

# Oyster cultch–recruit patterns provide new insight into the restoration and management of a critical resource

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## ABSTRACT

**Objective:** Our objective was to quantify the relationship between oyster cultch mass ( $\text{kg}/\text{m}^3$ ) and density ( $\text{oysters}/\text{m}^2$ ) of live eastern oyster *Crassostrea virginica* on intertidal reefs in Suwannee Sound, Florida. We also evaluated the potential for a cultch-mass threshold below which recruitment declines (depensation) to inform oyster fishery management and restoration strategies.

**Methods:** During the winters of 2020–2022, we collected 185 standardized  $0.025\text{-m}^3$  grub-box samples of cultch from unrestored intertidal reefs in Suwannee Sound and conducted line-transect surveys to estimate live eastern oyster density. Cultch mass was converted to units of weight per area ( $\text{kg}/\text{m}^3$ ) for analysis. We modeled the relationship between cultch mass and live eastern oyster density using a Beverton–Holt recruitment framework coupled with two spat-settlement functions—one incorporating a minimum cultch threshold ( $H_{\min}$ ) and one without. Models were fit in a Bayesian framework using Template Model Builder and No-U-Turn-Sampler, Markov chain–Monte Carlo sampling. We compared two biologically plausible parameter cases and evaluated model performance using Pareto-smoothed importance sampling leave-one-out cross validation.

**Results:** Live eastern oyster density increased in a saturating fashion with cultch mass. Models that included a minimum cultch threshold yielded median estimates of  $H_{\min}$  near  $20\text{ kg}/\text{m}^3$ , with 86–88% of posterior samples exceeding  $5\text{ kg}/\text{m}^3$ . However, the Pareto-smoothed importance sampling leave-one-out cross-validation model comparison did not favor threshold models over those without a threshold, and posterior distributions for  $H_{\min}$  were broad and included substantial probability density near zero. These findings suggest that recruitment limitation at low cultch mass is a plausible dynamic, but the exact location or existence of a cultch threshold remains uncertain.

**Conclusions:** Our findings highlight the potential for a cultch-mass threshold below which eastern oyster recruitment may be limited, consistent with ecological theory and field observations that larval settlement depends on suitable substrate. Although the precise value of this threshold remains uncertain, model results suggest that recruitment may decline when cultch mass falls below approximately  $20\text{ kg}/\text{m}^3$ . We recommend that restoration and management efforts maintain cultch mass above a precautionary range of  $5\text{--}20\text{ kg}/\text{m}^3$  to reduce the risk of reef collapse and support recovery. Further research is needed to more precisely estimate system-specific thresholds and better understand how cultch mass interacts with other oyster reef characteristics.

**KEYWORDS:** fisheries management, habitat management, oyster restoration, restoration and enhancement

## LAY SUMMARY

Our research in Suwannee Sound suggests that oyster populations may need a minimum of 5 to  $20\text{ kg}$  of cultch per cubic meter of reef to support successful recruitment. While our models show a strong possibility that recruitment drops off below this level, the exact threshold is uncertain and may differ across locations. Because oyster larvae rely on suitable substrate (type and amount) to settle and grow, maintaining adequate cultch to support positive population growth should be a key focus for managing and restoring oyster reefs. More research is needed to refine these estimates and understand how cultch thresholds may vary across different reef systems.

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## INTRODUCTION

The most common oyster species in eastern North America—the eastern oyster *Crassostrea virginica* (hereafter referred to as “oyster”—are found on the Atlantic coast of North America from Nova Scotia to Central America (Arakawa, 1990). Oyster reefs and oyster fisheries across their range have declined over the past 200 years, with multiple causal factors proposed. These include overharvesting (Gross & Smyth, 1946; Rothschild et al., 1994; Wilberg et al., 2013), shell removal (Lenihan & Micheli, 2000), disease (Ford & Tripp, 1996; Wilberg et al., 2011), and water quality deterioration (Lenihan & Peterson, 1998; Seliger et al., 1985). Some of the most notable recent U.S. declines have occurred in Florida (Camp et al., 2015; Kelly, 2019; Pine et al., 2015).

Oysters have been an essential resource for people in the northeastern Gulf of Mexico since before European settlement (Barbour et al., 2019; Jenkins, 2017; Sassaman et al., 2017). Florida’s most productive oyster reefs (measured by fishery landings and trips) were historically in Apalachicola Bay, in the northern Gulf of Mexico, contributing approximately 90% of Florida’s and 10% of the USA’s oyster harvest (Arnold & Berrigan, 2002; Dugas et al., 1997). The Apalachicola Bay wild oyster fishery collapsed in 2012 for reasons that were disputed by the states of Florida and Georgia to the U.S. Supreme Court, and the fishery was closed in August 2020 by the Florida Fish and Wildlife Conservation Commission until December 2025 (Camp et al., 2015; Kelly, 2019; Pine et al., 2015).

Oyster restoration efforts are widespread across the United States. In the U.S. Gulf of Mexico region, approximately US\$200 million from the consolidated Deepwater Horizon oil spill settlements was allocated for oyster restoration (La Peyre et al., 2022; Pine et al., 2022; Smith et al., 2010). Every U.S. Gulf Coast state, along with most Atlantic coast states, has active oyster restoration initiatives (Bersoza Hernández et al., 2018; La Peyre et al., 2022). These efforts highlight two key points: (1) States recognize the ecological and economic importance of oysters and are committed to restoring degraded habitats, and (2) traditional management measures—such as harvest seasons, size limits, and bag limits—have not been sufficient to prevent oyster population declines. This suggests that either these regulations alone are inadequate for sustainable oyster harvest or that additional factors beyond harvest are contributing to the declines.

Traditional approaches used to assess and manage fisheries may not work well for oysters because oyster life history and stock–recruitment dynamics are different from those of most finfishes (Hilborn & Walters, 1992). As a result, traditional fisheries assessment and management approaches may overlook critical aspects of oyster ecology. Oyster life history is complex, as it involves multiple stages with distinct ecological roles. Larvae are free swimming, while spat are larvae that have settled from the water column. Successful recruitment depends on larvae settling on hard substrates such as naturally occurring cultch—a complex matrix of living and dead material composed of live oysters and the shells of previous generations (Mann et al., 2022; Mann & Powell, 2007). Adult oysters are obligate, demersal, and reef associated, meaning they rely on structured habitats for survival.

