

Validation of a habitat suitability index for oyster restoration

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SETH J. THEUERKAUF^{1,2,3} AND ROMUALD N. LIPCIUS^{1,4}

¹*Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, VA 23062*

²*Department of Marine, Earth, and Atmospheric Sciences, Center for Marine Sciences and Technology, North Carolina State University, Morehead City, North Carolina 28557, USA. Tel.: + 1 252 222 6322*

³Email: sjtheuer@ncsu.edu

⁴Email: rom@vims.edu

Abstract. Habitat suitability index (HSI) models provide spatially explicit information on the capacity of a given habitat to support a species of interest, and their prevalence has increased dramatically in recent years. Despite caution that the reliability of HSIs must be validated using independent, quantitative data, most HSIs intended to inform terrestrial and marine species management remain unvalidated. Furthermore, of the eight HSI models developed for eastern oyster (*Crassostrea virginica*) restoration and fishery production, none has been validated. Consequently, we developed, calibrated, and validated an HSI for the eastern oyster to identify optimal habitat for restoration in a tributary of Chesapeake Bay, the Great Wicomico River (GWR). The GWR harbors an unparalleled, restored oyster population, and therefore serves as an excellent model system for assessing the validity of the HSI. The HSI was derived from GIS layers of bottom type, salinity, and water depth (surrogate for dissolved oxygen), and was tested using live adult oyster density data from a survey of high vertical relief reefs (HRR) and low vertical relief reefs (LRR) in the sanctuary network. Live adult oyster density was a statistically-significant sigmoid function of the HSI, which validates the HSI as a robust predictor of suitable oyster reef habitat for rehabilitation or restoration. In addition, HRR had on average 103-116 more adults m^{-2} than LRR at a given level of the HSI. For HRR, HSI values ≥ 0.3 exceeded the accepted restoration target of 50 live adult oysters m^{-2} . For LRR, the HSI was generally able to predict live adult oyster densities that meet or exceed the target at HSI values ≥ 0.3 . The HSI indicated that there remain large areas of suitable habitat for restoration in the GWR. This study provides a robust framework for HSI model development and validation, which can be refined and applied to other systems and previously developed HSIs to improve the efficacy of native oyster restoration.

Key words: *Habitat Suitability Index, oyster restoration, eastern oyster, C.*

2 *virginica.*

INTRODUCTION

4 Habitat suitability indices (HSI) are a commonly developed and often robust spatially
explicit, decision support model used to identify the capacity of a given habitat to support
6 a species of interest (U. S. Fish and Wildlife Service 1981, Roloff and Kernohan 1999). In
1981, the United States Fish and Wildlife Service proposed and developed the first HSI
8 models, which were intended to quantify the value of habitats when considering
management alternatives in species-specific conservation and restoration (U. S. Fish and
10 Wildlife Service 1981). HSIs are commonly generated through application of
wildlife-habitat relationships to relevant geospatial environmental data within a
12 Geographic Information System (GIS) to develop a composite HSI score with a range of 0
to 1, representing unsuitable to optimal habitat (Brooks 1997). Depending on the
14 relevance of the selected habitat variables, quality of the geospatial environmental data,
and reliability of the applied wildlife-habitat relationships, these models can serve as
16 robust spatial tools to inform species management.

Although the USFWS emphasized the need for validation of HSIs, or the quantitative
18 assessment of an HSI's ability to predict habitat suitability via an independent data set,
most HSIs intended to inform the management of terrestrial and marine species have not
20 been validated (Brooks 1997, Araújo and Guisan 2006). Recent HSI validation studies
have indicated that unvalidated HSIs can be unreliable indicators of habitat quality
22 (Reiley et al. 2014). Although widely used, HSI models have been criticized as unreliable
and lacking scientific rigor (Cole and Smith 1983, Roloff and Kernohan 1999). Despite the
24 potential cost associated with obtaining these independent datasets, the validation process
is required to determine the reliability and utility of these models if they are to inform
26 species conservation and management (Brooks 1997, Tirpak et al. 2009, Reiley et al.

2014).

2 To implement HSI models confidently, they must be tested for accuracy in a four-step
process (Brooks 1997, Tirpak et al. 2009, Reiley et al. 2014): development, calibration,
4 verification, and validation. Development involves the use of wildlife-habitat relationships
to generate an HSI ranging from 0, representing unsuitable habitat, to 1, representing
6 optimal habitat. Calibration aims to ensure that the HSI spans the full range of values
from 0 to 1. Brooks (1997) notes: "The intent is for sites of excellent habitat quality to
8 receive high scores (e.g., 0.7-1.0), and sites of poor habitat quality to receive low scores
(e.g., 0-0.3). If the HSI scores do not ordinate across the entire range of values from 0 to 1,
10 then they will be of little use in describing differences among sites." Verification entails
assessment of performance of an HSI model against independent qualitative or categorical
12 (ranked) data. A positive correlation of ranked data, such as presence/absence, and HSI
values would provide verification. Validation involves testing the performance of an HSI
14 model against independent quantitative data in space and time, such as against population
density or abundance. If validation has been accomplished, verification is not necessary. A
16 note of caution pertains to the use of different, non-independent data for validation. For
example, a dataset for a single ecosystem, such as a tributary, could be split in half. One
18 half of the dataset could be used to develop an HSI, and the second half used to test the
fit of the HSI model. This would not constitute validation because the data used to test
20 the HSI are not statistically independent of the data used to develop the model.

Few HSIs developed for marine or estuarine species of conservation interest have been
22 verified or validated through use of independent data. Brown and Hartwick (1988) were
the first to validate an HSI for a marine species, though it was for aquaculture of the
24 introduced Pacific oyster *Crasostrea gigas* in British Columbia, Canada, not for native
oyster restoration. Brown et al. (2000) verified HSI models for various fish and
26 invertebrate species (alewife *Alosa pseudoharengus*, American sand lance *Ammodytes
americanus*, Atlantic salmon *Salmo salar*, Atlantic tomcod *Microgadus tomcod*, common

mummichog *Fundulus heteroclitus*, winter flounder *Pleuronectes americanus*, American
2 lobster *Homarus americanus*, and soft-shell clam *Mya arenaria*) in an estuarine system.
Validation of HSI models was also accomplished for the distribution of juvenile Atlantic
4 salmon *S. salar* in a river (Guay et al. 2000) and coastal aquaculture farms of Pacific
oyster *C. gigas* (Cho et al. 2012). Note that in this study, we focus on HSI models, and
6 not on species distribution models such as MAXENT (Phillips and Dudík 2008), which
have also been used to predict the distribution of marine species as a function of habitat
8 features (e.g., Elsässer et al. (2010)).

