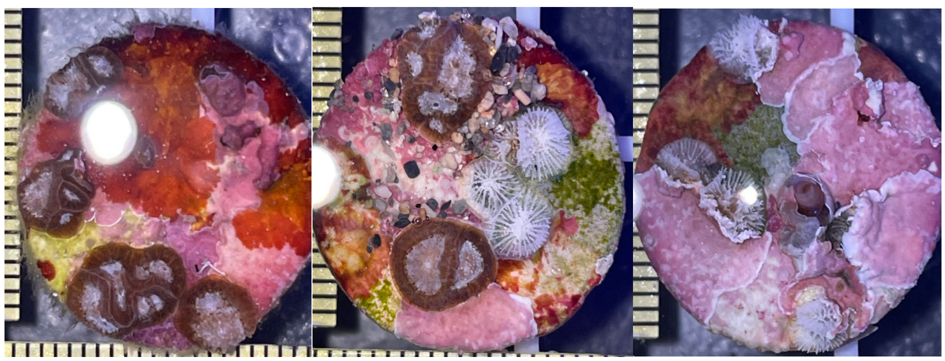
Understanding the effects of sediment on coral settlement and coral recruits



Understanding the effects of sediment on coral settlement and coral recruits

Final Report

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Management Summary
We conducted experimental studies to assess the impact of the presence of sediments and substrate burial on larval settlement and recruit survival for multiple reef-building coral species (*Acropora cervicornis*, *Colpophyllia natans*, *Diplora labyrinthiformis*, *Orbicella faveolata*, *Pseudodiploria clivosa*, and *Pseudodiploria strigosa*). The burial of suitable substrate drastically decreased the probability of settlement for all species tested, with just 2 mm of sediment decreasing settlement probability to 25% or less, and 4 mm suppressing settlement entirely. Similarly, the burial of recruits under 4 mm of sediment significantly decreased survival probability to 31% or less within ten days. Surprisingly, this strong negative response was consistent for recruits of multiple age/size groups ranging from 1-month to 18-months of age, highlighting the extreme sensitivity of coral recruits to sedimentation stress throughout at least the first 1.5 years of their lifespan. Coastal development projects such as the dredging of port channels and beach renourishment efforts can produce sediment layers between 0.5 and 10 cm thick, yet even the relatively shallow sediment layers we tested (≤0.4 cm) were enough to cause drastic decreases in larval settlement and recruit survival. These results underscore the strong potential for sediments to reduce or completely inhibit coral recruitment, reflecting the urgent need to identify the main sedimentary sources on reefs to limit future declines in reef-habitat quality. Our data provide an essential tool for managers to assess the impacts of future sedimentation events on the juvenile assemblages of key reef-building species and to assist them in mitigating their future loss to maximize future coral recovery.

Executive Summary
This project aimed to identify the impacts of the presence of sediments and substrate burial on larval settlement and recruit survival across multiple species of coral found on Florida's Coral Reef (*A. cervicornis*, *C. natans*, *D. labyrinthiformis*, *O. faveolata*, *P. clivosa*, and *P. strigosa*), age groups (1–6 months old), size classes approximating corals aged 6 to 18 months, and time intervals (1–10 days). We found variations in settlement success across the six species we tested, with *C. natans* larvae being the most sensitive to the burial of substrate; with the mere presence of sediment on a settlement substrate causing the near-complete suppression of larval settlement altogether. By contrast, *D. labyrinthiformis* larvae were still able to settle at 4 mm of sediment, albeit at extremely low rates compared to control trials with no sediment present (10% settlement probability vs. 58%). When coral recruits were buried under different sediment depths, we found high variability in survival rates among species but a clear decrease in survivorship across species when buried for ten days. Multiple species had individuals that were able to survive burial under 2 mm across a timespan of ten days (1- and 3-month-old *C.*

natans, 6-month-old *D. labyrinthiformis*, 1- and 3-month-old *O. faveolata,* and 1-month-old *P. strigosa*). Other species and age cohorts, however, were highly susceptible to 2 mm of sediment (3-month-old *A. cervicornis*, 3-month-old *P. strigosa*, and 12- and 18-month-old *O. faveolata*). For the 4 mm trials, all species across all age/size groups (1–18 months old) we tested were highly susceptible to mortality and exhibited consistent, drastic declines in survival within ten days of being buried under this amount of sediment. These trends provide tangible evidence of the extreme susceptibility corals have to sediment stress for at least the first 1.5 years of their lifespan. These findings highlight the need to address sedimentary stressors across the Florida Reef Tract to promote future coral recovery via sexual reproduction. These data could be of further use for predicting how future sedimentation events could impact the stock of juvenile corals, allowing managers to address the impact of multiple proposed scenarios. Importantly, these experiments were conducted using coarse sediments, rather than the fine sediments often generated by dredging projects, which may have different impacts on coral recruitment. Therefore, future research should address variation in coral settlement and survival across different sediment grain types to provide accurate data on the response of reef-building corals to sediments that are more representative of what is usually produced by coastal development projects such as port dredging.

Main Findings

Larval settlement assays

Burial of settlement substrate severely reduced the potential for the settlement for all coral species tested. Burial of settlement substrate by 2mm of sediment **decreased the predicted probability of settlement by 65-100%. Burial of settlement substrate by 4mm of sediment resulted in near-complete settlement inhibition for all species except *D. labyrinthiformis.***

Effects of sediment on coral recruits

Sediment burial for 10 days severely reduces the survivorship of coral recruits aged 1-month, 3-month, and 6-month. Predicted survival probability of 1-month and 3-month-old corals **decreased by 70–100% after 10 days of burial under 4mm of sediment.** Burial under 2mm of sediment decreased survival probability 10–90%, the effect sizes were not significant

Management recommendations:

Larger corals (live tissue area 1cm^2 to 4cm^2) were highly susceptible to mortality by burial under 4mm of sediment after 10 days. These findings suggest that even large coral recruits that are near juvenile sized remain highly sensitive to impacts from sedimentation.

Table of Contents

List of Figures

fluorescent green polyps with live tissue represent healthy, living coral recruits and the dull, bare skeletons represent coral recruits that died after 10 days of burial.

Figure 5: Scatterplots depicting (**A–E**) the binary response of the settlement of coral larvae to ceramic tiles surrounded by sediment layers of varying depths, and (**F–J**) the binary response of the settlement of coral larvae to ceramic tiles buried by sediment layers of varying depths. The black curves depict the best-fit logistic generalized mixed-effects models that predict the probability of settlement for each species across the sedimentary gradient; the shaded areas represent the 95% confidence intervals of the models. The red curves for plots **F**, **H**, and **J** represent the sole effect of sediment burial on larval settlement, which was estimated by incorporating the coefficients from the "Sediment Present" models (**A**, **C**, and **E**) into the sediment burial models (**F**, **H**, and **J**). Cnat = *Colpophyllia natans*, Dlab = *Diploria labyrinthiformis*, Ofav = *Orbicella faveolata*, Pcli = *Pseudodiploria clivosa*, Pstr = *Pseudodiploria strigosa*.

Figure 6: Kaplan-Meier curves (left) and forest plots (right) showing decreases in survival for 1-month-old recruits of 4 different coral species under different sediment burial treatments across a timespan of 10 days: **(A)** *C. natans*, **(B)** *O. faveolata*, and (**C**) *P. strigosa*. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$) hazard of that experimental treatment relative to the control treatment (no sediment burial).

Figure 7: Kaplan-Meier curves (left) and forest plots (right) showing decreases in survival for 3-month-old recruits of 4 different coral species under different sediment burial treatments across a timespan of 10 days: **(A)** *A. cervicornis*, **(B)** *C. natans*, **(C)** *O. faveolata*, and **(D)** *P. strigosa*. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$) hazard of that experimental treatment relative to the control treatment (no sediment burial).

Figure 8: Kaplan-Meier curve (left) and forest plot (right) showing a decrease in the probability of survival for 6-month-old recruits of *D. labyrinthiformis* under different sediment burial treatments across a timespan of 10 days. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$) hazard of that experimental treatment relative to the control treatment (no sediment burial).

