



Bottom-Use Conflicts in Shallow Coastal Zones: Hard Clam (*Mercenaria mercenaria*) Aquaculture and Restored Seagrass (*Zostera marina*)

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Abstract

Multiple-use conflicts of the marine benthos (“bottom-use conflicts”) are increasing as humans expand use of the coastal zone. These conflicts necessitate balanced policies that consider the economic and ecological benefits of different bottom uses. In the Virginia coastal lagoons on the US east coast, there is a potential bottom-use conflict between hard clam (*Mercenaria mercenaria*) aquaculture and seagrass (*Zostera marina*) meadows. We leveraged two decades (2001–2021) of aerial imagery and environmental data to quantify historic trends in bottom use, assess the realized niche of seagrass and clam aquaculture across depth, sand fraction, root mean square (RMS) velocity, fetch, and sea surface temperature (SST) anomaly, and used random forest models to predict the potential extent of seagrass, clam aquaculture, and bottom-use conflict. We found growth in the coverage of both seagrass (+3373%) and clam aquaculture (+140%) over the past 20 years with a corresponding increase in bottom-use conflict (+2579%), though conflict area remained relatively minor. Seagrass occurred in deeper areas with higher fetch, a higher frequency of SST anomalies, lower sand fraction, and similar RMS velocities to areas containing clam aquaculture. Our random forest models predicted potential for the expansion of seagrass (+62%) and clam aquaculture (+263.9%) with a relatively small area of predicted spatial overlap (12.3%) under current conditions. These results illustrate how species distribution models can help us understand the spatial impacts of aquaculture on natural ecosystems and inform managers and policy makers to create objective policies that balance socioeconomic and ecologic needs.

Keywords Benthic monitoring · Coastal zone management

Introduction

User conflicts in the coastal zone have increased in frequency as the human population expands and more people utilize near-shore areas for recreation, industry, and development (Steins & van Ginkel, 2001). Marine aquaculture is one use of the coastal benthos that is competing for space

with both other human activities and with biogenic habitats (Primavera, 2006; Sanchez-Jerez et al., 2016). Aquaculture development has received resistance from “not in my backyard” attitudes (Beckensteiner et al., 2020; Hanes, 2018), commercial wild-catch fishermen who fear aquaculture will depreciate product prices or reduce access to good fishing grounds (Knapp & Rubino, 2016; Steins & van Ginkel, 2001), and the public who may find aquaculture incompatible with recreation (Shafer et al., 2010). The interaction between aquaculture and natural habitats may result in competition over space and resources, creating potential conflicts between two or more potential uses of the coastal zone (Diana, 2009; Primavera, 2006; Steins & van Ginkel, 2001).

Conflicts have been observed between the expanding marine aquaculture industry and vulnerable coastal habitats around the world. For example, mangroves have lost area due to aquaculture (Luo et al., 2022; Primavera, 2000; Tengku Hashim et al., 2021). Since the global aquaculture boom that started in the 1970s, it is estimated that 28%

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of mangrove habitat area in Asia has been converted into aquaculture ponds primarily for fish, shrimp, and crabs (Hamilton, 2013; Primavera, 2000; Tengku Hashim et al., 2021). Aquaculture also detrimentally impacts other threatened coastal habitats such as salt marshes, coral reefs, and seagrass meadows both through direct habitat loss due to conversion to aquaculture and through mechanisms such as nutrient pollution and increased sedimentation (Gu et al., 2018; Hedberg et al., 2017; Howarth et al., 2022; Naylor et al., 2000). Coastal habitats are valuable (Costanza et al., 1997) and threatened (Halpern et al., 2008; He & Silliman, 2019; Orth et al., 2006a, 2006b; Polidoro et al., 2010; Waycott et al., 2009); thus, active conservation and restoration are critical for habitat protection and for sustaining ecosystem services against anthropogenic stressors such as aquaculture expansion.

However, aquaculture is also extremely important, providing numerous socioeconomic benefits and ecosystem services. Aquaculture has been identified as one of the most viable methods for meeting a growing global demand for protein stemming from increasing population growth and economic prosperity worldwide (Cai & Leung, 2017; Hinchion et al., 2017). While terrestrial agriculture is increasingly limited by land and water availability and yields from wild capture fisheries have plateaued (FAO, 2022; Kite-Powell et al., 2013), global aquaculture production increased by 609% between 1990 and 2020 (FAO, 2022) and per capita consumption of marine aquaculture products increased by 177% between 1996 and 2019 (Gephart et al., 2024). In addition to its socioeconomic value, shellfish aquaculture delivers ecosystem services such as habitat provisioning (Dumbauld et al., 2009; Kling, 2012; Powers et al., 2007), nutrient cycling (Doering et al., 1986; Dumbauld et al., 2009; Murphy et al., 2015, 2016), and improved water quality (Dumbauld et al., 2009; Kreeger et al., 2018). Given the importance of both marine aquaculture and natural habitats, it is critical to understand drivers of the spatial distributions of different uses of the coastal zone and quantify the potential for conflict between these uses to effectively inform coastal management.

Here, we examine the conflict between restored seagrass (eelgrass—*Zostera marina*) meadows and hard clam (*Mercenaria mercenaria*) aquaculture in the coastal lagoons of Virginia, USA. Over the past several decades, there has been concurrent growth of the clam aquaculture industry and the successful and ongoing restoration of seagrass meadows in these coastal lagoons, resulting in the potential for a significant spatial conflict between these two bottom uses (“bottom-use conflict”) due to similar habitat requirements (Center for Coastal Resources Management, 1999; Hadley et al., 1997; Oreska et al., 2021; Woods, 2001). It is unclear precisely how much overlap exists between clam aquaculture activities and seagrass in the Virginia coastal lagoons and,

similarly, what proportion of currently unvegetated bottom habitat is suitable for both clam aquaculture and seagrass. While previous studies have attempted to use habitat suitability modeling to predict areas where shellfish aquaculture or seagrass may spread in the future, most of this work has focused on the Chesapeake Bay (Berman, 2008; Center for Coastal Resources Management, 1999; Grignano, 1994; Woods, 2001). Previous studies conducted in the Virginia coastal lagoons have either focused solely on seagrass expansion (Oreska et al., 2021) or had very coarse resolution (Luckenbach & Ross, 2011). Thus, there is a need to quantify bottom use overlap to assess current and future conflict and how that may impact both the clam industry and seagrass meadows under possible management scenarios. To address this need, we leveraged two decades of spatial coverage data from the Virginia coastal lagoons to (1) evaluate temporal trends in seagrass and clam aquaculture growth and overlap (“conflict”), (2) identify and compare the realized niche of seagrass and clam aquaculture across five environmental variables—depth, sand fraction, root mean square (RMS) velocity, fetch, and sea surface temperature anomaly, and (3) predict where seagrass and clam aquaculture are likely to spread in the future, with particular emphasis placed on areas of potential overlap. We then discuss the potential for coexistence between these bottom uses, the regional policy implications of our findings, and lessons that can be applied to similar conflicts elsewhere.

Methods

Study Site Background

Our study site is a series of dynamic coastal lagoons sheltered between a chain of undeveloped barrier islands to the east and the Delmarva Peninsula, VA, USA, to the west (Fig. 1). This marsh-lagoon-barrier island system contains the Virginia Coast Reserve Long-Term Ecological Research site (VCR-LTER) and extends from Fisherman’s Island in the south to Wallops Island in the north. These lagoons consist of shallow mud flats, oyster reefs, and salt marshes crossed by a few deep channels (Hayden et al., 1991; Luckenbach & Ross, 2011; Orth et al., 2006a, 2006b). Average lagoon depth is -1.0 meters (m) mean sea level with semi-diurnal tides and a mean tidal range of 1.2 m (Safak et al., 2015). These lagoons have variable water residence times ranging from several hours to several weeks (Safak et al., 2015). The system spans a slight population and development gradient on the Delmarva Peninsula, which increases northward, but anthropogenic nutrient loading remains low across the study region (Cole, 2011; Giordano et al., 2011; Orth et al., 2006a, 2006b).