Numerous HSI models have been developed to guide aquaculture, fishery production,
10 and restoration of oyster species (Table 1). The first to derive a model of habitat quality
for an oyster species was Galtsoff (1964) for the eastern oyster *C. virginica*. Galtsoff (1964)
12 developed a mathematically simple model to evaluate potentially productive oyster bottom
in Gulf of Mexico and south Atlantic coastal habitats. He used the sum of bottom
14 condition, water movement, water temperature, salinity, food availability, sedimentation,
diseases, competition, predation, and pollution, each of which ranged from 0-10. The
16 model integrated singular point measurements for each variable to generate a composite
score that would characterize a broad region and therefore cannot be considered an HSI.
18 Galtsoff (1964) recognized that the model was overly simplistic because it weighted all of
the variables equally and because the model needed to be revised for different geographic
20 areas. Unfortunately, the model was additive in its habitat quality elements, such that a
value of 0 in one habitat characteristic did not produce an index of 0, unlike contemporary
22 HSI models.

Cake (1983) developed the first true HSI for the eastern oyster in the Gulf of Mexico,
24 meaning that it was intended to be employed using spatially-explicit datasets to determine
relative suitability of locations within a given system for fishery production. The Cake
26 (1983) model represents a comprehensive oyster HSI that incorporates a broad suite of
relevant environmental variables (Table 2). Soniat and Brody (1988) utilized

spatially-explicit environmental and oyster density datasets collected for 38 reef and
2 non-reef sites to apply and verify the Cake (1983) HSI for Galveston Bay, Texas. Using
oyster density data, the authors attempted to validate the original Cake (1983) model
4 using a regression approach. However, the authors encountered the issue of lack of
statistical independence due to oyster density (their response variable) also being
6 incorporated as a variable in their model, and therefore recognized that the model could
not be considered validated. The authors did benefit from removing oyster density from
8 the model, testing the relationship between oyster density and various combinations of the
variables incorporated into the original model (i.e., a model verification procedure), and
10 subsequently developed a modified HSI that incorporated the significant explanatory
variables.

12 With the advent of contemporary geographic information systems (GIS) software,
many HSIs for oysters have been developed within the past decade (Table 2). The
14 variables included within these models have varied widely, however, the most common
variables utilized are salinity, bottom type or substrate, and water depth. Other variables,
16 such as predator intensity, food availability, or pH are of unknown relevance for all systems
and their integration into HSI models requires additional spatially-explicit datasets that
18 rarely exist for most systems. Interestingly, the two most recent published models (Soniati
et al. 2013, Swannack et al. 2014) and this study have converged on a simplified model
20 structure that includes varied combinations of the most common variables utilized in
previous HSIs (i.e., salinity, bottom type or substrate, and water depth), although the
22 Soniat et al. (2013) and Swannack et al. (2014) models do not include water depth, which
is a critical variable for Chesapeake Bay subtidal oyster reefs. Additionally, of the eight
24 published oyster restoration HSIs, none has been validated using an independent,
quantitative population dataset. Thus, the reliability of these HSI models for informing
26 oyster restoration and management remains uncertain.

We developed, calibrated and validated an HSI for the eastern oyster in a tributary of

Chesapeake Bay, the Great Wicomico River (GWR). In 2004, the U.S. Army Corps of
2 Engineers (ACE) constructed 34.4 ha of sanctuary oyster reef within the system (Schulte
et al. 2009). Today, the GWR harbors an unparalleled, restored oyster population (Schulte
4 et al. 2009), and therefore serves as an excellent model system for assessing the validity of
an oyster HSI. Here, we describe the development of a simple, reliable HSI for the eastern
6 oyster and present the results from a direct field validation of the model.

MATERIAL AND METHODS

8

Study area

The GWR is a tributary on the western shore of the lower Chesapeake Bay (Figure 1).
10 The GWR is located approximately 10 km south of the Potomac River and 25 km north of
the Rappahannock River, and has a small watershed consisting predominately of forested
12 and agricultural lands (Southworth et al. 2010). The GWR is mesohaline and is considered
a trap-type estuary with gyre-like water circulation patterns that has contributed to its
14 history of significant natural oyster recruitment (Andrews 1979, Southworth et al. 2010).
The system is characterized by a single, central deep channel with an extensive sand shoal
16 near the river mouth (Southworth et al. 2010). Oysters within the system exist on public
oyster grounds, private lease areas, and no-harvest oyster sanctuaries (Schulte et al. 2009,
18 Southworth et al. 2010).

HSI development

20 This HSI was developed in ESRI ArcGIS 10.1 (Environmental Systems Research Institute
2011), and followed a standard logical framework used in the development of previous HSI
22 models (Cake 1983, Battista 1999), except that we added a validation step with
independent survey data. The steps in HSI development were as follows:

- 24 (i) Assimilation of data sets on environmental variables (e.g., salinity);
- (ii) Assessment of habitat requirements for eastern oyster from a literature review;

(iii) Construction of ArcGIS environmental layers;

(iv) Formulation of suitability functions for each of the environmental variables;

(v) Calculation of the HSI for the river system;

(vi) Collection of eastern oyster abundance data for the system from a population survey; and,

(vii) Comparison of HSI values and oyster abundance.

The HSI was derived from Geographic Information System (GIS) layers of environmental and biotic variables, including bottom type, land use, salinity, existence of private oyster leases and public oyster grounds, seagrass cover, dissolved oxygen, and water depth for most of the GWR at depths deeper than 2 m. From these variables, we selected those of greatest relevance to site suitability for oyster restoration in the GWR and for which there was river-wide data, which included bottom type, depth, and salinity (Figure 2). Bottom type was included in this study as oyster reefs constructed on sand, rock or oyster shell are less likely to subside than those built on mud or silt bottom (Schulte et al. 2009). Depth was included as benthic community abundance and diversity decline significantly at low dissolved oxygen (DO) levels (Long and Seitz 2009, Seitz et al. 2009), and depth is a robust surrogate for DO (Powers et al. 2005). During the summer in western shore tributaries of Chesapeake Bay, such as the GWR, DO remains high down to about 4 m (Seitz et al. 2009), after which it declines sharply to 0 mg l⁻¹ around 5 m. This general trend is due to seasonal benthic anoxia and hypoxia events induced by decomposition of plankton and subsequent stratification of the water column (Kemp et al. 2005). Salinity was included as the eastern oyster cannot tolerate extremely low or high salinities for long periods, and prefers upper mesohaline to polyhaline salinities (Battista 1999, Barnes et al. 2007, Carnegie and Burreson 2011, Battista 1999).