Figure 9: Kaplan-Meier curve (left) and forest plot (right) showing a decrease in the probability of survival for (**A**) 1 cm^2 fragments, (**B**) 2.3 cm^2 fragments, (**C**) and 4 cm^2 fragments of *O. faveolata*, under different sediment burial treatments across a timespan of 10 days. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$) hazard of that experimental treatment relative to the control treatment (no sediment burial).

1. BACKGROUND/INTRODUCTION

Coral recruitment and juvenile survival are critical components of resilient coral reefs. The life cycle of broadcast-spawning corals is a complex process that entails the release of sperm and eggs, fertilization, larval development and settlement, recruit survival, and the growth of corals. Settlement success often depends on numerous factors, with a major driver being the availability of suitable substrate for settlement. Coral settlement and survival also depend on factors such as larval supply, water flow, and microhabitat conditions including sediment abundance, substrate position, roughness, color, and benthic composition. Sediments can negatively affect corals through a variety of mechanisms, causing partial or full coral mortality. Although we have a general understanding of the effects of sediments on corals, we lack information on the species-specific effects of sediments on Atlantic coral species. Moreover, we lack information on the effects of sediments on the early life history stages of corals, arguably the time at which they may be most vulnerable to the impacts of sediments. Understanding how sediments affect larval settlement and recruit survival — critical life history stages when corals are most vulnerable to mortality — is essential to establishing biologically relevant benchmarks regarding sediment accumulation and identifying potential actions that can be taken to improve coral survival on Florida's reefs.

The overarching goal of this project was to understand the effect of sediment presence and deposition on the early life history stages of corals. To do so, we conducted a series of aquaria-based experiments to address two main goals: (1) understand the effect of sediment presence/absence and depth on coral settlement rates and preferences, and (2) understand the effect of sediment presence/absence and depth on recruit survivorship across different life history stages. This project addresses research priority 1; objective 1; '*Reduce Water Quality Impacts and Establish Coral-Specific Water Quality Standards*', and research priority 1; objective 3; '*Restoration Planning and Site Selection; Action: Enhance benthic habitat conditions to optimize conditions for natural larval settlement for coral and other reef obligate species*', which were outlined in FDEP's Resilience Action Plan for Florida's Coral Reef (2021–2026). Additionally, the project also addresses research priorities 4: '*Restoration Planning; 4.2 - Restoration Site Selection*' and 5: '*Direct Restoration Activities; 5.6 - Optimization of Restoration Sites to Promote*

Natural Larval Settlement' of the state of Florida's restoration priorities for Florida's coral reef (2021–2026).

1.1. Goal 1: Understand the effect of sediment presence/absence and depth on coral settlement rates

Objective 1 – Assess the effects of sediments on coral larval settlement rates

> *Rationale:* Sedimentation reduces suitable habitat space for larval settlement. To understand the mechanisms through which sedimentation inhibits future coral recovery, it is essential to understand the response of larvae from multiple coral species to the presence of sediment around suitable substrate and the burial of this substrate under varying sediment depths.

1.2. Goal 2: Understand the effect of sediment depth on recruit survivorship across different life history stages.

Objective 2 – Assess the effect of sediments on the survivorship of 1-month old recruits

> *Rationale:* Although coral larvae may successfully settle onto suitable substrates, post-settlement burial could kill off young recruits. Therefore, it is important to address how different sediment depths decrease survivorship for the earliest life stages of coral recruits, starting with 1-month olds.

Objective 3 – Assess the effect of sediments on the survivorship of 3-month-old recruits

Objective 4 – Assess the effect of sediments on the survivorship of 6-month-old recruits

Objective 5 – Assess the effect of sediments on the survivorship of coral fragments approximating 6-, 12-, and 18-month-old recruits

> *Rationale:* Assessing survivorship under different sediment depths for 3-month and 6-month-old coral recruits, and fragments approximating corals aged 6-, 12-, and 18-months old, can shed light on whether survivorship increases with age or if recruits remain vulnerable across this time span of their life cycle.

1.3 Reef Management Application

Outcomes of this project have multiple potential applications for improved reef management. New knowledge, techniques, and capabilities generated by this project may aid restoration efforts, improve planning for projects that include the potential to generate sedimentation on coral reefs, and may be applied to increase coral resilience through:

- Improved understanding on the influence of sedimentary stress on juvenile corals and, therefore, insights into its contribution to the lack of coral recovery in Florida.
- The quantification of survivorship trends for multiple coral species at different life stages can be used to predict decreases in the stock of juvenile corals through time in the context of sedimentation events.
- Develop and implement practices to minimize the impact of future events that may promote an increase in sedimentary stress on reefs, such as beach renourishment projects and dredging activities.

2. METHODS

The purpose and intended use of the data generated by the described activities are to inform regional and local management, specifically active restoration activities, aimed at improving the health and resilience of Florida's Coral Reef. Activities detailed herein were conducted under the advisement of relevant groups associated with and staff of the Florida DEP Coral Protection and Restoration Program. This was done to ensure that methodologies were not duplicated, best practices were employed, and project results were effectively communicated to all stakeholders. All required state and federal permits were obtained prior to the beginning of the work.

2.1. Task 1 – Conduct coral settlement assays

We conducted settlement rate assays in August and September of 2023 using larvae from coral spawning during the August and September spawning windows. Settlement assays were conducted in individual glass chambers (118 ml capacity, 6.5 x 8 cm, diam. x H). We placed settlement chambers into water baths (35 L capacity, 62 x 43 x 17 cm; L x W x H) in a random block design. Each water bath contained 30 individual chambers, such that a single replicate (n = 45 chambers) was spread across two water baths. Water baths were maintained at 28 °C using digital temperature controllers (Finnex HC-810M, ISK Merchandising Inc. USA) and 300 W titanium heaters (Finnex TH-303005 titanium heater, ISK Merchandising Inc. USA). A powerhead (Eco Wave EW-10 Wave Pump, Sea Side Aquatics, LLC, Anaheim, CA USA) consistently circulated water throughout each bath, and temperature data loggers (HOBO Pendant MX Temperature/Light Data Logger, Onset Corporation, Bourne, MA USA) recorded water temperature every 10 minutes.

Each chamber received a single 3.8 x 3.8 x 0.5 cm ceramic tile (Boston Aquafarms, Boston, MA USA; L x W x H) and then was filled with 100 ml of filtered (20 µm mesh size) and UV-sterilized seawater originating from Bear Cut, Miami, FL USA. This water source and level of filtration are routinely used by our team for larval settlement and recruit rearing without issue. Before adding sediments to the chambers, the top surface of each tile received a standardized amount of crushed crustose-coralline algae (CCA) to encourage settlement. CCA was harvested from a single aquarium using a razor blade and thus was of consistent origin and identity for all treatments and replicates. To create a gradient of sediment presence and depth of substrate burial, sediment treatments consisted of 0.15 g of sediment, which provided a ‘sprinkle’ of sediment across the settlement substrate, 2.15 g of sediment, which covered the settlement substrate with 2 mm of sediment, or 4.30 g of sediment, which covered the substrate with 4mm of sediment. Dried sediments were pre-weighed to standardize the amount of sediment added to each settlement chamber. For the “Sediment Present” treatments, sediments were added to the bottom of the chamber surrounding the tile (i.e., no sediments present on top of the settlement substrate), while for the “Sediment Burial” treatments the sediments were added directly on top of the settlement substrate. The “Sediment Present” treatments were designed to explicitly test the effect of the presence of sediments in the chamber but not physically covering the settlement substrate, and the “Sediment Burial” treatments were designed to test the effect of sediments physically covering the settlement substrate (**Figure 1**). We also tested the effect of sediment source by using sediments sourced from nearby Port Everglades; (PEV) or from an offshore reef site in Key Largo (KL). Each chamber was assigned one of eight experimental sediment treatments or a control, which received no sediment addition. Altogether, each settlement assay consisted of nine different treatments:

- Control (no sediment present)
- +0.15 g PEV Sediment Burial
- +2 mm PEV Sediment Present
- +4 mm PEV Sediment Present
- +2 mm PEV Sediment Burial
- +4 mm PEV Sediment Burial
- +0.15 g KL Sediment Burial
- +2 mm KL Sediment Present
- +2 mm KL Sediment Burial

All sediments were collected via SCUBA in July of 2023. Sediments were collected using a glass scoop and were placed into 2-gallon teflon bags that were sealed underwater. Upon surfacing, bags were drained of as much seawater as possible, sealed, and placed on ice for transport to the lab, where they were frozen at -20 °C until they were dried. All sediments were dried at 60 °C until they reached a consistent weight, at which point they were sieved to remove any material >5 mm diameter and were placed into teflon bags and sealed until use in experiments. There was no significant difference in settlement success between the treatments that contained Key Largo sediments and the treatments that contained Port Everglades sediments. Therefore, we combined these trials in our final analyses to assess the general response of larval settlement to sediments.

