Habitat Enhancement Over Trophic Control: Spatial Patterns in Benthic Invertebrate Production Around Artificial Reefs

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Abstract

Artificial reefs (ARs) are a widely used tool to enhance marine habitat and fisheries productivity, yet their broader ecological effects on adjacent benthic communities remain poorly understood. While reef-associated fishes are known to influence surrounding habitats through both nutrient subsidies and predation, it remains unclear whether these processes generate spatially structured gradients in invertebrate production and biomass. To address this, this study quantified prey item invertebrate production, biomass, and community composition along distance gradients from five ARs in The Bahamas. Prey item production and biomass declined sharply and non-linearly with distance, peaking at 1m and stabilizing beyond 3m, yet the proportional contribution of prey item invertebrates to the broader community remained constant across distances. Fish production and biomass were not consistent predictors of invertebrate patterns across distances. These results indicate that ARs generate spatially constrained hotspots of benthic productivity driven primarily by bottom-up habitat processes rather than top-down fish predation, enhancing overall prey availability in adjacent seagrass ecosystems without restructuring community composition. These findings highlight the importance of spatial scale in reef-seagrass connectivity and have direct implications for AR placement and coastal ecosystem management.

1. Introduction

Coral reef ecosystems are among the most biodiverse and productive environments on Earth, yet they are increasingly threatened by climate change, ocean acidification, pollution, and coastal development (Hughes et al., 2017; Moberg & Folke, 1999). As coral cover declines globally due to these stressors, the ecological functions these reefs provide, such as habitat structure, nutrient cycling, and support for biodiversity, are being lost at an alarming rate (Graham & Nash, 2013). In response, artificial reefs (ARs) have emerged as a widely adopted management tool aimed at mitigating these losses. ARs are commonly known as human-made structures that mimic patch reefs to support coral reef ecosystems. These structures provide a hard substrate in otherwise soft-bottom environments, ranging from old tires to cinder blocks, in order to create structural complexity that attracts and supports marine life from all trophic levels (Baine, 2001). ARs have been increasingly deployed and built worldwide to support fisheries enhancement, habitat restoration, biodiversity conservation, and even ecotourism (Seaman, 2007).

While much of the research on ARs has focused on their role in increasing community biodiversity and abundance on the reef, their ecological influence extends beyond the structure itself into surrounding benthic habitats. Artificial reefs are frequently located adjacent to seagrass beds, which are highly productive ecosystems that support diverse invertebrate communities, forming the base of coastal food webs (Orth et al., 2006). These benthic invertebrates represent an important pathway through which production is transferred to higher trophic levels, particularly reef-associated fishes. Specifically, invertebrates that are susceptible prey items, such as small crustaceans and polychaetes, therefore represent a critical link between benthic

production and secondary consumers (DeFelice & Parrish, 2003). Understanding the spatial variation in these invertebrate communities is essential for evaluating energy flow and trophic dynamics in AR systems.

Within these food webs, reef-associated fishes can influence benthic communities through both bottom-up and top-down pathways (Allgeier et al., 2017). Through excretion, fishes recycle essential nutrients such as nitrogen and phosphorus, enhancing primary production in nutrient-limited ecosystems (Schindler & Eby, 1997). In tropical ecosystems, these nutrient subsidies can extend beyond reef boundaries into adjacent seagrass habitats, increasing benthic production (Allgeier et al., 2013). As a result, seagrass areas close to reefs may experience elevated resource availability that can indirectly influence benthic invertebrate production.

In addition to these bottom-up pathways, reef-associated fishes also influence trophic linkages through predation on benthic invertebrates. While top-down effects can be strong at the species level, they are often weak or inconsistent at the community level. This is likely due to high species diversity and complex trophic interactions that buffer strong predatory control, as well as variation in predator identity, habitat structure, and spatial scale (Hammerschlag-Peyer et al., 2013; Heck Jr. et al., 2000). Together, these findings suggest that reef fish communities can influence adjacent ecosystems through both nutrient-mediated increases in productivity and spatially variable predation pressure, potentially producing non-linear or non-intuitive patterns in invertebrate distribution across reef-seagrass gradients.

These spatial patterns are further shaped by the movement behavior of reef fishes, which can determine how far reef-derived effects are extending into adjacent habitats. Many species, such as the white grunt, exhibit diel migrations between reef shelter sites and seagrass foraging grounds, while others remain more reef associated (Ogden & Ehrlich, 1977). This behavioral

distinction is ecologically significant because species that forage off the reef are likely exerting top-down pressure at greater distances from the structure, while reef-resident species may concentrate their effects closer to the reef, creating the potential for spatially partitioned trophic impacts that vary with consumer identity. Together, all of these processes suggest that reef-associated fishes may generate spatial gradients in benthic invertebrate communities that reflect both nutrient enrichment and species-specific foraging behavior across reef-seagrass boundaries.

Despite recognition that reef-associated fishes link reef and seagrass ecosystems through nutrient recycling and predation, few studies have quantified how these processes are structuring AR benthic invertebrate production and biomass (Rouse et al., 2020). In particular, it remains unclear how prey item invertebrates are represented across reef-seagrass gradients, how these patterns compare with those of the broader invertebrate community, and how reef-associated fishes modify these patterns through bottom-up and top-down processes.

This study addresses these questions by examining (1) how the production and biomass of prey item invertebrates vary with distance from artificial reefs, and how these patterns compare to the broader invertebrate community, and (2) how reef-associated fish influence prey item invertebrate production and biomass across this spatial gradient. This study hypothesized that prey item invertebrate production and biomass will be highest near reefs and decline with distance, reflecting increased habitat complexity and nutrient enrichment associated with reef proximity, and that their relative contribution to the broader invertebrate community will similarly decrease with distance. In concurrence, this study further hypothesized that reef-associated fishes will reduce prey item invertebrate production and biomass through

top-down predation, with stronger effects where mobile foragers, such as white grunts, are foraging off the reef.

2. Methods

2.1: Field Data Collection

Data collection took place in The Bight of Old Robinson, Abaco, The Bahamas, a shallow bay located on the southern side of Abaco Island (Figure 1). Sampling was conducted at five ARs (LH1, LH2, LH4, LH5, and LH6) located within The Bight during May-June 2021 (Figure 2). At each reef, a single north-facing transect was established extending away from the AR. Invertebrate samples were collected at multiple distances along each transect (1, 2, 3, 4, 6, 8, 12, and 20m).