Data for GIS layers of bottom type were derived from multiple sources including: 1) a 2009 NOAA acoustic seabed mapping survey (1 m x 1 m resolution), and 2) field notes taken by VIMS researchers during the 2012 reef monitoring sampling of the ACE reefs

(Bruce et al. 2010). Bottom type data derived from the 2009 NOAA acoustic seabed
2 mapping survey included the majority of downriver bottom, but excluded inshore areas
shallower than 2 m due to the inability of the research vessel to navigate shallow waters
4 (Bruce et al. 2010). Bottom type data derived from field notes (approximately 40 points
per reef) were imported into ArcGIS (Environmental Systems Research Institute 2011) as
6 point data and were subsequently used along with the bottom type data derived from the
2009 NOAA acoustic seabed mapping survey to supplement the delineation of bottom type
8 contours of characteristic grain sizes (e.g., muddy sand). Bottom type information derived
from the 2009 NOAA acoustic seabed mapping survey was utilized for the areas outside of
10 the ACE constructed oyster reef polygons, while bottom type information from the field
sampling notes taken by VIMS researchers was also utilized for the areas within the ACE
12 constructed oyster reef polygons. This provided a baseline (i.e., pre-construction) bottom
type dataset for integration into the HSI. This baseline bottom type dataset was necessary
14 as some of the reefs within the sanctuary reef network were originally constructed on
unsuitable bottom and have degraded since the 2009 NOAA acoustic seabed mapping
16 survey.

Mean bottom salinity data were derived from a VIMS hydrodynamic model developed
18 for tributaries of Chesapeake Bay (J. Shen, unpublished data). Salinity data were
imported into ArcGIS (Environmental Systems Research Institute 2011) as point data (1
20 m nodes), and were subsequently converted to produce a raster grid (1 m x 1 m
resolution). Bathymetric data were derived from a NOAA bathymetric digital elevation
22 model of the Chesapeake Bay (1 m x 1 m resolution) (Bruce et al. 2010).

Within ArcGIS (Environmental Systems Research Institute 2011), each input variable
24 layer was assigned suitability index values based on physiological tolerance ranges available
in the literature, or from on-going research of the ACE reefs in the GWR. Data cells
26 within each input variable layer were classified on a gradient between 0, indicating highly
unsuitable habitat, and 1, indicating highly suitable habitat, with varying degrees of

suitability in between. In order to ensure that the HSI would assign a particular location a value of '0' (unsuitable) if any single input variable layer had a value of '0,' the geometric mean of each input variable layer was calculated to produce the HSI. Mathematically, the HSI was computed as follows:

$$HSI = \sqrt[3]{BottomType * Depth * Salinity} \quad (1)$$

HSI validation

In Chesapeake Bay, a live adult oyster density of 50 m⁻² is the abundance target for a restored reef to be considered successful by the Sustainable Fisheries Goal Implementation Team of the Chesapeake Bay Program (Sustainable Fisheries Goal Implementation Team 2011). Thus, live adult oyster density data derived from the 2011 VIMS monitoring survey of the ACE restored reefs in the GWR were used to validate the model.

The 2011 VIMS monitoring survey involved sampling HRR and LRR sanctuary oyster reefs (Figure 3) via patent tong. The sampling methodology followed standard procedures under Stratified Random Sampling (Cochran 1977, Thompson 2012). Reef types were then apportioned into strata (i.e., HRR, LRR) using information from side-scan sonar maps. Stratum area and variance estimates were used to generate random, stratum-specific nominal sampling sites and backup sites within a grid surrounding each of the reef polygons (Figure 3), using stratified random sampling with sample allocation proportional to stratum area and variance (Cochran 1977, Thompson 2012). Sampling sites were located by GPS coordinates, and sampled in the order in which they were generated to assure random sampling within each stratum. At each sampling site, the vessel was triple-anchored to maintain position. Next, a patent tong (1 m wide) was deployed, the sample was retrieved on a processing table aboard the vessel, and a photo taken of the sample with its identification number visible on a whiteboard. A complete 0.5 m² section of the 1 m² tong sample was rinsed and retained for lab processing. Samples were

processed in the laboratory, rather than in the field, due to the high probability that
2 individual oysters would not be easily seen in the field, resulting in biased (inaccurate)
samples. Parameter estimates for density and abundance were obtained using the R
4 statistics package (R Core Team 2015).

RESULTS

6 *HSI distribution in the Great Wicomico River*

Bottom type and depth were the primary drivers of a particular site's suitability (Figure
8 4). The river's bathymetry, which consists of a deep, soft bottom channel flanked by
shallow, hard bottom shelves mirrors the observed suitability trends. Despite the most
10 suitable locations existing in shallow depth areas, patches of unsuitable bottom intermixed
in these areas constrain their extent. Additionally, in upriver locations, lower salinity
12 waters reduces the extent of highly suitable habitat.

HSI calibration and validation

14 After computation of the HSI, the model was calibrated through linear rescaling of the
HSI values to ensure the model ranged from 0 to 1. Live adult oyster density was a
16 statistically-significant sigmoid function of the HSI (Figure 5), thereby validating the HSI
as a robust predictor of suitable oyster reef habitat for rehabilitation or restoration in the
18 GWR. In addition, high-relief reef had on average 103-116 more adults m^{-2} than low-relief
reef at a given level of the HSI. For high-relief reefs, HSI values ≥ 0.3 exceeded the 50 live
20 adult oysters m^{-2} target (Figure 5). For low-relief reefs, the HSI was generally able to
predict live adult oyster densities that meet or exceed the target at HSI values ≥ 0.3 .
22 However, for low-relief reefs, there was more variation between the HSI value and the
corresponding live adult oyster density than for high-relief reefs. To maximize the
24 potential for success of oyster reef restoration and rehabilitation, suitable oyster habitat
was defined as all areas with an HSI value ≥ 0.5 , and marginal oyster habitat was defined

as all areas with an HSI value ≥ 0.3 .

2

Suitable habitat

This study identified that approximately 157.8 ha of suitable oyster habitat (e.g., cells
4 with a HSI value between 0.5 and 1.0) occur in the GWR. Approximately 2.4 ha of
marginally suitable oyster habitat (e.g., cells with an HSI value between 0.3 and 0.5) occur
6 in the GWR. Approximately 92.7 ha of suitable oyster habitat lay within private shellfish
aquaculture leases, along with approximately 0.8 ha of marginally suitable oyster habitat.
8 Within the 288.5 ha of public oyster harvest grounds, approximately 52.6 ha of suitable
oyster habitat and 0 ha of marginally suitable oyster habitat exist. On the ACE high-relief
10 reef, approximately 13.4 ha of suitable oyster habitat and approximately 0.2 ha of
marginally suitable habitat exist. On the ACE low-relief reef, approximately 9.7 ha of
12 suitable oyster habitat and approximately 0.2 ha of marginally suitable oyster habitat
exist. It is important to note that, due to the lack of available bottom type data for
14 shallow areas, the total amount of suitable habitat available in the GWR is greater than
the amount estimated here. As the majority of shallow areas in the GWR are held in the
16 form of private shellfish aquaculture leases, most of this additional suitable habitat is likely
contained within the private shellfish aquaculture leases.

