Oyster reef habitat depends on environmental conditions and management across large spatial scales

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ABSTRACT: Oyster reefs provide important services to ecosystems and people, with many of these benefits depending on structurally complex reef habitat. Despite the key role of oyster reef habitat, we have yet to understand natural and anthropogenic drivers of subtidal reef habitat over large spatial scales (>200 km). Chesapeake Bay (USA) offers a valuable system to explore how salinity, restoration, and harvest compare in their influence on subtidal oyster reef habitat because of its broad environmental gradient and mosaic of management types. We applied a remote rapid assessment method using underwater photographs to survey oyster reef habitat in 12 tributaries and scored images based on estimates of oyster percent cover and vertical relief. The broad spatial scale (~215 km) of the survey includes reefs that vary in management status and salinity. Bay-wide habitat scores were higher with greater estimated oyster percent cover and vertical relief on unharvested and restored reefs. Salinity also contributed to Chesapeake Bay-wide patterns, but the relationship depended on harvest status. In assessing the separate management jurisdictions, scores were higher on restored reefs in Maryland and on anthropogenic (i.e. artificially supplemented) reefs in Virginia. A time series over 4 yr in 2 Maryland tributaries showed high and persistent habitat scores in restored sanctuaries, but habitat scores increased for all reefs over time. The results highlight the combined roles of the natural environment and management decisions on oyster reef habitat. The effect of harvest and restoration on habitat underscores the importance of local management decisions in determining the future status of oyster reefs.

KEY WORDS: Oyster reef · *Crassostrea virginica* · Habitat · Harvest · Restoration · Foundation species

1. INTRODUCTION

Oysters and other marine foundation species form complex habitat that supports biodiversity, ecosystem function, and ecosystem services in the ocean. Unfortunately, population crashes have affected oysters around the world (Beck et al. 2011). Anthropogenic stressors are major contributors to oyster declines and include water pollution, overfishing, ocean acidification, disease, dredging, and development (Rothschild et al. 1994, Beck et al. 2011, Lemasson et al. 2017). Understanding how anthropogenic activity affects oyster habitat in the context of natural environmental conditions is essential for restoring and protecting coastal ecosystems, with relevance to global restoration challenges for marine foundation species.

On many present-day oyster reefs, it is difficult to disentangle anthropogenic drivers of reef habitat from natural drivers. Research on the eastern oyster *Crassostrea virginica* highlights the diversity of con-

ditions affecting reef habitat. Harvest is one determinant of reef habitat, especially for subtidal reefs that can be harvested with dredges. Long-term survey data show decreasing acreage of subtidal oyster reefs in Chesapeake Bay, USA (Rothschild et al. 1994), while harvesting on subtidal reefs in North Carolina reliably reduced reef height (Lenihan & Peterson 2004). Increasing reef habitat is one of the goals of Chesapeake Bay oyster sanctuaries, or no-take reserves. However, protection from harvest alone does not reliably rebuild reefs, as unrestored sanctuaries can have low oyster populations and little reef structure (Heggie & Ogburn 2021, MORIW 2021). Thus, restoration activity in sanctuaries has been a key tool for structurally complex and self-sustaining oyster habitat (Rodney & Paynter 2006, Powers et al. 2009, Schulte et al. 2009, MORIW 2021), aiming to amplify the benefits for biodiversity, nitrogen removal (Ray et al. 2021), and other services (Ziegler et al. 2018, De Santiago et al. 2019, Smith et al. 2023). Restoration in Chesapeake Bay focuses on adding oyster shell, alternative substrates, and oyster spat to reefs (MVORIW 2022).

Natural drivers that influence *C. virginica* reef habitat include environmental conditions that affect oyster growth, reproduction, and survival. Salinity is a known determinant, with *C. virginica* preferring mesohaline and polyhaline zones based on minimum salinity thresholds for growth (Davis & Calabrese 1964, Loosanoff 1965, Kennedy 1996) and fecundity (Loosanoff 1953, Calabrese & Davis 1970, Shumway 1996). However, increasing salinities can also lead to higher levels of predation (Gregalis et al. 2009, Theuerkauf & Lipcius 2016), infectious disease (Bushek et al. 2012), and shell bioeroders (Hopkins 1962). The number of oysters at a site also depends on dissolved oxygen (Powers et al. 2009, Patterson et al. 2014), the larval supply (Gregalis et al. 2009, Knights & Walters 2010), and subsidence and burial by sediment (Powers et al. 2009, Colden & Lipcius 2015, Caretti et al. 2021). The impact of sedimentation is lower on higher reefs with greater complexity, corresponding to greater reef success and persistence (Schulte et al. 2009, Colden et al. 2017). However, studies on the environmental conditions that influence reef habitat often focus on one driver at a time and a limited spatial scale, such as a single tributary. Larger-scale surveys that cover a broader range of environmental drivers and management regimes are necessary to identify which drivers are site-specific and which are generalizable.

Chesapeake Bay is a hub for research on *C. virginica* and serves as one of the key case studies for global oyster management due its size, variety of management types, and novel restoration projects. As the largest estuary in North America, its broad salinity gradient and other environmental gradients make it a natural laboratory for gaining insight into global oyster issues. The Bay also has a mosaic of management types, due in part to the fact that it is split between Maryland and Virginia (Fig. 1; Kennedy et al. 2011, MORIW 2021). For example, Virginia manages some reefs with rotational harvest every 3 yr and includes many private leases with different harvest practices. In contrast, Maryland reefs are harvested on an annual basis and there are fewer private leases. Finally, Chesapeake Bay is the target of the largest oyster restoration project in the world. The 'Ten Tributaries' initiative under the 2014 Chesapeake Bay Watershed Agreement aims to restore oyster reefs in 10 tributaries across the Bay by 2025 using structural enhancement (e.g. stone and shell) as well as spat enhancement (CBWA 2014, MORIW 2021, MVORIW 2022), and has already included the completion of the 2 largest oyster reef restoration projects in the world by acreage (MVORIW 2022). As a result, Chesapeake Bay offers a unique opportunity to study how the environment and management practices drive oyster habitat over a large spatial scale.