After establishing sediment treatments, coral larvae were placed into each settlement chamber (n = 20 larvae/chamber for *Orbicella faveolata*, n = 15 larvae/chamber for *Colpophyllia natans*, *Diploria labyrinthiformis*, *Psuedodiploria clivosa*, and *P. strigosa*). Larvae were deemed ready for use in experiments when we observed the onset of settlement within the main larvae holding tanks. Coral larvae were removed from their main holding tank via pipette and placed into individual 0.2 ml wells for transfer to experimental settlement chambers. Once larvae were introduced, the chambers were sealed shut to prevent evaporation and changes in salinity. We quantified larval settlement rates in each treatment after 72 hours by closely inspecting each tile using a dissecting microscope and fluorescent lights. For Sediment Burial treatments, we first inspected the surface of the sediments for the presence of any coral settlers. Then, while looking under the microscope, we gently pipetted the sediment off the tile to reveal the settlement substrate below to allow observation of any coral settlers. Settlers were recorded as either "settled", meaning that they had metamorphosed into a flat, disk-like shape to adhere to the substrate, or "attached", whereby they had firmly attached themselves to the substrate but had not yet metamorphosed. The number of larvae settled and attached was recorded for the upward-facing surface of each settlement substrate, the tile side, and the bottom of the tile (**Figure 2**). Only settlers recorded as settled or attached on the upward facing surface of settlement substrates were included as larvae that successfully settled in the analyses.

2.2. Task 2 – Conduct coral recruit sediment burial assays

We tested the influence of sediment burial on the survival of recruits across five different Caribbean coral species: *Acropora cervicornis*, *C. natans*, *D. labyrinthiformis*, *O. faveolata*, and *P. strigosa*. To test how survival to sediment burial may change with coral age, we used recruits of different ages, including 1-month old recruits (*C. natans*, *O. faveolata*, and *P. strigosa*), 3-month old recruits (*A. cervicornis*, *C. natans*, *O. favelata*, *P. strigosa*), and 6-month old recruits (*D. labyrinthiformis*). Since we did not have enough surviving *O. faveolata* recruits for older life stages, we tested the effect of sediment burial on fragments of *O. faveolata* approximating the size of 6-month-, 12-month- and 18-month-old recruits. This was accomplished by fragmenting established *O. faveolata* colonies into size classes representative of each age group: 1 x 1 cm (1 cm^2) for 6-month old recruits, 1.5 x 1.5 cm (2.3 cm^2) for 12-month old recruits, and 2 x 2 cm (4 cm^2) for 18-month old recruits. To test survival of recruits and different sized fragments through time, we exposed the corals to sediment burial for 1, 2, 3, 5, 7, and 10 days. Our experimental design was fully orthogonal and thus exposed all possible species combinations, life stages, and burial duration. For these experiments, we exposed coral recruits to three treatments: a control (no sediment present), burial under 2 mm of sediment, or burial under 4 mm of sediment (**Figure 3**).

Our species selection was based on the availability of recruits generated from summer 2023 coral spawning activities and species' relevance in terms of ecological importance and susceptibility to current stressors. For instance, *A. cervicornis* and *O. faveolata* are key reef-building species on Florida's reefs, and their populations have been on a steep decline over the last few decades from bleaching events, disease outbreaks, and poor water quality among other stressors. Similarly, *C. natans*, and *P. strigosa* are massive, reef-building coral species highly susceptible to stony coral tissue loss disease (SCTLD), which decimated their populations across the Caribbean over the last decade.

The coral recruits we used for the sediment burial exposure experiments were reared from larvae settled from the summer of 2023 coral spawning windows (August and

September). Larvae were settled on to 3.8 x 3.8 x 0.5 cm ceramic tiles. The resulting recruits were reared in aquaria at NOAA's Coral Reef Assessment and Research Lab (CoRAL) facility in Miami, FL. These aquaria consist of 20-gallon tanks with 20-gallon sumps fed filtered (20-micron) and UV-sterilized seawater with a turnover rate of ~6x per day. Lighting was consistent for each cohort via Radion XR30 G6 Pro LED aquarium lights (EcoTech Marine, PA USA), and temperature was kept consistent at ~28 °C using 300W titanium heaters (Finnex TH-303005 titanium heater, ISK Merchandising Inc. USA) controlled by an Apex Neptune controller system.

We built recruit sediment burial chambers consisting of PVC chambers (5 x 5 cm each) oriented in a 6 x 3 grid. Each individual chamber was designed to house a single tile, with each row of 3 tiles containing the three treatments (control, 2 mm, 4 mm) that was assessed on each timepoint (days 1, 2, 3, 5, 7, and 10). We established four tanks per species per age/size group (24 tanks total), each consisting of one replicate per species per age/size group. On day 0 before initiating the experiment, we counted, photographed, and mapped the location of all recruits present on each tile using a dissecting microscope (**Figure 4**). The tiles were then placed into their respective chambers and sediment was added to the tiles undergoing experimental treatments (2 mm and 4 mm) using a pipette. At each timepoint, sediment was removed from the respective tiles using a siphon and survivorship as assessed by counting the number of living and dead coral recruits.

3. RESULTS

3.1. Task 1 – Coral settlement assays

Sediments decreased larval settlement across all species, with 4 mm of sediments on the tile causing near-complete inhibition of settlement. The presence of sediment around the settlement tiles led to a significant decrease in survival probability for three out of the five species we tested: *C. natans*, *O. faveolata*, and *P. strigosa*; however, the effect of burial of the settlement substrate on settlement was far stronger (**Figure 5**). The predicted settlement probability for *C. natans* when no sediment was present was 80%, and it decreased to 50% when 2 mm of sediment were present around the tile and to 25% when 4 mm of sediment were present around the tile (**Figure 5A**). *O. faveolata* larvae exhibited the lowest settlement success, including trials with no sediment present (**Figure 5C**). The probability of settlement decreased to 22% when 2 mm of sediment were present around the settlement tile and further down to 7% when 4 mm of sediment were present around the settlement tile. For *P. strigosa*, the predicted settlement probability when no sediment was present was 85%, and it decreased to 73% when 2 mm of sediment were present around the tile and to 54% when 4 mm of sediment were present around the tile (**Figure 5A**).

The burial of settlement tiles under sediment led to a significant decrease in settlement probability for all of the five species that we tested: *C. natans*, *D. labirynthiformis*, *O. faveolata*, *P. clivosa*, and *P. strigosa*, and 4 mm of sediment were enough to suppress settlement entirely for all but *D. labyrinthiformis* (**Figure 5**). *Colpophylia natans* larvae were the most susceptible to our lowest level of substrate sediment burial. Predicted probability of settlement for *C. natans* in the absence of sediment was 82% but decreased to 25% when only a "sprinkle" (only partial (<25%) coverage of substrate) of sediment was present and to 0% at 2 mm (black curve, **Figure 5F**). In contrast, *D. labyrinthiformis* larvae appeared to be the most robust to substrate burial unlike the other species tested. Settlement probability for *D. labyrinthiformis* did not drop to 0% under 4 mm of substrate burial. Instead, settlement probability dropped to 28% and 10% under the 2 mm and 4 mm substrate burial treatments, respectively (black curve, **Figure 5G**). *Orbicella faveolata* larvae exhibited the lowest predicted settlement probability in the trials that contained no sediment (47%), and this probability decreased to just 4% when the substrate was buried under 2 mm of sediment and further down to 0% under 4 mm (black curve, **Figure 5H**). Although *P. clivosa* had high settlement rates when no sediment was present (96%) and were unaffected by the presence of sediment around the tile, just 2 mm of sediment on top of the substrate was enough to decrease settlement probability to 10%, and 4 mm of sediment suppressed settlement entirely (black curve, **Figure 5I**). Similarly, for *P. strigosa*, predicted settlement probability was 73% in the absence of sediments, but decreased to 12% with 2 mm of sediment on the tile and to 0% with 4 mm on the tile (black curve, **Figure 5J**).