18

DISCUSSION

Habitat suitability indices provide a quantitative tool that integrates the best available
20 environmental data and corresponding science to identify locations with the most potential
for successful restoration (U. S. Fish and Wildlife Service 1981, Roloff and Kernohan
22 1999), but their efficacy depends critically on validation with independent data (Araújo
and Guisan 2006, Brooks 1997, Tirpak et al. 2009, Reiley et al. 2014). Of the eight
24 published HSI models used in native oyster restoration and fishery production (Table 1),
none has been validated. Our key contributions are thus the (i) development, calibration

and validation of a relatively simple HSI model for restoration of the eastern oyster

2 *Crassostrea virginica*, (ii) demonstration of the value of including a key factor, in this case
reef relief, in the implementation of the HSI model, and (iii) identification of oyster
4 abundance as a sigmoid function of the HSI. The HSI was validated with data from a
metapopulation undergoing restoration in the GWR (Schulte et al. 2009), and depended
6 largely on bottom type, salinity, and water depth, a surrogate for dissolved oxygen
concentration. Given the extensive effort being dedicated to eastern oyster restoration
8 across the Atlantic and Gulf of Mexico coasts, our findings should enhance the efficiency
and effectiveness of such efforts, and likely for other native oyster species worldwide.

10 Some of the previous oyster HSI models have included additional variables, such as
turbidity and predation intensity (Table 2), for smaller or more intensively studied
12 waterbodies, where these spatial data sets are available. For larger or less studied
waterbodies, spatial data sets for large suites of environmental variables are often rare.
14 Further, based on the wide range of environmental and biotic variables included in prior
HSI models (Table 2), it is clear that a "one size fits all" approach to HSI modeling is
16 inappropriate. While many variables that determine habitat suitability overlap between
species and systems, variables that are significant drivers in a given system may not be as
18 critical as other variables. For instance, of the four oyster HSI models developed for
specific systems (i.e., Caloosahatchee Estuary, Florida by Barnes et al. (2007), Hudson
20 River, New York by Starke et al. (2011), Mission-Aransas Estuary, Texas by Pollack et al.
(2012), Mississippi River, Louisiana by Soniat et al. (2013)), only a single variable was
22 used by all four (i.e., average salinity), yet they used a total of seven other variables that
were not in common (Table 2).

24 The eastern oyster provides an excellent example of this variability in requirements in
that its geographic range encompasses the (i) Atlantic coast from Canada to Florida, (ii)
26 Gulf of Mexico coast, and (iii) Caribbean from the Yucatan Peninsula to the West Indies
(Buroker 1983), which spans no less than five biogeographic provinces containing a diverse

suite of habitats across temperate, subtropical and tropical areas (Kennedy et al. 1996).

2 When using HSI models that incorporate a small subset of variables, such as only salinity
and substrate (e.g., Soniat et al. (2013), Swannack et al. (2014)), it is especially valuable
4 to conduct model validation. Such simple models trade incorporation of large suites of
environmental layers (for which there are rarely comprehensive spatial datasets for large
6 areas) for broader spatial coverage, with the underlying assumption being that oyster
habitat suitability can be adequately described by salinity and substrate alone. In the case
8 of Chesapeake Bay, for which seasonal anoxia and hypoxia are prevalent in deeper waters,
omission of a variable that encapsulated dissolved oxygen (i.e., water depth) may lead to
10 an HSI erroneously overstating the extent of suitable oyster habitat for restoration. In this
case, water depth was an effective, if imperfect, surrogate for dissolved oxygen, and was
12 largely accountable for the performance of the HSI model along with bottom type.

Bathymetric information is often available for most waterbodies, and an understanding of
14 the relationship between depth and dissolved oxygen concentrations can be useful to
eliminate areas of hypoxia or anoxia in restoration efforts by use of HSI models. In the
16 case of the GWR, seasonal hypoxia in areas deeper than 4 m, reduced salinity in upriver
locations, and subsidence of reef material in areas of soft sediments had previously been
18 identified as priority factors that could negatively impact the success of oyster restoration.
Thus, developing an HSI that integrates the variables known to be major drivers of
20 restoration success in a particular system with subsequent validation and model refinement
is the optimal, robust approach.

22 Given the commonly stated goal for oyster restoration projects of oyster abundance
and biomass enhancement, live adult oyster density data derived from the 2011 survey of
24 the ACE restored reefs in the GWR were used to validate the model. Our use of live adult
oyster density data from seven years post-restoration allowed us to avoid biases resulting
26 from anomalous recruitment events. In addition, when using oyster density data to
conduct HSI model validation, it is important to differentiate live adult oyster density and

total live oyster density. Immediately following restoration, oyster sanctuaries can
2 experience major recruitment pulses that can temporarily inflate total oyster density with
size structure skewed towards high densities of recruits and sub-adults, which have reduced
4 probabilities of survival relative to adults (Puckett and Eggleston 2012).

Our division of the analysis of live adult oyster densities and corresponding HSI values
6 into low- and high-relief reef categories was necessary as some of the low-relief reefs
constructed in the GWR had degraded due to sedimentation and subsidence into mud
8 seabottom. For low-relief reefs, reef persistence depends greatly on whether live oyster
shell accretion outpaces subsidence and sedimentation (Schulte et al. 2009, Jordan-Cooley
10 et al. 2011, Colden and Lipcius 2015, Lipcius et al. 2015). In several cases, low-relief reefs
in the GWR with HSI values ≥ 0.3 exhibited low live adult oyster densities. These
12 low-relief reefs containing suitable oyster habitat should be examined as candidates for
rehabilitation to high-relief reefs through the placement of additional shell material on the
14 low relief sites. The majority of high-relief reefs in the GWR have persisted due to the
accretion of additional shell material, which allows the reef matrix to outpace subsidence
16 and sedimentation and thereby maintain a positive shell budget (Powell et al. 2012).
These finding lends support to the existence of bistability (i.e., alternative stable
18 states—persistent reef or degraded reef—existing under similar environmental conditions) on
the restored oyster reefs in the GWR. In the persistent state, high-relief reefs (i) offset
20 heavy sedimentation, (ii) promote larval settlement and survival, juvenile survival and
growth, and adult disease resistance and survival, (iii) lead to elevated adult abundance
22 and reef accretion, and (iv) have high adult abundance which enhances settlement and
recruitment, thereby constituting a positive feedback cycle. In contrast, in the low-relief
24 degraded state (i) there is heavy sediment deposition, (ii) thick sediments on the reef
inhibit larval settlement and juvenile/adult survival, (iii) low adult abundance limits reef
26 accretion, and (iv) depressed adult abundance and reef height preclude high settlement
and facilitate heavy sediment accumulation, leading to a downward spiral towards a

degraded reef and local extinction of the oyster population (Jordan-Cooley et al. 2011).

