Sediment source and dose influence the larval performance of the threatened coral *Orbicella faveolata*

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Abstract

The effects of turbidity and sedimentation stress on early life stages of corals are poorly understood, particularly in Atlantic species. Dredging operations, beach nourishment, and other coastal construction activities can increase sedimentation and turbidity in nearby coral reef habitats and have the potential to negatively affect coral larval development and metamorphosis, reducing sexual reproduction success. In this study, we investigated the performance of larvae of the threatened Caribbean coral species *Orbicella faveolata* exposed to sediments collected from a reef site in southeast Florida recently impacted by dredging (Port Miami), and compared it to the performance of larvae exposed to sediments collected from the offshore, natal reef of the parent colonies. In a laboratory experiment, we tested whether low and high doses of each of these sediment types affected the survival, settlement, and respiration of coral larvae compared to a no-sediment control treatment. In addition, we analyzed the sediments used in the experiments with 16S rRNA gene amplicon sequencing to assess differences in the microbial communities present in the Port versus Reef sediments, and their potential impact on coral performance. Overall, *O. faveolata* larvae exposed to high doses of either sediment type (Port or Reef) exhibited reduced survival and settlement rates, but only the Port sediments resulted in adverse effects in the low-dose treatment. Sediments collected near the Port also contained different microbiomes than Reef sediments, and higher relative abundances of the bacteria Desulfobacterales, which has been associated with coral disease. We hypothesize that differences in microbiomes between the two sediments may be a contributing factor in explaining the observed differences in larval performance. Together, these results suggest that the settlement success and survival of *O. faveolata* larvae are more readily compromised by encountering port inlet sediments compared to

45 reef sediments, with potentially important consequences for the recruitment success of this species

46 in affected areas.

Introduction

Dredging and port construction activities can induce chronic sedimentation and turbidity stress in surrounding coral reef habitats [1-6]. Sedimentation caused by dredging is often more harmful to corals than sedimentation caused by other activities, due to its acute onset and often long duration, typically lasting many months to years [1, 7]. Sedimentation effects vary depending on grain size and composition (e.g., [7-12]), and dredging activities can release large quantities of sediments in the water column that are typically of finer grain size compared to naturally occurring sediments (<63 μm, [7]). These finer sediments tend to attenuate more light and are more prone to being resuspended, thus causing a greater net reduction in light essential for photosynthesis [10]. Finer sediments also have an adhesive, clay-like texture that is more resistant to bioturbation when deposited [13], can lead to a change in the bacterial community [12], and is more likely to become anoxic [8, 14]. Finally, suspended sediment plumes, especially those with finer grain size, can also travel several km away from the dredging site (e.g., [9, 15, 16]), and can also release contaminants [17-19] and pathogens [11, 20, 21] which may potentially transmit coral diseases such as Stony Coral Tissue Loss Disease [22].

Sediments can negatively affect corals throughout their life cycle, suppressing coral health, condition, and survival via multiple mechanisms (reviewed in [7, 12, 13, 23]). Reported effects on early life stages of corals include reductions in the fecundity of parent colonies [24], fertilization [25, 26], larval settlement [27-31], and recruit survival [5, 27, 32, 33]. Tolerance to sedimentation exposure is estimated to be an order of magnitude lower for coral recruits compared to adults [13, 23, 34], although most of this work has been conducted on Pacific coral species (reviewed in [12, 13, 23]). Much less is known regarding the effects of sediments on coral larvae and recruits for Atlantic coral species, and this information is critical for developing appropriate conservation

70 plans for these species. Poor understanding of coral responses to sediment disturbances during
71 their most susceptible stages can result in inappropriate management of dredging projects, lead to
72 preventable coral losses, and unnecessarily high costs to adaptively manage operations (corrective
73 actions) and provide compensatory mitigation to offset impacts.

74 Sediments may interfere with the ability of coral larvae to find a suitable substrate on which
75 to settle, which is key to successful recruitment and survival [31, 35, 36]. Even a thin layer of
76 sediments not harmful to adult corals can be detrimental to coral larvae [23, 28, 31, 37-39], both
77 by physically obstructing settlement surfaces [27, 30], and impairing biotic settlement cues such
78 as those from crustose coralline algae (CCA) [30]. However, the mechanisms and cues by which
79 sediments can affect settlement and recruitment success, or benthic habitat quality (e.g., [31]) are
80 poorly understood. Recent work suggests that coral larvae show a preference for distinct microbial
81 and/or chemical signature types in certain types of CCA [40-43], suggesting that specific bacterial
82 communities can serve as environmental cues for coral settlement [40, 42]. How and whether
83 microbial communities present in sediments can negatively affect the ability of coral larvae to
84 identify these cues remains an open question.

85 The aim of the present study was to investigate the performance of coral larvae of an
86 important Caribbean reef-building species (*Orbicella faveolata*) following a short-term (pulse)
87 sediment exposure. *O. faveolata* (Ellis and Solander, 1786) is listed as threatened under the U.S.
88 Endangered Species Act [44] but is present in southeast Florida in the vicinity of two large ports
89 with expansions (deepening/widening) planned in the near future (Port Everglades and Port
90 Miami). The most recent large-scale deepening project at Port Miami (which occurred from 2013-
91 2015) resulted in severe sedimentation impacts to local coral reef habitats [1, 3, 15, 45], although
92 the severity of those impacts has been disputed [46]. In addition, recent work exposed adult *O.*

93 *faveolata* corals to Port Miami sediments during a 96-hr period and showed adverse effects on
94 tissue regeneration capacity compared to no sediment controls [47]. In this study, we exposed *O.*
95 *faveolata* larvae to sediments collected near the Port Miami channel and compared their
96 performance with larvae exposed to reef sediments collected from the natal reef of the parent
97 colonies in the Florida Keys. We compared the effects of the two different sediment types on the
98 survival, settlement, and respiration of coral larvae, and also characterized the bacterial
99 communities of these sediments using 16S rRNA gene amplicon sequencing to assess the potential
100 role of microbial communities in affecting coral performance. To our knowledge, this is the first
101 study to investigate the effects of suspended sediments on larvae of western Atlantic (Caribbean)
102 coral species, and the first to use sediments that have not been dried or sterilized prior to exposure,
103 which may have masked some of the biological or chemical effects of sedimentation in previous
104 studies.
105

106 # Methods

107 ## Coral larvae collection

108 *O. faveolata* larvae were collected and cultured as described in [48] and [49]. Gamete
109 bundles were collected seven nights after the full moon (night of 14th August 2017) from colonies
110 that spawned at two reefs in the upper Florida Keys (Horseshoe and Sand Island reefs). Once the
111 bundles broke apart, equal volumes of gametes from 3-4 parental genets were combined for
112 fertilization. Resulting embryos were maintained in water collected from their natal reef at a land-
113 based facility in the Keys (either in static bins with regular water changes or in a recirculating
114 system with mesh-floored bins and a constant drip input) and cultured for ~2 days so that

unfertilized eggs would disintegrate, leaving behind only developing larvae. Embryos were kept in a shaded area under ambient light conditions and a mean temperature of 29°C. Larvae were then transferred to the University of Miami for experiments.