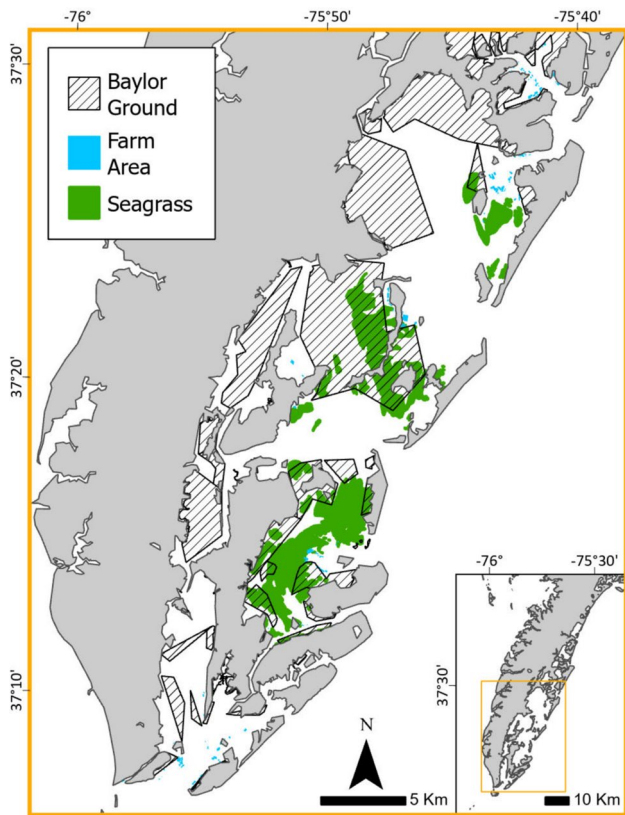


Fig. 1 Map of the southern Virginia coastal lagoons with the 2021 distribution of seagrass (dark green), clam farm areas (light blue), and Baylor Grounds (hashed)

Historically, the Virginia coastal lagoons were home to expansive seagrass meadows and wild-harvest shellfish industries (e.g., bay scallops, eastern oysters, hard clams); however, these both collapsed during the early to mid-twentieth century. Even prior to complete population collapse, Virginia established Baylor Grounds in 1895 to delineate and preserve natural, productive oyster reefs for public use as private aquaculture practices became more common in Virginia (Baylor, 1895). Eelgrass was abundant in the lagoons until 1932 when it was locally extirpated during an epidemic of seagrass wasting disease that spread across the Atlantic basin (Cottam, 1934; Muehlstein, 1989; Short et al., 1987). While eelgrass in neighboring systems like the Chesapeake Bay recolonized due to surviving populations that persisted in the fresher portions of riverine estuaries, the spatially isolated and high salinity Virginia seaside lagoons did not naturally recover (Orth et al., 2006a, 2006b).

The late-1990s began a period of recovery of both natural ecosystems and industry on the Virginia seaside. Hard clam aquaculture methods were developed by the Virginia Institute of Marine Science (VIMS) and the industry subsequently increased in Virginia's coastal lagoons (Castagna & Kraeuter, 1981; Mann et al., 2005; Orth et al., 2017).

Virginia has since become the leading producer of hard clams in the USA, with the coastal lagoons serving as the epicenter of this production (Gonçalves et al., 2022; Hudson, 2019). Around the same time, observations of a small, naturally established eelgrass patch near Wreck Island spurred the launch of a sustained and extremely successful eelgrass restoration project by VIMS that continues today, covering more than 4416.2 hectares (ha) of bottom by 2023 (Orth et al., 2020, 2006a, 2006b; Patrick et al., 2024).

The Virginia coastal lagoons provide a prime example of a region where there are shellfish industry and management concerns about current and future bottom-use conflicts between seagrass and shellfish aquaculture. In Virginia, hard clam aquaculture and seagrass meadows are regulated as mutually exclusive bottom uses that require similar habitat (e.g., shallow, sandy bottom) (Center for Coastal Resources Management, 1999; Hadley et al., 1997; Oreska et al., 2021; Woods, 2001). During the grow-out phase of clam aquaculture, mesh exclusion nets are placed over juvenile clams to protect them from predators for approximately two years until the clams have reached market size and are ready for harvest (Center for Coastal Resources Management, 1999; Hadley et al., 1997; Whetstone et al., 2005). These exclusion nets become overgrown with algae and block light, killing existing seagrass and preventing seagrass establishment (Center for Coastal Resources Management, 1999). Furthermore, grower activities including boat and foot traffic around the nets create additional disturbances that can affect seagrass.

In Virginia, submerged bottom is a state-owned resource managed by the Virginia Marine Resource Commission (VMRC), the agency that develops resource management policies and reviews and approves applications to lease these areas for aquaculture activity. The existing regulatory framework established by the VMRC concerning interactions between seagrass and aquaculture forms the basis for aquaculture industry concerns regarding the potential for bottom-use conflicts in the coastal lagoons. Suitable area available for new aquaculture lease applications is primarily limited by depth and tidal range (which varies throughout Virginia), the presence of designated public shellfish grounds ("Baylor Grounds"; areas mapped as natural oyster habitat in a survey conducted in 1894–1895) that are preserved for public use and may not be leased to citizens or companies (Luckenbach & Ross, 2011), and the potential impact of proposed activities on benthic natural resources (such as seagrass). Current policy for all tidal waters of Virginia protects seagrass by preventing approval of new aquaculture activities where seagrass has occurred within the past five years and limits changing the scope and spatial layout of existing operations where seagrass has grown around extant structures (Virginia Marine Resources Commission, 2017, 2016; Orth et al., 2002). These policies were developed with the declining seagrass meadows in the Chesapeake Bay in mind

and do not consider the functional differences between the Bay and coastal lagoons (e.g., lower nutrient loading, cooler water temperatures) that contribute to better outcomes for seagrass restoration and survival in the coastal lagoons (Orth & Moore, 1983; Orth et al., 2006a, 2006b; McGlathery et al., 2007; Orth, 2013; Orth et al., 2010; Giordano et al., 2011; McGlathery et al., 2012; Murphy et al., 2016; Lefcheck et al., 2017; Oreska et al., 2021). Given that the availability of leasable bottom suitable for clam aquaculture is the primary factor limiting the future expansion of the clam aquaculture industry (Luckenbach & Ross, 2011), factors that reduce this resource are a cause for industry concern. Under current regulations, there is the potential for rapidly expanding seagrass to outpace aquaculture expansion, effectively removing bottom habitat for future aquaculture activities as well as stymieing current operations.

Data Sources

Aerial Imagery and Spatial Data

We collected and analyzed annual aerial imagery of the study system for the years 2001–2021 from the VIMS SAV Monitoring Program, the National Agriculture Imagery Program (NAIP, years: 2005, 2009, 2011, 2012, 2013, 2016, 2018, 2021), and the Virginia Base Mapping Program (VBMP, years: 2002, 2007, 2013, 2017, 2021). The VIMS aerial imagery was used as the primary source, with NAIP and VBMP providing additional coverage to form as complete aerial coverage of the Virginia coastal lagoons through time as possible. The resulting imagery mosaic provided complete coverage of the Virginia coastal lagoons for ten of the years between 2001 and 2021 (2002, 2006, 2007, 2009, 2011, 2012, 2013, 2017, 2018, 2021), while other years contained substantial yet incomplete coverage of the region. The imagery was used to identify and delineate the location of clam nets and seagrass meadows. Spatial data on clam aquaculture leases were obtained from the 2021 aquaculture lease polygons throughout Virginia waters (Virginia Marine Resource Commission 2021).

Environmental Variables

We summarized data on five environmental variables—depth, sand fraction, root mean square (RMS) water velocity, fetch, and sea surface temperature anomaly into a polygon grid with a spatial resolution of 25 m². These variables were selected as abiotic conditions that represent key drivers of both seagrass and hard clam aquaculture survival and success (Castagna & Kraeuter, 1981; Roegner and Mann 1991; Hadley et al., 1997; Fonseca & Uhrin, 2009; Oreska et al., 2021). When compiling our dataset, we incorporated environmental variables with an initial spatial resolution smaller than 25 m² by calculating zonal statistics for the data

contained within each of our 25 m² grid cells and utilized the mean value for each polygon cell. For environmental variables with an initial spatial resolution larger than 25 m², we resampled the dataset to fit the resolution of our polygons.

Depth data were derived from the *Integrated Topography and Bathymetry for the Eastern Shore of Virginia* raster published by the VCR-LTER and generated using data collected from multiple sources (Richardson et al., 2014). The original dataset has a spatial resolution of 3.04 m² and models elevation (e.g., depth) in meters relative to the NAVD 88 vertical datum (NOAA National Geodetic Survey, 2018). We integrated these data into our analysis but changed values in the area near Godwin Island with low data resolution by taking out generalized values and interpolating depth data points around clam nets using data from the *Bathymetry of South Bay, VA 2020* single beam echo survey by the VCR-LTER (Barnes & Wiberg, 2023).

The sand fraction dataset represents benthic sediment grain size and has a resolution of 3.04 m² (Wiberg et al., 2015). Data for the full study system were extrapolated based on the relationship between grain size and residence time calculated from samples collected from four transects conducted in the Virginia coastal lagoons that spanned large hydrodynamic gradients (Wiberg et al. 2015). Sand fraction is defined here as the proportion of sediment comprised of particles larger than 64 µm (Wiberg et al., 2015).