2 Live adult oyster density was a sigmoid function of the HSI for both low- and
high-relief reefs. The sigmoid relationship differs from the linear relationship between
4 density and HSI in previous validated studies (Reiley et al. 2014, Cho et al. 2012). The
sigmoid relationship implies, for both low- and high-relief reef categories, a stasis in oyster
6 density below an HSI of 0.3, and a rapid increase in oyster density with increasing HSI to
a value likely corresponding with a site's carrying capacity. Low-relief reefs in areas with
8 an HSI ≤ 0.3 are unlikely to exceed performance standards, such as that of the Sustainable
Fisheries Goal Implementation Team (2011)—live adult oyster density target of 50 m⁻².
10 However, in areas of low-relief reef with an HSI ≥ 0.3 , density rapidly increases to nearly
double the 50 live adult oysters m⁻² target in low-relief reef areas with an HSI of 1.
12 Contrasting this, for high-relief reef in areas with an HSI as low as 0, the 50 live adult
oysters m⁻² target is exceeded with a rapid increase in density to nearly 5x the target at
14 an HSI of 1, although the long-term sustainability of reefs in areas with low associated HSI
values is questionable. This finding also provides further support to the existence of
16 bistability on the restored oyster reefs in the GWR in that under similar environmental
conditions (i.e., for a given level of HSI), low- and high-relief reefs remain differentiated by
18 oyster density.

With the increasing availability of spatial datasets for environmental variables in
20 marine and estuarine systems, habitat suitability indices will likely continue to be
developed to inform species conservation and management. However, as cautioned by the
22 USFWS shortly after the development of the first HSIs in the 1980s, the performance of
these models must be quantitatively assessed via an independent dataset. This study
24 provides a robust framework for HSI model development and validation, which can be
refined and applied to other systems and previously developed HSIs to improve the efficacy
26 of native oyster restoration.

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LITERATURE CITED

- 14 Andrews, J., 1979. Pelecypoda: Ostreidae. Pages 293–341 *in* A. Giese and J. Pearse, editors.
Reproduction of Marine Invertebrates. Academic Press.
- 16 Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling.
Journal of Biogeography **33**:1677–1688.
- 18 Barnes, T., A. Volety, K. Chartier, F. Mazzotti, and L. Pearlstine. 2007. A habitat suitability
index model for the eastern oyster *Crassostrea virginica*, a tool for restoration of the
20 Caloosahatchee Estuary, Florida. Journal of Shellfish Research **26**:949–959.
- Battista, T., 1999. Habitat suitability index for the eastern oyster *Crassostrea virginica*, in the
22 Chesapeake Bay: a geographic information system approach. University of Maryland at College
Park Masters Thesis.
- 24 Brooks, R. P. 1997. Improving habitat suitability index models. Wildlife Society Bulletin
25:163–167.

- 1 Brown, J., and E. Hartwick. 1988. A habitat suitability index model for suspended tray culture of
2 the Pacific oyster, *Crassostrea gigas* Thunberg. *Aquaculture Research* **19**:109–126.
- 3
4 Brown, S. K., K. R. Buja, S. H. Jury, M. E. Monaco, and A. Banner. 2000. Habitat suitability
5 index models for eight fish and invertebrate species in Casco and Sheepscot Bays, Maine.
6 *North American Journal of Fisheries Management* **20**:408–435.
- 7
8 Bruce, D., J. Lazar, and S. Giordano. 2010. Acoustic seabed mapping in the Great Wicomico
9 River (2009). NOAA Chesapeake Bay Office Habitat Assessment Team Final Report .
- 10
11 Buroker, N. E. 1983. Population genetics of the American oyster *Crassostrea virginica* along the
12 Atlantic coast and the Gulf of Mexico. *Marine Biology* **75**:99–112.
- 13
14 Cake, E. 1983. Habitat suitability index models: Gulf of Mexico American Oyster. *FWS/OBS*
15 **82**:1–37.
- 16
17 Carnegie, R. B., and E. M. Burreson. 2011. Declining impact of an introduced pathogen:
18 *Haplosporidium nelsoni* in the oyster *Crassostrea virginica* in Chesapeake Bay. *Marine Ecology*
19 *Progress Series* **432**:1–15.
- 20
21 Cho, Y., W.-C. Lee, S. Hong, H.-C. Kim, and J. B. Kim. 2012. GIS-based suitable site selection
22 using habitat suitability index for oyster farms in Geoje-Hansan Bay, Korea. *Ocean & Coastal*
23 *Management* **56**:10–16.
- 24
25 Cochran, W. 1977. Stratified random sampling. *Sampling techniques* pages 89–114.
- 26
27 Colden, A. M., and R. N. Lipcius. 2015. Lethal and sublethal effects of sediment burial on the
28 eastern oyster *Crassostrea virginica*. *Marine Ecology Progress Series* **527**:105.
- 29
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Environmental Systems Research Institute, 2011. ArcGIS desktop: Release 10.1. Redlands,
2 California.

Galtsoff, P. S. 1964. The American Oyster. Fishery Bulletin, US Fish and Wildlife Service
4 **64**:1–480.

Guay, J., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development
6 and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*).
Canadian Journal of Fisheries and Aquatic Sciences **57**:2065–2075.

Jordan-Cooley, W. C., R. N. Lipcius, L. B. Shaw, J. Shen, and J. Shi. 2011. Bistability in a
8 differential equation model of oyster reef height and sediment accumulation. Journal of
Theoretical Biology **289**:1–11.
10

Kemp, W., W. Boynton, J. Adolf, D. Boesch, W. Boicourt, G. Brush, J. Cornwell, T. Fisher,
12 P. Glibert, J. Hagy, et al. 2005. Eutrophication of Chesapeake Bay: historical trends and
ecological interactions. Marine Ecology Progress Series **303**:1–29.

14 Kennedy, V., R. Newell, and A. Eble. 1996. The Eastern Oyster *Crassostrea virginica*. Maryland
Sea Grant.

Lipcius, R. N., R. P. Burke, D. N. McCulloch, S. J. Schreiber, D. M. Schulte, R. D. Seitz, and
16 J. Shen. 2015. Overcoming restoration paradigms: value of the historical record and
metapopulation dynamics in native oyster restoration. Frontiers in Marine Science **2**:65.
18

Long, W. C., and R. D. Seitz. 2009. Hypoxia in Chesapeake Bay tributaries: worsening effects on
20 macrobenthic community structure in the York River. Estuaries and Coasts **32**:287–297.

Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new
22 extensions and a comprehensive evaluation. Ecography **31**:161–175.

