	High frequency in shallow mud flats towards center of Florida Bay, abundant on seagrass through entire year	Bock (1967)
Biloculina eburnea (d'Orbigny)	Primary weed fauna, more important on seagrass than in sediments	Bock (1967), Brasier (1975b)
Cyclogyra involvens (Reuss)	Low frequency, abundant on seagrass	Bock (1967), Brasier (1975b)
Discorbis mira Cushman,	Medium frequency, most common in shallow waters adjacent to lower Florida Keys, found living on *Thalassia* in small populations	Brasier (1975a), Grant et al. (1973), Martin and Wright (1988), Steinker and Raynor (1987)
Miliolinella fichtelliana (d'Orbigny)	Random distribution with low-medium frequency, abundant on seagrass through entire year	Bock (1967), Brasier (1975b)
Pyrgo denticulata Brady	Low frequency, limited to waters adjacent to lower Keys, common on seagrass	Bock (1967), Grant et al. (1973)
Quinqueloculina agglutinans (d'Orbigny)	Frequent in Florida Bay, highest frequencies with coarsest sediment suggest sorting by wave action, dissappears in brackish and deeper waters	Bock (1967)
Quinqueloculina polygona (d'Orbigny)	Limited to carbonate platform and shoals associated with high-diversity, miliolid-dominated enviroments; medium frequencies in Florida Bay, appears mainly restricted to shallow waters	Bock (1967)
Rosalina floridana (Cushman)	Primary weed fauna, more important on seagrass than in sediments	Bock (1967), Brasier (1975a, b), Steinker and Raynor (1987)
Sorites marginalis (Lamarck)	Commonly adheres flush to blades of seagrass	Bock (1967), Brasier (1975b), Martin and Wright (1988), Steinker and Raynor (1987), Steinker and Steinker (1976)
Spirillina vivipara Ehrenberg	Low frequency, common on seagrass	Bock (1967), Brasier (1975a)
Triloculina linneiana d'Orbigny	Restricted to carbonate platform and shoals associated with high-diversity, miliolid-dominated assemblages	Bock (1967)
Triloculina rotunda (d'Orbigny)	Primary weed fauna, more important on seagrass than in sediments	Brasier (1975a, b), Grant et al. (1973)

was obtained for each group using the discriminant model developed, as well as under a jackknife procedure. This procedure, although biased, does provide some information for future sampling results.

The Assemblage Turnover Index (ATI) measured the percent turnover, or change in SAF as a community, from one foraminiferal assemblage to the next youngest. The ATI quantifies the percentage of change overall in species' proportions to identify the times of greatest community change (Hayek and Wilson 2013).

$$\mathrm{ATI} = \sum_{\mathrm{i}} |p_{i2} - p_{i1}| \quad (1)$$

in which p_{i1} and p_{i2} are the proportional abundances of the *i*th species, i = 1,…, s, in the samples or assmblages on either side of a predetermined cutpoint or boundary. Note that although for each sample

$$\Sigma p_i = 1 \quad (2)$$

the measure ATI can be > 1.

Results

The proxy for seagrass abundance was based on seagrass-associated foraminifera (SAF) in South Florida and the Caribbean (Table 2). To test the set of 13 SAF species selected for the proxy from 76 taxa previously enumerated in Florida Bay (Cheng et al. 2012), we compared their relative abundances during the intervals (1) before the seagrass-die-off, 1970–1986; (2) the seagrass die-off's first phase in 1987–1991; and (3) the second phase in 1992–2002. ^{210}Pb ages from ~ 1970 to 2001 (Fig. 2, ESM1) have an error range of < ± 2 years.

The most abundant SAF taxa in the six cores (Cheng et al. 2012) were *Biloculina eburnea* (d'Orbigny), *Quinqueloculina polygona* d'Orbigny, *Rosalina floridana* (Cushman) and *Triloculina rotunda* (d'Orbigny). Percentages of SAF in all cores (Fig. 3) declined from the early 1970s to mid-1980s, before the seagrass die-off, and, with the exception of Trout Cove, reached even lower values during the die-off. A discriminant analysis of SAF in the three intervals shows only the pre-die-off interval 1970–1985 to be significantly distinct (Fig. 4). Although SAF percentages in the five cores from Bob Allen Bank, Russell Key and Ninemile Bank were higher after the first die-off phase, the first and second die-off phases were not significantly different. *Miliolinella fichtelliana* (d'Orbigny), *R. floridana* and *T. rotunda* were significant in separating the pre-die-off from the die-off phases, and Fisher's classification functions and the jackknife estimates classified correctly 66.1% of the originally grouped cases. In contrast, a discriminant analysis of the total assemblages of all 76 foraminiferal taxa shows no significant differences between the pre-die-off and die-off intervals, and *T. rotunda* was the only taxon that separated the pre-die-off from the two die-off phases. The Assemblage Turnover Index (ATI) also indicates larger turnovers in SAF assemblages around 1986 ± 2 years, because the turnover or change per sample for each core is about 2% maximum, compared to much higher values between the pre-die-off interval and beginning of the die-off (Table 3). In addition, although the discriminant analysis showed differences between the two die-off phases to be nonsignificant, the ATI indicated a high SAF assemblage turnover between the two phases.

Beginning with permanent human settlement in South Florida in the late 1880s, the ^{210}Pb-dated record of seagrass abundance using the SAF proxy (with age error of ± 5 years before ~ 1970) shows much variation in trends (Fig. 5). In addition to the mostly lower values during the seagrass die-off, other trends seen in five of six cores are a substantial increase 1919–1925 ± 5 years, and a large drop between 1934 and 1940 ± 5 years with a subsequent rise.

To analyze SAF assemblages in relation to documented anthropogenic and climatic influences, the 1880–2001 record was divided into five intervals defined by land use and, for comparison, the seagrass die-off (Table 4). Percentages of SAF during the die-off (Interval 5) were lowest with a mean of 11%, compared with 17–20% for other intervals. A discriminant model to test differences between intervals (Fig. 6) excluded Trout Cove, at the mouth of Trout Creek, because it contains sparse seagrass beds due to long-term low salinities. The discriminant analysis of SAF assemblages significantly separated the seagrass die-off from the other four time intervals. Interval 1, initial permanent settlement, and Interval 2, agricultural buildup and construction of canals, roads and a coastal railroad, were also significantly different from Interval 4, the period of intensification of agriculture and water management. Classification of the original grouped cases for the five cores was 39–79%, as compared to 28% for the Trout Cove cases using the five-core model.

