

Quantifying and mapping intertidal oyster reefs utilizing LiDAR-based remote sensing

Sara Hogan*, Matthew A. Reidenbach

Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904, USA

ABSTRACT: Restoration and conservation of the eastern oyster *Crassostrea virginica* requires information on its distribution and abundance, which is logistically difficult to obtain. We demonstrate how light detecting and ranging (LiDAR) can be used to obtain this information in a model intertidal system within the Virginia Coast Reserve (VCR) on the eastern shore of Virginia, USA. Specifically, we determined how LiDAR-derived data can be used to classify land cover and identify intertidal oyster reefs. We used the locations of existing reefs to determine the physical characteristics of oyster habitat through the use of elevation, fetch, and water residence time data for the region. Trained with elevation, intensity, surface slope, and curvature data, the land cover classification identified oyster land cover with an accuracy of 81%. Ground-truth patches were small, with the 50th percentiles for area and perimeter being 11.6 m² and 14.5 m, respectively. Reef crests occurred in a narrow range of elevation (−0.81 to −0.18 m relative to NAVD88) and patches had an average vertical relief of 0.14 m. The habitat suitability analysis located 52.4 km² of total oyster suitable habitat, or 12.03% of the mapped area with elevation, fetch, and residence time characteristics similar to those of existing reef area. This suggests that there is ample viable intertidal area for future oyster population restoration. Results also indicate that LiDAR data, coupled with physical attributes of existing reefs, can be used to target and prioritize locations for future restoration efforts in intertidal habitats.

KEY WORDS: Oyster · LiDAR · Remote sensing · Ecosystem restoration

—Resale or republication not permitted without written consent of the publisher—

1. INTRODUCTION

The native eastern oyster *Crassostrea virginica* is a dominant species in the intertidal zone of coastal bays on the eastern shore of Virginia, USA. Eastern oysters were historically abundant in Chesapeake Bay and the bordering coastal bays; however, due to overharvesting compounded by poor water quality and disease, the population rapidly declined in the latter half of the 20th century, collapsing commercial harvest (Rothschild et al. 1994, Kemp et al. 2005). Largely due to partnerships including federal and state agencies, universities and non-profits, oyster populations have begun to recover in Chesapeake Bay (Schulte et al. 2009, Lipcius et al. 2015) and on the eastern shore (Wesson et al. 1999, Ross & Luckenbach 2009). On the eastern shore, over 20 ha of reefs

have been successfully created and populated by oysters in the past decade largely by introducing hard substrate as habitat that creates suitable settlement locations for oyster larvae and, ultimately, oyster growth. The recovery of the eastern oyster is important because the species is economically significant as a fishery and provides many ecological services, including water filtration (Coen et al. 2007, Van der Zee et al. 2012, Reidenbach et al. 2013) and mitigation of wave energy that erodes shorelines (Piazza et al. 2005, Scyphers et al. 2011, Wiberg et al. 2019).

To understand the progress of restoration and current populations of oysters on Virginia's eastern shore, it is imperative to have accurate information regarding oyster stock and location. Remote sensing is a way to acquire environmental data from a distance and can be beneficial to visualizing landscape

*Corresponding author: sh8kj@virginia.edu

cover and environmental change on different temporal and spatial scales (Morgan et al. 2010). Airborne-based light detecting and ranging (LiDAR) is a recent form of remote sensing that can be used to estimate elevation based on the return time of laser lights emitted from the aircraft and reflected from the land below. Advantages of LiDAR include robust data with high data density and vertical elevation accuracy (Schenk & Csatho 2002).

Due to these advantages, LiDAR elevation data sets have been used in coastal and estuarine environments to understand inundation (Gesch 2009), marsh classification and sedimentation (Morris et al. 2005, Marion et al. 2009), and classification of seagrass beds (Ishiguro et al. 2016) and intertidal habitat (Garono et al. 2004, Halls & Costin 2016).

While orthoimagery, i.e. geometrically corrected imagery, has been used previously to aid in oyster mapping, in itself, it presents the disadvantages of low spatial extent, and in many instances produces inconsistencies that cause intertidal land classification to change depending on when imagery was collected with respect to the tides. This is an important consideration because the majority of oysters found Virginia's eastern shore are intertidal (Ross & Luckenbach 2009).

One characteristic of oyster reefs that makes the use of LiDAR especially attractive is that oysters accrete vertically and differ in elevation from surrounding land area. Many studies have relied largely on orthoimagery (Grizzle et al. 2002, Ross & Luckenbach 2009) and hyperspectral data (Garono et al. 2004, Le Bris et al. 2016) to identify and survey reefs. The greater inaccuracies of earlier image interpretation are attributed to pixel size, and with greater pixel resolution came improved analysis (Grizzle et al. 2002, Schill et al. 2006, Halls & Costin 2016, Le Bris et al. 2016). With high-resolution satellite imagery, intertidal landscapes for oysters have been classified with accuracies greater than 70% (Green & Lopez 2007, Le Bris et al. 2016). Moreover, by pairing LiDAR elevation data with aerial imagery and other terrain data, intertidal land classification can be improved (Smith et al. 2015, Halls & Costin 2016), with oyster classification accuracies reaching 85%. In the past, few researchers have investigated the use of LiDAR-derived data alone to classify intertidal land cover, and those that have experienced limited success (Schill et al. 2006). With greater availability and knowledge on how to acquire accurate LiDAR data by mitigating error propagation from sensors, flight missions, and processing (Baltasvias 1999, Ahokas et al. 2003, Hodgson & Bresnahan 2004, May & Toth

2007, Triglav-Čekada et al. 2009), it remained to be determined whether LiDAR-derived data alone can successfully classify intertidal oyster reefs.

Given previous success in other habitats, LiDAR data may provide an alternative technique to estimate distributions and abundances of intertidal oyster reefs. Marked difficulties in mapping oyster reefs include differences in size, location, origin (restored, natural, public, private), and overlap with habitats including mudflats and coarse beaches (Garono et al. 2004, Schill et al. 2006, Halls & Costin 2016). In addition, airborne-based LiDAR data have limitations in land classification (i.e. oyster versus marsh) because LiDAR returns do not provide scene information (Schenk & Csatho 2002). Similarly, LiDAR has limited ability to penetrate dense vegetation and water surfaces (Schmid et al. 2011), such that oyster reefs below the water surface cannot be identified using LiDAR. Because airborne-based LiDAR vertical elevation accuracy is typically on the order of 10s of centimeters, it is unable to detect all differences in land covers that are similar in elevation. Similarly, if the horizontal spatial resolution of the airborne-based LiDAR data is too large (typically 0.5 to 1 m), small oyster patches may go undetected.

To continue successful restoration efforts, in addition to identifying suitable oyster elevation habitat, it is also necessary to understand the physical environments that foster successful larval recruitment and oyster growth (Fodrie et al. 2014). Successful larval recruitment and survival of oysters to maturity along the eastern shore of Virginia rely upon hard substrate for attachment (Whitman & Reidenbach 2012). In addition, oysters depend upon currents to transport larvae, and locations with higher tidal energy and flow speed have been associated with greater oyster growth (Lenihan 1999, Byers et al. 2015). High flow velocities and turbulence act to transport and increase the supply of larvae, increase incidence of larvae encountering substrate, and reduce mortality from sedimentation (Lenihan 1999, Hendriks et al. 2006, Fuchs et al. 2013, Hubbard & Reidenbach 2015). However, if velocities adjacent to benthic surfaces are too high, this can prevent successful settlement (Crimaldi et al. 2002, Reidenbach et al. 2009). Often, high-energy environments that include significant wave activity limit successful recruitment of oysters (Ortega 1981, Bushek 1988, O'Beirn et al. 1995).

By understanding where and under what physical conditions oyster reefs exist, we can gain an understanding of suitable habitat to better manage and restore oyster populations (Schulte et al. 2009, Fodrie et al. 2014, Colden & Lipcius 2015, Lipcius et al. 2015,

Theuerkauf & Lipcius 2016, Colden et al. 2017). Because reef elevation controls the amount of time oysters are exposed, it can also be considered the primary variable in determining the fate of oysters (Fodrie et al. 2014). In addition to elevation, the local hydrodynamic environment determines oyster growth and larval recruitment (Bartol et al. 1999, Lenihan 1999, Schulte et al. 2009, Colden et al. 2017). Therefore, the 3 main objectives of this study were to: (1) determine whether LiDAR elevation data can be used to identify and map oyster reefs within intertidal regions; (2) describe the physical environment where oysters are found in relation to elevation, and the hydrodynamic factors of fetch and water residence time; and (3) identify existing intertidal regions within the Virginia Coast Reserve (VCR) with similar physical environments that can be used as target regions for future restoration efforts.

2. MATERIALS AND METHODS

2.1. Study site and areas of interest

This study focused on oysters within the intertidal region of the VCR, located on the Atlantic Ocean side of the Delmarva Peninsula, on the eastern shore of Virginia. Within the coastal habitat of the VCR, which extends along approximately 100 km of coastline and contains coastal bays and barrier islands that extend towards the open ocean, 16 areas (500 × 500 m, 0.25 km²) were analyzed for oyster land cover (Fig. 1). These areas were chosen because they contained intertidal reef patches that represented some of the more densely populated areas. They also provided spatial distribution across the VCR. The areas were used to create ground-truth data, train, and test a supervised classification for oyster and non-oyster land cover. The patchy and vertical accretions of oysters in the VCR are shown in Fig. 2. To determine suitable habitat, a total area of 436.4 km² encompassing intertidal and coastal bay area was analyzed.