Pollack, J., A. Cleveland, T. Palmer, A. Reisinger, and P. Montagna. 2012. A restoration
24 suitability index model for the eastern oyster *Crassostrea virginica* in the Mission-Aransas
Estuary, TX, USA. PloS one **7**:e40839.

- Powell, E. N., J. M. Klinck, K. Ashton-Alcox, E. E. Hofmann, and J. Morson. 2012. The rise and
2 fall of *Crassostrea virginica* oyster reefs: the role of disease and fishing in their demise and a
vignette on their management. *Journal of Marine Research* **70**:505–558.
- 4 Powers, S. P., C. H. Peterson, R. R. Christian, E. Sullivan, M. J. Powers, M. J. Bishop, and C. P.
Buzzelli. 2005. Effects of eutrophication on bottom habitat and prey resources of demersal
6 fishes. *Marine Ecology Progress Series* **302**:233–243.
- Puckett, B. J., and D. B. Eggleston. 2012. Oyster demographics in a network of no-take reserves:
8 recruitment, growth, survival, and density dependence. *Marine and Coastal Fisheries*
4:605–627.
- 10 R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation
for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org>.
- 12 Reiley, B. M., J. C. Bednarz, and J. D. Brown. 2014. A test of the Swainson’s warbler habitat
suitability index model. *Wildlife Society Bulletin* **38**:297–304.
- 14 Roloff, G. J., and B. J. Kernohan. 1999. Evaluating reliability of habitat suitability index models.
Wildlife Society Bulletin **27**:973–985.
- 16 Schulte, D. M., R. P. Burke, and R. N. Lipcius. 2009. Unprecedented restoration of a native
oyster metapopulation. *Science* **325**:1124–1128.
- 18 Seitz, R. D., D. M. Dauer, R. J. Llansó, and W. C. Long. 2009. Broad-scale effects of hypoxia on
benthic community structure in Chesapeake Bay, USA. *Journal of Experimental Marine*
20 *Biology and Ecology* **381**:S4–S12.
- Soniat, T. M., and M. S. Brody. 1988. Field validation of a habitat suitability index model for
22 the American oyster. *Estuaries* **11**:87–95.
- Soniat, T. M., C. P. Conzelmann, J. D. Byrd, D. P. Roszell, J. L. Bridevaux, K. J. Suir, and S. B.
24 Colley. 2013. Predicting the effects of proposed Mississippi River diversions on oyster habitat
quality: application of an oyster habitat suitability index model. *Journal of Shellfish Research*
26 **32**:629–638.

- Southworth, M., J. M. Harding, J. A. Wesson, and R. Mann. 2010. Oyster (*Crassostrea virginica*,
2 Gmelin 1791) population dynamics on public reefs in the Great Wicomico River, Virginia,
USA. *Journal of Shellfish Research* **29**:271–290.
- 4 Starke, A., J. Levinton, and M. Doall. 2011. Restoration of *Crassostrea virginica* (Gmelin) to the
Hudson River, USA: A spatiotemporal modeling approach. *Journal of Shellfish Research*
6 **30**:671–684.
- Sustainable Fisheries Goal Implementation Team. 2011. Restoration goals, quantitative metrics,
8 and assessment protocols for evaluating success on restored oyster reef sanctuaries. Report of
the Sustainable Fisheries Goal Implementation Team of the Chesapeake Bay Program .
- 10 Swannack, T. M., M. Reif, and T. M. Soniat. 2014. A robust, spatially explicit model for
identifying oyster restoration sites: case studies on the Atlantic and Gulf coasts. *Journal of*
12 *Shellfish Research* **33**:395–408.
- Thompson, S. K. 2012. *Sampling*. 3rd edition. Wiley series in probability and statistics, John
14 Wiley & Sons, Hoboken, NJ.
- Tirpak, J. M., D. Jones-Farrand, F. R. Thompson, D. J. Twedt, C. K. Baxter, J. A. Fitzgerald,
16 and W. B. Uihlein. 2009. Assessing ecoregional-scale habitat suitability index models for
priority landbirds. *Journal of Wildlife Management* **73**:1307–1315.
- 18 U. S. Fish and Wildlife Service, 1981. Standards for the development of Habitat Suitability Index
models. Technical Report 103 ESM, USDI Fish and Wildlife Service, Division of Ecological
20 Services, Washington, D.C.

TABLE CAPTIONS

2 TABLE 1. Habitat suitability index models developed for oyster aquaculture, fishery
production, and restoration. Calibration is achieved when the HSI approximately spans
4 the full range from 0 to 1. Verification is achieved when the HSI values are positively
correlated with independent qualitative or categorical (ranked) data, such as
6 presence/absence data. Validation is achieved when the HSI values correlate positively
with independent quantitative data in space and time, such as population density or
8 abundance. If validation has been accomplished, verification is not necessary.

TABLE 2. Variables used in habitat suitability index models developed for oyster
10 aquaculture, fishery production and restoration, and the models using each variable.
1–Barnes et al. (2007), 2–Battista (1999), 3–Brown and Hartwick (1988), 4–Cake (1983),
12 5–Cho et al. (2012), 6–Pollack et al. (2012), 7–Soniati and Brody (1988), 8–Soniati et al.
(2013), 9–Starke et al. (2011), 10–Swannack et al. (2014), 11–This study.

TABLE 1. Habitat suitability index models developed for oyster aquaculture, fishery production, and restoration. Calibration is achieved when the HSI approximately spans the full range from 0 to 1. Verification is achieved when the HSI values are positively correlated with independent qualitative or categorical (ranked) data, such as presence/absence data. Validation is achieved when the HSI values correlate positively with independent quantitative data in space and time, such as population density or abundance. If validation has been accomplished, verification is not necessary.

Authors	Species	Calibrated?	Verified?	Validated?
<i>Aquaculture</i>				
Brown and Hartwick (1988)	<i>C. gigas</i>	No *	Yes †	Yes
Cho et al. (2012)	<i>C. gigas</i>	No *	Yes †	Yes
<i>Fishery production</i>				
Cake (1983)	<i>C. virginica</i>	Yes	No	No
Soniat and Brody (1988)	<i>C. virginica</i>	Yes	Yes	No
<i>Restoration</i>				
Battista (1999)	<i>C. virginica</i>	Unknown §	No	No
Barnes et al. (2007)	<i>C. virginica</i>	Yes	No	No
Starke et al. (2011)	<i>C. virginica</i>	Yes	No	No
Pollack et al. (2012)	<i>C. virginica</i>	Unknown §	Yes ‡	No
Soniat et al. (2013)	<i>C. virginica</i>	Yes	No	No
Swannack et al. (2014)	<i>C. virginica</i>	Yes	No	No
This study	<i>C. virginia</i>	Yes	Yes †	Yes

* The HSI was not calibrated because index values did not span the range from 0 to 1.

§ The HSI calibration status is unknown because index values are reported as a range from low to high, and not from 0 to 1.