When the effect of sediment presence was incorporated into the sediment burial curves to determine the sole contribution of the physical burial component of sediments, the physical burial of the settlement tiles explained most of the trend of decreasing settlement probability for *C. natans*, *O. faveolata*, and *P. strigosa*. For *C. natans*, the curve remained practically unchanged due to the strong effect of sediments on this species. For *O. faveolata*, the physical burial of substrate under 2 mm of sediment contributed to a decrease in settlement probability of 15% (red curve, **Figure 5H)**. At 4 mm of sediment, settlement probability decreased to 3%. For *P. strigosa*, 2 mm of sediment over the settlement tile decreased absolute settlement probability to 22% (red curve, **Figure 5J**). At 4 mm of sediment, absolute settlement probability decreased to 3%. The curves for *P. clivosa* and *D. labyrinthiformis* did not requirecorrection because the presence of sediment did not have a significant influence on settlement probability for either species.

3.2. Task 2 – Coral recruit sediment burial assays

For the 1-month-old recruits, most species showed a consistent decrease in recruit survival through time when buried under 2 mm and 4 mm of sediment across a timespan of 10 days (**Figure 6**). Surprisingly, under 2 mm of sediment, the survival probability of 1-month old *C. natans* recruits only decreased to 94% (95% Confidence Interval (CI) = 77 – 100%), which was similar to the baseline survival probability from the control trials (probability for control = 92%; 95% CI = 0.83 – 1.00), but decreased to 31% (95% CI = 14 – 0.74%) under 4 mm of sediment (**Figure 6A**). The survival probability of 1-month old *O. faveolata* recruits decreased to 36% (95% CI = 13 – 100%) under 2 mm of sediment and to 0% under 4 mm of sediment, compared to 88% for controls. (**Figure 6B**). Similarly, the survival probability of 1-month old *P. strigosa* decreased to 45% (95% CI = 22 – 94%) under 2 mm of sediment and to 7% (95% CI = 1 – 0.47%) under 4 mm of sediment, compared to 82% for control corals (**Figure 6C**). Yet according to the Cox-Proportional Hazards (Cox-PH) models we ran for all species tested, only the hazard ratios of the 4 mm treatments were significantly higher than those of the control trials. A hazard ratio (HR) estimates the increased mortality risk of a treatment relative to the control group. For instance, the hazard ratio of 11.0 for the *C. natans* under the 4 mm treatment indicates that individuals of this species are 11 times more likely to die when buried under 4 mm of sediment than their unaffected counterparts (HR for *C. natans* at 4 mm = 11.0, 95% CI = 1.3 – 82.0, $p < 0.05$; HR for *O. faveolata* at 4 mm = 21.4, 95% CI = 2.8 – 163.0, $p < 0.01$; HR for *P. strigosa* at 4 mm = 9.3, 95% CI = 2.1 – 41.0, $p < 0.01$).

For the 3-month-old recruits, all species showed a decrease in recruit survival through time during the control trials and when buried under 2 mm and 4 mm of sediment (**Figure 7**). We observed decreased survivorship of recruits under the control treatments for *C. natans, O. faveolata,* and *P. strigosa*. This likely an artifact of the manner in which these recruits were attached to tiles, which created a small depression that inhibited cleaning and allowed algae to colonize and compete with coral recruits. It is important to note, that because survivorship in control treatments was low and hazard ratios are calculated relative to controls, significant hazard ratios for these assays represents a highly conservative estimate of the impacts of sediment burial on the survivorship of 3-month-old coral recruits. Across a timespan of 10 days, the survival probability of 3-month-old *A. cervicornis* recruits under control treatments was 92% (95% CI = 19 – 96%), but decreased to 14% (95% CI = 4 – 49%) under 2 mm of sediment and to 0% under 4 mm of sediment (**Figure 7A**). The survival probability of 3-month-old *C. natans* recruits was 43% (95% CI = 19 – 96%) during the control trials, 61% (95% CI = 40 – 92%) under 2 mm of sediment, and 0% under 4 mm of sediment (**Figure 7B**). The survival probability of *O. faveolata* was 54% (95% CI = 23 – 100%) during the control trials, 15% (95% CI = 3 – 85%) under 2 mm of sediment, and 9% (95% CI = 1 – 58%) under 4 mm of sediment (**Figure 7C**). For 3-month-old *P. strigosa* recruits, the survival probability was 86% (95% CI = 70 – 100%) during the control trials, 14% (95% CI = 2 – 83%) under 2 mm of sediment, and 0% under 4 mm of sediment (**Figure 7D**). Similar to the trends from the 1-month-old recruits, the Cox-PH models for the 3-month-old recruits of *C. natans* and *O. faveolata* determined that only the hazard ratios of the 4 mm treatments were significantly higher than the hazard ratios of the control trials. For *A. cervicornis* and *P. strigosa*, however, the hazard ratios of the 2 mm (HR for *A. cervicornis* at 2 mm = 16.3, 95% CI = 2.1 – 123.8, $p < 0.01$; HR for *P. strigosa* at 2 mm = 5.5, 95% CI = 1.2 – 25.0, $p < 0.05$) and 4 mm treatments (HR for *A. cervicornis* at 4 mm = 25.0, 95% CI = 3.3 – 186.8, $p < 0.01$; HR for *P. strigosa* at 4 mm = 12.6, 95% CI = 2.9 – 55.0, $p < 0.001$) were significantly higher than the hazard ratio of the control trials.

For the 6-month-old recruits, *D. labyrinthiformis* showed an evident decrease in recruit survival through time when buried under 4 mm of sediment across a timespan of 10 days, though survival for the 2 mm trials similar to the control trials (**Figure 8**). According to the Cox-PH model, 6-month-old recruits of *D. labyrinthiformis* were more than 14 times more likely to die when buried under 4 mm of sediment for ten days relative to the mortality rate of corals not buried under sediments (HR for *D. labyrinthiformis* at 4 mm =

14.2, 95% CI = 1.8 – 111.9, $p < 0.05$; **Figure 8**). The 1 cm^2 fragments of *O. faveolata*, which were representative of 6-month-old recruits, showed similar survival trends under 2 mm and 4 mm of sediments, with the probability of survival decreasing to 10% (95% CI = 2 – 64%) after ten days under 2 mm of sediment, and to 12% (95% CI = 2 – 70%) after ten days under 4 mm of sediment (**Figure 9A**). The Cox-PH model indicated that recruits buried under 2 mm and 4 mm of sediment were 13 and 12 times (respectively) more likely to die relative to the mortality rate of corals not buried under sediments (HR for 1 cm^2 *O. faveolata* at 2 mm = 12.7, 95% CI = 1.6 – 99.7, $p < 0.05$; HR for 1 cm^2 *O. faveolata* at 4 mm = 12.3, 95% CI = 1.6 – 96.1, $p < 0.05$; **Figure 9A**).