The root mean square (RMS) water velocity dataset came from Safak et al. (2015) and has a resolution of 3.04 m². RMS velocity was produced by a 3-D unstructured grid finite-volume coastal ocean model (Chen et al., 2003; Safak et al., 2015) and compared to field measurements conducted in the Virginia coastal lagoons using an acoustic current meter (Safak et al., 2015).

Data on fetch were derived from *Modeled Wind Fetch for the Bays of the Virginia Coast Reserve* (Kremer & Reidenbach, 2021). This dataset represents the mean modeled fetch, defined as the length of unobstructed distance over which wind can blow (Fagherazzi & Wiberg, 2009), from the summers of 2014 and 2015 based on weighted observations of wind direction over the course of those two time periods and has a spatial resolution of 30 m² (Kremer & Reidenbach, 2021). We averaged the 2 years to get a single, average fetch dataset for our analyses.

Sea surface temperature anomaly came from the Rutgers University Coastal Ocean Observation Laboratory Database and consisted of temperature percentages associated with a coordinate pair. The initial resolution was 350 m². We transformed these points into an interpolative raster using the Bayesian Krig method (Esri, 2024) to fit the resolution of our dataset. In this work, sea surface temperature anomaly represents the proportion of days in which the temperature exceeded 28 °C, comparable to the established heat stress threshold (28.6 °C) for eelgrass in this system (Berger & Berg, 2024), in June, July,

and August of 2010 as recorded by the NOAA-15, 17, and 18 Advanced Very High Resolution Radiometer (AVHRR) satellites (Rutgers Center for Ocean Observing Leadership 2025).

Analyses

Spatial Analyses

All spatial analyses were performed in ArcGIS Pro (v3.1.0). Aquaculture activities were manually delineated within the study region for each year of available imagery between 2001 and 2021. Clam nets were identified by their uniform rectangular shape and spectral signature, and the center of each net was recorded as a point. The region within a 25 m radius of these clam net centers was computed to create polygons representative of “farm areas.” The 25 m radius was chosen based on the observed dimensions of the clam nets from year to year and represents a slight overestimation of the physical boundaries of the nets to better evaluate areas (“farms”) where the clam nets and aquaculture operations had the most influence. Farm areas provide an areal estimate of the footprint of direct aquaculture activity, compared with lease areas which do not represent the presence or areal extent of active aquaculture operations. Leases just denote where aquaculture is permitted. Seagrass bed polygons were derived for each year of aerial imagery from the VIMS SAV Monitoring Program.

The area of each bottom use was calculated by summing the area of all GIS polygons representing that bottom type for a given year. The area of bottom-use conflict was generated by directly overlaying polygon layers and summing the area of the overlap for that year.

The polygon grid containing the environmental data was coded to reflect the presence and absence of benthic features of interest, including leased bottom, unleased available bottom, Baylor Grounds, seagrass presence and density, and aquaculture activity (e.g., clam nets, farm areas). All spatial data were summarized and exported for analysis in R (v4.3.2) (R Core Team, 2023).

Data Analyses

We used the non-parametric Mann–Kendall test from the Kendall package (McLeod 2005) (v2.2.1) to determine if the patterns exhibited by our bottom uses of interest exhibited a monotonic trend over the course of our study period. We tested for the presence and rate of temporal trends in total seagrass (area), clam aquaculture (farm area), and their spatial overlap (overlap area) with each other and features of interest (e.g., unleased bottom, Baylor Ground) between 2001 and 2021 for years where the coastal lagoons were completely covered by the annual

imagery mosaic ($n = 10$); only these years were utilized for this analysis due to the reliance on complete data to accurately analyze areal trends from year to year.

To assess differences between bottom use (seagrass or aquaculture) and environmental covariates (depth, sand fraction, RMS velocity, fetch, sea surface temperature anomaly), we compared the distribution of environmental conditions of the different bottom uses using a Wilcoxon rank-sum test with the `wilcox.test` function within the `stats` library (R Core Team, 2023) (v4.3.2). For these analyses, we utilized all years (2001–2021) of data since these results are not significantly biased by missing small areas of spatial coverage within our imagery. The complete dataset was analyzed for RMS velocity, fetch, and sea surface temperature anomaly whereas a data subset generated by stratified random sampling was analyzed for the depth and sand fraction data. We used stratified random sampling to select a subset of the depth data to correct for artifacts stemming from utilizing interpolation to correct for low observation density within certain areas of the original dataset. The depth data were stratified by 0.1 m depth increments (e.g., 0 to –0.1 m, –0.1 to –0.2 m), and 5000 observations were randomly selected within each stratum from 0 to –2.5 m deep (observed depth maximum for > 90% of observations of features of interest), yielding 125,000 observations in the new dataset, approximately 9% of the original dataset. Similar to the depth data, we used stratified random sampling to select a subset of the sand fraction data to correct for artifacts within the data. Subsampling was done using 10% increments (e.g., 0–0.1, 0.1–0.2) across the full range of the variable (0.0–1.0) with 12,500 observations per strata, yielding 125,000 observations in the new dataset. To contextualize the statistical differences in the distribution of clam aquaculture and seagrass across each environmental variable, we calculated effect size $\frac{Z}{\sqrt{n}}$ using the `wilcox_effsize` function from the `rstatix` package (Tomczak & Tomczak-Łukaszewska, 2014; Kassambara, 2023) (v0.7.2).

We then compared the realized niche of clam nets present between 2001 and 2010 and those present in 2011 and 2021 (split to reflect periods with little seagrass coverage and significant seagrass coverage) to explore whether current policies regarding the protection of seagrass influenced clam net placement and thus their distribution across our environmental variables. The distribution of clam nets across our five environmental variables was compared between the two time periods using a Wilcoxon rank-sum test, and a corresponding effect size was compared using a Wilcoxon effect size test.

Species Distribution Models

To predict the potential spread of seagrass and clam aquaculture, we used random forest models based on methods

derived from species distribution modeling to develop spatially explicit predictions of the potential future extent of each bottom type and their areas of overlap. Random forest models consist of an ensemble of decision trees designed to iteratively split variable values until a decision or outcome is reached (Breiman, 2001; Cutler et al., 2007; Liaw & Wiener, 2002; Oreska et al., 2021). The model can be used to predict outcomes by running observations in a dataset through each tree to determine the predicted outcome and classifying the result based on the majority vote of all trees in the model (ties are randomly decided) (Breiman, 2001; Cutler et al., 2007). Random forest models are better suited to species distribution modeling than regression-based models (Cutler et al., 2007; Valle et al., 2013) and are robust to overfitting (Breiman, 2001).

Given that seagrass has been spreading from south to north within the study region and northern areas remain lightly or completely unvegetated, the model creation was based on data from the southern bays where seagrass expansion had mostly stabilized as of 2021. Grid cells within this region of relatively stable seagrass meadow that had seagrass present during any of the years between 2001 and 2021 were fed to the model as presence observations while those that had never contained seagrass were considered absences. This reduced the potential bias caused by pseudoabsences in regions where seagrass had yet to colonize due to dispersal limitation rather than habitat suitability. Further, a significant imbalance between the majority (absence) and minority (presence) classes within a categorical dataset can generate predictive models that systematically misclassify minority cases (Barbet-Massin et al., 2012; Chawla et al., 2002). To correct for the imbalances within our training dataset (seagrass—28% of area, clam nets—2.1% of area), we applied a synthetic minority oversampling technique (SMOTE) to the seagrass and clam net data (Chawla et al., 2002) using the SMOTE function from the DMwR package (Torgo, 2010) (v0.4.1). This method combines over-sampling of the minority class and under-sampling of the majority class to generalize the decision region of the minority class for a machine learning model. Working in “feature space” (multidimensional space defined by the set of variables being analyzed), SMOTE over-sampling randomly selects a number between zero and one and multiplies it by the differences between a minority observation and k of its nearest neighbors. We used the recommended k value of five (Chawla et al., 2002). This value is then added back to the original observation and the resulting value becomes a new, synthetic observation of the minority class. At the same time, the majority class is under-sampled by randomly removing majority class observations. For both the seagrass and clam net data, we opted for a combination of over- and under-sampling that balanced presence and absence observations to within 10% of one another. The balanced datasets were randomly subsampled

to create a training dataset with 70% of the data and a test dataset with the remaining 30%.