2.2. LiDAR data sources and derived spatial layers

An airborne-based LiDAR data set accessed through the VCR data portal (Dewburg 2016) was collected for the project area. LiDAR data acquisition was completed by Leading Edge Geomatics, while classification, products, and quality assurances were completed by Dewberry, the primary contractor. Data were acquired between 11 and 24 April 2015 (Dewberry 2016). Flights were conducted within 2 h of the lowest low tide for the 2 wk that flights were completed. Sys-

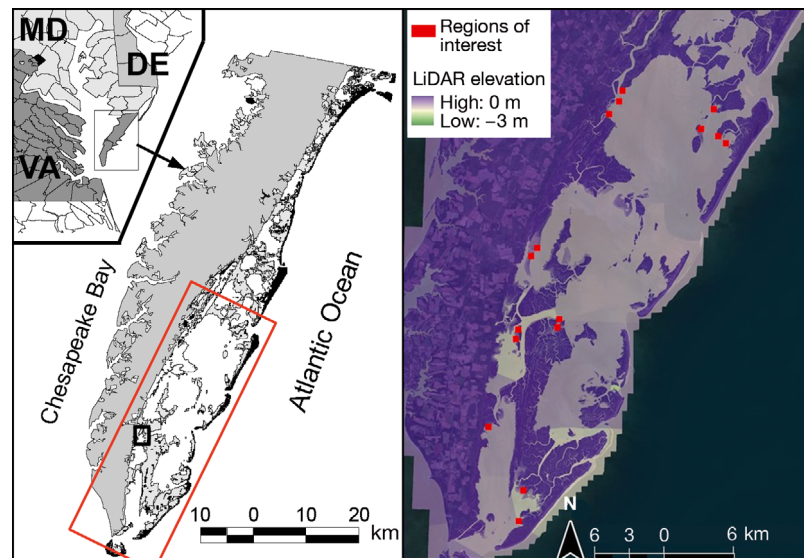


Fig. 1. Left: The Delmarva Peninsula, VA, USA, with land shown in grey and water in white, is a landmass between the Chesapeake Bay and the Atlantic Ocean. The Virginia Coast Reserve (VCR) is composed of the marshes, coastal bays, and barrier islands on the Atlantic Ocean side of this peninsula. The black box on the peninsula shows the location of Hillcrest oyster reefs, a site of healthy natural and restored reefs. The red box is extent of the image on the right. Right: the sixteen 0.25 km² regions (red) of interest chosen throughout the VCR for oyster reef mapping. LiDAR data (purple) were flown for the extent of the peninsula. Service layer credits: ESRI World Imagery

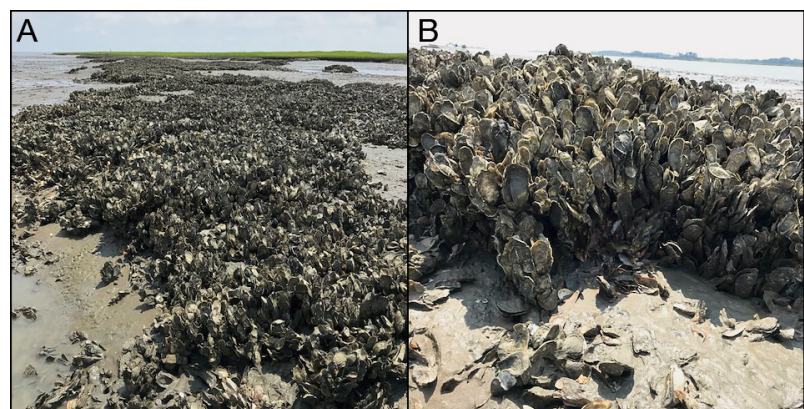


Fig. 2. Intertidal oysters photographed within the Virginia Coast Reserve showing their (A) patchy distributions and (B) vertical growth

tem specifications included a flight altitude of 1000 m, a speed of 100 knots, and a pulse rate of 200 kHz. The vertical accuracy reported for non-vegetated terrain had a 95% confidence level RMSE of 12.5 cm. Though not statistically significant (only based on 17 of 113 checkpoints) the horizontal accuracy was 64.9 cm (Dewberry 2016). Ground surface returns were filtered and breaklines made to distinguish land and water. Editing corrected misclassified land cover and artifacts and uneven water surfaces due to tidal and wave action were flattened. The LiDAR point data were used to create an elevation model layer with square pixels sized 0.76 m^2 and an aggregate nominal point density of 3.45 points per m^2 . The original layer was then projected with horizontal (WGS84 UTM 18N) and vertical datums (NAVD88) in meters. All elevations in this study are relative to NAVD88 unless specified. Some reefs were located below sea level during the time of flight when LiDAR data were collected, and therefore were not visible in the data set, preventing a complete oyster population survey. For many intertidal locations, reefs were easily distinguishable within LiDAR elevation maps and appeared different than surrounding land cover due to their distinct elevation change.

The LiDAR elevation data also included intensity data, a measure of the strength of return, from the flight paths. Mosaic raster layers of intensity values were created for the area covering the 16 regions of interest. Additionally, a slope layer was derived from the elevation layer using the neighborhood of immediate cells (3×3) for the same regions. A final slope of the slope layer was computed forming the curvature layer which measures the convexity or concavity of a surface and can account for additional textural differences between land covers (Pittman et al. 2009). ArcMap 10.5 GIS software was used to analyze and map the LiDAR data.

2.3. Ground-truth and surveyed oyster data

ArcMap 10.5 GIS software was also used to create ground-truth data. To create a ground-truth map of oyster land cover in the areas of interest, the 16 regions were delineated on the elevation layer. Satellite imagery and GPS tracks were used to determine the appearance of oyster reef patches on the elevation layer and validate the patches seen. The base-map provided by ESRI via ArcMap (ESRI 2017) was used as the source of the satellite imagery. The imagery was used to validate the patches of reef mapped on the elevation layer, but primarily served

to determine the appearance of oyster reefs on the elevation layer, where oyster patches were only visualized in terms of elevation. Specifically, images from ESRI World Imagery with up to 0.3 m resolution satellite images during low tide for 24 September, 27 April, and 16 April 2017 were used based on availability for individual locations. As an additional check to determine whether mapped patches were in the same locations of intertidal reefs, GPS tracks were made *in situ* using a handheld Garmin GPSMAP 64s (maximum accuracy of 3 m) during the summer of 2017 for portions of 8 of the 16 regions of interest (Red Bank [3 areas], Hillcrest, Narrows, Ramshorn [2 areas] and Mockhorn), which were easily accessible and known for healthy, dense patches of oyster reef. These GPS tracks were imported into GIS as line features and manually edited to make closed polygons. Polygons with an area less than 10 m^2 were discarded, while those greater than 10 m^2 in area but less than 1 m apart were aggregated. The resulting polygons were then imported onto the elevation layer. Because imagery was from 2017, while LiDAR elevation data were from 2015, only one data set, the elevation layer, was used to map reef patches. An oyster reef layer was created by drawing polygons around the perimeter of visible patches. As a check on digitally mapped reef accuracy, the GPS tracks served to determine whether LiDAR-mapped reefs were present within the GPS tracks. Although ground-truth oysters covered only 0.07 km^2 , or 1.8% of the 4 km^2 of total intertidal land cover within the 16 regions, greater than 86% of GPS tracks contained LiDAR elevation mapped patches. Hence, the digitized reefs served as a good proxy for ground-truth data and were used instead of *in situ* tracks for ground-truth oyster land cover in this study.

2.4. Supervised classification of oyster reefs in the VCR

2.4.1. Creating an oyster reef signature for maximum likelihood classification

Spatial data on elevation, intensity, slope, and curvature were used to provide training data to complete a maximum likelihood image classification in GIS. In total, 4 layers were made to create signatures for oyster patches. Multi-band rasters were created with the different data types as different bands, which were then used to determine which of the variables are most useful in identifying oysters. First, analysis from signatures using individual elevation,

intensity, and slope layers were completed, followed by 2-layer composites of all combinations of elevation, intensity, and slope, then a 3-layer composite of elevation, intensity, and slope. Finally, a 4-layer composite was computed with curvature added. Adding layers to a multi-band composite adds a dimension of data for each location in space; therefore, with more data, a greater amount of descriptive information can be used to create signatures from the input data.

Training samples were created from 8 oyster regions (half of the 16 total regions) by manually drawing polygons on the elevation layer identifying different land cover types, including water, marsh, and mud of differing elevations and appearances. Previously described oyster reef polygons were used to identify oyster land cover. Reefs for each of the 8 oyster regions were grouped as separate land covers to represent 8 potential types of oyster cover to account for regional differences in the signature. Because we were interested in classifying land for oyster land cover, this was done to make the signature more robust to identify oysters of varying size, shape, age, and appearance. Only reefs that covered areas equivalent to at least 50 pixels (11.6 m²) or greater were included to provide enough of a signature to be able to classify the data as an oyster patch. In total, 13 classes of land cover were discriminated, including the 8 representing oysters, high, medium, and low elevated muds, marsh, and water. Average elevation, intensity, slope, and curvature for training samples of oyster land cover within each of the 8 training regions are stated in Table 1. Data from the multi-band rasters (ranging from 1 to 4 bands of elevation, intensity, slope, and curvature) were extracted to the shapefile made from the training samples for all land cover types to produce the respective signature files. The signature for each land cover category was based on the mean and covariance of the data in training samples so that for each land cover, a statis-

tical representation of what each land cover type looks like in terms of elevation, slope, intensity, and curvature was formulated. A sensitivity analysis was conducted to determine the best combination of LiDAR-derived data to use in a supervised classification to identify oyster reefs.

2.4.2. Maximum likelihood classification in ArcMap 10.5 and interpretation of output

The maximum likelihood classification tool in ArcMap 10.5 was used to produce a classified raster on the remaining 8 oyster regions, referred to as test regions, using the created signature files. This is a pixel-based classification method that classifies images by placing pixels into different classes based on statistical probability using class means and covariances informed by the sample-based signature. The pixels classified to be similar to samples of oyster reefs from the training regions were reclassified to create one larger oyster class. The remaining classes of pixels for different land covers were reclassified to represent one class of non-oyster land cover. Although these data could be used to classify land cover, such as marsh and mud, in this study we were concerned only with success in identifying oyster reefs and generated ground-truth data for just this land cover.

