ORGANIC MATTER CYCLING AND NUTRIENT REMINERALIZATION BY SMALL- VERSUS LARGE-BODIED SEA CUCUMBERS ON CORAL REEFS

BY

Rachael Meredith Keighan

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Sea cucumbers play a crucial role in coral reef ecosystems by recycling organic matter (OM) into inorganic nutrients that fuel ecosystem productivity. Despite widespread overexploitation of sea cucumber stocks, studies that link changes in density or composition of holothuroid communities to ecosystem outcomes remain limited. A cage experiment was conducted to examine changes in sediment OM and pore water ammonium at depleted, natural, and high holothuroid densities while accounting for environmental covariates (precipitation and tide) and sea cucumber body size. Equal biomasses of two harvested species of differing body sizes were compared: the small but abundant black lollyfish (*Holothuria atra*) and the large, commercially prized black teatfish (*H. whitmaei*). OM accumulation was significantly greater when sea cucumbers were excluded compared to both natural and high densities. However, among high-density treatments, reductions in OM only occurred in plots containing the larger species, *H. whitmaei*. The negative effect of high sea cucumber density on OM was three times greater in *H. whitmaei* treatments than *H. atra* treatments, indicative of an allometric relationship between body size and resource access or metabolic demand. In contrast to OM dynamics, treatments did not influence changes in pore water ammonium, likely due to the large influence of environmental covariates. Precipitation and tidal exchange helped to predict OM and ammonium dynamics, without which sea cucumber treatment effects would have been diminished or masked. Our findings highlight the importance of maintaining both holothuroid density and diversity to support OM processing and nutrient remineralization, and the ensuing ecosystem benefits for seagrasses and corals. Regular monitoring and species restrictions will be important to preserve stocks of large species that provide disproportionate ecosystem services. These recommendations are particularly important for degraded reefs to avoid the cascading consequences of OM accumulation including sediment stratification, oxygen depletion, and opportunistic boom-and-bust cycles of algae and cyanobacteria that can promote coral-algal phase shifts.

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decreased organic matter. For environmental covariates (II), positive values indicate a positive relationship between the covariate and OM accumulation. Finally, for method-related effects (III), positive values indicate greater values reported from loss-on-ignition data than hydrogen peroxide digestion data (dashed line) and negative values indicate smaller values reported from loss-on-ignition data. Bolded values indicate statistical significance, and asterisks indicate the degree of significance.

Figure 6. Proportional changes in salinity (Sal_t/Sal_0) (a) and ammonium (NH_{4-t}/NH_{4-0}) (b). Colours indicate holothuroid treatments, ordered from low density (left) to high density (right). The dashed red line indicates no change from T0. Error bars indicate 95% confidence intervals.

Figure 7. The effects of holothuroid treatments and environmental covariates on proportional changes in salinity and ammonium. Points are means and error bars indicate the 5th (lower) and 95th (upper) confidence percentiles. For holothuroid treatments (I), positive values indicate greater ammonium/salinity compared to cage controls (dashed line), and negative values indicate decreased organic matter. For environmental covariates (II), positive values indicate a positive relationship between the specific covariate and salinity/ammonium. Bolded values indicate statistical significance, and asterisks indicate the degree of significance.

I. Introduction

In most coastal coral reefs, over a third of the shallow-water benthic environment consists of sandy patches and dunes that play an important role in maintaining reef ecosystems. Shallow-water carbonate sediments act as a biocatalytic filter; their high porosity facilitates the capture of particulate organic matter (POM) where it can be metabolised by deposit-feeding fauna (Yingst 1976, Slater et al. 2011) and the benthic microbial community (Wild et al. 2005). This conversion of POM to dissolved inorganic nutrients fuels the high productivity of coral reefs in oligotrophic waters (Rasheed et al. 2002). Sandy shallow-water habitats such as reef flats, seagrass beds, and lagoons are fertile grounds for organic matter production and turnover (Hansen et al. 1992, Miyajima et al. 1998). However, as anthropogenic development and agriculture intensify nutrient delivery and organic matter (OM) loading in coastal reef environments, the resulting spikes in benthic microbial respiration can create suboptimal conditions for many reef-associated flora and fauna.

In carbonate sediments, the depth of transition between aerobic and anaerobic decomposition of organic matter is influenced by pore-water advection of dissolved oxygen and organic carbon (Werner et al. 2006). Excess OM accumulation can alter the depth of this chemocline, leading to increased microbial respiration and localised hypoxia. Furthermore, cascading effects of anaerobic metabolism include decreased pH and the production of hydrogen sulphide that can harm corals (Weber et al. 2012) and seagrasses (Koch and Erskine 2001). As such, processes that mitigate POM accumulation and increase sediment oxygenation are crucial for maintaining ecosystem health.

Bioturbators such as sea cucumbers (Holothuroidea) influence the physical and chemical composition of sediments through particle reworking and bioirrigation (Kristensen et al. 2012). By disturbing or transporting sediment, bioturbators can promote water advection, increase oxygen penetration depth, and stimulate aerobic POM decomposition (Volkenborn et al. 2007, Kristensen et al. 2012, Lee et al. 2018). Of all bioturbators, deposit-feeding fauna are credited with the greatest proportion of sediment turnover (Jumars and Wheatcroft 1989). Deposit-feeders ingest large volumes of sediment to metabolise trapped OM and may facilitate the breakdown of partially digested POM by other fauna and bacteria (MacTavish et al. 2012, Costa et al. 2014). Yet, the magnitude of the role that bioturbators play in breaking down POM remains unclear.

In recent decades, the scale of bioturbation by deposit-feeding sea cucumbers has become better understood. For instance, on Heron Island, Australia, total bioturbation by all holothuroids was conservatively estimated at 64 000 metric tons of sediment per year, roughly equivalent to the mass of five Eiffel Towers (Williamson et al. 2021). Bioturbation rates vary between species depending on body size, environmental condition, seasonality, and behaviour (Uthicke 1999, 2001b, Roberts et al. 2000). For example, estimates of sediment turnover by the small, but abundant black lollyfish (*Holothuria atra*), which feeds consistently throughout the day, range between 14 and 25 kg annually (Uthicke 1999, Williamson et al. 2021). In contrast, the larger black teatfish (*H. whitmaei*), which feeds primarily in the late afternoon, can rework 30 to 60 kg of sediment annually (Shiell and Knott 2010). Although bioturbation capacity tends to increase with body size, little is known about the relationship between body size and nutrient ‘remineralization’, or the breakdown of organic compounds into inorganic nutrients.

Holothuroids process POM including microalgae, bacteria, and detritus captured in sediments. While sea cucumbers were once assumed to be passive grazers, some species appear to actively move towards areas of higher organic content (Slater et al. 2011). As they lack vision, this is likely facilitated by using chemosensory receptors on their tentacles (Marquet et al. 2020). Several studies have also noted significantly greater concentrations of organic matter and algal pigments in the holothuroid foregut compared to adjacent sediments, suggesting that sea cucumbers employ selective feeding (Zamora and Jeffs 2011, Slater et al. 2011, Navarro et al. 2013, Viyakarn et al. 2020). Active particle selection may contribute to the processing of 30-80% more organic matter than if feeding was non-selective (Slater et al. 2011). While holothuroids do not remove all organics from ingested sediments, estimates of dietary organic carbon absorption range between 10 to 40% (Webb et al. 1977, Moriarty et al. 1985, Mangion et al. 2004).

Incompletely digested sediments and waste matter are defecated in organic-rich faecal pellets that disintegrate over the course of several hours, redistributing their contents for further remineralization by bacteria and other fauna (Navarro et al. 2013). Dissolved metabolic waste products are excreted primarily as ammonium with trace amounts of nitrate, nitrite, and phosphate that help support ecosystem productivity (Uthicke 2001a, 2001b, MacTavish et al. 2012). Like bioturbation rates, nutrient excretion rates may differ even among species of similar body size (Uthicke 2001b). Yet, we do not fully understand how the mineralization process could change in the absence of bioturbators and what the ultimate ecosystem consequences of their removal are.

In-situ exclusion of *H. atra* resulted in increased benthic algal cover, indicating that holothuroids play an important role in controlling benthic algal productivity (Viyakarn et al. 2020). While holothuroid-derived dissolved inorganic nitrogen (DIN) benefits algal growth (Uthicke 2001a), microalgal proliferation appears to be moderated by grazing pressure (Uthicke

2001a, Viyakarn et al. 2020). Therefore, net productivity may be either positive or negative depending on bioturbation and grazing intensity (Uthicke 2001a). Mechanisms that control algal biomass may increase resource availability for other non-dietary primary producers such as seagrasses or corals which play an important role in carbon storage and habitat formation.