The longest core, from Ninemile Bank, contained the oldest sediments and was examined with ^{210}Pb and ^{14}C ages (Fig. 7). The mollusk samples analyzed for ^{14}C produced conventional radiocarbon ages (± 40, YBP) sequentially downcore of 2750, 3210, 3400, 3590 and 3720 YBP, with no reversals. Two-sigma age ranges are 2660–2340, 3150–2920, 3360–3200, 3580–3390, and 3800–3530 cal years BP.

Over the past ~ 3800 years, SAF increased rapidly during initial inundation by seawater, attained a relatively low abundance from ~ 3600 to 2300 cal years BP, and increased to a high ~ 1919 A.D. before gradually decreasing to relatively low percentages again during the 1987–2001 seagrass die-off. We conducted analyses on four intervals over which we suspected SAF would have changed: (1) initial flooding, (2) pristine conditions before ~ 1880, when humans permanently settled South Florida and began constructing canals in central Florida to divert freshwater, (3) anthropogenically-influenced coastal conditions 1880–1986, and (4) the

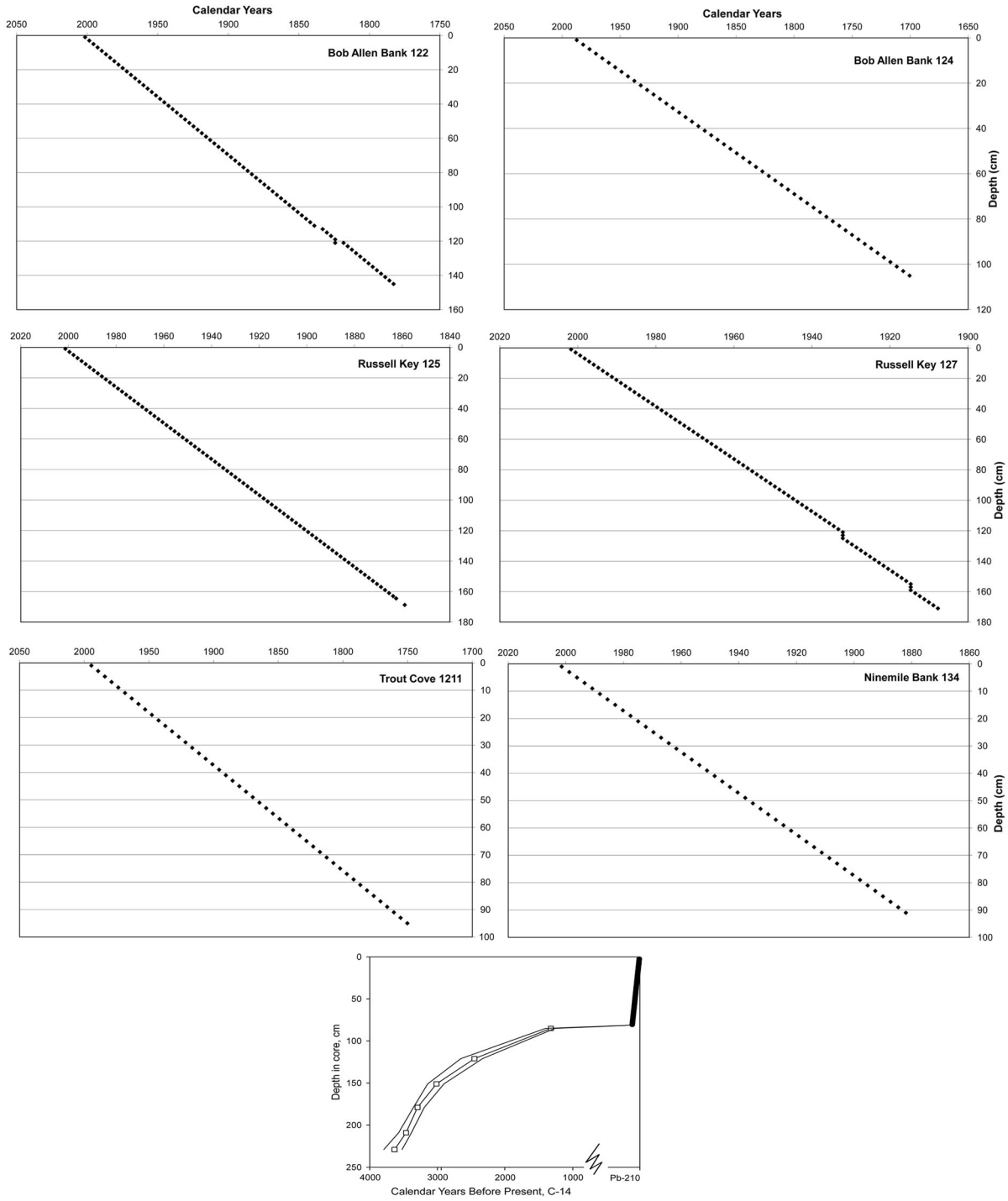

Fig. 2 Ages determined with ^{210}Pb (six plots at top, and broad line with error at bottom) and ^{14}C for Ninemile Bank (at bottom, open squares, error within lines, break in scale between older ^{14}C and younger ^{210}Pb ages)

recent seagrass die-off. A discriminant analysis (Fig. 8) clearly separates the two SAF assemblages in Group 1 (initial flooding of the bay, marked by mangrove peat) from the rest, and although assemblages in the other three groups overlap on the first two canonical axes, each of the four defined groups