Sediment collections and maintenance

Immediately prior to starting the larval experiments (24 - 48 h), two batches of sediments were collected for experiments, one from a "Reef" origin and another from a "Port" origin. Reef sediments were collected at Horseshoe Reef in Key Largo, from the same site where the coral parent colonies occurred (25°8'19"N, 80°17'41"W, Fig 1). Port sediments were collected from a site located ~200 m north of the recently-dredged channel of Port Miami (25°45'50"N, 80°5'56"W, Fig 1), reported in [3] as having detrimental effects from dredging-induced sedimentation on adult corals. This site was shown by [3] as the most severely impacted location surveyed, with the highest sediment cover (43%) and highest prevalence of sediment "halos" (indicating partial mortality) compared to the reference stations.

Fig 1. (A) Map of locations on the coast of southeastern Florida where Port and Reef sediments were collected from (near Port Miami and Horseshoe reef in Key Largo). (B) Map of coral reef habitats around the Port of Miami federal channel. (C) Port sediments were collected from a site within the Inner Reef located ~200 m north of the recently dredged channel of Port Miami (circled in red), which was the most severely impacted location surveyed due to sedimentation compared to the reference stations by [3]. (D) Representative photo of the sediments collected near the Port of Miami. (E) Representative photo of the sediments collected at Horseshoe reef.

138 All sediments were taken from the upper ~3 cm of the sediment layer (surficial layer) by
139 sliding a metal tool below the sediment-water interface and then scooping them into a certified-
140 clean HPDE sample container. Three to four containers were collected per site and combined to
141 produce a single "batch" for experiments. Sediments were then brought to the laboratory,
142 homogenized in a beaker of seawater and kept in continuous movement and aeration until used in
143 experiments. Prior to use, sediments were allowed to settle and water was siphoned out with care
144 to avoid disturbing the fine particles on the surface. Sediments were then wet-weighed (adjusting
145 for water content) to avoid killing any microorganisms present while retaining as many fine
146 particles as possible. The treatments were conducted using freshly collected sediments to be able
147 to assess any physical (e.g., abrasion) and biological (e.g., pathogenic) stress responses.

148 A subset of the sediments was analyzed for grain size by sieving and pipetting after drying
149 the sediments thoroughly in an oven. Grain size limits were defined according to the Udden-
150 Wentworth US standard classification [50], while statistical parameters were determined using
151 graphical measures from the cumulative size distributions as shown in S1 Fig. A summary of these
152 parameters are provided in S1 Table. Reef sediments can be described as a well-sorted medium
153 sand with virtually no silt or gravel. Conversely, Port sediments can be described as a poorly-
154 sorted, medium sand with small amounts of gravel (approx. 1.97% >2000 μm) and silt and clay-
155 sized particles (also referred as "mud", approx. 1.25% <63 μm). No chemical or organic matter
156 analysis of the sediments were conducted.

157 Experimental setup

158 Fifty 8-day-old larvae were added to individual glass vials containing 45 mL filtered
159 seawater (5 μm). Vials were allocated randomly to one of five different treatments: (1) a control

160 treatment (no sediment), (2) a low "Reef" suspended sediment treatment (20 mg/L of homogenized
161 sediment from Horseshoe Reef added), (3) a low "Port" sediment treatment (20 mg/L sediment
162 from the Port site added), (4) a high "Reef" sediment treatment (100 mg/L sediment from
163 Horseshoe reef added), and (5) a high "Port" sediment treatment (100 mg/L sediment from the
164 Port site added). Nine to ten replicates were used per treatment. Vials were attached to a titer plate
165 shaker set to 300 rpm to continuously maintain sediments in suspension for 24 h. Initial trials were
166 conducted to assess the best exposure times that caused minimal mortality in control larvae and
167 maintained both fine and coarse sediment particles in continuous suspension.

168 Treatments were chosen to characterize sub-lethal and lethal responses to suspended
169 sediment concentrations for "tolerant" versus "sensitive" species as described by [12]. In addition,
170 our goal was to test a low-concentration of suspended sediment (20 mg/L) representing typical
171 conditions near dredging operations. Jones et al. [13] analyzed suspended sediment concentrations
172 over a 30-day running mean period during the Barrow Island dredging project in Australia and
173 found that the 95th percentile was 21 mg/L for 7 sites located at distances <1 km from the dredging.
174 Similarly, although our 100 mg/L (high-dose) suspended sediment treatments were approximately
175 5 times higher than those typically observed during dredging operations, such conditions do occur
176 over short periods (see [51]).

177 24 hour treatment exposure: larval survival assays

178 After 24 h of exposure, swimming larvae remaining in each vial were pipetted out, counted
179 and examined with a microscope to determine the proportion that had survived. The vial was also
180 carefully examined for potential settlers. A subset of larvae (N=6 per vial) was used to assess
181 changes in respiration rates. Remaining larvae were allowed to recover for one week in filtered

182 seawater (without sediments) in the same vials before being transported to the Florida Keys to
183 conduct the settlement assays.

184 1-week post-exposure: larval settlement assays

185 Settlement assays were conducted by pooling all the larvae remaining in each treatment
186 and then redistributing N=15 larvae to individual vials containing filtered seawater and a piece of
187 rubble collected from Horseshoe reef to act as settlement cue. A total of 10 replicate glass vials
188 per treatment were used to quantify larval settlement per treatment. After 24 h, the total number of
189 larvae still swimming, or that had settled on the rubble, was manually scored using fluorescence
190 microscopy. Larvae were classified as "settlers" only if they displayed visible signs of settlement
191 (attachment to the substrate) and metamorphosis (i.e., transition from pear-shaped to flat/disc
192 shape). To determine the cumulative percentage of larval settlement, the total number of settled
193 corals (spat) was divided by the initial number of larvae added to each container.

194 24 hour and 1-week assessment of coral larval respiration

195 Respiration was measured using a microplate reader developed by Loligo Systems
196 (Denmark), which allows measuring real-time respiration rates in each one of 24 wells using an
197 optical fluorescence oxygen sensing technology (SDR SensorDish Reader®, PreSens, Germany)
198 as described in [52-54]. This system comes pre-calibrated specifically for the reader used, and
199 oxygen solubility is continuously calculated with oxygen sensors (optrodes) attached to the bottom
200 of each well. Larval respiration rates were assessed at two time points, immediately after the 24 h
201 treatment exposure and 1-week post-exposure. At each time point, larvae (N=6) were taken at
202 random from each vial and placed in each of the wells of a sealed glass 125-µL microplate (without
203 any sediments). A total of 8-10 replicate wells were used per treatment. Four additional control

204 wells were used in each plate without any larvae to measure any background respiration in the
205 treatment water.