For instance, seagrasses appear to benefit when sea cucumber abundances are high. Houk et al. (2013) noted that tropical seagrass-macroalgal ratios in *Halodule uninervis* seagrass beds were predicted by holothuroid abundance in addition to several watershed factors. Manipulative studies (Wolkenhauer et al. 2010, Arnull et al. 2021) in tropical seagrass beds have noted that high densities of the holothuroid sandfish (*H. scabra*) increased the productivity of *Thalassia* sp. and had beneficial to neutral effects on *Cymodocea* sp. growth. Stocking of sandfish in reef flats also reduced sediment oxygen consumption and increased oxygen penetration depth (Lee et al. 2018). Together, these studies suggested that increased seagrass productivity may result from a combination of increased availability of holothuroid-derived nutrients (Uthicke 2001b), reduced sediment hypoxia (Lee et al. 2018), and decreased competition with micro- (Viyakarn et al. 2020) and macroalgae (Houk et al. 2013).

Further support for the ecosystem-level role sea cucumbers may play comes from a comparison of two fringing reefs with different levels of anthropogenic nutrient input around the island of Réunion (Mangion et al. 2004). While a eutrophic reef supported much higher holothuroid biomass than an oligotrophic reef, the organic content of the sediments at both sites were similar. These findings imply that a substantial proportion of the organic matter at the eutrophic site was stored as holothuroid biomass. Clearly our limited knowledge of the ecosystem services provided by tropical sea cucumbers presents a critical knowledge gap in light of their overexploitation globally by fisheries.

Holothuroids are exported to major markets in Hong Kong, South Korea, Singapore, and Taiwan where they are sold brined, salted, frozen, and most commonly in the traditional dried form known as trepang or bêche-de-mer (Anderson et al. 2011, Eriksson and Clarke 2015). While commercial sea cucumber fisheries have existed for centuries, demand has dramatically increased since the late 1980s and remains high despite international concerns regarding overexploitation (Anderson et al. 2011, Eriksson and Clarke 2015, Conand 2018). Between 2009 and 2014, tropical sea cucumber fisheries harvested over 16000 tons dry weight (Conand 2018), excluding subsistence and illegal harvests. Fisheries often prioritise larger-bodied, long-lived species with thick body walls; however, abundant small-bodied species may be harvested to maximise total yield and can make up a large proportion of overall catch (Kinch et al. 2008, Friedman et al. 2011). In recent decades, approximately 80% of regional fisheries have reported holothuroid population declines due to overharvesting, as well as a reduction in average body size by 35% (Anderson et al. 2011). Global overexploitation has resulted in both spatial (inshore to offshore) and compositional (high to low value) shifts in holothuroid communities (Anderson et al. 2011). These community shifts may have significant repercussions on nutrient cycling and POM control.

Understanding the functional ecology of different holothuroid species will generate insight into how human activities impact nutrient recycling in reef ecosystems. As a result of the global overexploitation of sea cucumber stocks, regulating agencies have been encouraged to adopt an ecosystem approach to fisheries (EAF) management which holistically considers both stakeholder values and ecological thresholds (Purcell et al. 2014). Crucially, an EAF accounts for minimum sea cucumber densities needed to sustain a population; however, more information is needed to understand the effect of sea cucumber harvest on the surrounding environment. By understanding how species influence organic matter recycling, regulatory organisations may be able integrate metrics of environmental condition to determine where populations require protection and where harvest may have less impact. Currently employed management strategies include the implementation of area closures, catch quotas, minimum harvest lengths, and species restrictions (Purcell 2014, Baker-Médard and Ohl 2019). Yet, some of these strategies can be ineffective when applied broadly in multispecies fisheries due to differences in life histories between species. As the market for sea cucumber products continues to grow, it is critical that fisheries management decisions are supported by information on how resource exploitation will affect ecosystem function.

The present study evaluated the influences of two commercially important sea cucumbers, *H. whitmaei* and *H. atra*, on organic matter recycling and nitrogen remineralization in a nearshore coral-reef environment. These species were selected given their importance for the economy and ecology of the Pacific Islands (Friedman et al. 2008, Kinch et al. 2008), as well as their contrasting body sizes. We undertook a two-month long cage experiment to assess the impacts of each species on sediment organic matter content and pore water ammonium. While previous studies have compared how inclusion or exclusion of holothuroids influences sediment OM content across two to three timepoints (Wolkenhauer et al. 2010, Grayson et al. 2022), the present study accounted for natural fluctuations in organic matter by increasing sampling regularity and integrating environmental covariates into our analysis. Further differences include using species with contrasting body sizes and investigating both sediment OM and pore water ammonium on a reef flat with significant nutrient input from groundwater and three urbanised rivers.

II. Methods

Site Description

Guam is the southernmost island of the Mariana Archipelago, located in the tropical western Pacific (Fig. 1a). The island supports a high human population density, with approximately 169 000 permanent residents across a land area of 549 km^2. The island’s growing human footprint has had consequences for both marine and freshwater habitats, particularly for marine resources along the leeward western coast (Burdick et al. 2008, Prouty et al. 2014, Houk et al. 2022). While commercial sea cucumber fisheries have not been present on Guam for several decades, harvest of up to 100 animals per person per day is permitted outside of marine protected areas (MPA), and no additional regulations exist regarding factors like species or body size.

This study was conducted within the Piti Bomb Holes Marine Preserve, located in Asan Bay on the central-western side of Guam (Fig. 1b). The preserve, which was established in 1997, is one of Guam’s five MPAs and encompasses 3.64 square kilometres of fringing reef and lagoon habitat. Approximately 40% of the preserve is dominated by an extensive reef flat (Kottermair 2012) that supports high holothuroid densities. The nearshore reef flat, where experimental cages were established, experiences freshwater input from the Taguag river mainly, but also from two nearby rivers depending on the tide and current. In addition, groundwater contributes to the nutrient dynamics of Guam’s coastline due to the presence of substantial karst watersheds (Taboroši et al. 2005).

Study species

The black teatfish (*H. whitmaei*) is a commercially prized species of large-bodied sea cucumber found at relatively low densities throughout the tropical Pacific. This species is found in a wide range of habitats to a depth of 25 m, with body sizes typically increasing with depth (Kerr et al. 2017). On protected reefs in Australia, densities of black teatfish range from 19 to 27 individuals/ha; however, aggregations of 123 and 275 individuals/ha have been reported in more remote regions including Western Australia (Shiell and Knott 2010) and New Caledonia (Conand 1989), respectively. Unfortunately, the black teatfish exhibits slow recruitment rates and many compromised stocks remain well below these reference levels long after harvest (Uthicke and Benzie 2003, Friedman et al. 2011, Purcell et al. 2013). In 2010, *H. whitmaei* was assessed for the IUCN Red List of Threatened Species (IUCN 2010) and was listed as endangered due to significant population declines (60–90%) in the majority of its range (Conand et al. 2013b). Similarly in 2019, an advisory panel found that *H. whitmaei* met the listing criteria outlined by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II. However, a recent review conducted through the National Oceanic and Atmospheric Administration (NOAA) determined that listing the black teatfish under the US Endangered Species Act was not warranted (NOAA, 2021).

In contrast, the black lollyfish (*H. atra*) is one of the most abundant species of tropical sea cucumber with densities that can exceed 1000 individuals/ha in some regions (Uthicke 1999, Mangion et al. 2004, Viyakarn et al. 2020). This species is often highly abundant in reef flats and reef slopes to a depth of 10 m (Kerr et al. 2017). Despite its small body size and low commercial value, lollyfish can make up a significant proportion of catch composition when higher value species become scarce (Kinch et al. 2008). Black lollyfish populations appear to withstand harvesting pressure better than many other commercial species as they reproduce both sexually and asexually through transverse fission (Conand et al. 2002, Lee et al. 2008). Due to its high abundance, extensive distribution, and low commercial importance, the black lollyfish is listed as Least Concern by the IUCN (Conand et al. 2013a).

