TAPHONOMIC DISPARITY IN FORAMINIFERA AS A PALEO-INDICATOR FOR SEAGRASS

SIMON A.F. DARROCH,[1,2] EMMA R. LOCATELLI,[1] VICTORIA E. MCCOY,[1] ELIZABETH G. CLARK,[1] ROSS P. ANDERSON,[1] LIDYA G. TARHAN,[1] AND PINCELLI M. HULL[1]

[1]Department of Geology and Geophysics, Yale University, 210 Whitney Avenue, New Haven, Connecticut 06511, USA
[2]Smithsonian Institution, PO Box 37012, MRC 121, Washington, DC 20013-7012, USA
email: emma.locatelli@yale.edu

ABSTRACT: Seagrass meadows are a key component of marine ecosystems that play a variety of prominent geobiological roles in modern coastal environments. However, seagrass itself has low preservation potential, and consequently seagrass meadows are hard to identify in the rock record. In this study we combine observational taphonomic data from a modern sparse seagrass meadow with actualistic taphonomic experiments, in order to test whether taphonomic disparity (i.e., evenness in the distribution of taphonomic grades among multiple individuals) in the larger benthic foraminiferan *Archaias angulatus* has potential as a paleo-indicator for seagrass dominated communities. Our observational study demonstrates that sparse seagrass meadows possess a higher proportion of both pristine and highly altered tests than non-seagrass settings. Our taphonomic experiments, conducted over a six-month period, demonstrate a greater magnitude of bioerosion and diversity of bioerosion types in foraminifera deployed within sparse seagrass patches, than those deployed in patches without any seagrass cover. Although our experimental results in particular have high variability, these combined approaches provide a link between pattern (high taphonomic disparity) and process (higher rates of bioerosion) in developing the taphonomic signature of seagrass meadows. On the basis of these results we suggest several taphonomic criteria that could be used to identify seagrass meadows in the rock record. These criteria are potentially species-independent, and so may have greater utility as seagrass proxies than invertebrate indicator species that frequently have limited temporal or spatial distributions.

INTRODUCTION

Seagrass meadows are a key component of modern marine ecosystems. They occupy as much as 10% of the world's coastal ocean seafloor (Charpy-Roubaud and Sournia 1990; Hemminga and Duarte 2000) and play a prominent role in carbonate platform geomorphology, coastal nutrient cycling, sediment production and baffling, and in providing habitats for a diverse array of marine organisms including juveniles of economically important reef fish (Ginsburg and Lowenstam 1958; Tucker and Wright 1990; Beavington-Penney et al. 2004; Reich 2014; Reich et al. 2015). Although Caribbean seagrass meadows are dominated by marine angiosperms such as *Thallassia* and *Syringodium*, seagrass meadows also frequently contain abundant calcifying green algae such as *Halimeda* and *Penicillus* (see Buchan and Lewis 2009). Seagrasses evolved in the Tethys Ocean during the Late Cretaceous, and diversified during the Miocene (Beavington-Penney et al. 2004; Reich 2014). Modern seagrasses have a near-worldwide distribution, and are found in coastal environments around every continent except Antarctica (Reich et al. 2015). However, seagrasses have a low preservation potential and records of exceptionally well-preserved and/or silicified plant material from marine settings are rare (Den Hartog 1970; Ivany et al. 1990; Beavington-Penney et al. 2004). Consequently, these paleoenvironments are difficult to identify in the rock record (Brasier 1975; Domning 2001; Buchan and Lewis 2009; Reich et al. 2015), and there is a strong incentive to develop sedimentological and paleontological proxies for the presence of seagrass-dominated ecosystems.

Previous studies have identified key 'indicator' taxa of higher preservation potential that live closely associated with seagrass. Examples include species of coralline red algae with distinct 'hooked' morphology (Beavington-Penney et al. 2004), and large discoidal foraminifera adapted for epiphytic lifestyles (Brasier 1975; Eva 1980; Beavington-Penney et al. 2004). More recently, Reich (2014) demonstrated that Bahamian seagrass meadows are commonly associated with faunal assemblages dominated by herbivorous gastropods, suggesting that this particular gastropod bio-assemblage may potentially serve as a useful seagrass indicator. However, when indicator species or morphologies are rare (Reich 2014) or are characterized by limited spatial or temporal distributions, use of taxon- or morphology-based proxies can prove challenging. In these instances, a species-independent proxy would represent a valuable geological and paleoecological tool. Reich et al. (2015) provide an exhaustive review of proxies, termed Indirect Paleo-Seagrass Indicators (IPSIs), and evaluate their usefulness in terms of their potential geographic distribution, preservation potential, specificity, and temporal range. Here, we propose an additional IPSI based on the taphonomy of foraminifera that is potentially species independent, and which may extend back in time as far as the Oligocene.

Buchan and Lewis (2009) were the first to suggest that the "taphonomic grade" (i.e., the extent of postmortem alteration) of foraminiferal tests may represent a species-independent proxy for seagrass meadows (although see Leonard-Pingel 2005 for an example using mollusks). This proxy hinges on the important geobiological role seagrass plays in current baffling. These authors found that material recovered from seagrass patches tended to have a higher percentage of 'pristine' foraminiferal tests than in other environments, which they attributed to lower current velocities and incidences of abrasion during storm events. However, there are a number of additional factors governing the taphonomy of biomineralized material such as foraminiferal tests. The first of these is deep-tier bioturbators such as callianassid shrimp and polychaete worms, which are common in

modern carbonate platform sediments, including certain seagrass-populated settings worldwide (e.g., Vonk et al. 2008). These organisms efficiently exhume bioclastic material from depth back into the "taphonomically active zone" (TAZ), defined as the sediment zone in which carbonate shells are subjected to processes of dissolution, bioerosion, and mechanical destruction (Walker and Goldstein 1999). Callianassid shrimp in particular are capable of highly efficient transportation of sediment from depth up to the sediment-water interface (at rates of up to 55 cm^3 per individual per day; MacGintie and MacGintie 1949; although sediment also typically cascades passively down into burrows). With callianassid densities of up to 200 individuals per m^2 (for example in Cholla Bay, Meldahl 1987), this results in the recycling of prodigious volumes of sediment; deep-tier infauna such as callianassid shrimp and certain groups of polychaete worms are thus termed 'conveyer belt bioturbators' (Meldahl 1987; Martin et al. 1996). The activity of these organisms should therefore lead to an increase in highly altered and bioeroded material as tests are moved into zones where taphonomic processes operate. Although callianassid shrimp can be excluded from very dense seagrass meadows (where the density of root networks discourages burrowing activity, e.g. Suchanek et al. 1983), they are common in sparser seagrass (Berkenbusch et al. 2007), in particular those occurring in the vicinity of San Salvador, the Bahamas (Curran and Williams 1997).

In addition, the carbonate saturation state of pore waters in sediments underlying seagrasses is lower than in nearby, seagrass-free sediments. Burdige et al. (2010) demonstrated that aerobic bacteria associated with the roots of *Thalassia*-type seagrasses typically produce CO_2 in quantities sufficient to significantly lower pore-water pH compared to un-vegetated areas, resulting in higher rates of carbonate dissolution. Together with the recycling role played by deep-tier bioturbators, this aspect of seagrass ecology should also act to enhance taphonomic alteration of shell material.

In this study, we examine these hypothesized links between seagrass meadows and taphonomic processes using a combination of observational and experimental approaches in San Salvador, and test whether the taphonomy of foraminifera can be used as a proxy for seagrass meadows in the rock record. We focus on the large benthic foraminifer *Archaias angulatus* (Fichtel and Moll 1798), family Soritidae, which is an abundant taxon in Caribbean and Bahamian back-reef environments (Cottey and Hallock 1988). The genus *Archaias* is known from the Oligocene to Recent (Smout and Eames 1958); *Archaias angulatus* possesses a discoidal and porcelaneous test that is robust to many forms of corrasion (Peebles and Lewis 1991), and has been used frequently in previous taphonomic studies (Cottey and Hallock 1988; Kotler et al. 1992; Peebles and Lewis 1991; Buchan and Lewis 2009). Moreover, *A. angulatus* can be readily identified even after undergoing extensive mechanical and bioerosive alteration (see Buchan and Lewis 2009), making it an ideal model organism for assessment as a paleo-indicator for seagrass.

Seagrass Meadows and Taphonomy of A. angulatus

Previous work on both the ecology and taphonomy of *A. angulatus* (e.g., Fujita and Hallock 1999; Buchan and Lewis 2009) allows specific predictions to be made for the taphonomic grade of tests within and outside of seagrass meadows. *Archaias angulatus* is largely epiphytic in life habit, living attached to the blades of seagrasses and (less commonly) calcifying algae such as *Halimeda* and *Penicillis* (Fujita and Hallock 1999; Morgan and Lewis 2010). As a result, the relative abundance of living *A. angulatus* is far higher within seagrass meadows than outside, and there is a much higher flux of pristine (i.e., recently dead) tests to the sediment in these settings (Martin and Wright 1988; Buchan and Lewis 2009). In addition, seagrasses are efficient current bafflers, which results in lower rates of test abrasion due to agitation and transport along the sediment surface (Buchan and Lewis 2009). The high abundance of biomineralizing invertebrates (such as foraminifera and small mollusks) and calcifying algae (such as

Halimeda) in seagrass meadows result in extremely high sediment production and retention rates (exacerbated by current baffling) relative to uncolonized environments (Gacia et al. 2003). This means that that recently dead test material can become rapidly buried within the accumulating sedimentary pile. These processes should therefore produce high frequencies of relatively pristine (i.e., unaltered) tests in environments colonized by seagrass and other marine algae. Operating counter to this, sparsely vegetated seagrass meadows (on San Salvador in particular) are frequently home to dense populations of polychaetes and callianassid shrimp (*Glypturus acanthocinus* Stimpson 1866). Both of these organisms are capable of recycling tests from depth back into the TAZ (see Meldahl 1987) where they become prone to mechanical destruction and shell degradation by endolithic bacteria and fungi (which are typically more abundant within seagrass beds than outside—see Cottey and Hallock 1988; Harborne et al. 2006). Rates of dissolution underneath seagrass meadows are also higher (Burdige et al. 2010), likely resulting in relatively high incidences (and intensity) of test surface etching (Cottey and Hallock 1988). Accumulations of foraminifera in seagrass meadows should therefore contain high frequencies of both pristine and highly altered tests, reflecting the high flux of recently dead tests to sediments, as well as the high intensity of taphonomic processes specific to this environment. We also note that selective (and total) destruction of tests is an ongoing process that typically leaves assemblages enriched in abrasion-resistant species (see e.g., Li et al. 1997, and Buchan and Lewis 2009). To the best of our knowledge, the rate at which pristine tests are added to sediments relative to the rate at which highly altered tests are typically completely lost has not been quantified, however, in theory this could also have an effect on the predicted frequencies of taphonomic grades. However, in the absence of this data we do not consider this effect further.

In contrast, outside of seagrass meadows the abundance of living *A. angulatus* is far lower, and the majority of *A. angulatus* tests found in non-seagrass sediments are likely transported from elsewhere; this results in low rates of delivery of recently deceased individuals, and thus low rates of delivery of relatively pristine tests to the sediment pile (Buchan and Lewis 2009; Darroch 2012). In addition, without the baffling effect of seagrass, tests are likely to undergo much higher levels of mechanical abrasion during storm events (see e.g., Peebles and Lewis 1991; Buchan and Lewis 2009). However, where frequencies of deep-tier and conveyer-belt bioturbators are lower, individual tests have a greater chance of entering the sedimentary record without exhumation and repeated exposure to mechanical, geochemical, and bioerosive processes (and thus should result in fewer tests reaching the highest, i.e., 'most altered' taphonomic grades). Accumulations of foraminifera in non-seagrass settings without abundant bioturbation should therefore contain lower frequencies of both pristine and highly altered tests than those found in seagrass meadows.

These summed processes therefore predict that:

1. Seagrass meadow settings should possess a more even distribution of pristine and highly altered tests than non-seagrass settings.
2. In sparsely vegetated seagrass meadows with callianassid mounds, the proportions of highly altered tests should be homogenized between the surface and subsurface, reflecting the mixing effect of deep-tier bioturbators.
3. In non-seagrass settings without callianassid mounds, there should be a higher proportion of less-altered tests at the surface and more-altered tests in the subsurface, reflecting the lower intensity of sediment mixing. Moreover, these differences in rates and character of taphonomic processes should be observable in actualistic experiments.