Studies characterizing oyster reef habitat have historically used the percent cover and density of oysters (Schulte et al. 2009, MORIW 2021). However, these metrics lack information on the 3-dimensional structure that gives reefs much of their value to ecosystems and people. Three-dimensional, rugose structure provides hiding places for diverse prey species and settlement surfaces for benthic organisms. Thus, benthic macrofauna are often more abundant on more structurally complex reefs, including oyster and coral reefs (Rodney & Paynter 2006, Karp et al. 2018, De Santiago et al. 2019, Santoso et al. 2022). Measurements of vertical relief (reef height) or reef rugosity (a measure of structural complexity) on subtidal reefs using traditional methods are labor-intensive because they require SCUBA diving (Rodney & Paynter 2006, Santoso et al. 2022). Remote imaging methods, including underwater videography and sonar, have emerged as solutions to measure characteristics of reef complexity more efficiently on subtidal reefs (Grizzle et al. 2008, Caretti et al. 2021, Heggie & Ogburn 2021). Recently, we developed a remote rapid assessment method using underwater photographs to characterize oyster reef habitat with qualitative scores based on percent cover and vertical relief (Heggie & Ogburn 2021). The results differentiate between reef management types (e.g.
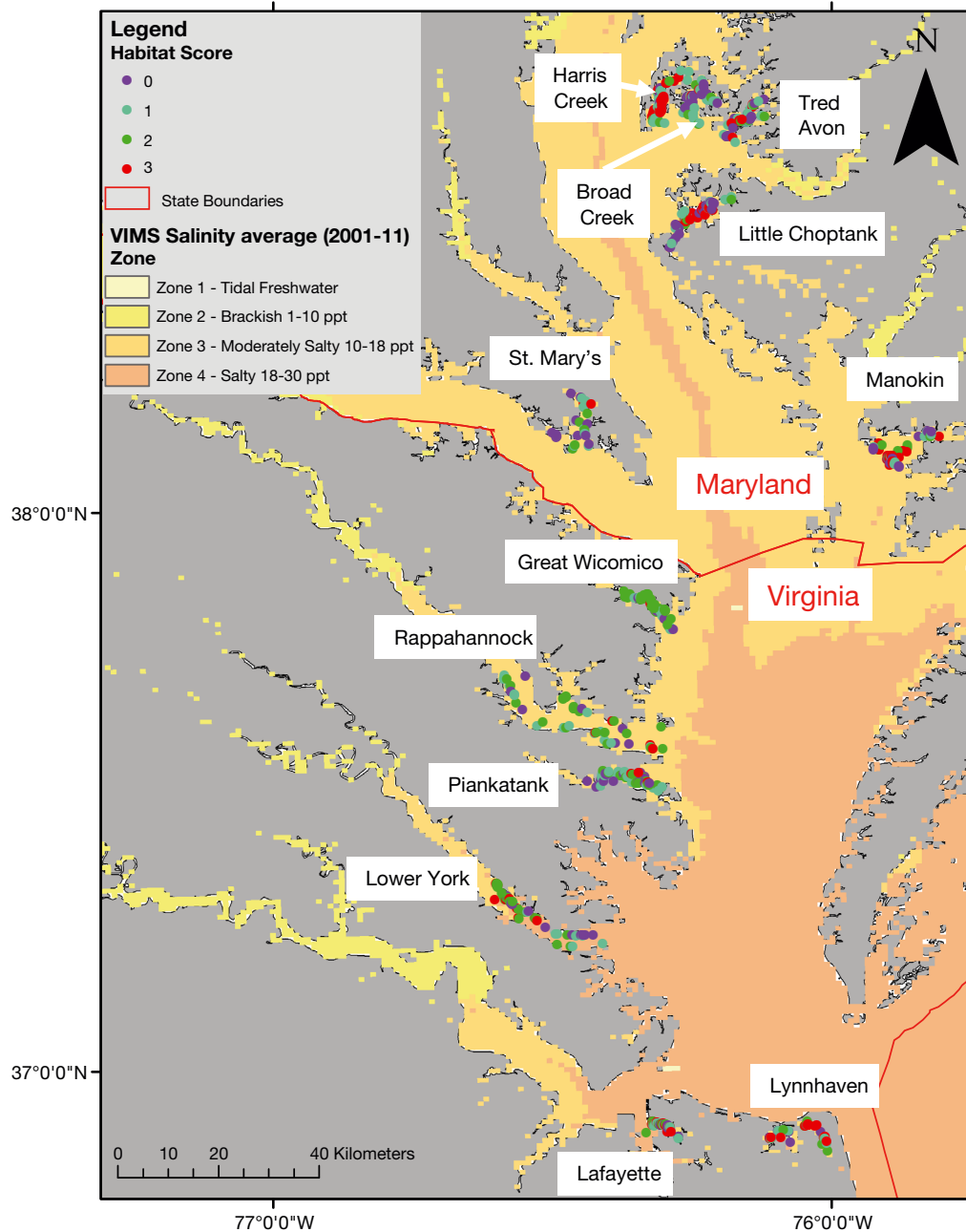
Fig. 1. Locations (n = 566) surveyed in 12 tributaries across salinity zones (VIMS 2023) and both the Maryland and Virginia sections of Chesapeake Bay. VIMS: Virginia Institute of Marine Sciences

restored vs. unrestored) and recapitulate measurements collected manually (typically by SCUBA divers in Chesapeake Bay) of oyster density, biomass, vertical relief, and rugosity in Chesapeake Bay (Heggie & Ogburn 2021, A. M. Tracy et al. unpubl. data).

We leveraged the remote rapid assessment method from Heggie & Ogburn (2021) to conduct an estuary-wide study of environmental and management drivers of oyster habitat. Although Chesapeake Bay is

well-studied, there are no Bay-wide surveys of oyster habitat across the broad range of environmental gradients and management types using a consistent survey method. This is due in part to the historical separation of management in the Maryland and Virginia portions of Chesapeake Bay (Kennedy et al. 2011, Schulte 2017), as well as to logistical challenges of surveying reefs that occur in 10 major rivers across more than 200 km. The increased efficiency of the remote rapid assessment method (Heggie & Ogburn

2021) reduces these logistical challenges, illustrating an approach that could be adapted for managing subtidal oyster reefs around the world.

We first tested the hypotheses that oyster habitat has greater percent cover and vertical relief in unharvested vs. harvested areas, in restored vs. unrestored areas, and with increasing salinity. We used stratified random sampling of habitat in 12 Chesapeake Bay tributaries to determine what factors predict these habitat characteristics. We then used the Maryland and Virginia subsets of the survey data to test the hypothesis that predictors of oyster reef habitat differ in the 2 states (or management zones) with their distinct practices (e.g. leases and rotational harvest). Finally, we tested the hypothesis that habitat increased in restored areas and decreased in harvested areas from 2017 to 2021. To test this hypothesis, we used data collected at timepoints in 2017, 2019, and 2021 for only 2 of the 12 tributaries to determine whether oyster habitat characteristics changed over time and as a function of reef restoration and harvest status. This unique, estuary-wide analysis of oyster habitat provides baseline data at the early stage of restoration efforts in Chesapeake Bay and can inform regional and global oyster management to maximize the ecosystem services provided by these critical foundation species.

2. MATERIALS AND METHODS

2.1. Study sites and sampling

Bay-wide reef surveys targeted the 10 tidal tributaries designated for restoration by the Chesapeake Bay Watershed Agreement (CBWA 2014), as well as 2 tributaries not receiving large-scale restoration (Broad Creek, MD, and the Rappahannock River, VA), which we added to include enough harvested locations to assess our first hypothesis (Figs. 1 & 2). The linear distance sampled within each tributary ranged from 5.2 to 29.0 km. Tributaries included reefs with completed restoration (restored sanctuaries), reefs within sanctuaries but not receiving restoration (unrestored sanctuaries), and harvested reefs (Table S1 in the Supplement at www.int-res.com/articles/suppl/m721p103_supp.pdf).

Tributaries in Maryland were defined with a straight-line boundary where the tributary meets the mainstem, matching the concept of state survey boundaries in Virginia (Virginia Oyster Stock

Assessment and Replenishment Archive, https://cmap22.vims.edu/VOSARA/). The sampling area in the Rappahannock River was a smaller subset of this larger tributary to make the sampling effort feasible and comparable to sampling in the other tributaries. In Virginia, reefs in the Rappahannock, Great Wicomico, and Lower York Rivers are managed on a rotational schedule with a given site being harvested every 3 yr, which contrasts with annual harvest in Maryland tributaries. We surveyed Maryland tributaries in fall 2019 and Virginia tributaries in fall 2020.