Background Densities

Baseline population surveys were conducted during the day in the reef flat on the eastern side of the Marine Preserve prior to the beginning of the experiment. Three 50 m transects were established within the study site, perpendicular to shore and ranging between 0.75 and 1 m in depth. All holothuroid species within 2.5 m of either side of the transect were counted, for a total survey area of 750 m^2. A total of ten sea cucumber species were identified within the study area, and average holothuroid density was 1.51 individuals/m^2. The sea cucumber community was dominated by the two species of lollyfish (*H. atra* and *H. edulis*) which made up 97.9% of all observations. One individual *H. whitmaei* was also noted within the survey area, consistent with the low densities and declining trends reported throughout Micronesia (Houk et al. 2016).

Experimental Design

In the present study, we carried out an in-situ cage experiment that investigated the influence of *H. atra* and *H. whitmaei* on sediment OM and pore water ammonium. This study was conducted approximately 150 m from the coastline in the vicinity of the Matague River, along the southeastern boundary of the Piti Bomb Holes Marine Preserve. Twenty 1.5 m x 1.5 m plots were established in the sandy reef flat, each randomly assigned to one of five cage treatments (n = 4 cages per treatment) based upon the baseline surveys noted above. Treatments included: exclusion (zero individuals/m^2), cage control (open on one side, natural density or 1.51

individuals/m^2), natural control (no cage structure, natural density or 1.51 individuals/m^2), *H. atra* (high density, six individuals or 2.7 individuals/m^2), and *H. whitmaei* (high density, one individual or 0.4 individuals/m^2). High-density *H. atra* treatments were stocked with six individuals to represent double the natural holothuroid density, and *H. whitmaei* treatments were stocked with a single animal of equivalent biomass (*H. atra*: 200.1 ± 3.6 g (SE) per individual & treatment density 533.7 ± 1.6 g/m^2; *H. whitmaei*: 1205.8 ± 9.2 g per individual, treatment density 535.9 ± 4.1 g/m^2). All animals used in this study were collected from within the reef flat and were returned following the experiment's completion (Guam Division of Aquatic and Wildlife Resources Permit SR-MPA-22-009/A). Two instances of binary fission were noted within *H. atra* treatments, and these animals were replaced with another individual of a mass equal to the sum of the fission products.

Cages were constructed from 1.5 m x 1.5 m weighted PVC pipe surrounded by a fine fibreglass screen with 4 mm^2 square pores. Each cage extended 30 cm above the sediment surface and 10 cm below the surface (where possible) to exclude burrowing sea cucumber species from the enclosure. All cages were left open on the top to allow access by benthic-feeding fish. Following establishment, plots remained for two months, and were inspected each week to ensure there was no change in sea cucumber biomass and to minimise biofouling. Cage controls were constructed similarly to treatment cages; however, these were open on one side to allow the passage of sea cucumbers. Natural control plots did not contain cage structures and were denoted at each corner using metal stakes. Natural controls and cage controls were compared to account for potential cage effects.

Surface sediments were collected at two-week intervals for the duration of the experiment. During each sampling event, three sediment cores (3.0 cm ⌀) were randomly collected from each cage. The top 30 mm were retained from each core, and these samples were sealed and placed on ice for transport to the University of Guam Marine Laboratory. Sediments were rinsed twice with purified water to remove excess salt, and were centrifuged at 2000 rpm for five minutes following each rinse to settle suspended particulate matter prior to decanting. Samples were dried at 60 ˚C for 72 hrs. Samples were then divided in half, and each subsample was analysed for OM content using one of two methods. First, crude organic matter content was determined by hydrogen peroxide digestion (HPD) following the protocols described by Tebbett et al. (2022; Supplementary Material S5), adapted for smaller sample sizes. This included adding 1 mL of 30% H_2O_2 twice each day for 14 days, after which samples were dried and reweighed. Second, combustible organic matter was also determined by heating samples in an ashing furnace for two hours at 550˚C and measuring the loss on ignition (LOI).

Pore water samples were also collected during each sampling event. Samples were slowly syphoned from the upper layer of sediment using 60 mL syringes and were field-filtered using Cole-Parmer 0.45 µm syringe filters before being stored at -20 ˚C for further analysis. Water samples were analysed for ammonium (NH_4-N) concentrations using a Trilogy Lab fluorometer following the procedures outlined by Holmes et al. (1999). To account for potential variations in groundwater discharge throughout the study site, sample salinity was also measured using a YSI Professional Plus multiparameter water quality instrument.

Environmental variables

Environmental data were gathered to serve as predictor terms, or covariates, in our analyses. Tide predictions were acquired from the National Oceanic and Atmospheric Agency's (NOAA) Tide Predictions for Apra Harbor (Station 1630000). From these data, cumulative tidal exchange was calculated as the sum of the differences between high and low tides. Tidal exchange was used as a metric of lagoonal flushing, current, and potential groundwater input (Houk et al. 2013). Precipitation data for Guam were also collected from the NOAA Daily Summaries for Guam International Airport (Station GQW00041415) and were used as a metric of nutrient and OM input from adjacent watersheds (Houk et al. 2022). Data for precipitation two days prior to sampling were also used in our analysis. Other potential covariates examined included maximum wave height and water temperature; however, these data did not predict sediment OM or ammonium alone or in combination with other factors. Therefore, these factors were excluded from further analysis.

Statistical analysis

All statistical analyses were conducted using R version 4.2.3 (R Core Team 2022). Data on % OM from both the LOI and HPD methods were evaluated at both the sample level and after aggregation to the cage level by averaging within-cage replicates. First, sample-level OM data were used to examine the covariance between the differing OM detection methods through linear regression. Second, to account for differing starting points among cages, we calculated the proportional change in OM, ammonium, and salinity for each cage as:

$$\Delta X = X_t / X_0$$

Data at all levels of aggregation were then normalised using a log transformation, and were analysed using a linear mixed-effects model approach through the *lme4* package (Bates et al. 2015). The modelling process worked to fit the relationship between dependent variables (OM, salinity, and ammonium) against treatments, environmental variables, methods (for OM only), and any potential interactions. Random effects were the individual replicate cages within each treatment. The best-fit model was determined by comparing the chi-square examination of the residuals, Akaike information criterion (AIC) and Bayesian information criterion (BIC) from models with varying interactions between predictor variables. Environmental data were examined with and without transformations. Prior to modelling, relationships between predictor variables were visualised through correlation testing using the packages *corrplot* (Wei and Simko 2021) and *ellipse* (Murdoch and Chow 2023). Following model comparison and fitting, all final models followed a similar structure that is furthered in the results:

$$\log(\%OM) \text{ and } \log(OM_t/OM_0) \sim (Treatment + Tidal\ exchange + \log(Precipitation)) * Method + (1|Cage)$$

or

$$\log(NH4_t/NH4_0) \sim Treatment + Tidal\ exchange + \log(Precipitation) + (1|Cage)$$

$$\log(Sal_t/Sal_0) \sim Treatment + Tidal\ exchange + \log(Precipitation) + (1|Cage)$$

III. Results

Organic Matter Analysis

At T_0, mean OM content determined by LOI accounted for 3.23% ± 0.07% (SE) of total sediment mass across all treatment plots whereas OM content determined by HPD accounted for only 0.31 % ± 0.03% (SE). Despite the magnitude of order difference, a positive relationship existed between methods for % OM content across treatments and time for both raw data ($p <$ 0.0001, $R^2 = 0.346$) and data aggregated at the cage level ($p < 0.0001$, $R^2 = 0.443$; Fig. 2). The correlation of % OM determined by LOI and HPD suggested that both OM metrics may have been influenced similarly by the treatment groups and environmental factors, supporting a combined modelling approach to investigate treatment effects.

Initial analyses of the % OM data revealed two key environmental covariates were relevant to changes through time (Table 1). A significant relationship existed between % OM and precipitation (estimate = 0.216 ± 0.034, $p < 0.0001$), and a marginally-significant relationship was noted with cumulative tidal exchange (i.e., extreme high and low tides; estimate = -0.135 ± 0.072, $p = 0.063$, Table 1). Although time was also a significant predictor of % OM, it was significantly correlated with precipitation and tidal exchange (i.e., the study timeframe included dry to wet season transition and neap to spring tide transition) and had a lower predictive power. As such, the best-fit model included precipitation and tide, although the correlation with time should be appreciated. Finally, because the starting % OM in each individual cage was unique, we did not expect or observe significant treatment effects using raw data. Instead, we converted our OM data into proportional change prior to our final modelling to interpret treatment effects.

