

# **Assessing Oyster Size Distributions Within Intertidal Eastern Oyster *Crassostrea virginica* (Gmelin, 1791) Populations across Restoration Sites, Harvest Zones, and Spatial Locations in the Big Bend of Florida**

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## ASSESSING OYSTER SIZE DISTRIBUTIONS WITHIN INTERTIDAL EASTERN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN, 1791) POPULATIONS ACROSS RESTORATION SITES, HARVEST ZONES, AND SPATIAL LOCATIONS IN THE BIG BEND OF FLORIDA

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**ABSTRACT** Eastern oyster *Crassostrea virginica* (Gmelin, 1791) shell height from more than 27,000 individuals were sampled over 12 y from control and restored intertidal oyster reefs in the Big Bend region of Florida to evaluate how spatial variation, harvest status, and restoration influence size structure. Analysis with Bayesian regression models (fixed and random effects) showed that spatial differences, especially across relic shoreline zones, were the primary determinants of oyster height. Inshore intertidal reefs supported the largest oysters (mean  $\approx$  37.1 mm), whereas offshore intertidal reefs supported the smallest (mean  $\approx$  25.0 mm). Harvest status had modest effects, typically shifting mean heights by less than 1 mm after accounting for spatial structure. In contrast, restoration produced strong, rapid responses in oyster heights. At Lone Cabbage (LC) Reef (offshore site), restoration increased mean oyster height in areas closed to harvest from 24.0 to 30.4 mm (about  $+6$  mm) and to 33.5 mm (about  $+9$  mm) in areas open to harvest. Restoration response was rapid, as within 2 y restored offshore reefs exhibited size structures approaching those of viable unrestored inshore reefs, indicating that intertidal restoration can succeed even where harvest occurs. These results highlight the key role of spatial setting and the roles of substrate and reef elevation in promoting intertidal oyster population size structure.

**KEY WORDS:** *Crassostrea virginica*, restoration, intertidal oyster, size structure

### INTRODUCTION

Eastern oyster *Crassostrea virginica* are estuarine bivalves distributed across coastal ecosystems in eastern North and South America and the Caribbean basin. As ecosystem engineers, oyster reefs create habitat for many demersal species and fill large ecological niches both through living biomass and their legacy of dead shell (Coen et al. 2007, Grabowski & Peterson 2007, Pace et al. 2023). Although oysters support commercial fisheries throughout their range, many of these fisheries have declined sharply or closed in recent decades (Rothschild et al. 1994, Kirby 2004, Pine et al. 2015). Ecosystem services provided by oysters, including water quality improvements, may exceed the value of the fishery itself (Nelson et al. 2004, Grizzle et al. 2006, Coen et al. 2007, Grabowski & Peterson 2007, La Peyre et al. 2014a, 2014b). The ecological and fishery value of oysters has motivated restoration efforts (Lenihan et al. 2001, Grabowski et al. 2005, Lipcius et al. 2015, Davenport et al. 2021, Smith et al. 2023), and committed restoration funding now exceeds annual fishery value in the Gulf of Mexico (Pine et al. 2022).

In response to oyster population declines, management agencies, local governments, and nongovernmental organizations have launched substantial restoration efforts, over \$199 million has been committed from the Deepwater Horizon settlements alone, yet restoration success has been mixed across the U.S.

Gulf of America (formerly Gulf of Mexico; Beroza Hernández et al. 2018, La Peyre et al. 2022, Pine et al. 2023). Although individual projects vary in goals, most aim to shift degraded reefs toward higher productivity states that provide greater ecological and fishery benefits (Coen & Luckenbach 2000). A key challenge in designing such projects, particularly at large scales, is the autogenic nature of oyster population dynamics, which requires restoring and maintaining shell biomass, surface area, and elevation at recruitment sites (Powell et al. 2012, Soniat et al. 2019, Johnson et al. 2022, Solinger et al. 2022).

Quantifying restoration goals in terms of population dynamics is critical for evaluating project success and informing adaptive restoration strategies. Baggett et al. (2015), in a comprehensive review of oyster restoration practices and response metrics, identified size-frequency distributions as a simple but effective metric to track recruitment, mortality, and overall population status. Oyster year class and growth estimates are typically derived from indirect methods such as size-frequency analyses (Coakley 2004, Manley et al. 2008, Grizzle et al. 2018, Harding 2020). In Chesapeake Bay, VA, the presence of at least two oyster age classes, reflected in size structure, has been adopted as a key performance metric for assessing restoration success (Allen et al. 2011).

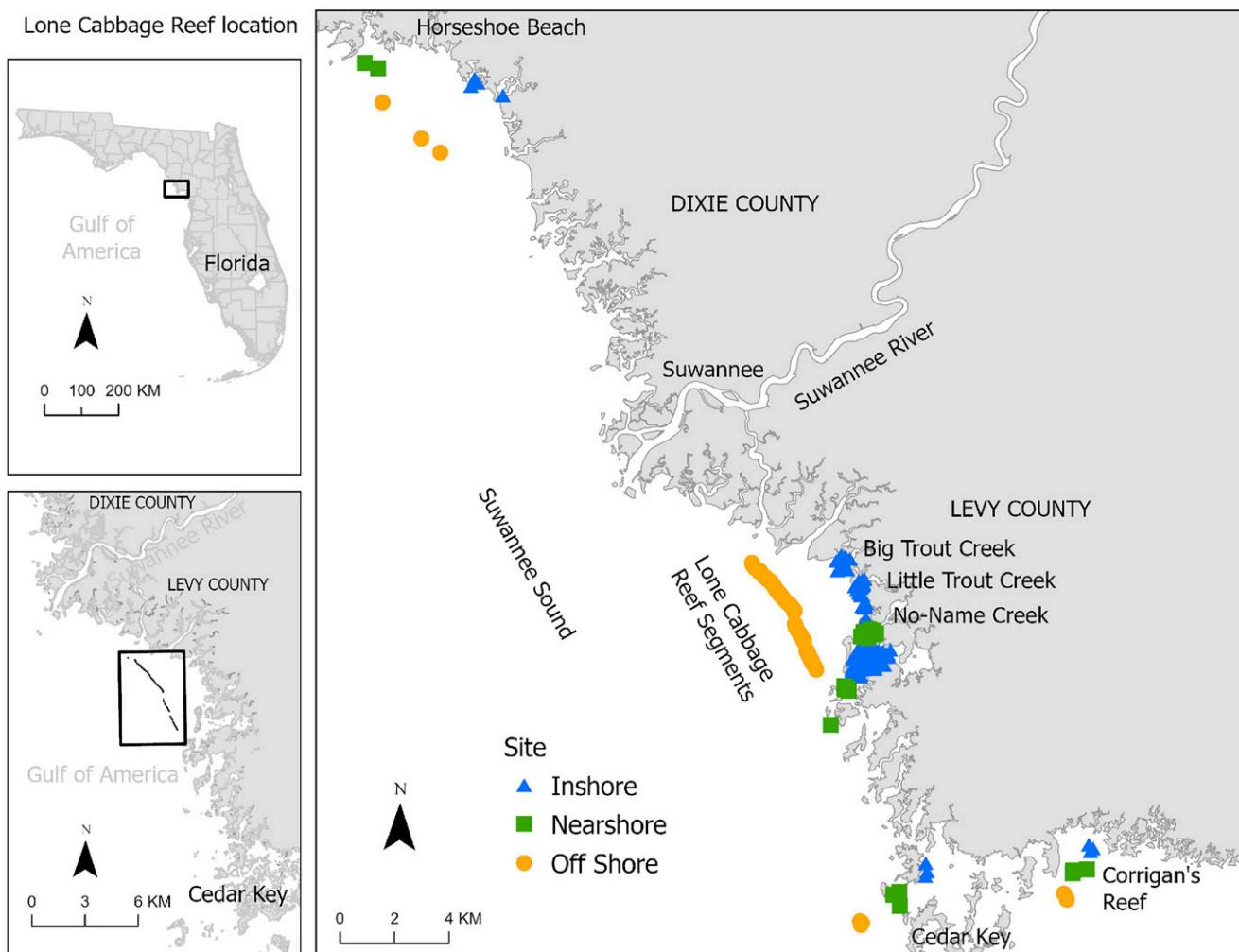
The southern Big Bend region of the northeastern Gulf of America (Fig. 1; Taylor, Levy, and Dixie counties, Florida) is a low-energy, open-ocean-facing lagoon of high conservation importance, bordered by state and federal protected estuarine (e.g., Big Bend Seagrass Aquatic Preserve) and upland (e.g., Cedar Keys and Lower Suwannee National Wildlife Refuges) habitats. With low human population density, the economy of the region remains closely tied to natural resources, including forestry, fisheries, and shellfish aquaculture (Mattson 2002, Southwick Associates 2021) and the region is experiencing

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**Figure 1.** Oyster reefs sampled throughout the Big Bend region of Florida for oyster height data from 2010 to 2022. The localities shown on the main map are Big Trout Creek (BT), Cedar Key (CK), Corrigan's Reef (CR), Horseshoe Beach (HB), Lone Cabbage (LC), Little Trout Creek (LT), and No Name Creek (NN). The two inset maps demonstrate the location of the study region with an emphasis on Lone Cabbage Reef as the location where oyster reef restoration occurred.

tropicalization likely due to changing climate (Sinnickson et al. 2021). Suwannee Sound, at the mouth of the Suwannee River, has supported oyster harvests for thousands of years (Wallis et al. 2022). Since 2017, the Big Bend has sustained the largest commercial oyster fishery in Florida (by trips and landings), harvested by small vessels using hand tongs or bare hands, and remains one of the few wild oyster fisheries in the U.S. Gulf of America.

Two main oyster-reef types occur in Suwannee Sound: subtidal and intertidal. Subtidal reefs stay submerged throughout the tidal cycle and often occupy channels between intertidal reefs. Intertidal reefs, which are the focus of this study, are widespread across the region and likely account for 60%–80% of total reef area. They typically form ridges parallel to shore that reflect relic shorelines from past sea levels. Because intertidal oysters are exposed to air for part of each tidal cycle, their growth is restricted (Roegner & Mann 1995). The commercial fishery concentrates on subtidal reefs, where oysters grow larger under continuously submerged conditions (Baillie & Grabowski 2019, Powers et al. 2025).