Within each tributary, we surveyed reef habitat using remotely collected underwater photographs as described by Heggie & Ogburn (2021). We deployed 2 horizontally mounted GoPro cameras to the bay bottom and recorded videos for approximately 2 min at 50 latitude and longitude pairs (hereafter 'loca-
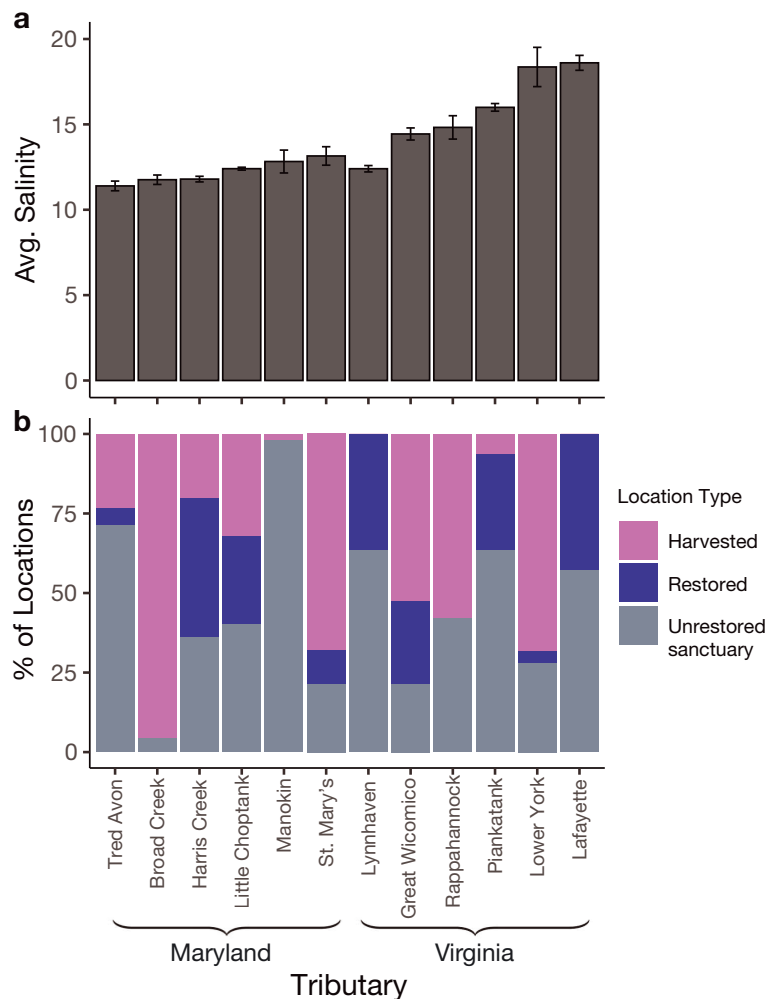

Fig. 2. Summary of 12 tributaries surveyed with respect to (a) average salinity of 50 locations (±SD), using a single 2001–2011 average per location (VIMS 2023) and (b) percent of locations classified as harvested, restored, or unrestored sanctuary

tions') per tributary. At the point of deployment, the depth-finder on the boat (Garmin, accuracy of 0.1 m) recorded water depth, which ranged from 0.5 to 9.7 m.

The 50 locations in each tributary were selected to represent 2 types of bay bottom (anthropogenic and biogenic) identified as oyster reef in GIS layers based on the Chesapeake Coastal and Marine Ecological Classification Standard (CMECS), the only habitat dataset available for all study sites. The CMECS dataset designates bay bottom expected to be anthropogenic (artificially supplemented with shell or alternative substrate) or biogenic (naturally occurring) oyster reef based on grain size and sediment type (NMFS Office of Habitat Conservation 2021). The CMECS anthropogenic habitat differs from restored habitat under the 'Ten Tributaries' initiative because it is based on sonar data and can occur on both harvested and unharvested reefs, whereas restoration is only on unharvested reefs.

We split the 50 locations per tributary between anthropogenic and biogenic habitat using generalized random tessellation stratified sampling (GRTS) on the CMECS GIS layer to generate 50 latitude–longitude pairs per tributary (Stevens & Olsen 2004, NMFS Office of Habitat Conservation 2021). In Maryland, we split the 50 locations per tributary between the 2 CMECS strata, i.e. 25 on biogenic habitat and 25 on anthropogenic habitat. The Tred Avon River had 52 locations (25 anthropogenic and 27 biogenic) to include 1 location on each of 2 large biogenic reefs that were missed by chance with stratified sampling. The St. Mary's River had 25 biogenic locations, but only 3 anthropogenic locations (for a total of 28 locations) because there was only a small area of anthropogenic habitat present in the entire tributary. In Virginia, we used a different method for selecting the 50 locations. In addition to the anthropogenic and biogenic CMECS designations used in Maryland, we also included restoration blueprints from the 'Ten Tributaries' initiative as input for GRTS site selection because these blueprints provide further information on where anthropogenic bay bottom is located (for example, see MORIW 2013). Restoration blueprints for the 'Ten Tributaries' initiative are GIS layers that show polygons designated for restoration in a tributary (not necessarily included in the CMECS dataset), previously restored reefs, and the restoration treatment for each reef (substrate addition and/or seed). Thus, the 50 locations in each Virginia tributary were selected to include 25 biogenic locations using CMECS (as in Maryland), but the 25 anthropogenic locations combine 15 CMECS anthro-

pogenic locations and 10 locations from polygons designated for future restoration in the blueprint. The 50 locations in each of the Maryland tributaries do not incorporate blueprints because they were selected prior to the publication of all restoration blueprints. Overall, the study design captured restored locations in all Maryland tributaries, but there was low representation of areas selected for restoration in the Tred Avon River (Table S2). All sampled reefs were ultimately subject to the same criteria for considering a reef to be restored (see Section 2.3).

For the analyses of temporal patterns in oyster habitat from 2017 to 2019 to 2021, we used the 94 locations of the 100 planned locations in Harris and Broad Creeks for which we were able to collect clear images at all 3 timepoints. We limited biennial sampling to these 2 Maryland tributaries due to their proximity to the Smithsonian Environmental Research Center. These were categorized as harvested (N = 52), unrestored sanctuary (N = 20), and restored sanctuary (N = 22). Harris Creek was closed to harvest in 2010 and restoration was conducted from 2012 to 2015, meaning all restored sites were 2 to 5 yr old at the first timepoint in 2017.

2.2. Image scoring

The remotely collected underwater photographs for 580 locations were processed and scored based on habitat characteristics as described by Heggie & Ogburn (2021). In brief, horizontal images were scored using the clearest frame selected from the 2 min of video for both cameras at a given location. The image received a score of 0, 1, 2, or 3 as a qualitative rating of oyster habitat. Images received a score of 0 if only sand or mud was present; a score of 1 if hard substrate covered <50% of the bottom; a score of 2 if hard substrate covered >50% of the bottom with a reef height of less than 1 adult oyster; and a score of 3 if hard substrate covered >50% of the bottom with a reef height of more than 1 adult oyster. In our experience, scores of 3 require oysters growing upwards and younger oysters growing attached to older oysters to gain sufficient height, while piles of shell score a 2 because tall piles either do not persist in the environment with water motion or are broad enough that they would be considered the substrate from which we would assess reef height. No locations had high percentages or high relief of alternative substrate. The height of 1 adult oyster was a relative metric estimated from oysters in each image. Analyses of photos for a separate dataset

show habitat scores are not biased by visibility (A. M. Tracy et al. unpubl.). Images from 13 of the 580 locations (2.2%) had insufficient visibility for scoring and were omitted from statistical analyses, as was 1 Lafayette site that was outside the reef polygon and thus could not be assigned characteristics. This left a total of 566 locations (Table S2).