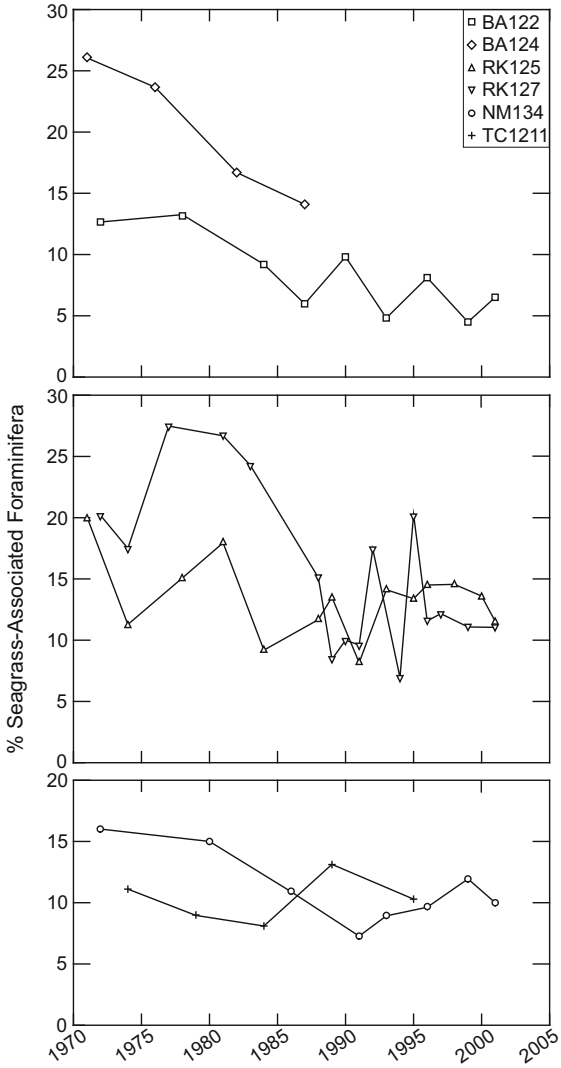

Fig. 3 Percentages of seagrass-associated benthic foraminifera in the six cores, 1970–2001. ^{210}Pb ages, ± ~ 2 years. Note decreasing trend preceding seagrass die-off that began in 1987, and generally lower values afterward, except for Trout Cove site

separated significantly ($p < 0.01$). In all, 70.7% of the original grouped cases were correctly classified. The ATI shows that across the boundaries between each two successive intervals, the greatest difference was a 62% change in species between initial flooding and more normal, pristine conditions, with the other boundary changes only ~ 2%.

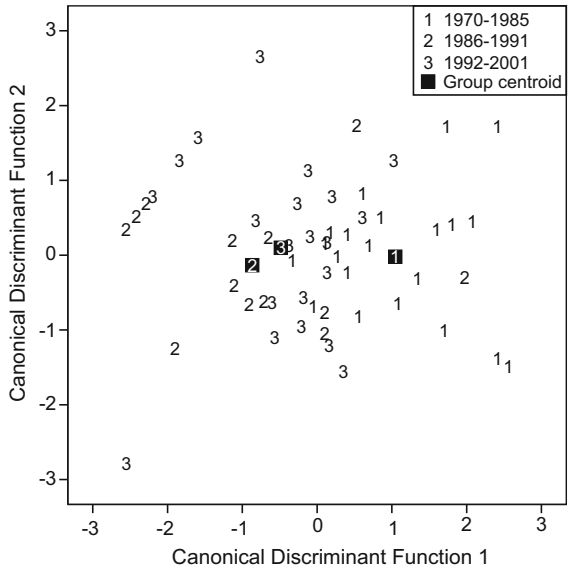

Fig. 4 Plot of discriminant analysis scores on first two axes for seagrass-associated foraminifera (SAF), 1970–2001. SAF assemblages in 1970–1985 (Group 1) and 1986–2001 (Groups 2 and 3 combined) differed significantly, validating the SAF proxy

Discussion

Seagrass-associated foraminifera, 1987–2002 seagrass die-off

Seagrass-associated foraminifera (SAF) in Florida Bay and the Keys (Table 2) typically occur on the broad blades of *Thalassia testudinum* Banks ex König, by far the most widespread and abundant local seagrass, which provides a larger substratum than thinner types and local algae (Bock 1969; Fujita and Hallock 1999). Over 95% of foraminiferal species living in seagrass or macroalgal substrates are permanently or temporarily motile (Langer 1993), so the criterion used was for SAF taxa found more often in seagrass beds or on seagrass than in sediments. A preliminary study (Collins et al. 2004) indicated that foraminifera found on seagrass could distinguish between dense and sparse seagrass beds, but most of the living taxa were delicate forms and less useful because of their poor chance of preservation in sediments over time.

The SAF proxy was tested against the well-documented 1987–2002 seagrass die-off. Prior to the die-off, the seagrasses *Syringodium filiforme* Kuetz, *Halodule wrightii* Asch and *T. testudinum*

Table 3 Assemblage Turnover Index (ATI) percentages for 1970–2001 seagrass-associated foraminifera

Core	Pre-die-off to Die-off Phase 1		Die-off Phase 1 to Phase 2	
	No. of samples	ATI%	No. of samples	ATI%
BA122	3–3	31	3–3	23
BA124	3–1	12	–	–
RK125	4–4	8[a]	4–5	30
RK 127	5–6	47	6–5	47
NM134	3–2	38	2–3	33
TC1211	3–2	20	–	–

[a]If cutpoint moved to 1989–1991, ATI = 73%; – indicates truncation of core

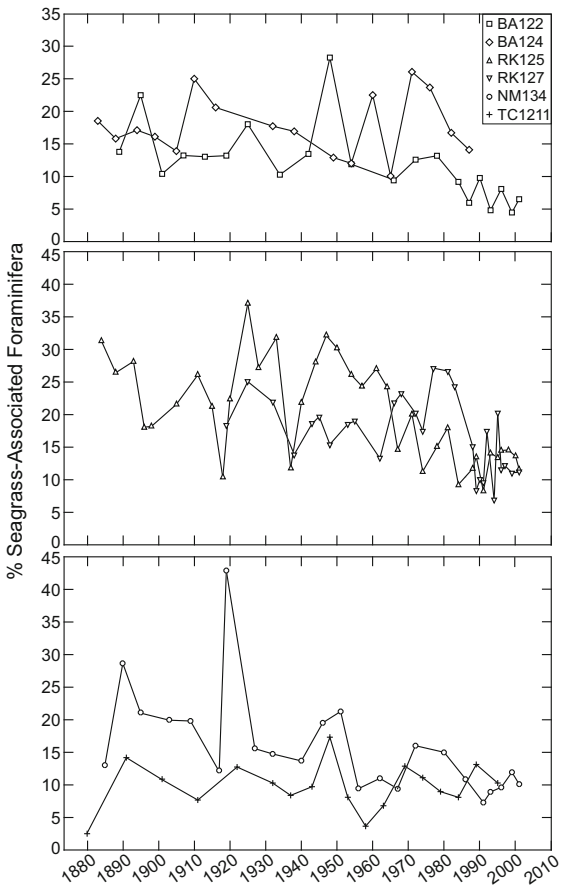

Fig. 5 Percentages of seagrass-associated benthic foraminifera in the six cores, 1885–2001. The largest decreases observed for all sites is for 1934–1940 (± ~ 5 years, ^{210}Pb ages), corresponding to an intense hurrican interval, and in 1987–2002, during the seagrass die-off