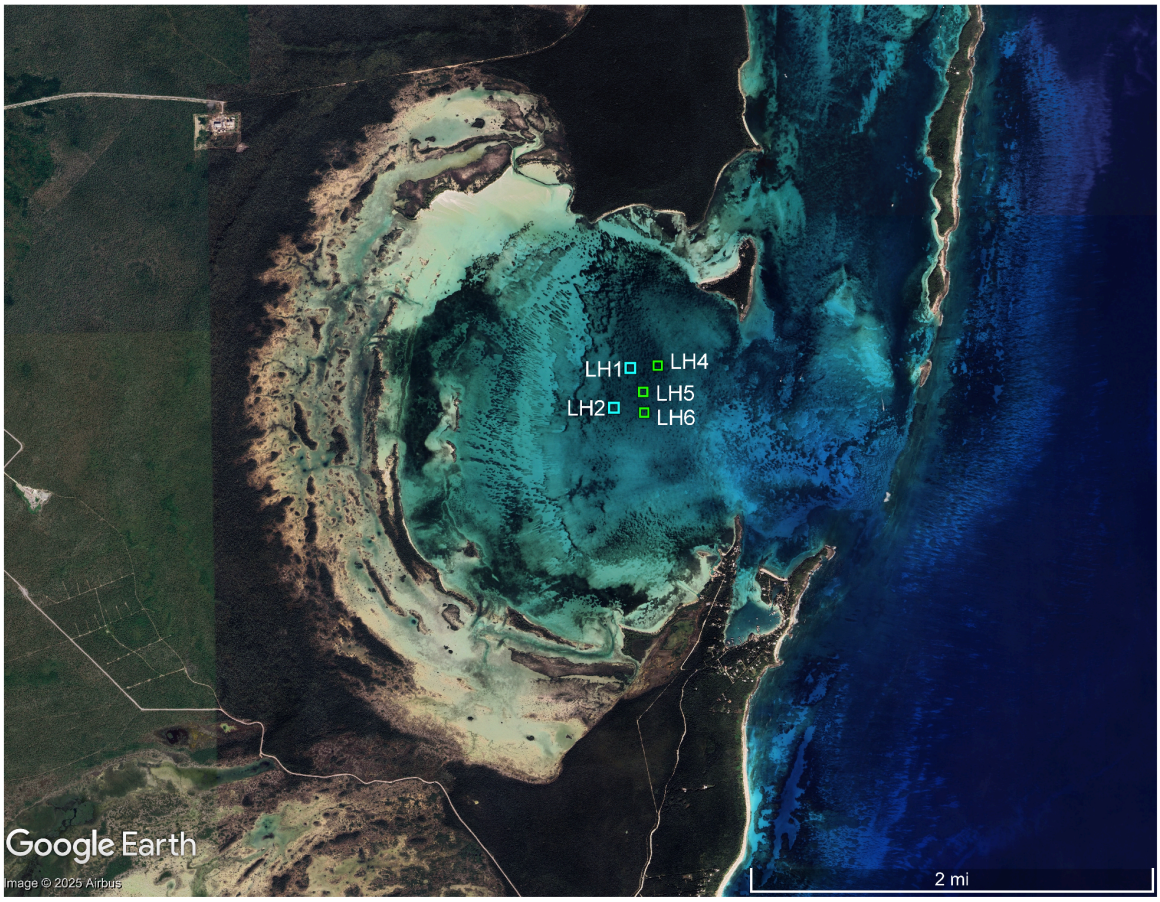


Figure 1: Map of study site, The Bight of Old Robinson, Abaco, The Bahamas. Square boxes representing the five artificial reefs used in this study. Courtesy of Jacob Allgeier.

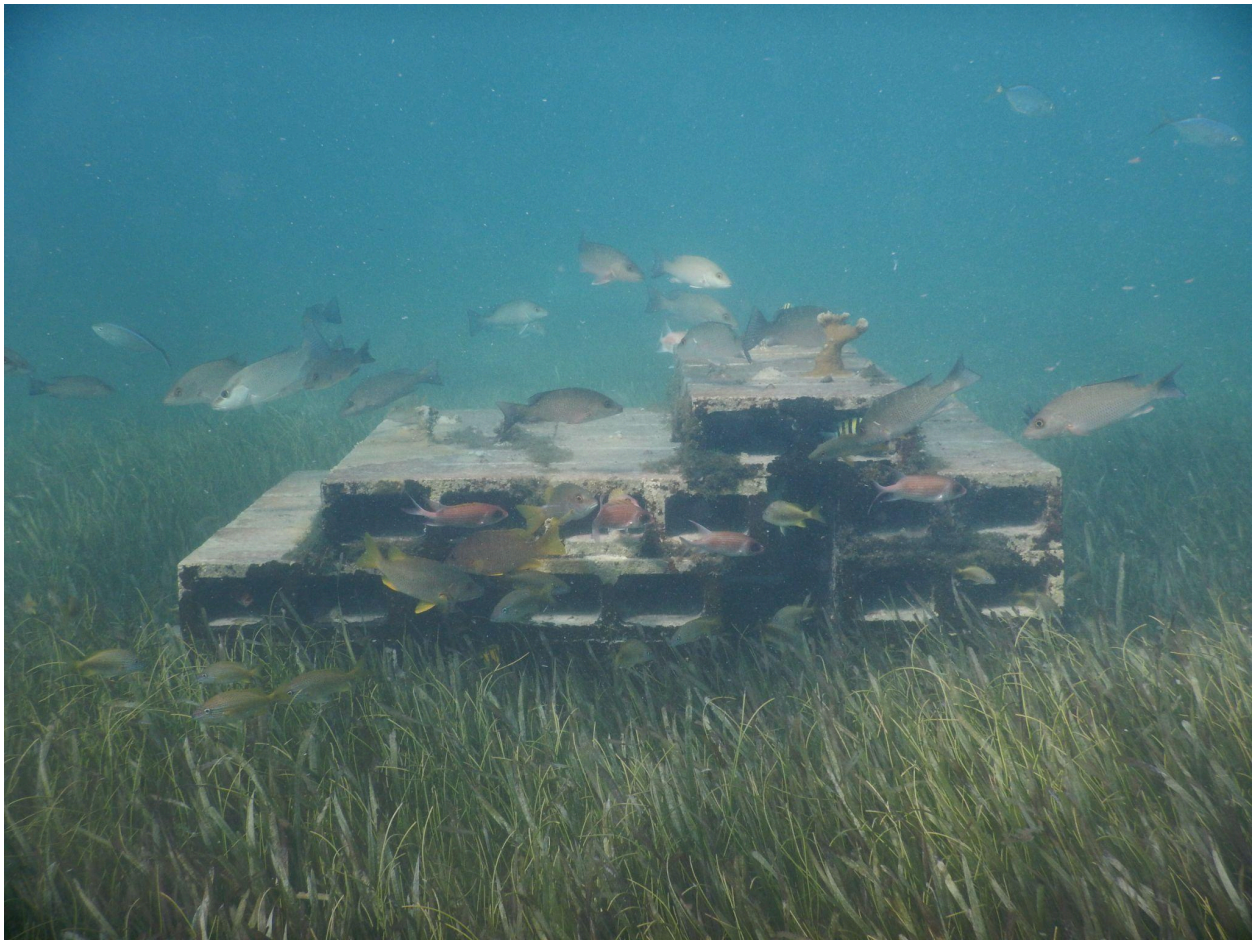


Figure 2: Image of artificial reef LH2. Courtesy of Jacob Allgeier.