206 Larvae were visually inspected for normal swimming behavior prior to each run. After each
207 plate was prepared, wells were inspected to ensure there were no air bubbles, and an oxygen-
208 impermeable seal was created using a silicone membrane covered with parafilm and a compression
209 block. To maintain constant temperature, the microplate was placed inside a temperature-
210 controlled flow-through water bath (included as part of the system), in a light-controlled room.
211 The plate was then placed in a titer shaker at a low speed to maintain constant water motion.
212 Finally, measurements of oxygen concentrations were taken every 15 seconds throughout the
213 duration of the run and recorded using the SDR v 4.0.0 software (PreSens, Germany). Oxygen
214 concentration was plotted as a function of time for individual wells and the first 10-20% (pO_2 in
215 % air saturation) linear decreases in oxygen were used to calculate the oxygen consumption rate
216 (an example plot of oxygen consumption over time for 6 *O. faveolata* larvae placed in a single
217 well of the microplate is shown in S2 Fig). Any portion of the slope that dipped below 70% air
218 saturation was not used for analysis. Respiration rates were then corrected for background
219 respiration and calculated as nanomoles of oxygen consumed per larva per minute.

220 16S sequencing of sediment samples

221 Immediately upon collection, ~1 gram from each of the Port and Reef sediment samples
222 collected per site was preserved in RNAlater for 16S sequencing. The DNA was extracted and
223 PCR amplified with 16S rRNA gene V4 primers [55] with the Platinum Hot Start PCR Master Mix
224 (2X) (ThermoFisher Scientific, Waltham, MA). The master mix was a 48-µl reaction and 2 µl of
225 DNA template was used. The DNA was then amplified as follows: 94 °C for 3 minutes (1X), 94 °C
226 for 45 seconds (35X), 50 °C for 60 seconds (35X), 72 °C for 90 seconds (35X), and 72 °C for

227 10 minutes (1X). Amplified products were cleaned using AMPure XP beads (Beckman Coulter,
228 Brea, CA), normalized to 4 nM, and 5 µl of each normalized sample was pooled. The samples were
229 sequenced on a MiSeq with PE-300v3 kits at the Halmos College of Natural Sciences and
230 Oceanography at Nova Southeastern University.

231 Statistical analysis

232 Larval performance

233 All analyses of larval performance data were done in R v.4.1.2. The effects of the sediment
234 treatments on the proportion of larval survivorship and settlement were analyzed using binomial
235 generalized linear models (GLM) with the lme4 package [56]. The models included sediment
236 treatment as a fixed effect and replicate (vial) as a random effect. Model predictions (survivorship
237 and settlement probabilities as well as the odds ratio between the control and the treatments) were
238 plotted using the plot_model function from the sjPlot package [57] including 95% confidence
239 intervals. Larval respiration rates after 24 h of treatment exposure and 1-week post-exposure were
240 analyzed using a linear mixed-effects model (LMEM) with the lme4 package. The model included
241 sediment treatment and time point (exposure and recovery) as fixed interactive effects, and vial,
242 plate, and well as random effects. All data and code for larva survivorship, settlement and oxygen
243 consumption can be found at Zenodo [58].

244 Microbiome analysis of sediment samples

245 DNA sequences were demultiplexed and further processed with Qiime2-2022.11 [59].
246 Since the reverse reads were of poor quality only the forward reads were analyzed. Using the
247 program Cutadapt the primers were removed [60], and Amplicon Sequence Variants (ASVs) were
248 generated with the program DADA2 [61] trimmed at the 10 and 205 bp positions. The ASVs were

249 taxonomically classified with the classify-consensus-vsearch function and the silva 138 99
250 database [62]. If the sequences were annotated as chloroplast or mitochondria they were removed
251 from the analysis. The data were then uploaded to R and converted into a Phyloseq v1.26.1 data
252 object for analysis and graphical display of phylogenetic sequencing data.

253 Alpha-diversity was evaluated by rarefying to a minimum sequence depth of 60,000. Three
254 alpha-diversity metrics, richness, Shannon-Wiener, and the Inverse Simpson index, were
255 generated with the phyloseq estimate_richness function. The respective values were then tested
256 for normality using qqnorm, qqline, and the Shapiro test. Upon passing normality, significance
257 between sites was tested with an Analysis of Variance (ANOVA).

258 For beta-diversity, ASVs were filtered if they summed to <10 in 30% of the data. The
259 filtered data were then transformed to centered log ratios (CLR) using the package Microbiome
260 v0.9.99. The Vegan v2.5.4 package was used for beta-diversity testing for both within and between
261 group differences. Dispersion of the samples (within group) was tested by using the function
262 Vegdist (method = "Euclidean", Permutations = 999) and Betadisper and was tested for
263 significance with a permutation test. A permutational multivariate analysis of variance
264 (PERMANOVA, function Adonis, method = "Euclidean", Permutations = 999) was used to
265 evaluate significance between groups.

266 To identify differentially abundant microbial ASVs between sites, the program Analysis of
267 Compositions of Microbiomes with Bias Correction (ANCOM_BC) was used [63]. ANCOM_BC
268 was used with an alpha <0.001 and a W statistic was >90. The ASVs were further evaluated if they
269 had a log-fold change < -3.5 or > 3.5.

270

Results

Larval performance

Sediment treatments significantly impacted the performance of *O. faveolata* larvae (Fig 2, S2 Table). In general, sediment exposure negatively impacted larval survival and settlement for both Port and Reef sediment types. However, the effect of sediment concentration was important depending on the sediment type used in the treatment. Whereas both high and low Port sediment concentrations negatively impacted larval survival and settlement, only the high-dose Reef sediment treatment resulted in adverse effects (Figs 2 and S3). Specifically, survival proportions after 24 h in the treatments were above 93% for Control and Low Reef, but exposure to Low Port, High Reef, and High Port reduced survival probabilities to 90%, 86%, and 81%, respectively ($p<0.05$, df = 4, S2 and S3 Tables), resulting in significantly lower odds ratios of survivorship for these treatments (<0.6) compared to the Control (S3 Fig). Larval settlement probabilities 1-week after treatments were 21-22% in the Control and Low Reef treatments, but were reduced to less than 12% in the Low Port, High Reef, and High Port treatments ($p<0.05$, df = 4, S2 and S3 Tables). This resulted in lower (<0.5) odds ratios for settlement in the Low Port, High Reef, and High Port treatments compared to the Control (S3 Fig).

Fig 2. Effects of sediments on *Orbicella faveolata* larvae (model estimated values ± 95% CI). (A) Proportion of larval survival after a 24 h exposure to experimental treatments. (B) Proportion of larval settlement after one week of recovery from experimental treatments. Asterisks denote significant differences in a sediment treatment compared to controls with no sediment added (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$). Colors match Figs 3 and 4 and denote either Port or Reef sediment treatments.

None of the sediment treatments affected the larval respiration rates at either of the time points (S4 Table, S4 Fig). Average respiration rates per larva were $9.33 \times 10^{-4} \pm 2.53 \times 10^{-4}$ nmol O_2 min^{-1} (mean ± SD) across treatments after 24 h of exposure and declined to $6.01 \times 10^{-4} \pm 1.97 \times 10^{-4}$ nmol O_2 min^{-1} after a week of recovery, but this was only marginally significant ($p<0.06$, df = 1, F = 15.83, S4 Table).