2.4.3. Accuracy assessment: comparing classified and ground-truth oyster land cover

To validate the classification and determine which combined data layers created the best signature for oyster reefs, accuracy assessments were completed for classified test regions. In a similar way to reclassifying the classified outputs to have 2 categories, oyster and non-oyster land cover, a ground-truth data raster layer was made where digitized (ground-truth) oysters comprised the oyster class and all other land was classified as non-oyster. The raster matched the projection and resolution of the classified layers (WGS 1984 UTM zone 18N, 0.76 m² resolution). A total of 500 points spread across the regions were generated, using an equalized stratified random sampling technique, such that the 500 points were distributed randomly for the total area, but an equal number of

Table 1. Summary of the means (\pm SD) for elevation, intensity, slope, and curvature data within oyster patches for each training region

	Elevation (m, relative to NAVD88)	Intensity	Slope (degree)	Curvature
Hillcrest	-0.23 \pm 0.14	66.46 \pm 27.39	3.67 \pm 2.85	51.45 \pm 19.85
Mockhorn	-0.51 \pm 0.22	146.58 \pm 67.63	4.24 \pm 2.66	51.83 \pm 18.93
North1	-0.22 \pm 0.10	133.22 \pm 46.56	2.15 \pm 2.15	52.90 \pm 17.26
North2	-0.39 \pm 0.08	176.06 \pm 57.41	3.40 \pm 2.19	50.38 \pm 17.83
Ramshorn	-0.26 \pm 0.10	80.91 \pm 30.44	4.28 \pm 2.58	56.01 \pm 17.29
RedBank1	-0.32 \pm 0.2	92.25 \pm 38.38	6.70 \pm 5.09	64.46 \pm 17.58
RedBank2	-0.27 \pm 0.11	129.04 \pm 44.32	4.21 \pm 2.81	56.10 \pm 18.84
South1	-0.21 \pm 0.12	197.92 \pm 61.58	4.43 \pm 2.34	51.51 \pm 20.87

points were randomly assigned to oyster and non-oyster classes based on the ground-truth data layer. Stratified sampling has the advantage of including categories of data that are rarer and less likely to appear with simple random sampling, and has proven to work accurately with habitat and remotely sensed data (Congalton 1991, Hirzel & Guisan 2002). The ground-truth land cover type for each point was compared to the land cover type on the classified layer assessed, and a confusion matrix was generated to determine the accuracy of the classified layer in identifying oyster and non-oyster land covers. In addition to overall accuracy, the confusion matrices determined user and producer accuracies for oyster and kappa coefficients.

Confusion matrices, also known as error matrices, provide a means to determine what portion of classified data is correctly classified based on reference data (Story & Congalton 1986). Reference and classified data are organized in columns and rows, respectively, and separated into categories, in this case whether the points were found in pixels categorized as oyster or non-oyster. Agreement between the reference and the classified data is along the matrix's major diagonal. This is used to determine the overall accuracy by adding all the correctly classified data points for both categories and dividing by the sum of all random points. To assess individual category accuracy, the correctly classified data points are divided by the total ground-truth data points for that category. In this scenario, this is all the random points correctly classified as oyster divided by the total number of ground-truth oyster points. This measures the producer accuracy, which is suggestive of errors of omission (omission error = $1 - \text{producer accuracy}$), which can be defined as the percent of ground-truth oysters not correctly classified (i.e. oyster area omitted from the produced map). User accuracy for a category is calculated by dividing the number of correctly classified points by the total number of points classified as that category (Story & Congalton 1986). This is a measure of error of commission (commission error = $1 - \text{user accuracy}$), a determinant of the rate of false positives. It explains the chance of discovering a location classified on the map as oyster to be a different land cover in reality. A kappa value takes the classifier as a whole and compares the observed agreement between the classified and reference data and the agreement that is likely to occur by chance if observations were independent. In this way, it is the proportional agreement between data that has been corrected for chance. A value of 1 would indicate complete agreement between the observed and clas-

sified data, a value of 0 is indicative of no difference with what is expected by chance, and a value of -1 would indicate complete disagreement after considering corrections for chance (Agyemang et al. 2011).

To compare how the classification differed by test region, individual accuracy assessments for oyster and non-oyster land cover for each region were also performed, in a similar way, by generating 500 random points, equally stratified for oyster and non-oyster land covers for each of the 8 test regions. This analysis was completed using the classified raster produced from the most successful composite determined through the sensitivity analysis. The mean of the difference between elevation of oyster patch crests and the buffered 2 m of adjoining land, mean oyster patch area, and mean patch perimeter per region were quantified. To calculate mean elevations for patches and surrounding land, all points within each polygon were averaged, where elevation points were spaced 0.75 m apart set by the LiDAR point density. Regression analyses were performed to determine whether differences in local accuracies were explained by these variables. The elevation was also made relative to local mean sea level (lmsl) by adding a conversion factor layer to the LiDAR elevation layer available through the VCR (Richardson 2013) to determine the local position of reefs. It was hypothesized that with (1) greater difference in elevation between reef crests and surrounding land and (2) larger oyster patches, the classification and identification of oysters would be more successful.

2.5. Using digitized reefs to determine suitable habitat within the VCR

In addition to the LiDAR data set, water residence time and fetch data layers were created in GIS using model output from Safak et al. (2015) and Wiberg et al. (2019) to characterize intertidal lands suitable for oysters. Water residence time was modeled with a 3-dimensional coastal ocean model utilizing particle tracking and validated with field observations, while fetch was weighted by wind direction. In the present study, water residence time and fetch serve as proxies for water mean velocity and wave energy from winds, respectively. Residence time data can also predict the exchange of water masses, which is likely an important factor in not only providing reefs with food, but also enhancing larval exchange. These layers were projected and resampled using the nearest neighbor method to match the datum and resolution of the LiDAR elevation data (WGS 84 UTM zone 18N, resolu-

tion of 0.762 m²). The data were then extracted to overlapping ground-truth oyster reef polygons from all 16 regions to find the mean for each oyster patch using zonal statistics, where mean values for each variable were calculated per reef. Suitable habitat analysis for the VCR was restricted to the area where data were available for all 3 variables, eliminating land features that had no water residence time or fetch data. The range for elevation of land surrounding oyster patches within 2 m was computed, and the middle 99% of oyster patch elevation (range from the 0.5 to 99.5 percentiles) was set as suitable elevation. The surrounding land rather than the elevation of patches (reef crests) was used for suitable elevation because this is more representative of the elevation of land oysters are recruited to and more useful to target land for restoration. However, an examination using the same method but with reef crest elevation was also completed for comparison. Using the elevation range from the middle 99% of the sample excluded some extreme data that may have been wrongly identified as oyster habitat. This range also excluded much of the subtidal areas that would not be visible on the LiDAR data set. Next, the area of suitable habitat was further restricted by eliminating areas where fetch was not suitable, and finally reduced by excluding area with unsuitable water residence time. Fetch and water residence time were not affected by errors in the modeled elevation, so the full range of data (maximum to minimum average values found in the oyster sample) were used to categorize areas suitable and less suitable for these variables. The combination of elevation and water residence time was also examined to help determine which variable, water residence time or fetch, was a more useful criterion in determining suitable oyster habitat.

The results of suitable habitat using elevation defined by land surrounding oyster patches were then compared to the most recent oyster survey conducted within the VCR completed in 2007 by Ross & Luckenbach (2009). This survey combined ground-truth data with aerial images from 2007 to determine oyster area. This survey was input as a GIS layer and then the polygon layer was converted to a raster with resolution matching the LiDAR data. Then, the suitable land cover product was extracted to the reefs for the sixteen 0.25 km² regions used to create ground-truth oysters.

3. RESULTS

3.1. LiDAR classification

Satellite orthoimagery and GPS tracks were useful in helping to determine how oyster patches appear on an elevation layer. Greater than 86% (151/175) of GPS tracks intersected digitally mapped reefs based on LiDAR elevation (Fig. 3); 90.3% of the GPS tracks were within 3 m of digitized reefs. There were apparent differences in the overlap for the different areas surveyed. Most of the unaccounted tracks were in the regions near Red Bank (3 regions), which accounted for 15 of the total 24 tracks that did not overlap digitized reefs.

In the sensitivity analysis, the classified raster became more accurate as more layers were used to create signatures (Table 2). Confusion matrices using information from random points showed that overall accuracy of land classification increased when composites of multiple layers were formed to provide signatures for land cover (Table 2). Of the analyses performed on the individual layers of elevation, slope, and intensity, slope performed the best with a high overall accuracy (0.77). When data from elevation, intensity, and slope layers were combined, the overall accuracy and kappa value increased to 0.79 and 0.58, respectively, values similar to slope alone. However, with the signature informed by 3 layers, the kappa value increased while also creating more balanced errors of omission (26%) and commission (17%). Additionally, with more layers added, the re-

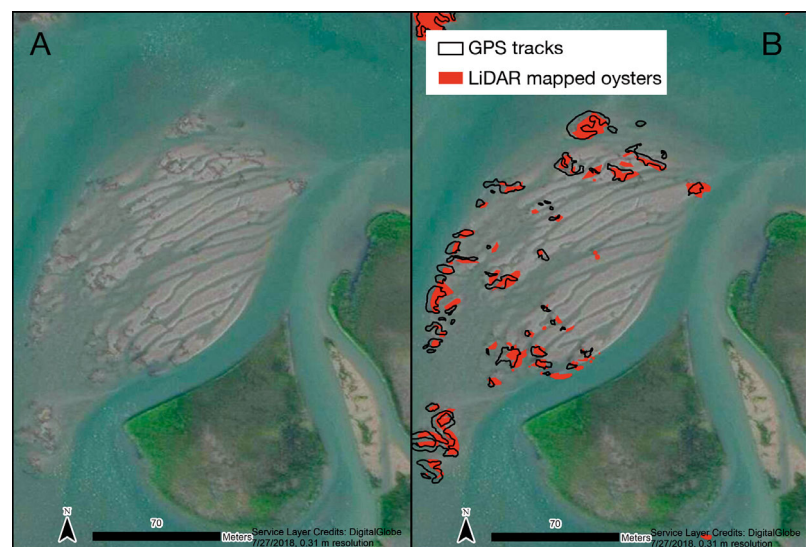


Fig. 3. (A) A birds-eye view of the Narrows region visualized with satellite imagery (ESRI World Imagery 7/27/18) and (B) the LiDAR-mapped oyster patches (red) and GPS tracks completed (black outline) for this region