We therefore also predict that, in seagrass meadows characterized by high rates of bioturbation:

4. Per unit time, foraminiferal tests retained on the sediment surface should display higher rates of bioerosion and diversity of bioerosion types (reflecting the higher biovolume and diversity of bioerosive and endolithic organisms in these habitats).

5. Foraminiferal tests sequestered in the subsurface should exhibit higher rates of test dissolution (reflecting the decreased carbonate saturation state of pore waters beneath seagrass meadows—see Burdige et al. 2010) than those held at the surface.

6. This surface-subsurface discrepancy in extent/rates of test dissolution should be particularly pronounced in seagrass meadows.

In the event that these six predictions are supported, high relative abundances of both pristine and highly altered tests (high 'taphonomic disparity'—essentially high 'evenness' of taphonomic grades) in accumulations of large benthic foraminifera may serve as a species-independent proxy for seagrass communities (specifically those characterized by dense conveyor-belt burrow systems) in the geological record.

METHODS

We test the predictions listed above in two ways. First, to test for bulk taphonomic differences between environments (hypotheses 1–3), we sampled both surface and subsurface foraminiferal assemblages from environments with and without seagrass, and scored collected *A. angulatus* tests for taphonomic grades. Second, to test for differences in rates and patterns of test alteration in an actualistic fashion (hypotheses 4–6) we deployed recently dead *A. angulatus* tests in a variety of seagrass-dominated subenvironments, and at two different depths with respect to the sediment-water interface.

Taphonomic differences between environments.—To compare bulk taphonomic differences between environments with and without seagrass, we selected two sites north and east of San Salvador Island (Fig. 1). Both localities are open marine. Graham's Harbor represents a windward inner lagoon environment at the northeast end of the Island, characterized by rippled and bioturbated carbonate sand with areas of sparse to dense seagrass (Colby and Boardman 1988). In contrast, Fernandez Bay represents a leeward mid-shelf lagoon setting characterized by coral patch reefs, and largely without seagrass meadows.

Graham's Harbor.—Grahams Harbor (24.12044°, –74.465824°; Fig. 1B, 1C) is a shallow-water environment (~ 1.5 m depth) with patchy seagrass beds dominated by *Thalassia*, and a variety of calcifying algae including *Halimeda*. Seagrass beds also possess abundant *Glypturus* mounds (Fig. 2). Sediments are typically poorly sorted with respect to size, and individual grains appear frosted (Colby and Boardman 1988). Grains are predominantly bioclastic, containing abundant fragments of *Halimeda*, benthic foraminifera, bivalve and ostracode valves, high-spired microgastropods, ophiuroid debris, and asteroid plates (Darroch 2012). Peloids are relatively uncommon, but where found are generally large (up to 1 mm in the long axis) and ellipsoidal.

Fernandez Bay.—The locality at Fernandez Bay (24.035442, –74.531585; Fig. 1B) is deeper than at Graham's Harbor (~ 5 m depth), and is situated near to several patch reefs (the nearest being Snapshot Reef). *Glypturus* mounds are absent. Sediment is typically highly polished, moderately well sorted with respect to size, and contains frequent grain aggregates (Darroch 2012). Bioclasts are extremely common and dominated by benthic foraminifera, coral debris, bivalves, high-spired microgastropods, echinoid spines, and sponge spicules, and also rare ophiuroid debris and crinoid ossicles.

Sediment samples were collected along transects in both Graham's Harbor and Fernandez Bay. In Graham's Harbor, samples were taken from within a large seagrass meadow possessing abundant *Glypturus* mounds (Fig. 2). Three individual samples were taken from each locality, spaced at 5-m intervals parallel to shoreline. Given the high density of *Glypturus* in Graham's Harbor, sampling points frequently intersected with the margins and 'splay' from exhumed sediment mounds. Surface assemblages were collected by gathering 5 g of sediment from the upper ~ 1 cm of the seafloor using a plastic container; subsurface assemblages were collected directly beneath surface samples using a simple corer (PVC pipe ~ 2.5 cm in diameter) to a consistent depth of 60 cm (see also Darroch 2012). At this depth the sediment was sufficiently consolidated for a disc of sediment to be recovered.

Tests of *A. angulatus* were picked and scored for taphonomic grade with reference to the index published by Buchan and Lewis (2009). Specifically, taphonomic grade 1='pristine'; 2='good'; 3='altered'; 4='highly altered'. These grades are defined on the basis of several qualitative characteristics (described in detail below), and represent the summed effect of mechanical, bioerosive, and dissolution processes operating in each environment. 'Pristine' specimens are those in life condition (i.e., showing no detectable damage), 'good' specimens show mild postmortem alteration (such as slight test breakage), 'altered' specimens show more severe damage to the test along with some loss of ornamentation, and 'highly altered' show almost total loss of ornamentation along with a high level of outer wall damage (Buchan and Lewis 2009, fig. 2). To avoid possible taphonomic grade-related bias during picking, each sample was spread onto a picking tray divided into 1 cm^2 grid squares; grid squares were then chosen at random under the microscope field of view, and all dead foraminifera in that square were picked and scored for taphonomic grade until either 100 individuals had been picked, or no individual *A. angulatus* remained in the sample (see also Darroch 2012). Overall abundances of *A. angulatus* were much lower at Fernandez Bay, and thus the number of individuals per sample in this setting was typically smaller. Numbers of individual foraminifera graded in each sample are given in Table 1.

Taphonomic Experiments.—To test for rates and patterns of alteration, we deployed pristine foraminifera in Graham's Harbor close to the boat pier that serves the Gerace Research Center, within three subenvironments characterized by varying densities of vegetation (GPS coordinates given in Table 2): high-density vegetation, low-density vegetation, and no vegetation (Figs. 3, 4). Relative vegetation densities were established using counts of algal thalli and individual *Thalassia* seagrass blades within three 0.25 m^2 PVC frame quadrats scattered randomly around the sampling site (Fig. 3; see Buchan and Lewis 2009; Reich 2014); these are recorded in Table 2. Vegetation in all quadrats was dominated by *Thalassia* seagrass, with minor *Syringodium* and *Halimeda*.

We designed an experimental rig that allowed us to suspend and recover foraminiferal tests both above and below the sediment-water interface (Fig. 4). 'Pristine' tests of *A. angulatus* were picked from sediment collected around Graham's Harbor, dried, and two foraminifera each were affixed to the centers of glass slides using circlets of sticky carbon tape. We only selected foraminifera preserving the remains of soft protoplasm tissue inside tests (identified by wetting tests with the end of a brush—see Buchan and Lewis 2009), thus establishing that they were most likely living at the time of sampling (prior to drying). Slides were then wrapped in microfilament gauze bags with 150 μm mesh size, and placed inside plastic sample tubes sealed with screw tops. Open 5 × 25 mm 'windows' were then cut into opposite sides of tubes at the height at which slides and foraminifera were suspended and covered with additional sheets of 150 μm gauze, in order to allow water to flow freely through sample tubes. A complete sample rig was comprised of two sample tubes connected to a PVC rod that could be inserted into the sediment. The two tubes were attached 15 cm apart on rods to ensure that while the upper tube was suspended at the sediment-water interface (with the foraminifera suspended 1–3 cm above the sediment surface), the lower was positioned
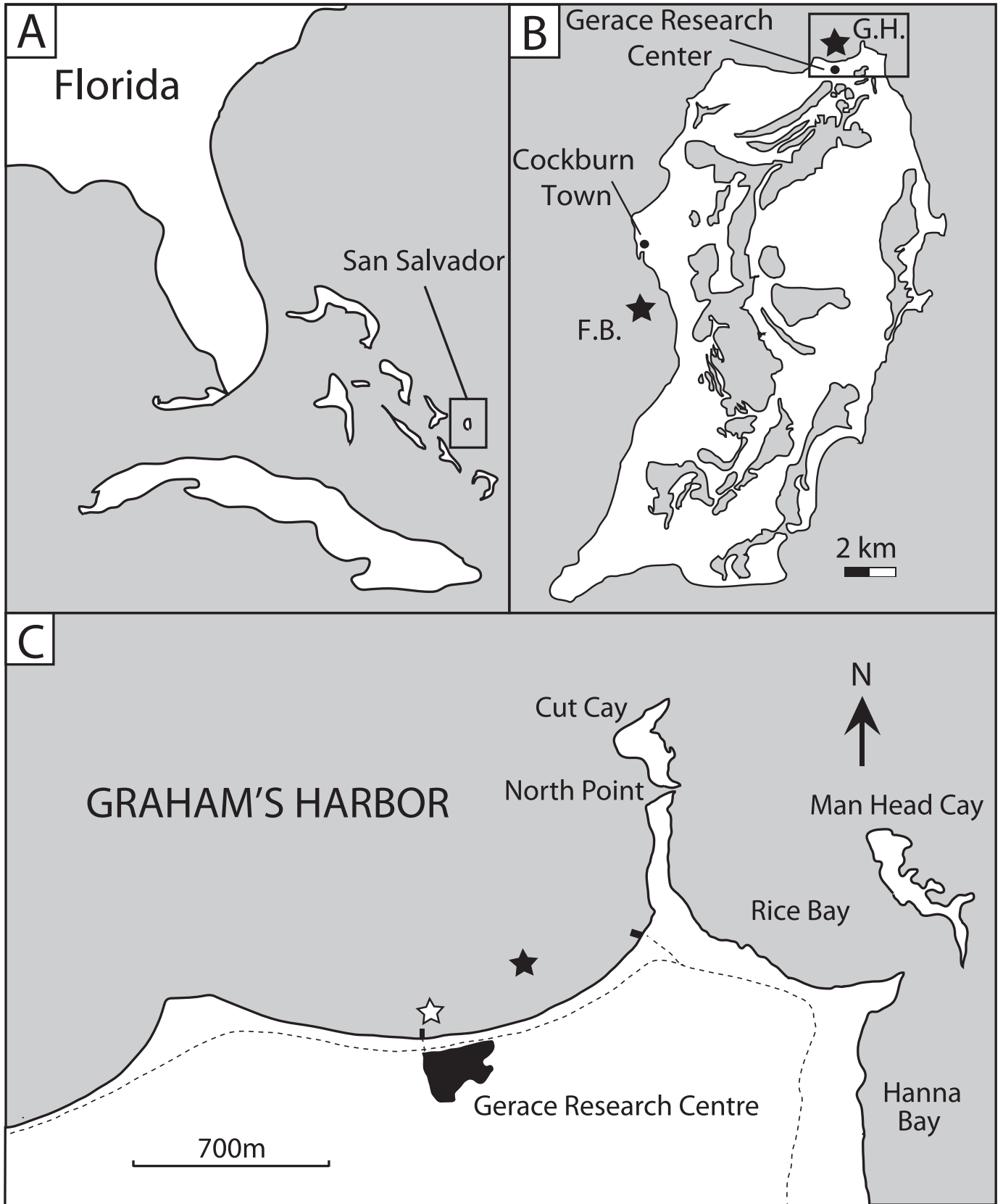
FIG. 1.—Location map. **A)** The position of San Salvador relative to the Bahamas platform. **B)** Sampling sites (filled stars) for observational studies ('G.H.'=Graham's Harbor, 'F.B.'=Fernandez Bay). **C)** Sample site (open star) for experimental study.

S.A.F. DARROCH ET AL.

Fig. 2.—Image illustrating a typical seagrass meadow in Graham's Harbor, the Bahamas, characterized by abundant mounds produced by *Glypturus acanthocinus* shrimp.

15 cm below the sediment-water interface (Fig. 4). Our design therefore allowed for a free flow of current- and pore-waters through the upper and lower sample tubes, respectively, while ensuring that individual tests could be reliably recovered after deployment. The 150 μm gauze also protected the foraminifera from macro-scavengers, while still allowing access to small meio- and micro-fauna and -flora. Sample rigs were deployed for a period of approximately six months, from February 12 to August 8 2012.