Microbiome analysis

A total of seven sediment samples (Port N=3 and Reef N=4) resulted in sequence counts between 93,626 and 419,403 (median=171,281). After processing and filtering, 1,852 ASVs were used for the analysis. The median alpha-diversity was slightly higher in the Reef sediments (richness: Reef=3604 vs Port=3001, Shannon-Wiener: Reef=7.26 vs Port=7.20, and Inverse Simpson: Reef=654.24 vs Port=584.8), but this difference was not significant between sites (Fig 3A). In contrast, within-group (permutest, p=0.023) and between-group beta-diversity were significantly different (PERMANOVA, Fmodel=6.127, R^2=0.55 p=0.03, Fig 3B), with the microbial communities in Reef sediments having a more dispersed beta-diversity compared to Port sediments (average distance to centroid: Reef=55.76 vs Port=41.99). Of the seven most relatively abundant bacteria orders, the Reef and Port sediments shared four taxa (57%) with NB1-J and Cyanobacteriales being unique to Reef sediments, and Desulfobacterales being unique to the Port sediments (Fig 3C).

Fig 3. Microbial communities found in Port and Reef sediments. (A) Alpha diversity differences between Reef and Port samples using three diversity metrics: (1) Species richness (2) Shannon diversity Index, and (3) Inverse Simpson Index. (B) Beta diversity of microbial

317 composition between Port and Reef sediment samples. (C) The cumulative relative abundances of
318 the most abundant (0.05>) microbial order per sample grouped by the site of sediment collections.
319

320 Differential abundance analysis was conducted to identify the differences between sites,
321 resulting in 293 significant ASVs (Fig 4). Of these, there were a total of 74 orders, 82 families,
322 and 96 genera. The most prevalent differentially abundant orders were Steroidobacterales (N=29),
323 Desulfobacterales (N=19), and Pirellulales (N=15). The Port sediments had more enriched ASVs
324 (N=223) compared to Reef sediments (N=70). More specifically, the ASVs most enriched in Port
325 sediments were from the orders Ectothiorhodospirales (family *Ectothiorhodospiraceae*, genus
326 *Thiogranum*), an uncultured genus from the Class Gammaproteobacteria, Desulfobacterales
327 (*Desulfosarcinaceae*, Sva0081 sediment group), and Steroidobacterales (*Woeseiaceae*, *Woeseia*).
328 In the Reef sediments, the most enriched orders were Alteromonadales (*Moritellaceae* from an
329 uncultured genus), Steroidobacterales *(Woeseiaceae*, *Woeseia*), and Nitrosococcales
330 (*Nitrosococcaceae*, *AqS1*).
331

332 **Fig 4. Microbial Amplicon Sequence Variants (ASVs) associated with Reef or Port**
333 **sediments.** Differential abundances between Reef and Port, where the y-axis shows significant
334 ASVs (padj<0.001, W statistic >90) grouped by order. Only ASVs with a log-fold change <-3.5
335 and >3.5 were visualized.

336 Discussion

337 In this study, we investigated differences in the survival and settlement of larvae from the
338 threatened Caribbean coral *Orbicella faveolata* after short-term exposure to sediments collected

339 near the recently dredged Port Miami channel (considered anthropogenically modified) versus
340 sediments collected from the natal reef of the parent colonies in the Florida Keys (considered
341 natural or unmodified). Neither of the sediment types were dried or sterilized to avoid changing
342 their biological or chemical properties. Overall, we found that although *O. faveolata* larvae
343 exposed to high doses of both sediment types ("Port" and "Reef") exhibited adverse survival and
344 settlement rates, only the Port sediments resulted in adverse effects when exposed to low-dose
345 treatments, characteristic of conditions near actual dredging projects (e.g., [13]). The low-dose
346 Reef sediment treatment was not detrimental to coral larvae, and showed similar outcome odds of
347 survival and settlement compared to the no sediment (control) treatment (see S3 Fig).

348 Port sediments had different microbiome profiles and significantly higher abundances of
349 potentially pathogenic bacteria compared to Reef sediments, which may explain the reduced larval
350 survival and settlement observed even in the low-dose treatment. We speculate that Port sediments
351 could have been more detrimental to larvae compared to reef sediments due to differences in their
352 physical and chemical composition (e.g., grain size and sediment composition), and other
353 biological differences (e.g., different microbial communities). Together, these findings suggest
354 that, although suspended sediments may be generally detrimental to the survival and recruitment
355 potential of *O. faveolata* larvae, anthropogenic sediments, such as those occurring adjacent to
356 recent dredging projects, may incur greater harm compared to natural reef sediments.

357 Effects on larval survival

358 Both of our sediment sources significantly impacted the survival of *O. faveolata* larvae,
359 however, exposure to both the low- and high-dose Port sediment treatments reduced survival
360 proportions to 86% and 81%, respectively (compared to the control treatment), while the high-

361 dose Reef sediment treatment only reduced the survival proportion to 90% (Fig 2A). Suspended
362 sediments may reduce larval survival through physical abrasion [38] and reduced light over
363 prolonged periods can also lead to decreased photosynthetic efficiency of larval symbionts and
364 subsequent larval mortality from starvation [23]. However, in our study, decreased light was
365 unlikely the driver of our results, given the short exposure to sediments (24 h) and the use of
366 aposymbiotic (symbiont-free) larvae. Instead, we suspect that reduced larval survival in both of
367 our high-dose sediment treatments (Fig 2A) could have been caused by continuous physical
368 abrasion from suspended sediments during exposure. Given the pelagic nature of coral larvae, this
369 stage is likely to be more prone to physical abrasion from moving sediment particles compared to
370 coral recruits, on which sediment can accumulate on the growing coral tissue.

371 Increased mortality of *O. faveolata* larvae in both of our Port sediment treatments
372 (compared to Reef sediments) could have also been due to chemical or microbial differences in
373 the sediment composition and/or grain size. A recent study [32] assessed the effects of
374 sedimentation on recruits from the brooding coral *Porites astreoides* using either reef sediments
375 collected from the site of adult colonies, or sediments collected near Port Everglades (Fort
376 Lauderdale, Florida) to resemble the grain size composition often found in dredging areas. Similar
377 to our study, the authors found that reef sediments did not negatively affect coral survival, but Port
378 sediments did. However, since there were only trace amounts of mud-sized particles in our Port
379 sediments (approximately 1.25%), we hypothesize that Port sediments may be more likely to have
380 affected coral larvae through microbial processes leading to decreased survival.

381 ## Effects on larval settlement

382 Except for the low-dose Reef sediment treatment, we showed significant effects of both
383 sediment types (Port and Reef) after one week of sediment exposure, resulting in approximately
384 50-60% reduction in settlement in *O. faveolata* larvae compared to the control treatment (Figs 2B
385 and S1). Reduced larval settlement has been documented for a few Pacific coral species in the
386 presence of suspended sediments (in concentrations less than 10 mg/L, [23]), presumably due to
387 changes in light quality and quantity (as a result of increased light attenuation). Sediment-covered
388 surfaces have also been shown to decrease larval settlement in various coral species such as
389 *Pocillopora damicornis* [64], *Acropora digitifera* [38], *Acropora millepora* [38], and *O. faveolata*
390 [31], likely due to limited space to settle (preventing larvae from accessing and attaching to suitable
391 substrate), higher risk of abrasion, smothering/burial by deposited sediments, and masking of
392 appropriate chemical cues for settlement [23].