At each distance, benthic material such as sediment, seagrass, detritus, and invertebrates was collected using a suction dredge system. A hose dredged the top sediment from a 0.3421 m^2 area at each distance and reef, for a total of 40 samples. Samples were collected underwater in the vacuum apparatus, and were then transferred into Ziploc bags. Sampling time was not standardized, and instead was conducted until the area was considered exhaustively sampled by researchers.

Collected samples were stored either through freezing or being placed in ethanol. Variation in preservation occurred across reefs, including inefficient ethanol preservation and

partial sieving of samples in the field. These differences may have impacted the retention of soft bodied individuals.

Fish surveys were conducted by one or two observers around ARs in either June or December of 2021, based on the procedures described by Allgeier et al. (2013, 2018). All fish were identified to the lowest possible taxonomic level and the total length was estimated to the nearest centimeter. Transient and cryptic species were removed from surveys. All surveys were conducted at least one calendar year following reef construction to ensure sufficient time for fish colonization. Fish production values were obtained from Esch et al. (in review). Where multiple surveys were conducted on the same reef within the same month, production and biomass estimates were averaged across survey dates prior to analysis.

2.2: Laboratory Methods

Frozen samples were thawed before processing. Each sample was rinsed through a series of sieves (12.5mm, 8mm, 5.6mm, 4mm, 2.8mm, 2mm, 1.4mm, 1mm, 710μm, and 500μm) in order to separate the material into size classes. Samples were divided into a "large" group (12.5mm-2.8mm) and a "small" group (2mm-500μm).

For the large group, seagrass ("green material") and detritus were separated into Ziploc bags. Invertebrates were removed, preserved in ethanol, and counted and identified to the lowest taxonomic group possible. For the small group, samples were preserved in ethanol with a rose bengal stain to aid in organism detection. Samples were sorted either with the naked eye or under a microscope, and invertebrates were organized into four major taxonomic groups (bivalves, gastropods, crustaceans, and others). Crustaceans were further classified into intermediate

morphological groups (shrimp, hermit crabs, other crabs, amphipods, and other crustaceans), while bivalves, gastropods, and other taxa were not subdivided further.

Sorted invertebrates were placed into pre-labeled tins by group and sample and dried using a freeze dryer for a minimum of 24 hours to remove all moisture. Freeze drying was done to ensure that mass measurements reflected dry tissue weight rather than water content.

Following the freeze drying, samples were transferred to pre-weighted aluminium tins and weighed using a microbalance to obtain a dry weight (DW). Each tin containing a group of individuals was weighed and values were recorded. Samples were then placed in crucibles and combusted in a muffle furnace overnight to remove organic material. After combustion, samples were re-weighted in the same tins to obtain a post-ash mass. The difference between DW and post-ash mass was used to calculate the ash-free dry weight (AFDW), which represents organic biomass (AFDW = Dry Weight - Post-Ash Weight). AFDW was used as the primary measurement of invertebrate biomass.

Total invertebrate biomass at each sample was calculated by summing AFDW across all groups. Secondary production was estimated from biomass using established production to biomass relationships from Esch et al. (in review), allowing comparisons of energy availability across distances from reefs.

Prey item invertebrates were classified based on published diet data of reef-associated fishes. Classifications were informed by trophic ecology studies describing “shelled invertebrate feeders,” defined as fishes capable of consuming hard-bodied prey such as gastropods, bivalves, echinoderms, and crustaceans through specialized jaw or pharyngeal structures (Randall, 1967). Fish survey and production data were cross-referenced with these feeding guilds to identify dominant consumers, including wrasses, porcupinefish, and grunts.

Although gastropods and bivalves are included in the diets of some reef fishes, quantitative stomach content analyses indicate that these taxa contribute relatively little to the diets of key species in this system, particularly grunts (<6% contribution; Randall, 1967). Additionally, fishes that consume higher proportions of shelled invertebrates, such as some wrasses and porcupinefish, represented a relatively small proportion of total fish production and biomass in this study. Therefore, inclusion of these taxa would likely overestimate their ecological importance as prey.

Based on these considerations, prey item invertebrates were defined to include taxa that represent primary and consistent components of reef fish diets, such as mobile crustaceans and other soft-bodied benthic invertebrates, while gastropods and bivalves were excluded.

2.3: Statistical Analysis

All statistical analyses were conducted in RStudio version 4.4.3. Prior to all analyses, residuals were assessed for normality using the Shapiro-Wilk normality test and the Lilliefors test. Visual inspection of residual diagnostic plots including residuals vs. fitted, Q-Q plots, scale-location, and residuals vs. leverage plots was also used to confirm model assumptions were met. Where normality was violated, appropriate transformations were applied as described below.

To examine how prey item invertebrate production and biomass varied with distance from artificial reefs, Analysis of Covariance (ANCOVA) models were fit with reef identity (referring to LH1, LH2, LH4, LH5, and LH6) as a fixed factor and log-transformed distance as a continuous predictor. Distance was log-transformed to account for a normality violation. An interaction term between reef identity and log-transformed distance was included to assess

whether the effect of distance differed among reefs. Separate models were run for prey item invertebrate production and biomass as response variables. The model used for production was: aov(Prey Item Production ~ Reef Identity + log(Distance) + Reef:log(Distance)). The model used for biomass was: aov(Prey Item Biomass ~ Reef Identity + log(Distance) + Reef:log(Distance)).

To assess whether the relative contribution of prey item invertebrates to the total invertebrate community changed with distance, additional ANCOVA models were run using the log-transformed ratio of prey item production or biomass to other invertebrate production or biomass as the response variable. The ratio and the distance variable were log-transformed to meet normality assumptions. The model used for production was: aov(log(Prey Item Production Ratio) ~ Reef + log(Distance) + Reef:log(Distance). The model used for biomass was: aov(log(Prey Item Biomass Ratio) ~ Reef + log(Distance) + Reef:log(Distance).

Fish production and biomass were quantified at the reef level and were not measured at the same spatial resolution as benthic invertebrate samples. As a result, fish metrics were treated as reef-level predictors and were held constant across all distance intervals within a given reef when examining relationships with invertebrate responses. This approach allowed fish-invertebrate relationships to be evaluated across spatial gradients in invertebrate communities, while acknowledging that fish production and biomass represent integrated reef-scale estimates rather than distance-specific measurements.