In order to quantify the types and extent of taphonomic alteration to foraminiferal tests, we surveyed tests from all deployments using scanning electron microscopy (SEM), described the morphologies of the various 'damage types' found on test surfaces, and compared these to published accounts of damage types found on foraminifera (e.g., Perkins and Halsey 1971; Golubic et al. 1975; Cottey and Hallock 1988; Peebles and Lewis

1988). As a control (i.e., to establish confidence that taphonomic damage to tests had occurred post-, rather than pre-burial), we performed the same survey on a 'pristine' test, collected in the same way as the others (i.e., alive at the time of capture), which had not been buried. Ideally, we would have surveyed the tests used in experiments both before and after the experimental treatment. However, preparing tests for SEM analysis (i.e., coating in Au/C) would likely have impacted colonization potential by bioeroding organisms, and thus may have biased results. Consequently, although we did not see any test alteration or damage in our 'control' specimen, it is possible that, prior to deployment, the actual tests used in deployment may have possessed damage on scales below that detectable under light microscopy. However, given that live (or very recently deceased) individuals were used for this experiment, the amount of pre-deployment bioerosion was likely minimal.

Following collection, we quantified the relative abundance and diversity of damage characterizing each test using an equal-area approach using SEM. To do this, we took five randomly spaced images with identical working distance and magnification for each specimen (hereafter referred to as 'views'), being sure to include both the center and edge of the tests. Each SEM view was overlain with a 16×12 grid using ImageJ software. We counted the number of grid cells containing each damage type. Because the features associated with our surveyed 'damage types' occupied a wide range of sizes, we consistently counted damage at a magnification of 967× (resulting in 76.5 μm^2 grid cells) which allowed reliable identification of all features. We quantified differences between tubes held at the surface vs. subsurface and between the three subenvironments using Welch t-tests in the open-access statistical software R (R Development Core Team 2013).

RESULTS

Taphonomic Differences between Graham's Harbor and Fernandez Bay

In this section we refer to single samples (e.g., GH1) as 'individual samples'. Where we combine all surface or subsurface samples from a

TABLE 1.—*Taphonomic grade frequencies for* A. angulatus *in individual and aggregated samples, from both surface and subsurface collections. 'TG'=taphonomic grade. Samples with '-1' suffix indicate those taken from the subsurface at each locality (see also Figs. 6, 7).*

	Individual											
	Graham's Harbor						Fernandez Bay					
TG	G1	G2	G3	G1-1	G2-1	G3-1	F1	F2	F3	F1-1	F2-1	F3-1
1	20	18	30	12	14	14	22	9	3	7	1	5
2	42	20	32	22	29	42	45	30	5	40	9	43
3	23	11	20	17	16	22	23	13	1	18	6	41
4	15	11	18	9	11	22	10	8	0	15	4	11
TOTAL	100	60	100	60	70	100	100	60	9	80	20	60

	Aggregated					
	Graham's Harbor			Fernandez Bay		
TG	surface	subsurface	All G.H.	surface	subsurface	All F.B.
1	68	40	108	34	13	47
2	94	93	187	80	92	172
3	54	55	109	37	65	102
4	44	42	86	18	30	48
TOTAL	260	230	490	169	200	369

TABLE 2.—*Vegetation densities (*Thalassia *seagrass and* Halimeda *algae) in experimental subenvironments.*

Locality/grid (GPS: 24.12044°, −74.465824°)	*Thalassia* count	*Halimeda* count	Sum *Thalassia*	Mean *Thalassia*
High-density seagrass 1	89	6		
High-density seagrass 2	93	2		
High-density seagrass 3	87	0	269	89.67
Low-density seagrass 1	37	1		
Low-density seagrass 2	54	0		
Low density seagrass 3	31	0	122	40.67
No seagrass 1	0	0		
No seagrass 2	0	0		
No seagrass 3	0	0	0	0

single locality (e.g., GH1, GH2 and GH3), we refer to these as 'aggregated samples'. Taphonomic indices for individual (Graham's Harbor, Fig. 5; Fernandez Bay, Fig. 6) and aggregated samples were plotted as percentage frequency histograms (Fig. 7). Taphonomic disparity was quantified using standard ecological evenness and diversity metrics: Simpson index and Shannon's H. Raw data are given in Table 2; descriptive statistics (mean

taphonomic grade, standard deviations, and evenness/diversity indices) are given in Tables 3 and 4 (for individual and aggregated samples, respectively).

In all individual and aggregated samples, evenness and diversity indices for taphonomic grades (TGs) are universally higher (i.e., higher disparity of taphonomic grade and greater number of damage types) in the seagrass-rich Graham's Harbor than at the seagrass-poor Fernandez Bay. This is illustrated in percentage frequency histograms (Figs. 5–7) where Fernandez Bay samples show positive (right) skew when compared to those from Graham's Harbor.

In all individual and aggregated samples from both localities, TGs were higher in subsurface samples. In order to test the significance of these differences we performed Kolmogorov-Smirnov tests on all surface-subsurface pairs of samples (both individual and aggregated; Table 5); these show that mean taphonomic grades between surface and subsurface are statistically indistinguishable pairs in Graham's Harbor, but significantly different ($p < 0.05$) in Fernandez Bay for the aggregated sample pair.

Taken together, these results show: (1) taphonomic grades have higher evenness at Graham's Harbor than at Fernandez Bay; (2) surface and subsurface taphonomic grades are significantly different at Fernandez Bay, but not so (i.e., are essentially homogenous) in Graham's Harbor; and, (3)
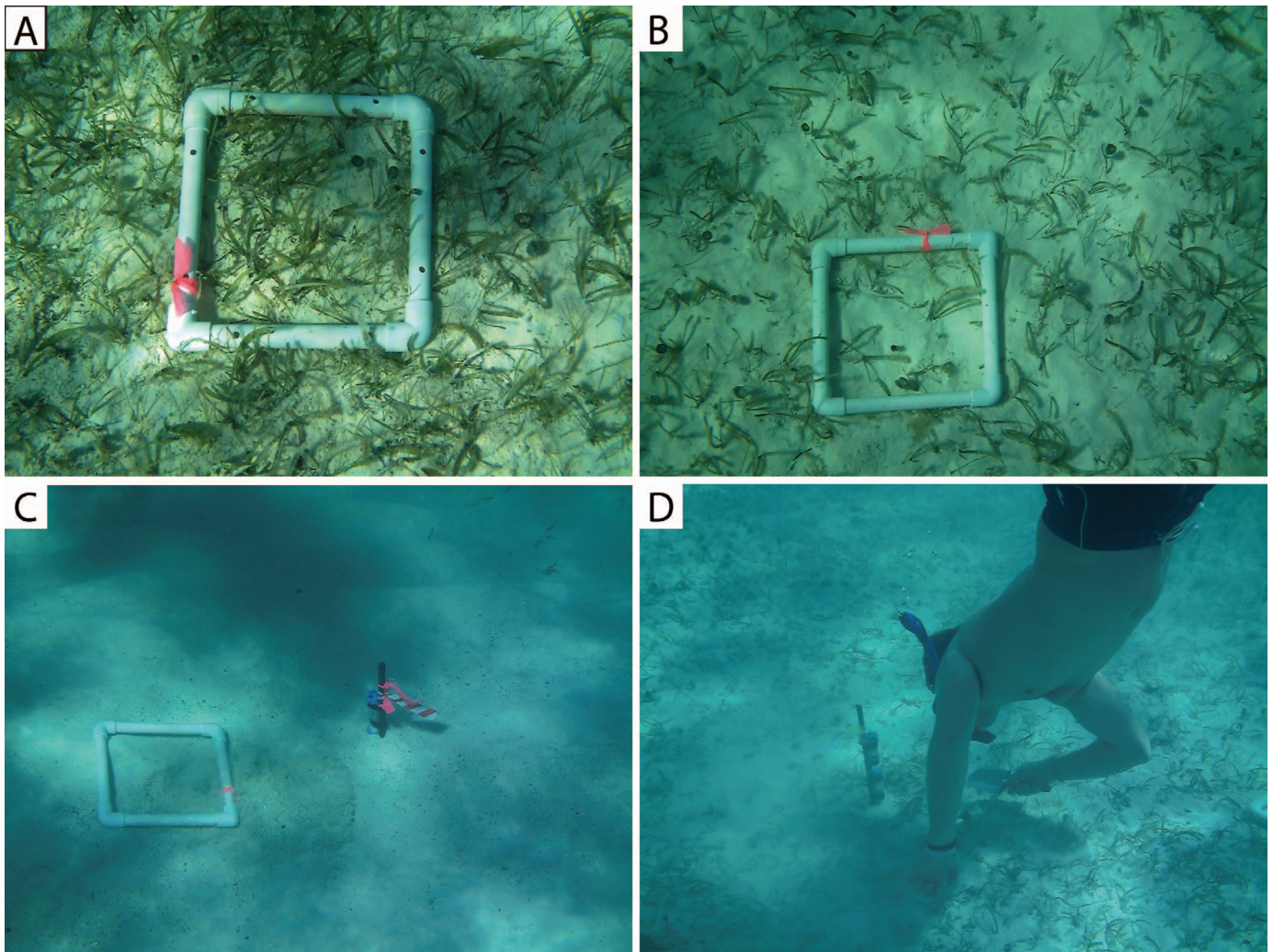

FIG. 3.—Experimental deployment areas of foraminifera. **A)** 'Dense seagrass' subenvironment. **B)** 'Intermediate seagrass' subenvironment. **C)** 'No seagrass' subenvironment. **D)** A preliminary attempt by the lead author at deploying an experimental rig (low-density vegetation subenvironment).
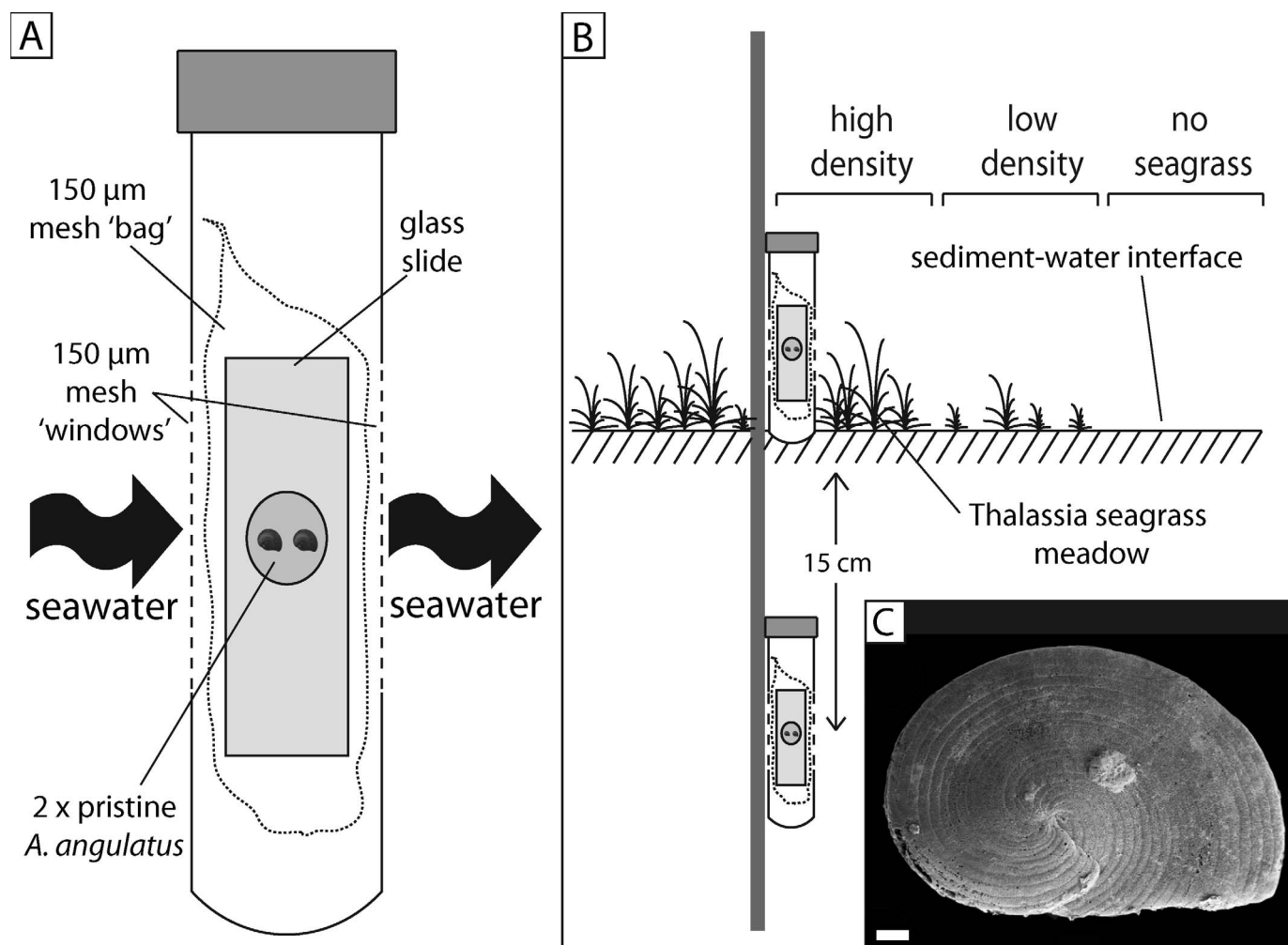
Fig. 4.—**A**, **B**) Experimental design. **C**) SEM image of individual *Archaias angulatus* formaminifer collected from San Salvador (modified from Darroch 2012, fig. 5; scale bar 200 μm).

subsurface sediments at Fernandez Bay contain significantly more taphonomically altered tests than surface samples.