Two random forest models, one for seagrass and one for clam nets, were trained on the training data using the randomForest function from the randomForest library (Breiman et al., 2001) (v.4.7–1.1). We generated 500 trees for both our seagrass and clam net models. In addition to out-of-bag error estimates, the models were validated on the 30% remaining test data using area under the receiver operating characteristic curve (AUC) scores in conjunction with a consideration of majority and minority class error (used to determine if one class was systematically misclassified compared to the other) (Chawla et al., 2002). We then used the fitted seagrass and clam net models to predict their presence and absence across the full study system on a cell-by-cell basis (716,127 25 m² cells) based on the mean environmental conditions present within each cell.

We evaluated the relative importance of each environmental variable to each model using mean decrease Gini (MDG) scores. MDG represents the average decrease in node impurities (measured by the Gini index) resulting from splitting the data using a particular variable, averaged across all trees in a random forest model (Han et al., 2016). Larger MDG scores indicate that a variable is more important for the classification of the dataset (Han et al., 2016).

We compared the results of our seagrass random forest model with the combined random forest (RF) and boosted regression tree (BRT) model created by Oreska et al. (2021) by overlaying and comparing our predicted presence and absence data with their raster containing the probability of seagrass presence. We converted their probabilities (of seagrass presence) into binary presence/absence data using their probability threshold cut-off of 0.6 (where probabilities ≥ 0.6 represented seagrass presence and those < 0.6 represented seagrass absence) (Oreska et al., 2021). We compared model agreement based on four categories: presence-presence and absence-absence agreement and presence-absence and absence-presence disagreement.

Results

Historic Trends

Between 2002 (our first year of complete imagery coverage) and 2021, seagrass, clam aquaculture, and bottom-use conflict all increased in area (Fig. 2). Seagrass area increased from 105.3 to 3,658.5 ha (3373% increase; Mann–Kendall test, $\tau = 0.911$, $p = 0.003$). Clam farm area increased from 86.9 to 208.4 ha (140% increase, $\tau = 0.689$, $p = 0.007$). On average, farmed areas within leases represented just 7.3% of active lease area across all years. The area of seagrass present within clam farms increased from 0.1 to 3.5 ha (2579% increase, $\tau = 0.690$, $p = 0.008$) while the proportion of

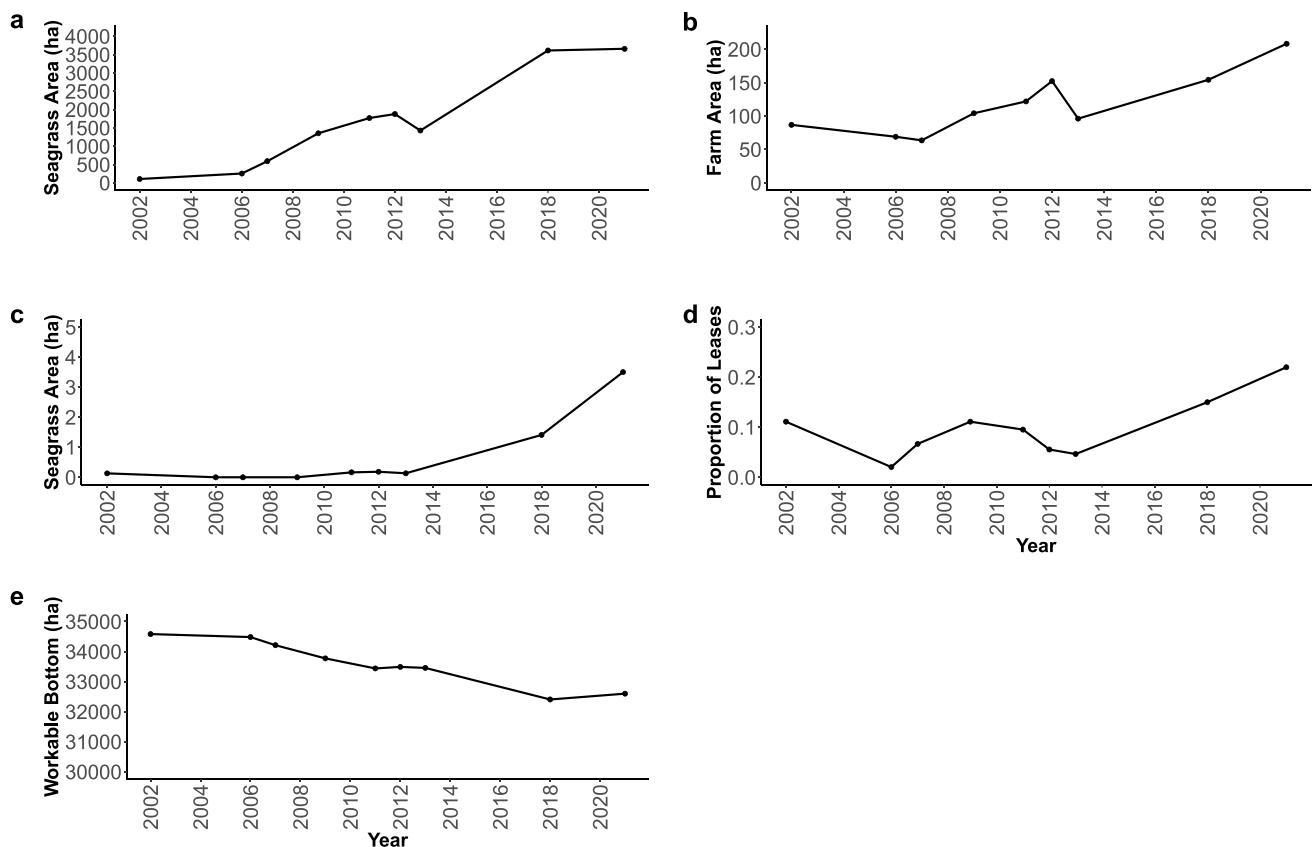


Fig. 2 Historic bottom use trends between 2002 and 2021 for years with complete coverage of the study system by the imagery ($n=10$). **a** Total seagrass meadow area in hectares, **b** total area of clam farms, **c** total seagrass area within clam farm boundaries, **d** the proportion

of aquaculture leases containing active clam operations that had seagrass within lease boundaries, and **e** the area of bottom that was either leased for aquaculture purposes or was available to lease for aquaculture

all privately leased bottom that contained both active clam operations (does not include vacant leases) and seagrass within the lease boundaries increased from 0.11 to 0.22 but not significantly so ($\tau=0.315$, $p=0.243$). As seagrass area expanded, the area of total bottom available for aquaculture (total area outside of Baylor Grounds minus seagrass area outside of Baylor Grounds) decreased from 64,272.3 to 62,289.6 ha (3.1% decline, $\tau=-0.833$, $p=0.002$).

Realized Niche

Seagrass occurred deeper (median = -1.01 m) than clam nets (median = -0.73 m) (Wilcoxon rank-sum test, $p=6.88e-11$, Wilcoxon effect size = 0.060), in more exposed areas (median fetch = 3,928 m vs 2,923 m, respectively; $p<2.2e-16$, effect size = 0.167), in areas with a greater frequency of sea surface temperature exceeding 28°C (median sea surface temperature anomaly = 0.33 vs 0.25, respectively; $p<2.2e-16$, effect size = 0.275), and in sediments containing a lower sand fraction (median sand fraction = 0.63 vs 0.69, respectively; $p=5.13e-5$, effect size = 0.038). RMS velocity was not functionally different