Seavey et al. (2011) and Moore et al. (2020) documented major declines of intertidal oysters in Suwannee Sound, estimating a 66% loss of reef area since 1982 based on aerial imagery and field surveys. Frederick et al. (2016) showed that adding durable substrate can reverse losses at the reef scale, suggesting substrate limitation rather than limited spat supply. Building on small-scale success at LC Reef, where dolomite limestone was used to restore degraded oyster cultch (Frederick et al. 2016), the approach was expanded along the relic reef footprint, creating an approximately 5-km chain of restored reefs (Pine et al. 2022, Aufmuth et al. 2025).

This study evaluates how intertidal oyster size structure varies across combinations of restoration and harvest status, using standardized, fisheries-independent sampling at multiple locations in the Big Bend region of Florida over 12 y. Although oysters on intertidal reefs are usually too small for commercial harvest (minimum legal size 76.2 mm), managers and restoration practitioners still debate whether harvest and restoration can coexist in these settings and whether broad harvest closures are warranted where restoration occurs.

This analysis investigated spatial and management drivers of shell height on unrestored intertidal reefs through three hierarchical questions:

- (1) Do oyster shell heights differ among major localities across the Big Bend?
- (2) Do shell heights differ among individual sites within those localities?
- (3) Do oyster heights differ between reefs open and closed to commercial harvest?

These questions span nested ecological and management scales from broad geographic patterns to local harvest effects.

The analysis further examined restoration effects on intertidal oyster size structure at LC Reef through comparisons of restored versus unrestored reefs across open and closed harvest areas. This framework facilitates evaluation of how restoration and harvest jointly influence oyster population structure.

Oyster shell height was analyzed using a Bayesian hierarchical regression framework applied to data from multiple intertidal reef sites across successive monitoring periods. Two model classes were fit: (1) fixed-effects models including restoration treatment, harvest status, and their interaction and (2) hierarchical models with random intercepts for sampling station and monitoring period to account for spatial and temporal heterogeneity. Posterior predictions were compared with raw data to assess fit and estimate treatment effects.

Variation in oyster height on control (unrestored) reefs was examined using four fixed-effects specifications—locality-only, site-only (inshore, nearshore, and offshore), harvest-only (open versus closed), and site + harvest. To assess robustness, the leading fixed-effects models were refit with a random intercept for monitoring period. At LC (the only locality with restoration), additional site-specific models summarized local restoration effects and displayed posterior predictions of restoration impacts on oyster heights. Collectively, these analyses yield quantitative guidance for adaptive oyster harvest and restoration across the Big Bend region.

## MATERIALS AND METHODS

### Study Area

The Big Bend region of the West Coast of Florida is a shallow, low-energy, open-coast estuarine system, with depths generally less than 2 m. It contains some of the lowest human population densities in coastal Florida, largely because extensive state and federal conservation lands protect most uplands (Geselbracht et al. 2011). As a result, relatively undisturbed shorelines dominated by salt marshes, oyster reefs, mangrove swamps, and mudflats have persisted (Orlando 1993, Wright et al. 2005, Moore et al. 2020). The region lies along a climatic ecotone between temperate and subtropical zones, and community composition has shifted toward subtropical taxa in recent decades, likely in response to climate change. For example, Black Mangrove *Avicennia germinans* has expanded into salt marshes, and the neonative Common Snook *Centropomus undecimalis* has extended its range northward (Stevens et al. 2006, Purtlebaugh et al. 2020, Sinnickson et al. 2021).

### Oyster Reef Monitoring and Restoration Processes

Characterization of intertidal oyster reefs in this region and small-scale restoration testing on LC Reef and regional intertidal oyster monitoring to inform this analysis began in 2010 using aerial mapping and on-the-ground assessments of oyster heights, density, and coverage of reef area (Seavey et al. 2011, Frederick et al. 2016).

Oyster height data were collected in the Big Bend from 2010 to 2022 at restored and wild intertidal oyster reefs as part of a standardized line-transect sampling program (Moore et al. 2020) in which intertidal oyster reefs were randomly selected for assessing oyster density from three strata: (1) open/closed to harvest, (2) control (unrestored)/rocks (restored), and (3) locality; Big Trout Creek (BT), Cedar Key, Corrigan's Reef, Horseshoe Beach, LC, Little Trout Creek (LT), and No Name Creek (NN); Figure 1.

Restoration proceeded in two phases. Phase 1 placed 360 m<sup>3</sup> of limestone across four restored-control site pairs and was surveyed in 2013 (prerestoration) and 2015 (postrestoration; Frederick et al. 2016). Phase 2, began in 2018 and expanded the effort to 26 reefs with approximately 13,000 m<sup>3</sup> of limestone, with postrestoration monitoring starting in 2019 (Aufmuth et al. 2025). In both phases, high-resolution on-water surveys mapped the footprint and elevation of relic reefs, and nearby healthy reefs provided elevation targets. Volumetric estimates then determined the rock required to build each reef to the target height. Phase-1 reefs were later augmented to the Phase-2 specification, producing an average elevation increase of about 0.36 m to match adjacent wild reefs. The total area of restoration built to elevation is about 2.95 ha (Aufmuth et al. 2025). The northern two-third of the restored area is closed to commercial harvest; the southern third is seasonally open (Aufmuth et al. 2025).

All sampling was timed to low-water windows when tidal height remained below -0.24 m mean lower low water for at least 120 min, as forecast by NOAA Cedar Key station (8727520). These conditions occur on roughly 50 days per year from October to March and allow intertidal reefs to dewater sufficiently for line-transect sampling. Candidate sampling dates were identified in R (R Core Team 2025) using rtide (Thorley et al. 2024) and suncalc (Thieurmel & Elmarhraoui 2022), adjusting field schedules as needed for wind effects.

Sampling dates were grouped into discrete biannual periods: winter (October–March) labeled as even-numbered periods and summer (April–September) as odd-numbered periods, from period 1 (summer 2010) through period 24 (winter 2021 to 2022; Table A1). Standardized postrestoration monitoring was generally focused on winter periods after the pilot restoration in period 9 (summer 2014) and the larger restoration in period 17 (summer 2018) to reduce variability from new recruitment and episodic mortality and better isolate restoration effects.

Oyster heights were measured at random locations on reefs using either a randomly selected 2.5-m line-transect segment or a randomly placed quadrat (Frederick et al. 2016, Moore et al. 2020, Moore & Pine 2021). Field crews typically measured the first 50 oysters encountered at random; if fewer than 50 were obtained, an additional transect segment or quadrat was sampled until greater than or equal to 50 oysters were measured. Heights were measured along the longest axis (umbo to farthest

point). The legal harvest size is 76.2 mm. Measurements within each period are treated as instantaneous.

#### Statistical Analysis

#### Study Factors and Stratification

Each oyster measured was classified into one of seven coastal localities (Fig. 1) and into a site (inshore, nearshore, and offshore) category that approximates natural visual orientation and distance from shore. These site categories follow the chains of reefs that parallel the coast and likely reflect relic shorelines. Subtidal reefs also occur in the region but were not the focus here. Restoration was implemented only at LC Reef (offshore sites).

#### Descriptive Summaries

Individual shell heights were summarized by restoration and harvest treatment to describe broad patterns. Each oyster from 2010 to 2022 was assigned to one of four groups: control (unrestored) or restored and then open or closed to harvest. Standard frequentist summaries of oyster height and normal approximations to measure uncertainty were computed for each group, and observed distributions were displayed as box plots with overlaid raw points (Tables 1 and A1, Fig. 2).

#### Modeling Framework

A Bayesian generalized linear models with a gamma likelihood and log-link was used to quantify variation in shell height across space and management regimes. Posterior inference was conducted on the response (mm) scale via population-average predictions with 95% credible intervals (CrI). Model adequacy was evaluated with posterior predictive diagnostics; Bayesian  $R^2$  was reported and models were compared using PSIS-LOO.

#### Analysis 1: Unrestored (Control) Reefs

To identify the main drivers of variation on wild reefs, four fixed-effects specifications were fit: (1) locality-only, (2) site-only (inshore, nearshore, and offshore), (3) harvest-only (open versus closed to harvest), and (4) site + harvest. As a sensitivity check, the best-performing fixed-effects model was refit with a random intercept for monitoring period to assess potential temporal heterogeneity (see Appendix).

#### Analysis 2: Restoration Effects at LC (Site = Offshore)

Restoration outcomes at limestone-cultched intertidal reefs (LC Reef, offshore sites; Fig. 1; Aufmuth et al. 2025) were evaluated using site-specific gamma regression models with a log-link, including fixed effects for treatment (restored versus wild) and harvest (open versus closed), with and without interaction terms. Population-level posterior predictions were summarized for each treatment  $\times$  harvest combination.

#### Implementation Details

All analyses were conducted in R (R Core Team 2025) with brms (Bürkner 2017) using CmdStan via cmdstanr as the Stan backend (Carpenter et al. 2017). Weakly informative priors [Normal(0, 1) on fixed effects; default weak priors on other parameters] were used and ran four MCMC chains (4,000 iterations per chain and 1,000 warm-up). This Bayesian approach provides full posterior distributions for parameters and derived quantities, supporting direct probability statements about treatment effects and their uncertainty.