Survival for the 2.3 cm^2 fragments of *O. faveolata*, which were representative of 12-month-old recruits, showed similar survival trends to younger recruits under 2 mm and 4 mm of sediments, with the probability of survival decreasing to 31% (95% CI = 10 – 96%) after ten days under 2 mm of sediment, and to 10% (95% CI = 2 – 62%) after ten days under 4 mm of sediment (**Figure 9B**). The Cox-PH model determined that only the recruits buried under 4 mm of sediment were 13 times more likely to die relative to the mortality rate of corals not buried under sediments (HR for 2.3 cm^2 *O. faveolata* at 4 mm = 13.2, 95% CI = 1.7 – 103.9, $p < 0.05$; **Figure 9B**). The 4 cm^2 fragments of *O. faveolata*, which were representative of 18-month-old recruits, exhibited drastic declines in survival when buried under 2 mm and 4 mm of sediments, with the probability of survival decreasing to 12% (95% CI = 2 – 73%) after 10 days under 2 mm of sediment, and to 0% after ten days under 4 mm of sediment (**Figure 9C**). The Cox-PH model determined that recruits buried under 2 mm and 4 mm of sediment were 13 and 17 times (respectively) more likely to die relative to the mortality rate of corals not buried under sediments (HR for 4 cm^2 *O. faveolata* at 2 mm = 12.9 , 95% CI = 1.6 – 101.8, $p < 0.05$; HR for 4 cm^2 *O. faveolata* at 4 mm = 16.9 , 95% CI = 2.1 – 132.4, $p < 0.05$; **Figure 9C**).

4. DISCUSSION

4.1. Coral settlement

These experiments were designed to identify relevant biological benchmarks regarding the impacts of sedimentation on coral settlement and specifically targeted levels well below what is currently considered relevant for sedimentation (i.e., on the scale of mm instead of cm). Surprisingly, even the minimal amounts of sediment we tested were sufficient to cause severe decreases in larval settlement.

The burial of substrate by sediments drastically affected all species and settlement was inhibited by 4 mm of substrate burial for all but one species, *D. labyrinthiformis*. Nevertheless, even though the larvae of *D. labyrinthiformis* were slightly more tolerant to sediments, their probability of settlement still decreased well below 25% when the settlement substrate was buried under 4mm of sediment, further reducing their chances of establishing viable coral recruits to replenish this species' population. The mere presence of sediment decreased the probability of settlement for three out of the five species we tested, indicating that sediments may not only be a physical deterrent to settlement but also impact settlement via different mechanisms, in this case likely by decreasing the surrounding water quality. Further experiments like these that assess changes in water quality through time with different sediment loads could help shed light on the potential deterring effect of declining water quality, exacerbated by sediments, on larval settlement. Indeed, *O. faveolata* was the most susceptible species to sediment presence, with the presence of probability dropping near 0 with 4 mm present. Yet these results are the product of experiments within a small, controlled environment. Coral reef habitats, on the other hand, are much larger in scale and highly dynamic. Therefore, we cannot draw any solid conclusions on the relationship between sediments, declining water quality, and coral settlement unless it is tested in a setting that possesses a higher resemblance to natural conditions.

These experiments reveal that coral larvae of numerous species in Florida are extremely sensitive to even minimal amounts of sediment deposition. These trends have important management implications and indicate that disturbances that induce sediment stress have the potential to significantly impact or even inhibit the settlement of coral larvae. Therefore, minimizing sedimentation stress on coral-reef habitats during peak settlement periods is prudent to maximize the chances of successful coral recruitment and promote the recovery of coral populations via sexual reproduction.

4.2. Recruit survival

Although there was variability in survival for the 2 mm trials among species, all of the species at all of the life stages we tested were drastically impacted by 4 mm of sediment, decreasing their survival probability from 31% to 0% in just ten days. Contrary to our predictions that older recruits would exhibit higher survival when challenged with sediment burial, even our fragments that approximated 18-month-old recruits exhibited similar mortality patterns to 1-month old recruits. These surprisingly consistent trends reflect the extreme sensitivity that coral recruits have to sedimentation disturbances and suggest that the impacts of sediment burial are not reduced even when corals reach sizes of 4 cm^2.

Quantification of how survival rates for multiple species at multiple life stages are impacted by sediment burial, and how these effects change with burial duration provides much needed data to inform managers in the risks associated with disturbances that lead to increased sediment stress on coral-reef habitats, especially to a myriad of important reef-building species. These data can also further benefit future research that would be highly impactful for managers, such as using the risk factors we estimated for each species to predict future decreases in the stock of juvenile corals in the face of future sedimentation events. Our experiments were conducted using coarse sediments (>250 µm), which are representative of what is usually found on coral reefs; however, coastal development projects tend to deposit much finer sediments (≤62 µm) onto reef habitats. Therefore, future research should focus on assessing the survival of juvenile corals across different sediment grain sizes to further expand our understanding on the influence of sedimentary stress to coral survival in the face of human-induced stressors such as dredging and beach renourishment projects.

5. MANAGEMENT RECOMMENDATIONS

- Develop strategies for coastal development projects, in particular large-scale dredging projects, to avoid sediment deposits and habitat burial in areas that support reefs.
- Include sediment depth monitoring as part of dredge projects and broader coral reef monitoring programs to help assess changes in the ability of the habitat to support recruits and juvenile corals.
- Consider time of year restrictions for dredging that would allow for coral. spawning, larval competency period, and recruitment to occur without additional stress from sediment.
- Adaptively manage dredging projects, to allow for timely course corrections if sediment deposits or habitat burial occurs in hardbottom areas.
- Conduct complementary studies using fine-grained material and tiles conditioned with long, sediment-laden algal turfs.

6. TABLES AND FIGURES

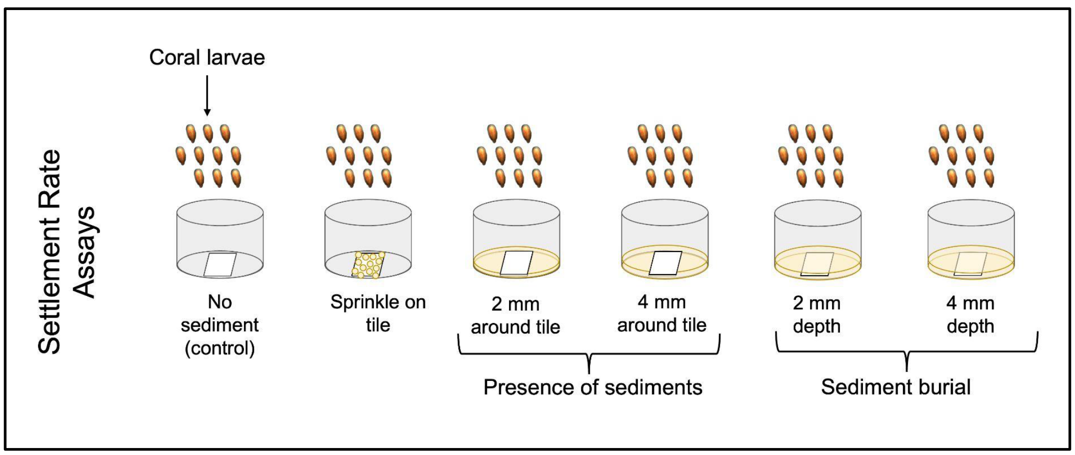

Figure 1: Figure 1: Schematic representation of the larval settlement assays depicting the different treatments established to test the response of larval settlement to the presence of sediments around the substrate and the burial of the substrate by sediments.

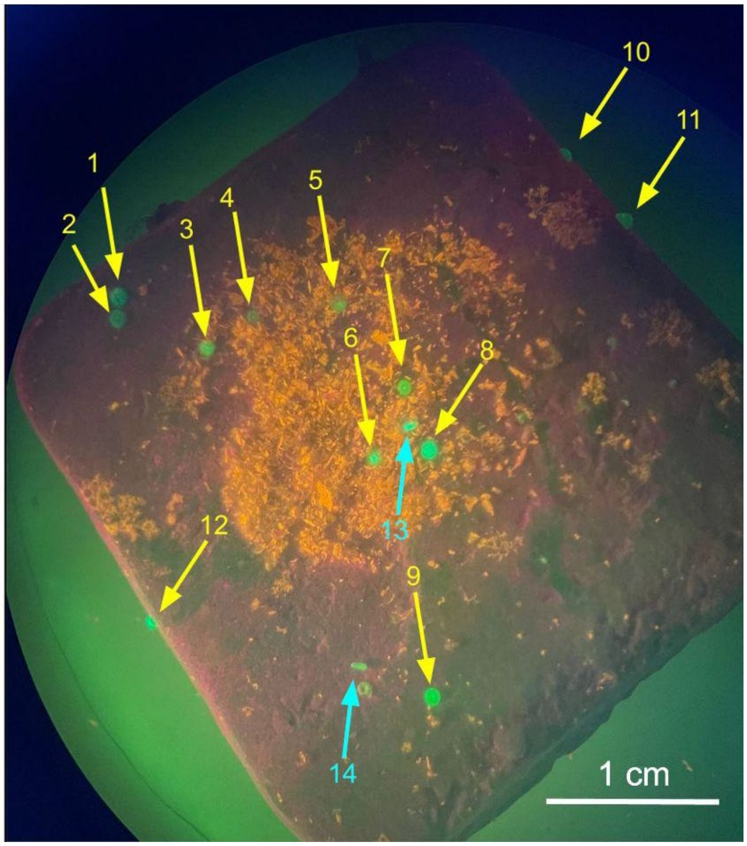

Figure 2: Photograph of a settlement tile after 72 hours. The fluorescent green dots are coral larvae that have settled or attached onto the tile. The yellow arrows point to larvae that have successfully settled and metamorphosed into a flat, disk-like shape to adhere to the substrate. The cyan arrows point to larvae that have firmly attached themselves to the substrate but have not yet metamorphosed. The orange areas are crushed CCA allocated to each tile to encourage coral settlement.