covered > 80% of Florida Bay's seafloor (Zieman et al. 1989; Hall et al. 1999). From 1987 to 1991, an initial die-off phase extended from the west to the southeast central bay and only *T. testudinum* experienced significant decline, but by 1991, over 40 km^2 of seagrass beds were denuded and another 240 km^2 were also affected (Fourqurean and Robblee 1999). No pronounced decreases in water clarity or increases in algal abundance were observed before the 1987 die-off, which was caused by chronic hypersalinity, probably hypoxia and sulfide toxicity, and possibly high temperature, and the combined effects of multiple stressors such as a multiyear, late-1980s drought and long-term water management (Borum et al. 2005; Koch et al. 2007). Initial losses resulted in sediment resuspension and phytoplankton blooms leading to extensive, persistent water turbidity, declines in water clarity, and thus, pronounced light attenuation that threatened more seagrass habitat (Fourqurean and Robblee 1999; Fourqurean et al. 2002). From 1991 to 1994, a second phase of the die-off resulted from widespread declines in water clarity due to erosion of the seafloor left bare by the first phase, and from nutrients released from the decaying seagrass biomass, which may, in turn, have led to decreased light attenuation and two interrelated consequences: algal blooms and sediment resuspension (Butler et al. 1995; Zieman et al. 1999; Hall et al. 1999; Durako et al. 2002). From 1995 to 1998, western basins exhibited great losses in biomass, although other parts periodically subjected to low salinities changed little (Durako et al. 2002). Finally, from 1999 to 2002, declines in overall abundance slowed, and seagrass coverage began to increase afterwards (Hall 2012).

The decline in SAF percentages during the 1970s to mid-1980s in all cores except Trout Cove (Fig. 3) suggests that environmental stresses on seagrasses had increased prior to the 1987 die-off. (Trout Cove contains sparse seagrass beds due to long-term low salinity, and SAF percentages conformed less to those in the other five cores throughout the study.) It may be that water allocation plans and drought in the 1970s, and droughts in 1980–1982 and 1985 (Nuttle et al.

Table 4 Time intervals defined by land-use activities and recent seagrass die-off, used in discriminant analysis

	Time	Events
Interval 1	1880–905	Initial permanent settlement; pre-agricultural buildup
Interval 2	1906–1930	Agricultural buildup; Flagler Railroad, Tamiami Trail and canal construction
Interval 3	1931–1950	Agriculture without additional construction of canals
Interval 4	1951–1986	Agriculture intensification with construction of more canals, Water Retention Areas, and a series of water management plans
Interval 5	1987–2001	Seagrass dieoff phase 1 (1986–1991) and phase 2 (1992–2001)

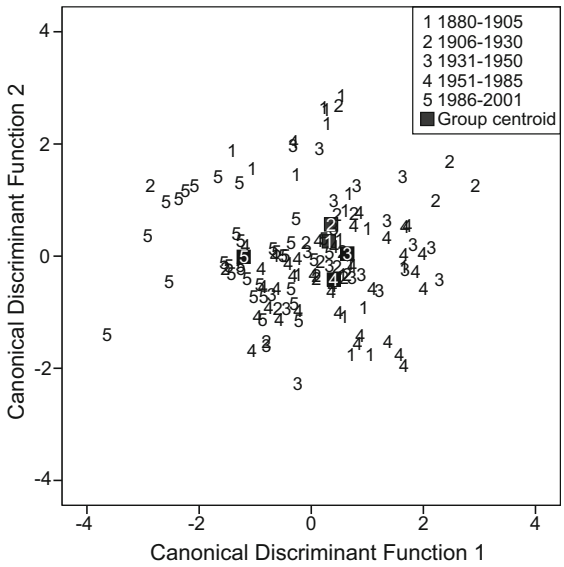

Fig. 6 Plot of discriminant analysis scores on first two axes for seagrass-associated foraminifera excluding Trout Cove site, 1885–2001. Time intervals (Table 4) defined by land-use activities (Intervals 1–4) and recent seagrass die-off (Interval 5). Interval 5 was significantly different from the others. Intervals 1 and 2 differed significantly from Interval 4

2000), possible precursors of the 1987 seagrass die-off, began the decline in SAF before the larger die-off was observed.

Between 1987 and 1994, seagrass abundance dramatically decreased in the central bay (Hall et al. 1999). During this time, three of the four central bay cores (BA122, BA124, RK127) show mostly continued decreases in SAF percentages; the fourth (RK125) shows an increase in the late 1980s before dropping to its lowest value in 1991 (Fig. 3). SAF percentages also decreased in the late 1980s—early 1990s at Ninemile Bank, where water is exchanged with the Gulf of Mexico (Stumpf et al. 1999). In contrast, seagrass surveys between 1984 and 1994 in that area showed stable standing crops with only a few stations recording a slight decrease, although in some nearby areas such as Rabbit Key, a great amount of seagrass died between 1987 and 1994 (Hall et al. 1999). The Ninemile Bank record of SAF suggests that even if local seagrass loss was minimal, severe SAF losses in other parts of the bay were felt by SAF beyond the locally affected area.

During the seagrass die-off, SAF in the Trout Cove core had a trajectory opposite to those in the other five cores, showing higher SAF percentages in the late 1980s to early 1990s compared with the 1970s to early 1980s (Fig. 3). Trout Cove receives much freshwater runoff from Trout Creek and Taylor Slough (Fig. 1) and its lower salinity results in a sparse stand of seagrass, possibly due to the interaction of phosphorus and salinity in controlling seagrass density in that area (Herbert and Fourqurean 2009). No seagrass die-off was observed at nearby Duck Key, either (Zieman et al. 1999). A seagrass biomarker study (Xu et al. 2007) also suggested less effect of the seagrass dieoff in this area relative to other Florida Bay sites.

