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NOTE

Long-term data reveal greater intertidal oyster biomass in predicted suitable habitat

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ABSTRACT: Habitat suitability models have been used for decades to develop spatially explicit predictions of landscape capacity to support populations of target species. As high-resolution remote sensing data are increasingly included in habitat suitability models that inform spatial conservation and restoration decisions, it is essential to validate model predictions with independent, quantitative data collected over sustained time frames. Here, we used data collected from 12 reefs over a 14 yr sampling period to validate a recently developed physical habitat suitability model for intertidal oyster reefs in coastal Virginia, USA. The model used intertidal elevation, water residence time, and fetch to predict the likelihood of suitable conditions for eastern oysters *Crassostrea virginica* across a coastal landscape, and remotely sensed elevation was the most restrictive parameter in the model. Model validation revealed that adult oyster biomass was on average 1.5 times greater on oyster reefs located in predicted 'suitable' habitat relative to reefs located in predicted 'less suitable' habitat over the 14 yr sampling period. By validating this model with long-term population data, we highlight the importance of elevation as a driver of sustained intertidal oyster success. These findings extend the validation of habitat suitability models by quantitatively supporting the inclusion of remotely sensed data in habitat suitability models for intertidal species. Our results suggest that future oyster restoration and aquaculture projects could enhance oyster biomass by using habitat suitability models to select optimal site locations.

KEY WORDS: Eastern oyster · *Crassostrea virginica* · Elevation · LiDAR · Habitat suitability model · Oyster restoration · Remote sensing

1. INTRODUCTION

Habitat suitability models inform species management, restoration, and conservation by predicting landscape capacity to support target populations and identifying specific areas of heightened habitat suitability (Thuiller & Münkemüller 2010). As remotely sensed data become more accessible, high resolution, and spatially dense, they are increasingly included in a range of habitat suitability models, particularly for species that are discernible with aerial/satellite platforms or associated with physical attributes that can be resolved remotely (Tattoni et al. 2012, Hogan & Reidenbach 2019). To ensure reliability, habitat suitability models should undergo calibration, verification, and validation procedures (Brooks 1997), yet many models are not validated with independent, quantitative population data. Moreover, because populations can vary over time, validation should ideally include data

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collected over sustained time periods (Roloff & Kernohan 1999).

Habitat suitability models are commonly used to advise placement of oyster restoration and aquaculture projects (Theuerkauf & Lipcius 2016). Most existing habitat suitability models for oyster populations are habitat suitability index models, which apply known wildlife–habitat relationships to spatially explicit environmental data (Brooks 1997). These models incorporate various mechanisms that influence oyster persistence, including water quality measures (e.g. salinity, temperature, dissolved oxygen), hydrodynamic attributes (e.g. water depth, flow velocity), and biological variables (e.g. substrate type, predator abundance, larval dispersal; Cake 1983, Theuerkauf & Lipcius 2016, Puckett et al. 2018, Chowdhury et al. 2019). Although oysters can exist in both subtidal and intertidal habitats, most oyster habitat suitability models are for subtidal populations (Cake 1983, Theuerkauf & Lipcius 2016, Puckett et al. 2018; but see Chowdhury et al. 2019).

Compared to subtidal oysters, intertidal oysters are constrained by additional factors that should be incorporated into habitat suitability models (Baillie & Grabowski 2019). For example, hydrodynamic conditions such as water residence time and fetch may be useful for predicting the locations of intertidal reefs (Theuerkauf et al. 2017), which are directly exposed to waves and are intermittently submerged. Intertidal reefs require enough water flow to deliver oyster larvae from distant sources, but too much wave exposure and/or water velocity can prevent settlement or erode suitable substrate (Whitman & Reidenbach 2012, Theuerkauf et al. 2017). Substrate elevation is also important; oysters in deeper water can suffer sedimentation and heightened predation (Lenihan 1999), whereas high intertidal oysters are vulnerable to desiccation stress, starvation, and limited recruitment (Fodrie et al. 2014). Importantly, immersion of intertidal reefs depends on the interaction of absolute reef elevation and the tidal regime (Morris et al. 2021).