Proportional change in OM was significantly influenced by precipitation, tidal exchange, and analytical method. Although time was not a significant predictor of change in OM in the best-fit model, time was collinear with both precipitation (R = 0.64) and tidal exchange (R = 0.55, Fig. 3), similarly noted above. Thus, when interpreting the best-fit model, the influences of precipitation and tidal exchange were independent from each other, but both covaried with time.

Cumulative tidal exchange did not significantly influence proportional changes in OM (*p* = 0.175; Table 1, Fig. 4). Meanwhile, precipitation had the strongest positive influence on change in OM, resulting in a 34.2% increase per mm rainfall (estimate = 0.342 ± 0.034, *p* < 0.0001).

By accounting for environmental variation, the model revealed significant differences in the proportional change in OM across sea cucumber treatment groups. The greatest change in OM was observed within exclusion treatments, which were on average 84.1% ± 23.6% greater than the background-density cage control treatments (Fig. 5). Conversely, among both high-density sea cucumber treatments, only *H. whitmaei* cages were significantly different from background density. Proportional changes in OM were on average 43.6% ± 23.6% lower in plots containing the large-bodied sea cucumber, *H. whitmaei* (estimate = -0.249, *p* = 0.0123). Meanwhile, non-significant declines of only 14.4% ± 23.6% were noted for the smaller sea cucumber, *H. atra* (estimate = -0.0639, *p* = 0.494). Thus, despite similar sea cucumber biomass, only cages with the larger species resulted in a significant decline in OM relative to cage controls.

While both the LOI and HPD metrics of OM were influenced by treatment and environmental conditions similarly, the magnitude of the experimental effects differed. Proportional change in OM was approximately 83.7% ± 21.3% smaller among LOI replicates than HPD replicates (estimate = -0.788, *p* = 0.000345; Fig. 5). Additionally, the effect of precipitation was 17.6% ± 4.8% lower among LOI replicates (estimate = -0.176, *p* =0.000345), whereas the influence of tidal exchange was 64.1% ± 26.5% greater (estimate = 0.215, *p* = 0.0376). Finally, while treatments were significant for both methods, differences between exclusion and cage control treatments were 40.2% lower among LOI replicates (estimate = -

0.223, $p = 0.00914$) and differences between *H. whitmaei* and cage control treatments were 61.1% greater (estimate = 0.207, $p = 0.0152$).

Pore Water Analysis

Similar to OM, pore water chemistry was significantly influenced by precipitation and tidal exchange. Throughout the experiment, pore water salinity averaged 31.61 ± 0.69 ppt (Fig. 6a). Changes in salinity were primarily driven by precipitation, increasing by 13% per mm rainfall (estimate = 0.056, $p < 0.0001$; Table 2; Fig. 7a). Additionally tidal exchange had a marginally significant but positive relationship with salinity (estimate = 0.0770, $p = 0.098$); however, the random effect of cage was significant. Together, these findings suggested that pore water salinity was influenced more by precipitation compared to groundwater, with notable heterogeneous groundwater input throughout the study site as evidenced by random effects at the cage level (Supplemental Table S1). Unsurprisingly, no differences were measured in the proportional change in salinity between sea cucumber treatments.

Ammonium concentrations within sediment pore water averaged 132.18 ± 6.85 µg/L (Fig. 6b). In contrast to salinity, proportional changes in pore water ammonium were most strongly influenced by tidal exchange and were not associated with precipitation (Fig. 7b). We revealed a 58% decrease in proportional change in ammonium per m tidal exchange (estimate = -0.378, $p = 0.0007$). Neither changes in salinity nor changes in organic matter were associated with changes in pore water ammonium concentrations (Fig. 3). Finally, while treatment had no significant effect on ammonium, ammonium tended to be greater in our high-density treatments (Fig. 7b).

IV. Discussion

The dramatic rise in sea cucumber harvesting since the 1970s has generated international concern for the health of depleted reefs due to the cascading consequences of OM accumulation on coral reef ecosystems. In this study, we confirmed that sea cucumbers act as important buffers against natural pulses in OM and expanded upon the existing knowledge base in several ways. Sea cucumbers are well known to process OM and enhance nutrient cycling; however, few studies have examined their role in situ. Of those few studies, almost all have focused on a single species (*H. scabra*) and none have compared the influences of different species, examined changes in nutrient concentrations, or accounted for natural fluctuations in environmental conditions. The present study addressed these knowledge gaps by: i) comparing the influences of holothuroids at depleted, natural, and high densities on both sediment OM and pore water ammonium, ii) comparing two species with differing body sizes, iii) using two methods to cross-validate our findings for changes in sediment OM, and iv) integrating environmental covariates in our analyses. One key finding was the disproportionate role the larger species, *H. whitmaei*, played in processing three times more OM compared to a similar biomass of the smaller species, *H. atra*. However, these and other treatment effects would have been diminished or masked without accounting for environmental covariates that helped scale our experimental effect sizes.

Changes in OM were primarily influenced by precipitation and (to a lesser degree) tidal exchange and, by accounting for these variables, the consequences of sea cucumber removal on sediment heath became clear. In exclusion plots, changes in OM were on average 84.1% greater than for plots at background holothuroid density, and were between 98% and 128% greater than high-density cages that were representative of coral reefs with limited human presence. In support, Lee et al. (2018) demonstrated a two-fold increase in sediment oxygen consumption where the burying sea cucumber, *H. scabra,* was excluded. Our findings reinforce their conclusion that sea cucumber removal would first cause OM to accumulate in the sediment, which would subsequently lead to depletion of interstitial oxygen through microbial and infaunal activity. Further, exclusion of sea cucumbers has also been linked with greater sediment chlorophyll-*a* (Plotieau et al. 2013, Viyakarn et al. 2020) and bacterial abundance (Moriarty et al. 1985, Plotieau et al. 2013), likely due to decreased grazing pressure. We synthesise that the aforementioned conditions associated with sea cucumber exclusion offer competitive advantages to algae and (cyano)bacteria over seagrasses and corals, with consequences for nutrient cycling (Silveira et al. 2017), habitat complexity (McManus and Polsenberg 2004, Burkholder et al. 2007), and disease prevalence (Grayson et al. 2022). Given the suite of detrimental effects associated with OM loading (Kline et al. 2006, Fabricius 2010, Brocke et al. 2015), the overharvest of sea cucumbers may have additional consequences for habitat condition, yet studies formally linking sea cucumber densities to ecosystem outcomes remain limited despite their importance.

OM accumulation was expected to decline in high density treatments compared to background densities; however, OM only declined in cages containing the larger species, *H. whitmaei*. Our findings likely result from a non-linear relationship between body size and resource access (Lokrantz et al. 2008, Lange et al. 2020) and/or metabolism (Brown et al. 2004, Durden et al. 2019). Larger individuals may be able to access organic-rich particulates deeper in the sediment or particulates of greater size. In agreement with metabolic ecology, increased resource access would help support the disproportionately-large energy demand needed for both maintenance and growth that is characteristic of species of greater body size (Lokrantz et al.

2008). In this study we compare only two species; however, at present 65 holothuroid species of varying body sizes have been described for Guam (Michonneau et al. 2013, Kerr et al. 2017), and no studies have compared holothuroid species sizes and ecosystem functions. Further work will be necessary to determine if a non-linear relationship is consistent throughout the family *Holothuroidea*.

The trends we described regarding OM were cross-validated using two common methods of OM determination that allowed us to account for the inherent benefits and potential shortcomings of each method. LOI, which is one of the most common methods for determining organic matter content in marine sediments, can process large batches at a single time; however, for sediments derived from calcareous organisms like corals, particulate decarbonation can lead to significant overestimation of organic matter when compared to more-precise methods (Purcell 1997, Frangipane et al. 2009). Additionally, LOI requires the use of specialized equipment such as a muffle furnace, which may not be as feasible for small-scale monitoring agencies. The use of HPD circumvented the issue of decarbonation, and these data better represented typical values for coral reef sediments determined by high precision analytical methods (Purcell 1997). However, HPD requires additional time, labour, and the handling of a corrosive and oxidising reagent. Despite variations between LOI and HPD, both methods uncovered similar trends regarding treatments. Thus, while comparing the results of studies using different methods should be avoided, both prove effective tools for analysing rates of change in OM.