393 An important distinction of our study compared to previous work on the effects of
394 sedimentation on coral larvae is that we tested potential latent effects of sediment exposure on
395 eventual settlement one week after acute exposure. Thus, the settlement environment (i.e., light
396 and condition or exposure of settlement substrates) were the same across treatments, and
397 consequently neither sediment deposition on the coral surfaces or settlement substrates, nor
398 changes in light, were drivers of the reduced settlement observed in the exposed larvae.
399 Furthermore, since our low-dose Reef sediment treatment was not detrimental to coral settlement
400 (but the low-dose Port sediment treatment was), we speculate that disruption of potential
401 settlement cues in larvae exposed to Port sediments may have resulted from biological/chemical
402 damage (potential interactions with any contaminants or bacterial pathogens present in the Port
403 sediments). Sediment-stressed larvae could also have had lower energy reserves available for

allocation to settlement and subsequent metamorphosis, although no significant respiration rate differences were observed among treatments (see S4 Fig). One reason why our study may have found latent effects is that previous studies conducted experiments using sediments that had been dried prior to exposure. Oven drying can change the chemical composition of the sediments and kill bacteria [5], masking these potentially important biological or chemical effects. The inclusion of wet sediments in our study may therefore have helped preserve these properties and allowed us to explore how bacterial assemblages can affect larval survival and settlement.

Microbiome analysis of sediment samples and potential implications for coral survival and settlement

Coral settlement is the result of complex behavioral responses that are modulated by distinct microbial signatures in CCA [40-43]. In this study, we hypothesized that microbial differences among the two sediment types may have resulted in decreases in survivorship and potential impairment of the ability of larvae to detect cues for settlement and metamorphosis. The microbiome analysis of the sediment samples collected near the Port revealed differences in microbial beta-diversity and differentially abundant bacteria taxa compared to Reef sediments (Figs 3BC and 4). Relative abundance analysis of the most abundant taxa showed that Desulfobacterales were unique to the Port sediments (Fig 3C). These taxa have been found to be enriched in microbial communities from other inlets in southeast Florida [65] and have also been associated with black band disease [66], suggesting that this bacterial taxa may play a role in coral health and its enrichment in Port sediments may have contributed to the reduced survival and settlement in larvae exposed to both low- and high-doses of these sediments (Fig 2A). Moreover, Desulfobacterales are anaerobic sulfate-reducing bacteria [67] that reduce sulfate (SO_4^{2-}) to hydrogen sulfide (H_2S). Desulfobacterales are abundant in organic-rich and high nutrient

427 environments linked to eutrophication [68], and their waste product, H_2S, is correlated with coral
428 tissue degradation [11], and algal mortality [69]. Port sediments enriched in Desulfobacterales (Fig
429 4) may therefore reflect elevated H_2S and stressful hypoxic conditions that may have resulted in
430 lower survival and settlement rates.

431 Sediments may also act as vectors for the transmission of diseases such as Stony Coral
432 Tissue Loss Disease [22], which is documented to have appeared for the first time near Port Miami
433 in 2014 [70, 71]. Also, bacteria genera from two common human pathogens, *Staphylococcus* and
434 *Streptococcus*, have been found across multiple time points in surface water and sediment samples
435 near Port Everglades [65, 72], another southeast Florida inlet subject to dredging impacts. Our
436 findings add to these studies and also suggest that port inlets may carry potentially pathogenic
437 bacteria which may be transported to nearby reefs through various sediment transport processes
438 (natural or anthropogenic), resulting in potential exposure to coral larvae and other downstream
439 health impacts.

440 Effects on coral larval respiration

441 Despite significant effects of sedimentation on *O. faveolata* larval survival and settlement
442 (Figs 2 and S3), none of the sediment treatments had significant effects on coral larval respiration
443 (S4 Fig and S4 Table). Sedimentation has been shown to decrease photosynthesis to respiration
444 (P/R) ratios in adult corals, via decreased photosynthesis of the algal symbionts and increased
445 respiration of the host (e.g., [73]). However, in this study, we used aposymbiotic larvae, which
446 may explain the lack of significant effects on respiration. Alternatively, changes in respiration may
447 have not been detected because it is not possible to maintain the sediment treatments in the
448 microplate reader while respiration measurements are taken. Lower respiration rates across all

449 treatments at the 1-week recovery period (compared to the 24-hr sediment exposure, see S3 Fig)
450 could have resulted from ontogenetic and/or behavioral differences during those two time points
451 (active swimming versus exploration of suitable substrate for settlement), e.g. [74]).

452 Management implications for the conservation of corals

453 Our study is the first to examine the effects of suspended sediments on larvae from an
454 Atlantic coral species. With the two major commercial shipping ports in southeast Florida planning
455 major expansions which require multi-year dredge projects, this information is important for
456 understanding the impacts of sedimentation on susceptible life stages of corals, and assisting with
457 the development of protective management strategies. *O. faveolata* is listed under the US
458 Endangered Species Act (ESA) and already shows poor recruitment [49, 75, 76]. Recent work
459 confirms the ESA Critical Habitat (legal) requirements that larvae require substrates free of
460 sediment for settlement [31]. Importantly, our study showed that while sediments have detrimental
461 effects on the survival and settlement of *O. faveolata* larvae at high doses, even brief exposures to
462 low doses of anthropogenic sediments found near a recently dredged Port during the pelagic phase
463 could reduce larval survival and disrupt settlement, potentially compromising the recruitment
464 success and recovery potential of this species. Furthermore, we showed substantial direct mortality
465 from short-term sediment exposure, but also an additional significant latent effect on the surviving
466 larvae's capacity to successfully settle one week after sediment exposure. These results indicate
467 that sediments which remain adjacent to a dredging project even after ~2 years may still have
468 significant effects on early life stages of corals during relatively short-term resuspension events
469 (e.g., storms). This highlights the potential for long-term impacts of dredging (e.g., critical habitat
470 modification) as a result of resuspension of anthropogenic sediments. However, it is unclear how
471 long such sediments can persist in the area, or how often resuspension events might happen.

472 Our findings also highlight the importance of setting temporary moratoriums as a
473 management tool during dredging operations. Since 1993 dredging projects in Western Australia
474 conducted near coral reefs have been required to implement a coral environmental ("stand-down")
475 window spanning five days before spawning to seven days after spawning [13, 77]. The *O.*
476 *faveolata* larvae used in our experiments were eight days old and were adversely impacted by both
477 sediment types with just 24 h of exposure, with detrimental latent effects still detectable after one
478 week. Consequently, a one-week "stand down" period may be insufficient for broadcast spawner
479 coral species such as *O. faveolata* given the length of time it takes for larvae to become competent
480 and find suitable substrate for settlement. Based on our results, we recommend setting
481 environmental windows which encompass the months of peak spawning (typically August and
482 September for *O. faveolata* [78, 79]), plus an additional period of at least two to three weeks after
483 spawning to prevent negative effects on settlement. These months are also typically the peak period
484 for heat-stressed induced coral bleaching, and avoiding dredging during these months would
485 therefore have multiple benefits.