To examine whether relationships between fish and prey item invertebrates varied with distance from the ARs, separate linear models were fit relating prey item production or biomass to reef fish production or biomass, with an interaction term between the fish metrics and distance in order to test whether slopes differed across distances. Separate models were run for white

grunt and all other fish species combined to account for differences in foraging behavior between species that forage off the reef nocturnally, such as white grunt, and those that remain reef-associated. For white grunt production, the model used was: lm(Prey Item Production ~ White Grunt Production + Distance:White Grunt Production). For other fish production, the model used was: lm(Prey Item Production ~ log(Other Fish Production) + Distance:log(Other Fish Production)). For white grunt biomass, the model used was: lm(Prey Item Biomass ~ White Grunt Biomass + Distance:log(White Grunt Biomass)). Finally, for other fish biomass, the model used was: lm(Prey Item Biomass ~ log(Other Fish Biomass) + Distance:log(Other Fish Biomass)). Normality assumptions were met for the white grunt production model, however the white grunt biomass, other fish production, and other fish biomass models violated normality assumptions so therefore the predictor variable was log transformed prior to analysis, after which normality assumptions were adequately met. To evaluate whether the strength of fish-prey relationships differed among distances, estimated marginal slopes were calculated separately for each distance using trend analyses (emtrends, emmeans package), and significance of slopes was assessed using associated p-values.

3. Results

3.1: Effects of reef and distance on prey item production and biomass

3.1.1: Production

Mean prey item invertebrate production varied across distances from the reef, ranging from a high of ~0.004g/day at 1m to a low of ~0.001g/day at 3m, before stabilizing from 4m to 20m. The ANCOVA test revealed that prey item production significantly declined with distance

from the reef after accounting for reef identity ($F(1,30) = 5.55$, $p = 0.03$). However, reef identity did not have a significant effect on prey item production after accounting for distance ($F(4,30) = 2.07$, $p = 0.11$), and the interaction between reef and distance was also non-significant ($F(4, 30) = 1.40$, $p = 0.26$) (Figure 3).

3.1.2: Biomass

Mean prey item invertebrate biomass varied across distances from the reef, ranging from a high of ~4g at 1m to a low of 0.05g at 3m, before stabilizing from 4m to 20m. The ANCOVA test revealed that prey item biomass also declined significantly with distance from the reef after accounting for reef identity ($F(1,30) = 7.21$, $p = 0.01$). However, reef identity did not have a significant effect on prey item biomass after accounting for distance ($F(4,30) = 1.20$, $p = 0.33$). The interaction between reef and log-transformed distance was also non-significant ($F(4, 30) = 1.32$, $p = 0.29$) (Figure 3).

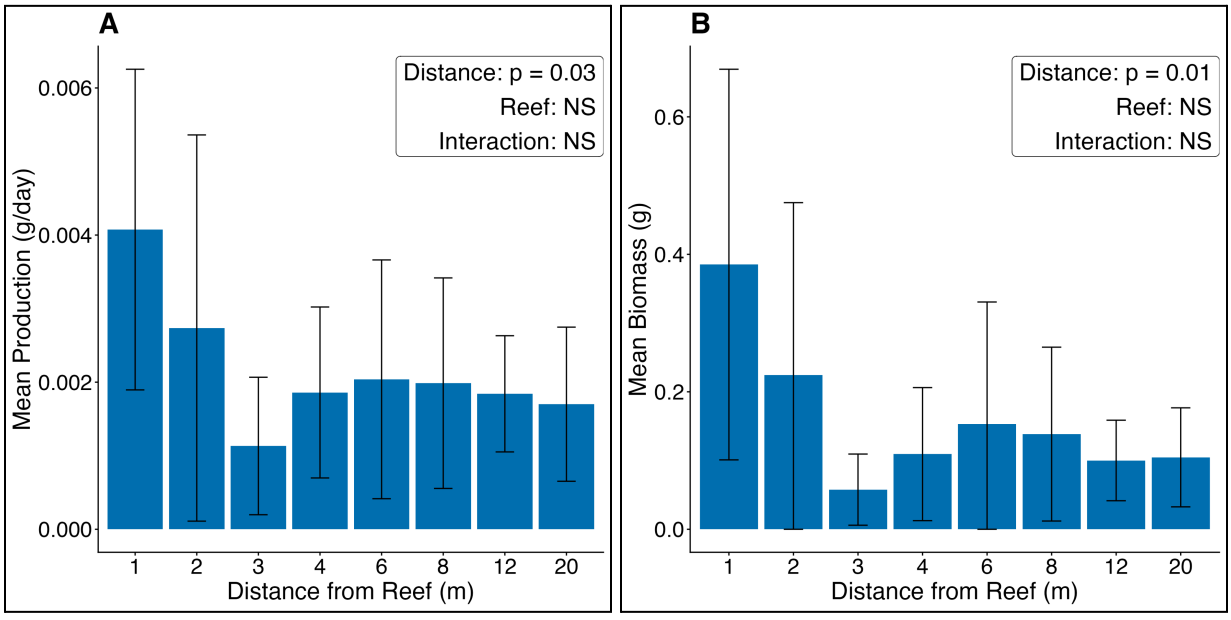


Figure 3: A) The average value across all five reefs of prey item production at each distance from the reef. **B)** The average value across all five reefs of prey item biomass at each distance from the reef. Error bars in each figure indicate standard deviation.

3.2: Comparison of prey item invertebrates:other invertebrates ratio across distances

3.2.1: Production

The ratio of prey item production to other invertebrate production did not significantly vary with distance ($F(1, 30) = 0.01$, $p = 0.93$), nor did reef identity ($F(4, 30) = 2.15$, $p = 0.1$) or the reef by distance interaction ($F(4, 30) = 0.81$, $p = 0.53$) (Figure 5).

3.2.2: Biomass

Similarly to production, the ratio of prey item biomass to other invertebrate biomass did not significantly vary with distance ($F(1, 30) = 0.02$, $p = 0.89$), reef identity ($F(4, 30) = 2.29$, $p = 0.08$), or their interaction ($F(4, 30) = 0.53$, $p = 0.72$) (Figure 5).