In contrast to subtidal reefs that are always submerged, intertidal reefs can be visually detected from airborne measurements at low tide. Increasingly accessible remotely sensed technologies, such as airborne light detecting and ranging (LiDAR) methods, can estimate elevation across intertidal gradients and distinguish the vertical relief (reef height aboveground) of intertidal oyster reefs from surrounding areas. Recently, Hogan & Reidenbach (2019) presented the first habitat suitability model for intertidal oysters based partially on remotely sensed data. Their model combined LiDAR-based elevation data (collected in 2015; 12.5 cm vertical accuracy; 0.5776 m^2 grid cells) with modeled estimates of water residence time and fetch (Safak et al. 2015, Kremer & Reidenbach 2021) to identify suitable habitat for intertidal eastern oysters *Crassostrea virginica* in coastal Virginia, USA. Elevation was the dominant predictor of oyster habitat suitability. However, like many habitat suitability models, this model has yet to be validated with independent population data.

Here, we used 14 yr of oyster population monitoring data to validate this physical habitat suitability model. Our results show that habitat suitability models developed with remotely sensed data can accurately predict areas of sustained high oyster biomass, which can inform spatial planning for oyster populations. More broadly, as the first validation of a habitat suitability model for intertidal oyster reefs that uses remotely sensed methods, our study supports the expanded use of remote sensing for coastal habitat suitability modeling, particularly when paired with long-term quantitative assessments.

2. MATERIALS AND METHODS

2.1. Study site

We sought to validate a physical habitat suitability model for intertidal eastern oyster populations within the Virginia Coast Reserve (VCR) (Hogan & Reidenbach 2019). The VCR is a landscape of intertidal marshes and mudflats, shallow bays, and barrier islands spanning >100 km of coastline on the Eastern Shore of Virginia (Fig. 1). This region is polyhaline (28.8 ± 5.9 psu; mean ± SD), with semidiurnal tides (0.75–1.5 m; −0.688 m mean lower low water). As in the nearby Chesapeake Bay, overharvesting and disease drastically reduced native oyster populations in the VCR during the mid-1900s. Some remnant intertidal oyster populations naturally rebounded during the early 2000s without human intervention. We monitored these remnant reefs to assess population recovery and stability of oyster reefs that naturally recovered from overharvesting. We selected remnant reefs that covered a wide spatial extent of the VCR (Fig. 1) that were characterized by high oyster densities, pronounced vertical structure, and multiple oyster size classes.

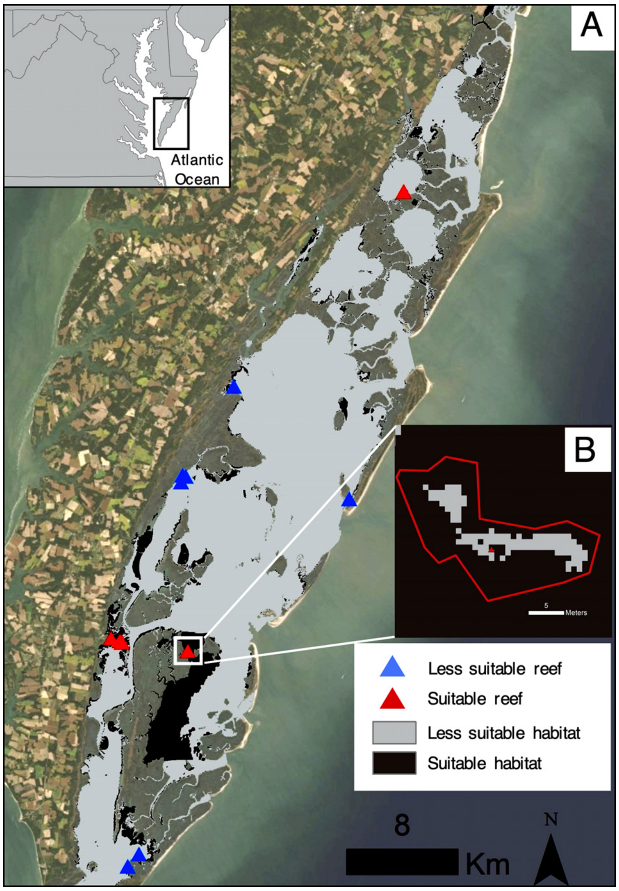

Fig. 1. (A) Predicted suitable (red triangles) and less suitable (blue triangles) oyster reefs monitored in the coastal bays of Virginia's Eastern Shore. (B) Example reef (red outline) overlaid on areas of predicted suitable habitat (black pixels) and less suitable habitat (gray pixels), based on Hogan & Reidenbach (2019)

2.2. Field data collection

From 2006 to 2019, we monitored oyster populations on 12 remnant reefs in the VCR (Fig. 1A; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m683p221_supp.pdf). The sampling frequency of each reef varied by year and season over the 14 yr sampling period (mean ± SD no. of sampling events per reef: 5.83 ± 2.55, range = 1–9). Prior to field sampling, we mapped the outline of each reef with a hand-held GPS and randomly chose at least 3 sampling points per reef for each sampling event. At each location, we excavated all reef substrate from a 0.0625 m^2 quadrat (15–30 cm depth), although in 2006 we used a 0.25 m^2 quadrat. We converted all data to units per m^2.