Table 2. Accuracy assessment results for classified land cover produced from signatures created using different combinations of elevation, intensity, slope, and curvature data. User and producer accuracy for oyster classes, in addition to overall accuracy and kappa coefficients, were computed for land cover classified as oyster or non-oyster. Accuracies range from 0 to 1 and the kappa coefficients range from -1 to 1

No. of layers	Combination of data	Oyster user accuracy	Oyster producer accuracy	Overall accuracy	Kappa coefficient
1	Elevation	0.62	0.48	0.59	0.19
	Slope	0.83	0.68	0.77	0.54
	Intensity	0.66	0.66	0.66	0.32
2	Elevation & slope	0.66	0.78	0.72	0.48
	Elevation & intensity	0.73	0.72	0.73	0.46
	Intensity & slope	0.87	0.6	0.76	0.51
3	Elevation, intensity, & slope	0.83	0.74	0.79	0.58
4	Elevation, intensity, slope, & curvature	0.81	0.80	0.81	0.62

Table 3. Confusion matrix created for the classification produced by signature with the 4-layer composite for land classified as oyster and non-oyster. For each of the 500 random points, the table lists whether they are categorized as oyster or non-oyster according to ground-truth and classified data. Accuracies range from 0 to 1 and the kappa coefficient ranges from -1 to 1

Classified land cover	Ground-truth land cover			User accuracy	Kappa
	Non-oyster	Oyster	Total		
Non-oyster	204	49	253	0.81	
Oyster	46	201	247	0.81	
Total	250	250	500		
Producer accuracy	0.82	0.80		0.81	
Kappa					0.62

sulting land cover result more accurately reflected the training data, where all 13 categories were represented, whereas only a few categories were produced with single layers. When the additional layer of curvature was added to provide greater textural information for the signature, the accuracies again increased and this 4-layer composite was analyzed further and used to investigate regional differences.

In the accuracy assessment for the classification trained using all data layers (Table 3), the error of commission (19%) was almost balanced with the error of omission (20%) for oyster land cover, given the user accuracy of 0.81 and the producer accuracy of 0.80. This suggests that there was a 20% chance that true oyster cover at a location was omitted from the map, and a 19% chance that a pixel classified as oyster was a false positive. This balance of omission and commission was improved compared to the 3-layer results, omission error being reduced from 26 to 20%. The overall accuracy in classifying land as oyster or non-oyster was 0.81 and the kappa coefficient was 0.62. The high kappa coefficient supports the conclusion that there was a reduced chance that the

similarity between the classified and ground-truth data layers was due to chance alone (Table 3).

In total, 80.8% of the area of ground-truth reefs was correctly classified as oysters. Additionally, ground-truth reef polygons were analyzed to determine whether they contained pixels that were classified as oysters. This measured the classified raster's ability to detect oyster patches, if not their entire area. Of the 1259 ground-truth oyster reef polygons located in the test regions, 1218, or 97%, contained at least one pixel that was

classified as oyster. Therefore, almost all ground-truth reefs were at least partly represented in the classified map.

A visual comparison for a sample of classified test regions compared with ground-truth oyster reefs is seen in Fig. 4. The overall accuracy for individual test regions ranged from 0.65 to 0.92, while kappa values were lower and had a greater range from 0.30 to 0.83 (Table 4). The average patch elevation (reef crest) for oysters within the test regions was -0.31 m relative to NAVD88. The difference between mean oyster elevation and surrounding land elevation provides an estimate of the average vertical relief of oysters in each region, which ranged from 0.103 to 0.225 m for the different test regions (Table 4), supporting that reef patches were positioned higher than the surrounding land cover. The overall average for oyster relief in test regions was 0.14 m. For the VCR, local mean sea level was below NAVD88, ranging in magnitude from 0.039 to 0.149 m. The mean patch elevation was at -0.207 m lmsl and the average patch elevation for each region ranged from -0.308 to -0.065 m lmsl (Table 4).

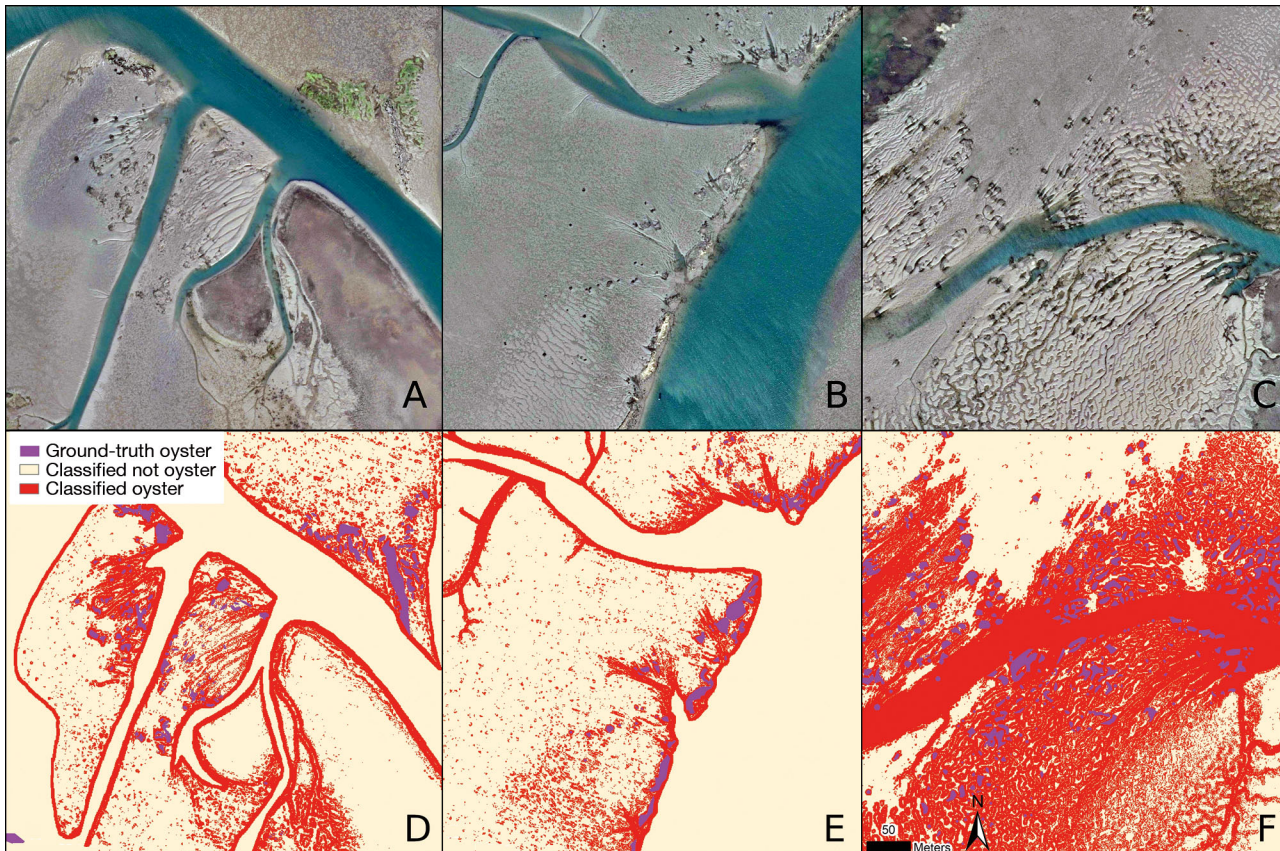


Fig. 4. Aerial images of 3 test regions named (A) Narrows, (B) Ramshorn, and (C) Mockhorn. The classified rasters (D–F) are shown below their respective regions. Red indicates areas classified as raster, yellow indicates area classified as non-oyster land cover, and purple represents ground-truth polygons. Overall accuracy and kappa values for Narrows, Ramshorn, and Mockhorn regions were 0.71, 0.81, and 0.67 and 0.43, 0.63, and 0.34, respectively. Image layer credits: ESRI World Imagery (A,B) 27 April 2017 and (C) 24 September 2017

Table 4. Quantified characteristics for each of the classified test regions describing region overall accuracy, mean elevation, mean oyster elevation, the mean difference in elevation between oyster patch crests and surrounding land, mean oyster patch area, and mean oyster patch perimeter for the patches located in each region

	Overall accuracy	Kappa	Oyster elevation (m lmsl)	Oyster elevation (m NAVD88)	Difference between crest and land elevation (m NAVD88)	Patch area (m ²)	Patch perimeter (m)
Narrows	0.71	0.43	-0.308	-0.408	0.103	33.1	22.0
Mockhorn	0.67	0.34	-0.213	-0.322	0.169	24.9	19.5
Ramshorn	0.81	0.63	-0.161	-0.268	0.143	41.6	25.0
Red Bank	0.72	0.45	-0.145	-0.247	0.126	48.0	32.8
North1	0.92	0.83	-0.420	-0.522	0.130	91.7	44.4
North2	0.85	0.71	-0.201	-0.306	0.135	8.5	11.0
South1	0.65	0.30	-0.071	-0.179	0.116	13.9	15.2
South2	0.91	0.81	-0.065	-0.183	0.225	159.4	68.5

There was no significant relationship between region overall accuracy and vertical relief ($r^2 = 0.25$, $p = 0.21$; Fig. 5A). There were positive relationships between region accuracy and mean patch area with 94 %

confidence ($r^2 = 0.47$, $p = 0.06$) and mean patch perimeter with 91 % confidence ($r^2 = 0.41$, $p = 0.0.9$). These strong positive relationships may indicate that with larger reefs there is increased accuracy (Fig. 5B,C).