Experimental Deployment of Foraminifera

Damage Types Encountered During Surveys.—After surveying all buried foraminifera, we identified six distinct damage types that were each found preserved on multiple individual tests. Our control specimen showed no evidence for any damage types, supporting inference that all described damage occurred subsequent to deployment and the start of the experiment. All damage types are described below and illustrated in Figures 8 and 9:

1. *Type 1 patches*: Rough, often ellipsoidal or elongate patches with shallow topographic relief in the test surface. These are distinct from Type 2 patches in being relatively localized and possessing sharply defined edges (Fig. 8A, 8B).

2. *Type 2 patches*: Broad areas showing rough texture, and often seen grading smoothly into nearby non-pitted areas (Fig. 8C, 8D).

3. *Type 1 trails*: Linear features typically 8–10 μm in width, with relatively deep scalloped-shaped bases. Trails commonly anastomose and split, and only rarely intersect with pseudopores. We included in

this damage type instances of 'scalloping' around the margins of pores in the test wall (Fig. 9A, 9B).

4. *Type 2 trails:* Linear features 2–4 μm in width forming smooth, continuous, and sinuous trails, which commonly anastomose and split (Fig. 9C, 9D).

5. *Type 3 trails*: Linear features comprising discontinuous trails of small, dark holes in the test surface, 4–5 μm in diameter (Fig. 9E–9G).

6. *Holes*: These are circular openings in the test wall with (relatively) rough edges, typically 8–10 μm in diameter (i.e., larger than the majority of pseudopores) (Fig. 9H).

Test Damage Assessed as a Function of Sub-Environment and Burial Depth.—The abundances of damage types calculated for individual tests are given in online Supplementary Data Table 1. The most common types of damage found on the surfaces of tests were Type 1 trails (mean 8.58 grid cells per view) and Type 2 trails (mean 8.15 grid cells). In contrast, Holes (mean 0.42 grid cells) and Type 3 trails (mean 2.6 grid cells) were comparatively rare.

Between subenvironments, mean per-view damage scores were highest in sediments collected from sites characterized by high-density vegetation (23.85 grid cells), lower in low-density vegetation (20.25 grid cells), and
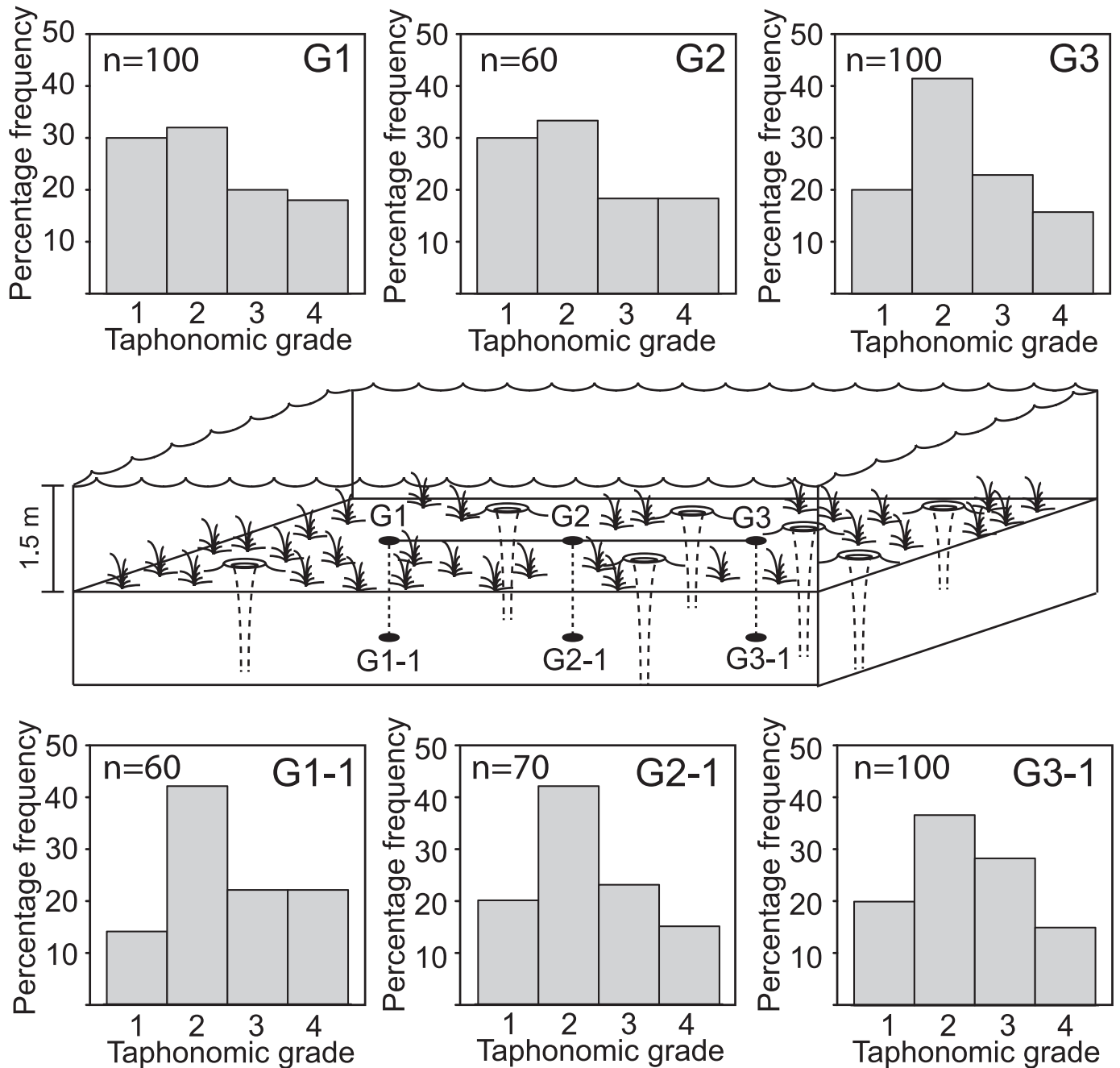
Graham's Harbor

FIG. 5.—Sampling strategy and individual results of taphonomic grade counts (as histograms) for sampling localities at Graham's Harbor, illustrating environmental characteristics of each sampling point. Samples with '-1′ suffix indicate those taken from the subsurface. Taphonomic grades assigned as: 1='pristine', 2='good', 3='altered, 4='highly altered' (see Buchan and Lewis 2009).

lowest in no vegetation (15.15 grid cells), however, these differences were not statistically significant (see Table 6). Comparison of overall damage scores between surface and subsurface samples reveals that foraminifera held in the subsurface accumulated more damage in environments characterized by high-density vegetation (45.1 grid cells) and no vegetation (20.7 grid cells). In the low-density vegetation environment, overall damage scores were higher at the surface (27.4 grid cells) than in the subsurface. Comparison of individual damage types between sub-

environments reveals some general trends correlative to the high-density vegetation to no vegetation gradient; Holes and Type 2 patches are rarest in high-density vegetation, more common in low-density vegetation, and most common in environments with no vegetation. In both high-density vegetation and areas without vegetation, Holes were more common in the subsurface than at the surface (the trend is reversed in low-density vegetation). Type 2 patches were more common at the surface in high-density vegetation, whereas for both low-density vegetation and no
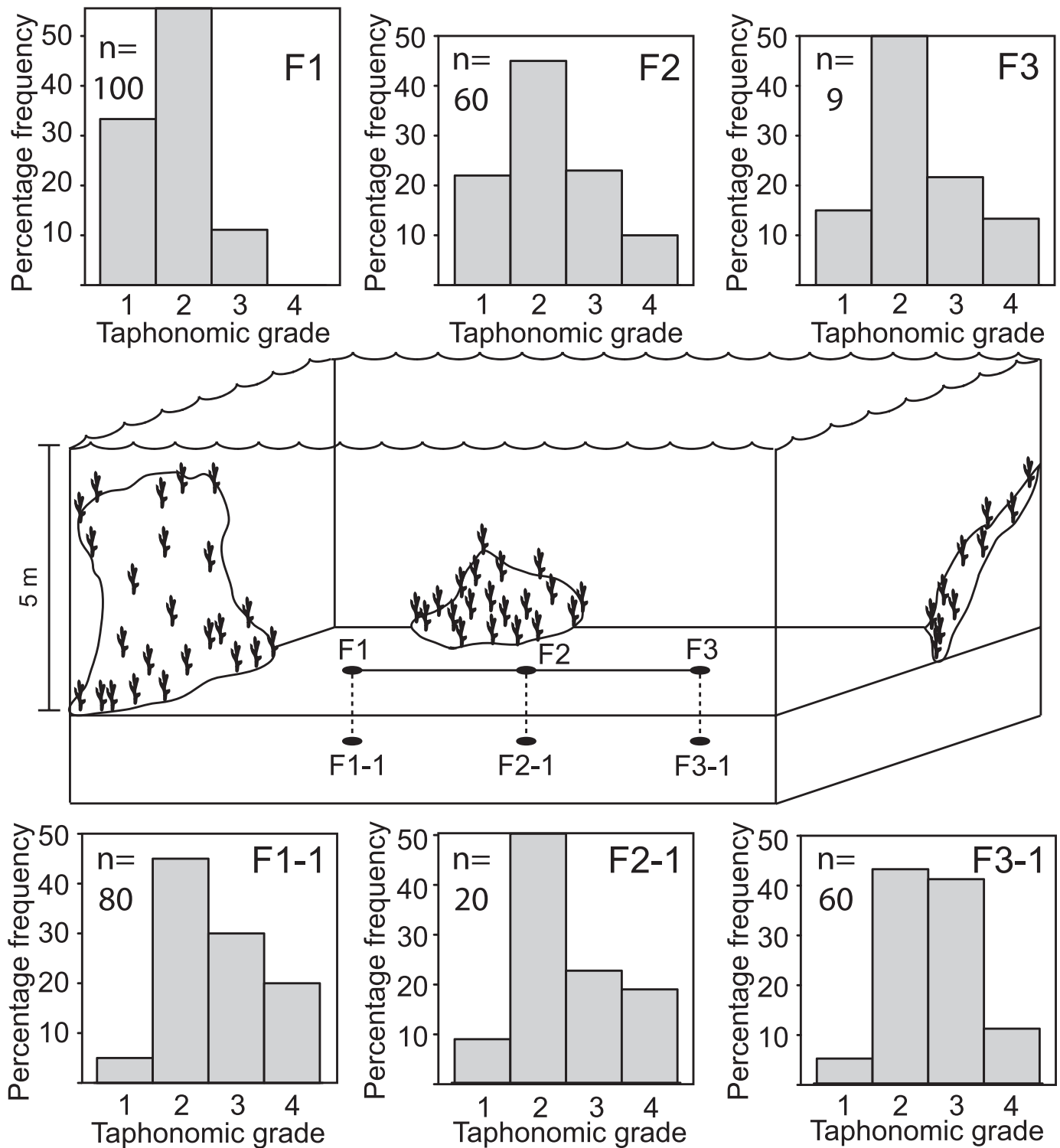
Fernandez Bay