Although this dependency on cultch seems straightforward, it creates unique and potentially complex population dynamics

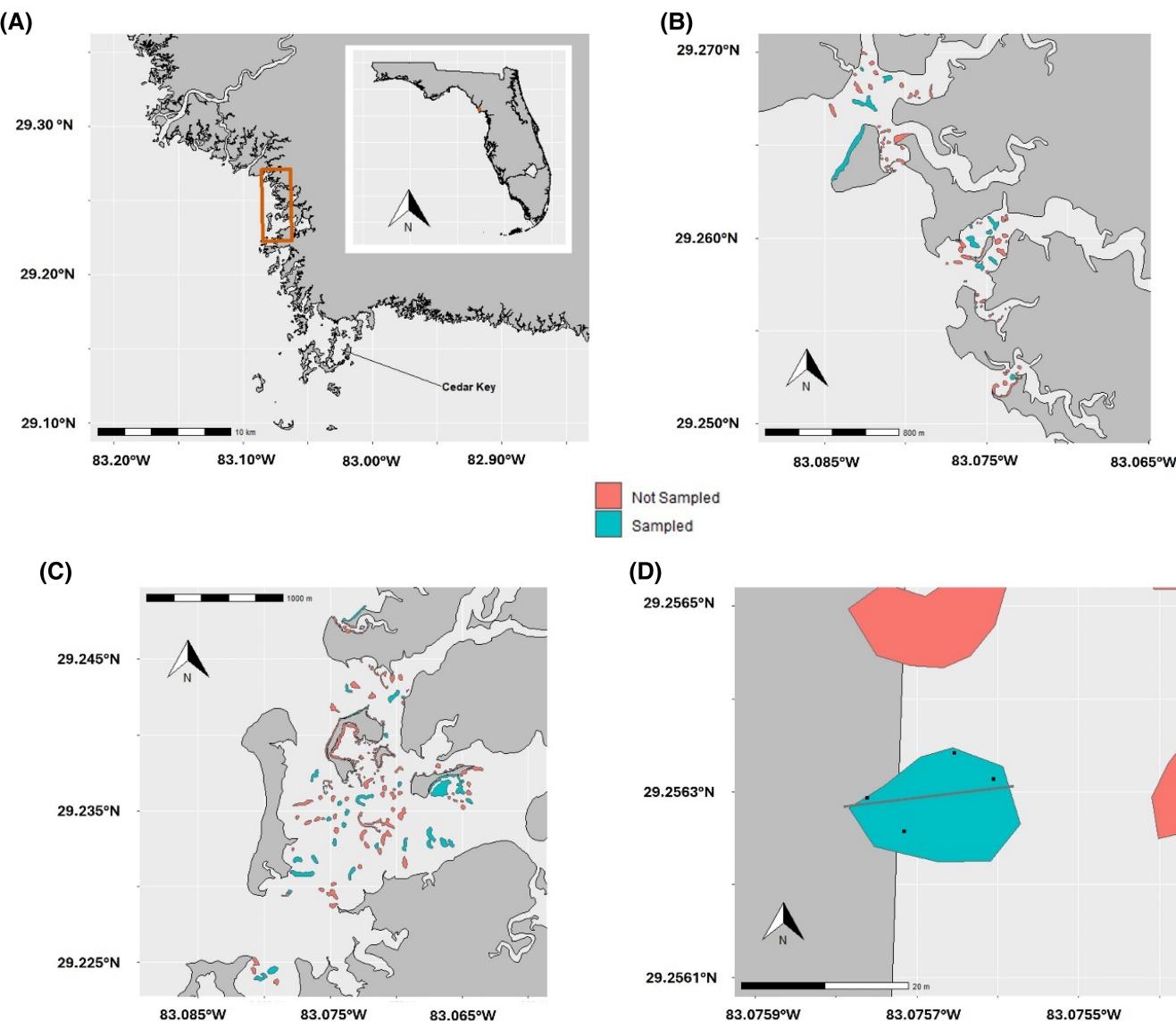
because successful recruitment relies on both living and dead oysters (Powell et al., 2012; Solinger et al., 2022; Soniat et al., 2019; see also Walters & Kitchell, 2001). The persistence of these “material legacies” (Kopecky et al., 2023)—dead structural components that influence ecosystem resilience—has been demonstrated in forests (Johnstone et al., 2016); corals (Kopecky et al., 2023; Schmitt et al., 2022; Vieira, 2020); and most relevant to this study, oyster reefs (Lenihan & Peterson, 1998; Powell & Klinck, 2007).

The removal of oyster shells through harvest (a structure-removing disturbance; Kopecky et al., 2023), dissolution (Pace et al., 2023; Waldbusser et al., 2011), or displacement to unsuitable habitat directly limits the potential for future population growth (Solinger et al., 2022). Failing to account for these ecological constraints could reduce the effectiveness of oyster management and restoration efforts (Johnson et al., 2022; Pine et al., 2023; Powell & Klinck, 2007; Wilberg et al., 2013).

In the Big Bend region of Florida (northeastern Gulf of Mexico), Seavey et al. (2011) documented a 66% net decline in intertidal oyster reefs between 1982 and 2011. The hypothesis that loss of cultch leads to the loss of oyster reef was tested by Frederick et al. (2016) by placing durable substrate (locally sourced dolomite limestone rocks) as a replacement cultch on the degraded Lone Cabbage Reef in Suwannee Sound. In this experiment, the rocks would serve as settlement sites for oyster larvae, creating a reef substrate similar to natural cultch. This experiment was successful, demonstrating that oyster reefs in Suwannee Sound are cultch and not larvae limited (Frederick et al., 2016; Pine et al., 2022). This work aligns with a broader understanding that suitable, and adequate, cultch is a necessary component of oyster restoration (Dunn et al., 2014; Goelz et al., 2020; Graham et al., 2017; Powell & Klinck, 2007; Solinger et al., 2022; Theuerkauf et al., 2015).

The use of oyster cultch in managing oyster fisheries was first practiced in the Suwannee Sound region more than 2,500 years ago (Jenkins, 2017). Legal management of oysters by the State of Florida began in 1881, and oyster shells were recognized by statute as valuable assets belonging to the state even after an oyster was harvested and the meat processed. In the 1980s, a series of changes to oyster regulations in Florida removed 50% of the public trust ownership by the state and exempted oysters sold in the half-shell market from the public trust ownership of the shells (Palmer et al., 2022). These weakened regulations of oyster shells and changes in cultching restoration practices (reduced frequency and amount of cultch) over the past three decades demonstrate major changes in the ecological and economic value of oyster cultch and restoration approaches in Florida that likely contributed to the current highly degraded state of oyster fisheries in the state (Berrigan, 1988, 1990; Pine et al., 2015; Radabaugh et al., 2019).

Uncertainty remains about the functional relationships between cultch characteristics (e.g., type, mass, and elevation) and live oyster density, which are critical for guiding oyster fishery management and restoration efforts (Colden et al., 2017; Goelz et al., 2020; Lipcius et al., 2021; Pine et al., 2023). To address this gap, we conducted a field study and a simple modeling assessment to examine the relationship between cultch shell mass and live oyster counts. We focused on unrestored intertidal oyster reefs in Suwannee Sound, Florida, within the



**Figure 1.** Maps of the study area in Suwannee Sound, Florida, showing (A) the study area, outlined with a rectangle, in relation to the Suwannee River and Cedar Key, (B) the north end of the study area, (C) the south end of the study area with Deer Island in the center, and (D) an example of one of the reefs sampled, with the grub-box locations indicated with points and the transect indicated with a line.

northeastern Gulf of Mexico (Figure 1). This work provides valuable insights for management and restoration by establishing a reference point—a standard for evaluation, assessment, or comparison—that can be used to monitor cultch mass in the field. By identifying thresholds that signal an increased risk of oyster reef collapse or poor restoration outcomes, these findings help refine conservation strategies and improve the long-term sustainability of oyster populations.