Around 1995, some recovery in seagrass occurred in the central bay, but from 1995 to 1998 western basins exhibited great losses in biomass while other parts periodically experiencing low salinities changed little (Durako et al. 2002). In three of the four cores covering post-1995 (RK 125, RK 127, NM 134), SAF percentages were higher after 1995 than during the die-off's first phase (1987–1991), but still lower than values prior to the die-off.

Similar to post-1991 periods of partial seagrass recovery in some areas combined with severe losses in others, statistical measures of the timing of SAF changes are a bit mixed. The greatest amount of turnover in SAF between the first die-off phase (1993/1994 samples) and the second phase (1995/1996 samples) indicated by the Assemblage Turnover Index (Table 3) suggests substantial changes to SAF assemblages, but discriminant analysis showed no significant difference between SAF assemblages 1986–1991

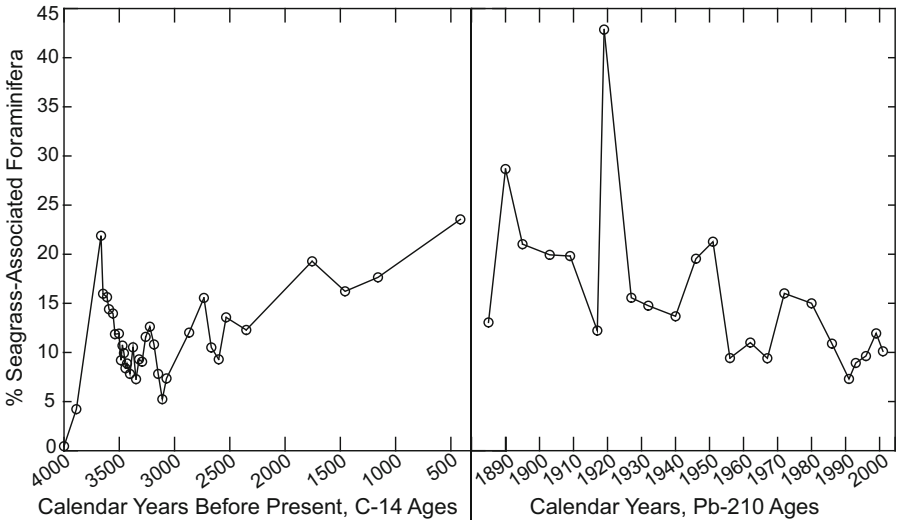

Fig. 7 Percentages of seagrass-associated benthic foraminifera (SAF) at Ninemile Bank, ~ 3800 cal years YBP—2001 A.D. The ^{14}C ages shown are (except for the base) interpolations between midpoints of two-sigma age ranges (e.g. 2660–2340, cal years BP) of five dated samples of molluscan material. ^{14}C ages younger than 2500 cal years BP were interpolated between last ^{210}Pb age of 1885 cal years and youngest ^{14}C age of 2500 cal years BP. SAF assemblages indicate the 1987 die-off resulted in extremely low coverage that was comparable to inundation and development of the benthic ecosystem > 2500 YBP

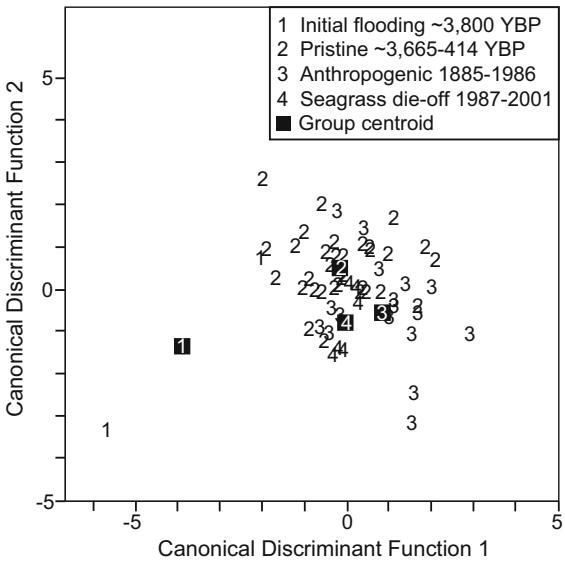

Fig. 8 Plot of discriminant analysis scores on first two axes for seagrass-associated foraminifera at Ninemile Bank, ~ 3800 YBP—2001 A.D. SAF assemblages were significantly different over the four intervals of (1) initial flooding, (2) pristine conditions before human occupation, (3) anthropogenic influences after the beginning of agriculture and canal construction, and (4) the seagrass die-off

and 1992–2001 (Fig. 4), which agrees with the general pattern that seagrass recovery post-1991 was neither strong nor sustained. Overall, the conclusion from testing the seagrass abundance proxy is that the initiation of a large seagrass die-off is detectable in the sedimentary record of Florida Bay using the SAF proxy.

Seagrass-associated foraminifera, 1880–2002

At the centennial scale, the 1987 seagrass die-off was truly deleterious to SAF, as seen in their lower percentages (Fig. 5). Results of the discriminant analysis (Fig. 6) also showed that only the 1986–2001 time interval was different from the other four anthropogenically defined intervals (Table 4). However, most SAF assemblages were correctly classified by the five time intervals for the four Bob Allen Bank and Russell Key cores (53–71%), so changes in central bay SAF were detectable if not significantly separable. Correct classification of Ninemile Bank SAF at 39% and Trout Cove at 28% reflect damped effects, probably due to their proximity to the Gulf of Mexico and Taylor Slough, respectively. We should note that classification is not part of the discriminant analysis model and is biased because the

same species that are used to develop the model are being classified, but it is standard practice to run ad-hoc classifications.

Besides the severe decrease in SAF during the seagrass die-off, two other times of larger change occurred (Fig. 5). A large increase 1919–1925 ± 5 years is seen at Ninemile Bank and Russell Key, with moderate increases in the Bob Allen Bank #122 and Trout Cove cores. During that period, there occurred so many overlapping climatic and meteorologic events (e.g., Atlantic Multidecadal Oscillation cool phase, ENSO cycle of higher precipitation, strong hurricanes, droughts), and construction that blocked freshwater flow to the Bay (e.g., Tamiami Trail road, Tamiami Canal, Lake Okeechobee Levee and other canals in central Florida), that they cannot be isolated and related chronologically to SAF changes. It may also be that there is no single, bay-wide cause of a decrease at any one time, but rather, random variation and localized changes.