486 Finally, we showed that sediments collected near the Port contained higher abundances of
487 potentially pathogenic bacteria compared to Reef sediments, aligning with previous work
488 conducted in the vicinity of the Port Everglades inlet [65, 72]. These studies highlight the
489 importance of monitoring for potential contaminants in sediments and changes in the microbiome
490 which may result from dredging. In addition, although we only looked at the effects of suspended
491 sediments on coral larval performance, suspended sediments can act in concert with other stressors
492 typically associated with dredging. For example, [51] showed that elevated suspended sediment
493 concentrations, when simultaneously combined with reduced light levels, resulted in partial
494 mortality for multiple Pacific coral species. These findings emphasize the importance of

495 monitoring both suspended sediments and benthic light availability (PAR) during large-scale
496 dredging projects, and highlight the need for similar studies for Atlantic coral species.

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Supporting information

S1 Fig. Composite display of grain size analysis of sediment samples. Two replicates per sediment type (Port versus Reef) were used.

S2 Fig. Example plot of oxygen consumption over time for 6 *Orbicella faveolata* larvae placed in a single well of the microplate. The R^2 value is given for the linear trend. The first 10–20% (pO2 in % air saturation) linear decreases in oxygen were used to calculate respiration

751 rates per larva. Any portion of the slope that dipped below 70% air saturation was not used for
752 data analysis.

753 **S3 Fig. Odds ratios (OR) for the association between *Orbicella faveolata* larvae exposure to**
754 **sediment treatments.** (A) larval survival after 24 h of treatments, and (B) larval settlement after
755 one week of recovery from experimental treatments. OR=1 Exposure does not affect odds of
756 outcome, OR>1 Exposure associated with higher odds of outcome, and OR<1 Exposure
757 associated with lower odds of outcome.

758 **S4 Fig. Respiration rates (mean ± 95 CI) in *Orbicella faveolata* larvae** after a 24 h exposure to
759 experimental treatments (left panel) and after one week of recovery from experimental
760 treatments (right panel). White dots denote individual replicate wells.

761 **S1 Table. Size fraction analysis of sediment samples.** Values correspond to graphic in S1 Fig.

762 **S2 Table.** Generalized linear mixed-effect models outputs for *Orbicella faveolata* larvae
763 performance. DF: Degrees of freedom

764 **S3 Table. Results of the final generalized linear mixed-effect models for *Orbicella faveolata***
765 **performance.** A) larval survival after 24 h of treatments, and B) larval settlement after one week
766 of recovery from experimental treatments (shown in Fig 1). The coefficient estimates describe
767 the change in the log odds for each treatment level compared to the base level (control).
768 Asterisks denote significant differences in a sediment treatment compared to controls with no
769 sediment added (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

770 **S4 Table.** Linear mixed-effect model outputs for *Orbicella faveolata* larvae respiration.

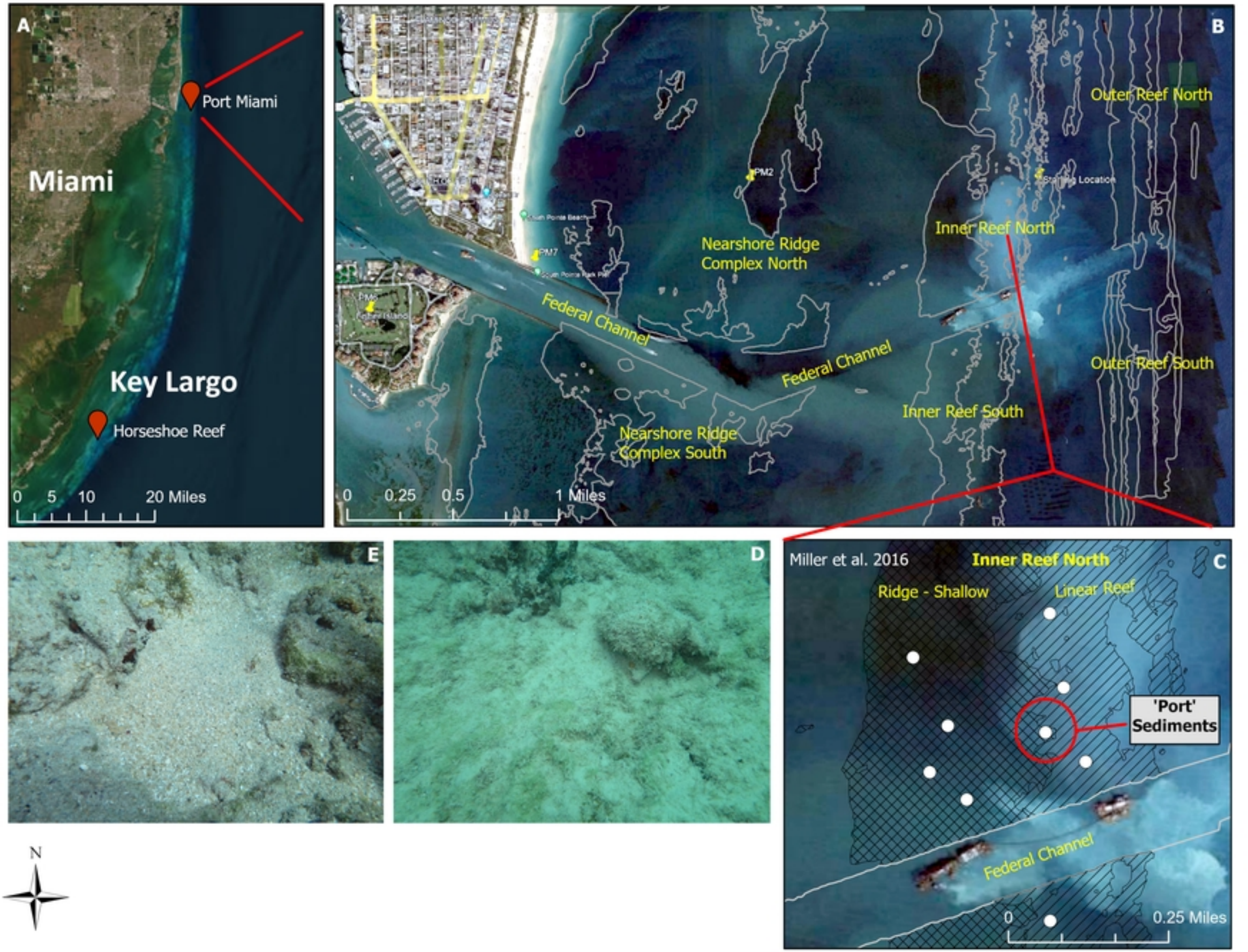
A
Port Miami
Miami
Key Largo
Horseshoe Reef
0 5 10 20 Miles
B
Outer Reef North
Inner Reef North
Nearshore Ridge Complex North
Federal Channel
Federal Channel
Outer Reef South
Inner Reef South
Nearshore Ridge Complex South
0 0.25 0.5 1 Miles
E
D
Miller et al. 2016
Inner Reef North
C
Ridge - Shallow
Linear Reef
'Port' Sediments
Federal Channel
0 0.25 Miles
N