Through the metabolism of OM, holothuroids redistribute inorganic nutrients such as ammonium into the sediment surface interface which helps fuel benthic productivity. Here, we found that changes in pore water ammonium were strongly influenced by tidal exchange, agreeing with previous studies (Montani et al. 1998, Tanaka and Choo 2000), although changes in ammonium were not influenced by environmental factors or sea cucumber treatments. Given that ex situ studies have shown localised increases in ammonium concentrations from holothuroids (Uthicke and Klumpp 1998, Uthicke 2001b, MacTavish et al. 2012), it is likely that nutrients mineralized by sea cucumbers in our cages were redistributed more rapidly than could be detected through biweekly sampling. Further research will be necessary to evaluate how changes in OM relate to nutrient excretion using finer scale and more frequent measurements, or through ecosystem attributes such as seagrass growth (e.g. Wolkenhauer et al. 2010) and microalgal growth (e.g. Uthicke et al. 1999) that respond differently to nutrient enrichment (McManus and Polsenberg 2004, Burkholder et al. 2007).

Healthy populations of detritivores including sea cucumbers are crucial for removing waste matter from reefs and facilitating the transfer of energy to different trophic levels. Consequently, maintaining healthy sea cucumber populations may be critical for avoiding the consequences of OM loading and nutrification, which tend to favour algal dominance over slow-growing, habitat-forming taxa like corals and sea grasses (McManus and Polsenberg 2004, Lapointe et al. 2019). In support, Houk and colleagues (2013) found greater seagrass to macroalgal ratios in areas of high sea cucumber abundance. However, we demonstrate that the benefits provided by sea cucumbers depend on body size and not just biomass. Unsustainable harvesting of large sea cucumbers is expected to have disproportionate impacts to the affected reef habitats. These findings will help support an EAF for sea cucumber management, considering not only population densities but ecosystem condition. Regular monitoring which documents environmental condition, sea cucumber community composition, and population density, will establish what areas and populations require additional protection. In regions where sea cucumber fisheries provide important sources of income, it will be critical to establish and enforce fisheries management plans that preserve the diversity and size structure of sea cucumber populations, and to set harvesting limits that align with their ecosystem functions.

V. Tables

Table I.

		Sample level	*Cage level*
		Dependent variable	
		log (% OM)	$\log (OM_t / OM_0)$
Treatments	Exclusion	0.034	**0.265****
		(0.069)	(0.092)
	Holothuria atra	-0.014	-0.064
		(0.068)	(0.092)
	Holothuria whitmaei	-0.019	**-0.249***
		(0.068)	(0.092)
	Natural control	0.012	-0.068
		(0.069)	(0.092)
Covariates	log (Precipitation)	**0.216*****	**0.342*****
		(0.034)	(0.034)
	Tidal exchange	-0.135	0.099
		(0.072)	(0.072)
Variation associated with method	Method (LOI)	-0.0003	**-0.788****
		(0.241)	(0.244)
	Exclusion : Method (LOI)	-0.011	**-0.223****
		(0.076)	(0.084)
	Holothuria atra : Method (LOI)	0.023	0.064
		(0.076)	(0.084)
	Holothuria whitmaei : Method (LOI)	0.023	**0.207***
		(0.076)	(0.084)
	Natural control : Method (LOI)	0.0004	0.103
		(0.076)	(0.084)
	log (Precipitation) : Method (LOI)	-0.082	**-0.176*****
		(0.048)	(0.048)
	Tidal exchange : Method (LOI)	**0.382*****	**0.215***
		(0.102)	(0.102)
	Constant	-0.125	**2.016*****
		(0.174)	(0.179)
	Observations	591	160
	Log likelihood	-142.842	24.303
	AIC	317.842	-16.605
	BIC	387.794	32.597
	R^2	0.739	0.773

Note: Asterisks indicate the degree of significance
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table II.

		Dependent variable	
		log ($Salinity_t/Salinity_0$)	log ($NH_{4\,t}$/ $NH_{4\,0}$)
Treatments	Exclusion	-0.054 (0.045)	-0.122 (0.144)
	Holothuria atra	0.010 (0.045)	0.132 (0.144)
	Holothuria whitmaei	-0.044 (0.045)	0.097 (0.144)
	Natural control	0.002 (0.045)	-0.119 (0.144)
Covariates	log (Precipitation)	**0.056**** (0.021)	0.011 (0.049)
	Tidal exchange	0.077 (0.046)	**-0.378***** (0.106)
	Constant	-0.0187 (0.110)	**0.978***** (0.264)
	Observations	80	80
	Log likelihood	47.924	-17.997
	AIC	-77.847	53.994
	BIC	-56.409	75.432
	R2	0.230	0.443

Note: Asterisks indicate the degree of significance
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

VI. Figures

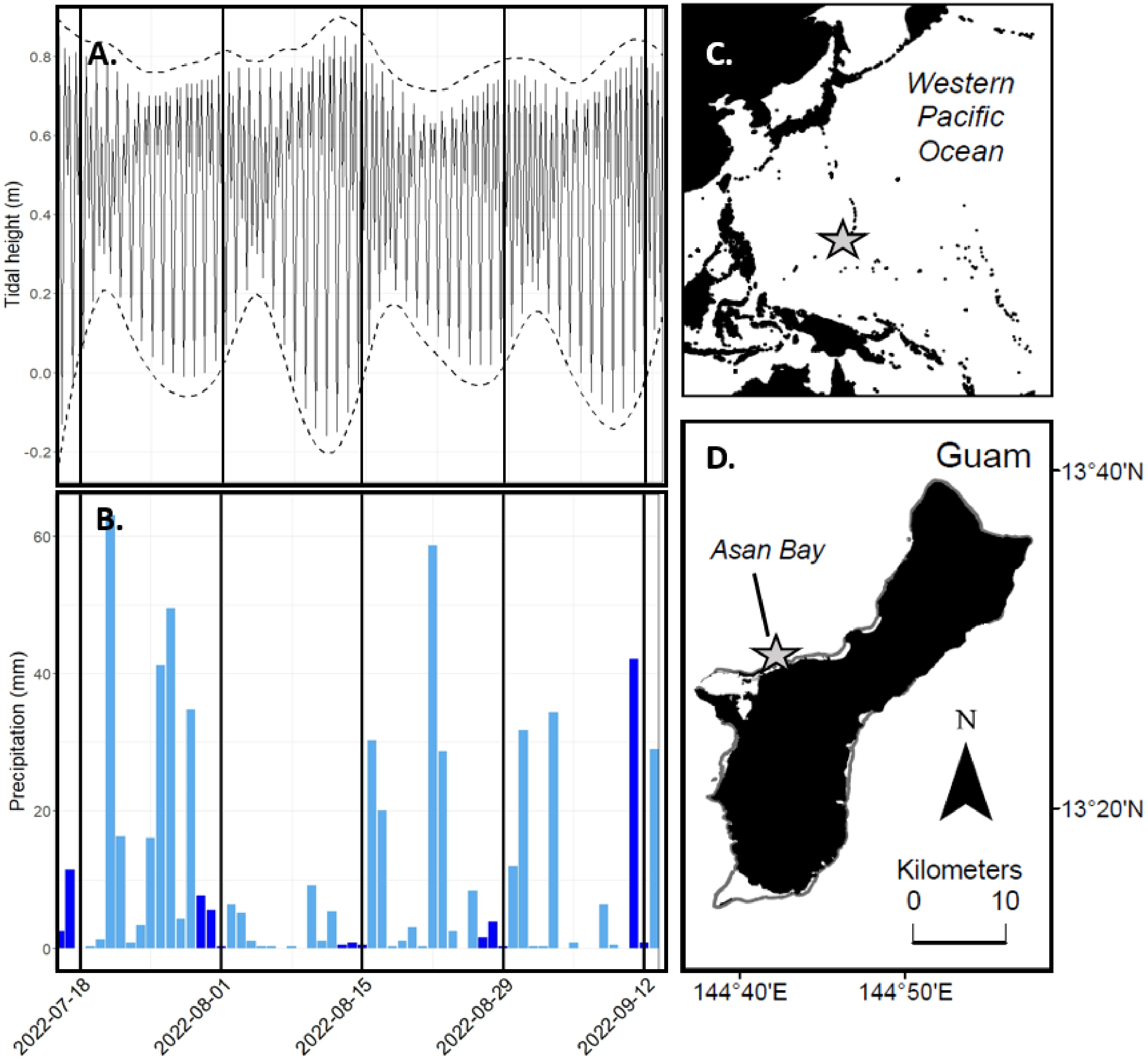


Figure 1.