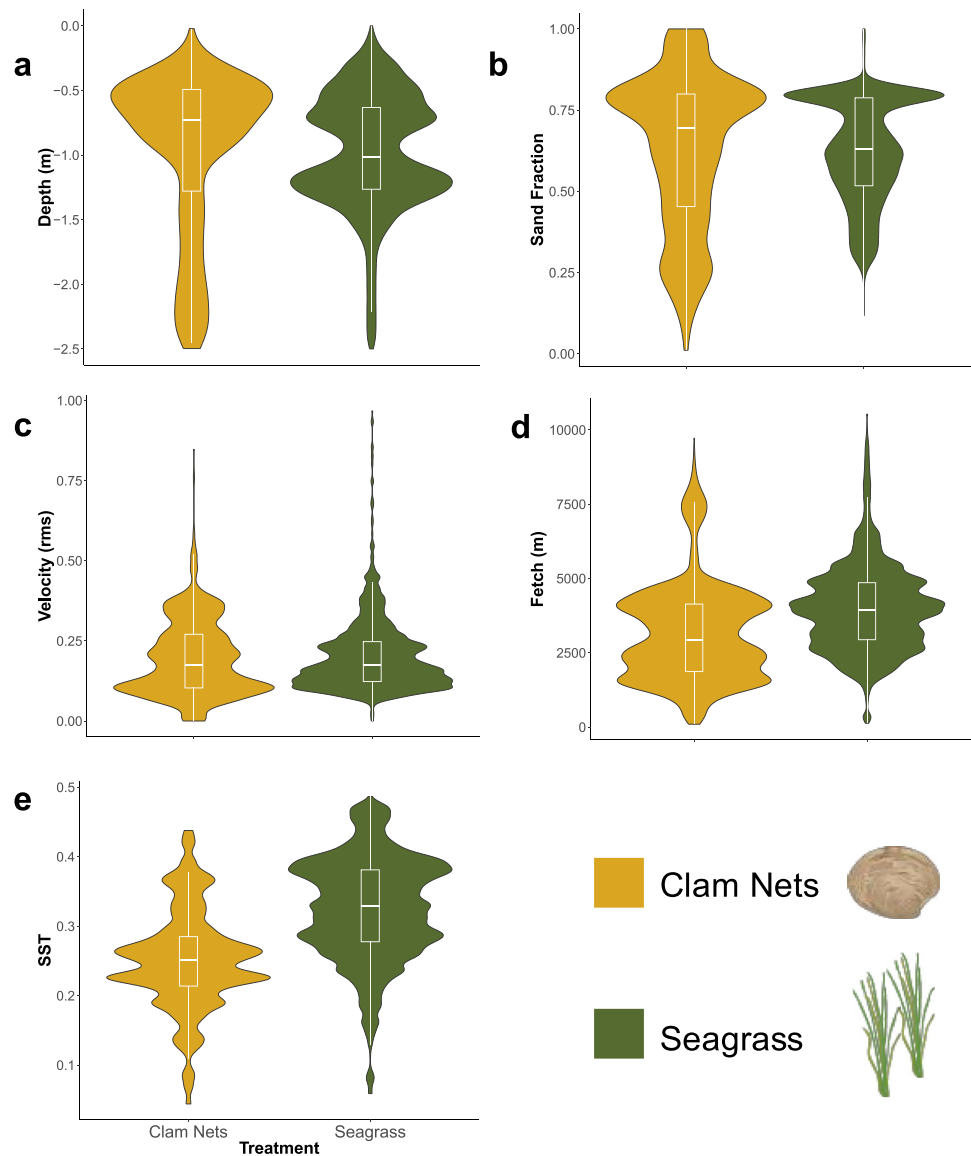
between bottom uses despite statistically different distributions (median RMS velocity = 0.173 vs 0.174, respectively; $p<2.2e-16$, effect size = 0.029) (Fig. 3).

Clam nets present between 2001 and 2010 (“early”) and those present between 2011 and 2021 (“late”) did not significantly differ in depth between the two time periods (Wilcoxon rank-sum test, $p=0.530$). Sand fraction ($p<2.2e-16$, Wilcoxon effect size = 0.289), RMS velocity ($p<2.2e-16$, effect size = 0.193), fetch ($p=0.019$, effect size = 0.026), and sea surface temperature anomaly ($p<2.2e-16$, effect size = 0.213) had differing distributions between the early and late groups, but only sand fraction, RMS velocity, and sea surface temperature anomaly had meaningful, though relatively small, effect sizes (0.1 = small effect, 0.3 = medium effect, 0.5 = large effect; Fritz et al., 2011) (Fig. 4).

Species Distribution Models

The seagrass model had an out-of-bag estimate of error rate of 1.24% that was balanced across the presence and absence data (1.0% and 1.5%, respectively) and an AUC score of

Fig. 3 A comparison of the distribution of clam nets (gold, left paired plots) and seagrass (green, right paired plots) (x-axis) across the five environmental variables utilized in our random forest models (y-axis): **a** depth (meters), **b** sand fraction, **c** root mean squared (RMS) velocity, **d** fetch (meters), and **e** sea surface temperature (SST) anomaly. Figure contains box plots nested inside violin plots utilizing a kernel density estimate to smooth the data distribution



0.988 indicating an excellent model fit (Pearce & Ferrier, 2000). The clam net model had an out-of-bag estimate of error rate of 0.93% that was relatively balanced across the presence and absence data (1.64% and 0.28%) and an AUC score of 0.990 indicating an excellent model fit (Pearce & Ferrier, 2000).

Sea surface temperature anomaly and depth were the two most important determinants of seagrass and clam net presence for both of our models based on mean decrease Gini scores (Calle & Urrea, 2010), with sea surface temperature anomaly being more important for seagrass and depth being more important for clam nets. In terms of variable importance, fetch was a close third for both models, followed by sand fraction and finally RMS velocity as the least important predictor variable (Fig. 5).

The seagrass model predicted 5,932.3 ha of seagrass at maximum extent under the environmental conditions measured at the time of data collection, which represents a 62% increase from 2021. The clam net model predicted 994.8 ha of clam nets at maximum extent under current conditions, representing a 377% increase from 2021. Since presence predictions were made on a cell-by-cell areal basis (rather than predicting individual clam nets), this model prediction roughly equates to an estimate of future clam farm area. For all bottom across the study system, the models generated overlapping presence predictions for 116.8 ha, representing a potential overlap between 11.7% of predicted farm area and 2% of predicted seagrass area (Fig. 6). However, within these predicted distributions, 2,439.8 ha (41.1%) of seagrass, 236.2 ha (23.7%) of clam nets, and 23.4 ha (20%) of overlap

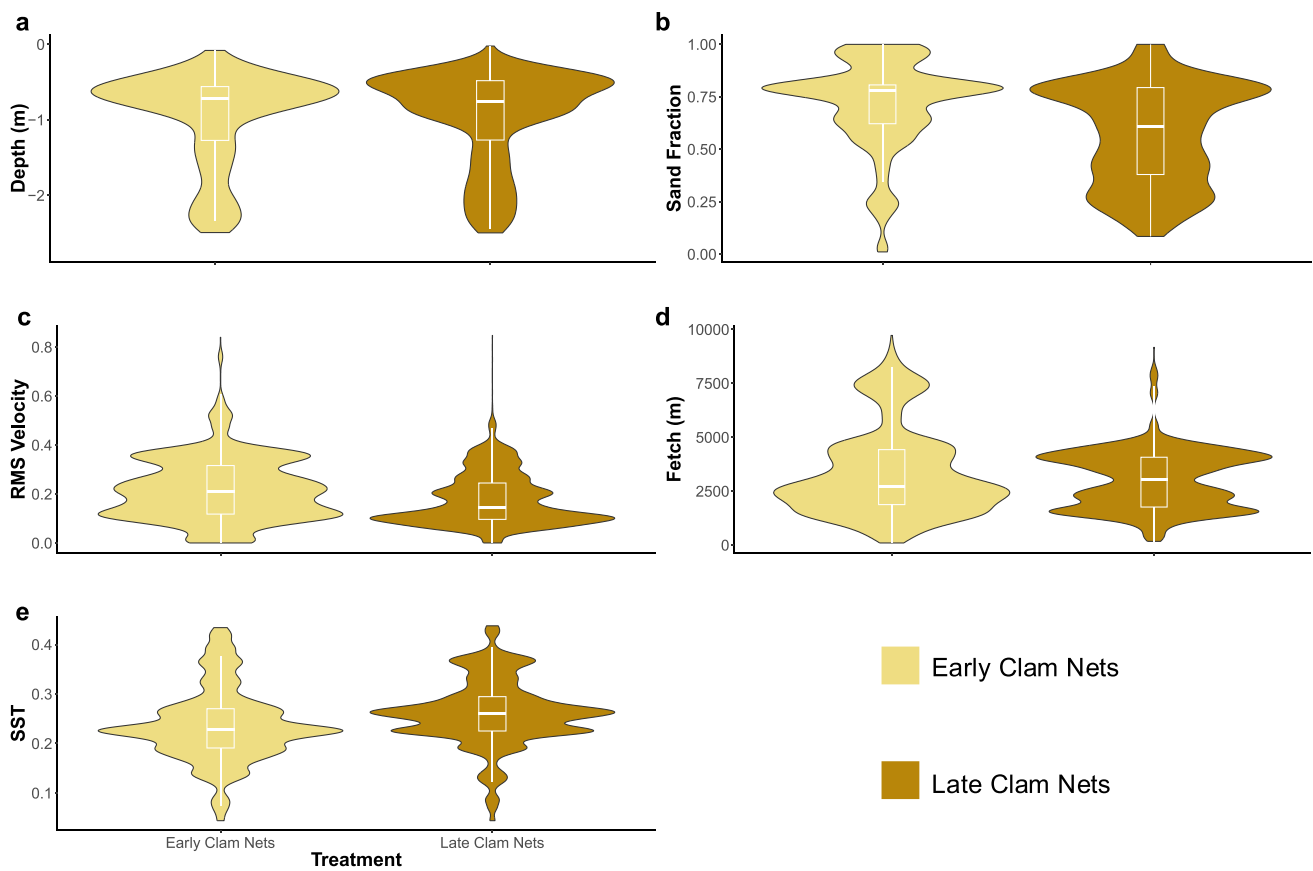
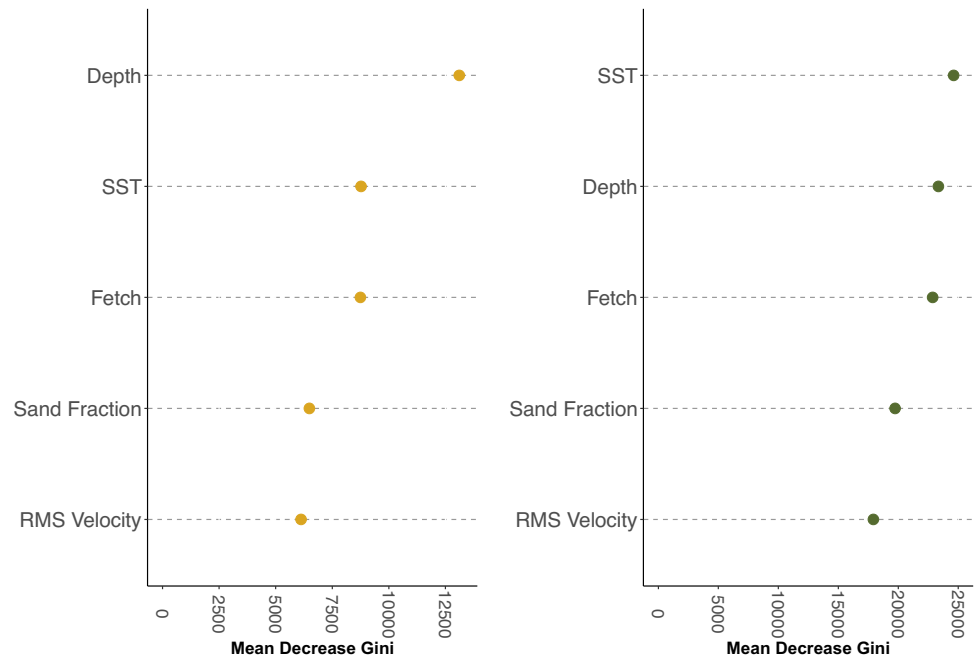