#### Simple Bayesian Regression (Fixed Effects)

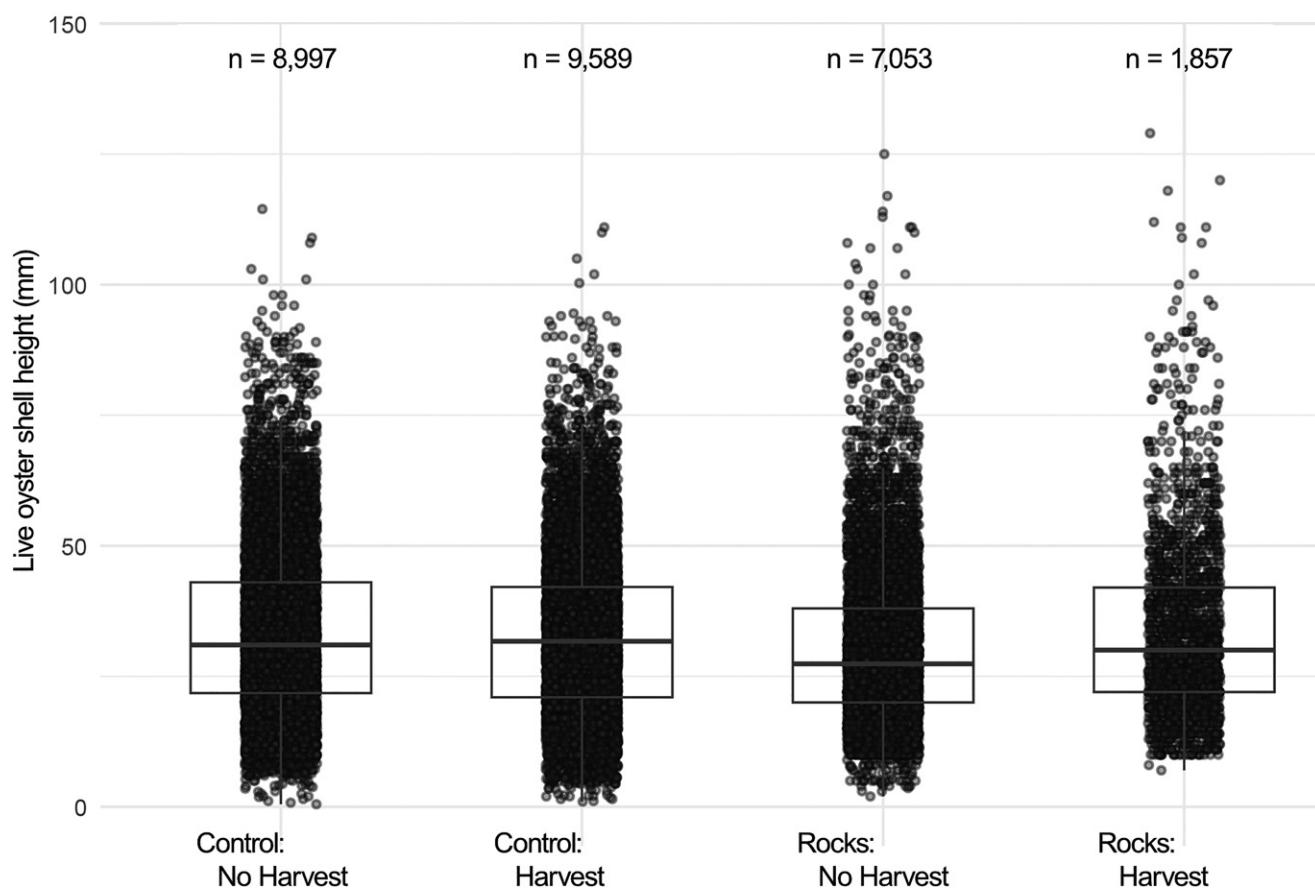
To evaluate restoration outcomes at LC (offshore site is the only site where restoration occurred), oyster shell height across

TABLE 1.

**Raw data summary of live oyster shell heights across restoration treatment and harvest status categories. Values represent simple descriptive statistics for the full dataset, including all sampled localities and sites, and are intended to illustrate general differences across key management factors. Each locality, site, treatment (control or restored), and harvest category are listed. For each group, the table reports sample size (N), mean shell height (mm), SD, SE, and the t-based 95% confidence interval (CI) for the mean shell height.**

Locality	Site	Treatment	Harvest	N	Mean	SD	Mean (95% CI)
BT	I	Control	Closed	678	38.88	18.16	38.88 (37.51–40.25)
CK	I	Control	Open	715	40.99	12.85	40.99 (40.05–41.93)
CK	N	Control	Open	503	37.93	14.56	37.93 (36.65–39.20)
CK	O	Control	Open	255	19.42	14.35	19.42 (17.65–21.19)
CR	I	Control	Closed	1,734	36.71	11.11	36.71 (36.18–37.23)
CR	N	Control	Open	1,340	32.98	14.1	32.98 (32.23–33.74)
CR	O	Control	Open	697	36.06	14.73	36.06 (34.97–37.16)
HB	I	Control	Closed	770	36.25	11.91	36.25 (35.40–37.09)
HB	I	Control	Open	1,366	33.73	12.14	33.73 (33.08–34.37)
HB	N	Control	Open	1,048	19.95	11.85	19.95 (19.23–20.67)
HB	O	Control	Open	318	13.16	6.43	13.16 (12.45–13.87)
LC	I	Control	Closed	1,823	36.96	15.33	36.96 (36.26–37.67)
LC	I	Control	Open	2,231	37.47	15.43	37.47 (36.83–38.11)
LC	N	Control	Closed	55	26.91	13.9	26.91 (23.15–30.67)
LC	N	Control	Open	1,116	32.59	16.71	32.59 (31.60–33.57)
LC	O	Control	Closed	2,800	24.04	13.63	24.04 (23.54–24.55)
LC	O	Rocks	Closed	7,053	30.39	14.96	30.39 (30.04–30.74)
LC	O	Rocks	Open	1,857	33.55	17.18	33.55 (32.77–34.33)
LT	I	Control	Closed	705	40.76	16.7	40.76 (39.53–41.99)
NN	I	Control	Closed	432	40.28	16.92	40.28 (38.68–41.88)

### Distribution of live oyster shell heights (mm)



**Figure 2.** Distribution of live oyster shell heights (mm) by reef treatment and harvest status across all localities and sites. Box plots summarize the distribution of individual shell height measurements for each group: control reefs closed to harvest (control: no harvest), control reefs open to harvest (control: harvest), restored reefs closed to harvest (rocks: no harvest), and restored reefs open to harvest (rocks: harvest). Boxes show the interquartile range (IQR), which spans the middle 50% of the data from the 25<sup>th</sup> percentile (Q1) to the 75<sup>th</sup> percentile (Q3), with the median indicated by a horizontal line inside each box. Whiskers extend to 1.5 times the IQR from Q1 and Q3. Individual observations are plotted as semitransparent points, and sample sizes (*n*) are displayed above each group. The *y*-axis is limited to 150 mm to emphasize central tendencies and between-group differences. This *y*-axis limit removes two oysters from the more than 27,000 measured.

four groups defined by treatment (control versus rocks) and harvest status (closed versus open) were compared. Because major restoration occurred in summer 2018 (period 17), the analysis focused on the first postrestoration winter (period 18) and the next two winters (periods 20 and 22). For each period  $\times$  treatment  $\times$  harvest group, standard summary statistics were computed, followed by fitting Bayesian gamma regressions with a log-link and fixed effects for treatment and harvest (and their interaction), using weakly informative priors. Population-average posterior predictions were generated on the millimeter scale for the four groups, summarized by posterior means and 95% CrI, and visualized with half-eye plots. Model fit and parsimony was assessed using PSIS-LOO. Finally, posterior predictions with period-specific raw summaries were plotted to assess the magnitude and timing of restoration effects.

#### Model Evaluation

Model fit was assessed with posterior predictive checks by comparing observed heights to data simulated from the posterior predictive distribution of each model. Predictive histograms

and density overlays based on 100 posterior draws were examined to verify that the models reproduced location, spread, and distributional shape without systematic bias. Bayesian  $R^2$  is reported as a measure of variance explained.

Leave-one-out cross-validation with PSIS (loo in the loo package) to compare out-of-sample performance and ranked models by expected log predictive density (ELPD). Larger ELPD indicates better predictive accuracy. For the four fixed-effects models (Analysis 1; locality-only, site-only, harvest-only, and site + harvest), PSIS-LOO was computed for each model and summarized  $\Delta$ ELPD. Data and basic code for this model are available in the Git repository ([https://github.com/billpine/LCR\\_Heights\\_JSR.git](https://github.com/billpine/LCR_Heights_JSR.git)).

#### Full Bayesian Regression Model (Fixed and Random Effects)

A multilevel Bayesian regression was fit to quantify treatment and harvest effects, whereas accounting for spatial and temporal heterogeneity. Oyster height was modeled with a gamma likelihood and log-link. Fixed effects included restoration treatment

(unrestored control versus restored with rocks) and harvest status (open versus closed). Random intercepts were added to capture unexplained variation for sampling station and monitoring period. Weakly informative priors were used for fixed effects [Normal(0, 1)] and for the gamma shape parameter [gamma(1, 1)]; group-level SD used default weakly informative priors. Models were fit in *R* with brms as described above. Convergence was assessed by standard diagnostics (trace plots,  $\hat{R} \approx 1.00$ , effective sample sizes), and calibration was checked with posterior predictive plots. For inference on group means, population-average predictions on the millimeter scale were generated by marginalizing over random effects, and posterior means with 95% CI were summarized. An interaction variant (treatment  $\times$  harvest) was also fit and its predictive performance compared using PSIS-LOO. The simpler additive specification was retained for main-text summaries, with interaction results provided in the Appendix.