We were interested in exploring the potential for a tipping point—a critical threshold where small changes in habitat or environmental conditions can trigger a rapid shift between stable states. For example, a once-productive, self-sustaining oyster reef may transition to a collapsed state with limited potential for natural recovery. Such shifts may exhibit hysteresis, where reversing collapse requires substantially greater effort than the initial disturbance. This conceptual framework also relates to depensation, a process in which oyster recruitment declines

disproportionately at low population densities, creating feedback loops that hinder population recovery at both reef and ecosystem scales (Johnson et al., 2022, 2023).

## METHODS

### Fieldwork

We quantified the relationships between oyster cultch mass ( $\text{kg}/\text{m}^3$ ) and live oyster density ( $\text{number}/\text{m}^2$ ) in Suwannee Sound, Florida. Sampling was part of ongoing monitoring assessing the response of oyster populations on the restored Lone Cabbage Reef and adjacent control (unrestored) reefs (Moore et al., 2020; Pine et al., 2023). These live oyster monitoring efforts have occurred irregularly since 2010 (Moore et al., 2020; Seavey et al., 2011) but became regular winter-season sampling events in 2018–2022. These efforts take advantage of winter low-tide events, where tidal height descends below

–0.24 m mean lower low water, dewatering large areas of the intertidal oyster bar.

Using existing GIS layers of oyster reef distribution for the region (Florida Fish and Wildlife Conservation Commission, 2023), possible line-transect locations to estimate live oyster abundance were identified on oyster reefs, and then transects were randomly selected for sampling from a list of possible sites. The tidal heights are available approximately 30–40 d per year, and on these days, it is only feasible to sample a few hours per day. Sites were selected randomly from the list of possible locations within each stratum (open or closed to fishing) in GIS until the total transect length for the strata was reached from individual transect segments. The amount of sampling was determined by a power analysis (Moore & Pine, 2021), which allowed us to allocate additional sampling to areas with greater variability in oyster counts. We counted live oysters greater than 18 mm (a U.S. dime coin), as oysters larger than this size are distinguishable from other bivalves, reducing the likelihood of misidentification. Oysters greater than the minimum were counted following standard methods (Moore et al., 2020). Intertidal oysters in the Big Bend region demonstrate a truncated size structure due to aerial exposure, with oyster heights during winter demonstrating a single peak in size frequency of around 33 mm (Sinnickson et al., 2025). Thus, we did not separate our analyses by size-classes.

We examined the estimated density of live oysters from the ongoing monitoring efforts within the strata (Table 1). We attempted to sample cultch mass in areas open and closed to commercial harvest across the full range of observed live oyster densities to fully characterize the relationship between live oysters and shell mass across these densities.

Cultch mass was estimated on the same wild unrestored oyster reefs as the line-transect samples to estimate live oyster density using a metal frame 50 × 50 × 10 cm in size (a grub box). Four grub-box locations were selected randomly per transect chosen to estimate live oyster density. Most grub-box sites were chosen by placing a 10-m buffer around the randomly chosen transect using ArcPro (157 of 185 grub-box sites). Within this buffer, grub-box locations were randomly selected by leaving a 1-m buffer between sample sites and ensuring that the sample site did not overlap with the transect. Sites not selected using ArcPro were selected using random numbers that specified a linear distance along and away from the transect (28 of 185 grub-box sites). When the transect was oriented east to west, the direction from the transect for the grub box was north or south, and when the transect was oriented north to south, the direction from the transect was east or west.

The grub box was hammered into the reef using a sledge-hammer until the top was flush with the reef surface (Figure 2), creating a fixed surface area and depth from which to remove shell material. A depth of 10 cm was chosen to standardize the amount of material sampled on each reef that would include cultch material that is available for spat settlement and other material that promotes reef elevation, stability, or other physical factors. Sampling to a fixed area and depth standardized the area of reef excavated for cultch.

Once the grub box was in place, all live and dead shell material was excavated to the depth of the box and placed in a large bucket. Oyster clusters (multiple oysters growing from a single

**Table 1.** The number of reefs sampled for live eastern oyster density estimates and the number of grub boxes collected for cultch mass estimation in each sampling year (November–February) in areas open (Yes) and closed (No) to fishing.

Location	2020–2021		2021–2022	
	Yes	No	Yes	No
Reefs	15	19	6	7
Grub boxes	58	75	24	28



**Figure 2.** An excavated grub box in Suwannee Sound, Florida. Material excavated from the fixed areas of the grub box was rinsed and sieved before weighing. Photo credit: T. S. Coleman.

source) that were intersected by the box were broken at the intersection point, and the portion of the cluster within the box was included in the mass estimate. Three different sieves were used to wash the material and remove silt and shell hash that would not be suitable for oyster spat settlement. The large sieve had square openings 10 × 10 cm and retained only the largest shell and cultch material. The medium sieve openings were 5 × 5 cm and captured only the medium-sized clusters, and the small sieve had openings 2.5 × 2.5 cm and retained only small oyster clusters and large individual shells. Larger oyster clusters were then hand-washed and sieved through the large and medium sieves to prevent them from breaking. Any oyster clusters that were hand-sieved but fit through the large and medium sieves were placed in a separate bucket until the small material was washed and then returned to the bucket for weighing.

Smaller material—mostly silt, mud, and shell hash—was removed by placing the material in a plastic bucket with 1-× 1-cm holes and a sieve screen above the base. The sieve in the rinse bucket was raised off the bottom to wash the material more efficiently by preventing it from touching the muddy bottom. The material was then taken to the reef edge and rinsed of mud and shells smaller than 2.5cm. The bucket was shaken, swished, and agitated vigorously enough to wash the material but carefully enough that no material was lost from the bucket. The cultch material was then sieved through the 10- and 5-cm sieves to ensure that no large clusters were missed in the original sorting. Then, all material too large to fit through each of the different sieve sizes was placed in separate tared buckets, weighed, and then returned to the space on the reef from which it was sourced.

We collected 185 grub-box samples during winter 2020–2021 and 2021–2022 and combined data for both seasons for analyses. Of these, 103 samples were from areas closed to commercial harvest and 82 were in areas open to harvest (Table 1). For analysis, the yields from all grub boxes on a given reef were combined by summing the mass of the material from each category into a single total amount of cultch material for each reef and standardizing the volume of reef sampled with the grub boxes to kilograms per cubic meter as standard unit instead of units of grub box.

## Analysis

### Fitting effective cultch–live oyster models to data

#### Predicting probability of oyster spat settlement

Oyster recruitment predictions were made by first predicting the probability of oyster spat settlement,  $P(S)$ , on cultch using two different models that describe the relationship between a constant regional larval abundance ( $L$ ) and different sizes of cultch mass ( $H$ , in kg/ m<sup>3</sup>) measured in Suwannee Sound. Note that given a constant larval supply is assumed,  $L$  is not necessary in any of the following equations.