FIG. 6.—Sampling strategy and individual results of taphonomic grade counts (as histograms) for sampling localities at Fernandez Bay, illustrating environmental characteristics of each sampling point. Samples with '-1' suffix indicate those taken from the subsurface. Taphonomic grades assigned as: 1='pristine', 2='good', 3='altered', 4='highly altered' (see Buchan and Lewis 2009).
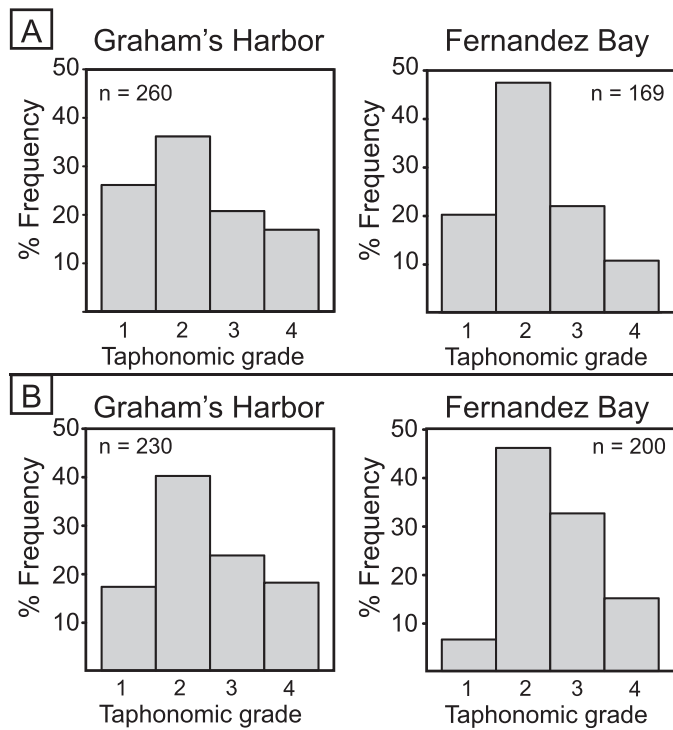
FIG. 7.—Aggregated results of taphonomic grade counts as histograms for (left) Graham's Harbor, and (right) Fernandez Bay. **A**) Surface samples. **B**) Subsurface samples.

vegetation it was more common in the subsurface. Type 2 trails, by contrast, were most common in high-density vegetation, less common in low-density and entirely absent in no vegetation environments. In both high- and low-density vegetation, Type 2 trails were more common in the subsurface than in the surface.

Among the other damage types, Type 1 patches and Type 3 trails were most common in low-density vegetation, less common in no vegetation, and rare in high-density vegetation. Of these, Type 1 patches were more common at the surface in high-density vegetation, but less common at the

TABLE 3.—*Descriptive statistics for taphonomic indices among collected foraminifera in individual samples, for both surface and subsurface samples. 'G'=Graham's Harbor; 'F'=Fernandez Bay. 'SD'=standard deviation; 'Simpson's'=Simpsons diversity index; 'H'=Shannon's diversity index.*

Sample	Mean	SD	Simpson's	H
		Surface		
G1	2.33	0.96	0.73	1.35
G2	2.25	1.08	0.71	1.31
G3	2.26	1.08	0.74	1.36
F1	2.21	0.9	0.57	0.94
F2	2.33	0.9	0.69	1.26
F3	1.78	0.67	0.66	1.23
		Subsurface		
G1-1	2.52	0.99	0.71	1.32
G2-1	2.38	0.98	0.72	1.33
G3-1	2.34	0.98	0.71	1.31
F1-1	2.51	0.9	0.63	1.19
F2-1	2.65	0.88	0.66	1.21
F3-1	2.58	0.75	0.67	1.12

TABLE 4.—*Descriptive statistics for taphonomic indices among collected foraminifera in aggregated samples, for both surface and subsurface samples. 'GH'=Graham's Harbor; 'FB'=Fernandez Bay.*

Sample	Mean	SD	Simpson's	H
		Surface		
GH	2.28	1.03	0.73	1.35
FB	2.23	0.89	0.68	1.25
		Subsurface		
GH	2.43	0.98	0.72	1.32
FB	2.56	0.82	0.66	1.19
		Surface + subsurface		
GH	2.35	1.01	0.73	1.34
FB	2.41	0.87	0.67	1.24

surface in low-density vegetation. Type 3 trails are more common at the sub-surface in high-density vegetation and no vegetation, but more common at the surface in low-density vegetation. Type 1 trails were most common in low-density vegetation, and rare in both the high-density and no vegetation environments. Type 1 trails were found only on the surface in low-density vegetation, only in the sub-surface for no vegetation, and in approximately equal proportion on the surface and in the sub-surface in high-density vegetation.

In summary, test damage is higher in environments possessing vegetation (both high- and low-density) than without. In addition, a larger variety of damage types was found in environments possessing vegetation than without, as Type 2 trails were absent from the no-vegetation environment. This difference is accentuated if results are restricted to surface samples—Holes, Type 2 trails, and Type 3 trails were all absent from the no-vegetation environment, but present in both high- and low-density vegetation. The relatively low sample numbers used for comparison in each case (five views each of two individual foraminifera, totaling 10 views per sample) does, however, result in low statistical power, so that few comparisons produce significant differences (see Table 6; Fig. 10). Despite this low statistical power, Welch t-tests reveal that overall damage scores are significantly lower in surface samples within high-density vegetation than in either low-density vegetation or no vegetation (p=0.0028 and p=0.046 respectively; Table 6). In addition, overall damage scores (i.e., sum of all grid cells with any type of damage) are significantly

TABLE 5.—*P-values for comparisons (Kolmogorov-Smirnov) between surface-subsurface sample pairs for collected foraminiferal samples (observational study); significant values highlighted in bold.*

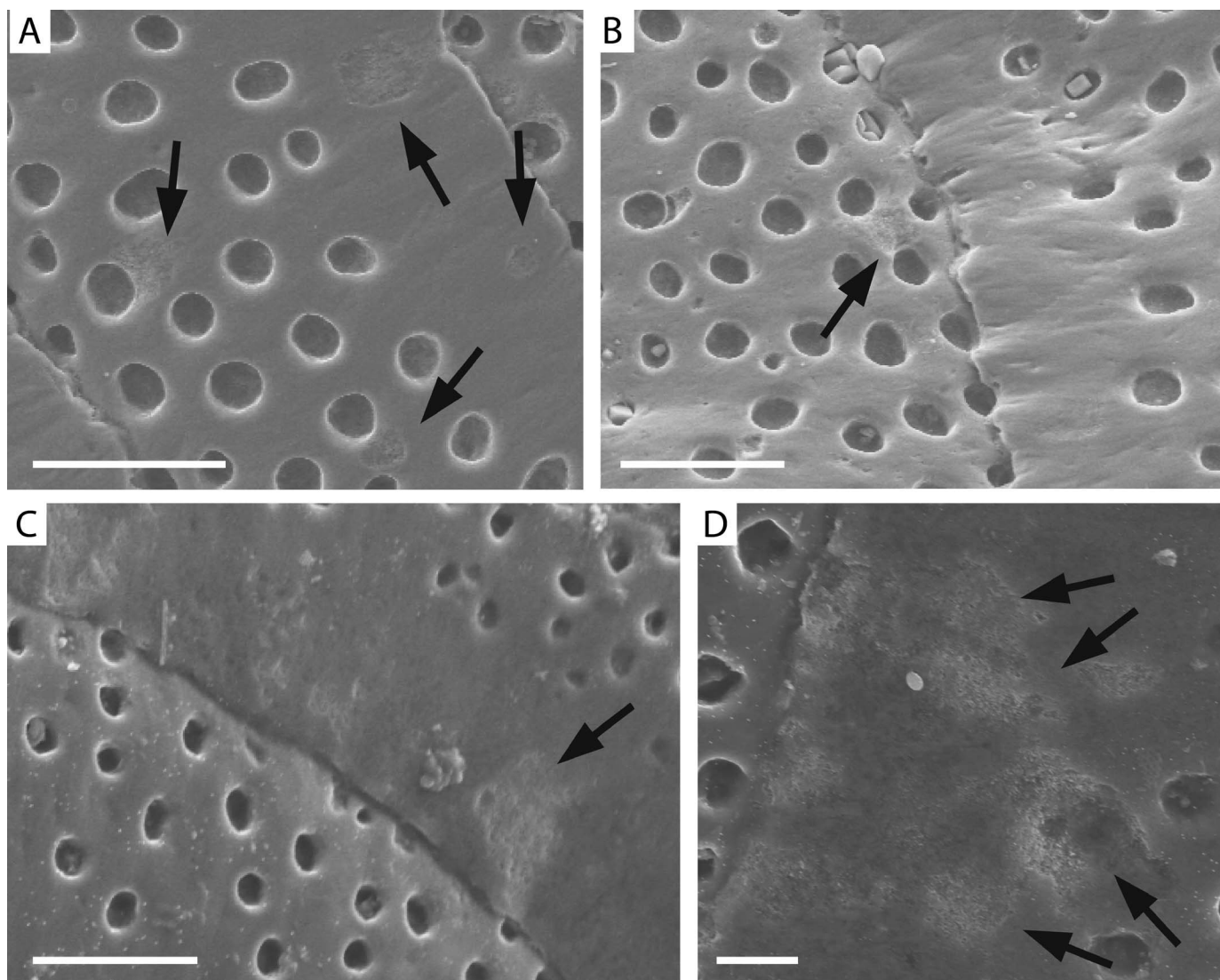| Surface	Subsurface			
	G1-1	G2-1	G3-1	All GH. sub.
G1	0.9032			
G2		0.9999		
G3			0.1545	
All G.H. sur.				0.3059
Surface	Subsurface			
	F1-1	F2-1	F3-1	All F.B. sub.
F1	0.3049			
F2		0.4162		
F3			0.2286	
All F.B. sur.				**0.03322**

FIG. 8.—SEM images illustrating surveyed damage types, showing: **A**, **B**) Type 1 patches (note relatively smooth gradations between adjacent damaged and non-damaged areas). **C**, **D**) Type 2 patches (note well-defined margins to damaged areas).

higher in surface samples within low-density vegetation than in no vegetation (p=0.02).

DISCUSSION

Biotic and Abiotic Sources of Test Damage on A. angulatus

Prior to addressing the six hypotheses associated with our general taphonomic model (see introduction), we first attempted to link our observed

TABLE 6.—*P-values (Welch tests) for tests of significance in differences between number of cells with damage in surface/subsurface pairs and among paleoenvironments; significant values highlighted in bold.*