From 1934 to 1940 ± 5 years, a large decrease in SAF percentages to low points is seen in all cores except BA124. During this period there were no major natural events or anthropogenic changes other than a series of three powerful, relatively wet hurricanes in 1926, 1928 and 1935 that hit South Florida. Seagrass biomarkers from the same cores suggested decreased abundance from 1932 to 1949 (Xu et al. 2007), which agrees in part with our SAF pattern. From 1928 to 1938 ± 5 years, concurrent peaks of the brackish *Ammonia* foraminiferal association in these cores may reflect temporary freshening of the bay by the hurricanes (Cheng et al. 2012). *Thalassia* thrives in a fairly narrow salinity range with maximal productivity at 28–30 psu (Zieman 1975; Lirman and Cropper 2003), so the SAF decrease may be a lagged response to decreased salinity and, subsequently, seagrass cover.

In the 1940s, SAF percentages returned to higher levels in all cores except BA124, then generally decreased to the end of all core records except those of BA124 and RK127, which recorded higher values in the 1960s to early 1980s. Salinity proxies of ostracod taxa and stable isotopes of oxygen indicated that a multiyear drought in the early 1940s led to hypersalinity in the central bay (Dwyer and Cronin 2001; Swart et al. 1999), which would have decreased seagrass abundance, not in agreement with the SAF data. Additionally, the 1940s–2001 SAF pattern of decline is opposite to that shown by epiphytal ostracods that suggested a higher abundance of aquatic vegetation after 1950 in central and eastern Florida Bay (Cronin et al. 2001). Although ostracods have potential as seagrass indicators (Forsey 2016), this study of seagrass and macroalgal variability did not show a decline in epiphytal taxa during the large 1987–2002 seagrass die-off, as the SAF taxa did.

Decreases of SAF in most cores during the 1960s to early 1980s were concurrent with a period of droughts, in 1961–1963, 1971–1974, 1980–1982 and 1985. These SAF decreases might have resulted from intensified freshwater management that included completion of the Water Retention Areas in the Everglades in 1960–1963, the Everglades National Park-South Dade Conveyance System in 1968, the South Florida Water Management District's (SFWMD) Minimum Allocation Plan for freshwater flow in 1965–1970, the SFWMD's Monthly Allocation Plan for flow to Taylor Slough in 1970 to early 1980s, and the SFWMD's Rainfall Plan for flow to Shark River and Taylor sloughs in the mid-1980s (Light and Dineen 1994).

A pattern seen across all six cores is the degree of variability in total foraminiferal assemblages (Cheng et al. 2012) and SAF assemblages within the two central bay areas of coring that is as great as that between the four cored areas. This large variability at any one time can be explained by localized habitat differences and subsequent bioturbation, as well as age error. Sediment accumulation rates were also different; for example, one Bob Allen Bank core reflected rates twice as high as the other (Cheng et al. 2012). All of this variability emphasizes the need for multiple cores and sites in studies of shallow coastal waters, which reflect highly localized conditions.

Seagrass abundance over ~ 3800 years

Approximately 3800 cal years BP, when seawater initially flooded Florida Bay (Wanless et al. 1994), mangroves were replaced by seagrass beds. At Ninemile Bank, the brackish *Ammonia* foraminiferal association dominated the basal sediments that included mangrove peats (Cheng et al. 2012), and the extremely low percentages of SAF (Fig. 7) indicate that seagrass abundance was near zero for the two bottom core samples. During the subsequent sea level rise, Florida Bay gradually became a more

hospitable habitat for seagrass as indicated by a trend of increasing SAF percentages until the very high peak at ~ 1919 A.D., a high also seen in most of the other cores. It may be that during initial inundation, severe phosphorus limitation minimized seagrass biomass, and benthic systems did not accumulate phosphorus from the Gulf of Mexico source for millennia. Although sea level rise was probably not a generally smooth rise as is often shown (Robbin 1984), and the sedimentology of archeological sites in southwest Florida even suggests a highstand ~ 1.2 m higher than today ~ 1750–1450 cal years BP (Walker et al. 1995), the effect of that difference in water depth on seagrass abundance would be minimal (as compared to phosphorus accumulation) in determining seagrass abundance.

Ninemile Bank SAF assemblages were significantly different between periods of the initial flooding, pristine conditions ~ 3665–414 cal years BP, anthropogenic influence 1885–1986 ± 5 years, and the 1987–2001 ± 2 years seagrass die-off (Fig. 8). Percentages of SAF during the die-off were as low as values > 2500 cal years BP, suggesting that seagrasses had not yet become well established. The much greater difference in SAF assemblage composition between initial flooding and pristine conditions than with the other boundary changes, as shown by the Assemblage Turnover Index values, supports the mangrove peat-marine sediment transition as a far greater change in seagrass abundance than any subsequent fluctuations.

Conclusions

A foraminiferal proxy for regional seagrass abundance was developed from the literature, tested successfully against the large seagrass die-off that began in 1987, and used to construct a record of seagrass variability for Florida Bay since initial flooding ~ 3800 cal years BP. Total percentages of seagrass-associated foraminifera (SAF) responded to the die-off with significant decreases in five of six sediment cores. The sixth (Trout Cove) core, from a low-salinity area with sparse seagrass beds, is more influenced by freshwater runoff than typical bay-wide conditions. The SAF proxy performed well for the seagrass die-off, so we applied it to the 1880–2001 record in detail (± 5 years), and to the ~ 3800-year record at a larger scale.

From 1880 to 2001, the largest overall decrease in SAF occurred during the seagrass die-off that began in 1987. Discriminant analysis showed that SAF assemblages beginning in 1987 were significantly different from the previous four anthropogenically defined intervals back to 1880. There are two other large SAF changes in most of the cores: (1) Between 1919 and 1925 ± 5 years, a large increase in SAF percentages in three cores and a moderate increase in two other cores occurred during a time interval that included so many anthropogenic, climatic and meteorologic events that any correspondence in timing cannot be disentangled. (2) From 1934 to 1940 ± 5 years, a large decrease in SAF percentages to relative lows in all cores except one occurred during a time of three powerful, wet hurricanes in South Florida that may have caused freshening and lower salinities (Cheng et al. 2012) that, in turn, could have diminished seagrass abundance and coverage.