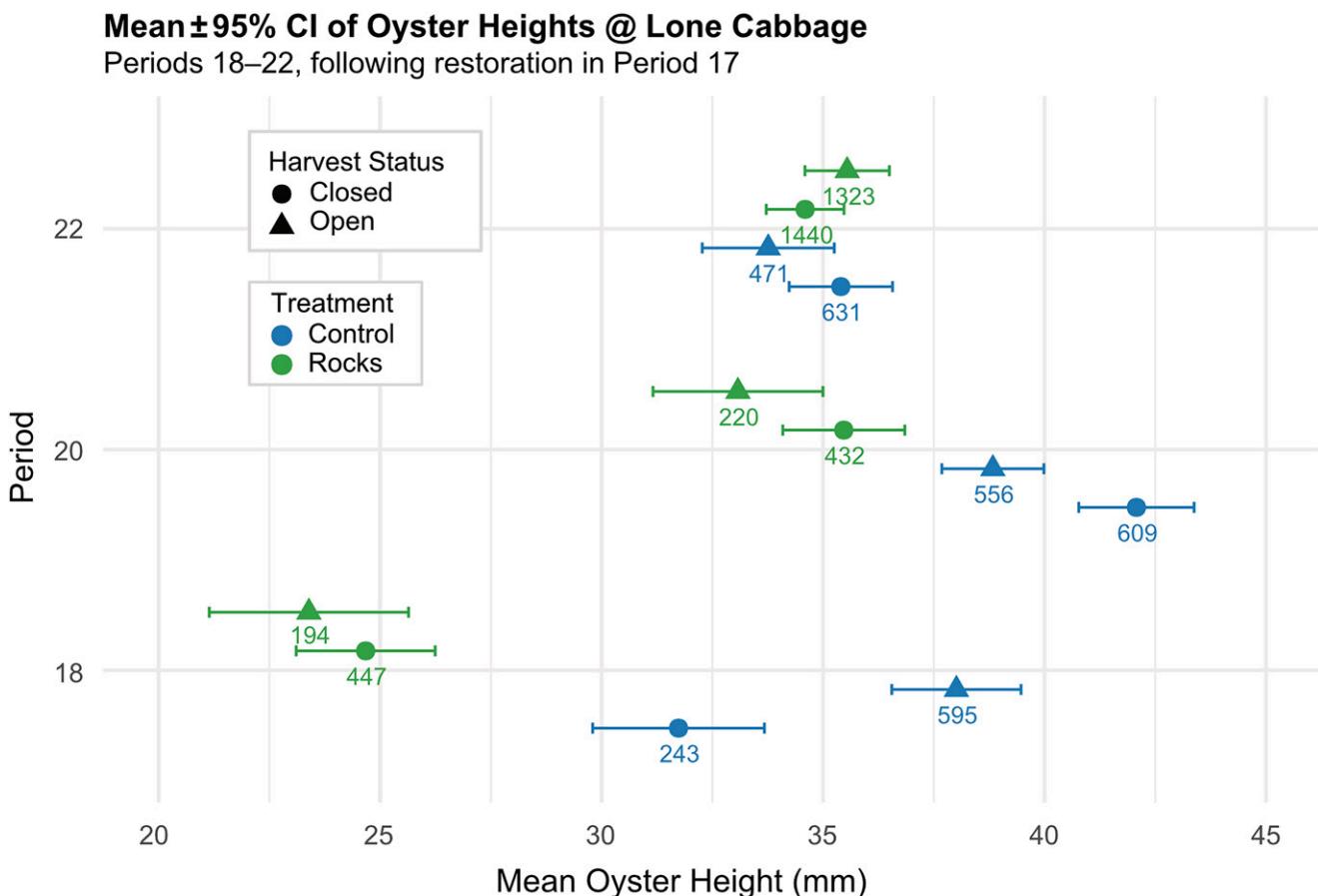
## RESULTS

A total of 27,496 live oysters were measured across all reef-harvest combinations: 8,997 on control reefs closed to harvest, 9,589 on control reefs open to harvest, 7,053 on restored reefs closed to harvest, and 1,857 on restored reefs open to harvest.

Mean shell height varied across these four groups (Fig. 2): on control reefs, oysters were slightly smaller in harvested areas [32.7 mm; 95% confidence interval (CI): 32.4–33.0] than in closed areas (33.4 mm; 95% CI: 33.1–33.7). In contrast, on restored reefs, oysters were larger in areas open to harvest (33.6 mm; 95% CI: 32.8–34.3) than areas closed to harvest (30.4 mm; 95% CI: 30.0–30.7). This reversal between control and restored reefs highlights the interaction between restoration and harvest effects on oyster growth (Table 1).

Legal-size oysters were relatively rare, with only 409 legal-size individuals (1.5% of the total) observed. By group, 137 legal oysters (1.5%) occurred on control (unrestored) reefs that were closed to harvest, 105 (1.1%) on control reefs that were open to harvest, 106 (1.5%) on restored reefs closed to harvest, and 61 (3.3%) on restored reefs that were open to harvest.

Oyster heights on restored control and rock (restored) reefs were generally similar within 1.5 y following restoration (Fig. 3). For example, about 1.5 y following the restoration of LC Reef (period 17), the differences in oyster heights were small between control and restored reefs (period 20), and within 3 y (period 22), the heights were similar (confidence intervals overlapped between control and restored reefs), and these similarities persisted (Fig. 3). No further analysis of oyster size over time was completed because of the observed similarities



**Figure 3.** Lone Cabbage (site offshore): mean oyster shell height (mm) by monitoring period with 95% confidence intervals, separated by treatment (control versus rocks; color) and harvest status (closed to harvest versus open to harvest; shape). Points are raw period means with *t*-based 95% CIs; adjacent numbers give sample sizes (N). Only periods where all four treatment  $\times$  harvest combinations were sampled (control/closed, control/open, rocks/closed, rocks/open) are shown (e.g., periods 18–22), following the large restoration completed just before period 17. These summaries are descriptive (not model-based) and illustrate the postrestoration increase in oyster height across harvest regimes.

and uncertainty in model predictive power in areas where restoration did not take place because restoration only occurred at LC (discussed below).

#### **Model Evaluation (Bayesian Regression Model with Fixed-Effects Model)**

The simple fixed-effects model accurately recovered the mean shell heights on control (unrestored) reefs observed in each of the four treatment-harvest groups, indicating that it effectively captured the primary treatment signal (Fig. 4). The posterior predictive distributions closely overlapped the empirical data histograms across the full range of oyster shell heights indicating adequate fit (Fig. 5). No strong evidence of model misfit was observed in terms of mean estimates or tail behavior. This suggests that each of the candidate models captured the primary structure of variation present in the data and were appropriate for subsequent model comparisons and interpretation of estimated effects.

#### **Locality-Only Model Results**

Population-average mean shell height varied by locality from about 28 to 41 mm. The largest oysters were at LT and NN, with LT estimated at 40.8 mm (95% CrI: 39.4–42.2;  $n = 705$ ) and NN at 40.3 mm (95% CrI: 38.5–42.2;  $n = 432$ ). Big Trout Creek (BT) was slightly lower at 38.9 mm (95% CrI: 37.5–40.3;  $n = 678$ ).

Cedar Key and Corrigan's Reef were intermediate, 36.2 mm (95% CrI: 35.3–37.1;  $n = 1,473$ ) and 35.3 mm (95% CrI: 34.7–35.8;  $n = 3,771$ ), respectively. Lone Cabbage was lower at 31.9 mm (95% CrI: 31.6–32.3;  $n = 8,025$ ), and Horseshoe Beach had the smallest mean at 28.3 mm (95% CrI: 27.8–28.8;  $n = 3,502$ ). Overall, these estimates indicate pronounced regional differences, with LT and NN highest, BT next, Cedar Key and Corrigan's Reef intermediate, and LC and Horseshoe Beach lowest.

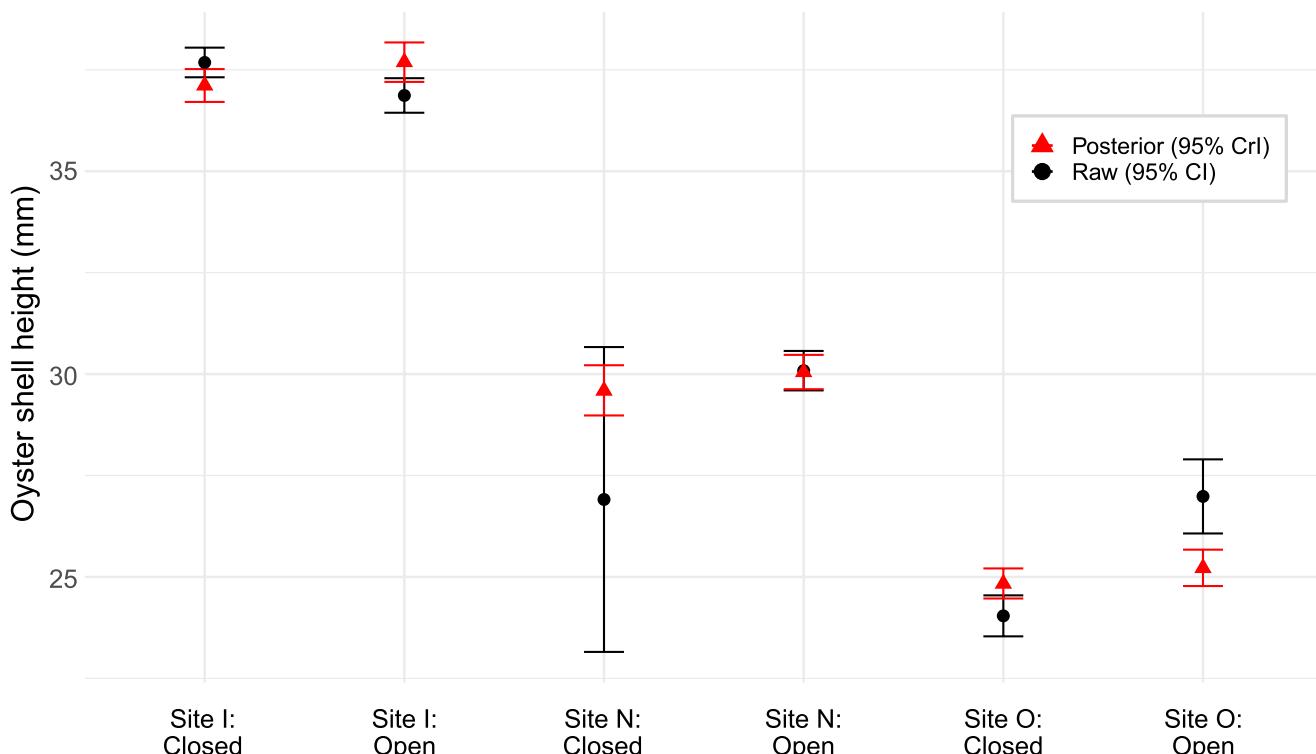
#### **Site-Only Model Results**

Population-average mean shell height differed across reef zones, declining from inshore to offshore. Inshore (I) reefs averaged 37.3 mm (95% CrI: 37.0–37.7;  $n = 10,454$ ), nearshore (N) averaged 30.0 mm (95% CrI: 29.6–30.5;  $n = 4,062$ ), and offshore (O) averaged 25.0 mm (95% CrI: 24.6–25.3;  $n = 4,070$ ). These estimates indicate a clear spatial gradient in oyster size, with inshore reefs supporting the largest oysters, followed by nearshore and then offshore reefs.