† The HSI was not verified before being validated, but because it was validated, it is also considered to be verified.

‡ Abundance data was collected using an oyster dredge, which provides qualitative, not quantitative, estimates of density. Consequently, the HSI was verified, not validated.

FIGURE CAPTIONS

2 FIGURE 1. Map showing the location of the Great Wicomico River in relation to
Chesapeake Bay.

4 FIGURE 2. Relationships between the actual value of environmental variables and
associated habitat suitability values for (a) water depth (surrogate variable for dissolved
6 oxygen), (b) salinity, and (c) bottom type (MC = muddy clay, SM = sandy mud, MS =
muddy sand, S = sand, HB = hard bottom). Scores of 0 are unsuitable and values of 1 are
8 optimal.

FIGURE 3. Distribution of high vertical relief reefs (HRR) and low vertical relief reefs
10 (LRR) in the US Army Corps of Engineers network of sanctuary reefs in the Great
Wicomico River.

12 FIGURE 4. A) Depth suitability layer. B) Salinity suitability layer. C) Bottom type
suitability layer. D) Habitat suitability index output, red areas are unsuitable oyster
14 habitat, green areas are optimal oyster habitat.

FIGURE 5. Sigmoid relationship between habitat suitability index score and associated live
16 adult oyster density on HRR and LRR. The solid line represents the relationship for HRR
and the dashed line represents the relationship for LRR.

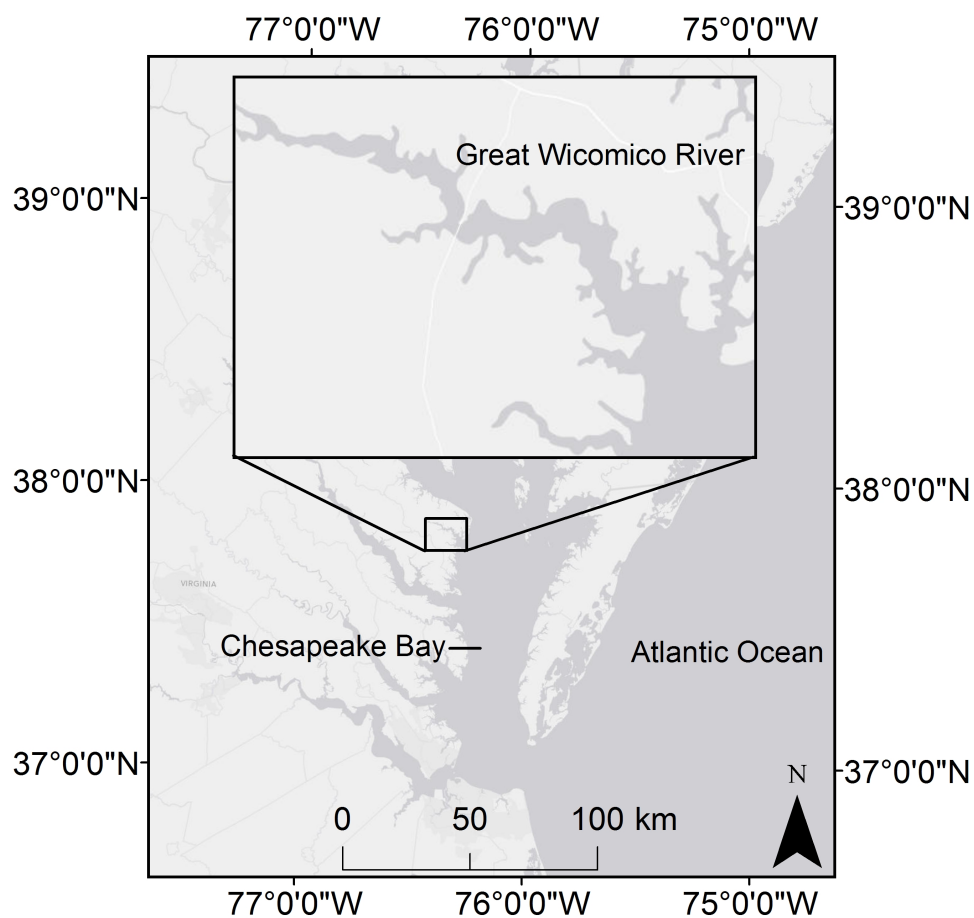


FIGURE 1. Map showing the location of the Great Wicomico River in relation to Chesapeake Bay.

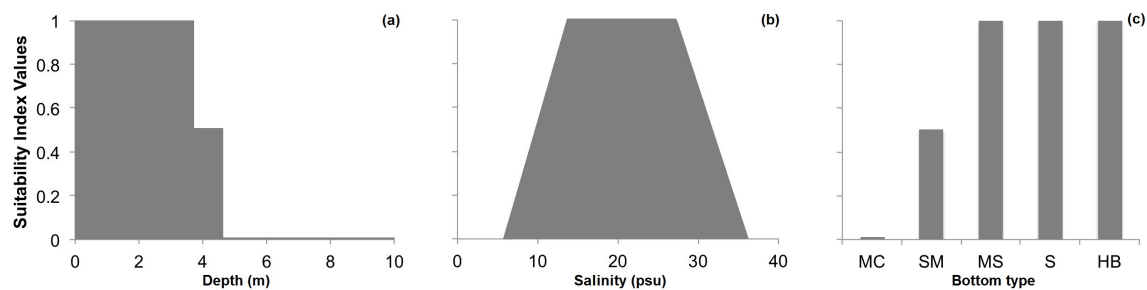


FIGURE 2. Relationships between the actual value of environmental variables and associated habitat suitability values for (a) water depth (surrogate variable for dissolved oxygen), (b) salinity, and (c) bottom type (MC = muddy clay, SM = sandy mud, MS = muddy sand, S = sand, HB = hard bottom). Scores of 0 are unsuitable and values of 1 are optimal.