2.3. Assigning location characteristics

We used GIS layers to assign characteristics to the 566 locations. We verified the CMECS strata (anthropogenic, biogenic, or none) based on the designation in the GIS layer (NMFS Office of Habitat Conservation 2021). In both states, restored reef in the blueprints from the 'Ten Tributaries' is unharvested. For the remaining reefs in Maryland, sanctuaries are marked with boundaries and a location was harvested if it fell outside the boundary in GIS. In Virginia, we used GIS layers from the Virginia Marine Resources Commission (VMRC) and assigned harvest based on GIS polygons and annual harvest tables (A. Button & M. Southworth pers. comm.). Private leases in Virginia were assigned as harvested because harvest is permitted, though these areas may not be actively harvested. Contaminant-closed areas in all tributaries were classified as unharvested because harvest is not permitted.

We considered locations to be restored if the restoration blueprint showed they had received restoration treatment (substrate addition and/or seed) at least 1 yr prior to video sampling (D. Bruce pers. comm.), allowing oysters time to grow to reach maturity. Reefs labeled as 'Premet' in the blueprint already meet oyster density (50 oysters m^{-2}) and other targets for the 'Ten Tributaries' initiative (MVORIW 2022), but they were only classified as 'restored' if the blueprint included a restoration year or leading organization. Of the sanctuary locations included in the survey, 28% were designated as 'restored' (Table S1).

Finally, we used spatial statistics in ArcGIS Pro (ESRI) and a publicly available GIS layer from the Virginia Institute of Marine Sciences (VIMS) to assign a salinity value for each location. The VIMS layer is a raster of salinity values based on annual averages between March and November from 2001 to 2011 with a cell size of 923 m (Peters 2023). Values were not available for 91 of the 566 points (16.1%), so we imputed values based on the closest point over water and only within the spatial scale of the cell size (<1 km). Salinity values ranged from 11.1 to 20.6 ppt.

2.4. Statistical analyses

We tested 5 predictors of oyster habitat score for the full Bay-wide dataset (N = 566) as well as for the Maryland subset of the data (N = 277) and the Virginia subset (N = 289). The 5 predictors are CMECS habitat stratum (anthropogenic, biogenic, or none), restoration status of the location (yes or no), harvest status of the location (yes or no), depth of the location, and salinity of the location. We analyzed the Maryland and Virginia subsets separately because state and year, which were confounded in the dataset, are significant predictors of habitat.

We tested the 5 predictors of habitat scores with multinomial logistic regression using package 'nnet' in the R statistical software (version 4.1.2, R Core Team 2021, Venables & Ripley 2002). Multinomial logistic regression is appropriate because it allows for more than 2 categorical response variables rather than the 2 possible for binomial distributions, which suits the response variables for the 4 habitat scores (0, 1, 2, and 3). It is the best alternative when models using ordinal logistic regression do not satisfy the Brant test for the proportional odds assumption (Brant 1990), which was the case. We set the habitat score of 3 as the reference response category for all analyses and used an alpha level of 0.05 for statistical significance.

We first used correlation tests to assess multicollinearity of numeric predictors. We assessed multicollinearity of categorical predictors by comparing estimates for pairwise sets of predictors singly and in an additive model. Variables with high multicollinearity were then tested in separate models (Table S3). For all analyses, model selection was performed using Akaike's information criterion (AIC), including confirming that the best model was better than the null model. We report results for the best model by AIC and for models that fall within approximately 2 AIC units that support contributions from additional predictors. Given the lack of diagnostic tests for multinomial logistic regressions, we used 3 separate logistic regressions to test diagnostics for each of the best models using a pseudo-R^2 (McFadden's R^2 in the R package 'pscl'; Jackman 2020), which calculates R^2 on a scale of 0 to 1 using the log likelihood of the best model relative to that of the null. Because the score of 3 is the reference level, the 3 component logistic regressions are 3 vs. 2, 3 vs. 1, and 3 vs. 0. Finally, we calculated the relative importance of all variables on a scale of 0 to 100 using the R package 'caret' (Kuhn 2022). For categorical variables, estimated probability differences were calcu-

lated using the R package 'emmeans', which compares the probability of each habitat score between categories on a scale of 0 to 1 (Lenth 2021). Plots were created using the R package 'ggplot2' (Wickham 2016).

For the full Bay-wide dataset, the Maryland subset of the data, and the Virginia subset of the data, we tested all potential additive models that avoided multicollinearity. We also tested models with an interaction between salinity and each categorical predictor, as well as models with an interaction between harvest and restoration status. While there could be differences in habitat across tributaries, the stratified sampling design is not suited for comparing across tributaries because it does not characterize habitat at the tributary scale.

We tested differences in habitat scores as a function of time and reef type by comparing habitat scores at 3 time points using the 94 sites that were sampled in 2017, 2019, and 2021 (N = 282). We tested the 5 predictors, year, and an interaction between each of the 5 predictors and year, using generalized linear mixed models in the R package 'lme4' to conduct logistic regression with location as a random effect to account for repeated measures (Bates et al. 2015). We used 3 sets of logistic regressions to compare the probability of habitat scores of 0, 1, and 2 relative to scores of 3. We created transition matrices to visualize locations transitioning between habitat scores over time using tables in R (R Core Team 2021), and plotted the transitions using the packages 'ggalluvial' (Brunson 2020), 'ggthemes' (Arnold 2021), and 'viridis' (Garnier et al. 2021).

3. RESULTS

3.1. Bay-wide habitat scores

Harvest status, restoration status, and average salinity are the most important predictors of oyster habitat scores across Chesapeake Bay. The best model for predicting the oyster reef habitat score for the full Bay-wide dataset (all Maryland and Virginia locations, 566 points across 12 tributaries) is better than the next model by 16 AIC units (Table S4). It includes restoration status and an interaction between harvest status and salinity. The binomial logit models used for diagnostics have McFadden's R^2 values of 0.23 (0 vs. 3), 0.16 (1 vs. 3), and 0.13 (2 vs. 3). A model with all 5 predictors could not be tested due to collinearity between the CMECS stratum (reef type of anthropogenic, biogenic, or none) and restoration

status. However, the lack of support for additional predictors is demonstrated from the poor performance of the models with depth and CMECS stratum (Tables S4 & S5).

Within the best model, harvest status has the highest relative importance (21.6), followed by restoration status (5.1), the interaction of harvest and salinity (1.3), and salinity (0.4). Reef habitat with the greatest relative height and percent cover, denoted by a score of 3, is more common in unharvested and restored locations, whereas lower scores are more common in harvested and unrestored locations. Harvested locations have a significantly lower probability of the highest habitat scores of 3 relative to unharvested locations (estimated probability difference = 0.201, p = 0.0007), and a significantly higher probability of scores of 2, denoting high percent cover but low reef height (estimated probability difference = 0.186, p = 0.0036) (Fig. 3; Tables S5–S7). Restored locations have a significantly higher probability of habitat scores of 3 relative to unrestored locations (estimated probability difference = 0.260, p < 0.0001), a significantly lower probability of scores of 0 that denote the absence of hard substrate (unrestored–restored estimated probability difference = 0.234, p = 0.0311), and a significantly lower probability of scores of 1 that denote low percent cover and low reef height (estimated probability difference = 0.151, p = 0.0484) (Fig. 3; Tables S5–S7).
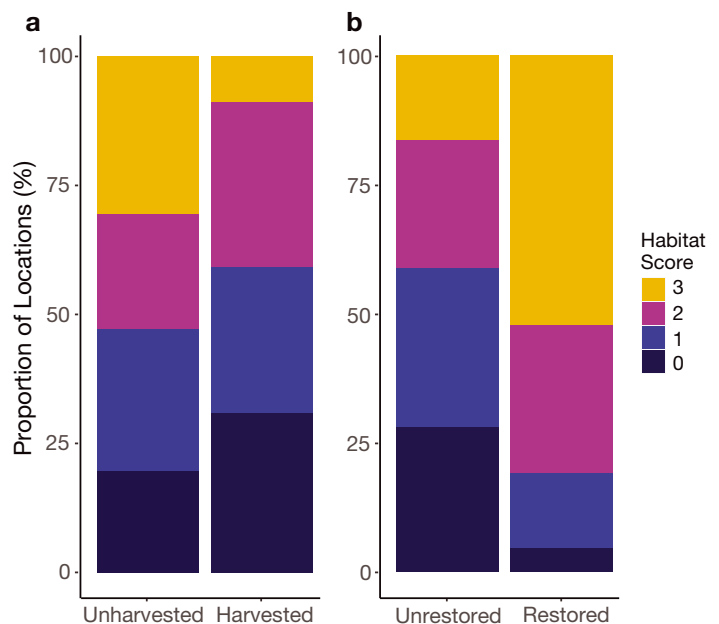