Vegetation	Surface + subsurface	Surface	Subsurface
high vs. low	0.7629	**0.0028**	0.1475
high vs. none	0.4163	0.0464	0.2177
low vs. none	0.5084	**0.0209**	0.5768

damage types to the activity of specific organisms and/or environmental factors. Comparison of our six recorded damage types to other accounts of foraminiferal test alteration allows tentative identification of each as the result of either biotic (i.e., bioerosive) or abiotic (mechanical destruction and/or dissolution) processes. Our Type 1 trails (Fig. 9A, 9B) are readily identifiable as incipient *Fascichnus* isp. based on characteristic 'scalloped' bases, and which likely represents endolithic boring activity by the cyanobacterium *Hyella* (Radtke and Golubic 2011; Cherchi et al. 2012). Although these bacteria are individually coccoidal, they commonly produce tubular borings similar to those of filamentous organisms, and in the fossil record the trails they produce have been subdivided into ichnospecies on the basis of tube diameters (Radtke 1991). In this case, borings display consistent widths of 8–10 μm, and are thus interpreted as incipient *F. dactylus*. Instances of pore-enlargement (resembling our 'scalloping' around pseudopores) have been attributed to similar groups of endolithic cyanobacteria (Radtke and Golubic 2011). Scalloping around pseudopores can be clearly seen where Type 1 trails meander to avoid these features, suggesting that they represent similar processes. We therefore group the 8–10μm trails and scalloping around pseudopores into a single category. Type
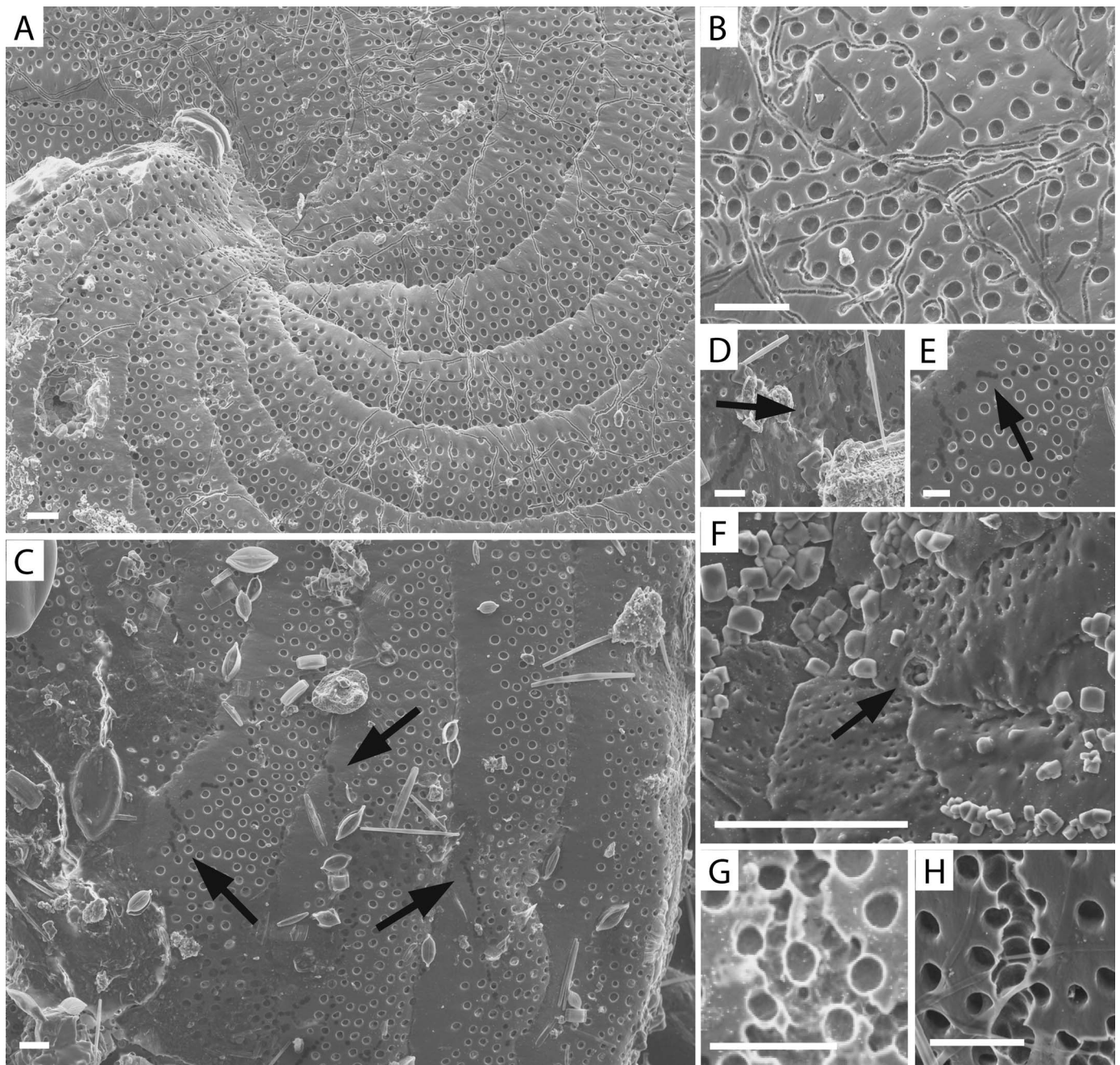
Fɪɢ. 9.—SEM images illustrating surveyed damage types. **A, B)** Type 1 trails (note distinctive 'scalloping' of test surface, and avoidance of pseudopores). **C, D)** Type 2 trails. **E, G)** Type 3 trails. **H)** Holes.

2 trails have much smaller widths and lack scalloped bases, and are thus readily identifiable as microborings left by fungal hyphae. Fungal hyphae leave slightly curved filamentous traces characteristically 1–4 μm in width; they typically appear on carbonate substrates after initial colonization by endolithic algae, which they may actually parasitize (Perkins and Halsey 1971; Golubic et al. 1975; Cherchi et al. 2012). Unlike borings by endolithic algae, however, relatively little work has been done tying bore morphologies to specific fungal species, and so the precise identity of the boring fungi active in these settings is unknown. The identity of our Type 3 trails (Fig. 9E–9G) is much harder to establish, although they bear a close similarity to borings figured by Cherchi et al. (2012, fig. 3F; see also Freiwald 1994, fig. 4) in which these features were attributed to bacteria—possibly even

cyanobacteria. The identity of organisms responsible for Holes (Fig. 9H) is also not clear. Similar features have been figured by several previous studies (see Cherchi et al. 2012, figs. 2, 3), but these typically have much smaller diameters than the features found on our specimens. Hallock et al. (1998) described boreholes of similar size in *Amphistegina*, attributed to the predatory foraminifer *Floresina amphiphega*, however, these leave a characteristic pattern of radiating grooves surrounding the borehole that is not seen here. Consequently, the identity of Hole-makers is left open, but they may represent an instance of predation/scavenging by another species of foraminifera.

Type 1 patches (Fig. 8A, 8B) are distinguished from other damage types by the presence of sharply defined margins, and are broadly consistent with

interpretation as impact structures (cf. Cottey and Hallock 1998, pl. 2). These features are excluded from bulk analyses (i.e., where different damages are summed); however, including/excluding this damage type does not alter either the relative ordering of tests in different subenvironments (Fig. 9) in terms of overall damage score, or the significance of comparisons shown in Table 6.

In contrast to Type 1 patches, Type 2 patches (Fig. 8C, 8D) tend to have much more diffuse margins, and are consistent with interpretation as the result of dissolution (cf. 'etching' traces of Cottey and Hallock 1988, pls. 1, 3). These authors reported much faster rates of dissolution in their experiments than were seen in ours, but suggested that rates of test etching may have been increased by the respiratory products from abundant tunicates which colonized the suspended bags.

Robustness of the Generalized Taphonomic Model

We tested six predictions of our hypothesized general model of differing taphonomic processes in seagrass-dominated versus non-seagrass environments. Hypothesis 1 (seagrass meadow settings should possess a higher proportion of both pristine and highly altered tests than non-seagrass settings) is supported. The data show universally higher taphonomic disparity (i.e., higher evenness among taphonomic grades) in samples from seagrass-dominated Graham's Harbor than in seagrass-poor Fernandez Bay. This is true for both individual (i.e., single) samples and aggregated samples where all taphonomic grades from either surface or subsurface collections were summed. Our other measure of taphonomic disparity (Simpson's diversity, which essentially indicates the extent to which certain taphonomic grades are 'rare') shows the same results—these indices are universally higher in Graham's Harbor, indicating a more even distribution of altered and unaltered tests in this locality. Hypothesis 2 (the proportions of pristine and highly altered tests in seagrass meadows should be homogeneous between the surface and subsurface) is also supported. In all (i.e., both individual and aggregate) paired samples in Graham's Harbor, Kolmogorov-Smirnov tests indicate that mean taphonomic grades are statistically indistinguishable ($p > 0.05$) between surface and subsurface samples (Table 5). In contrast, the aggregated sample pair in Fernandez Bay (FB1/FB-1) reveals significant differences between mean taphonomic grade in surface and subsurface samples. Moreover, *A. angulatus* tests from the subsurface in this locality are more altered (i.e., have higher taphonomic grade) than those on the surface (Tables 3, 4). This last observation also supports the third hypothesis (settings without seagrass should contain a higher proportion of less altered tests at the surface, and more altered tests in the subsurface), as the higher mean taphonomic grade of subsurface tests in Fernandez Bay is shown to be statistically significant.

Actualistic experiments using collected foraminifera reveal a variety of both biotic and abiotic sources of test damage, and allow us to test for differences in rates of test alteration (i.e., overall extent of alteration over a six month period) within and outside of seagrass meadows (hypotheses 4–6). Hypothesis four (per unit time, foraminiferal tests retained at the sediment surface should display higher rates and diversity of bioerosion types within seagrass meadows than outside) is partially supported. Tests held at the sediment-water interface in the seagrass (both high- and low density) subenvironment do display a wider variety of bioerosion types than the no-seagrass environment, where Holes, Type 2 trails, and Type 3 trails were all absent. In addition, in terms of overall rates of bioerosion our surface specimens in low-density vegetation developed significantly higher mean per-view damage coverage than in no vegetation (Welch t-test; p=0.02). However, mean per-view damage coverage in high-density vegetation was significantly lower than in environments without vegetation (p=0.046), suggesting that denser vegetation may provide protection from some bioeroding organisms (specifically those responsible for forming Type 1 trails and Type 3 trails). This finding runs counter to that of Leonard-Pingel (2005) who found highest rates of bioerosion within dense seagrass patches, albeit using mollusks rather than foraminifera), but corroborates observations made by Buchan and Lewis (2009), who noted that low-density seagrass beds were characterized by the lowest quality of preservation seen in their study, and reinforces inference that dense seagrass may play an (as yet) unappreciated role in excluding endolithic parasites and scavengers. Hypothesis five (foraminiferal tests held in the subsurface beneath seagrass beds should exhibit higher rates of test dissolution) and six (surface-subsurface discrepancy in extent/rates of test dissolution should be less apparent outside of seagrass meadows) are not supported. Although both total and mean area of subsurface dissolution (our 'Type 1 patches') are highest in low-density vegetation, this difference is not significantly higher than the no-vegetation subenvironment (Welch t-test; p-value=0.46). In addition, both total and mean area of subsurface dissolution is lower (albeit not significantly) in high-density seagrass than in either low-density vegetation or no vegetation. There are likewise no significant differences in extent of dissolution between surface and subsurface specimens; although subsurface dissolution is higher than surface in low-density vegetation, the opposite is true in high-density vegetation (but is consistent in no vegetation, where no difference was predicted).

In summary, the actualistic experiments provide support for the general hypothesis that rates of bioerosion (and diversity of bioeroders) are higher in seagrass meadows than environments without seagrass. When taken together with observation of larger numbers of living foraminifera (and hence larger flux of pristine tests to the sediment pile) in seagrass-dominated communities (Buchan and Lewis 2009; Darroch 2012), this supports our model for higher taphonomic disparity among foraminiferal tests in environments with seagrass. However, we find no support for the predicted role of seagrass in elevating rates of dissolution in the sediment subsurface beneath meadows (*sensu* Burdige et al. 2010).