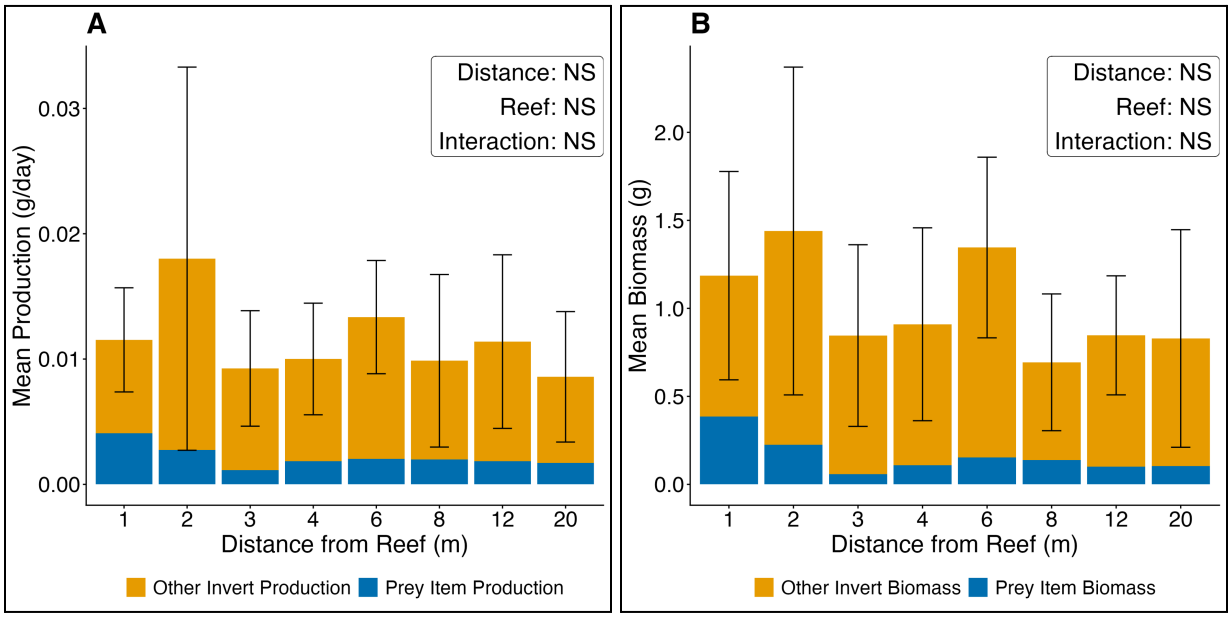


Figure 4: A) The average value across all five reefs of total invertebrate production at each distance from the reef, with mean prey item production (blue) separated from the remaining invertebrate production (orange). **B)** The average value across all five reefs of total average invertebrate biomass at each distance from the reef, with mean prey item biomass (blue) separated from the remaining invertebrate biomass (orange). Error bars indicate standard deviation for total invertebrate production and biomass means, respectively. See figure 3 for prey item production and biomass error bars.

3.3: Relationship between prey item and fish production and biomass

3.3.1: Production

The relationship between white grunt production and prey item production was not significant at any distance from the reef (all $p > 0.05$), indicating that white grunt production did not predict prey item production at any sampled distance (Figure 5).

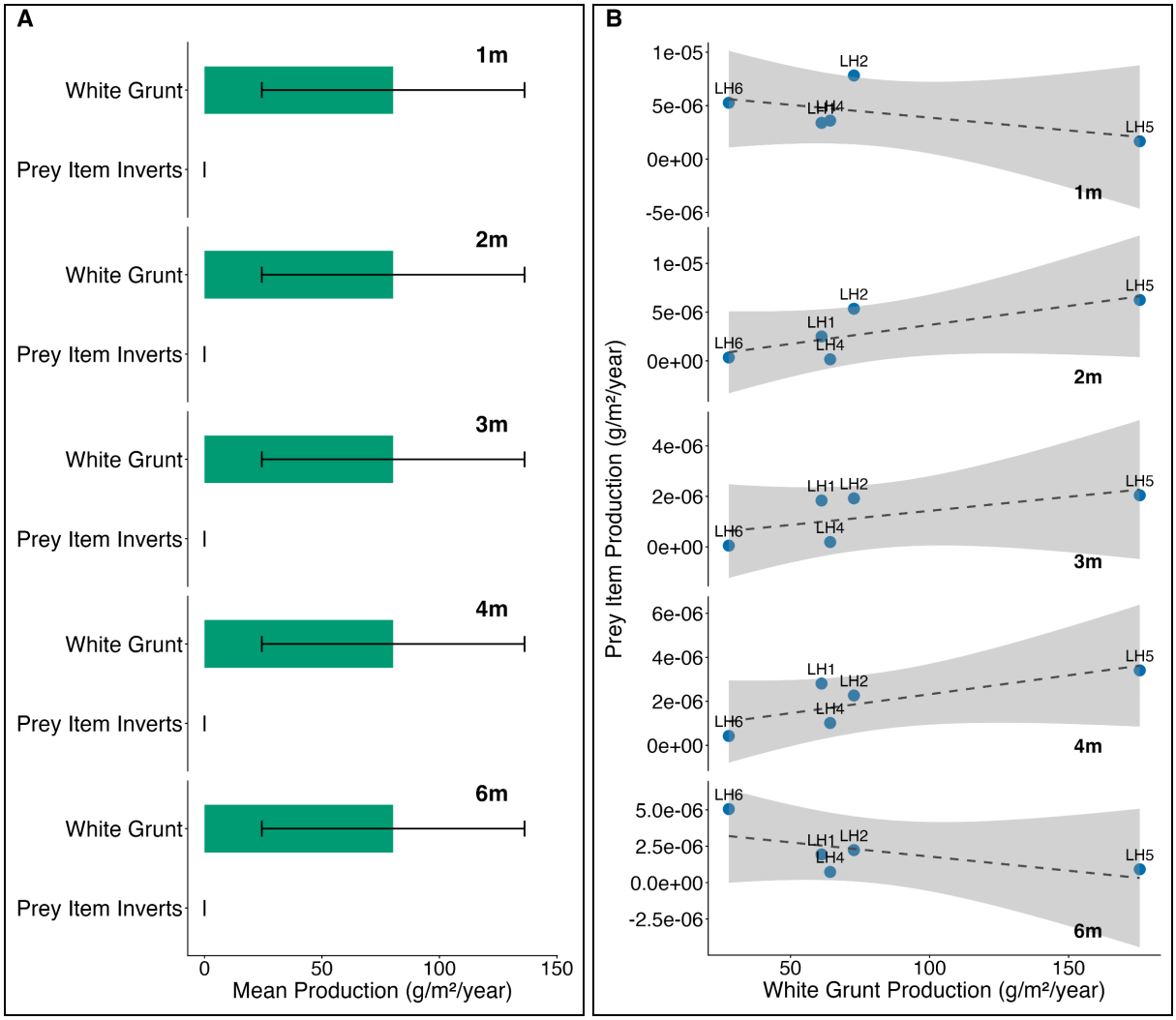


Figure 5: A) Average white grunt production and prey item invertebrate production at each distance from the reef (1, 2, 3, 4, and 6m), averaged across all five reefs. Error bars indicate standard deviation. Distance labels are shown in the top right corner of each panel. **B)** White grunt production versus prey item invertebrate production at each distance from the reef (1, 2, 3, 4, and 6m). Each point represents one reef (n = 5) and dashed lines represent linear regression fits with 95% confidence intervals shown in grey. Distance and r correlation coefficients shown in bottom right corner.

3.3.2: Other Fish Production

The relationship between other fish production and prey item production was not significant at any distance from the reef (all $p > 0.05$), indicating that other fish production did not predict prey item production across the reef distance gradient (Figure 6).