Fig. 3. Full Chesapeake Bay-wide dataset: habitat scores across Chesapeake Bay for (a) harvested and unharvested locations, and (b) restored and unrestored locations. See Section 2.2 for definitions of habitat scores
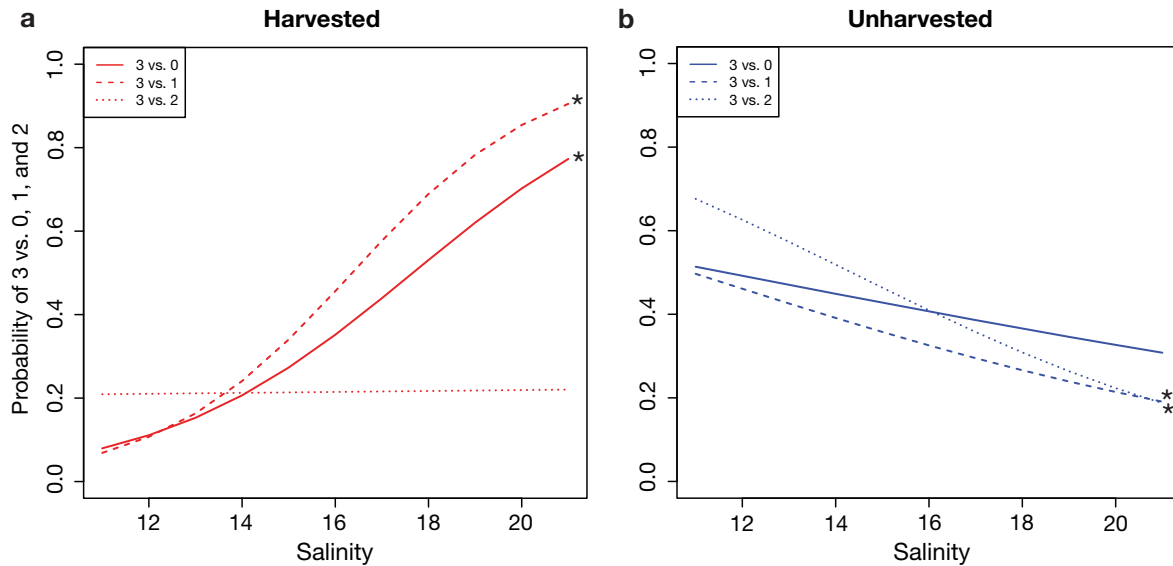
Fig. 4. Full Chesapeake Bay-wide dataset: habitat scores across Chesapeake Bay as a function of salinity in (a) harvested and (b) unharvested locations. Stars denote statistical significance at alpha = 0.05. See Section 2.2 for definitions of habitat scores

The effect of salinity depends on the harvest status, represented by the interaction between harvest and salinity. Increasing salinity corresponds to higher habitat scores in harvested areas (a higher probability of scores of 3 relative to 0 and 1). However, increasing salinity corresponds to lower habitat scores in unharvested areas (a lower probability of scores of 3 relative to 1 and 2) (Fig. 4; Table S5).

3.2. Maryland habitat scores

The Maryland subset of the data includes 277 points across the 6 Maryland tributaries. As in the full Bay-wide dataset, harvest status, restoration status, and average salinity are included in the best model of habitat across the 6 Maryland tributaries, which is better than the next model by 0.96 AIC units. The binomial logit models used for diagnostics have McFadden's R^2 values of 0.34 (0 vs. 3), 0.24 (1 vs. 3), and 0.20 (2 vs. 3). Unlike the Bay-wide data, there is no interaction between harvest status and salinity. Models that include depth or omit salinity also fall within 2 AIC units of the best model and contribute model weight. All top models include harvest status and restoration status, indicating the strongest support for these predictors. None of the top models includes the CMECS stratum (Table S8).

In the best model, restoration status has the highest relative importance (17.4), followed by harvest status (3.7) and salinity (1.2). The highest habitat scores of 3

are more common on unharvested and restored Maryland reefs. Restored locations have a significantly higher probability of habitat scores of 3 relative to unrestored locations (estimated probability difference = 0.604, p < 0.0001), and a significantly lower probability of 0 (estimated probability difference = 0.365, p < 0.0001) and 1 (estimated probability difference = 0.192, p = 0.0306) (Fig. 5; Tables S9–S11). Harvested locations have a significantly lower probability of habitat scores of 3 relative to unharvested locations (estimated probability difference = 0.177, p = 0.0307), with no difference in the probability of 0, 1, and 2 (Fig. 6; Tables S9–S11). Increasing salinity within Maryland corresponds to a greater probability of 3 relative to 1, though not 0 or 2 (Fig. 7; Table S9). In the second-best model, which includes depth, restoration status still has the highest relative importance (19.3), followed by harvest status (3.7), salinity (1.2), and finally depth (0.53). Greater depths correspond to a greater probability of 3 relative to 1 only (Table S12).

3.3. Virginia habitat scores

The Virginia subset of the data includes 289 points across the 6 Virginia tributaries. The results for Virginia differ from drivers in the full Bay-wide dataset and the Maryland subset because the harvest status and the CMECS stratum are the only predictors in the best model of oyster reef habitat, which is better
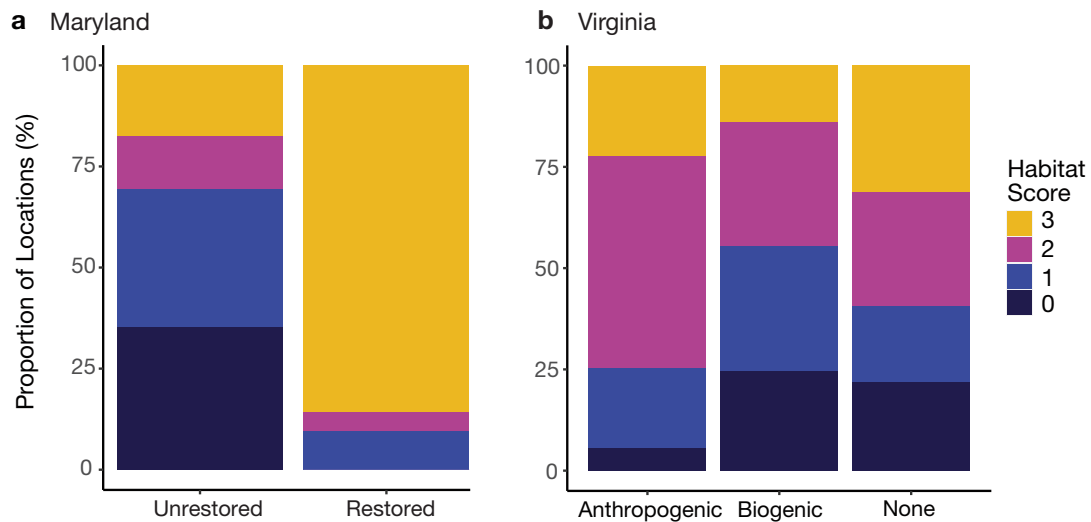
Fig. 5. (a) Habitat scores in restored and unrestored locations in the Maryland subset of the data. (b) Habitat scores for reefs classified as anthropogenic, biogenic, or none in the Chesapeake Coastal and Marine Ecological Classification Standard (CMECS) in the Virginia subset of the data. See Section 2.2 for definitions of habitat scores

than the next model by 2.05 AIC units (Tables S13 & S14). The binomial logit models used for diagnostics have McFadden's R^2 values of 0.13 (0 vs. 3), 0.05 (1 vs. 3), and 0.07 (2 vs. 3).