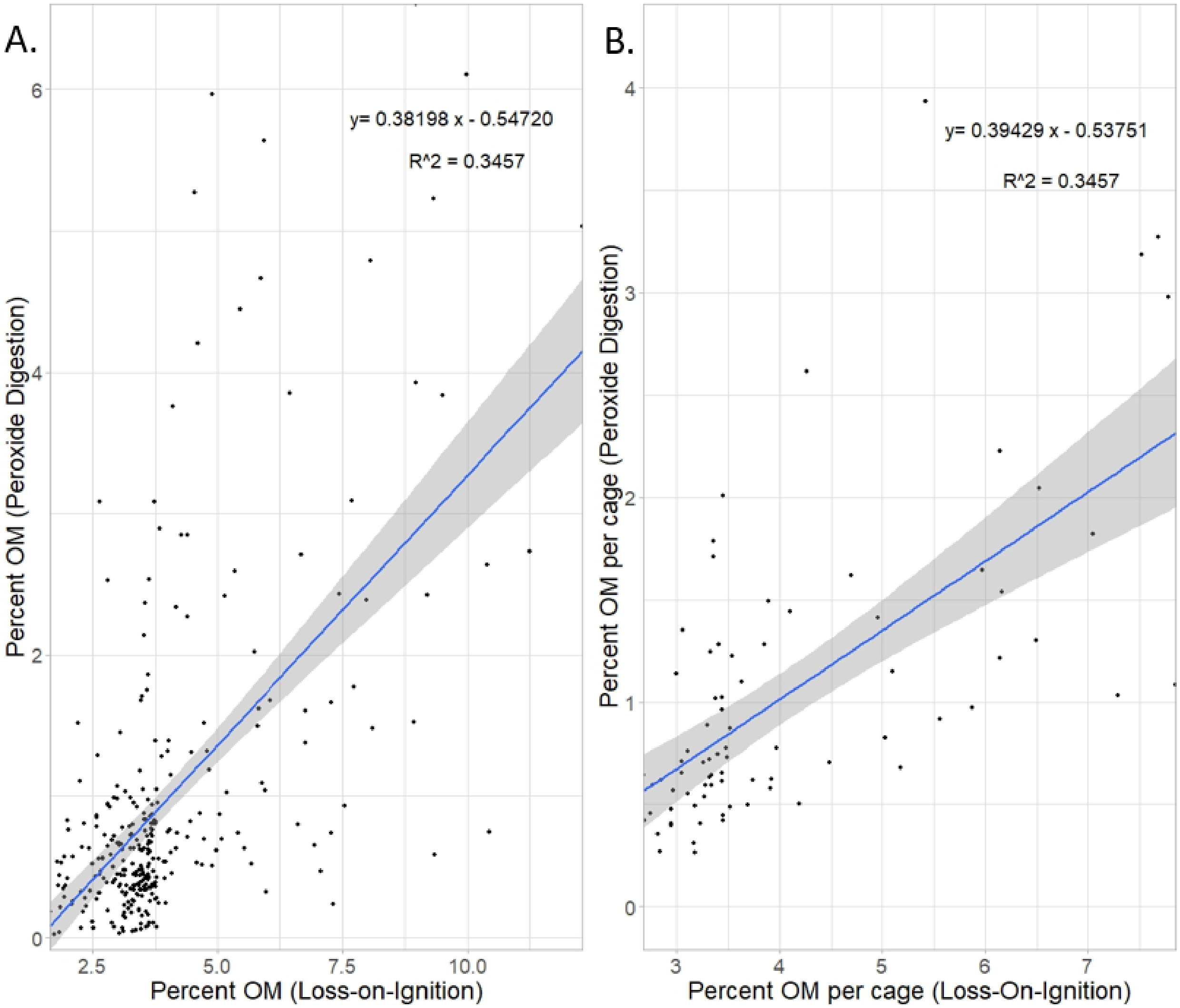
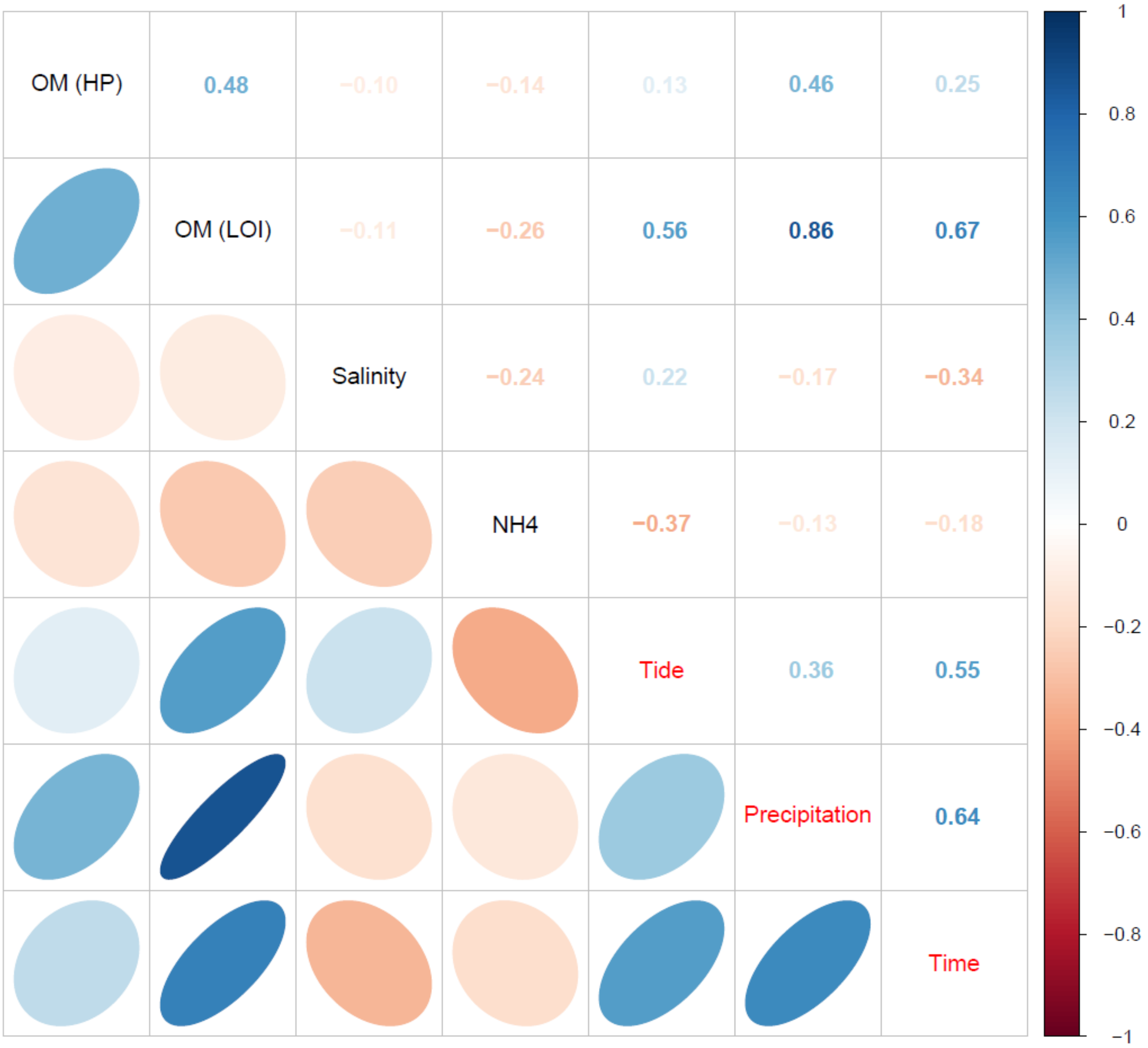

A.
y= 0.38198 x - 0.54720
R^2 = 0.3457
Percent OM (Peroxide Digestion)
Percent OM (Loss-on-Ignition)
0
2
4
6
2.5
5.0
7.5
10.0
B.
y= 0.39429 x - 0.53751
R^2 = 0.3457
Percent OM per cage (Peroxide Digestion)
Percent OM per cage (Loss-On-Ignition)
0
1
2
3
4
3
4
5
6
7

Figure 2.



OM (HP)
0.48
−0.10
−0.14
0.13
0.46
0.25
OM (LOI)
−0.11
−0.26
0.56
0.86
0.67
Salinity
−0.24
0.22
−0.17
−0.34
NH4
−0.37
−0.13
−0.18
Tide
0.36
0.55
Precipitation
0.64
Time
1
0.8
0.6
0.4
0.2
0
−0.2
−0.4
−0.6
−0.8
−1

Figure 3.