Fig. 4 A comparison of the distribution of early (2001–2010) clam nets (light yellow, left paired plots) and late (2011–2021) (brown, right paired plots) (x-axis) across the five environmental variables utilized in our random forest models (y-axis): **a** depth (meters), **b** sand

fraction, **c** root mean squared (RMS) velocity, **d** fetch (meters), and **e** sea surface temperature (SST) anomaly. Figure contains box plots nested inside violin plots utilizing a kernel density estimate to smooth the data distribution

Fig. 5 Variable importance plots (based on mean decrease Gini scores; x-axis) for the clam net (gold, left) and seagrass (green, right) for the five environmental variables used in our random forest models (y-axis; depth, sea surface temperature (SST), fetch, sand fraction, and root mean squared (RMS) velocity). Note the x-axes have a different scale



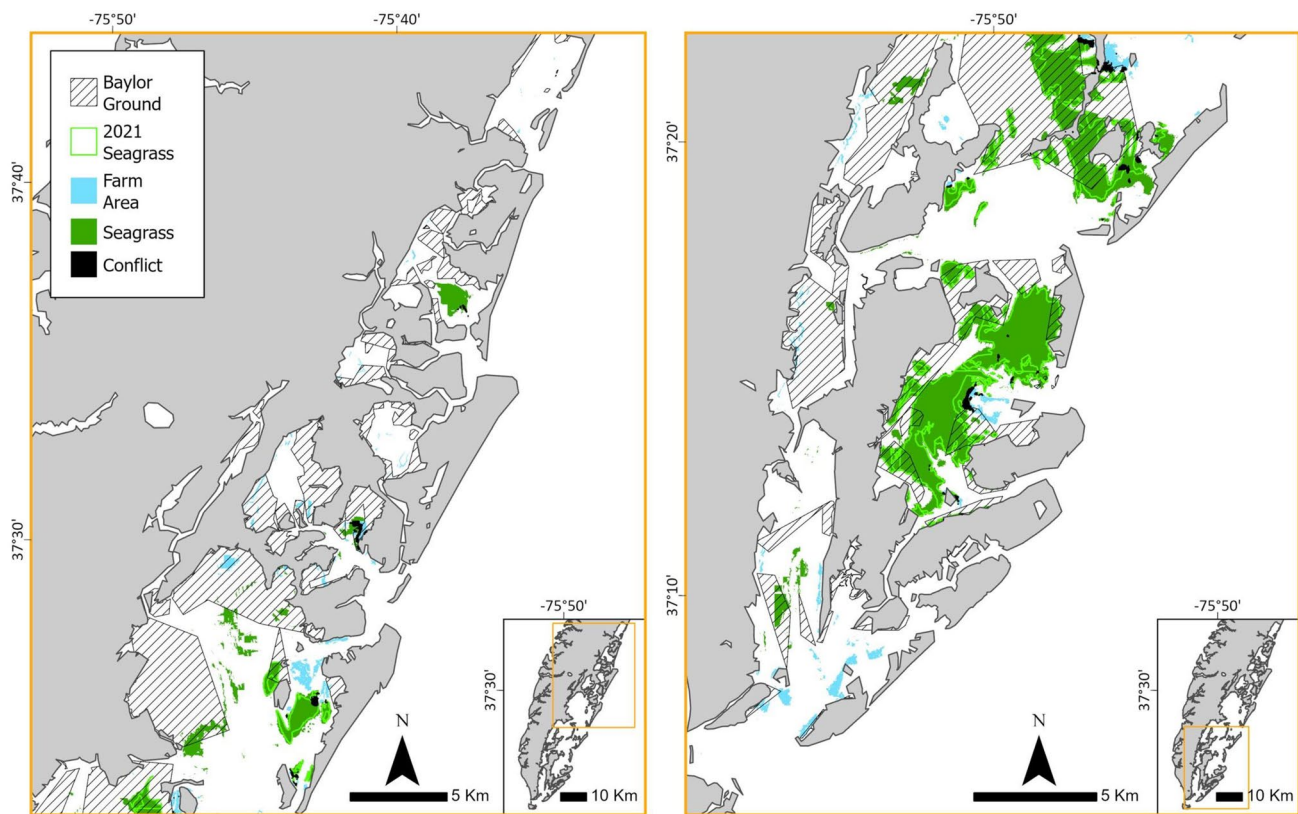


Fig. 6 Maps of model predictions of seagrass (dark green), farm areas (light blue), and bottom-use conflict (black) distributions across the northern (left) and southern (right) regions of the Virginia coastal

lagoons under current environmental conditions with Baylor Grounds (hashed) and 2021 seagrass meadow area (light green outline)

are predicted on Baylor Grounds. Given that clam nets cannot be placed on Baylor Grounds, the adjusted potential clam net area is 758.6 ha (263.9% increase) and the overlap area is 93.4 ha, representing 12.3% of adjusted predicted farm area and 1.6% of predicted seagrass area. On bottom that is available for lease (no inactive or active leases or Baylor Grounds present), the model predicts 2,494.1 ha of seagrass, 147.4 ha of clam nets, and 15.8 ha of conflict.

Our seagrass model predicted 59.3 km² (5,932.3 ha) of seagrass while the combined random forest and boosted regression tree model generated by Oreska et al. (2021) predicted 42.9 km² (4,290 ha). In terms of comparison, of the area covered by both models, our models agreed on 1,995.2 ha (5.8% of total bottom area) of seagrass area and 26,891.6 ha (77.9%) of bare sediment area. Our model predicted 3,477.7 ha (10.1%) of bottom with seagrass in areas that Oreska et al. (2021) predicted to be bare sediment while Oreska et al. (2021) predicted 2,136.9 ha (6.2%) of bottom with seagrass in areas that we predicted as bare bottom (Fig. 7). The models had high agreement for the classification of bare sediment and poor agreement for the classification of seagrass bottom.

Discussion

Over the past 20 years, both seagrass and clam aquaculture coverage in the Virginia coastal lagoons has expanded. With this expansion has come the increased potential for bottom-use conflict between natural habitat and aquaculture, as well as a small increase in actual bottom-use conflict. While we found positive trends for both seagrass and clam aquaculture and an associated increase in the total area of bottom-use conflict between 2001 and 2021, the proportional area of conflict remained relatively low throughout the past 20 years and in our future predictions. The 3.5 ha of seagrass found within farm areas in 2021 represents just 0.096% of total seagrass area and 1.68% of total farm area in 2021. We also predicted the potential for significant expansion of both seagrass and clam aquaculture, even if potential conflict areas are excluded. Our results indicate that both the clam aquaculture industry and seagrass can continue to expand without significantly impeding the other's growth. These results indicate managers can allow both uses to continue to grow and that the lack of conflict can be documented to alleviate industry concerns.