We disassembled each excavation to count and measure the shell length (mm) of all live oysters. We used a length–biomass relationship for adult live oysters in the VCR to estimate oyster biomass per sample (Biomass = 1.76 × 10^{-5} × Shell Length$^{2.4}$; Smith et al. unpubl.). Due to variability among years in the sampling season, we excluded spat oysters (shell length <25 mm) from analyses.

2.3. Model description

A previously developed oyster habitat suitability model combined LiDAR-derived elevation data with modeled water residence time (Safak et al. 2015) and fetch (Kremer & Reidenbach 2021) to identify regions of predicted suitable oyster habitat in the VCR (Hogan & Reidenbach 2019). Briefly, Hogan & Reidenbach (2019) used over 2000 digitized patch reefs to extract data for the intertidal elevation of land surrounding reefs, water residence time, and fetch distance. From these data, they created 'suitable' ranges for each parameter (Table 1). Suitable criteria for water residence time (23–2000 h) and fetch (40–4643 m) used the full range of data while elevation (–0.92 to –0.13 m NAVD88) used the middle 99th percentile of data to account for errors associated with bay hydroflattening. Where suitable ranges for all 3 parameters overlapped, they classified the landcover as suitable habitat (52.4 km^2, equivalent to

Table 1. Comparison of (A) the habitat suitability ranges for elevation, water residence time, and fetch parameters from the model of Hogan & Reidenbach (2019) relative to the (B) suitable reef mean ± SD, (C) suitable reef range (minimum to maximum), (D) less suitable reef mean ± SD, and (E) less suitable reef range of these physical parameters for oyster reefs sampled in this study (n = 12 reefs)

	Elevation (m; NAVD88)	Water residence time (h)	Fetch (m)
A. Habitat suitability range (Hogan & Reidenbach 2019)	–0.92 to –0.13	23 to 2000	40 to 4643
B. Suitable reef mean ± SD	–0.47 ± 0.15	406 ± 542	1144 ± 469
C. Suitable reef range (min. to max.)	–0.64 to –0.27	98 to 1370	542 to 1748
D. Less suitable reef mean ± SD	–0.87 ± 0.36	284 ± 240	2403 ± 750
E. Less suitable reef range (min. to max.)	–1.24 to –0.11	1 to 706	1189 to 3388

12% of available habitat in the study region) in an equally weighted, GIS-based additive model. Areas outside of the suitable range for one or more variables were categorized as 'less suitable' habitat. Suitable habitat was particularly limited by LiDAR-derived elevation, with the suitable elevation range found for only 19.1% (83.2 km^2) of the target area, compared to ~67% coverage for water residence time (295.2 km^2) and fetch (294.2 km^2). However, this habitat suitability map was not validated with oyster population measurements from areas with different predicted suitability.

To validate this model with population data, we overlaid the mapped reefs from the monitoring program with the habitat suitability model map (Fig. 1B). Monitored reefs did not overlap with locations of previously collected field measurements from the initial model ground-truthing (Table S1). For each reef, we calculated the number of pixels in predicted suitable and less suitable habitats (Table 1C), defining a reef as suitable if the habitat suitability model classified more than 90% of the pixels in the reef polygon as suitable; otherwise, reefs were categorized as less suitable. Using a 90% threshold ensured that most pixels were present in predicted suitable areas for suitable reefs, while maintaining a relatively balanced experimental design (n = 5 suitable reefs; n = 7 less suitable reefs).

2.4. Data analysis

To assess whether the oyster population data validated the predictions of the habitat suitability model, we used a linear mixed effects model to quantify the degree to which oyster biomass differed as a function of habitat suitability (suitable, less suitable), with sampling year as a random intercept to control for interannual variation (Zuur et al. 2009). To determine whether temporal trends in oyster biomass differed with habitat suitability, we fit a linear model with an interaction between habitat suitability and year, but we found no difference and dropped the interaction term (time × habitat suitability: $F_{1,66} = 0.64$, $p = 0.43$). For both models, we only included years when data were collected from reefs located in both predicted suitable and less suitable areas. We fit models in R version 4.05 with the 'lme4' package used for the mixed model (Zuur et al. 2009). We used the 'DHARMa' package to ensure that our models met assumptions of homogeneity and normality, and we square-root transformed biomass to meet model assumptions (Hartig 2019). Sample autocorrelation function analysis and semi-variograms showed no evidence of temporal or spatial autocorrelation, respectively (Zuur et al. 2009).