The effect of biogenic vs. anthropogenic CMECS stratum has the highest relative importance (3.1), followed by harvest status (2.4), and the effect of the anthropogenic CMECS stratum vs. habitat with no designation ('none') (2.1). The CMECS anthropogenic reef habitat has a lower probability of scores of 0 than the naturally occurring biogenic habitat

(anthropogenic–biogenic estimated probability difference = 0.194, p = 0.0013), and a higher probability of scores of 2 (anthropogenic–biogenic estimated probability difference = 0.274, p = 0.0016) (Fig. 5; Table S15).

As in the Maryland subset and the full Bay-wide dataset, harvested locations have a significantly lower probability of the highest habitat scores of 3 relative to unharvested locations (estimated probability difference = 0.141, p = 0.0136) (Fig. 6; Table S16). Like the Bay-wide dataset, but not the Maryland subset,
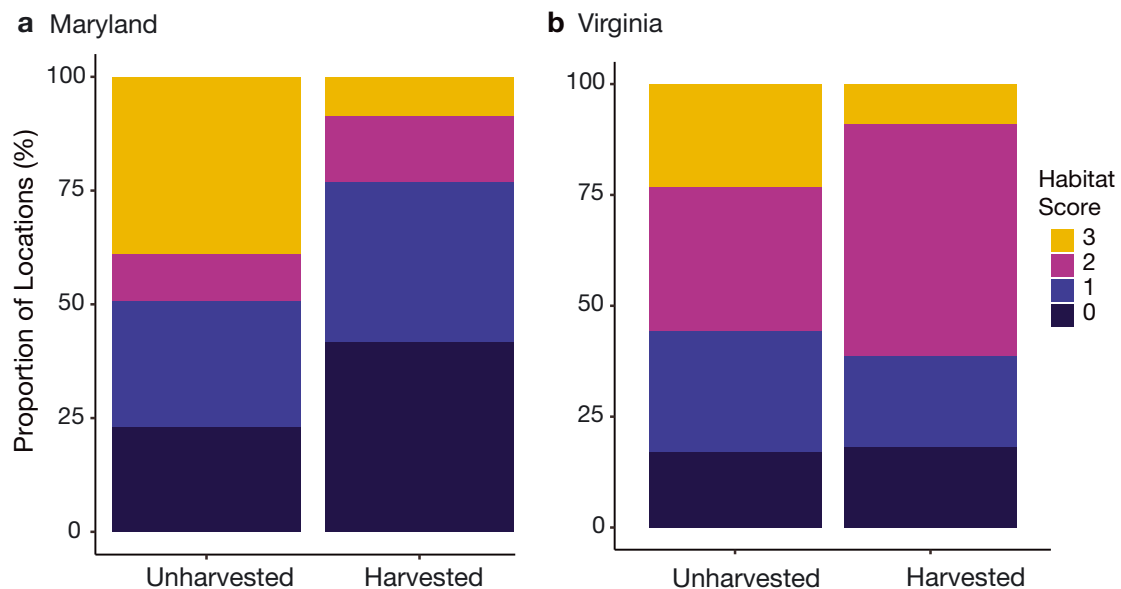

Fig. 6. Habitat scores in harvested vs. unharvested locations for the (a) Maryland and (b) Virginia subsets of the data. See Section 2.2 for definitions of habitat scores
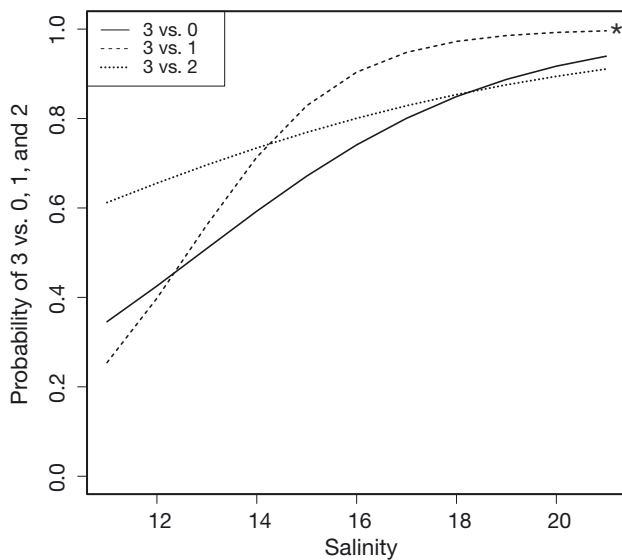
Fig. 7. Habitat scores in the 6 Maryland tributaries as a function of salinity. The star denotes statistical significance for the top line only at alpha = 0.05. See Section 2.2 for definitions of habitat scores

harvested sites in Virginia have a significantly higher probability of 2 (estimated probability difference = 0.257, p = 0.0021) (Fig. 6; Table S16). There is no difference in the probability of 0 and 1 (Fig. 6; Table S16).

Restoration status is included in the second-best model by AIC with evidence for more high scores of 3 and fewer low scores (1 and 0) on restored reefs, but the differences are not statistically significant (Tables S13 & S17, Fig. S1). Collinearity for salinity (with harvest status and the CMECS stratum) and depth (with the CMECS stratum) limited testing all possible models, but salinity and depth are not included in the top models (Table S13).

3.4. Change in oyster habitat over time

Harvest status and restoration status were the strongest predictors of habitat scores across 2017, 2019, and 2021, with additional variation across years (Fig. 8). Harvest was the only predictor in the best model of habitat scores of 0 relative to the highest scores of 3 (delta AIC 3.93), with unharvested reefs having a higher probability of 3 (Tables S18 & S19). Restoration status and year were included in the 2 best models of habitat scores of 1 relative to scores of 3, with support for an interaction between restoration and year (delta AIC = 1.78) (Table S20). The best model indicates a higher probability of high scores of 3 on restored reefs vs. non-restored reefs,

and in 2019 and 2021 relative to 2017 (Table S21). Harvest and year were included in the best model of habitat scores of 2 relative to 3 (delta AIC = 1.59), but a model with year and the 3 reef categories also contributed (Table S22). In the best model, there is a higher probability of 3 on unharvested reefs, as well as in 2019 and 2021 compared to 2017 (Table S23). The differences between years show more probabilities of 3 over time relative to 2 and 1.

Restored sanctuary reefs also have the most stable probabilities of 3, as all locations that scored a 3 in 2017 remained 3 in 2019 and 2021. Moreover, additional locations transitioned from lower scores of 1 and 2 into the highest score of 3. Although locations transitioned into 3 on the harvested and unrestored sanctuary reefs, these scores also downgraded to 1 and 2. This downgrading did not occur on restored sanctuary reefs (Tables S24–S27).