Over the time of Florida Bay's existence, seagrass at Ninemile Bank replaced mangroves ~ 3800–3530 cal years BP. The SAF indicate gradually increasing seagrass until the early 1900s when, except for an anomalous peak in 1919, abundance started to decline until the record's end at the 1987–2002 seagrass die-off. Assemblages of SAF during the four intervals of initial marine flooding, pre-anthropogenic times, anthropogenic times, and the seagrass die-off were significantly different, with basal samples reflecting lower-salinity, transitional peat-to-marine sediments being most different.

This is the first study using foraminifera as a proxy to reconstruct the seagrass history of an area. It should be emphasized that when using shallow-water foraminiferal ecologies to develop proxies, regions can be different in the species that are most useful. Because of local environmental controls, common, seagrass-associated foraminifera in one region may not be as common in another region, which may have others that are better seagrass markers. It is most expedient to study the local to regional patterns in the area in which a paleoenvironmental analysis is planned. This research introduced a new approach for developing a seagrass proxy: we identified species that are more abundant in seagrass beds than in other sediments, and tested them together as a proxy against a previously documented seagrass die-off, a method

that may be useful for future micropaleontological studies based in other regions.

Acknowledgements This research analyzed data from a dissertation by Cheng (2009). The National Park Service, Everglades National Park, permitted core collection and use of the Key Largo Multi-Agency Science Center for sample preparation. Core collection was directed by Charles Holmes (retired) and managed by Marci Marot, U.S. Geological Survey, St. Petersburg, Florida. Fishermen's Hospital, Marathon, graciously contributed their x-ray machine to examine the internal sedimentologic structure of the cores. We are grateful to FIU students, research staff, William Anderson, Rudolf Jaffe, and Evelyn Gaiser, who participated in collecting, x-raying and/or sampling the cores. This is contribution #120 from the Center for Coastal Oceans Research in the Institute of Water and Environment at Florida International University.

Funding This project was supported by the National Science Foundation, USA with Grant EAR-0126024 to Collins, Fourqurean and others.

References

Bock WD (1967) Monthly variation in the foraminiferal biofacies on Thalassia and sediment in the Big Pine Key area, Florida. Ph.D. dissertation, University of Miami, Florida

Bock WD (1969) *Thalassia* testudinum, a habitat and means of dispersal for shallow water benthonic foraminifera. Gulf Coast Assoc Geol Soc Trans 19:337–340

Bock WD, Lynts GW, Smith S et al (1971) A symposium of recent South Florida foraminifera. Miami Geol Soc Mem 1:1–245

Borum JO, Pedersen TM, Greve TA et al (2005) The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass *Thalassia testudinum*. J Ecol 93:148–158

Brasier MD (1975a) Ecology of recent sediment-dwelling and phytal foraminifera from the lagoons of Barbuda, West Indies. J Foraminifer Res 5:42–61

Brasier MD (1975b) The ecology and distribution of recent foraminifera from the reefs and shoals around Barbuda, West Indies. J Foraminifer Res 5:193–210

Brewster-Wingard GL, Ishman SE (1999) Historical trends in salinity and substrate in central Florida Bay: paleoecological reconstruction using modern analogue data. Estuaries 22:369–383

Butler MJ, Hunt JH, Herrnkind WF et al (1995) Cascading disturbances in Florida Bay, USA: cyanobacterial blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Mar Ecol Prog Ser 129:119–125

Buzas MA (1990) Another look at confidence limits for species proportions. J Paleontol 64:842–843

Buzas MA, Severin KP (1982) Distribution and systematics of foraminifera in the Indian River, Florida. Smithson Contrib Mar Sci 16:1–45

Cheng J (2009) Paleoenvironmental reconstruction of Florida Bay, South Florida, using benthic foraminifera. Ph.D. dissertation, Florida International University, Miami

Cheng J, Collins LS, Holmes C (2012) Four thousand years of habitat change in Florida Bay, as indicated by benthic foraminifera. J Foraminifer Res 42:3–17

Collins LS, Schultz S, Fourqurean JW (2004) Use of seagrass-associated foraminifera as indicators of past water quality. Geol Soc Am Ann Meet Abstr Program 36:382

Cronin TM, Holmes CW, Wingard GL et al (2001) Historical trends in epiphytal ostracodes from Florida Bay: implications for seagrass and macro-benthic algal variability. Bull Am Paleontol 361:159–197

Dennison WC, Orth RJ, Moore KA et al (1993) Assessing water quality with submersed aquatic vegetation. Bioscience 43:86–94

Durako MJ, Hall MO, Merello M (2002) Patterns of change in the seagrass dominated Florida Bay hydroscape. In: Porter JW, Porter KG (eds) The Everglades, Florida Bay, and coral reefs of the Florida Keys. CRC Press, Boca Raton, pp 523–537

Dwyer GS, Cronin TM (2001) Ostracode shell chemistry as a paleosalinity proxy in Florida Bay. Bull Am Paleontol 361:249–276

Ellis BF, Messina AR (1941–2009)) Catalogue of Foraminifera, vol 106. Micropaleontology Press, New York, pp 1–87000

Forsey GF (2016) Ostracods for past seagrass: a review. Palaeogeogr Palaeoclimatol Palaeoecol 447:22–28

Fourqurean JW, Robblee MB (1999) Florida Bay: a history of recent ecological changes. Estuaries 22:345–357

Fourqurean JW, Durako MJ, Hall MO et al (2002) Seagrass distribution in South Florida: a multi-agency coordinated monitoring program. In: Porter JW, Porter KG (eds) The Everglades, Florida Bay, and coral reefs of the Florida Keys. CRC Press, Boca Raton, pp 497–522

Fujita K, Hallock P (1999) A comparison of phytal substrate preferences of *Archaias angulatus* and *Sorites orbiculus* in mixed macroalgal-seagrass beds in Florida Bay. J Foraminifer Res 29:143–151