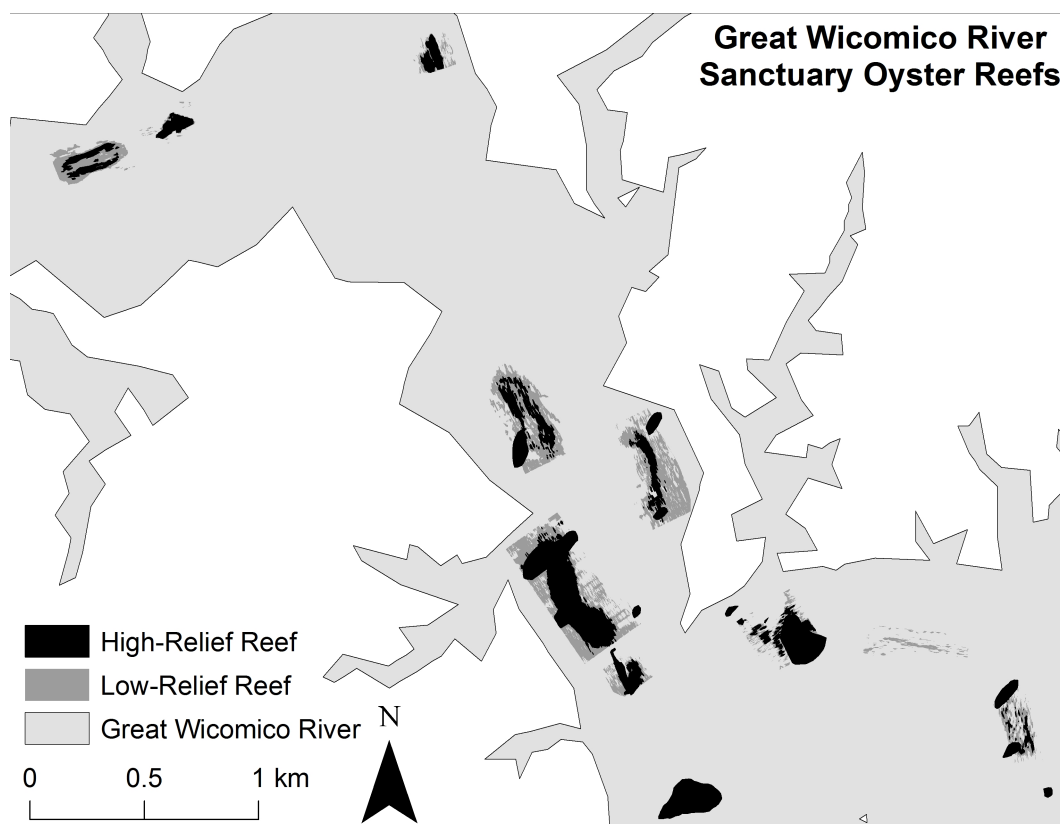


FIGURE 3. Distribution of high-relief reefs (HRR) and low-relief reefs (LRR) in the US Army Corps of Engineers network of sanctuary reefs in the Great Wicomico River.

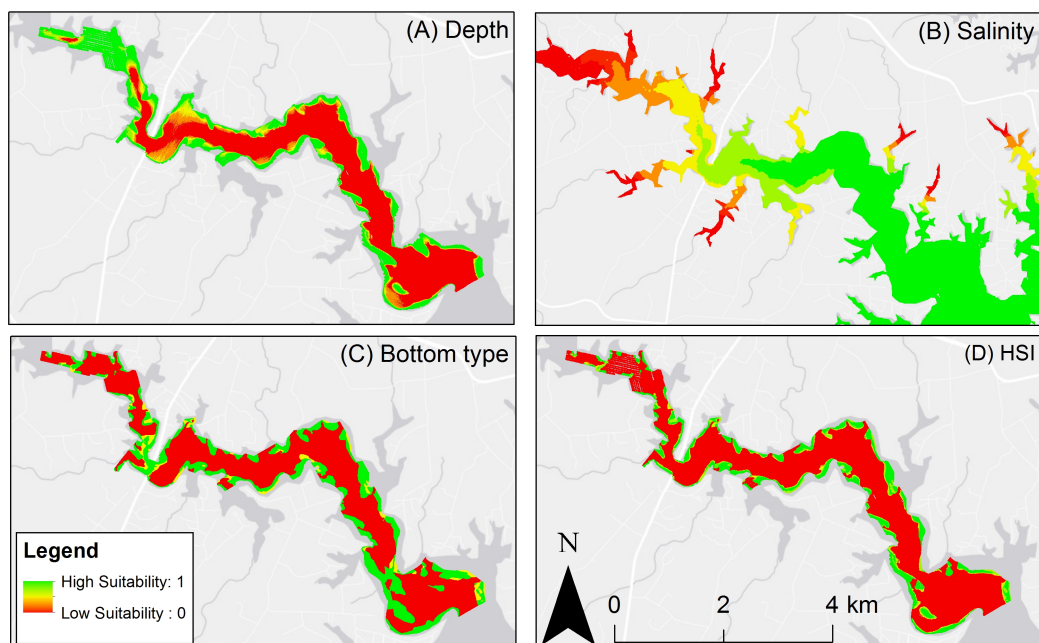


FIGURE 4. A) Depth suitability layer. B) Salinity suitability layer. C) Bottom type suitability layer. D) Habitat suitability index output, red areas are unsuitable oyster habitat, green areas are optimal oyster habitat.

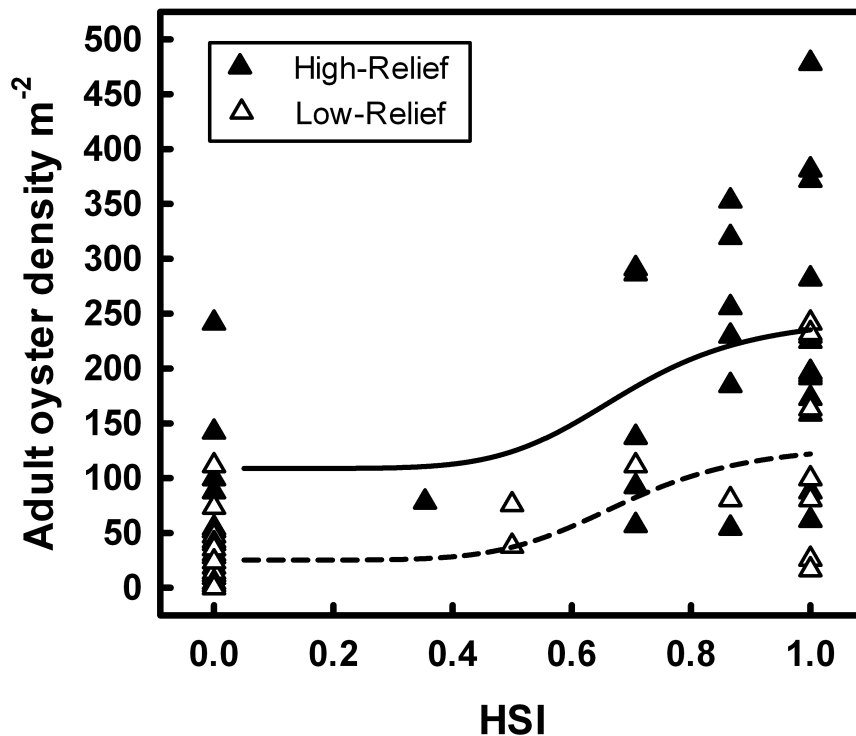


FIGURE 5. Sigmoid relationship between habitat suitability index score and associated live adult oyster density on HRR and LRR. The solid line represents the relationship for HRR and the dashed line represents the relationship for LRR.