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RESTORATION OF *CRASSOSTREA VIRGINICA* (GMELIN) TO THE HUDSON RIVER, USA: A SPATIOTEMPORAL MODELING APPROACH

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ABSTRACT As a result of its historical abundance and ecological significance, the eastern oyster, *Crassostrea virginica,* has been identified as a primary restoration target for the Hudson River–New York Harbor region. Prior to any large-scale restoration investments, a spatial assessment has been made to characterize the region's potential for hosting restored oyster populations. Using existing geographic data of the physical attributes of the river, a GIS-based restoration suitability index has been developed with the goal of identifying specific areas that hold a greater probability for success in oyster restoration. The results show that much of the river's restoration potential is initially limited by the physical environment, depth, and sediment type, and is reduced further by the salinity distribution. The results from this model should be used as a preliminary guide to focus future restoration efforts within the lower Hudson River and New York Harbor area as well as to investigate possible changes to the restoration potential with changing salinities brought on by regional climate change and hydrodynamic alterations.

KEY WORDS: oyster, restoration, *Crassostrea virginica*, Hudson River

INTRODUCTION

Oyster bars constructed by the eastern oyster, *Crassostrea virginica*, were once a major feature of shallow-water estuarine habitats of the Lower Hudson River and the New York Harbor regions, but have largely disappeared because of overharvesting, pollution, and habitat destruction (Franz 1982, USEPA 1998). *C. virginica* is a major potential economic resource, but in New York waters, restoration objectives center around the ecosystem services oyster reefs provide (Bain et al. 2007). The scope of ecosystem services provided by dense populations of *C. virginica* has been widely discussed (Coen et al. (2007) and references therein) and include reduction of phytoplankton density (Newell 1988, Gerritsen et al. 1994), indirect benefits of water clarity to seagrasses (Newell & Koch 2004), increase of nitrogen cycling especially through denitrification (Newell et al. 2002, Newell et al. 2005), and provision of habitat for numerous benthic invertebrates and demersal species (Lenihan 1999, Coen et al. 2007).

As a result of the enormity of change that the Hudson River has undergone from its precolonial days (Franz 1982), it is difficult to assess the potential long-term viability of restored oyster reef populations without a characterization of potential oyster habitat and a basic empirical understanding of the short-term challenges that restored populations may face. In addition, the costs, and even likelihood (Mann & Powell 2007), associated with oyster restoration are daunting, therefore careful plans must be made to maximize the return in investment. Keeping to these basic concepts, a restoration plan can be developed in which areas are selected based on the potential for successful recruitment, growth, and persistence, as well as areas that allow for careful monitoring and assessment that provides feedback for future work and maintenance of these oyster populations. We focus here on a habitat assessment model to characterize the areas best suited for restoration efforts.

A major challenge created by a lack of robust oyster populations is the scarcity of ideal substrate for recruitment. A stable oyster population relies on the continuing recruitment of juveniles to areas that will support survival and growth. These areas are typically provided by a reef structure containing the shells of prior oyster generations, both live individuals and remnant valves. Although the Hudson River currently provides some localized appropriate substrate—in relict oyster reefs, shell hash, rock, and gravelly sediments—it is likely that nearly all the substratum that once supported oysters now lacks the vertical 3-dimensional structure needed for oyster recruitment and survival (Soniat et al. 2004, Brumbaugh & Coen 2009, Powers et al. 2009). Many other formerly suitable areas have been altered substantially by dredging and pollutant discharge, and are now physiologically unsuitable for natural recovery.

Observed recruitment and vigorous growth on suspended shell bags (A. Starke, unpubl. data) along with frequent anecdotal reports of oyster settlement on a variety of other surfaces (e.g., mooring chains, docks, and ropes) indicate some spawning populations in a northern section of the estuary, known as the Tappan Zee–Haverstraw Bay (TZ-HB) region. Yet there remains a lack of expansive oyster reef communities, possibly indicating a shell substrate budget threshold having been crossed since the time that Hudson River oysters were reduced in abundance by overharvesting, dredging activities, or other human disturbances. Scattered oyster recruitment has also been observed in New York Harbor (Medley 2010), but not in Jamaica Bay (Levinton, unpubl. obs.).