3. RESULTS

Our classification method identified 5 oyster reefs in predicted suitable habitat and 7 oyster reefs in predicted less suitable habitat. From 2006 to 2019, adult oyster biomass on reefs in suitable habitat was 1.5 times greater than adult oyster biomass on reefs in predicted less suitable habitat (Fig. 2A; mean ± SE; 89.03 ± 6.52 g ash free dry weight [AFDW] m^{-2}, vs. 54.86 ± 10.57 g AFDW m^{-2}; $F_{1,60} = 8.99$, $p = 0.004$). Adult oyster biomass was consistently higher over time in predicted suitable habitats (Fig. 2B; main effect of habitat suitability: $F_{1,67} = 9.0$, $p = 0.004$) without a detectable temporal trend (main effect of year: $F_{1,67} = 2.2$, $p = 0.2$).

4. DISCUSSION

Our results validate an existing physical habitat suitability model for intertidal oysters (Hogan & Reidenbach 2019). Using 14 yr of independently collected monitoring data, we found that adult oyster biomass was greater in model-predicted suitable habitats relative to less suitable habitats, confirming that the model can predict areas of enhanced oyster suitability. Despite some temporal variation in population dynamics, adult oyster biomass was on average 1.5 times higher in 'suitable' areas. Increased oyster biomass supports additional oyster recruitment (Lenihan 1999), while simultaneously enhancing ecosystem functions such as water filtration and fisheries production that scale with oyster biomass (Grabowski et al. 2012). Furthermore, this sustained difference in oyster biomass increases confidence that these findings are not due to natural variability or transient dynamics. Most prior validations of oyster habitat suitability models only use data from a single year or short time frames (<5 yr) (Cake 1983, Theuerkauf & Lipcius 2016), whereas prior evaluation of habitat suitability models suggests that at least 3 yr of data are needed to validate models for species that reproduce annually, such as oysters (Roloff & Kernohan 1999). This work also extends the validation of oyster habitat suitability models by using oyster biomass, which integrates both density and size structure. Our results validate the use of this habitat suitability model to manage, restore, and conserve oyster populations in coastal Virginia. More