Figure 1

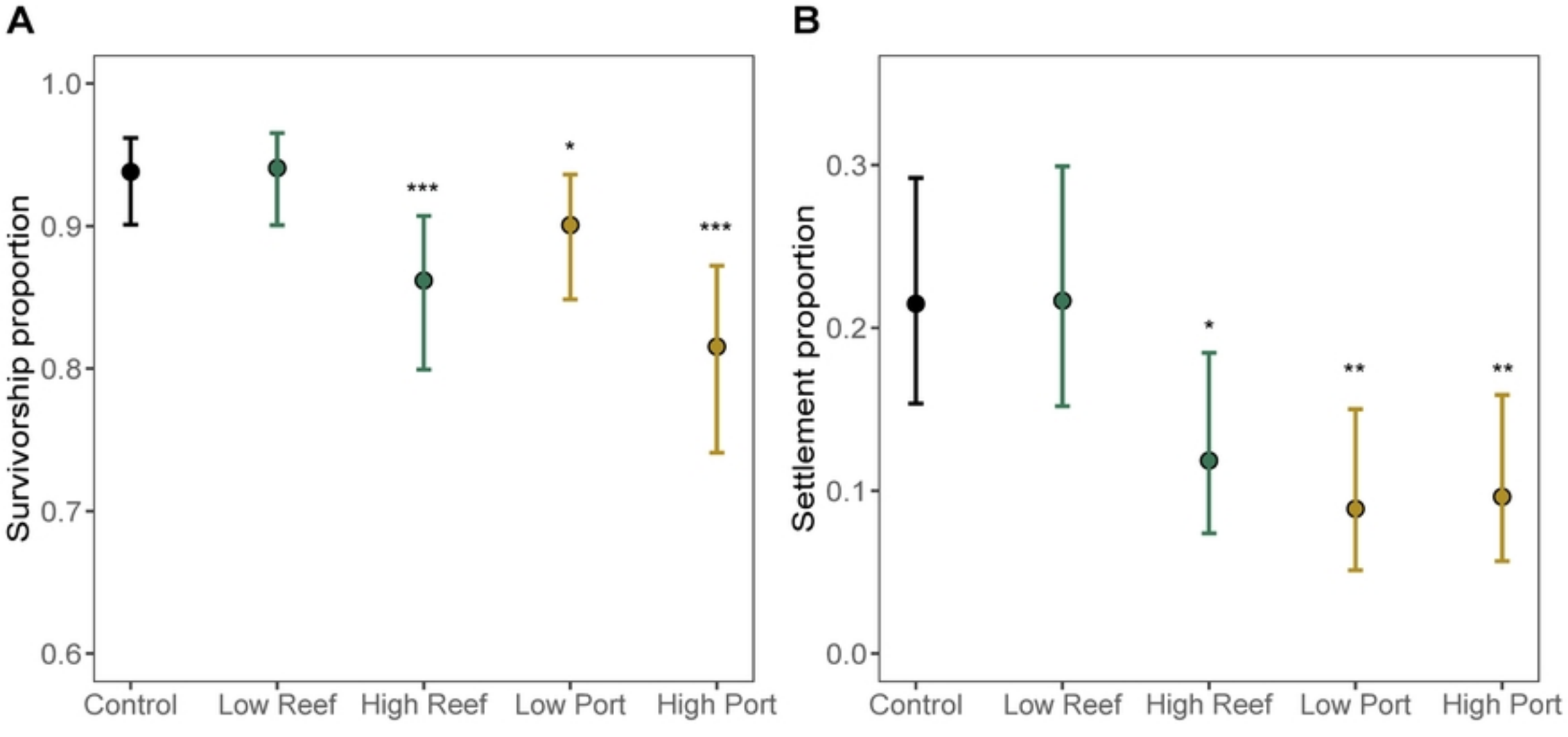
A
Survivorship proportion
1.0
0.9
0.8
0.7
0.6
***
*
***
Control
Low Reef
High Reef
Low Port
High Port
B
Settlement proportion
0.3
0.2
0.1
0.0
*
**
**
Control
Low Reef
High Reef
Low Port
High Port

Figure 2

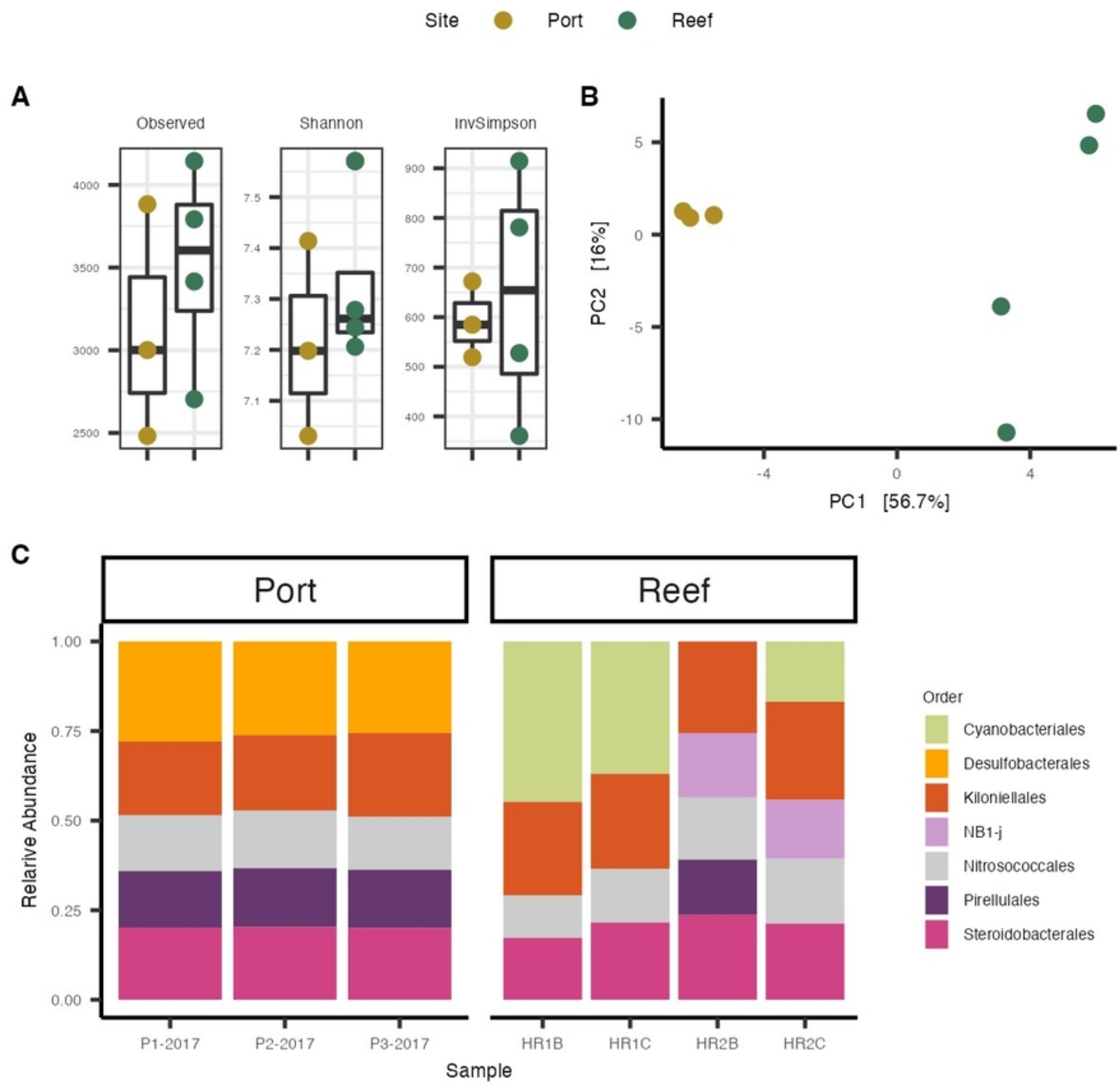
Site
Port
Reef
A
Observed
Shannon
invSimpson
4000
3500
3000
2500
7.5
7.4
7.3
7.2
7.1
900
800
700
600
500
400
B
PC2 [16%]
5
0
-5
-10
-4
0
4
PC1 [56.7%]
C
Port
Reef
Relative Abundance
1.00
0.75
0.50
0.25
0.00
P1-2017
P2-2017
P3-2017
HR1B
HR1C
HR2B
HR2C
Sample
Order
Cyanobacteriales
Desulfobacterales
Kiloniellales
NB1-j
Nitrosococcales
Pirellulales
Steroidobacterales