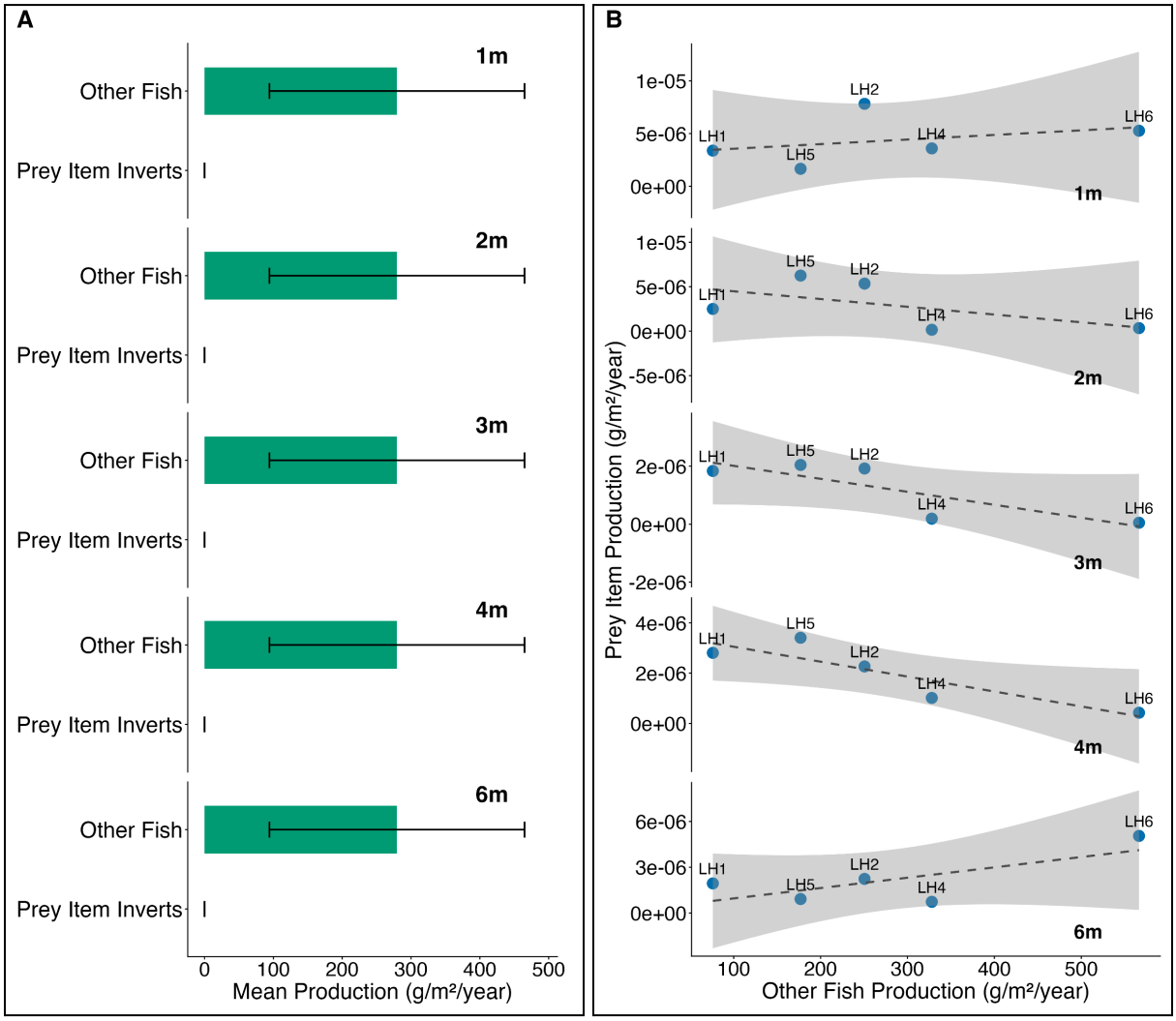


Figure 6: A) Average other fish production and prey item invertebrate production at each distance from the reef (1, 2, 3, 4, and 6m), averaged across all five reefs. Error bars indicate standard deviation. Distance labels are shown in the top right corner of each panel. **B)** Other fish production versus prey item invertebrate production at each distance from the reef (1, 2, 3, 4, and 6m). Each point represents one reef (n = 5) and dashed lines represent linear regression fits with 95% confidence intervals shown in grey. Distance and r correlation coefficients shown in bottom right corner.

3.3.3: White Grunt Biomass

The relationship between white grunt biomass and prey item biomass was not significant at any distance from the reef (all $p > 0.05$), indicating that white grunt biomass did not predict prey item biomass across distances (Figure 7).