Because bottoms with oyster shell are now rare in the Hudson, plans for restoration have emphasized restoring hard-shell bottoms, with the ambitious goal of restoring 500 acres of oyster reefs to the Hudson–Raritan estuary by 2012 (Bain et al. 2007). To achieve these goals, there needs to be an enormous investment of resources to the study, development, and implementation of restoration strategies in this system. Fortunately, there have been many efforts of oyster restoration along the Atlantic coast that can contribute to our understanding of how best to tackle restoration in the Hudson.

A number of oyster restoration projects have had some success using reef enhancement and construction techniques

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(Nestlerode et al. 2007, Gregalis et al. 2008, Powers et al. 2009, Schulte et al. 2009), with reef height seeming to be the vital component to their respective achievements. Finding appropriate locations for these restoration efforts is a cautious undertaking, because this type of work comes at a considerable expense. Selecting the location of these restoration sites needs to focus on areas that exhibit the potential to support oyster populations and that have sufficient physical properties for reef construction and maintenance. We therefore require appropriate quantitative habitat assessment methods to select priority sites for restoration.

Habitat suitability indices are a commonly used tool by resource managers in conservation and restoration planning (van Katwijk et al. 2000, Vincenzi et al. 2006, Barnes et al. 2007). To define the potential geographic range of a restoration, such indices are frequently built using a spatial correlation analysis between presence/absence or abundance data and known environmental conditions found within the study area. These methods are useful in identifying locations for preservation of crucial habitat but can also be modified to identify areas that have characteristics that may limit a species' local range. With diminished populations, such as those of *C. virginica* in the Hudson River, the development of such an index needs to be approached by identifying the conditions that will provide the best chances of reef restoration success and then identifying if and where these locations exist.

Keeping to this approach, our proposed index aims to identify areas spatially that have characteristics that not only identify currently suitable habitat, but also fit well with reef creation and enhancement practices. The methodology of this restoration suitability index (RSI) is based on similar habitat suitability models (van Katwijk et al. 2000, Van der Lee et al. 2006, Vincenzi et al. 2006, Barnes et al. 2007), with a focus on some basic habitat requirements for a successful reef restoration project. Figure 1 shows the study area within which we calculated the spatial variation of the RSI for *C. virginica*.

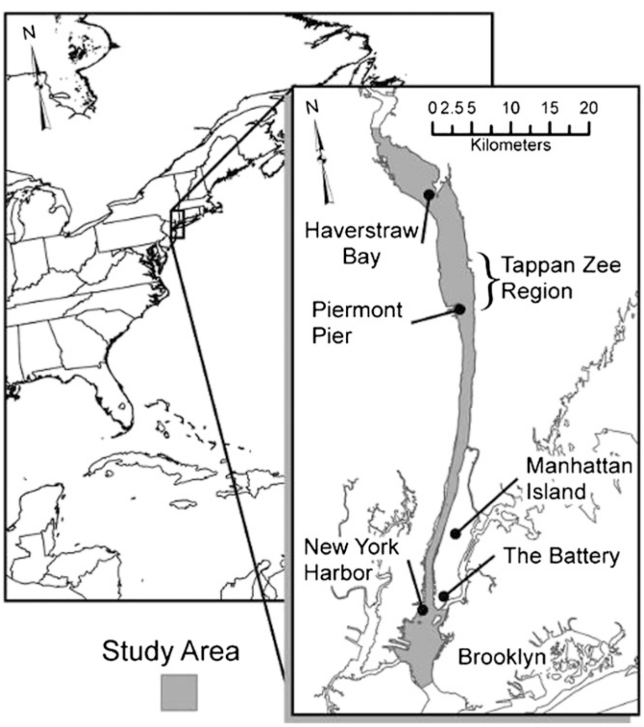

Figure 1. Study location, northern mid-Atlantic Ocean, Hudson River estuary encompassing the Tappan Zee–Haverstraw Bay, New York Harbor regions of the river. Restoration suitability index extent represented by shaded area.

Briefly, the model operates by organizing spatially explicit environmental data into raster or grid-based data sets (10 × 10-m cell size). These rasters are reclassified independently on a suitability scale and then combined to form a continuous map of spatially referenced restoration suitability across the study region. The structure of this model and the associated outputs do not act as an assessment of the region's capacity to restore reef systems; rather, they are designed to identify specific areas that offer the greatest potential for implementing reef construction and population restoration. Of course, we presume that such sites will also be loci of population growth. As our understanding of oyster physiology, disease dynamics, the physical nature of the Hudson River, and the interaction of all these variables improve, we will understand more fully the system's capacity to host restored oyster populations.