The apparent contradictions between the observational and experimental results can perhaps be explained due to the time scales involved in the experiments. The experimental data show that rates of bioerosion in two individuals within a single environment can be highly variable (for example, contrast individuals 11 and 12 in online Supplementary Data Table 1) suggesting that rates and patterns of infestation may be affected by a variety of stochastic processes on short timescales. Patterns of infestation may be subject to a number of positive feedbacks (for example, fungi frequently colonize tests only after initial infestation by algae [Golubic et al. 1975]), which may explain some of the differences in otherwise identically treated individuals, and which would likely become less disparate over longer deployments. In addition, the degree of time averaging in material counted in our observational study is unknown, however, test accumulations in many depositional environments likely represent a range of ages on the order of 10^0–10^3 years (based on both radiocarbon and amino acid racemization dates of bioclastic accumulations in modern settings, see Martin et al. 1996; Olszewski and Kaufman 2015; Strasser and Samankassou 2003; Kosnik et al. 2009; Krause et al. 2010), and so are unlikely to be faithfully represented in experiments run for six months. ^{14}C dates for accumulations of *Baculogypsina* large benthic foraminifera reported by Dawson et al. (2014) are younger (max. ~ 450 years), however, this genus is smaller and likely less robust than *A. angulatus*. For example, none of the experimentally treated individuals progressed beyond a taphonomic grade of two over the course of

→

FIG. 10.—Overall damage scores for experimentally treated surface and subsurface foraminifera, within all studied sub-environments. Results displayed as mean per-view damage values for all individuals (black), and broken down into surface (red) and subsurface (blue). Points indicate mean values; bars give 90% confidence intervals on the mean.
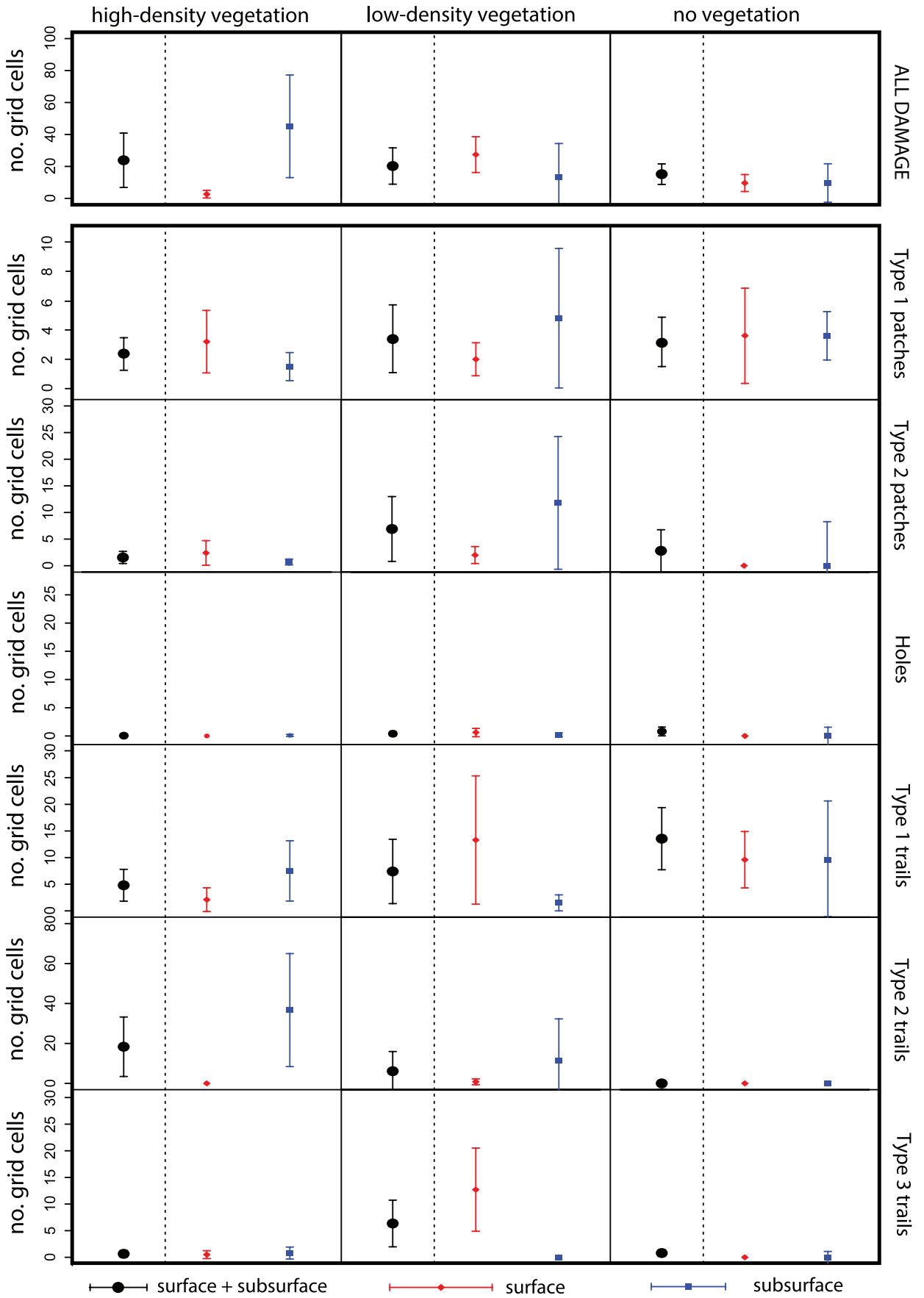
deployment. Despite these caveats, we express cautious optimism that the overall trends visible in the experiments (greatest extent of bioerosion, and highest diversity of bioerosion types in environments characterized by seagrass) represent processes that will eventually produce the patterns evident in the observational data. These combined datasets in turn suggest that taphonomic disparity may be a viable criterion for recognizing seagrass communities in the geological record.

Identifying Seagrass Communities in the Fossil Record

Only a subset of these results, and a subset of the components of the taphonomic model developed here, are potentially useful for identifying seagrass communities in the fossil record. We suggest two groups of criteria for identifying seagrass: (1) direct criteria, which can be used to identify whether any single site likely contained seagrass, and (2) comparative criteria, which can be used to assess which of two fossil deposits were more likely to have contained seagrass beds.

(1a) Type 2 trails (likely produced by endolithic fungi) were entirely absent from the non-vegetated setting. This suggests that seagrass meadows may be a favorable habitat for the tracemakers of these structures (or otherwise play a role in current baffling, preventing spores from being swept away and thus enhancing fungal colonization potential), and thus the presence of this trace may be indicative of seagrass meadow environments. The abundance of studies documenting this trace from other settings (especially those below the photic zone where seagrass is not present—see Golubic et al. 1975) does, however, make this a weak criterion.

(1b) Sparse seagrass meadows displayed a statistically higher evenness in the distribution of TGs (i.e., had higher taphonomic disparity) than the setting without seagrass.

(2a) The mean coverage (both surface and subsurface) of 'scallop trail' damage (likely produced by the cyanobacterium *Hyella*) was statistically higher in non-vegetated settings, than in high-density vegetation (Welch t-test; p-value=0.03, although this test was not significant with low-density vegetation). Consequently, sites characterized by high abundances of Type 1 trails are likely to be either lacking in, or only sparsely populated by seagrass.

(2b) When comparing two sites, the site with higher taphonomic disparity is more likely to be a seagrass meadow.

Review of indirect paleo-seagrass indictors by Reich et al. (2015) allow us to evaluate the strength of taphonomic disparity as a proxy in terms of their criteria, which include geographic and temporal distribution, preservation (fossilization) potential, and habitat restriction. With respect to geographic distribution, *Archaias angulatus* is currently known from shallow marine environments in the Bahamas, Florida, North Atlantic, the Gulf of Mexico, and into the Mediterranean (World Register of Marine Species), overlapping with only a small fraction of global seagrass bed distribution (see Reich et al. 2015). In a temporal context, *Archaias* is known from the Oligocene to Recent, and thus this proxy may be applicable as far back as the late Paleogene. In terms of preservation potential, this study is currently calibrated for only a single species of foraminiferan, possessing a robust test that remains identifiable even with extensive levels of endolithic infestation and mechanical damage. Given that tests with different constructions and compositions can respond very differently to taphonomic processes (both in terms of susceptibility to infestation: Peebles and Lewis 1988; and mechanical destruction: Peebles and Lewis 1991), we cannot yet unequivocally state that taphonomic disparity is easily applicable outside of *A. angulatus* as a seagrass proxy. However, the Soritidae are characterized by porcelaneous tests, and many of the constituent species likely possess equivalent resistance to corrosion and susceptibility to infestation (i.e., instances of heavy infestation are not limited to *Archaias*, see e.g., Peebles and Lewis 1988). It is therefore possible that our proxy may be applicable across the Soritidae (which have a near global distribution), however, this remains to be tested.

In terms of habitat restriction, this study is only calibrated for two specific environments (shallow water, high energy lagoon settings with and without seagrass), and it is conceivable that a 'seagrass-type' taphonomic signature could be produced elsewhere. This signature (i.e., high evenness of taphonomic grades) is reliant on: (1) high levels of bioerosion (itself potentially a consequence of a high biovolume of bioeroding organisms, possibly combined with 'conveyer-belt' bioturbation that repeatedly excavates buried material to the surface where it is subject to degradation by bioeroding organisms); and, (2) a high influx of pristine test material (from recently dead individuals) derived from a locally abundant living population of these organisms. Other environments possessing abundant bioeroders and dense populations of living benthic foraminifera (e.g., mangroves) could therefore be capable of producing the same signature. Along these lines, Golubic et al. (1975) noted a general depth-related zonation of common bioerosion 'types' even within the photic zone, suggesting that both rates and patterns of test infestation may differ between seagrass meadows and deeper water. In addition, there are several environmental differences between our two study sites that could be responsible for the differences in taphonomic grades; differences in grain size (and mechanisms of grain sorting), and differences in water energy (i.e., windward vs. leeward) are factors that may have an effect. Future work will therefore target a larger diversity of modern environments in order to test whether high taphonomic disparity is an exclusive signature for seagrass meadows. A robust test of this proxy will require comprehensive sampling of the great variety of seagrass-type environments that currently exist worldwide, as well as quantification of taphonomic disparity patterns across a broader swath of (non-seagrass-dominated) shallow marine carbonate environments.

It is also possible that taphonomic disparity as a proxy holds only for more sparse seagrass meadows colonized by deep-tier bioturbators. Although callianassid mounds are common components of seagrass-dominated communities across San Salvador (and worldwide, see e.g., Vonk et al. 2008), they are typically excluded from the densest seagrass meadows due to the effect of root-rhizome matrices in impeding mobility and burrowing (Brenchley 1982; Suchanek et al. 1983; Berkenbusch et al. 2007). As a result, there is an apparent threshold density level at which both seagrass meadows and callianassid shrimp can (and commonly do) coexist (Berkenbusch et al. 2007). This study demonstrates homogeneity in the distribution of taphonomic grades between surface and subsurface assemblages in a relatively sparse seagrass meadow in Graham's Harbor (Table 5). Although this homogeneity could also be produced by sediment mixing by storm and wave action, we consider this unlikely given both the current baffling effect of seagrass, and the observation of surface-subsurface heterogeneity in Fernandez Bay (which does not possess seagrass, and so might be expected to be more susceptible to storm-mixing). However, we do not test whether surface-subsurface assemblages are homogenous in denser seagrass meadows where the intensity of vertical bioturbation may be lower. Added to this, our taphonomic experiments support findings by previous authors that rates of bioerosion may be lower in dense seagrass than in sparse seagrass; consequently, dense seagrass meadows may possess a very different taphonomic signature. Future work will therefore investigate the homogeneity of surface and subsurface assemblages in seagrass meadows of varying density (including those without callianassid burrows), to establish the extent to which homogeneity may be controlled by bioturbation alone.

Given the caveats detailed above, it is likely that the proposed taphonomic disparity proxy for seagrass beds in the fossil record would currently qualify as only a 'weak' IPSI (cf. Reich et al. 2015). However, the taphonomic signature and grade of foraminiferal tests possess a number of strengths as potential proxies—foraminifera are extremely abundant in seagrass settings, have a high preservation potential, and we have shown that rates and patterns of test alteration can be significantly different in and outside of sparse seagrass beds. As a result, (and pending further studies)

we are therefore confident that taphonomic disparity has potential as a seagrass proxy applicable to a diversity of both extant and ancient species of foraminifera, and which merits further investigation.

CONCLUSIONS

In summary, these combined analyses demonstrate that: (1) sparse seagrass meadows sampled in Graham's Harbor characterized by higher density of vertical burrows possess a higher proportion of both pristine and highly altered tests (i.e., higher evenness in the distribution of taphonomic grades) than the non-seagrass setting sampled in Fernandez Bay; and (2) pristine foraminifera deployed for six months within the sampled seagrass meadow developed a greater extent and diversity of bioerosion than those deployed in a nearby non-seagrass setting. These approaches therefore provide a link between pattern (high taphonomic disparity) and process (higher rates of bioerosion) in the development of a 'seagrass-type' taphonomic signature that can potentially be used to recognize the signature of seagrass meadows in the geological record. We hypothesize that this signature is the result of both high rates of living test production in seagrass meadows, and vertical bioturbation which recycles tests to the sediment-water interface where they can be repeatedly subjected to bioerosive processes (thus reaching the highest taphonomic grades). However, if this hypothesis is correct, then the use of high taphonomic disparity as a paleoenvironmental proxy may be restricted to relatively sparse seagrass meadows possessing deep-tier bioturbators, and may not be useful for identifying much denser meadows where vertical bioturbators are excluded. Despite this, combined observational and experimental approaches show that taphonomic disparity in foraminiferal tests has potential utility as a species-independent proxy for seagrass-dominated communities, and future work will focus on the links between seagrass density, bioturbation intensity, the abundance of bioerosive organisms, and the abundance of living foraminifera in seagrass settings.