Figure 3

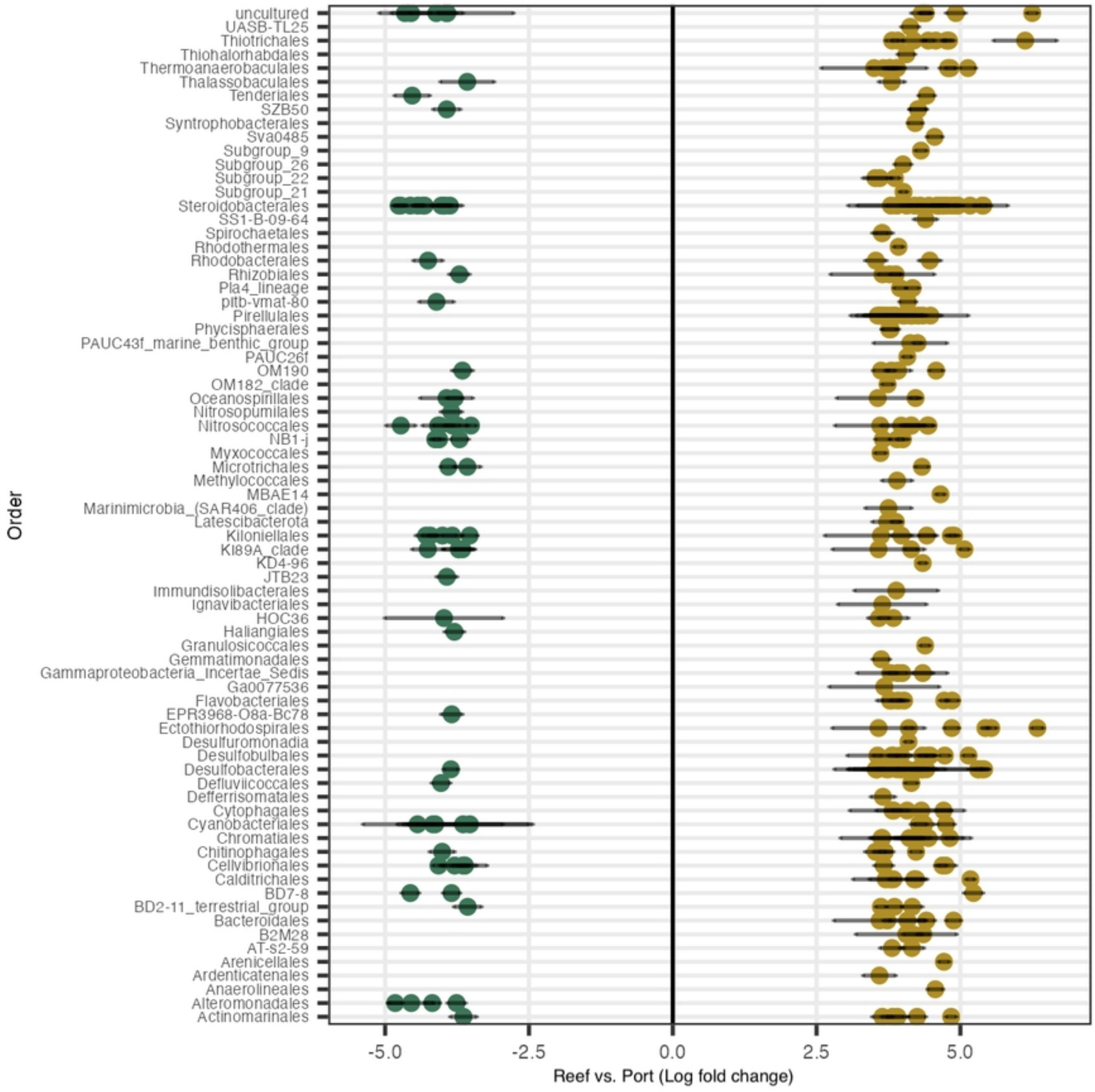
uncultured
UASB-TL25
Thiotrichales
Thiohalorhabdales
Thermoanaerobaculales
Thalassobaculales
Tenderiales
SZB50
Syntrophobacterales
Sva0485
Subgroup_9
Subgroup_26
Subgroup_22
Subgroup_21
Steroidobacterales
SS1-B-09-64
Spirochaetales
Rhodothermales
Rhodobacterales
Rhizobiales
Pla4_lineage
pltb-vmat-80
Pirellulales
Phycisphaerales
PAUC43f_marine_benthic_group
PAUC26f
OM190
OM182_clade
Oceanospirillales
Nitrosopumilales
Nitrosococcales
NB1-j
Myxococcales
Microtrichales
Methylococcales
MBAE14
Marinimicrobia_(SAR406_clade)
Latescibacterota
Kiloniellales
KI89A_clade
KD4-96
JTB23
Immundisolibacterales
Ignavibacteriales
HOC36
Haliangiales
Granulosicoccales
Gemmatimonadales
Gammaproteobacteria_Incertae_Sedis
Ga0077536
Flavobacteriales
EPR3968-O8a-Bc78
Ectothiorhodospirales
Desulfuromonadia
Desulfobulbales
Desulfobacterales
Defluviicoccales
Defferrisomatales
Cytophagales
Cyanobacteriales
Chromatiales
Chitinophagales
Cellvibrionales
Calditrichales
BD7-8
BD2-11_terrestrial_group
Bacteroidales
B2M28
AT-s2-59
Arenicellales
Ardenticatenales
Anaerolineales
Alteromonadales
Actinomarinales
Order
-5.0
-2.5
0.0
2.5
5.0
Reef vs. Port (Log fold change)

Figure 4