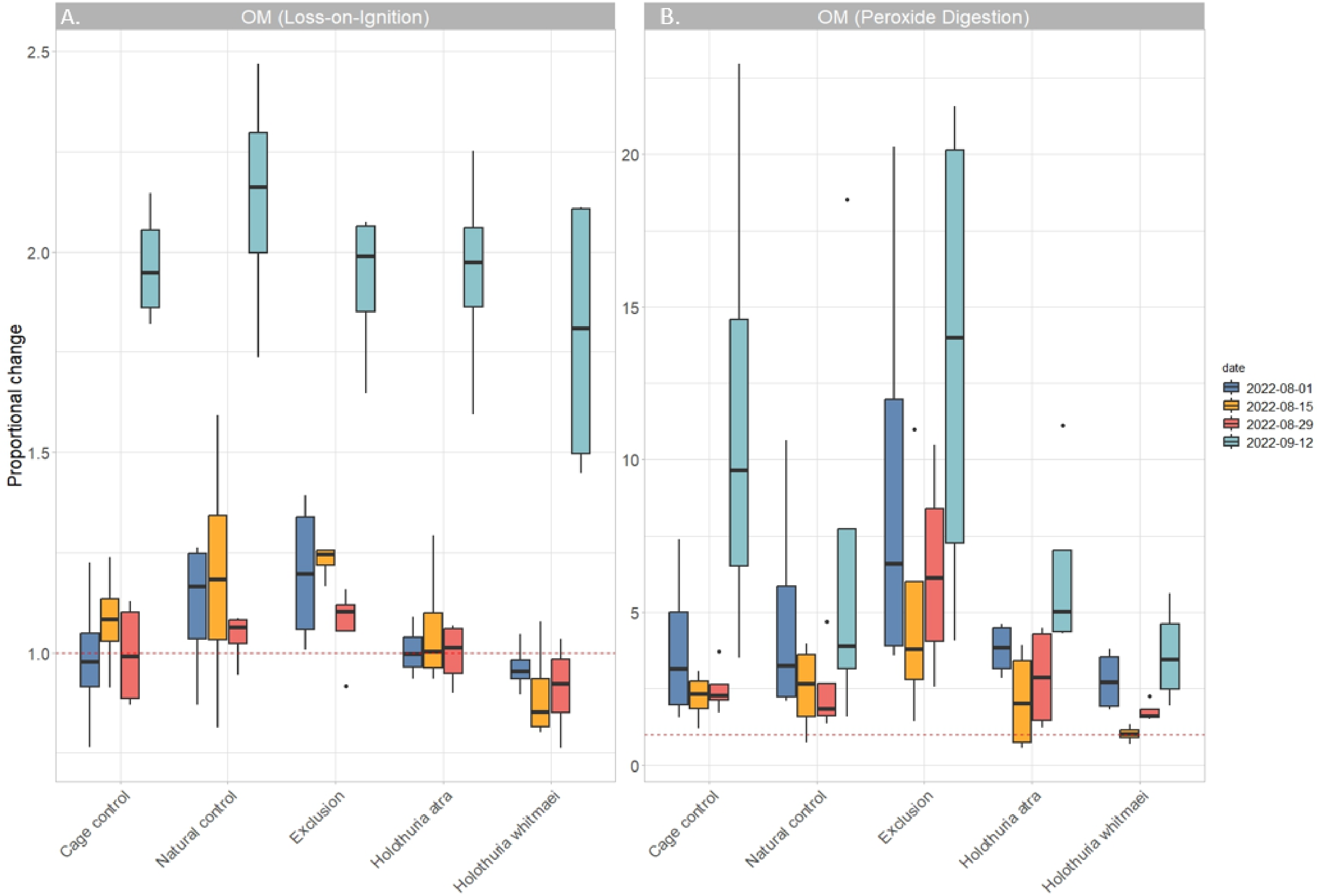

A.
OM (Loss-on-Ignition)
B.
OM (Peroxide Digestion)
Proportional change
2.5
2.0
1.5
1.0
20
15
10
5
0
Cage control
Natural control
Exclusion
Holothuria atra
Holothuria whitmaei
date
2022-08-01
2022-08-15
2022-08-29
2022-09-12

Figure 4.

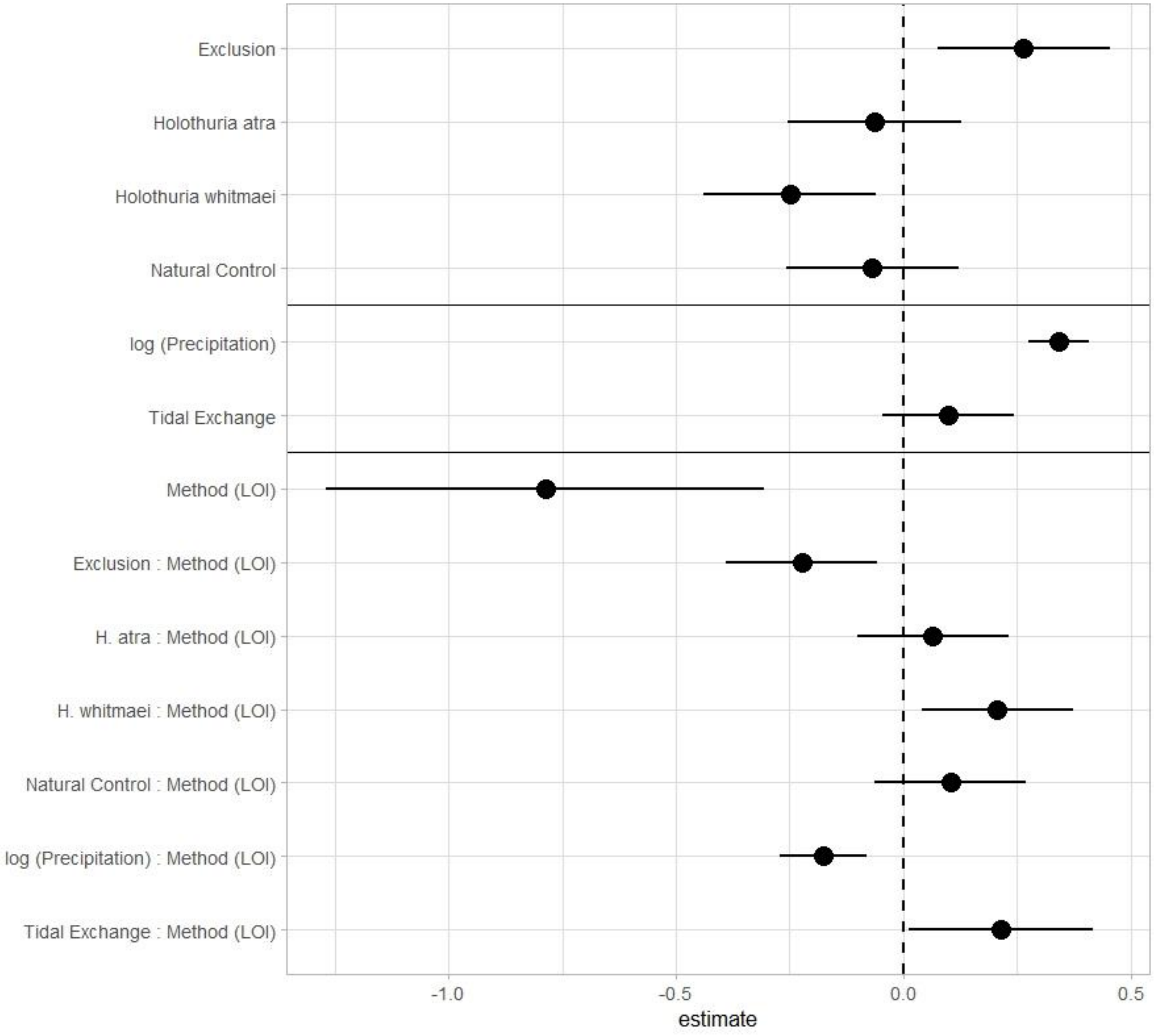

Exclusion
Holothuria atra
Holothuria whitmaei
Natural Control
log (Precipitation)
Tidal Exchange
Method (LOI)
Exclusion : Method (LOI)
H. atra : Method (LOI)
H. whitmaei : Method (LOI)
Natural Control : Method (LOI)
log (Precipitation) : Method (LOI)
Tidal Exchange : Method (LOI)
-1.0
-0.5
0.0
0.5
estimate

Figure 5.