Model 1 is a simple exponential relationship where  $P(S)$  varies with cultch mass as

$$P(S) = 1 - e^{-c \times H}, \quad (1)$$

where  $H$  = cultch mass and  $c$  = a power parameter, with larger values implying higher probabilities of settlement at low cultch mass.

Model 2 is similar to model 1, with the addition of a term,  $H_{\min}$ , describing the minimum cultch mass required for any spat settlement ( $P(S) > 0$ ), estimated from the Suwannee Sound data:

$$P(S) = 1 - e^{-c \times (H - H_{\min})}. \quad (2)$$

#### Predicting net oyster recruitment from predicted spat settlement

We then predicted net oyster recruitment ( $R$ ) from predicted spat settlement using a Beverton–Holt equation similar to Solinger et al. (2022; their Equation 13) with the different  $P(S)$  relationships (Equations 1 and 2):

$$R = \frac{a \times P(S)}{\left(1 + a \times \frac{P(S)}{R_{\max}}\right)}, \quad (3)$$

where  $a$  = maximum survival rate of settled spat and  $R_{\max}$  = asymptotic maximum oyster recruitment.

We fit the combined probability of settlement ( $P(S)$ ) and recruitment ( $R$ ) model (Equation 3) using a Bayesian framework in R, utilizing Template Model Builder (TMB; Kristensen, 2024; R Core Team, 2022) and Markov chain–Monte Carlo (MCMC) methods for parameter estimation and characterizing parameter uncertainty. We utilized a normal likelihood with an estimated SD term ( $\sigma$ ) to fit the data and placed uninformative uniform priors on all parameters (Supplementary Material A). Markov chain–Monte Carlo sampling was conducted using the No-U-Turn-Sampler (Monnahan & Kristensen, 2018), running four chains, each starting at the 0.05, 0.25, 0.75, and 0.95 quantiles of parameter posteriors from an initial chain run of the model (the initial chain began at maximum likelihood estimation estimates). Each chain was run for 1,000,000 iterations, with the first 50% of iterations discarded from the beginning of each chain as a warm-up. Specifically for model 2, an approximation for  $P(S)$  was implemented to avoid minimization issues with the break point. This was achieved by modifying Equation 2 to not allow a conditional change between predicting 0 and the exponential function at  $H = H_{\min}$ . For this approach, the exponential is multiplied by a very steep logistic function that increases from 0 to 1 over a narrow range of  $H$  values approaching and exceeding  $H_{\min}$ , where

$$P(S) = 0.000001 + \left(1 - e^{-\frac{c(H - H_{\min})}{500}}\right) \frac{H^{50}}{(H_{\min}^{50} + H^{50})},$$

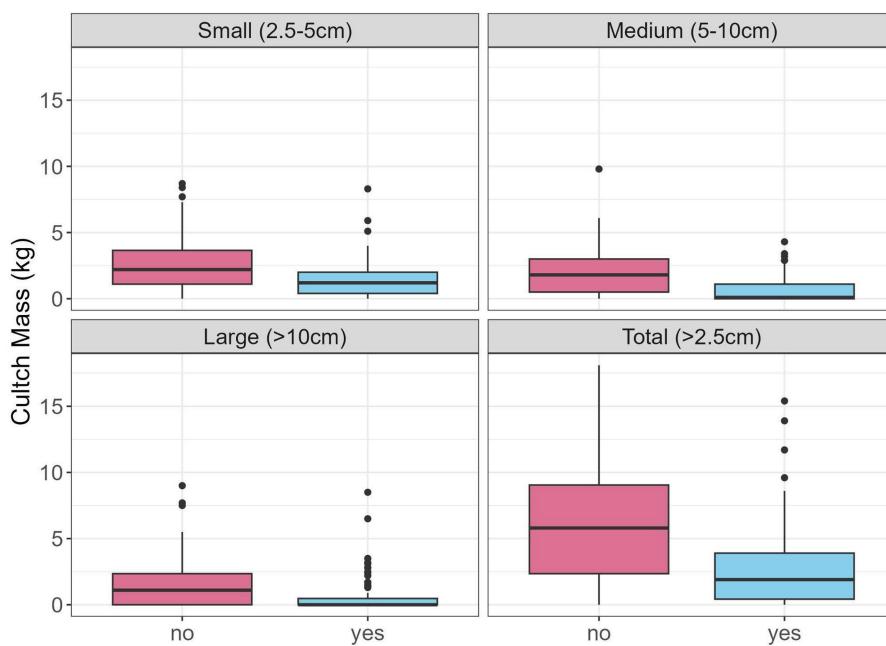
which uses a power function with power 50.

Initial attempts to predict  $R$  (Equation 3) using each model while estimating all four to five parameters were unsuccessful, as the posterior distributions of the parameters were uniform across a range of values. This is due to Equation 3 combining the effects of two saturating relationships that can give similar shape and fit to the data (Supplementary Material A). For this reason, we focused the analysis on two different biologically plausible cases for the Beverton–Holt parameters  $a$  and  $R_{\max}$  for each individual model fit:

Case 1: Fix  $R_{\max}$  at a very high value ( $1 \times 10^{10}$ ). This scenario approximates a system where oyster populations are limited by larval supply. In this case, we fixed  $R_{\max}$  at  $1 \times 10^{10}$  and estimated the other parameters.

Case 2: Fix  $a$  at a very high value ( $1 \times 10^6$ ). This scenario approximates a cultch-limited system (density-dependent mortality of larvae) as the survival rate of settled spat is high, thus the system is defined by the probability of settlement and estimated  $R_{\max}$ . In this case, we fixed parameter  $a$  at  $1 \times 10^6$  and estimated the other parameters.

We present the information criterion Pareto-smoothed importance sampling leave-one-out cross validation (PSIS-LOO; Vehtari et al., 2017) for model comparison between the



**Figure 3.** Cultch mass per grub box for areas closed to harvest (no) and open to harvest (yes). The thick black lines within the boxes represent the median, and the box frames the upper and lower quartiles. The whiskers extend 1.5 times the interquartile range, and black dots are data points that exceed this level. Cultch sizes are as follows: small = 2.5 to 5 cm, medium = >5 to 10 cm, and large = >10 cm.

**Table 2.** Summary information for three size-classes of oyster cultch collected in areas open or closed to harvest in Suwannee Sound, Florida. Each column represents a size of cultch (small [2.5 to 5 cm], medium [>5 to 10 cm], large [>10 cm], or all sizes combined) from areas that are harvested or not (yes or no).

Measurement	Small		Medium		Large		All sizes	
	No	Yes	No	Yes	No	Yes	No	Yes
Total cultch mass sampled (kg)	270.5	123.2	210.6	57.2	160.7	50.7	641.8	231.1
Number of grub boxes <sup>a</sup>	103	82	103	82	103	82	103	82
Mean cultch mass per grub box (kg)	2.63	1.5	2.04	0.7	1.56	0.62	6.23	2.82
SD of mean cultch mass per grub box	2.07	1.43	1.88	1.02	1.78	1.42	4.47	3.19
Maximum cultch mass per grub box (kg) <sup>b</sup>	8.7	8.3	9.8	4.3	9.0	8.5	18.1	15.4
Cultch mass (kg/m <sup>3</sup> )	105.05	60.1	81.79	27.9	62.41	24.73	249.24	112.73

<sup>a</sup>All grub boxes were 0.025 m<sup>3</sup> in volume.