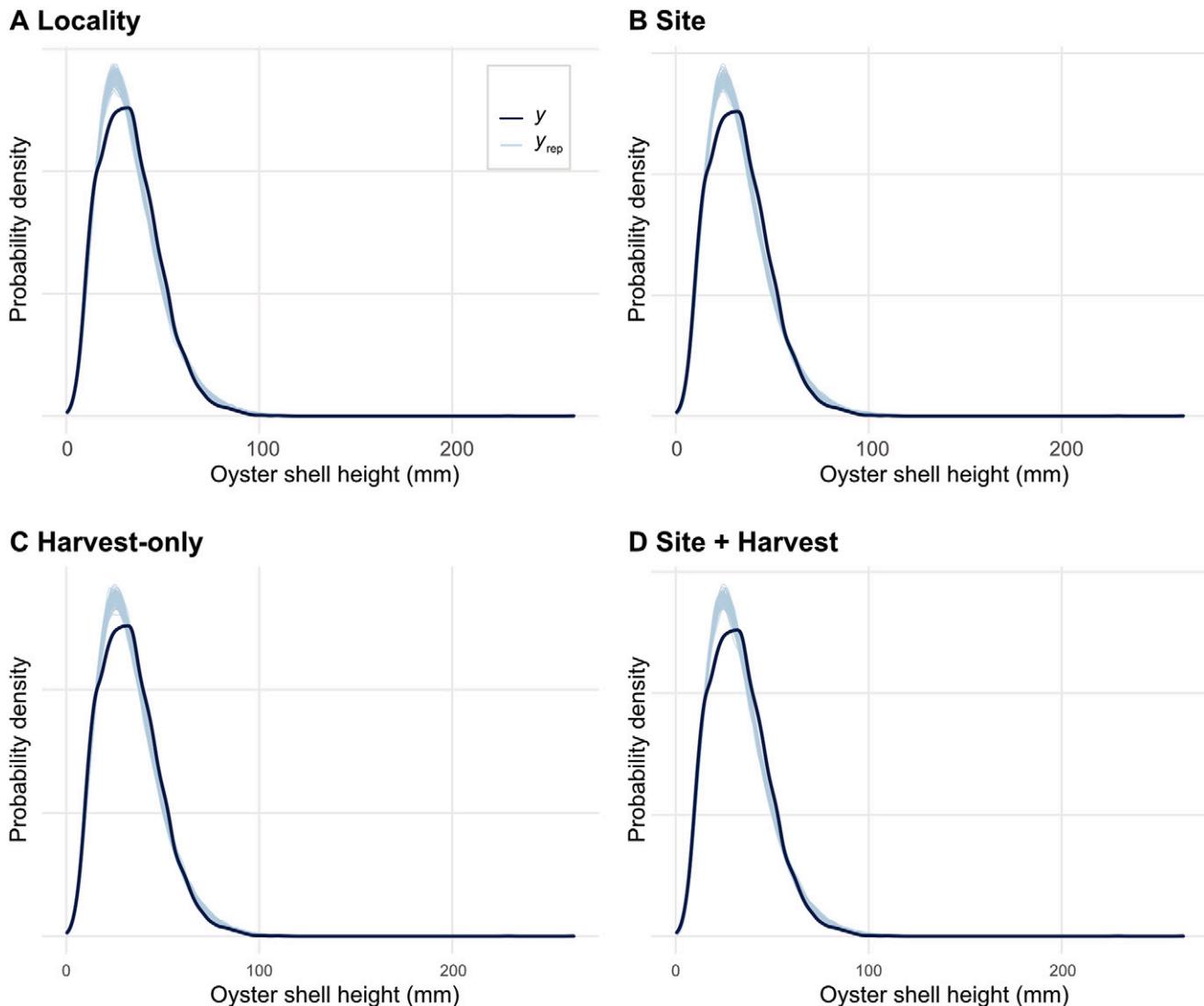
#### **Harvest-Only Model Results**

Across all control reefs, population-average mean shell height was slightly higher in closed areas than in open areas. Closed reefs averaged 33.4 mm (95% CrI: 33.0–33.7;  $n = 8,997$ ), whereas open reefs averaged 32.7 mm (95% CrI: 32.4–33.0;  $n = 9,589$ ). This corresponds to a modest difference of about 0.7 mm on average,

### **Control reefs: raw means vs posterior means (Site + Harvest)**



**Figure 4.** Comparison of raw data means (black) and posterior predicted means (red) from the Bayesian gamma regression model including site and harvest as fixed effects. Points represent posterior means or raw sample means; lines represent 95% credible intervals (posterior predictions) or 95% confidence intervals (raw data). Groupings reflect combinations of site (inshore, nearshore, and offshore) and harvest status (harvested or unharvested). The close agreement between raw means and posterior predictions indicates that the model accurately captures the observed differences among site-harvest groups.



**Figure 5.** Posterior predictive density overlays for four Bayesian gamma regression models fit to oyster shell height data from control (unrestored) reefs. Each panel represents one model: (A) locality model, (B) site model, (C) harvest model, and (D) site + harvest model. For each model, the observed distribution of oyster shell heights (black density curve) is compared with posterior predictive distributions generated from 100 draws from each posterior (blue density curves). Posterior predictive checks evaluate model fit by assessing whether the model can reproduce the shape and spread of the observed data.

indicating that harvest status alone explains only small variation in oyster size relative to spatial factors reported above.

#### Site × Harvest Interaction Model Results

Posterior predictions from the site + harvest model show strong spatial gradients and only modest within-site harvest differences (Table A2). At inshore reefs, mean shell height was 37.1 mm (95% CrI: 36.7–37.5;  $n = 6,142$ ) in closed areas and 37.7 mm (95% CrI: 37.2–38.2;  $n = 4,312$ ) in open areas ( $\approx 0.6$  mm higher when open). At nearshore reefs, means were 29.6 mm (95% CrI: 29.0–30.2;  $n = 55$ ) for closed and 30.0 mm (95% CrI: 29.6–30.5;  $n = 4,007$ ) for open ( $\approx 0.4$  mm difference; note the much smaller  $N$  for nearshore-closed). At offshore reefs, means were 24.8 mm (95% CrI: 24.5–25.2;  $n = 2,800$ ) in closed and 25.2 mm (95% CrI: 24.8–25.7;  $n = 1,270$ ) in open ( $\approx 0.4$  mm difference). Overall, zone-to-zone differences (inshore > nearshore > offshore) dominate

variation in shell height, whereas the harvest contrast within zones is consistently small (approximately 0.4–0.6 mm).

#### Comparison across Simple Fixed-Effects Models

The PSIS-LOO favored the site + harvest model (baseline,  $\Delta\text{ELPD} = 0$ ). The site-only model was statistically indistinguishable from it ( $\Delta\text{ELPD} = -0.98$ , SE = 1.96). In contrast, the locality-only ( $\Delta\text{ELPD} = -689.9$ , SE = 53.4) and harvest-only ( $\Delta\text{ELPD} = -1088.2$ , SE = 48.5) models had worse out-of-sample fit. Consistent with this, Bayes  $R^2$  was approximately 0.11 for both site + harvest (0.109; 95% CrI: 0.102–0.117) and site (0.109; 0.101–0.116), lower for locality (0.046; 0.040–0.053), and near-zero for harvest alone (0.0005; 0.00003–0.0013). On the millimeter scale for the site + harvest fit, population-average means were: inshore (closed to harvest) 37.1 mm (95% CrI: 36.7–37.5) versus inshore (open to harvest) 37.7 mm (37.2–38.2); nearshore (closed

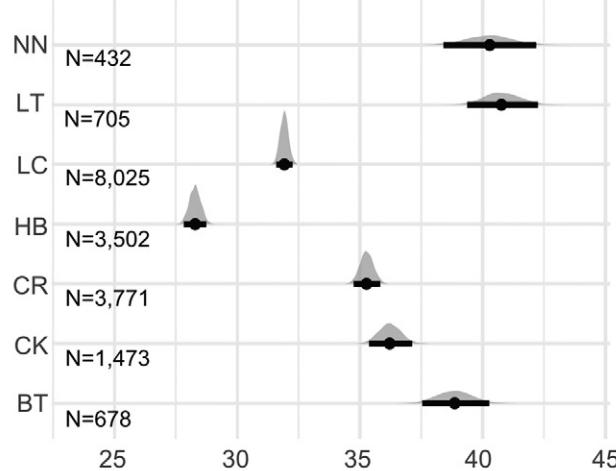
to harvest) 29.6 mm (29.0–30.2) versus nearshore (open to harvest) 30.0 mm (29.6–30.5); offshore (closed to harvest) 24.8 mm (24.5–25.2) versus offshore (open to harvest) 25.2 mm (24.8–25.7; Fig. 6). Thus, spatial (site) differences explain the bulk of variation and predictive performance, whereas harvest status adds only small shifts (approximately 0.4–0.6 mm) once site is included.