4. DISCUSSION

We conducted a large-scale, estuary-wide study across 12 tributaries in Chesapeake Bay that reveals how both management decisions and the environment shape oyster reef habitat. Surveys using a remote rapid assessment method show that reef habitat varies across the 12 tributaries depending primarily on management decisions. Habitat scores are higher at unharvested locations, reflecting greater percent cover and vertical relief. The presence of higher habitat scores on unharvested reefs is a clear and consistent result that emerges in the full Bay-wide dataset, as well as in the Maryland and Virginia subsets of the data. Restoration is also a strong predictor across the entire bay, with locations that received restoration treatment at least 1 yr prior to sampling having higher habitat scores relative to un-restored locations. These findings support our hypotheses on the effects of harvesting and restoration, verifying the importance of sanctuaries and restoration for high percent cover and structurally complex reefs. Oyster management around the world can benefit from large-scale studies of this kind that include many distinct subpopulations in a holistic evaluation of oyster reef habitat.

Restoration and harvest activity greatly influence reef habitat. However, there are differences depending on spatial scale. Harvest is a consistent driver across Chesapeake Bay and in both states, but other drivers in Maryland and Virginia show that we cannot extrapolate from the state level to understand Bay-wide drivers. For example, restoration status drives

scores in Maryland and Bay-wide, while the CMECS stratum is a significant driver of habitat scores in Virginia. Restoration and the CMECS anthropogenic stratum both lead to higher habitat scores, as they both reflect anthropogenic supplementation of reefs with shell or alternative substrate. However, the CMECS anthropogenic reefs in Virginia have more scores of 2 (high percent cover, low reef height) but not the highest scores of 3 (high percent cover and reef height). This lack of vertical relief may occur because CMECS anthropogenic habitat includes harvested reefs, whereas restoration is only in no-take oyster sanctuaries. Restoration status is also a more accurate encapsulation of anthropogenic supplementation in Chesapeake Bay because only 31% of anthropogenic CMECS sites are restored and 26% are stock-enhancement sites in harvest areas (Table S1), with the remaining 43% being former fishery stock-enhancement sites now in unrestored sanctuary areas. Another reason that restoration status is likely especially important in Maryland is because of the low natural recruitment in lower salinity (Tarnowski et al. 2020, 2022), and because restoration had progressed further in the Choptank River in the 'Ten Tributaries' initiative when this study was conducted (MVORIW 2022). The importance of CMECS anthropogenic habitat in Virginia may stem from the greater proportion of restored locations within anthropogenic habitat compared to Maryland (Table S1). It may also result from the higher salinities in Virginia because adding oyster shell or other substrate has a greater positive impact where oyster larvae are more likely to recruit and grow. While it is possible that temporal variation contributes to the state differences because photos were collected 1 yr apart, the 3 yr lifespan of oysters suggests that major changes occur on the scale of more than a single year. Longstanding environmental and management differences between the 2 sites also suggest that these are stable differences. Overall, the results support our hypothesis that drivers differ in Maryland and Virginia, which may stem from differences in both environmental and management conditions. The state-specific drivers we identify are valuable for management decisions that occur at the state level. Moreover, they indicate that it is unreliable to extrapolate state-specific habitat data to the Bay-wide scale.

Environmental conditions also play an important role in Bay-wide habitat. Salinity influences oyster reef habitat scores in the full Bay-wide dataset and in the Maryland subset, but depth has minimal impacts. At the Bay-wide scale, habitat scores increase with increasing salinity on harvested reefs, as hypothe-
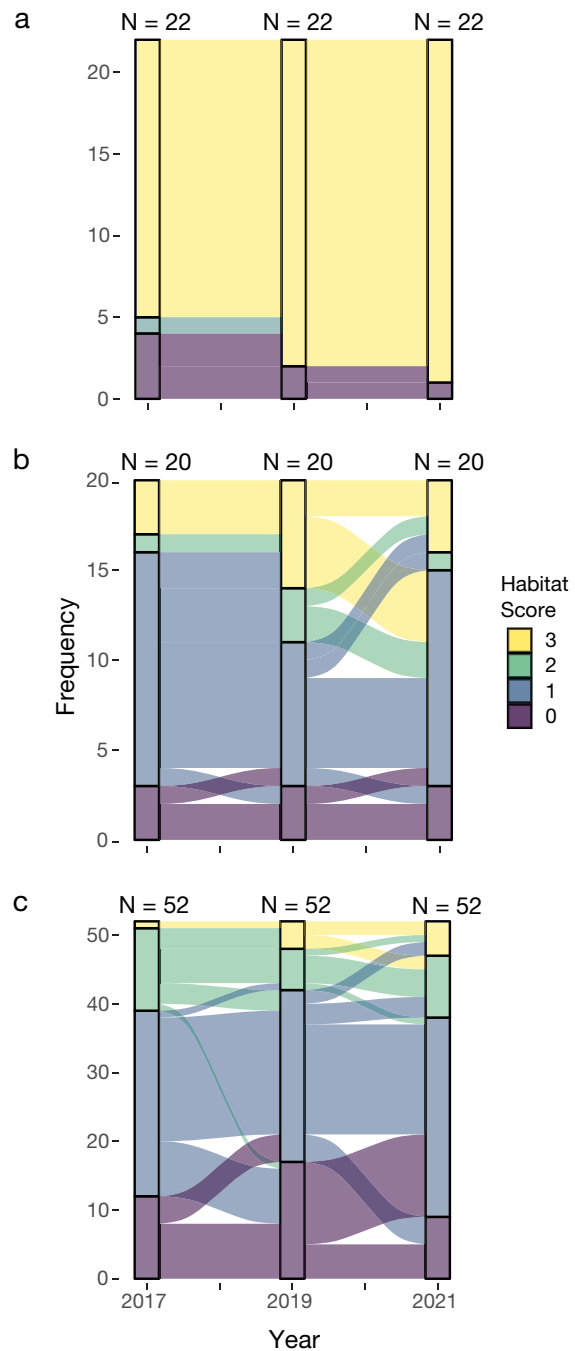

Fig. 8. Habitat scores in Harris and Broad Creeks (Maryland) from 2017 to 2019 to 2021 for (a) restored sanctuary locations, (b) unrestored sanctuary locations, and (c) harvested locations. The stacked barplots for each year reflect the proportion of scores in that year, while the curves and lines between years show the proportion of locations of a given score that stay the same or transition to higher or lower scores. N: sample sizes. See Section 2.2 for definitions of habitat scores

sized based on the physiological salinity preferences of *Crassostrea virginica*. However, scores decrease with salinity on unharvested reefs, contrary to our

hypothesis (Fig. 4). This decrease with salinity could result because some metrics of oyster success do not increase linearly with salinity. For example, growth and spawning require a minimum salinity threshold, but may not increase further as salinity increases (Kennedy 1996, Shumway 1996). It may also result if other environmental conditions change as salinity increases on unharvested reefs, such as bottom type, dissolved oxygen, or nutrient pollution. Additionally, the unexpected decrease with salinity may result if restoration activity, which occurs only on unharvested reefs, is overriding the natural effects of salinity. Thus, the observed pattern may reflect the fact that restoration projects under the 'Ten Tributaries' initiative have been completed earlier at lower-salinity Maryland sites and include more acreage of this recent restoration work (MVORIW 2022). The oyster reef habitat scores in the Maryland subset of the data increase with salinity despite the later restoration schedule of the saltier Manokin and St. Mary's tributaries, though salinity has a smaller effect size and weaker support than harvest and restoration status (Fig. 7; Table S8).