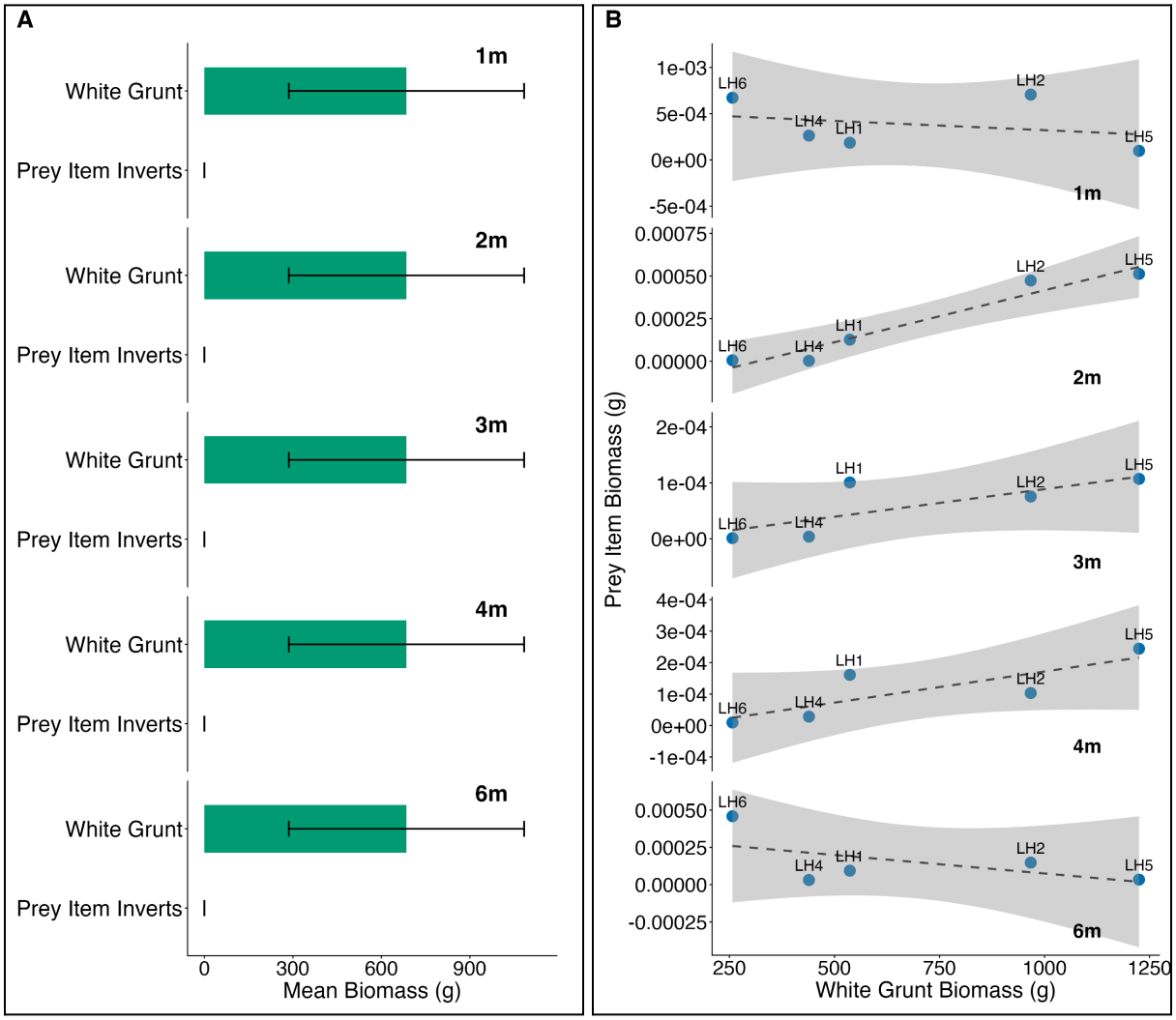


Figure 7: A) Average white grunt biomass and prey item invertebrate biomass at each distance from the reef (1, 2, 3, 4, and 6m), averaged across all five reefs. Error bars indicate standard deviation. Distance labels are shown in the top right corner of each panel. **B)** White grunt biomass versus prey item invertebrate biomass at each distance from the reef (1, 2, 3, 4, and 6m). Each point represents one reef (n = 5) and dashed lines represent linear regression fits with 95% confidence intervals shown in grey. Distance and r correlation coefficients shown in bottom right corner.

3.3.4: Other Fish Biomass

The relationship between other fish biomass and prey item biomass was not significant at any distance from the reef (all $p > 0.05$), indicating that other fish biomass did not predict prey item biomass across the reef distance gradient (Figure 8).

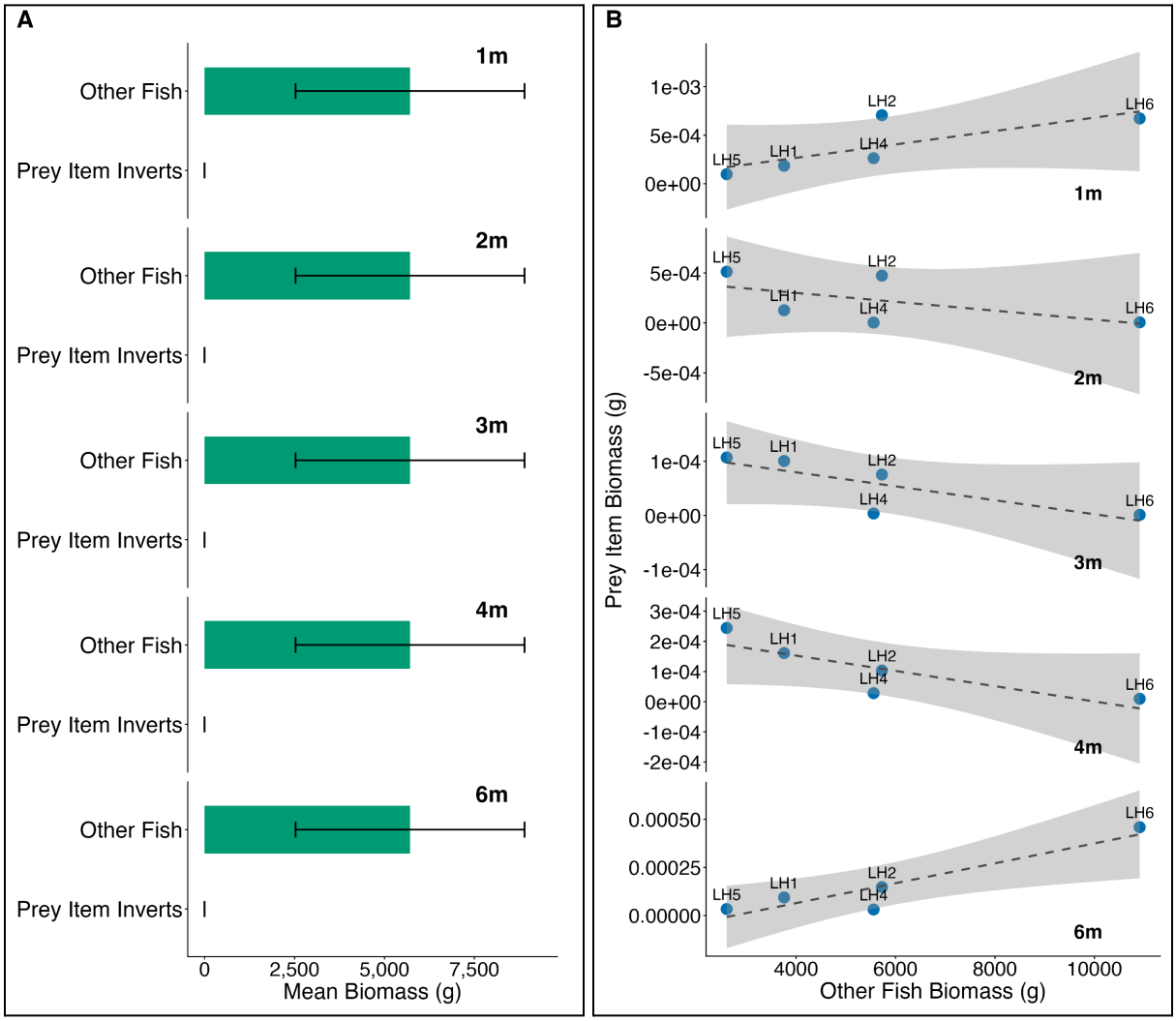


Figure 8: A) Average other fish biomass and prey item invertebrate biomass at each distance from the reef (1, 2, 3, 4, and 6m), averaged across all five reefs. Error bars indicate standard deviation. Distance labels are shown in the top right corner of each panel. **B)** Other fish biomass versus prey item invertebrate biomass at each distance from the reef (1, 2, 3, 4, and 6m). Each point represents one reef (n = 5) and dashed lines represent linear regression fits with 95% confidence intervals shown in grey. Distance and r correlation coefficients shown in bottom right corner.

4. Discussion

This study investigated how artificial reefs influence benthic food web structure in adjacent seagrass habitats and whether these effects are mediated by reef-associated fishes across spatial gradients. Specifically, it examined whether proximity to the reef alters benthic invertebrate production and biomass, and whether these patterns are consistent with bottom-up processes such as nutrient availability, or top-down processes such as fish predation. Overall, the results demonstrate that ARs strongly enhance benthic invertebrate production and biomass in the immediate vicinity of reef structures, but these effects decline rapidly with distance and are not accompanied by detectable fish-driven top-down control, which has important implications for understanding how ARs shape adjacent seagrass food webs.