#### *Restoration Effects on Heights—LC*

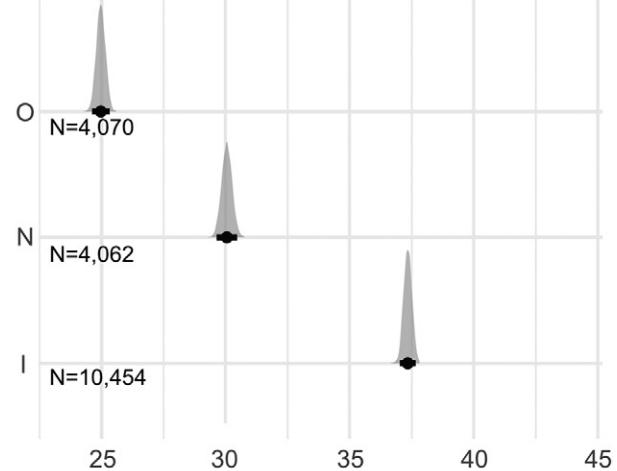
At LC (offshore), a Gamma-log model with two main effects was fit: restoration (control versus rocks) and harvest status (closed versus open). All four treatment  $\times$  harvest combinations (control/closed to harvest, control/open to harvest, rocks/closed to harvest, and rocks/open to harvest)

were represented in the data, although field time prioritized restored versus unrestored comparisons, so sample sizes were largest for restored reefs. In this main-effects parameterization, the Control/Closed group serves as the reference level, and the restoration and harvest coefficients describe multiplicative changes in mean shell height relative to this baseline. Sample sizes at LC (offshore) were  $N = 2,800$  for control/closed to harvest,  $N = 1,270$  for control/open to harvest,  $N = 7,053$  for rocks/closed to harvest, and  $N = 1,857$  for rocks/open to harvest. We summarized these data with a regression model that included main effects of restoration (control versus restored) and harvest status (closed versus open), using the control/closed group as the reference. In this model, the restoration and harvest terms describe how much larger or smaller mean

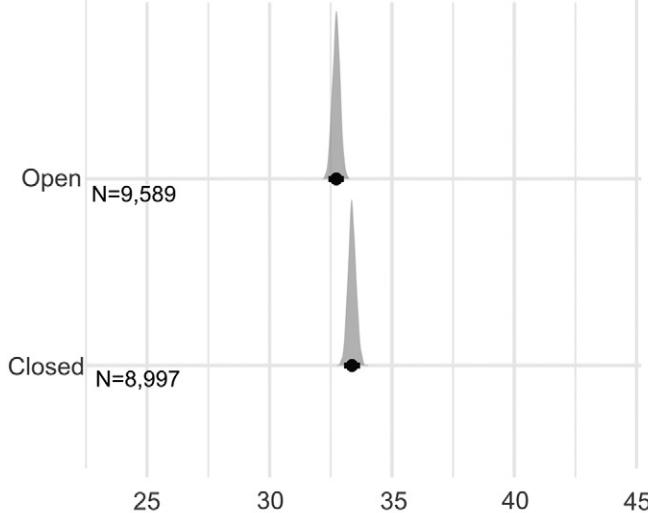
### A Locality effects



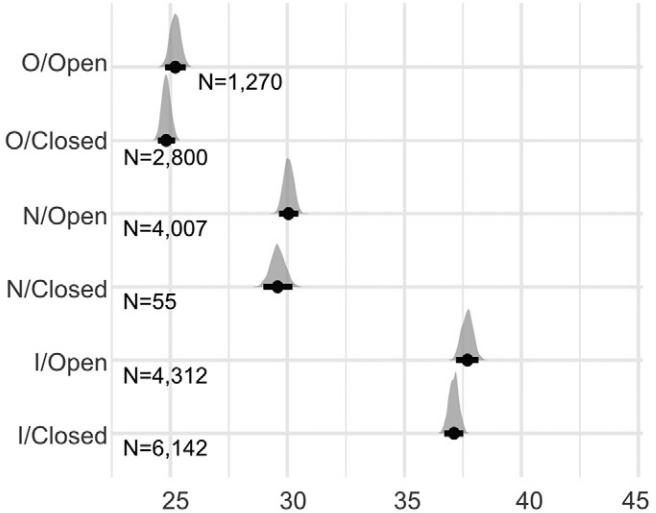
### B Site effects



### C Harvest effects

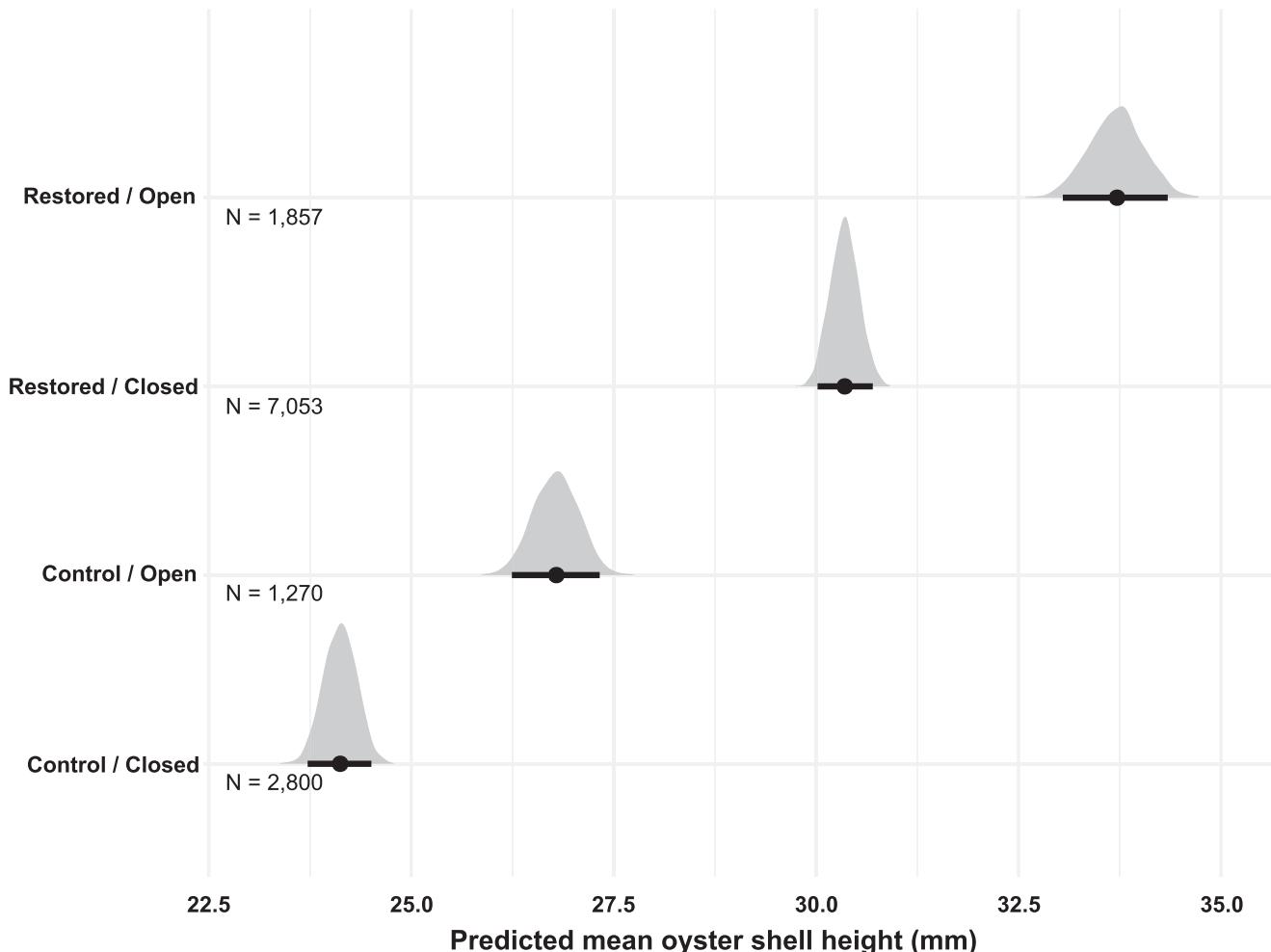


### D Site $\times$ Harvest effects



**Predicted mean oyster height (mm)**

**Figure 6.** Posterior predicted oyster shell heights from four Bayesian gamma regression models fit to unrestored (control) reefs. Panels show posterior distributions for (A) locality, (B) site, (C) harvest, and (D) site  $\times$  harvest effects. Models were fit in brms with weakly informative priors and a log-link. Points indicate posterior means with 95% credible intervals; half-eye shapes depict uncertainty in predicted mean shell height (mm) at each factor level. Comparisons across panels illustrate how variation is partitioned among spatial and harvest predictors; site-level differences explain far more of the observed variation in oyster height than harvest alone.



**Figure 7.** Posterior predictions of oyster shell height (mm) for the offshore Lone Cabbage reef (site = O), estimated using a Bayesian Gamma regression model with fixed effects for restoration (control versus restored) and harvest status (closed versus open). Half-eye plots show the full posterior distribution for each treatment  $\times$  harvest combination, with horizontal bars indicating 95% credible intervals; sample sizes (N) for each group are shown next to the corresponding distribution. These predictions illustrate that restoration increased oyster shell height relative to control reefs at site O, whereas harvest status had a smaller effect.

shell height is, on average, relative to that baseline. The main-effects model indicated that opening reefs to harvest increased mean shell height by roughly 10–15%, and that restored reefs had larger oysters than control reefs regardless of harvest status. Adding a treatment  $\times$  harvest interaction term did not change these conclusions: the interaction effect was close to zero, with a wide credible interval that included both positive and negative values, and the interaction model did not fit the data any better than the simpler main-effects model.

As a sensitivity check, a random intercept for monitoring period to control for period-specific baseline shifts was added to the model. In this model, the restoration effect remained positive (ratio = 1.23, 95% CrI: 1.19–1.26), whereas the harvest effect centered at one (ratio = 1.00, 95% CrI: 0.97–1.03). This suggests the small harvest signal in the main-effects model was largely explained by between-period differences. Note that this specification allows period-level baseline heterogeneity but assumes a constant harvest effect across periods. Overall, the LC offshore results show a consistent increase in oyster shell height with restoration, whereas harvest status has at most a small and

uncertain effect. For context, Bayesian  $R^2$  was approximately 0.043 for the main-effects and interaction models and approximately 0.11 when period was included as a random effect, reflecting that restoration explains part of the variation but that much of the variability remains due to other reasons.