A number of important abiotic and biotic environmental habitat characteristics are essential to the successful construction, maintenance, and persistence of oyster populations. The characteristics chosen for use in this model have been selected for the appropriate data availability, reliability, spatial extent, and stationarity (spatial variation). The model we use in this study focuses on distinct criteria while making the suitability assessment: the ability of a location to support the establishment and maintenance of a constructed reef, and the area's potential for successful oyster population growth.

The successful installation of a reef structure is dependent on the firmness of the seabed and its ability to support the weight of these large reef systems. Sediment types that offer firm support, such as sandy or gravelly sediments, are preferable, as are areas that are less prone to accumulation of soft sediments. The accumulation of sediments atop and surrounding the reef structure will inhibit the growth of oysters and other epibenthos on the installed reef and should be avoided. Tidal and other bottom currents often interact with fine sediments and cause resuspension, which inhibits suspension feeding (Rhoads & Young 1970, Urban & Kirchman 1992, Barille et al. 1997). Some of this negative effect is mitigated by enhancing the vertical relief of restored oyster reefs.

MATERIALS AND METHODS

Data Acquisition

The physical environmental data for this study was obtained from the New York State Department of Environmental Conservation GIS Clearinghouse (http://www.nysgis.state.ny.us/index.cfm) (Bell et al. 2006a, Bell et al. 2006b, Ladd 2008) and was gathered as part of the large-scale Benthic Mapping Project (Nitsche et al. 2004). Data were collected, compiled, and analyzed for depth, sediment type, and sediment environment, between 1998 and 2003 using a variety of techniques, including side-scan sonar, subbottom profiling, multibeam bathymetry, sediment cores, and grabs (Nitsche et al. 2004, Nitsche et al. 2007). The original sedimentary environment and sediment type data were converted from polygon shape file format to raster format (10-m cell size), and depth was resampled to a 10-m cell size for consistency of data inputs. Figure 2A–C displays these data as thematic maps.

The Hudson River is an active system that ranges from a well-mixed estuary during periods of low river flow and high