The patterns in oyster reef habitat over 4 yr (2017–2021) in Harris and Broad Creeks support our hypothesis that habitat differs depending on whether the reef was harvested or restored, in alignment with the Bay-wide results. The higher proportion of habitat scores of 3 relative to 1 in restored sanctuaries shows they have higher percent cover and reef height. Similarly, restored and unrestored sanctuary reefs have a higher proportion of 3 while harvested reefs have a higher proportion of 0 and 2. Contrary to our hypothesis, there is an additive contribution of year but no interactive effect with harvest or restoration status. Rather, the changes over time are consistent across reef types, with an overall increase in the proportion of the highest scores of 3 relative to 1 and 2. This supports our hypothesis that reef percent cover and height increase in restored areas over time but shows that there is also potential for this to occur on harvested reefs (Fig. 8; Tables S16–S19). The increase in habitat scores matches other evidence of thriving oyster populations in this time period. There were strong spat sets in 2020 and 2021, which were especially strong in Harris and Broad Creeks (Tarnowski et al. 2022, 2023). Additionally, the 2021 oyster biomass index in Maryland was the highest in 28 yr, and harvests were among the top 8 years, at 347 000 Maryland bushels (2800.9 cu in, 45.9 l) (Tarnowski et al. 2023). The forward progress of Bay-wide restoration from 2017 to 2021 may also have contributed to increases in habitat across reef types if restored reefs nearby bolster the larval supply in Broad Creek. There is

also stability in habitat scores, as half of the locations (47 out of 94) retain the same score from 2017 to 2019, to 2021. We estimate that scores from the same location are within a few meters of each other over time because the remote rapid assessment method cannot photograph the exact same reef location across years due to variability in GPS positioning and lowering the camera frame to the exact reef location. As a result, this method focuses on dramatic changes in percent cover and height between years, such as those caused by rapid population growth, large-scale sedimentation, or die-offs.

Despite encouraging numbers in both Harris and Broad Creeks in this time frame, the transition matrices do indicate differences in restored sanctuaries. The highest scores of 3 with high percent cover and vertical relief were robust against transitioning to lower scores in restored sanctuaries, whereas 3 in harvested and unrestored sanctuary reefs did not show this robustness. The lack of harvest alone was not sufficient for stable or increasing habitat scores over time, as indicated by the transitioning of higher scores of 2 and 3 from 2019 into lower scores in 2021 in the unrestored sanctuaries (Fig. 8). This finding aligns with other studies that show that limiting harvest alone, without accompanying restoration activity, is not sufficient to increase oyster densities or habitat (Heggie & Ogburn 2021, MORIW 2021), perhaps due to lack of hard substrate for spat to settle on, sedimentation, or the influx of freshwater with heavy rains in 2018 and 2019 (Tarnowski et al. 2020).

In comparison to a snapshot of habitat data, the time series is particularly important in understanding changes in habitat as a metric of reef success. The results for Harris and Broad Creeks demonstrate the influence of the environment because the positive impact of good years for oyster growth and recruitment occurs on all reef types. At the same time, the influence of management is clear in the differences across reef types. This is an important case study for oyster restoration projects around the world because it provides a specific example of how management and the environment can both influence reef habitat over time. It highlights the value of restored sanctuaries for increasing, and especially for maintaining, percent cover and reef height. It is also an example of why understanding connections between neighboring harvested and sanctuary reefs remains a high priority for oyster management in Chesapeake Bay and globally.

Beyond the implications for restoration, the analyses for all 12 tributaries and the time series provide valuable insights into habitat on harvested reefs. Habitat scores decrease in the presence of harvest

Bay-wide and are lower on harvested reefs in Harris and Broad Creeks from 2017 to 2021. Fewer scores of 3 show that there is lower vertical relief on harvested reefs, and yet harvested reefs can retain high percent cover. This confirms results found at smaller spatial scales that harvested areas often have high oyster densities but little structure (Lenihan & Peterson 2004, Heggie & Ogburn 2021). These flatter, less structurally complex harvested reefs are less valuable as habitat for some fish and crab species (Rodney & Paynter 2006). However, harvested oyster reefs provide different types of habitat rather than no habitat. Unrestored reefs that are similar in their lack of structure can be preferred by some species, with faunal communities that differ from restored reefs (Blomberg et al. 2018, Karp et al. 2018, Troast et al. 2022). Moreover, harvested sites may have high oyster productivity in terms of spat and biomass, which are separate but important metrics of value (Tarnowski et al. 2022). The multiple goals for oyster management in Chesapeake Bay and other regions, such as Europe (zu Ermgassen et al. 2021) and the Gulf of Mexico (Bendick et al. 2018), mean that it is essential to define the contributions of harvested reefs to habitat as part of the broader reef network. We show that reefs managed for the oyster fishery and restored sanctuaries both contribute to habitat, but with substantially different reef characteristics.

The remote rapid assessment method employed here (Heggie & Ogburn 2021) provided a unique opportunity to study oyster habitat with high resolution across a large spatial scale in Chesapeake Bay. We demonstrate the value of the remote rapid assessment tool from Heggie & Ogburn (2021), for which we now have a protocol and validation that is forthcoming (A. M. Tracy et al. unpubl. data). Similar methods can inform science and management for other estuaries with subtidal oyster reefs. However, underwater imagery is part of a suite of monitoring tools that provide insights into oyster and reef health. The present study highlights the value of estuary-wide oyster reef habitat data collected using a consistent method but does not meet all monitoring needs. Integrating the rapid assessments used in this study with quantitative oyster metrics at a subset of sites could yield important insights to inform future management of oyster reefs in Chesapeake Bay and in other estuaries with subtidal shellfish reefs, such as the Neuse River estuary in North Carolina (Lenihan & Peterson 1998), Botany Bay and Georges River estuary in Australia (The Nature Conservancy Australia 2021), and across the European range of *Ostrea edulis* (zu Ermgassen et al. 2021).

One limitation of our analyses is the simplification of harvest and restoration categories into presence/absence, which was necessary based on the available data. Future studies could dig deeper into variation within management status to complement the findings herein with comparisons between different restoration types, metrics of harvest intensity or gear used, time since harvest for rotational harvest sites, or other more detailed categories. Increasing the specificity of management conditions and features of the natural environment would also help explain further variation in habitat scores, as the pseudo-R^2 values reflect additional variation that remains unexplained. An evaluation of tributary-scale restoration impacts on habitat would also be informative, particularly at the conclusion of restoration efforts under the 'Ten Tributaries' initiative.

Oyster management in Chesapeake Bay and globally emphasizes the twin goals of a healthy ecosystem and a productive wild fishery. One of the critical ingredients of managing reefs for ecosystems and people is quantifying and evaluating oyster reef habitat because of the central role of structurally complex reefs in ecosystem services (Fitzsimons et al. 2019, Smith et al. 2023). It is important to know the type of habitat provided on harvested and restored reefs and understand how the effects of management work in the context of environmental drivers at multiple spatial scales. As one of the first large-scale analyses of subtidal oyster reef habitat, our study offers a new perspective by showing that restoration and sanctuaries are the main contributors to structurally complex reef habitat over more than 200 km and 12 distinct tributaries, despite a broad salinity gradient. We demonstrate that local spatial management decisions are an effective tool for managing habitat in the context of natural environmental drivers because they have high relative importance. Our findings will help guide coastal restoration projects of oysters and other species on a global scale by highlighting the need to understand the relative importance of environmental conditions and management. Furthermore, the data on habitat in Chesapeake Bay tributaries establish that harvested reefs and restored sanctuary reefs both contribute to oyster habitat, albeit in different ways.

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