<sup>b</sup>Minimum cultch mass per grub box was 0 kg.

models and cases. We interpret an appreciable difference as >3 deviance units (Burnham & Anderson, 2002). The posterior distributions of  $H_{\min}$  for the different models were also examined to provide approximate estimates of cultch mass as a reference point below which extinction may be likely. In particular, we calculate percentage of MCMC samples where  $H_{\min} > 5$  as an approximation for  $H_{\min}$  being appreciably different than 0 (alternatively what is the probability that  $H_{\min} \neq 0$ ).

## RESULTS

### Cultch mass

For all cultch sizes, the total cultch mass per grub box ranged from 0 to 18.1 kg for areas closed to harvest and 0 to 15.4 kg for areas open to harvest (Table 2). The mean cultch mass per grub box was higher in areas closed to harvest (mean = 6.23 kg, SE = 4.47) than in harvested areas (mean = 2.81 kg, SE = 3.19). Cultch mass for each size-class and harvest category was lower

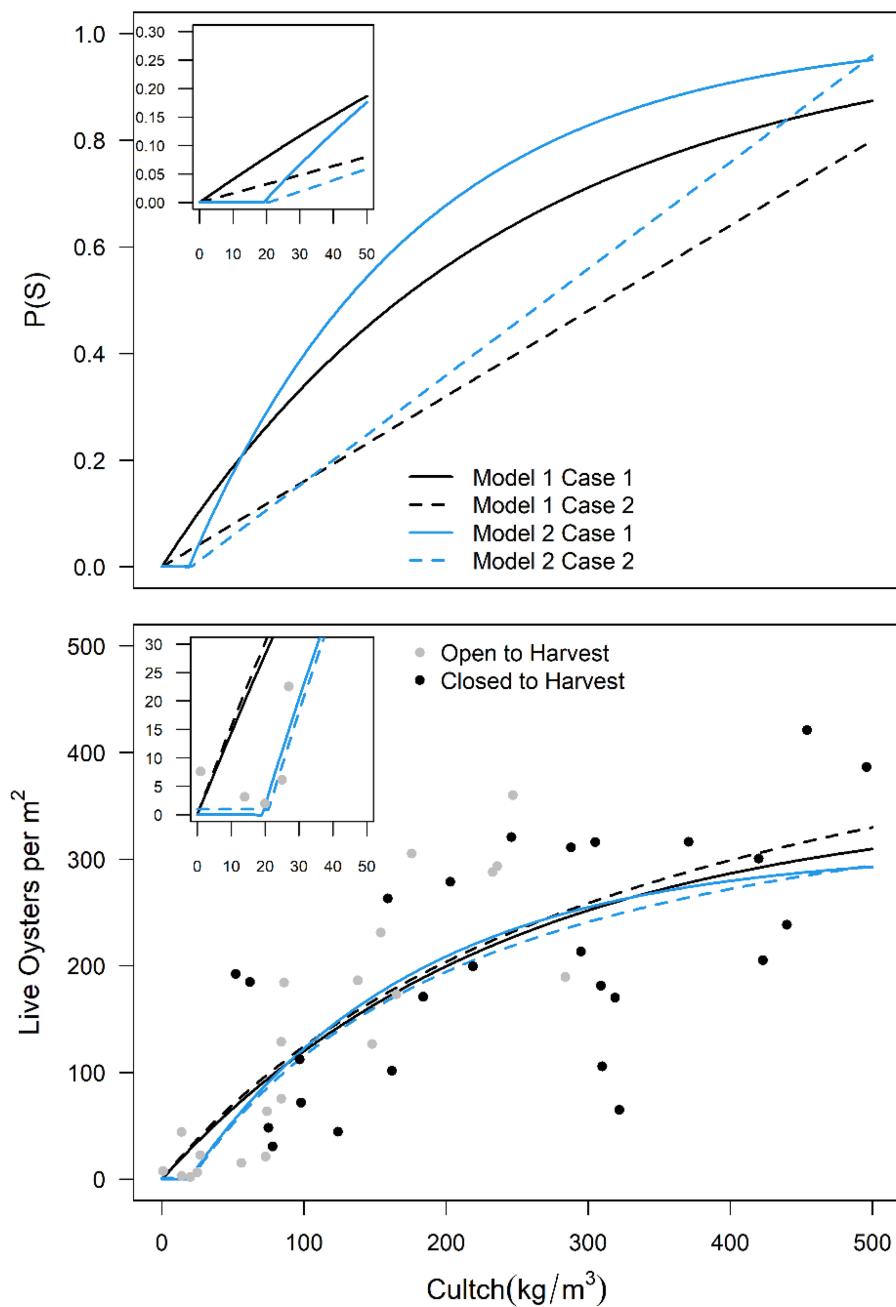
for areas open to harvest (Figure 3). For example, the mass (standardized to cubic meters by the grub-box sampling volume of 0.025 m<sup>3</sup>) of large cultch in areas open to harvest was about 25 kg/m<sup>3</sup> and about 62 kg/m<sup>3</sup> in areas closed to harvest (Table 2).

### Live oysters

The 21 line transects we completed in areas open to commercial harvest had mean live oyster densities from 1.97 to 359.95/m<sup>2</sup> (mean = 129.87/m<sup>2</sup>; SD = 116.44). On the 26 line transects we completed in no-harvest areas, the mean live oyster densities ranged from 30.6 to 421.1/m<sup>2</sup> (mean = 201.92/m<sup>2</sup>; SD = 109.30).

### Fitting effective cultch–live oyster models to data

Simple plots of shell mass versus live oyster density as a measure of recruitment show that as average shell mass per area increases, the number of live oysters per area also increases