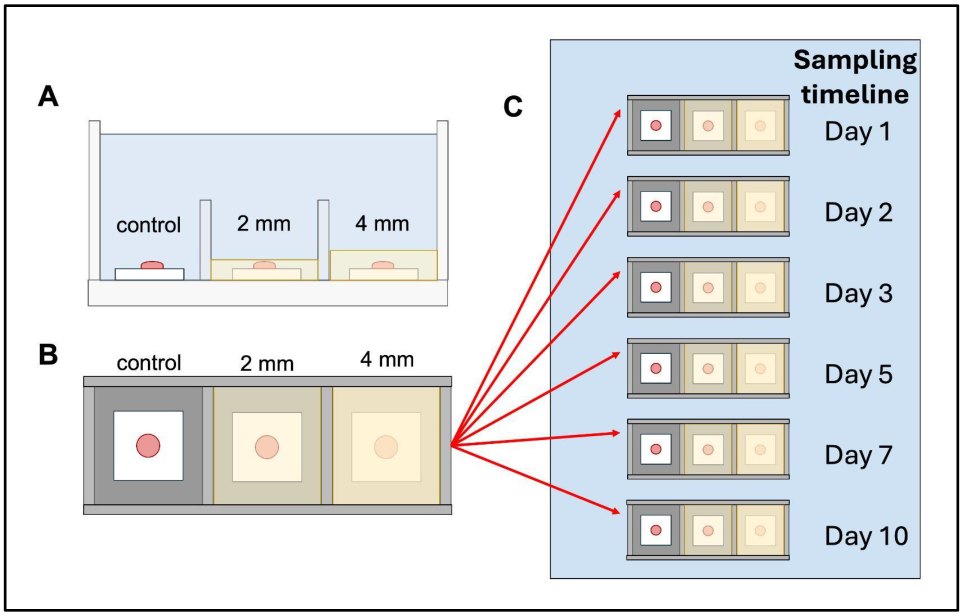

Figure 3: Schematic representation of the sediment burial assays depicting the different treatments we set up for each replicate to test the presence of sediments around the substrate and the burial of the substrate by sediments on the settlement rates of coral larvae.

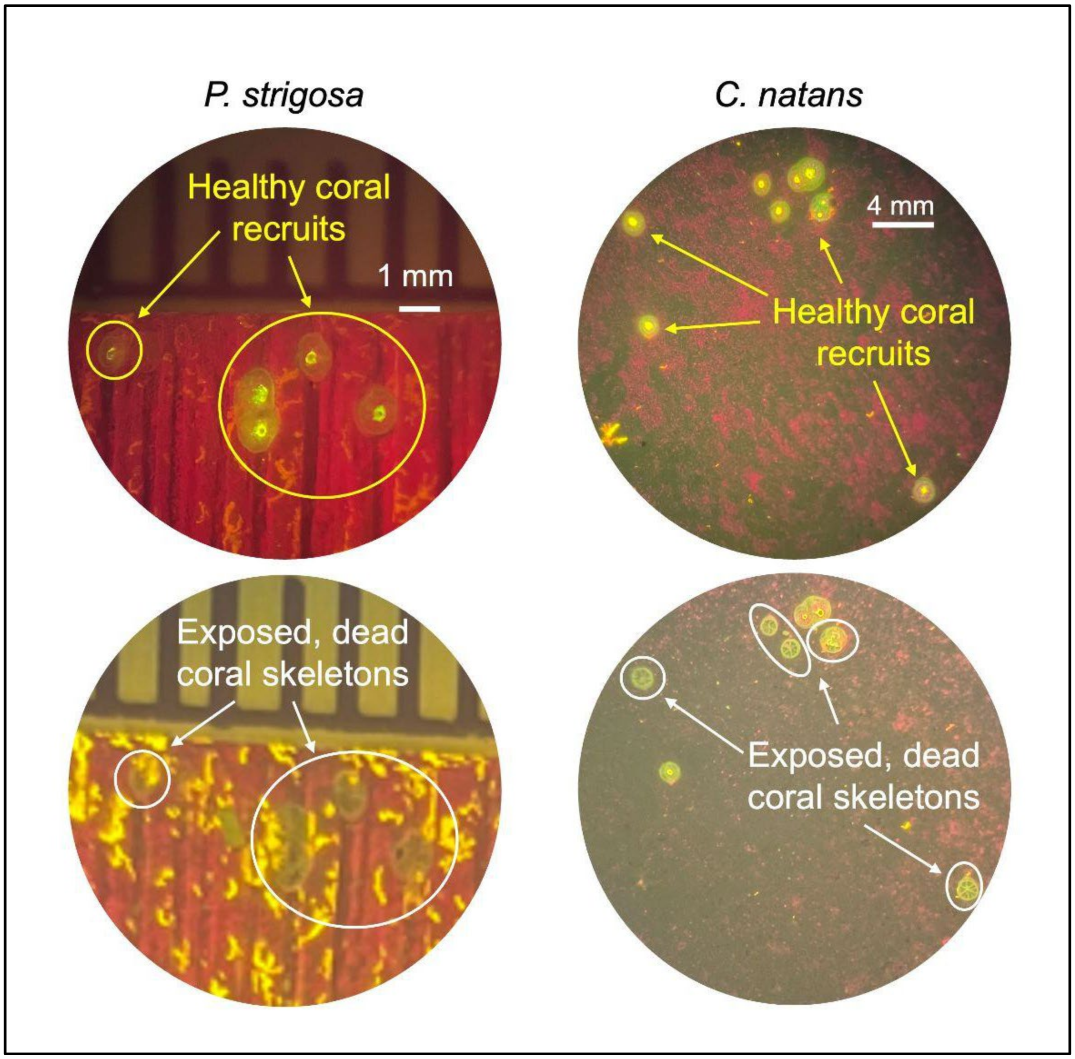

Figure 4: Photograph of 1-month-old *P. strigosa* and *C. natans* recruits before sediment burial (top) and after 10 days of burial under 4 mm of sediments (bottom). The fluorescent green polyps with live tissue represent healthy, living coral recruits and the dull, bare skeletons represent coral recruits that died after 10 days of burial.