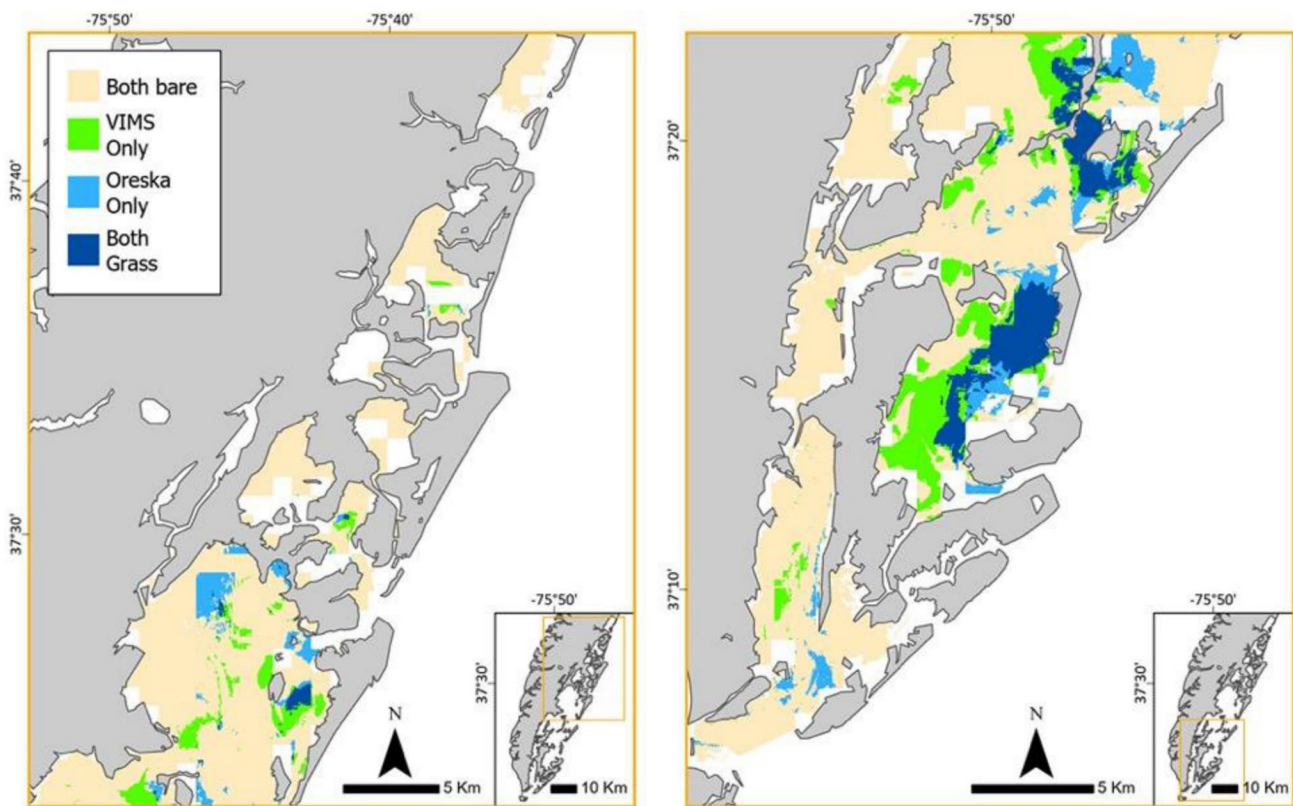


Fig. 7 Maps comparing model predictions with those of Oreska et al. (2021). Areas of model agreement for bare sediment (tan) and seagrass (dark blue) are shown along with areas of disagreement between our model (VIMS) and those of Oreska et al. (2021)

(presence-absence: green, absence-presence: light blue, respectively). Areas outside of one or both models' scope are shown in white. **a** Northern Virginia coastal lagoons and **b** southern Virginia coastal lagoons

Clam Aquaculture

Even under the most restrictive interpretation of our predicted clam aquaculture expansion (e.g., excluding nets predicted on Baylor Grounds or in conflict with seagrass), Virginia's clam industry can increase. In 2021, Virginia's 208.4 ha of clam farms produced hard clam landings valued at \$57.8 million (Hudson & McCarty, 2023). If we assume that the value of the industry will scale proportionally with area, the predicted farm area of 665.2 ha outside of Baylor Grounds and excluding seagrass bottom-use conflicts has the potential to bring in an additional \$184.5 million. If policies were changed to allow for some aquaculture on bottom containing seagrass or if the Baylor Ground areas were shifted to better reflect modern reef locations (Luckenbach & Ross, 2011), this number could be even higher.

In addition to its direct economic value, clam aquaculture provides several key ecosystem services that benefit humans, provide habitat, and impact ecosystem processes. The macroalgae that grow on clam nets provide habitat that, in some cases, can be comparable to that of other structured habitats such as seagrass (Powers et al., 2007). The biomass and composition of the invertebrate and

juvenile fish communities around clam nets tend to more similarly resemble those of seagrass habitat compared with unvegetated substrates (Kling, 2012; Powers et al., 2007). The habitat and resources provided by clam aquaculture may also contribute to enhanced fisheries production (Barrett et al., 2022; Powers et al., 2007; Theuerkauf et al., 2022) as well as nutrient cycling and carbon storage (Doering et al., 1986; Murphy et al., 2015, 2016). Management policies and regulations surrounding clam aquaculture should holistically consider both the potential and relative importance of ecosystem services lost and those gained from locating a lease on a particular area of bottom.

Seagrass

There are no complete quantitative records of seagrass meadow area prior to the wasting disease epidemic of the early 1930s, though reports indicate that it was abundant and dense throughout the region (Lynch et al. 1937; Cottam & Munro, 1954). The decades without vegetation undoubtedly led to shifts in environmental conditions in the area as the unstructured bottom was subject to the forces of wind and waves. Areas that once supported seagrass may no

longer be suitable, and areas that were unsuitable now may support vegetation due to changes in the environmental conditions over time. Our model predicts the potential seagrass extent under current environmental conditions, which can help set a target for modern restoration efforts. Continued seagrass restoration will support the ecosystem services provided by these meadows as well as enable the northward spread of seagrass into some of the coastal lagoons where natural expansion will be limited due to geologic or hydrologic barriers (Orth et al., 2006a, 2006b; Orth & McGlathery, 2012).

Our seagrass model predictions differed in several ways from those generated from a prior model (Oreska et al., 2021) but generated similar conclusions regarding the future of seagrass in the region. Oreska et al. estimated that seagrass cover could reach between 34 km² (3,400 ha) and 107 km² (10,700 ha). Our model prediction of 59.3 km² (5,932.3 ha) falls in the middle of their predictions. However, the spatial distributions differ, with less than 50% agreement in the seagrass presence locations on a cell-by-cell basis (based on their combined RF and BRT model).

A key difference between the model of Oreska et al. (2021) and our model is the seagrass presence and absence data used to train the models. Our model focused on an area of composite seagrass presence data from 2001 to 2021 that had stabilized by 2021 while Oreska et al. (2021) focused on areas of seagrass presence spread between restoration and natural recruitment plots established between 2001 and 2015. Our data had over two orders of magnitude more observations, likely increasing the accuracy and predictive performance of our model. The different data used to train the models likely explains an important difference between our model and that of Oreska et al. (2021), which is that our model predicted seagrass area to span from near-shore to offshore regions of the coastal lagoons, while Oreska et al. (2021) predicted seagrass in primarily near-shore locales. The use of data from restoration plots biases their model towards shallower, more near-shore locations because areas selected for restoration plots are typically shallower and in lower energy areas (e.g., shorter fetch, lower RMS velocities) to maximize seedling establishment in the absence of intraspecific facilitation by existing seagrass. This also biases their predictions towards greater bottom-use conflict with clam aquaculture, which also tends to be located in these shallower, near-shore locales.

Another key difference is that we balanced our presence and absence data using SMOTE in order to generate a model that did not systematically misclassify minority (presence) cases (Chawla et al., 2002). Oreska et al.'s (2021) AUC values were 0.89 for the BRT model and 0.86 for the RF model, whereas our model had an AUC score of 0.988, indicating a better overall fit (Pearce & Ferrier, 2000). Such a high AUC score may generate concerns about model overfitting, but

random forest models are generally robust to overfitting and our inferences are restricted to the spatial area where model fitting occurred (Breiman, 2001). Given this, we expect that our model results represent a strong target for seagrass restoration efforts within the system and validate our subsequent estimates of bottom-use conflict.