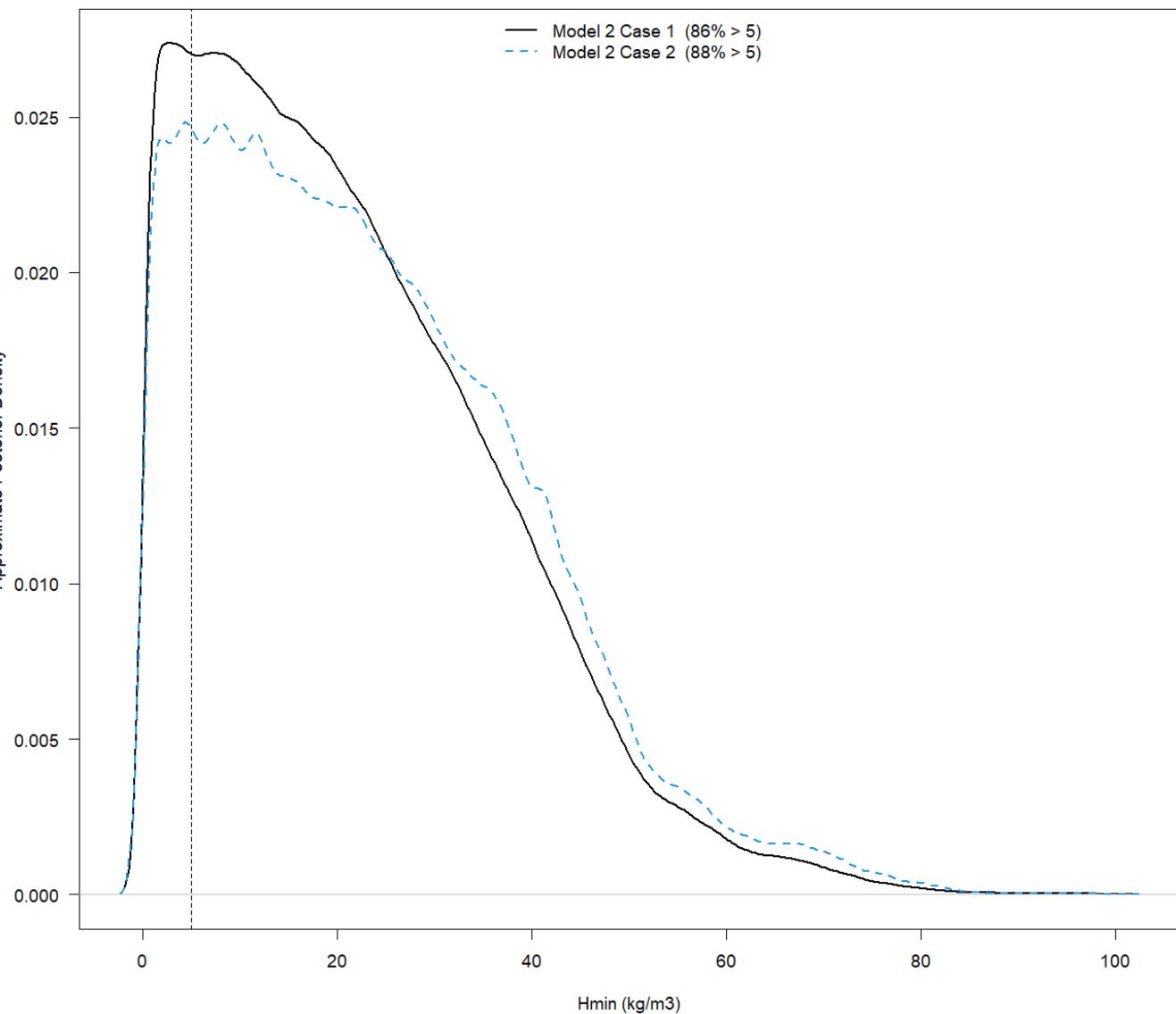
**Figure 4.** The top panel shows the predicted settlement probabilities  $P(S)$  from model 1: case 1 (solid black line), model 1: case 2 (dashed black line), model 2: case 1 (solid blue line), and model 2: case 2 (dashed blue line) multiplied by 1,000 to show shape. The inset plot is the same figure but zoomed in at low cultch biomass ( $\text{kg}/\text{m}^3$ ) to show the shape of the curves from each case near the origin. The bottom panel shows the observed and predicted live eastern oyster counts from model 1, model 2: case 1 (limited larval supply) and model 2: case 2 (density-dependent survival). Gray points are for sites open to commercial harvesting, and black points are areas closed to commercial harvest.

in an apparently saturating pattern (Figure 4). These plots also suggest that there may be an inflection point suggesting depensation below which the rate of increase in live oysters for a given increase in shell mass is lower than at higher levels of the two variables, i.e., that  $H_{\min}$  in model 2 (Equation 2) is greater than zero (see Figure 4 insert). We sampled over the widest possible range of live oyster densities and targeted field-sampling efforts in 2022 to sample areas at the lowest and highest cultch mass levels observed in 2021 to try and minimize the errors-in-variables problem.

### Modeling

All four models converged, as  $R$ -hat estimates were below 1.01 and each effective sample size was well above 400 (Vehtari et al., 2021; Supplementary Material A). Convergence diagnostics and approximate densities for each parameter estimated are shown in Supplementary Material A. The model selection criterion PSIS-LOO did not discriminate between any of the four models.

The model 1 spat settlement pattern ( $H_{\min}=0$ ) in the Beverton–Holt model resulted in model fits that generally



**Figure 5.** Posterior probabilities for  $H_{\min}$  (minimum cultch mass required for spat settlement) for the two cases of model 2. The percentage of Markov chain–Monte Carlo iterations where the parameter estimate for  $H_{\min}$  was greater than  $5 \text{ kg/m}^3$  is shown in the legend for each case, and a dashed vertical reference line is provided on the  $x$ -axis at  $H_{\min} = 5 \text{ kg/m}^3$ .

overestimated live oyster counts at low cultch mass and under-estimated live oyster counts at high cultch levels (regardless of case; Figure 4).

Using model 2, we found that the relationship between live oysters and cultch mass was fitted equally well from the two extreme parameter value cases, representing plausible but very different hypotheses about what causes an apparent limit on recruitment at high cultch masses. In the first parameter set for model 2 settlement (model 2: case 1), if we assume a  $P(S)$  spat settlement curve that has a nonzero cultch threshold for settlement and fix  $R_{\max}$  at a high value, the estimated  $P(S)$  has a relatively high fitted power parameter  $c$ , resulting in a strongly curved relationship between spat settlement and cultch mass and a median  $H_{\min}$  of approximately  $19 \text{ kg/m}^3$  (95% highest posterior density =  $0\text{--}49 \text{ kg/m}^3$ ; Supplementary Material A; Table 3). Additionally, in examining the posterior distributions of  $H_{\min}$ , 86% of the posterior MCMC samples were greater than  $5 \text{ kg/m}^3$

for model 2: case 1, providing evidence that  $H_{\min}$  is likely  $> 0$  (Figure 5). As  $R_{\max}$  is in the denominator of the Beverton–Holt equation (Equation 3), having a large value in the denominator reduces the Beverton–Holt equation to approach  $R = a \times P(S)$ , which results in a similar shape as the settlement curve. In this case, the Beverton–Holt slope parameter  $a$  is also an estimate of the asymptotic maximum recruitment given a low larval supply. This is equivalent biologically to where the larval supply is low,  $P(S)$  is high, and spat has low density-dependent mortality. Thus, recruitment is simply proportional to  $L \times P(S)$ .

Alternatively in the second case of model 2, where  $a$  was fixed at a very high value (the hypothesis of density-dependent mortality and limited recruitment), a very similar recruitment curve resulted (Figure 4). The model estimated a similar level for  $H_{\min}$ , with a median of approximately  $21 \text{ kg/m}^3$  (95% highest posterior density =  $0\text{--}52 \text{ kg/m}^3$ ). Under this scenario, larval supply would have to be very high to produce the patterns seen

**Table 3.** Median parameter estimates and Pareto-smoothed importance sampling leave-one-out cross-validation (PSIS-LOO) comparisons for each model. A bold parameter estimate signifies that it was fixed. Column definitions are as follows:  $c$  is a power parameter, with larger values implying higher probabilities of settlement at low cultch mass;  $H_{\min}$  is the minimum cultch mass level ( $\text{kg}/\text{m}^3$ );  $a$  is the maximum survival rate of settled spat;  $R_{\max}$  is the asymptotic maximum recruitment of spat; and delta PSIS-LOO is the difference in PSIS-LOO scores between the lowest scoring (delta PSIS-LOO = 0) and other models fit to the data.