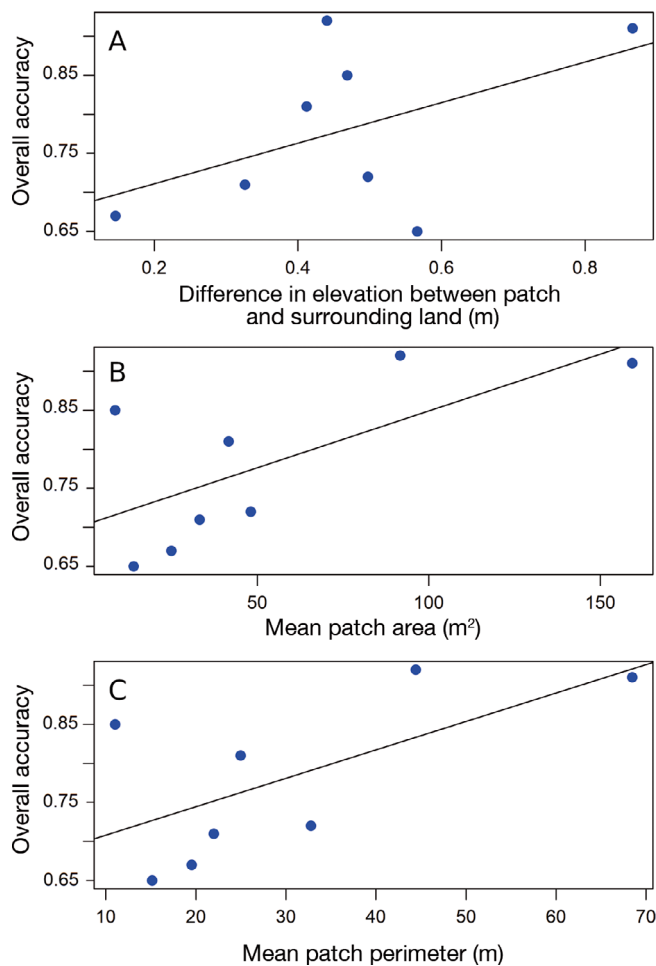


Fig. 5. Linear regressions plotted to determine relationships between region accuracy and (A) difference in mean surrounding land and oyster elevation, (B) mean patch area, and (C) mean patch perimeter

3.2. Physical environment and habitat suitability

The elevation range found for the middle 99% of land surrounding oysters was -0.92 to -0.13 m for oyster reefs ($n = 2089$). For the intertidal and coastal bay region analyzed within the VCR, 83.2 km², or 19.1% of the total 436.4 km², fell within the range of suitable elevation (Fig. 6A). Suitable elevation, when instead defined by reef crests, led to a suitable elevation range (middle 99%) of -0.81 to -0.18 m and covered 32.3 km² or 7.3% of the study area (Fig. 6B). Water residence time for 2026 oyster patches ranged from 23.2 to 2000 h, while fetch data for 1498 patches ranged from 40.0 to 4643.0 m. Area of suitable water residence time and fetch were much less restrictive, covering 294.2 and 295.2 km², respectively (Fig. 6C,D). Areas having both suitable fetch and residence time totaled

226.5 km², so that areas suitable for both these variables were often coincident. When the study area was subjected to the range of values to meet suitable criteria for elevation, water residence time, and fetch, a total of 52.4 km², or 12.0% of the study area, remained (Fig. 7). Areas of suitable habitat were distributed throughout the study area, but were often near higher areas of mud and marsh land covers. Using reef crest elevation led to a similar but more restrictive overall suitable habitat of 23.1 km² or 5.3% of the study area, though areas further from land and toward more open water were reduced. Greater than 83% of the ground-truth reefs area fell within suitable habitat with elevation set by surrounding land, after reefs were converted to raster. Some disagreement existed because the model was computed on a pixel basis, whereas the average values for elevation, fetch, and residence time were calculated for each oyster patch to set criteria (Fig. 8A). Also, some ground-truth reefs did not have modeled data because either fetch or water residence time was absent for areas of higher elevations.

3.3. Comparison to Ross & Luckenbach (2009) oyster survey

In the comparison between the suitable area within the sixteen 0.25 km² regions and the Ross & Luckenbach (2009) survey, most surveyed area overlapped with modeled suitable habitat that met all 3 criteria of elevation, fetch, and water residence time (Fig. 8B). Of the 0.21 km² of surveyed reef within these 16 regions for which suitable habitat was modeled, 0.138 km² or 66.3% was described as suitable. Total suitable land in the regions was 1.44 km² so that overlapping surveyed reefs accounted for about 10% of suitable area. While there was good agreement between the survey and suitable land for these regions, the comparison between the 2 data sets should be used with caution because many of the areas surveyed by Ross & Luckenbach (2009) were in hydro-flattened areas of the LiDAR elevation data.

4. DISCUSSION

The present study found that LiDAR data can be used to identify intertidal oyster reefs along the Virginia, USA, coastline and the locations of existing reefs can be used to identify the physical environments in which they are most often found. While producing a complete population survey is unachievable using this data due to the lack of subtidal and, at

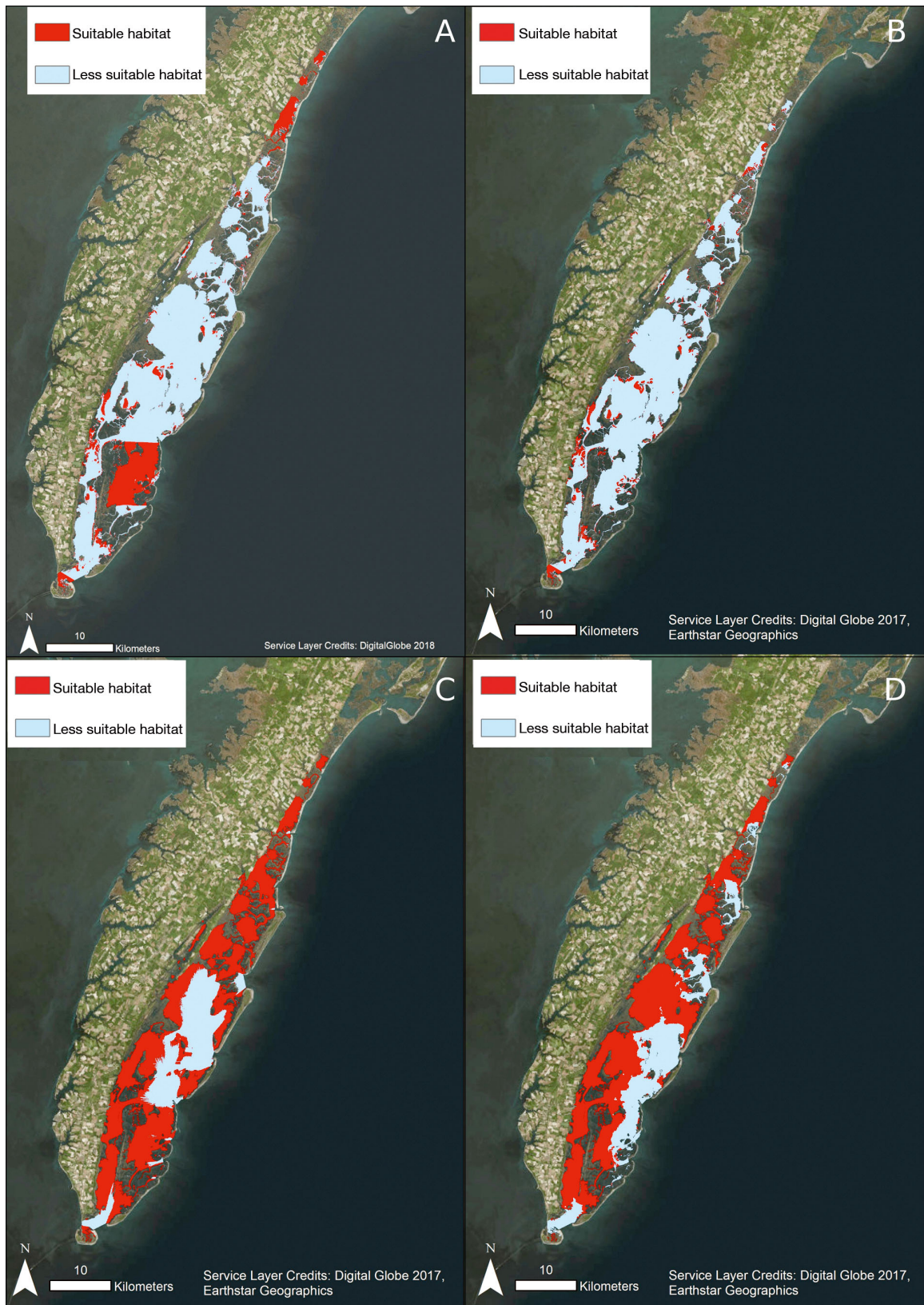


Fig. 6. Areas of suitable (red) and less suitable (blue) (A) elevation defined by land surrounding reefs, (B) elevation defined by reef crests, (C) fetch, and (D) water residence time for the Virginia Coast Reserve. Service layer credits: ESRI World Imagery

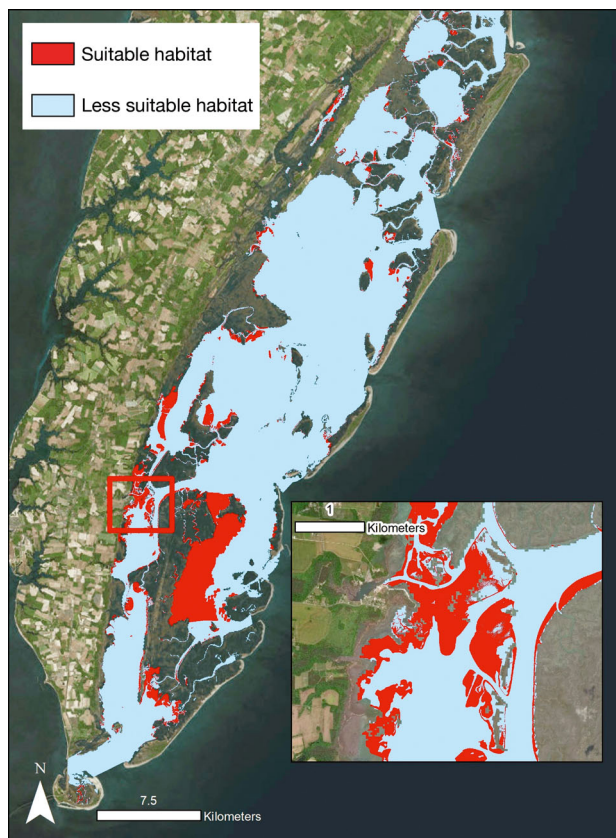


Fig. 7. Area of suitable elevation (red) remaining after areas with less suitable elevation, fetch, and water residence time were removed. Service layer credits: ESRI World Imagery

some locations low-intertidal LiDAR information, the study was successful in determining methods for automatic classification. By successfully quantifying elevation, fetch, and water residence time data over areas of existing reefs, the study also determined target regions within the VCR where oyster restoration is likely to be successful.