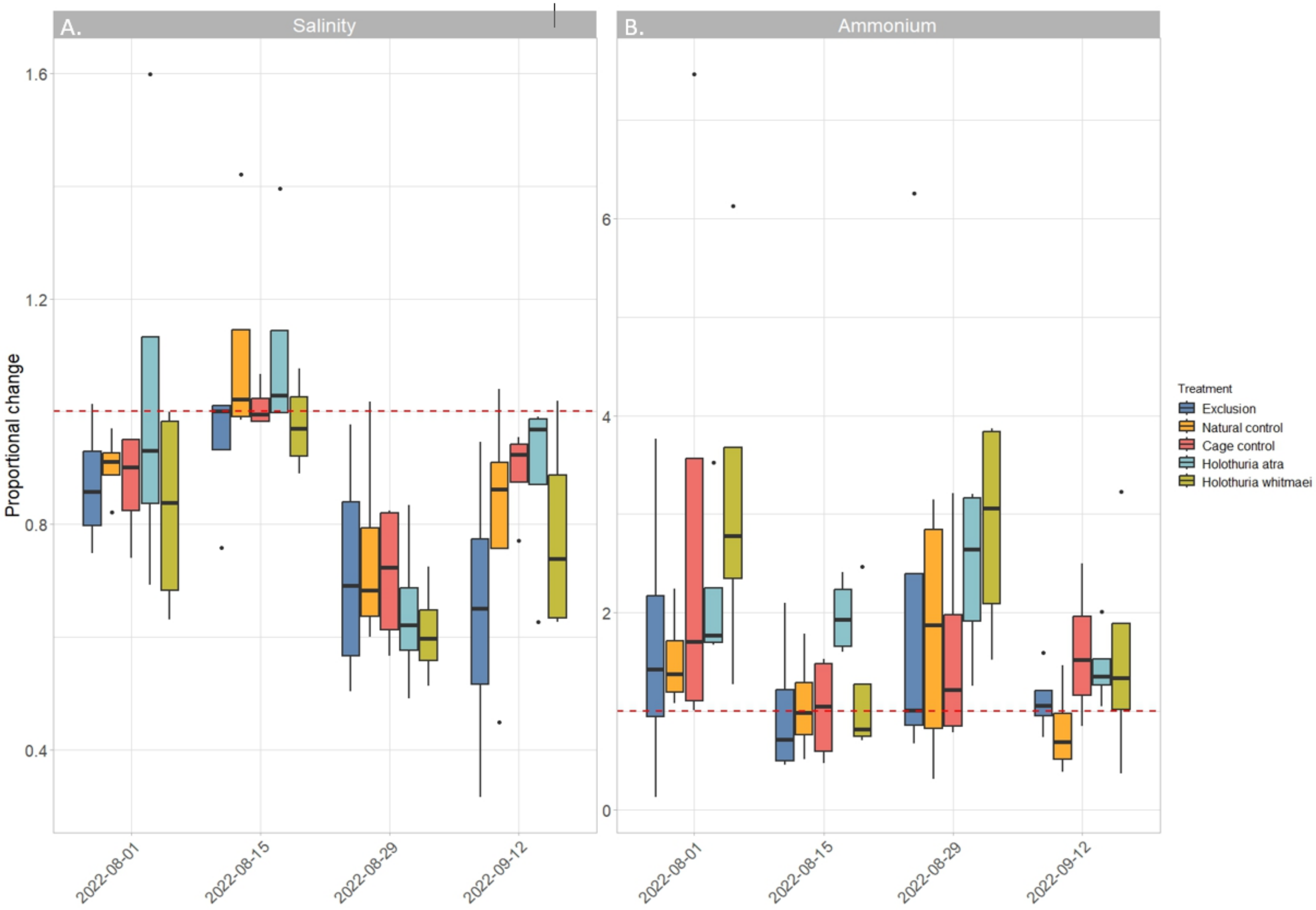

A.
Salinity
B.
Ammonium
Proportional change
1.6
1.2
0.8
0.4
6
4
2
0
2022-08-01
2022-08-15
2022-08-29
2022-09-12
Treatment
Exclusion
Natural control
Cage control
Holothuria atra
Holothuria whitmaei

Figure 6.

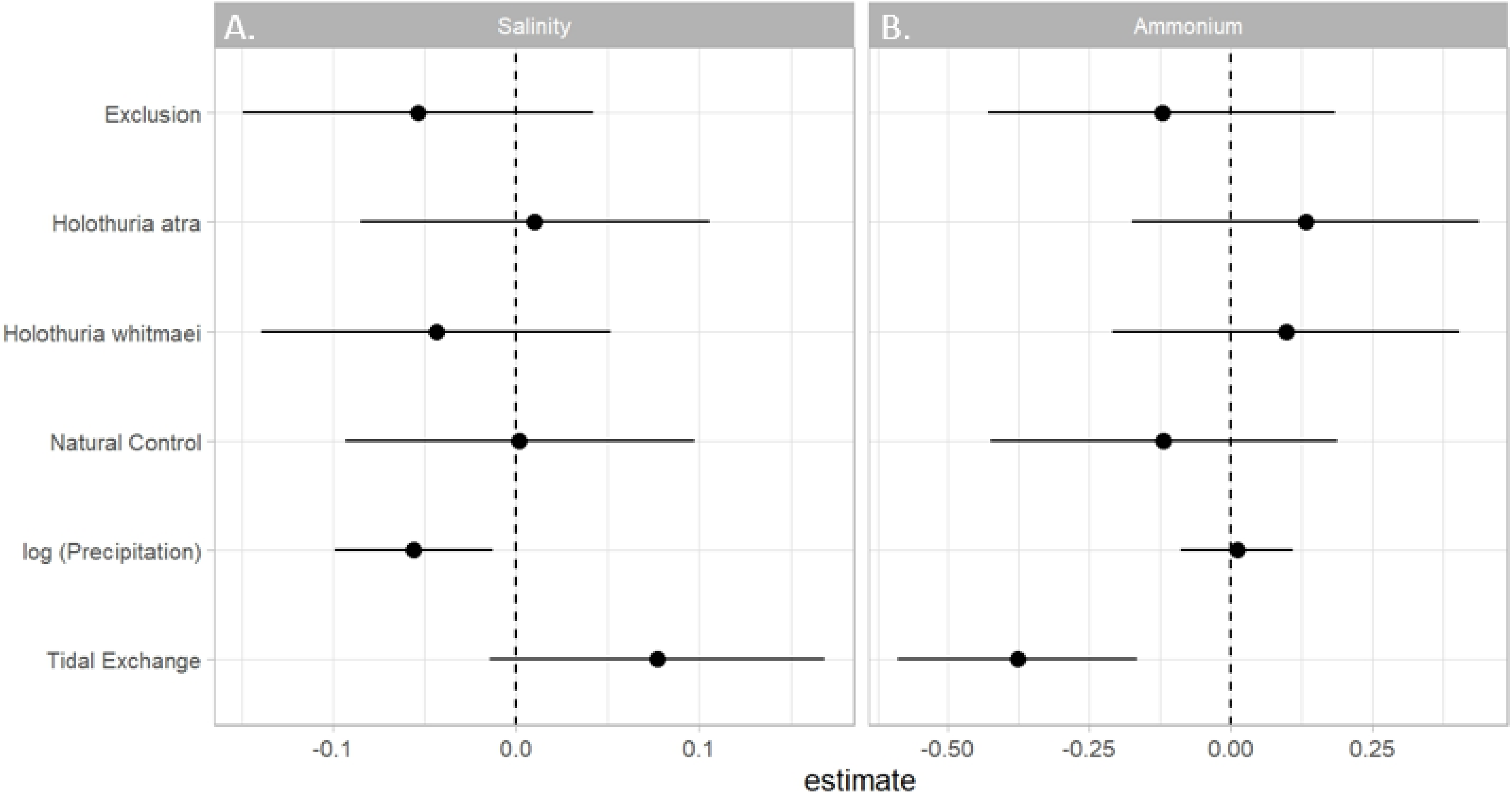

A.
Salinity
B.
Ammonium
Exclusion
Holothuria atra
Holothuria whitmaei
Natural Control
log (Precipitation)
Tidal Exchange
-0.1
0.0
0.1
-0.50
-0.25
0.00
0.25
estimate

Figure 7.

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