ACKNOWLEDGMENTS

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

REFERENCES

BEAVINGTON-PENNEY, S.J., WRIGHT, V.P., AND WEOLKERLING, W.J., 2004, Recognising macrophyte-vegetated environments in the rock record: a new criterion using 'hooked' forms of crustose coralline red algae: Sedimentology Geology, v. 166, p. 1–9.

BERKENBUSCH, K., ROWDEN, A.A., AND MYERS, T.E., 2007, Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages: Journal of Experimental Marine Biology and Ecology, v. 341, p. 70–84.

BRASIER, M.D., 1975, An outline history of seagrass communities: Palaeontology, v.18, p. 681–702.

BRENCHLEY, G.A., 1982, Mechanisms of spatial competition in marine soft-bottom communities: Journal of Experimental Marine Biology and Ecology, v. 60, p. 17–33.

BUCHAN, O.C. AND LEWIS, R.D., 2009, Recent benthic foraminifera as indicators of seagrass-bed characteristics, San Salvador, Bahamas: the addition of taphonomy, *in* Demchuk, T.D. and Gary, A.C. (eds.), Geologic Problem Solving with Microfossils: A Volume in Honor of Garry D. Jones: SEPM (Society for Sedimentary Geology) Special Publication, v. 93, p. 83–92.

BURDIGE, D.J., HU, X., AND ZIMMERMAN, R.C., 2010, The widespread occurrence of coupled carbonate dissolution/reprecipitation in surface sediments on the Bahamas Bank: American Journal of Science, v. 301, p. 492–521.

CHARPY-ROUBAUD, C. AND SOURNIA, A., 1990. A comparative estimation of phytoplanktonic and microphytobenthic production in the oceans: Marine Microbial Food Webs, v. 4, p. 31–57.

CHERCHI, A., BUOSI, C., ZUDDAS, P., AND DE GIUDICI, G., 2012, Bioerosion by microbial euendoliths in benthic foraminifera from heavy metal-polluted coastal environments of Portovesme (south-western Sardinia, Italy): Biogeosciences, v. 9, p. 4607–4620.

COLBY, N.D. AND BOARDMAN, M.R., 1988, Depositional environment of a windward, high-energy lagoon, Graham's Harbor, San Salvador, Bahamas: Journal of Sedimentary Petrology, v. 59, p. 819–834.

COTTEY, T.L. AND HALLOCK, P., 1988, Test surface degradation in *Archaias angulatus*: Journal of Sedimentary Research, v. 18, 187–202.

CURRAN, H.A. AND WILLIAMS, A.B., 1997, Ichnology of an intertidal carbonate sand flat: Pigeon Creek, San Salvador Island, Bahamas, *in* Carew, J.L. (ed.), Proceedings of the Eighth Symposium on the Geology of the Bahamas and Other Carbonate Regions: Gerace Research Centre, San Salvador, Bahamas, p. 33–46.

DARROCH, S.A.F., 2012, Carbonate facies control on the fidelity of surface-subsurface agreement in benthic foraminiferal assemblages: implications for index-based paleoecology: PALAIOS, v. 27, p. 137–150.

DAWSON, J.L., SMITHERS, S.G., AND HUA, Q., 2014, The importance of large benthic foraminifera to reef island sediment budget and dynamics at Raine Island, northern Great Barrier Reef: Geomorphology, v. 222, p. 68–81.

DEN HARTOG, C., 1970, Origin, evolution and geographical distribution of the seagrasses: Verhandelingen-Koninklijke Nederkindse Akademie van Wetenschappen Afdeling Natuurkunde, v. 59, p. 12–38.

DOMNING, D.P., 2001, Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 166, p. 27–50.

EVA, A.N., 1980, Pre-Miocene seagrass communities in the Caribbean: Palaeontology v. 23, v. 231–236.

FICHTEL, L.V. AND MOLL, J.P.C., 1798, Testacea microscopia, aliaque minuta ex generibus Argonauta et Nautilus, ad naturam delineata et descripta: A. Pichler, Wien, xii + 123 p., 24 pl.

FREIWALD, A., 1994, Bacteria-induced carbonate degradation: a taphonomic case, study of *Cibicides lobatulus* from a high-boreal carbonate setting: PALAIOS, v. 10, p. 337–346.

FUJITA K. AND HALLOCK, P., 1999, A comparison of phytal substrate preferences of *Archaias angulatus* and *Sorites orbiculus* in mixed macroalgal-seagrass beds in Florida Bay: Journal of Foraminiferal Research, v. 29, p. 143–151.

GACIA, E., DUARTE, C.M., MARBA, N., TERRADOS, J., KENNEDY, H., FORTES, M.D., AND TRI, N.H., 2003, Sediment deposition and production in SE-Asia seagrass meadows: Estuarine, Coastal and Shelf Science, v. 56, p. 909–919.

GINSBURG, R.N. AND LOWENSTAM, H.A., 1958, The influence of marine bottom communities on the depositional environment of sediments: The Journal of Geology, v. 66, p. 310–318.

GOLUBIC, S., PERKINS, R.D., AND LUKAS, K.J., 1975, Boring microorganisms in carbonate substrates, *in* Frey, R.W. (ed.), The Study of Trace Fossils: A Synthesis of Principals, Problems, and Procedures in Ichnology, Springer-Verlag, New York, p. 229–259.

HALLOCK, P., TALGE, H.K., WILLIAMS, D.E., AND HARNEY, J.N., 1998, Borings in amphistegina (foraminiferida): evidence of predation by floresina amphiphaga (foraminiferida): Historical Biology, v. 13, p. 73–76.

HARBORNE, A.R., MUMBY, P.J., MITCHELL, F., PERRY, C.T., DAHLGREN, C.P., HOLMES, K.E., AND BRUMBAUGH, D.R., 2006, The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes: Advances in Marine Biology, v. 50, p. 57–189.

HEMMINGA, M.A. AND DUARTE, C.M., 2000, Seagrass Ecology: Cambridge, UK, Cambridge University Press, 298 p.

IVANY, L.C., PORTELL, R.W., AND JONES, D.S., 1990. Animal-plant relationships and paleobiogeography of an Eocene seagrass community from Florida: PALAIOS, v. 5, p. 244–258.

KOSNIK, M.A., HUA, Q., KAUFMAN, D.S., AND WUST, R.A., 2009, Taphonomic bias and time-averaging in tropical molluscan death assemblages: differential shell halflives in Great Barrier Reef sediment: Paleobiology, v. 35, p. 565–586.

KOTLER, E., MARTIN, R.E., AND LIDDELL, W.D., 1992, Experimental analysis of abrasion and dissolution resistance of modern reef-dwelling foraminifera: implications for the preservation of biogenic carbonates: PALAIOS, v. 7, p. 244–276.

KRAUSE, R.A., JR., BARBOUR, S.L., KOWALEWSKI, M., KAUFMAN, D.S., ROMANEK, C.S., SIMOES, M.G., AND WEHMILLER, J.F., 2010, Quantitative comparisons and models of time-averaging in bivalve and brachiopod shell accumulations: Paleobiology, v. 36, p. 428–452.

LEONARD-PINGEL, J.S., 2005, Molluscan Taphonomy as a Proxy for Recognizing Fossil Seagrass Beds: Unpublished M.S. thesis, Louisina State University, Baton Rouge, 140 p.

LI, C., JONES, B., AND BLANCHON, P, 1997, Sediment deposition and production in SE-Asia seagrass meadows: Estuarine, Coastal and Shelf Science, v. 56, p. 909–919.

MACGINTIE, G.E. AND MACGINTIE, N., 1949, Natural History of Marine Animals: New York, McGraw-Hill, 473 p.

MARTIN, R.E. AND WRIGHT, R.C., 1988, Information loss in the transition from life to death assemblages of foraminifera in back reef environments, Key Largo, Florida: Journal of Paleontology, v. 62, p. 399–410.

MARTIN, R.E., WEHMILLER, J.F., SCOTT HARRIS, M., AND LIDDELL, W.D., 1996, Comparative taphonomy of bivalves and foraminifera from Holocene tidal flat sediments, Bahia la

Choya, Sonora, Mexico: taphonomic grades and temporal resolution: Paleobiology, v. 22, p. 80–90.

MELDAHL, K.H., 1987, Sedimentologic and taphonomic implications of biogenic stratification: PALAIOS, v. 2, p. 350–358.

MORGAN J.L. AND LEWIS, R.D., 2010, Benthic foraminiferal assemblages at Cut Cay: a microcosm study of the effect of water energy and substrate preference, San Salvador, Bahamas, *in* Siewers, F. and Martin, J. (eds.), Proceedings of the 14th Symposium on the Geology of the Bahamas and other Carbonate Regions, Gerace Research Centre, San Salvador, Bahamas, p. 150–162.

OLSZEWSKI, T.D. AND KAUFMAN, D.S., 2015, Tracing burial history and sediment recycling in a shallow estuarine setting (Copano Bay, Texas) using postmortem ages of the bivalve *Mulinia lateralis*: PALAIOS, v. 30, p. 224–237.

PEEBLES, M.W. AND LEWIS, R.D., 1988, Differential infestation of shallow-water benthic foraminifera by microboring organisms: possible biases in preservation potential: PALAIOS, v. 3, p. 345–351.

PEEBLES, M.W. AND LEWIS, R.D., 1991, Surface textures of benthic foraminifera from San Salvador, the Bahamas: Journal of Foraminiferal Research, v. 21, p. 285–292.

PERKINS, R.D. AND HALSEY, S.D., 1971, Geologic significance of microboring fungi and algae in Carolina shelf sediments: Journal of Sedimentary Petrology, v. 41, p. 843–853.

R DEVELOPMENT CORE TEAM, 2013, R: A language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/.

RADTKE, G., 1991, Die mikroendolithischen Spurenfossilien im Alt-Tertiar West-Europas und ihre palokologische Bedeutung: Courier Forschinst Senckenberg, v. 138, p. 1–185.

RADTKE G. AND GOLUBIC, S., 2011, Microbial euendolithic assemblages and microborings in intertidal and shallow marine habitats: insight in cyanobacterial speciation, *in* Reitner, J.N., Queric, V., and Arp, G. (eds.), Advances in Stromatolite Geobiology: Lecture Notes in Earth Sciences, v. 131, p. 213–244.

REICH, S., 2014, Gastropod associations as a proxy for seagrass vegetation in a tropical, carbonate setting (San Salvador, Bahamas): PALAIOS, v. 29, p. 467–482.

REICH, S., DI MARTINO, E., TODD, J.A., WESSELINGH, F.P., AND RENEMA, W., 2015, Indirect paleo-seagrass indicators (IPSIs): a review: Earth Science Reviews, v. 143, 161–186.

SMOUT, A.H. AND EAMES, F.E., 1958, The genus Archaias (Foraminifera) and it's stratigraphical distribution: Palaeontology, v. 1, p. 207–225.

STIMPSON, W., 1866, Descriptions of new genera and species of macrurous Crustacea from the coasts of North America: Proceedings of the Chicago Academy of Sciences, v. 1, p. 46–48.

STRASSER, A. AND SAMANKASSOU, E., 2003, Carbonate sedimentation rates today and in the past: Holocene of Florida Bay, Bahamas, and Bermuda vs. Upper Jurassic and Lower Cretaceous of the Jura Mountains (Switzerland and France): Geologica Croatica, v. 56, p. 1–18.

SUCHANEK, T.H., 1983, Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidia) bioturbation: Journal of Marine Research, v. 41, p. 281–298.

TUCKER, M.E. AND WRIGHT, V.P., 1990, Carbonate Sedimentology: Blackwell Scientific, Oxford. 482 p.

VONK, J.A., KNEER, D., STAPEL, J., AND ASMUS, H., 2008, Shrimp burrow in tropical seagrass meadows: an important sink for litter: Estuarine, Coastal and Shelf Science, v. 79, p. 79–85.

WALKER, S. AND GOLDSTEIN, S., 1999, Taphonomic tiering: experimental field taphonomy of molluscs and foraminifera above and below the sediment-water interface: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 227–244.