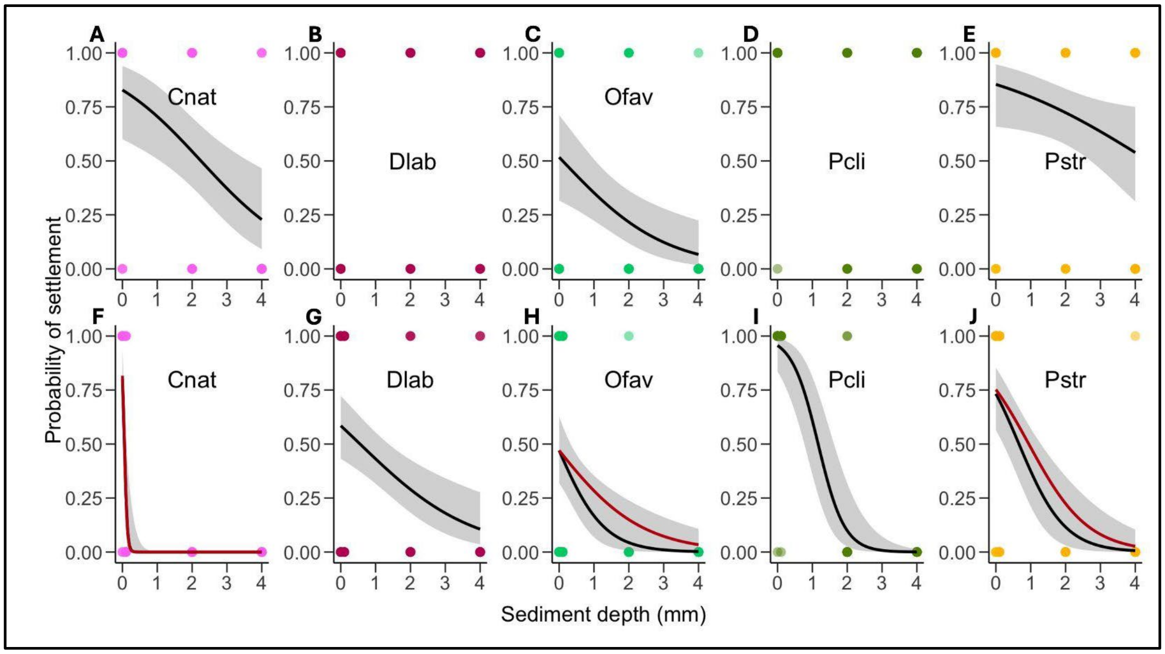

Figure 5: Scatterplots depicting (**A–E**) the binary response of the settlement of coral larvae to ceramic tiles surrounded by sediment layers of varying depths, and (**F–J**) the binary response of the settlement of coral larvae to ceramic tiles buried by sediment layers of varying depths. The black curves depict the best-fit logistic generalized mixed-effects models that predict the probability of settlement for each species across the sedimentary gradient; the shaded areas represent the 95% confidence intervals of the models. The red curves for plots **F**, **H**, and **J** represent the sole effect of sediment burial on larval settlement, which was estimated by incorporating the coefficients from the "Sediment Present" models (**A**, **C**, and **E**) into the sediment burial models (**F**, **H**, and **J**). Cnat = *Colpophyllia natans*, Dlab = *Diploria labyrinthiformis*, Ofav = *Orbicella faveolata*, Pcli = *Pseudodiploria clivosa*, Pstr = *Pseudodiploria strigosa*.

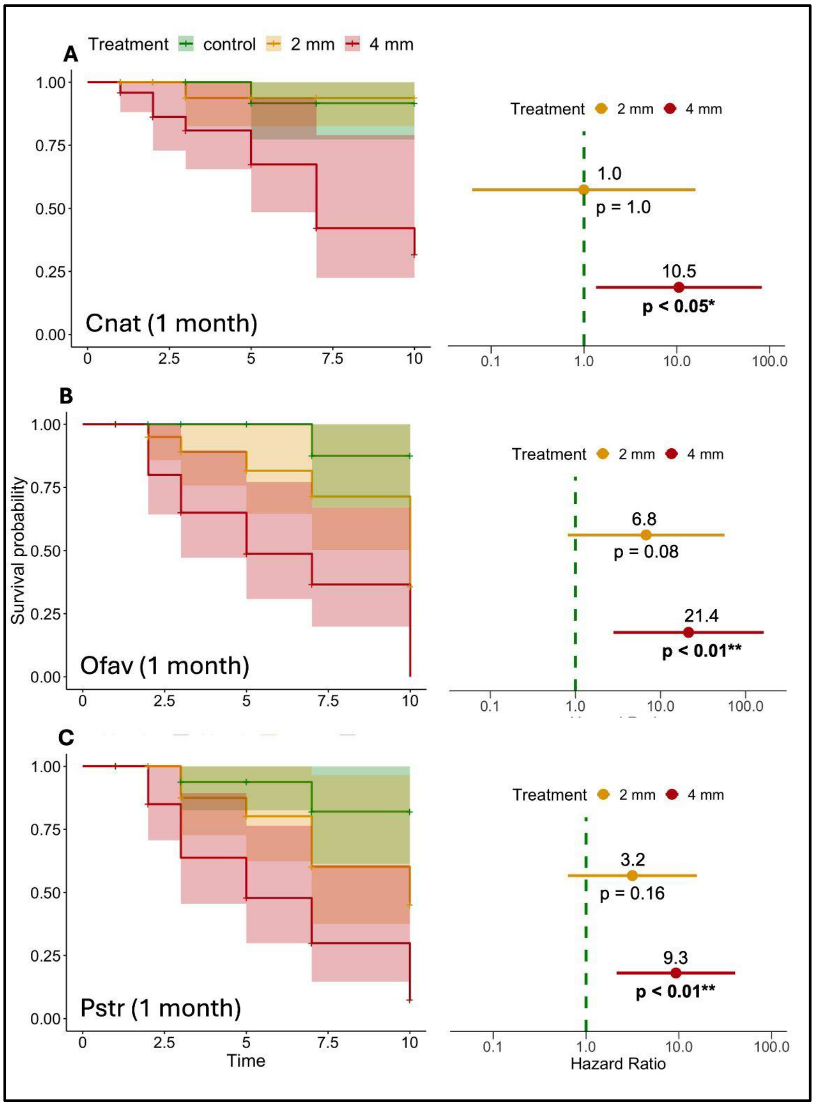

Figure 6: Kaplan-Meier curves (left) and forest plots (right) showing decreases in survival for 1-month-old recruits of 4 different coral species under different sediment burial treatments across a timespan of 10 days: **(A)** *C. natans*, **(B)** *O. faveolata*, and (**C)** *P. strigosa*. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$) hazard of that experimental treatment relative to the control treatment (no sediment burial).

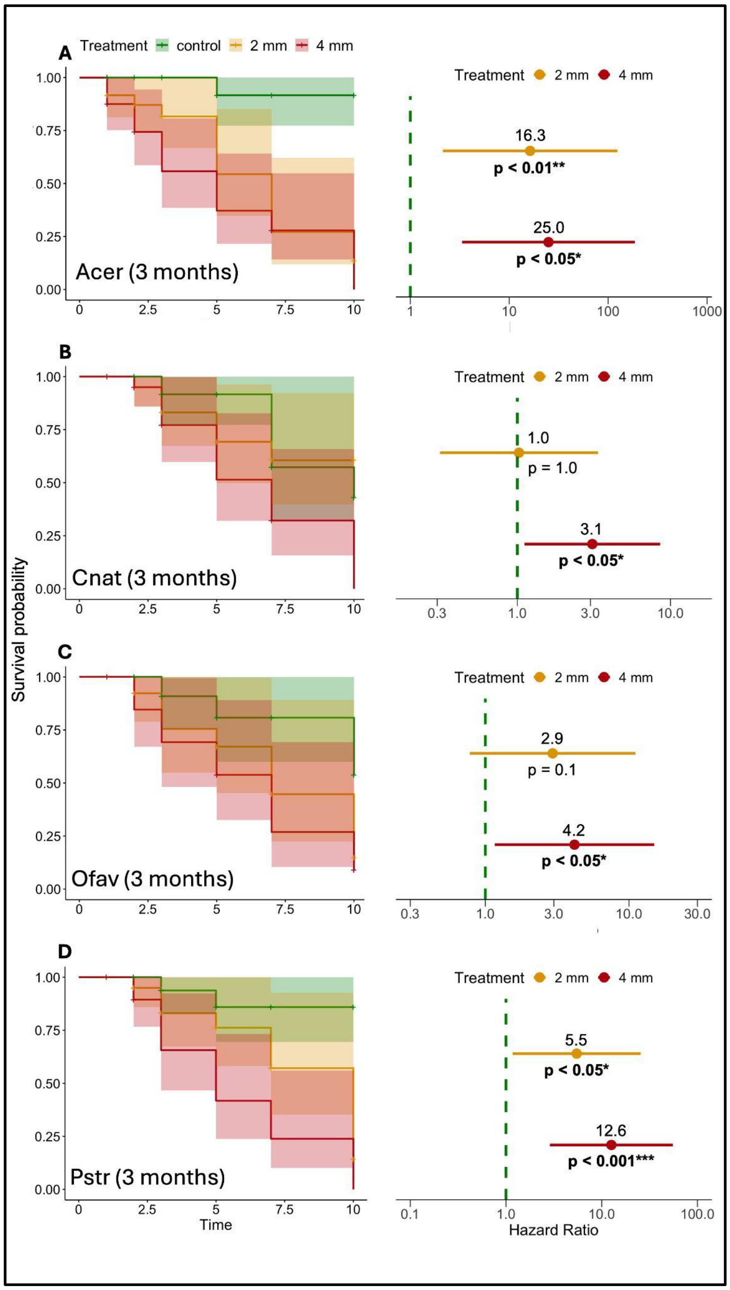

Figure 7: Kaplan-Meier curves (left) and forest plots (right) showing decreases in survival for 3-month-old recruits of 4 different coral species under different sediment burial treatments across a timespan of 10 days: **(A)** *A. cervicornis*, **(B)** *C. natans*, **(C)** *O. faveolata*, and **(D)** *P. strigosa*. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$)