4.1. Oyster land cover classification

A multi-band raster including elevation, intensity, slope, and curvature data increased the accuracy in identifying reefs (Table 3). This combination of data provided a signature that distinguished oysters from other land covers with high accuracy. This study took a simplified approach and used only layers derived from LiDAR. In this way, we tested the utility of LiDAR for classification of intertidal oysters. Other land classification studies included additional roughness parameters, such as surface rugosity, plan cur-

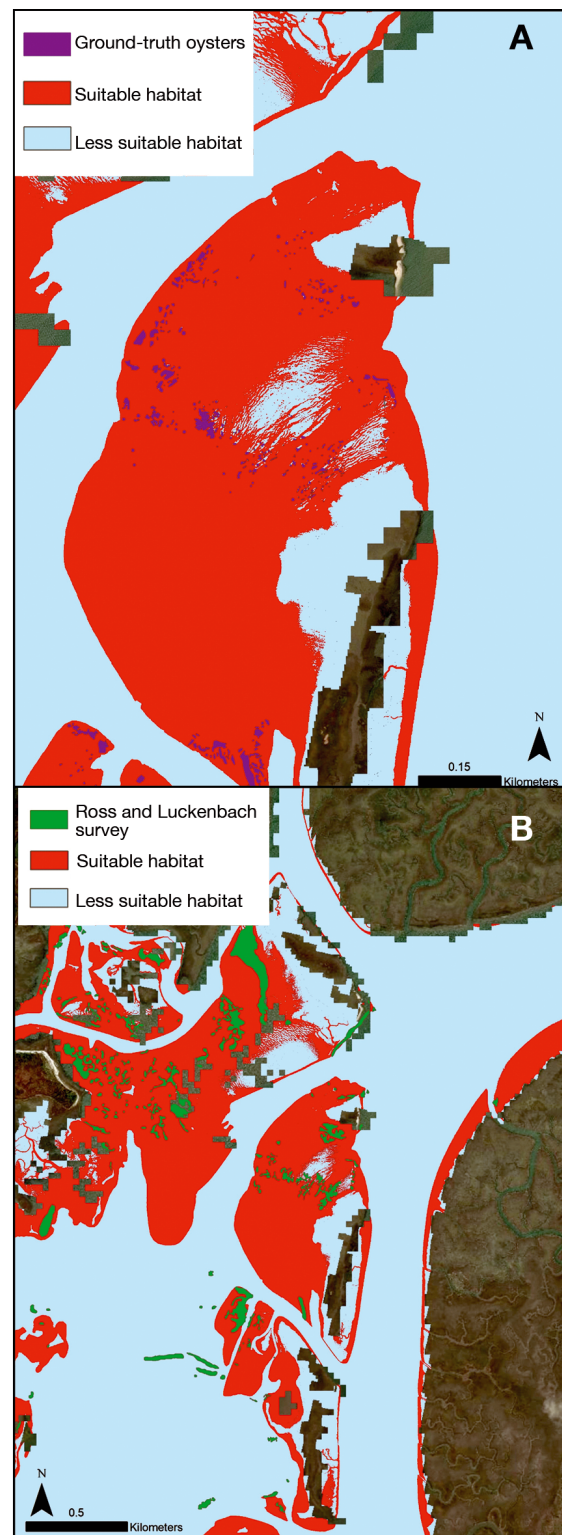


Fig. 8. (A) Ground-truth oysters (purple) and (B) Ross & Luckenbach (2009) reef polygons layered on the suitable habitat map, where suitable habitat is seen in red and less suitable habitat in blue. Both ground-truth and surveyed reef polygons greatly overlap with suitable habitat. Service layer credits: ESRI World Imagery

vature (concavity perpendicular to the maximum slope), and fractal dimension, to characterize landscapes (Pittman et al. 2009), which may prove more beneficial in other environments and particular land covers. The accuracy was not greatly improved by adding curvature to our analysis and did not warrant further additions. Different kernel (3×3 cells) statistics including maximum, minimum, standard deviation, and range for elevation, intensity, and slope were examined, but did not benefit the classification and were colinear with the other data. These layers were therefore excluded.

Our method of using data only derived from LiDAR supported the idea that LiDAR data can distinguish between land that is oyster and non-oyster with 81% accuracy, based on the confusion matrix created using 500 equally stratified random points. The kappa coefficient, 0.62, supported agreement between the classified and ground-truth land cover layers at 62%. This value may be more reflective of the accuracy, due to the small amount of land cover that is truly oyster reef. Oysters covered approximately 2%, or 0.04 km², of the total 2 km² of land within the test regions, and therefore there may have been some chance agreement involved in classifying non-oyster cover because it covered the vast majority of the land. In creating a method to classify oyster cover, it was important to not only identify reefs correctly, but also minimize the extent to which false positives were produced. This study successfully balanced the error of omission (20%) with the error of commission, or false positive rate (19%). One common error in the classified output was that the edges of mudflats were often denoted as being oyster cover. While this is an error of commission in many areas, oysters are commonly found fringing mudflats and marshes, and therefore are areas that are also likely to have elevations similar to those of ground-truth oyster samples. Additionally, while the overall accuracy was 81% in identifying oyster from non-oyster land cover, 80.8% of the ground-truth reef area was classified as reef and 97% of the ground-truth patches had at least one pixel classified as oyster. Therefore, the classification was successful in identifying almost all of the true reef patches, albeit lacking in identifying the total area. This suggests that portions of reef patches are more representative of the training data than others.

The classification scheme may be useful to define areas where oysters are located, although the results of this study support that ground-truth data or manual digitization using LiDAR is necessary to identify full cover. Certainly, using LiDAR to train classification tools to identify oyster reefs can narrow the area

with potential reef cover from remote locations. Therefore, this study supports that if LiDAR data are available for a different geography, elevation can be used to create ground-truth training data informed with derived layers (including elevation, intensity, slope, and curvature) to automatically classify land for oysters with a high accuracy. While the present study has shown that obtaining full oyster coverage using LiDAR is unlikely, LiDAR can be used to manually map known locations of oyster with greater patch definition compared to ground surveys. More precise patches can foster the ability to monitor change over time. Both growth and mortality might be quantified based on measurable changes in horizontal and vertical dimensions. For the VCR, past LiDAR surveys over the region were not conducted during low tide, preventing comparisons with the data used in this study. However, now knowing that patches can be mapped with LiDAR, monitoring can take place with future LiDAR surveys.

Mapping with LiDAR elevation, with the user trained with imagery and *in situ* data as described here, presents a more precise method to delineate area. Surveying on foot can cause larger tracks to be taken due to accessibility and effort. The GPS tracks in this study were not collected with the intention to assess accurate area or population size, but for a more qualitative comparison to learn how terrain is visualized on an elevation layer. Therefore, the accuracy was less meaningful and comparison with digitized reefs utilized a presence-absence method, which showed that reefs seen on LiDAR elevation were also present with *in situ* reef tracks, though areal comparison should be interpreted with caution. In addition to error introduced by the handheld GPS accuracy, the LiDAR data also has errors in horizontal accuracy and can only discriminate patches with discernible vertical relief. The regional differences seen in overlap between LiDAR-digitized reefs and GPS tracks indicates that differences in geographic position such as elevation or patch size may affect digitization, and it is difficult to resolve whether error is in the GPS or LiDAR data.

Past studies using various methodologies have reported similar results for accuracy and kappa coefficients for estuarine land covers including oyster reefs, which were difficult to distinguish remotely within coastal habitats (Halls & Costin 2016, Le Bris et al. 2016). Obstacles include misrepresentation of oyster patches with other land covers such as mud or gravel. These errors have been attributed to lower proportion of cover and sample data, similar textures and elevations between land covers, and the ephemeral

exposure within intertidal landscapes (Garono et al. 2004, Schill et al. 2006, Halls & Costin 2016). Studies successful in classifying coastal habitats often rely on combining different sources of data, including high-resolution and hyperspectral imagery (Grizzle et al. 2002, Schill et al. 2006, Chust et al. 2008, Dumbauld et al. 2011, Le Bris et al. 2016), and hydrodynamic (Smith et al. 2015), radar (Choe et al. 2012), and acoustic sonar (Smith et al. 2001, Allen et al. 2005). Even when high degrees of accuracy (greater than 80%) were achieved in intertidal habitat classifications, oysters were one of the least successful categories of cover (Halls & Costin 2016).