Model	$c$	$H_{\min}$	$a$	$R_{\max}$	$\sigma$	PSIS-LOO	Delta PSIS-LOO
Model 1: case 1	2.07	0	354.25	$1 \times 10^{10}$	77.48	545.8	0
Model 1: case 2	0.0008	0	$1 \times 10^6$	561.16	78.26	546.9	1.1
Model 2: case 1	3.13	19.08	307.97	$1 \times 10^{10}$	77.48	546.8	1
Model 2: case 2	0.001	21.08	$1 \times 10^6$	424.11	77.48	547	1.2

in the data, and the upper limit on recruitment is set by higher density-dependent mortality (larger effect of the denominator term  $aP(S)/R_{\max}$  representing density dependence in survival rate in [Equation 3](#)). Finally, in examining the posterior distributions of  $H_{\min}$ , 88% of the posterior MCMC samples were greater than 5  $\text{kg}/\text{m}^3$  for model 2: case 2, which gives additional support to  $H_{\min} > 0$ .

## DISCUSSION

Our results provide new insight into the relationship between cultch mass and live oyster density on unrestored intertidal reefs in Suwannee Sound. While our models suggest a saturating relationship between cultch mass and oyster recruitment, they also indicate a strong possibility that recruitment may decline at low cultch levels, consistent with depensatory dynamics ([Powell & Klinck, 2007](#); [Solinger et al., 2022](#); [Walters & Kitchell, 2001](#)). Specifically, models that include a minimum cultch threshold ( $H_{\min}$ ) yield median estimates near 20  $\text{kg}/\text{m}^3$ , with 86% (model 2: case 1) and 88% (model 2: case 2) of posterior samples exceeding 5  $\text{kg}/\text{m}^3$ . However, the posterior distributions for  $H_{\min}$  are wide and include substantial probability mass near zero, and model comparison did not distinguish between threshold and nonthreshold formulations. As such, we cannot precisely estimate a tipping point value. Nevertheless, given the biological necessity of suitable substrate for oyster settlement area, substrate type, reef height, and profile, all of which are well established in the literature ([Kopecky et al., 2023](#); [Lenihan & Peterson, 1998](#); [Mann & Powell, 2007](#); [Powell et al. 2001, 2012](#)), the possibility of a recruitment threshold should be considered in management and restoration planning, particularly when cultch mass is low. Our findings underscore the need for further research to better identify threshold dynamics and quantify how cultch loss contributes to reef collapse and recovery resistance ([Colden et al., 2017](#); [Johnson et al., 2022](#); [Lipcius et al., 2021](#); [Pace et al., 2023](#); [Solinger et al., 2022](#)), which can help guide large-scale oyster restoration efforts currently underway in the Gulf of Mexico. These insights are particularly relevant given the limited success observed in some oyster restoration initiatives ([Committee on Long-Term Environmental Trends in the Gulf of Mexico Gulf Research Program, 2022](#); [La Peyre et al., 2022](#); [Pine et al., 2023](#)).

We assessed how variation in larval supply would alter the predicted oyster recruitment in our models at different cultch mass levels ([Supplementary Material B](#)) and found similar patterns as reported in [Lipcius et al. \(2021\)](#), showing that a

threshold level of larval supply is required for successful oyster recruitment, even if  $H_{\min}$  cultch levels are met. Because necessary larval supply levels are currently met in Suwannee Sound, we recommend focusing restoration and management efforts on recovering and managing cultch to promote oyster populations and maintain adequate larval supply to prevent having to address the more complicated problem of having to recover both cultch and larval supply if the oyster population collapses near extinction. Assessing factors that influence the persistence of oyster cultch material and whether management can influence this persistence and maintenance is a critical need in this region ([Pace et al., 2020](#); [Powell et al., 2012](#)).

Our results help to quantify results in [Seavey et al. \(2011\)](#) from the Big Bend region of Florida, including Suwannee Sound, which documents a decline in oyster reef elevation and oyster cultch and subsequent reef collapse. These authors describe a declining trend in total oyster habitat in 1982–2001, with an unexpected increase in 2010. However, this increase was likely short-lived, as the overall decline was characterized by conversion from high-vertical-relief, high-oyster-density reefs to low-vertical-relief, low-oyster-density reefs that were primarily shell hash and sand. The uptick observed in 2010 was driven by the collapse of higher-elevation reefs whose cultch became unconsolidated, reducing the vertical relief and spreading the area of the cultch material. As these reefs continued to degrade, the oysters likely went locally extinct and, eventually, the reefs vanished ([Frederick et al., 2016](#); [Moore et al., 2020](#); [Seavey et al., 2011](#)). These low-vertical-relief reefs of shell hash and sand would have low mass in our grub-box samples because this small material would not be retained in the sieve, as it is small and unsuitable for oyster larvae to settle on ([Frederick et al., 2016](#); [Seavey et al., 2011](#)). This conversion of the oyster reef from suitable to unsuitable cultch, followed by reef collapse ([Seavey et al., 2011](#)), was the catalyst for our research and restoration efforts in this region in the subsequent decade.

Although we separated cultch material into size bins during field processing, we did not analyze recruitment patterns by size-class. Intertidal oyster reefs in Suwannee Sound are dominated by small oysters (20–37 mm in height; [Sinnickson et al., 2025](#)) that typically occur in irregularly shaped, multi-oyster clusters. These conglomerates make direct estimation of surface area impractical under field conditions. While cultch size likely influences settlement through structural complexity and orientation (e.g., 2D versus 3D configurations), the limited variation in oyster size and the irregular morphology of clusters constrained our ability to assess cultch quality beyond total mass in the field. Future studies incorporating high-resolution

measurements of reef architecture (e.g., photogrammetry) may offer more precise evaluations of how cultch structure affects settlement and recruitment.

While our results are from naturally occurring reefs, these results are likely applicable to informing oyster reef restoration design. In Suwannee Sound, we have demonstrated through replicated restoration experiments that degraded oyster reefs are limited by cultch and not larval supply (Aufmuth et al., 2025; Frederick et al., 2016; Pine et al., 2022). The observed positive response in oyster populations to restoration (Frederick et al., 2016; Pine et al., 2025) and our observations and simple models describing the cultch mass–live oyster relationship for unrestored reefs suggest that the degraded oyster reefs may be approaching or are below the  $H_{\min}$  threshold we have identified. Surveying  $H_{\min}$  and live oyster densities across a wide range of restored and unrestored reefs in Florida could provide insight into this relationship.