#### Full Bayesian Regression Model (Fixed and Random Effects)

To account for unmeasured spatial and temporal heterogeneity, a multilevel gamma-log model was fit with fixed effects for treatment (restored versus control) and harvest status (open versus closed), and random intercepts for sampling station (161 levels) and monitoring period (12 levels). The random-effect SD on the log scale were approximately 0.28 for stations and 0.16 for periods, and overall fit was good (Bayes  $R^2$  = 0.21, 95% CrI: 0.20–0.21). Population-average posterior means on the millimeter scale were 31.1 mm (28.0–34.4) for control/closed to harvest, 31.8 mm (95% CrI: 28.6–35.2) for control/open to harvest, 40.1 mm (35.9–44.7) for rocks/closed to harvest, and 41.1 mm (36.7–45.7) for rocks/open to harvest.

These estimates indicate a clear restoration effect of roughly +9–10 mm within a harvest category, whereas the contrast between oyster heights in areas open or closed to harvest was small at about +0.7–1.0 mm. A model with an interaction term provided only a very small improvement in predictive performance ( $\Delta\text{ELPD} = +12.7$ , SE = 4.4) and did not change conclusions. Given that treatment contrasts are the primary focus and fixed-effects models produce similar group-level predictions, fixed-effects results are reported in the main text, whereas complete multilevel results appear in Appendix.

## DISCUSSION

More than 27,000 oysters from control and restored intertidal reefs across the Big Bend region of Florida were analyzed to evaluate how spatial setting, harvest status, and restoration shape oyster heights. Spatial setting emerged as the primary driver. Predicted mean size declined from inshore = 37.1 mm (95% CrI: 36.7–37.5) to nearshore = 29.6 mm (29.0–30.2) to offshore = 24.8 mm (24.5–25.2; Fig. 6). By comparison, oyster heights in areas open to harvest versus closed to harvest changed mean size within a site by only about 0.4–0.6 mm, indicating that where an oyster reef is found on the landscape is a larger factor in explaining oyster size on intertidal reefs than whether that intertidal reef is in an area open or closed to harvest (Fig. 6).

Restoration produced clear biological gains in oyster height. At LC (offshore), adding limestone cultch increased mean shell height within a harvest category by roughly 6–10 mm: from 24.0 mm (95% CrI: 23.6–24.5) on unrestored reefs that were closed to harvest to 30.4 mm (95% CrI: 30.1–30.7) on restored reefs that were closed to harvest and to 33.6 mm (95% CrI: 32.8–34.3) on restored reefs open to harvest (Figs. 6 and 7). An alternative model with a random intercept for period retained a strong restoration effect (ratio = 1.23, 95% CrI: 1.19–1.26) whereas the harvest effect centered near one (ratio = 1.00, 95% CrI: 0.97–1.03). In practical terms, restoration delivered sustained increases in oyster height, and restored reefs that were open to harvest were actually predicted to have larger oysters than restored reefs that were closed to harvest.

### Mechanisms, Setting, and Long-Term Context

These results align with prior work indicating that cultch mass and reef elevation are key drivers of oyster abundance and size (Frederick et al. 2016, Aufmuth et al. 2025, Casteel et al. 2025, Pine et al. in review, this work). Durable, elevated substrate increases settlement area, stabilizes elevation, and creates positive feedback that sustain recruitment and growth (Lenihan & Peterson 1998, Schulte et al. 2009, Colden et al. 2017, Lipcius et al. 2021). Oyster reef elevation, driven by the accumulation of live and dead oysters, creates positive feedback that enhances persistence and resilience. For example, Schulte et al. (2009) showed that high-relief reefs in Chesapeake Bay supported oyster densities approximately four times greater than low-relief reefs, and that reef height was strongly linked to sustained recruitment, reduced sedimentation, and improved survival. Similar feedback between elevation, growth, and persistence likely operate in Suwannee Sound. Consistent with these results and prior studies, restoration that rebuilds cultch mass and elevation can promote both increased abundance (Frederick et al. 2016, Pine et al.

2022, Pine et al. in review) and larger oyster heights (this study), advancing overall ecosystem restoration success.

Growth differences between subtidal and intertidal oysters are well documented and likely reflect contrasts in aerial exposure, metabolic stress, and resource availability (Dame 1972, Peterson & Black 1987, Lawrence 1988, Littlewood 1988, Roegner & Mann 1995, Jenkins 2017). Subtidal oysters feed continuously but face higher exposure to aquatic predators and parasites such as boring clams *Diplothyra smithii* and sponges *Cliona* spp., which can suppress growth and survival (Littlewood 1988, Jenkins 2017). Intertidal oysters experience periodic dewatering that limits feeding but reduces predation and parasitism. That both subtidal and intertidal oysters are found in Suwannee Sound likely promotes resilience in oyster populations to different types of disease and predation threats.

The advantages of intertidal placement for restoration are echoed in other systems (Caretti et al. 2024). In North Carolina, Powers et al. (2009) reported substantially higher success for intertidal oyster reef restoration. Powers et al. (2009) found that 23 intertidal oyster sanctuaries met performance criteria, including mean densities greater than 205 oysters  $\text{m}^{-2}$ , biomass greater than 9.5 kg  $\text{m}^{-2}$ , and market-size densities greater than 105 oysters  $\text{m}^{-2}$ . Only 26 of 65 subtidal reefs (40%) met restoration goals and 39 (60%) failed. These outcomes highlight habitat setting as a major control on restoration performance. To reduce confounding from site and tide, sampling was standardized to low predicted tidal height at NOAA station 8727520 ( $\leq -0.24$  m mean lower low water for  $\geq 120$  min), allowing shell-height comparisons at comparable water elevations across periods. Although wind and exact field setup can introduce small deviations, using a consistent tidal window and the very low elevation gradient of intertidal reef surface in this area (Aufmuth et al. 2025) reduced inundation time artifacts in field sampling. Future work should incorporate full inundation histories by including subtidal oyster reefs to determine whether growth differences similar to those observed for intertidal oysters occur. Longer inundation times may help to explain the higher frequency of legal-size oysters in Powers et al. (2009) compared with the results of this study. Because larger oysters disproportionately provide greater ecosystem services understanding whether expanding restoration efforts to subtidal regions could provide ecosystem and fishery benefits (Coen et al. 2007, Allen et al. 2011, Caretti et al. 2024). Local oyster harvesters do target subtidal oysters near the restored LC Reef which are possibly individual oysters and oyster clumps that first settled on LC, grew, and then were displaced by wave action from the restored intertidal reef to subtidal areas. These oysters then grew to the larger sizes selected by the commercial fishery. This transport from the restored LC Reef to the unrestored, adjacent subtidal areas likely mimics the natural source sink dynamics between intertidal (source) and subtidal (sinks) reefs which may exist in the region. Understanding these source-sink dynamics and how this informs both restoration and fishery management is an important area of future work.

The spatial patterns observed in oyster heights across the inshore-to-offshore gradient may reflect a slow, geologic-scale trajectory of reef formation and degradation in Suwannee Sound. Along the west-central coast of Florida, a low-gradient, sediment-starved, karstic platform, long-term sea-level rise, and antecedent topography have shaped coastal morphology

for millennia (Hine et al. 1988). As sea level rose, oyster reefs likely began at inshore intertidal elevations that favored recruitment, growth, and bioherm development (Lenihan & Peterson 1998, Powell et al. 2001, Colden et al. 2017, Pace et al. 2020). Today, inshore reefs support the largest oysters and the highest densities (Fig. 4; Pine et al. *in review*), consistent with the prolonged accumulation of cultch mass and the stable structure required for persistent, and not transient, accretion, and accumulation of vertical relief (Aufmuth et al. 2025, Casteel et al. 2025). In contrast, offshore oyster reefs in this region have lost area, elevation, and abundance (Seavey et al. 2011, Moore et al. 2020, Aufmuth et al. 2025, Pine et al. *in review*), possibly because higher wave energy and sediment mobility under rising seas destabilize reef structure and accelerate cultch losses (Hine et al. 1988). As offshore reefs degrade, inshore complexes become increasingly important for sustaining oyster populations, both because of their intertidal setting and because they lie behind remnant offshore structures that continue to buffer wave energy until they are lost. These inshore complexes will also become offshore reefs as sea levels continue to rise. This is not a new process and is demonstrated by the practice in recent history of mining oyster shell at inland areas in Florida. Taken together, these lines of evidence suggest that the current spatial gradient represents different points along a continuum of reef evolution governed by interacting geological, biological, and hydrodynamic processes operating over long timescales (Wright et al. 2005). The restored LC Reef, built to a target elevation similar to remnant viable offshore reef on the northern end of LC and coincidentally similar to inshore elevations near Big and Little Trout creeks, may now function more like an inshore reef at the current sea level given its durable cultch and elevated profile (Aufmuth et al. 2025, Casteel et al. 2025).

It should be noted that oysters in this region have been harvested and restored through cultch addition for thousands of years, with alternating periods of intensive human use and abandonment spanning several centuries (Jenkins 2017, Sassaman et al. 2020). Archaeological evidence from Suwannee Sound, where oysters served as a major food source and were used in the construction of civic-ceremonial structures (Jenkins 2017), suggests that oysters harvested by native tribes may have exceeded the sizes observed on modern intertidal reefs. Preliminary analyses of shell heights from midden sites dated to AD 400–600 indicate mean and median oyster heights of 56.6 and 55.9 mm, respectively (Wallis and LeFebvre 2022, unpublished data, Florida Museum of Natural History). These findings suggest either larger intertidal oysters during this period or harvest from a combination of intertidal and subtidal habitats.

#### *Advantages of the Analytical Approach*

In this study, straightforward frequentist statistical summaries were paired with a Bayesian modeling framework to analyze oyster heights. The frequentist approach summarized the raw data by locality, site, treatment, and harvest (means, SD, and 95% CI), which provides an intuitive, design-based view

of the patterns in oyster heights in millimeters. The Bayesian models then build on those summaries. Because oyster heights are positive and can be right-skewed, using a gamma–log-link matches the data distribution and avoids normality assumptions in the modeling efforts. The reported posterior means with 95% CrI give an interpretable measure of uncertainty on the millimeter scale; and station and period effects account for where and when oysters were measured, so correlated observations are not treated as independent. Posterior predictive checks further assess how well fitted models reproduce the observed size distributions. Together, the raw frequentist summaries and the Bayesian models tell a consistent story and provide complementary evidence on how restoration and harvest relate to oyster size structure.