While most of the surveys completed in the past have relied on high-resolution imagery, the 2% of oyster cover found in the largely intertidal regions investigated in the present study is similar to other accounts for the VCR and along intertidal oyster habitats on the mid-Atlantic coast (Bahr 1976, Bahr & Lanier 1981, Ross & Luckenbach 2009). Notwithstanding recent successful restoration efforts (Schulte et al. 2009, Lipcius et al. 2015), the eastern oyster remains only a small percentage, about 1%, of its historical population size in Chesapeake Bay (Rothschild et al. 1994, Kemp et al. 2005), though the intertidal populations in the coastal lagoons adjacent to Chesapeake Bay (e.g. VCR) are somewhat higher (Ross & Luckenbach 2009). In the most recent stock survey, oyster reef land cover in the VCR area represented 0.4% of habitat mapped (Ross & Luckenbach 2009). This low percentage of cover appears to be common along the mid-Atlantic for the last few decades (Bahr 1976, Bahr & Lanier 1981). The percentage quantified from the present study, however, is likely inflated due to the concentrated mapping on areas chosen to be dense with oyster reefs.

The idea that mapping oyster with elevation data would be successful is based on the understanding that oysters grow vertically above surrounding land cover. Contrary to the hypothesis that differences in elevation between oyster and adjoining mudflat would be related to the ability to detect oysters, there was no significant relationship. The mean elevation difference between patches and surrounding land (2 m buffer), 0.14 m, likely represents the difference in elevation needed for reef recognition from LiDAR elevation data and may account for discrepancies in what was visible on LiDAR versus *in situ* mapping. This value can serve as a benchmark in deciding whether LiDAR data can be used to map reefs in different regions. In our regional analysis, the average oyster patch for each region fell within a narrow range of elevation relative to NAVD88 from -0.52 to

-0.17 m. Therefore, it is likely that within this approximately half meter of elevation, virtually all intertidal oysters exist. The spatial variation in *lmsl* could account for the range of average patch elevations relative to NAVD88. For all digitized oysters, the average crest elevation in terms of *lmsl* was -0.207 m. With the top of the oyster patches falling below *lmsl*, oysters are likely underwater for at least half the tidal cycle.

The regressions relating oyster identification with area and perimeter had positive trendlines, indicating that regions with larger patches were more accurate. The accuracy for individual test regions varied over a narrow range from 0.65 to 0.92, suggesting that areas with smaller average patch sizes still had a relatively high accuracy in identifying reefs. This is important for oysters in the VCR because the distribution of patch size from the sample of ground-truth oysters indicated that most oyster patches were small, with the 50th percentile being 11.6 m² and 14.5 m for area and perimeter, respectively. Knowing the size distribution of reefs in this area can help indicate the accuracy likely to be attained via LiDAR classification and lead to further understanding of spatial distributions.

4.2. Suitable habitat

The digitized reefs provided a large sample size that was spatially diverse, and therefore likely representative of oyster patches within the VCR. The suitability map created using 3 environmental variables (elevation, fetch, and water residence time) was successful in identifying areas that are likely to be highly suitable oyster habitat. Suitable water residence time and fetch covered much greater areas than suitable elevation. Individually, suitable elevation defined by land surrounding reefs, reef crests, fetch, and residence time covered approximately 83.2, 32.3, 294.2, and 295.2 km², respectively, of the total study area, which was 436.4 km². The low land cover for suitable habitat when all 3 variables are considered, 52.4 km² or 12.03% of the area, is therefore limited by suitable elevation, the most restrictive variable. When reef crests are used to determine suitable habitat, the model was even more restrictive, describing only 23.1 km² as suitable habitat. While it is likely that managers are more interested in the suitability of land without oysters that can be used to further restoration, represented here by the elevation of land surrounding reefs, reef crests also represent substrate that attracts larvae, and could be used to

consider a more conservative examination of suitable habitat.

Although most ground-truth reefs overlapping with the suitability model were in suitable habitat, a small percent was modeled as less suitable habitat. Unless additional unquantified variables play a significant role in preventing recruitment and growth, this suggests that oysters can survive beyond the boundaries set by the model for suitable habitat. The elevation criteria presented here are then likely to be conservative and represent areas that would be most suitable, or prime habitat for oyster restoration. Most of the suitable habitat was located near higher intertidal areas adjacent to mudflats and marshes, and more towards the mainland. In these locations, oysters are likely to experience a greater amount of protection from harsh wave action, explaining why the bays and areas near inlets were less suitable, where high wave energy was likely incompatible with oyster growth (Crimaldi et al. 2002, Reidenbach et al. 2009).

The area of suitable habitat was also compared with a past survey completed by Ross & Luckenbach (2009). This comparison was restricted to the 16 test regions because these represented locations where the LiDAR data were capable of accurately identifying oyster reefs. Comparing the total model area with the survey would not accurately reflect the agreement between the 2 data sets. For reefs within the entire modeled area, there was a significant difference in the elevation of the reefs with those surveyed by Ross & Luckenbach (2009), which typically were much lower in elevation than those in the present study, where mean patch elevations were -0.85 and -0.31 m relative to NAVD88, respectively. These lower reefs were likely located in areas that are subtidal or under water during the majority of the tidal cycle. While some of the reefs included in the survey by Ross & Luckenbach (2009) may not have been visible in our data set, others may no longer exist. When ground-truth tracks were taken for the present study, some areas indicated as reef on their map no longer existed. There may have been oyster cover at these locations in the past, but our analysis suggests that these regions are not the most suitable for oyster growth and survival. Nonetheless, the comparisons drawn between the two data sets should be viewed with caution. Differences between the data sets highlight the challenges in surveying intertidal environments and how differing survey techniques and sources of remotely sensed data can cause deviations in the detection of ephemerally exposed areas, such as intertidal oyster reefs.

The VCR is a dynamic environment in which the landscape is continuously changing due to external

drivers and internal feedbacks (McGlathery et al. 2013). Areas that may have been suitable environment for oysters in the past may have been transformed between the time that data were collected for present study and that by Ross & Luckenbach (2009). Historic documentation described oysters covering a much greater area (Schulte 2017), supporting that greater land area was favorable for habitat.

Many current restoration projects in coastal lagoons primarily seek to restore intertidal oyster reefs at higher elevations because they promote greater recruitment and growth (Schulte et al. 2009) while also adding coastal protection (Piazza et al. 2005, Borsje et al. 2011, Scyphers et al. 2011, Wiberg et al. 2019). Our results should prove useful in choosing locations for future projects with these goals. While the majority of the surveyed reefs were within suitable land area, the model also showed that total suitable habitat within the 16 test areas was 1.44 km², and within this habitat the total surveyed reef area was only 0.14 km². Therefore, the surveyed reefs only comprised about 10% of potential suitable habitat for oysters. Across the entire VCR region, spanning approximately 100 km of coastline, there may be various locations suitable for future oyster restoration.

Acknowledgements. We thank the staff of the Anheuser-Busch Coastal Research Center for field assistance and local expertise. This research was funded by the National Science Foundation to the Virginia Coast Reserve Long Term Ecological Research program (grant nos. DEB-1237733 and DEB-1832221) and by CAREER grant (OCE-1151314) to M.A.R.

LITERATURE CITED

- ✦ Agyemang TK, Heblinski J, Schmieder K, Sajadyan H, Vardanyan L (2011) Accuracy assessment of supervised classification of submersed macrophytes: the case of the Gavaraget region of Lake Sevan, Armenia. *Hydrobiologia* 661:85–96
- Ahokas E, Kaartinen H, Hyyppa J (2003) A quality assessment of airborne scanner data. *Int Arch Photogramm Remote Sens* 34:1–7
- ✦ Allen YC, Wilson CA, Roberts HH, Supan J (2005) High resolution mapping and classification of oyster habitat in nearshore Louisiana using sidescan sonar. *Estuaries* 28: 435–446
- ✦ Bahr LM (1976) Energetic aspects of the intertidal oyster reef community at Sapelo Island Georgia USA. *Ecology* 57:121–131
- Bahr LM, Lanier WP (1981) The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. FWS/OBS-81/15. US Fish and Wildlife Service, Office of Biological Services, Washington, DC
- ✦ Baltasvias EP (1999) Airborne laser scanning: basic relations and formulas. *ISPRS J Photogramm Remote Sens* 54: 199–214