Grant K, Hoare TB, Ferrall KW, Steinker DC (1973) Some habitats of foraminifera, Coupon Bight, Florida. Compass Sigma Gamma Epsil 59:11–16

Hall MO (2012) Seagrass communities in Florida Bay changed after the die-off. In: Kruczynski WL, Fletcher PJ (eds) Tropical connections. Ian Press, Cambridge, pp 281–282

Hall MO, Durako MJ, Fourqurean JW et al (1999) Decadal changes in seagrass distribution and abundance in Florida Bay. Estuaries 22:445–459

Hayek LC, Buzas MB (1997) Surveying natural populations. Columbia University Press, New York

Hayek LC, Wilson B (2013) Quantifying assemblage turnover and species contributions at ecologic boundaries. PLoS ONE 8(10):e74999. https://doi.org/10.1371/journal.pone.0074999

Herbert DA, Fourqurean JW (2009) Phosphorus availability and salinity control productivity and demography of the seagrass *Thalassia testudinum* in Florida Bay. Estuar Coast 32:188–201

Holmes CW, Robbins J, Halley R et al (2001) Sediment dynamics of Florida Bay mud banks on a decadal time scale. Bull Am Paleontol 361:31–40

Koch MS, Schopmeyer SA, Nielsen OI et al (2007) Conceptual model of seagrass die-off in Florida Bay: links to biogeochemical processes. J Exp Mar Biol Ecol 350:73–88

Langer MR (1993) Epiphytic foraminifera. Mar Micropaleontol 20:235–265

Light SS, Dineen WJ (1994) Water control in the Everglades: a historical perspective. In: Davis SM, Ogden JC (eds) Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, pp 47–84

Lirman D, Cropper WP (2003) The influence of salinity on seagrass growth, survivorship and distribution within Biscayne Bay, Florida: field, experimental, and modeling studies. Estuaries 26:131–141

Macreadie PI, Allen K, Kelaher BP et al (2012) Paleoreconstruction of estuarine sediments reveal human-induced weakening of coastal carbon sinks. Glob Change Biol 18:891–901

Martin RE, Wright RC (1988) Information loss in the transition from life to death assemblages of foraminifera in back reef environments, Key Largo, Florida. J Paleontol 62:399–410

Nuttle WK, Fourqurean JW, Cosby BJ et al (2000) Influence of net freshwater supply on salinity in Florida Bay. Water Resour Res 36:1805–1822

Orth RJ, Carruthers TJB, Dennison WC et al (2006) A global crisis for seagrass ecosystems. Bioscience 56:987–996

Purvaja R, Robin RS, Ganguly D et al (2018) Seagrass meadows as proxy for assessment of ecosystem health. Ocean Coast Manag 159:34–45. https://doi.org/10.1016/j.ocecoaman.2017.11.026

Robbin DM (1984) A new Holocene sea level curve for the upper Florida Keys and Florida reef tract. In: Gleason PJ (ed) Environments of South Florida, present and past II. Miami Geological Society, Miami, pp 437–458

Rose RP, Lidz BH (1977) Diagnostic foraminiferal assemblages of shallow-water modern environments: South Florida and the Bahamas. Sedimenta VI:1–63

Sansone FP, Hollibaugh JT, Vink SM, Chambers RM, Joye SB, Popp BN (1994) Diver-operated piston corer for nearshore use. Estuaries 17:716–720

Serrano O, Lavery P, Masque P et al (2016) Seagrass sediments reveal the long-term deterioration of an estuarine ecosystem. Glob Change Biol 22:1523–1531

Steinker PJ, Steinker DC (1976) Shallow-water foraminifera, Jewfish Cay, Bahamas. Mar Sedimentol Spec Publ 1:171–180

Steinker DC, Raynor AL (1987) Some habitats of nearshore foraminifera, St. Croix, U.S. Virgin Islands. Compass Sigma Gamma Epsil 59:15–26

Stuiver M, Reimer PJ, Bard E (1998) INTCAL98 radiocarbon age calibration, 24,000-0 cal B.P. Radiocarbon 40:1041–1083

Stumpf RP, Frayer ML, Durako MJ, Brock JC (1999) Variations in water clarity and bottom albedo in Florida Bay from 1985 to 1997. Estuaries 22:431–444

Swart PK, Healy G, Greer L et al (1999) The use of proxy chemical records in coral skeletons to ascertain past environmental conditions in Florida Bay. Estuaries 22:384–397

Talma AS, Vogel JC (1993) A simplified approach to calibrating 14C dates. Radiocarbon 35:317–322

Vélez-Juarbe J (2014) Ghost of seagrasses past: using sirenians as a proxy for historical distribution of seagrasses. Palaeogeogr Palaeoclimatol Palaeoecol 400:41–49

Wachnicka A, Collins LS, Gaiser E (2013) Response of diatom assemblages to 130 years of environmental change in Florida Bay (USA). J Paleolimnol 49:83–101

Walker KJ, Stapor FW, Marquardt WH (1995) Archaeological evidence for a 1750-1450 BP higher-than-present sea level along Florida's Gulf coast. J Coast Res Spec Issue 17:205–218

Wanless HR, Parkinson RW, Tedesco LP (1994) Sea level control on stability of Everglades wetlands. In: Davis SM, Ogden JC (eds) Everglades, the ecosystem and its restoration. St. Lucie Pr, Boca Raton, pp 199–223

Wantland KF (1967) Recent foraminifera of the British Honduras shelf. Ph.D. Dissertation, Rice University

Wardlaw BR (2001) Paleoecological studies in South Florida. Bull Am Paleontol 361:1–238

Waycott M, Duarte CM, Carruthers TJB et al (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:2377–12381

Xu Y, Holmes CW, Jaffe R (2007) Paleoenvironmental assessment of recent environmental changes in Florida Bay, USA: a biomarker based study. Estuar Coast Shelf Sci 73:201–210

Zieman JC (1975) Seasonal variation of turtle grass, *Thalassia testudinum* König, with reference to temperature and salinity effects. Aquat Bot 1:107–123

Zieman JC, Fourqurean WJ, Iverson RL (1989) Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. Bull Mar Sci 44:292–311

Zieman JC, Fourqurean JW, Frankovich TA (1999) Seagrass die-off in Florida Bay: long-term trends in abundance and growth of turtle grass, *Thalassia testudinum*. Estuaries 22:460–470