hazard of that experimental treatment relative to the control treatment (no sediment burial).

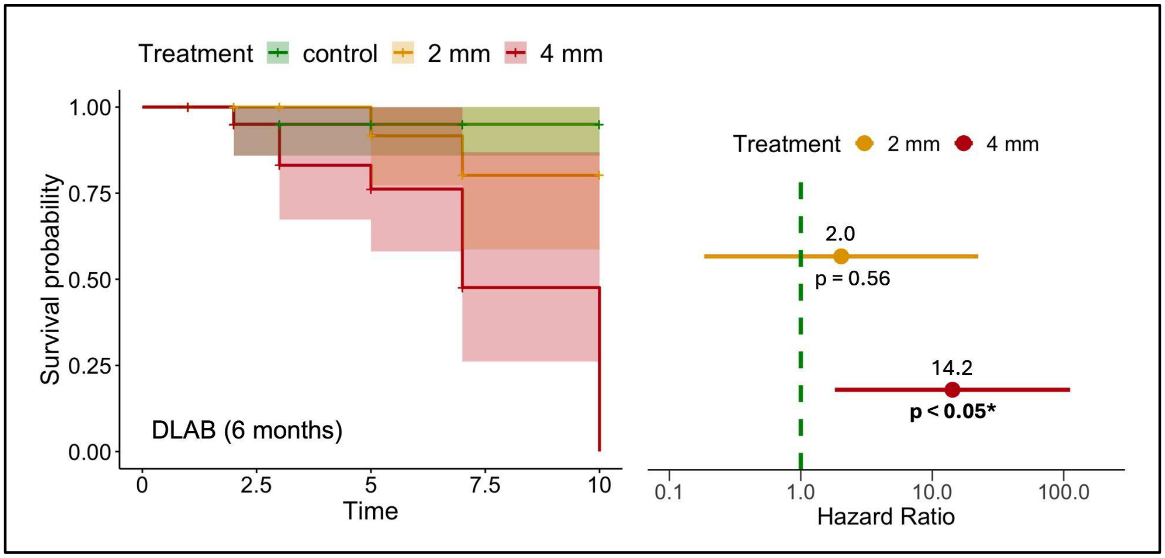

Figure 8: Kaplan-Meier curve (left) and forest plot (right) showing a decrease in the probability of survival for 6-month-old recruits of *D. labyrinthiformis* under different sediment burial treatments across a timespan of 10 days. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$) hazard of that experimental treatment relative to the control treatment (no sediment burial).

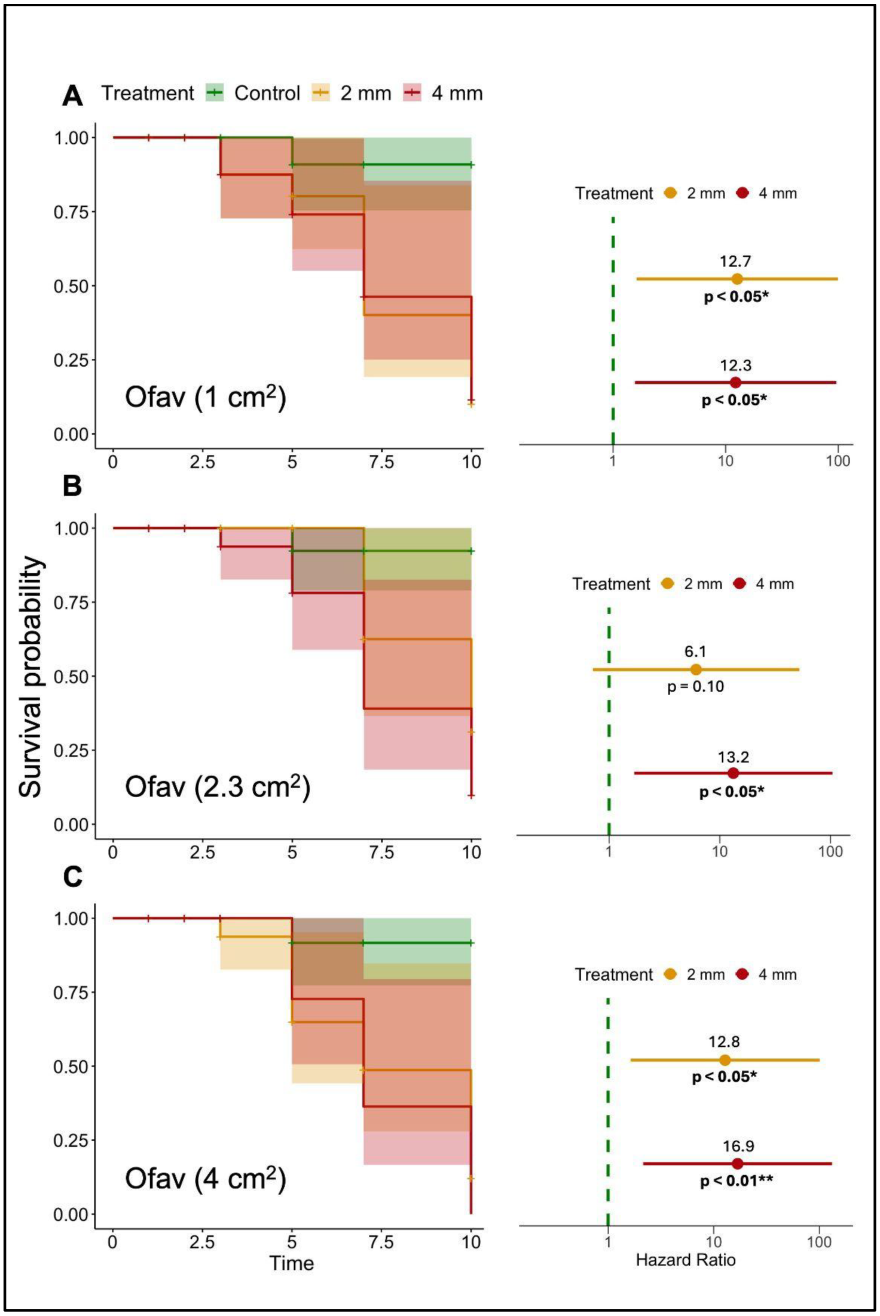

Figure 9: Kaplan-Meier curve (left) and forest plot (right) showing a decrease in the probability of survival for (**A**) 1 cm^2 fragments, (**B**) 2.3 cm^2 fragments, (**C**) and 4 cm^2 fragments of *O. faveolata*, under different sediment burial treatments across a timespan of 10 days. The forest plots depict the time-independent hazard ratios calculated by the Cox-proportional hazards models for each treatment. Any hazard ratio greater than 1 indicates increased mortality risk under the respective treatment. The dotted vertical lines represent the baseline hazard ratio of 1. The error bars depict the 95% CIs of the hazard ratios, which, if greater than 1, indicate a significant ($p < 0.05$) hazard of that experimental treatment relative to the control treatment (no sediment burial).