- Bartol IK, Mann R, Luckenbach M (1999) Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: effects of tidal height and substrate level. *J Exp Mar Biol Ecol* 237:157–184
- Borsje BW, van Wesenbeeck BK, Dekker F, Paalvast P, Bouma TJ, van Katwijk MM, De Vries MB (2011) How ecological engineering can serve in coastal protection. *Ecol Eng* 37:113–122
- Bushek D (1988) Settlement as a major determinant of intertidal oyster and barnacle distributions along a horizontal gradient. *J Exp Mar Biol Ecol* 122:1–18
- Byers JE, Grabowski JH, Piehler MF, Hughes A, Weiskel HW, Malek JC, Kimbro DL (2015) Geographic variation in intertidal oyster reef properties and the influence of tidal prism. *Limnol Oceanogr* 60:1051–1063
- Choe BH, Kim D, Hwang JH, Oh Y, Moon WM (2012) Detection of oyster habitat in tidal flats using multi-frequency polarimetric SAR data. *Estuar Coast Shelf Sci* 97:28–37
- Chust G, Galparsoro I, Borja A, Franco J, Uriarte A (2008) Coastal and estuarine habitat mapping, using LiDAR height and intensity and multi-spectral imagery. *Estuar Coast Shelf Sci* 78:633–643
- Coen LD, Brumbaugh RD, Bushek D, Grizzle R and others (2007) Ecosystem services related to oyster restoration. *Mar Ecol Prog Ser* 341:303–307
- Colden AM, Lipcius RN (2015) Lethal and sublethal effects of sediment burial on the eastern oyster *Crassostrea virginica*. *Mar Ecol Prog Ser* 527:105–117
- Colden AM, Latour RJ, Lipcius RN (2017) Reef height drives threshold dynamics of restored oyster reefs. *Mar Ecol Prog Ser* 582:1–13
- Congalton RG (1991) A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sens Environ* 37:35–46
- Crimaldi JP, Thompson JHR, Lowe RJ, Koseff JR (2002) Hydrodynamics of larval settlement: The influence of turbulent stress events at potential recruitment sites. *Limnol Oceanogr* 47:1137–1151
- Dewberry (2016) Eastern shore Virginia QL2 LiDAR BAA. Report produced for the U.S. Geological Survey. Dewberry & Davis LLC, Tampa, FL. USGS Contract: G10PC00013. Task Order G15PD00284, p 1–157
- Dumbauld BR, Kauffman BE, Trimble AC, Ruesink JL (2011) The Willapa Bay oyster reserves in Washington State: fishery collapse, creating a sustainable replacement, and the potential for habitat conservation and restoration. *J Shellfish Res* 30:71–83
- ESRI (2017) 'World Imagery' [basemap]. 0.31 – 0.5 m resolution. 'World Imagery map'. April 16, 24, 27, 2017. www.arcgis.com/home/ (2017–March 2019)
- Fodrie FJ, Rodriguez AB, Baillie CJ, Brodeur MC and others (2014) Classic paradigms in a novel environment: inserting food web and productivity lessons from rocky shores and saltmarshes into biogenic reef restoration. *J Appl Ecol* 51:1314–1325
- Fuchs HL, Hunter EJ, Schmitt EL, Guazzo RA (2013) Active downward propulsion by oyster larvae in turbulence. *J Exp Biol* 216:1458–1469
- Garono RJ, Simenstad CA, Robinson R, Ripley H (2004) Using high spatial resolution hyperspectral imagery to map intertidal habitat structure in Hood Canal, Washington, USA. *Can J Rem Sens* 30:54–63
- Gesch DB (2009) Analysis of lidar elevation data for improved identification and delineation of lands vulnerable to sea-level rise. *J Coast Res* 53:49–58
- Green K, Lopez C (2007) Using object-oriented classification of ADS40 data to map the benthic habitats of the state of Texas. *Photogramm Eng Remote Sensing* 73:861–865
- Grizzle RE, Adams JR, Walters LJ (2002) Historical changes in intertidal oyster (*Crassostrea virginica*) reefs in a Florida lagoon potentially related to boating activities. *J Shellfish Res* 21:749–756
- Halls J, Costin K (2016) Submerged and emergent land cover and bathymetric mapping of estuarine habitats using WorldView-2 and LiDAR imagery. *Remote Sens* 8:718
- Hendriks IE, van Duren LA, Herman PMJ (2006) Turbulence levels in a flume compared to the field: Implications for larval settlement studies. *J Sea Res* 55:15–29
- Hirzel A, Guisan A (2002) Which is the optimal sampling strategy for habitat suitability modelling. *Ecol Modell* 157:331–341
- Hodgson ME, Bresnahan P (2004) Accuracy of airborne Lidar-derived elevation: empirical assessment and error budget. *Photogramm Eng Remote Sensing* 70:331–339
- Hubbard AB, Reidenbach MA (2015) Effects of larval swimming behavior on the dispersal and settlement of the eastern oyster *Crassostrea virginica*. *Mar Ecol Prog Ser* 535:161–176
- Ishiguro S, Yamada K, Yamakita T, Yamano H, Oguma H, Matsunaga T (2016) Classification of seagrass beds by coupling airborne LiDAR bathymetry data and digital aerial photographs. In: Nakano S, Yahara T, Nakashiuka T (eds) Aquatic biodiversity conservation and ecosystem services. *Ecol Res Monogr Springer*, Singapore, p 57–70
- Kemp WM, Boynton WR, Adolf JE, Boesch DF and others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Mar Ecol Prog Ser* 303:1–29
- Le Bris A, Rosa P, Lerouxel A, Cognie B and others (2016) Hyperspectral remote sensing of wild oyster reefs. *Estuar Coast Shelf Sci* 172:1–12
- Lenihan HS (1999) Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. *Ecol Monogr* 69:251–275
- Lipcius RN, Burke RP, McCulloch DN, Schreiber SJ, Schulte DM, Seitz RD, Shen J (2015) Overcoming restoration paradigms: value of the historical record and metapopulation dynamics in native oyster restoration. *Front Mar Sci* 2:65
- Marion C, Anthony EJ, Trentesaux A (2009) Short-term (<2 yrs) estuarine mudflat and saltmarsh sedimentation: high-resolution data from ultrasonic altimetry, rod surface-elevation table, and filter traps. *Estuar Coast Shelf Sci* 83:475–484
- May NC, Toth CK (2007) Point positioning accuracy of airborne LiDAR systems: a rigorous analysis. In: Stilla U et al. (eds) PIA07 Munich. *Int Arch Photogramm Remote Sens* 36 (3/W49B): 107–111
- McGlathery KJ, Reidenbach MA, D'Odorico P, Fagherazzi S, Pace ML, Porter JH (2013) Nonlinear dynamics and alternative stable states in shallow coastal systems. *Oceanography (Wash DC)* 26:220–231
- Morgan JL, Gergel SE, Coops NC (2010) Aerial photography: a rapidly evolving tool for ecological management. *Bioscience* 60:47–59
- Morris JT, Porter D, Neet M, Noble PA, Schmidt L, Lapine LA, Jensen JR (2005) Integrating LiDAR elevation data, multi-spectral imagery and neural network modeling for marsh characterization. *Int J Remote Sens* 26:5221–5234
- O'Beirn FX, Heffernan PB, Walker RL (1995) Preliminary recruitment studies of the eastern oyster, *Crassostrea*

- virginica*, and their potential applications, in coastal Georgia. *Aquaculture* 136:231–242
- ✦ Ortega S (1981) Environmental stress, competition, and dominance of *Crassostrea virginica* near Beaufort, North Carolina, USA. *Mar Biol* 62:47–56
- ✦ Piazza BP, Banks PD, La Peyre MK (2005) The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. *Restor Ecol* 13:499–506
- ✦ Pittman SJ, Costa BM, Battista TA (2009) Using LiDAR bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *J Coast Res* 53:27–38
- ✦ Reidenbach MA, Koseff JR, Koehl MAR (2009) Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wave-driven flow. *Limnol Oceanogr* 54:318–330
- ✦ Reidenbach MA, Berg P, Hume A, Hansen JCR, Whitman ER (2013) Hydrodynamics of intertidal oyster reefs: the influence of boundary layer flow processes on sediment and oxygen exchange. *Limnol Oceanogr* 3:225–239
- ✦ Richardson D (2013) Tidal datum conversion grids for the Eastern Shore of Virginia and surrounding waters. Virginia Coast Reserve Long-Term Ecological Research Project Data Publication knb-lter-vc.219.5. doi:10.6073/pasta/aeb2fe3192348fe201bd6252b64a3af7
- Ross PG, Luckenbach MW (2009) Population assessment of eastern oysters (*Crassostrea virginica*) in the seaside coastal bays. Virginia Coastal Zone Management Program, Virginia Department of Environmental Quality, Richmond, VA
- ✦ Rothschild BJ, Ault JS, Gouletquer P, Jensen WP, Herald M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Mar Ecol Prog Ser* 111:29–39
- ✦ Safak I, Wiberg PL, Richardson DL, Kurum MO (2015) Controls on residence time and exchange in a system of shallow coastal bays. *Cont Shelf Res* 97:7–20
- Schenk T, Csatho B (2002) Fusion of LiDAR data and aerial imagery for a more complete surface description. *Int Arch Photogramm Remote Sens* 34:310–317
- Schill SR, Porter DE, Coen LD, Bushek D, Vincent J (2006) Development of an automated mapping Technique for monitoring and managing shellfish distributions. NOAA/UNH Cooperative Institute for Coastal and Estuarine Environmental Technology (CICEET), Durham, NH
- ✦ Schmid KA, Hadley BC, Wijekoon N (2011) Vertical accuracy and use of topographic LiDAR data in coastal marshes. *J Coast Res* 27:116–132
- ✦ Schulte DM (2017) History of the Virginia oyster fishery, Chesapeake Bay, USA. *Front Mar Sci* 4:127
- ✦ Schulte DM, Burke RP, Lipcius RN (2009) Unprecedented restoration of a native oyster metapopulation. *Science* 325:1124–1128
- ✦ Scyphers SB, Powers SP, Heck KL, Byron D (2011) Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. *PLOS ONE* 6:e22396
- ✦ Smith GF, Bruce DG, Roach EB (2001) Remote acoustic habitat assessment techniques used to characterize the quality and extent of oyster bottom in the Chesapeake Bay. *Mar Geod* 24:171–189
- ✦ Smith G, Yesilnacar E, Jiang J, Taylor C (2015) Marine habitat mapping incorporating both derivatives of LiDAR data and hydrodynamic conditions. *J Mar Sci Eng* 3:492–508
- Story M, Congalton G (1986) Accuracy assessment: a user's perspective. *Photogramm Eng Remote Sensing* 52:397–399
- ✦ Theuerkauf SJ, Lipcius RN (2016) Quantitative validation of a habitat suitability index for oyster restoration. *Front Mar Sci* 3:63
- ✦ Triglav-Čekada M, Crosilla F, Josmatin-Fras M (2009) A simplified analytical model for a-priori Lidar point-positioning error estimation and a review of Lidar error sources. *Photogramm Eng Remote Sensing* 75:1425–1439
- ✦ Van der Zee EM, van der Heide T, Donadi S, Eklof JS and others (2012) Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer–resource interactions. *Ecosystems* 15:664–673
- Wesson J, Mann R, Luckenbach M (1999) Oyster restoration efforts in Virginia. In: Luckenbach MW, Mann R, Wesson JA (eds) *Oyster reef habitat restoration: a synopsis and synthesis of approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, p 117–129
- ✦ Whitman ER, Reidenbach MA (2012) Benthic flow environments affect recruitment of *Crassostrea virginica* larvae to an intertidal oyster reef. *Mar Ecol Prog Ser* 463:177–191
- ✦ Wiberg PL, Taube SR, Ferguson AE, Kremer MR, Reidenbach MA (2019) Wave attenuation by oyster reefs in shallow coastal bays. *Estuar Coast* 42:331–347

Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

Submitted: April 3, 2019; Accepted: August 26, 2019
Proofs received from author(s): October 31, 2019