Bottom-Use Conflicts

Spatial differences in current and predicted future distributions of seagrass and clam nets are likely the result of differences in the combination of ideal habitat requirements for each bottom use. Specifically, these “habitat requirements” reflect both the clams biological limits and working conditions required by industry personnel.

Despite seagrass and clam aquaculture having significantly different distributions across all five of our environmental variables modeled here, only fetch and sea surface temperature anomaly were important as individual predictors based on an evaluation of effect size (Fritz et al., 2011), though in all cases, effect sizes were relatively small in magnitude. Still, our model predicted minimal spatial overlap, indicating that, despite small univariate effect sizes, the subtle differences in their distributions across the combinations of environmental variables generated relatively greater divergence in their spatial distributions. One explanation for this is that the interplay between these environmental variables generates unique habitat conditions that amplify the smaller differences observed when considering any one variable in isolation.

The overarching importance of depth in clam net and seagrass distributions in our machine learning models may be indicative of differences in tolerance to thermal stress and site workability. In our study system, eelgrass is at the southern end of its range (Fonseca & Uhrin, 2009; Jarvis et al., 2012), thus is subject to thermal stress (Fonseca & Uhrin, 2009; Orth & Moore, 1986), especially during summer months. Since the water quality in this system is generally good, greater light penetration depths allow eelgrass to find refuge from heat and desiccation stress in deeper parts of the coastal lagoons. In contrast, infaunal clams are protected from heat and desiccation stress beneath the sediment in the intertidal zone (Peterson, 1991). Furthermore, intertidal clam aquaculture operations benefit from the desiccation of macroalgae and other fouling organisms that occur at low tide (Castagna & Kraeuter, 1981; Hadley et al., 1997), reducing the labor needed to clean and maintain the nets. Additionally, the clams are available for visible inspection at low tide (Hadley et al., 1997). Shallow subtidal areas are still workable for clam aquaculture but require more effort to clean and maintain. Workability decreases as depth increases, and planting clams deeper than the shallow subtidal zone significantly increases the effort and equipment required, making deeper sites less profitable.

The inverse relationship between depth and thermal stress may help explain our predicted distribution of seagrass in deeper areas, but it is somewhat at odds with our finding that existing seagrass is located in regions with a greater frequency of sea surface temperature (SST) anomalies (defined here as surface temperatures exceeding 28 °C) compared to areas where clam nets are present. However, SST anomaly may be a better indicator of local hydrodynamic conditions (e.g., currents, residence time, water inputs) than actual thermal stress. Clam nets tend to be placed in areas near channels because there is greater food availability and flushing of excess organics and waste due to a lower residence time, and these regions are more accessible by boat. Areas near the channels typically have a lower SST due to the influx of cooler water from the Atlantic Ocean. Conversely, seagrass benefits from being further away from the channels because the lower energy areas enhance seedling establishment, removing it from direct ocean inputs and placing seagrass in areas with a higher frequency of SST anomalies. This is supported by the fact that SST anomaly in this system is inversely correlated with sand fraction and fetch, which we see reflected in the distribution of seagrass in areas with higher fetch, lower sand fraction, and higher SST anomaly and clam nets in areas with lower fetch, higher sand fraction, and lower SST anomaly.

The differing tolerance to exposure (fetch) between seagrass and clam nets may arise from the ability of seagrass to modify its environment to reduce wind-wave energy whereas clam nets are subject to the full force of the energy generated by increasing exposure. Established seagrass meadows can modify their environment, and their above-ground biomass (e.g., shoots) reduces wind-wave energy and creates positive feedback that allows seagrass to persist by reducing sediment resuspension and erosion (Carr et al., 2010; Contti Neto et al., 2022; Hansen & Reidenbach, 2021). This habitat modification does not occur with clam nets, which are at risk for becoming buried or washed away in high-energy (exposure) locations (Hadley et al., 1997). Consequently, clam growers often place nets in more sheltered locations, such as near a marsh or barrier island.

Our observation that clam nets occurred in slightly sandier sediments than seagrass is likely the result of a combination of site workability, habitat requirements, and the ability of seagrass to modify their environment. Clams can survive in most sediments but are more likely to be placed in sandier areas because they are easier to work in than those with finer sediment particles (Hadley et al., 1997). Eelgrass can also survive in a variety of sediments (Fonseca & Uhrin, 2009), but higher sand fractions are lower in nutrients than siltier regions, which may limit seagrass growth. Further, the seagrass canopy can slow water velocity and trap particles, resulting in the deposition of finer particles than would otherwise occur. However, finer sediments can result in an

accumulation of sulfides, which can stress eelgrass (Goodman et al., 1995); thus, a balance between fine and sandy substrates is required for seagrass growth.

An alternative hypothesis for the existing spatial divergence between the bottom uses is the effect of current policies. Given that new farms are not allowed to be situated in areas where seagrass already occurs, it stands to reason that newer farms have been concentrated in areas unsuitable for seagrass. When we compared the distribution of clam nets in 2001–2010 (small seagrass area) and 2011–2021 (large seagrass area) across each environmental variable, we found that the differences were statistically significant, but with relatively small effect sizes.

Interestingly, clam nets placed later—when seagrass was more abundant and thus existing policies generated greater restrictions on where nets could be located—shifted towards more similar habitat preferences to seagrass compared to nets placed earlier when there was less seagrass and thus less restrictions on net placement. Similarly, we did not observe much invasion of seagrass into farms that were established in areas of the lagoons prior to the seagrass expansion. These two concordant lines of evidence support the interpretation that the ideal bottom areas for each use type are significantly different from one another regardless of policy.

It is important to note that our reported predictions of bottom-use conflict are significantly lower than those of Oreska et al. (2021) (93.4 ha = 0.934 km² vs 876 ha = 8.76 km²), but this can be explained by a difference in our definitions of conflict. Oreska et al. (2021) reported bottom-use conflict as lease overlap, which greatly inflates the actual conflict because lease boundaries do not reflect the actual area farmed. Clam aquaculture leases in this region are typically large and span from the intertidal to subtidal waters. Only 7.3% of the average active lease was used for clam production over the course of our study, and our models suggest that an average of only 8.9% of current leased bottom is suitable for clam production, and 14.6% is suitable for seagrass. Seagrass presence on a lease is not indicative of a direct conflict since much of the lease area is unusable for aquaculture, and seagrass can exist on deeper sections of a lease without impacting operations. Our prediction of conflict is based on direct spatial conflict of seagrass within the clam farm (25 m buffered radius around clam nets). Further study on the physiological and ecological results of such direct interactions, including seagrass facilitation by or resistance to and recovery from interaction with aquaculture and impacts on aquaculture production by seagrass, would further benefit our understanding of these interactions on the fine scale.

Despite the perception of a significant and growing bottom-use conflict, we observed that, currently, there is relatively little direct conflict occurring in the region. Furthermore, we interpret the model predictions to suggest

that, with no policy change, the clam aquaculture industry has the potential to expand by 219.2% under the worst-case scenario for industry where seagrass colonizes all potential future conflict zones before farms are established. However, there may be opportunities for policy adjustments to further minimize industry concerns in the region without significant negative impacts on the seagrass. In a completely permissive scenario where farms can be sited anywhere regardless of the presence of seagrass, our model indicates that only 1.57% of seagrass bottom would be affected. However, this does represent 93.4 ha of seagrass loss, a potentially unpalatable amount when viewed within the context of global declines in this critical resource (Dunic et al., 2021; Orth et al., 2006a, 2006b).

An alternative approach might involve redrawing the lines for the Baylor Grounds (public shellfish grounds). The suitability of Baylor Grounds for shellfish has changed dramatically over 129 years since they were established in 1895. Only 56% of Baylor Ground area in Virginia coastal lagoons are still suitable for wild oysters, and less than 10% are deemed suitable for commercial wild clam harvest (Luckenbach & Ross, 2011), indicating a mismatch between their original purpose and current use. While there may be a resistance to such a move given their cultural and recreational significance, a redistribution of Baylor Ground boundaries could potentially reduce bottom-use conflict from 93.4 to 0 ha by opening 236.2 ha of Baylor Grounds suitable for clam farming but not seagrass to production and simultaneously moving the 93.4 ha of conflict zone on leasable bottom into Baylor Grounds.

Conclusions

As both conservation and aquaculture intensify in coastal regions, multiple-use conflicts will increase. Quantitative analysis in the example studied here indicates limited conflict between two types of uses in Virginia, USA. Detailed modeling of spatial processes at regional scales is an important direction for studying these interactions and potential conflicts and will help inform better resource management policy.

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Data Availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics Approval and Consent to Participate Not applicable.

Consent for Publication Not applicable.

Competing interests The authors declare no competing interests.

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