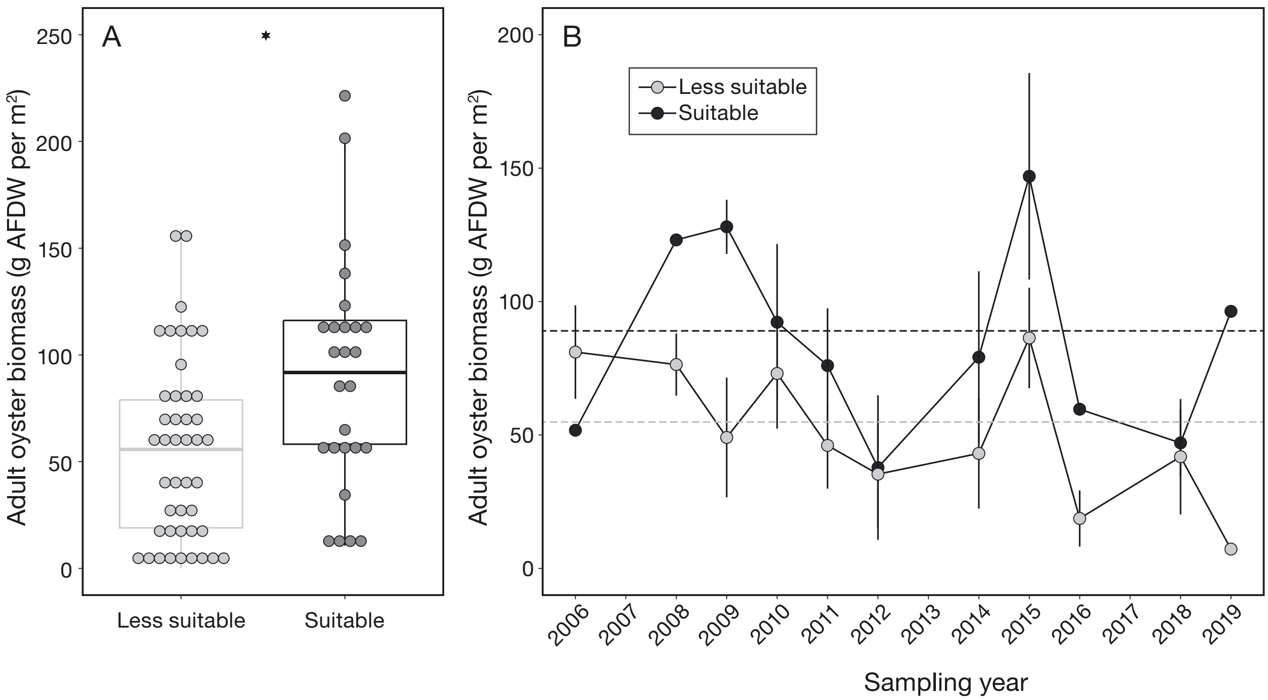

Fig. 2. (A) Adult oyster biomass on suitable and less suitable oyster reefs. Each point represents mean adult oyster biomass (averaged across quadrats) for a given sampling event (*$p < 0.05$; linear mixed effects model). Boxplots show median (bold lines) and interquarterile range (boxes), with outliers greater than 1.5 × IQR (whiskers). AFDW: ash-free dry weight. (B) Mean ± SE adult oyster biomass over the 14 yr sampling period. Dashed lines indicate mean adult oyster biomass, averaged across the 14 yr sampling period, for reefs in predicted suitable (black line) and less suitable (gray line) habitat.

broadly, our work also supports the inclusion of remotely sensed data in habitat suitability models for other intertidal ecosystems.

The habitat suitability model that we validated is the first to incorporate remotely sensed data for intertidal oysters, and LiDAR-derived elevation measurements were the most restrictive predictor of suitability (Hogan & Reidenbach 2019). Greater biomass of adult oysters in predicted suitable areas underscores the importance of elevation as a driver of intertidal oyster persistence (Lenihan 1999) and supports the inclusion of elevation in other habitat suitability models for intertidal oysters. As LiDAR and other remote-sensing methods are increasingly used to create baseline distribution maps for intertidal species, our work highlights that these methods can also inform habitat suitability models, especially for intertidal species that respond to subtle elevation differences or are easily resolvable in remotely sensed products. LiDAR data are ideal for integration into habitat suitability models, as they can be gathered using airborne platforms at high resolution (<1 m, with centimeter scale vertical accuracy) over large spatial scales relevant to conservation and restoration (hundreds to thousands of km^2).

Our validation of the physical habitat suitability model could improve regional management of oyster populations. Our finding that adult oyster biomass was enhanced in predicted suitable areas suggests that siting for future intertidal oyster restoration and aquaculture projects should be prioritized in areas with predicted suitable habitat. Thus, when establishing new projects, it is important to provide stable substrate within the known ranges of elevation, water residence time, and fetch that support oyster recruitment and growth. However, because elevation was the primary predictor of suitability in the model, it is important to consider how creating a new reef or placing on-bottom intertidal aquaculture structures will change oyster elevation relative to the surrounding seafloor and affect potential site suitability. The initial model used surrounding sediment elevation, not reef crest elevation, so it is important to consider the inherent elevation associated with any future built structure. In coastal Virginia, the range of suitable elevation is –0.92 to –0.13 m NAVD88, so future reefs should be built to fall within that range for successful oyster recruitment. Elsewhere, the absolute elevation of reefs should be considered relative to the tidal regime to optimize tidal immersion for intertidal reefs by placing reefs at elevations that are inundated at least 50% of the time (Morris et al. 2021). Depending on the characteristics of a site (e.g. bottom sediment type), oyster restoration or on-bottom intertidal aquaculture structures could enhance habitat suitability by increasing elevation to predicted suitable ranges. However, using habitat suitability models for project siting does not guarantee success, as other factors not captured in the model, such as larval supply or predation, can constrain restoration outcomes and may vary regionally based on the dominant physical and biotic drivers (Baillie & Grabowski 2019). Furthermore, the fact that oyster reefs exist in predicted less suitable areas indicates that some oysters can survive outside of the predicted suitable ranges of the model, albeit with lower biomass.

In summary, habitat suitability models based on remotely sensed data products can accurately predict the abundance of sessile intertidal organisms. Our validation study supports the expanded incorporation of remotely sensed data into habitat suitability models to inform the conservation and restoration of coastal ecosystems. Furthermore, our study highlights the benefits of sustained population monitoring for parameterizing and validating habitat suitability models.

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