4.1: Spatial effects of artificial reefs on benthic invertebrates

The strong decline in prey item invertebrate production and biomass with increasing distance from ARs indicates that reef proximity is a key determinant of benthic productivity in AR habitats. Rather than a gradual decline with distance, invertebrate abundance showed a sharp decrease within the first few meters of the reef followed by relatively stable values at greater distances. This pattern suggests that artificial reefs generate a localized zone of enhanced benthic invertebrate productivity that does not extend far into surrounding habitats.

This pattern is consistent with the idea that ARs function as structural “hotspots” that can modify local habitat conditions (Hammond et al., 2020). Habitat complexity is well known to increase local biodiversity and abundance by providing refuge from predation, increasing surface area for colonization, and altering local hydrodynamic conditions that influence larval settlement

and organic matter retention (Heck & Wetstone, 1977). In benthic systems, even relatively small-scale structural changes can strongly influence invertebrate distribution by altering sediment stability, food availability, and microhabitat diversity (Orth et al., 2006). Additionally, reef-associated fishes are also known to concentrate nutrient excretion near reef structures, generating localized nutrient hotspots that can enhance primary and secondary production in nutrient-limited systems (Allgeier et al., 2018). The rapid decline of these effects with distance likely reflects the spatial constraints of both structural influence and fish-mediated nutrient subsidies, which are concentrated near the reef and diminish quickly as structural complexity and fish density decline.

The lack of significant change in the ratio of prey item invertebrates to the broader invertebrate community suggests that reef proximity influences overall benthic abundance rather than selectively affecting certain functional groups. This indicates that environmental drivers associated with reefs such as habitat complexity or increased nutrient availability affect multiple invertebrate groups similarly, resulting in parallel declines rather than restructuring the entire community composition.

Despite strong effects of distance on prey item invertebrates alone, reef identity did not significantly influence invertebrate production or biomass after accounting for distance, nor was there a significant interaction between reef and distance. This suggests that proximity to reef structure is more important than reef-specific characteristics, and that the reefs included in this study are functionally similar in their ability to support invertebrate communities. The consistency of distance-decay patterns across all five reefs further indicates that the spatial processes documented here are generalizable across the AR system studied, rather than being the result of individual reef characteristics. This has important implications for scaling AR effects,

such that the predictability of these spatial patterns suggests that distance from reef structure may be a reliable predictor of benthic invertebrate productivity across AR systems more broadly.

This distinction between resource availability and community composition has important ecological implications. For reef-associated fishes, movement away from reefs likely results in reduced overall prey availability, but not necessarily a shift in prey type. This may help explain why many fishes remain closely associated with reef habitats, where prey abundance is highest. At the same time, the concentration of invertebrate production near reefs highlights the role of artificial reefs as main points of energy availability, supporting higher trophic levels in surrounding ecosystems.

4.2: Top-down control effects from reef-associated fish

In contrast to expectations of strong trophic interactions, reef-associated fish production and biomass were not significant predictors of prey item invertebrate production or biomass at any distance from reefs. This pattern was consistent across both white grunt and the broader fish community, and no spatial interaction effects were detected. Together, these results provide little evidence that fish predation exerts measurable top-down control on benthic invertebrate communities at the spatial scale examined in this study.

This lack of relationship is particularly notable given that white grunts were expected to exert localized foraging effects due to their known diel movement patterns between reef and adjacent habitats (Ogden & Ehrlich, 1977). Because this species actively forages in surrounding seagrass beds while using reefs as daytime refuge, it was hypothesized that white grunt biomass would show stronger associations with invertebrate prey availability across distance gradients. However, the absence of any significant relationship suggests that even behaviorally mobile

reef-associated consumers may not generate consistent or spatially structured top-down effects on benthic invertebrate communities in AR systems.

One explanation for this weak relationship is that benthic invertebrate communities may be structured primarily by habitat availability and recruitment processes rather than by control from predation. This interpretation is directly supported by the parallel declines in both prey item and non-prey invertebrates documented in section 4.1, which suggest that community-wide responses to habitat gradients outweigh any selective depletion by fish predation. If fish were exerting strong top-down control specifically on prey item taxa, we would expect the ratio of prey item to non-prey invertebrates to decline near the reef where predation pressure is highest, yet this ratio remained consistent across all distances, further arguing against predation as a primary structuring force.

It is also well established that top-down effects in coastal seagrass and reef-associated systems are highly context dependent, shaped by variation in habitat structure, consumer identity, prey density, and environmental conditions (Heck & Valentine, 2006). The structural complexity provided by ARs and adjacent seagrass may provide prey refuge that reduces predator encounter rates and foraging efficiency, buffering benthic invertebrate communities against strong predation effects (Hixon & Beets, 1993). Under these conditions, even abundant reef-associated predators may have limited capacity to exert detectable community-level top-down control.

4.3: Conclusion

Taken together, these results reveal a consistent pattern across all analyses: ARs act as localized centers of enhanced benthic productivity that influence surrounding seagrass ecosystems over spatially constrained scales, with effects strongest immediately adjacent to reef

structures and declining rapidly within the first few meters. This spatial pattern was consistent across all five reefs studied, suggesting it reflects a generalizable feature of AR-seagrass systems rather than site-specific variation.

While reef proximity strongly increased invertebrate production and biomass, it did not alter community composition or produce detectable top-down suppression by reef-associated fishes. Instead, the dominant processes shaping these spatial patterns appear to be bottom-up drivers associated with reef structure, including enhanced habitat complexity, localized nutrient availability from fish excretion, and favorable hydrodynamic conditions, which benefit the entire benthic invertebrate community rather than specific functional groups. These findings suggest that ARs function primarily as structural habitat additions that modify local ecological conditions, rather than as systems that restructure adjacent food webs through strong trophic cascades.

Importantly, this study highlights that predator-prey relationships in reef-adjacent ecosystems do not always conform to simple top-down expectations. Fish and invertebrate distributions may be more strongly linked through shared responses to habitat conditions associated with reef proximity than through direct trophic web patterns, resulting in spatially similar patterns rather than evidence of strong predatory control. This has broader implications for how we interpret the ecological role of reef-associated fish communities in AR systems. Their most important influence on adjacent benthic communities may be indirect, operating through nutrient subsidies and habitat modification rather than through direct consumption of invertebrate prey.

Future work should prioritize several directions to build on these findings. First, explicitly quantifying nutrient dynamics across reef-seagrass gradients, particularly the spatial

extent of fish-derived nutrient subsidies, would help clarify the bottom-up mechanisms driving the observed invertebrate patterns. Second, incorporating isotopic analysis of fish gut contents and benthic invertebrates across distance gradients would more directly test whether reef fish are selectively consuming prey item invertebrates near ARs and at what spatial scale these trophic interactions are detectable. Third, extending sampling transects beyond 20m and incorporating seasonal replication would help characterize the full extent of reef influence and assess whether the patterns documented here vary across time. Finally, examining how AR density and spacing influence the spatial extent of reef effects on adjacent invertebrate communities would provide actionable guidance for AR placement and management in seagrass ecosystems.

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