To date, Suwannee Sound oyster restoration efforts have focused on restoring oyster reefs using natural local material (dolomite limestone) as replacement cultch. This material supports oyster spat settlement in the natural environment, and the cultch sizes we use to restore degraded oyster reefs are large (0.1–0.3 m) and target restoring average vertical relief of reefs to 0.37 m (Aufmuth et al., 2025; Frederick et al., 2016). Most of this rock cultch is used to build the vertical reef structure, which drastically changes the elevation profile of the oyster reef, likely creating multiple types of positive feedback to promote oyster recruitment, survival, and ecosystem services (Colden et al., 2017). This type of restoration in Suwannee Sound has been successful, demonstrated by increasing  $P(S)$  and oyster recruitment compared with unrestored sites over 5 years of oyster population growth following restoration (Pine et al., 2025). In contrast, other restoration efforts in Florida (Pensacola, St. Andrew, and Apalachicola bays) have focused on building low-cultch-mass reef structures using smaller (mostly 0.02–0.04 m) cultch material spread over a large area, resulting in very low vertical relief (about 0.05 m). But because the material is a dense rock, the biomass per area can be high and exceed the  $H_{\min}$  levels we have identified for Suwannee Sound. Restoration efforts in Pensacola, St. Andrew, and Apalachicola bays have not resulted in reversing the degraded oyster reefs to a desired state for reasons that are not known. It could be the type, size, and quantity of cultch material, larval supply, or other factors in concert limiting recovery (Pine et al., 2023). In the Chesapeake Bay, threshold reef heights of 0.25–0.40 m have been identified for successful oyster reef restoration and persistence using oyster shell as cultch based on extensive field, experimental, and modeling efforts (Colden et al., 2017; Lipcius et al., 2015, 2021; Schulte et al., 2009). This is a critical point: If a minimum amount of cultch material of a suitable type ( $H_{\min}$ ) and reef elevation are required for successful  $P(S)$ , as our results and the literature suggests, then oyster reefs at or below these minimum levels may be in a state where they are less likely to respond to restoration or on a trajectory where they may collapse and go extinct (Johnson et al., 2022; Lipcius et al., 2021; Solinger et al., 2022). If other key factors, such as larval supply or the type and size of reef material used in restoration are not correct, then restoration may not be successful regardless of the amount of material. Understanding these

complexities in the various factors influencing successful oyster reef restoration at any specific location is difficult, which is why we advocate for an adaptive management approach to oyster restoration instead of prescriptive solutions (Pine et al., 2022).

Our field results show a positive, saturating relationship between oyster cultch mass and live oyster density, with model-based evidence suggesting the potential for depensatory dynamics—i.e., reduced settlement probability  $P(S)$  per unit of cultch—at low cultch mass values (Powell & Klinck, 2007; Solinger et al., 2022; Walters & Kitchell, 2001). While both threshold and nonthreshold models fit the data similarly, posterior estimates from threshold models indicate a strong possibility of recruitment limitation below approximately 20 kg/m<sup>3</sup>, with 86–88% of posterior samples for  $H_{\min}$  exceeding 5 kg/m<sup>3</sup>. However, the posterior distributions of  $H_{\min}$  are broad, include considerable density near zero, and do not allow a precise estimate of a tipping point. These findings nonetheless highlight the potential biological and management importance of maintaining sufficient cultch levels, particularly because cultch mass likely reflects multiple key reef characteristics, such as surface area for larval settlement, elevation, and substrate stability (Carette et al., 2024; Colden et al., 2017; Lenihan & Peterson, 1998; Lipcius et al., 2015; Pace et al., 2020; Powell et al., 2012). From a management and restoration perspective, it may be more effective to intervene before reef collapse, as significantly more cultch material is needed to rebuild vertical relief and habitat structure after collapse has occurred (Colden et al., 2017). Adaptive experimental policies that compare combinations of cultch mass and elevation on reefs at different degradation stages could help identify  $H_{\min}$  and the required elevation that would provide critical thresholds and refine restoration targets while addressing the uncertainty identified in our model results.

Research should be undertaken to understand why cultch biomass is being lost in Suwannee Sound in the first place. Seavey et al. (2011), in their assessment of oyster reef losses in this region, found declines in oyster reefs in areas open and closed to harvest. These authors proposed that a decadal period of higher salinity, related to more frequent periods of low freshwater discharge, led to higher oyster mortality and low recruitment, which resulted in destabilization of the oyster reef cultch and subsequent collapse. More than a decade of research since (Frederick et al., 2016; Moore et al., 2020; Pine et al., 2023) has demonstrated spat settlement and oyster population growth from multiple cohorts of oysters on restored oyster reefs in areas open and closed to fishing, while unrestored reefs are continuing to decline or persist at lower oyster densities than on restored reefs in both areas (Pine et al., 2025).

Innovative oyster management practices such as those in Alabama, where cultch levels and oyster removals are monitored before and during the fishing season (Alabama Marine Resources Division & National Oceanic and Atmospheric Administration, 2021) and the oyster fishery closed once certain live oyster removal thresholds are met, could provide insight into both the  $H_{\min}$  and live oyster removals that are sustainable in Mobile Bay. Simulations of oyster populations and field examples demonstrate that sustainable exploitation levels for oyster populations are very low

(<5%) without substantial efforts to replace cultch material removed through harvest (Johnson et al., 2022; Morson et al., 2022; Solinger et al., 2022). Marquardt et al. (2025) demonstrate the effects of cultching and spatial management of harvest on oyster reefs in the Rappahannock River, Chesapeake Bay, Virginia. Their findings suggest that a 3-year rotational harvest maintains reef structure, enhances recruitment, and increases market-sized oyster density, while low levels of cultching improve harvester efficiency and provide ecological and fishery benefits. Rotational oyster harvest policies have also been used successfully in Scotland and South Africa (de Bruyn et al., 2009; Eagling et al., 2015; Steyn et al., 2023), and these types of rotational practices could be designed to promote low exploitation rates and high cultch levels, which are likely necessary for long-term sustainable oyster harvest.

Our findings suggest the possibility of compensatory recruitment dynamics in oyster populations at low shell mass levels, where recruitment may be insufficient to sustain a positive population trajectory. Simulations from other oyster populations suggest that such declines could lead to hysteresis, where populations shift from a viable state to an unstable, low-density condition that resists restoration efforts (Johnson et al., 2022). Lipcius et al. (2021) further identify key factors—reef height, sedimentation rates, and larval supply—that can drive oyster reefs in the Chesapeake Bay toward extinction. We recommend that restoration and management efforts maintain oyster cultch mass above levels that may represent critical transition points to support reef persistence and recovery. Exceeding these precautionary thresholds, especially on degraded reefs, can reduce the risk of collapse. Preventing collapse is likely more effective and less costly than attempting to restore reefs after they have failed.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Marine and Coastal Fisheries* online.

## DATA AVAILABILITY

Data and code are available at the following location: [https://github.com/billpine/MCF\\_cultch\\_depensation.git](https://github.com/billpine/MCF_cultch_depensation.git).

## ETHICS STATEMENT

The research meets the ethical guidelines and legal requirements for observational studies in the United States.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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