#### *Management Implications*

This study documents that restoration creating stable, durable substrate suitable for larval settlement and providing vertical relief that confers multiple benefits to oyster populations (Lenihan & Peterson 1998, Schulte et al. 2009, Colden et al. 2017) can rapidly improve oyster abundance and size structure on degraded reefs in the Big Bend region of Florida, even under spatially managed harvest (Frederick et al. 2016, Pine et al. *in review*). Taken together, these findings emphasize both the potential and complexity of oyster restoration in the Big Bend region. Future restoration planning will benefit from integrating site selection criteria that explicitly consider cultch material, durability, and reef elevation, ensuring that restoration targets locations with strategies most likely to support long-term oyster persistence. The results also underscore the need for expanded restoration replication across sites and regions to further disentangle treatment effects from site-specific variability. An integrated restoration framework that pairs cultch addition, ongoing monitoring, adaptive management, and long-term assessment of reef elevation and structure will be essential to sustain oyster populations and restore ecosystem function under changing environmental conditions in the “Nature Coast” region of Florida.

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#### APPENDIX: Alternative Model Formulation

Preliminary checks suggested that adding random effects improved statistical fit relative to fixed-effects models, so a full Bayesian multilevel gamma-log model with fixed effects for treatment (control versus restored) and harvest status (closed versus open), and random intercepts for monitoring period and sampling station were fit using weakly informative priors consistent with the main analysis and summarized population-average predictions.

#### Main Multilevel Model

We modeled lived shell height using a gamma likelihood with a log link and the following linear predictor:

$$\text{height\_live} \sim \text{treatment} + \text{harvest} + (1|\text{station}) + (1|\text{period\_f})$$

We used weakly informative priors: fixed effects coefficients

$b \sim \text{Normal}(0,1)$ ; standard deviations of the station and period\_f random intercepts

$\sigma_{\text{station}}, \sigma_{\text{period\_f}} \sim \text{Exponential}(1)$ ; and the Gamma shape parameter

$$\phi \sim \text{Gamma}(1,1).$$

#### Interaction Model

To allow the effect of harvest to differ by treatment, we fit an interaction model:

$$\text{height\_live} \sim \text{treatment} * \text{harvest} + (1|\text{station}) + (1|\text{period\_f})$$

This model used the same likelihood (Gamma with log link) and the same priors as the main model:

$$b \sim \text{Normal}(0,1),$$

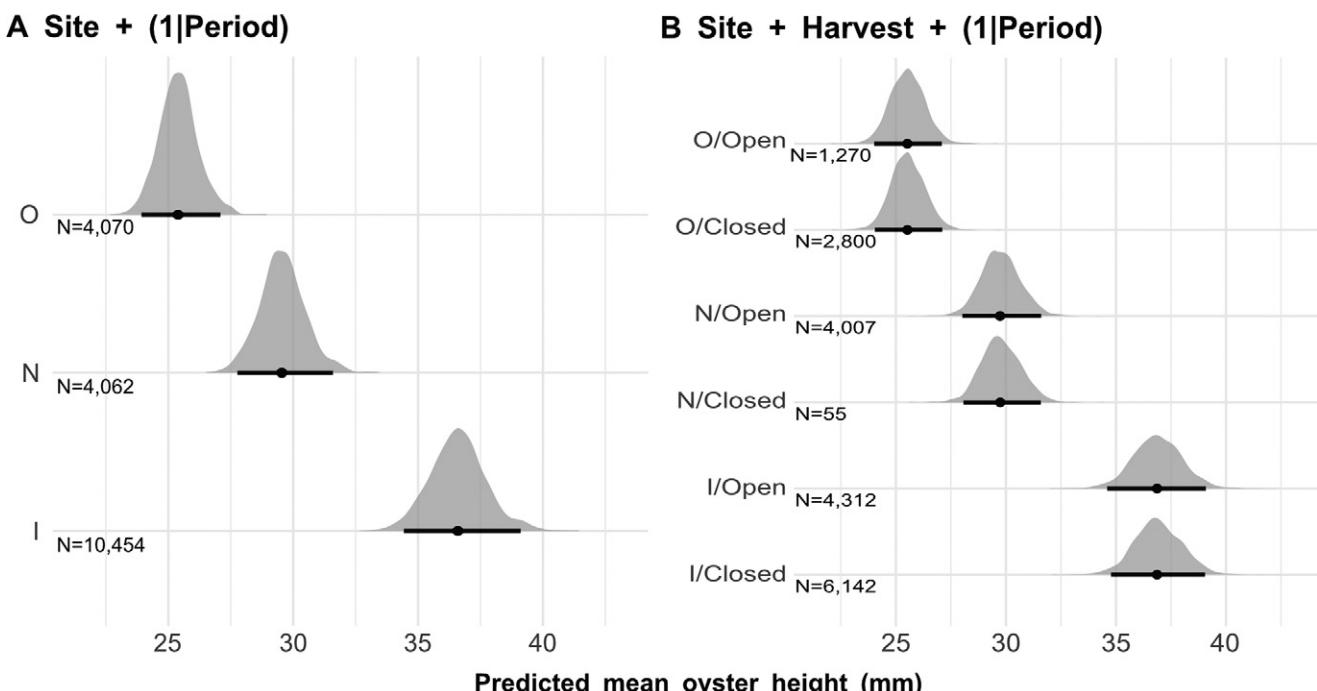
$$\sigma_{\text{station}}, \sigma_{\text{period\_f}} \sim \text{Exponential}(1),$$

$$\phi \sim \text{Gamma}(1,1).$$

The multilevel model fit well (Bayesian  $R^2 = 0.206$ , 95% CrI 0.199–0.213). On the log scale, the estimated SD of station intercepts was 0.28 (0.25–0.32), indicating spatial clustering, whereas period intercepts were smaller at 0.16 (0.10–0.25), consistent with a modest temporal component. Back-transformed, population-average mean oyster heights were 31.1 mm (95% CrI: 28.0–34.4) for control/closed to harvest, 31.8 mm (28.6–35.2) for control/open to harvest, 40.1 mm (35.9–44.7) for rocks/closed to harvest, and 41.1 mm (36.7–45.7) for rocks/open to harvest (Fig. A1). On the coefficient scale, the treatment effect was 0.26 (0.22–0.29), a multiplicative ratio of approximately 1.30 that implies a large, positive restoration effect on shell height. The harvest effect was 0.02 (−0.02 to 0.06), a ratio of approximately 1.02, indicating at most a small change once treatment and clustering are accounted for.

For completeness, an interaction variant with treatment × harvest was also fit. This model made only a very small improvement in predictive performance relative to the main multilevel model ( $\Delta\text{ELPD} \approx +12.7$ , SE = 4.4) and did not change the substantive conclusion: restoration drives the primary shift in mean size, whereas harvest contributes little after spatial and temporal heterogeneity are modeled.

Including random intercepts widened CrI, as expected, but group means remained broadly consistent with the



**Figure A1.** Posterior predicted oyster shell height (mm) for each site from two Bayesian GLMs fit to unrestored (control) reefs with gamma likelihood and period random intercept. Panel (A) shows predictions from the Site + (1|Period) model. Panel (B) shows predictions from the Site + Harvest + (1|Period) model. Predicted means and 95% credible intervals are displayed as half-eye plots. Adding harvest produces modest separation within sites, whereas site-level differences remain the dominant source of variation. Models were fit in brms with the cmdstanr backend.

**TABLE A1.**  
**Sample size (number of oysters measured) by locality and monitoring period.**

Locality	1	2	3	6	10	11	16	18	19	20	22	24	Total
BT	0	0	0	0	0	0	188	100	0	90	150	150	678
CK	1,182	0	0	221	0	0	0	0	70	0	0	0	1,473
CR	1,368	1,577	383	360	0	0	0	0	83	0	0	0	3,771
HB	1,380	1,234	582	257	0	0	0	0	49	0	0	0	3,502
LC	1,443	858	350	252	1,763	1,187	1,524	1,266	62	1,398	3,505	3,327	16,935
LT	0	0	0	0	0	0	185	70	0	210	120	120	705
NN	0	0	0	0	0	0	90	43	0	119	90	90	432
Total	5,373	3,669	1,315	1,090	1,763	1,187	1,987	1,479	264	1,817	3,865	3,687	27,496

Values represent the number of live oyster shell height observations collected at each locality across the 12 monitoring periods used in the analysis. The unbalanced structure reflects variation in sampling design and site accessibility over time.

**TABLE A2.**  
**Raw oyster shell height summary statistics by site and harvest status for unrestored (control) reefs.**

Site	Harvest	N	Mean_mm	Lower95_mm	Upper95_mm	Mean (95% CI)
I	Closed	6,142	37.68	37.32	38.05	37.68 (37.32–38.05)
I	Open	4,312	36.87	36.44	37.29	36.87 (36.44–37.29)
N	Closed	55	26.91	23.15	30.67	26.91 (23.15–30.67)
N	Open	4,007	30.08	29.6	30.57	30.08 (29.60–30.57)
O	Closed	2,800	24.04	23.54	24.55	24.04 (23.54–24.55)
O	Open	1,270	26.98	26.07	27.9	26.98 (26.07–27.90)

Values represent sample size (*N*), observed mean shell height (mm), and corresponding 95% confidence intervals based on SE calculated from the raw data.

simpler fixed-effects fits and with raw summaries. Visual inspection of control data over time did not reveal strong temporal trends, and the agreement between fixed-effects and multilevel predictions suggests that the main conclusions are not artifacts of unmodeled temporal variation or

of the unbalanced sampling design. Because the focus is on estimating treatment contrasts and the fixed-effects and multilevel results tell the same story, the main text reports fixed-effects results, with full multilevel summaries provided here for completeness.