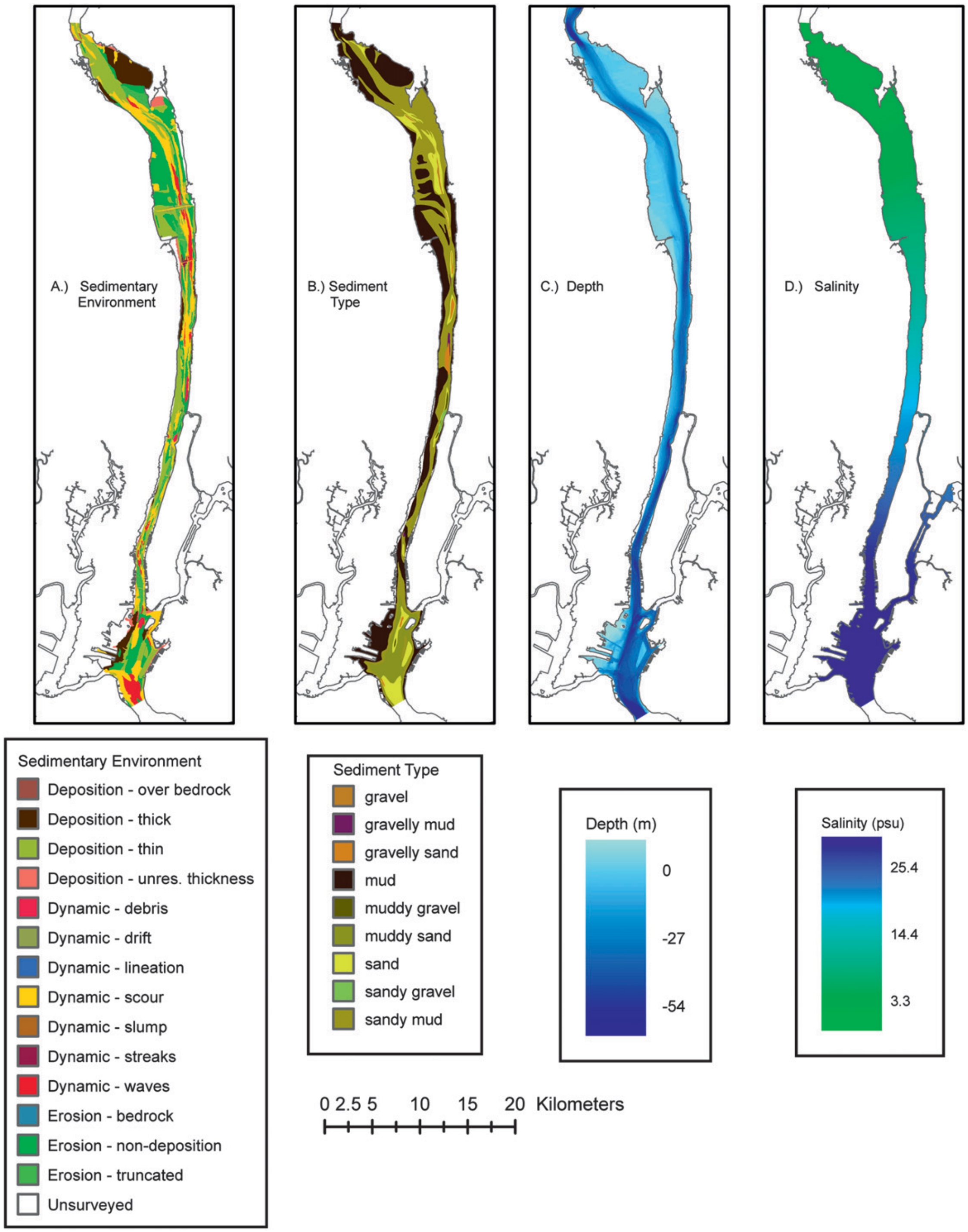

Figure 2. GIS maps of input environmental habitat characteristics. (A) Sedimentary environment. (b) Sediment type. (C) Depth. (A–C) Data obtained from NYSDEC GIS Clearinghouse (Bell et al. 2006a, Bell et al. 2006b, Ladd 2008). (D) Estimated salinity coverage interpolated from long-term longitudinal salinity data.

tidal amplitude, to a highly stratified estuary during periods of high river flow and low tidal amplitude (Geyer & Chant 2006). The river's dynamic nature makes it difficult to monitor and categorize salinity throughout the study region. We used outputs from a 2-dimensional hydrodynamic model to generate a simplified but reasonably accurate map of the salinity regime (Ralston et al. 2008, Ralston & Geyer 2009) to calculate a mean salinity across the study area. Data were subsampled for the period encompassing the biologically active growing and reproductive season (March 1 to November 1)—the time in which oysters are most sensitive to salinity (Shumway 1996). The model's output of basinwide daily mean bottom salinity was then averaged over the model's extended time period (1918 to 2005) for each model station point throughout the study area. Mean bottom salinities were then interpolated using the geostatistical process of kriging (Legendre & Legendre 1998) to produce a continuous coverage of salinity values across the study area (Fig.re 2D). Although the geostatistical model output reflects poorly the cross-basin salinity distribution observed in real-time latitudinal salinity measures, it mimics the source data (a basinwide average) well and provides a reasonable estimate of long-term salinity averages across the region, especially through the sensitive TZ-HB region.

River depth is an important consideration during and after the installation of a reef structure. Careful positioning of the reef substrate is often needed to maximize its effectiveness in attracting oyster recruits and to promote survival. Because of the strong tidal currents and often rapid sedimentation, installation of these structures in the strong bottom currents of the Hudson River (Geyer & Chant 2006) can be difficult and potentially dangerous. Postdeployment monitoring of the reef structures, a crucial step in a successful restoration project, would be unfeasible in deep, typically high-turbidity river water. On the other hand, the Hudson also has extensive ice formation, and ice usually accumulates in shallow shoreward areas each winter. Oyster reef structures would therefore need to be fitted between an ideal nearshore deployment and monitoring depth and depths to deep to have appropriate conditions of relatively low near-bottom turbidity. Our models (described next) therefore include some considerations of the difficulties of installing and monitoring, which are highly intercorrelated.

MODEL CONSTRUCTION

Restoration Suitability Index

Environmental parameters representing the sedimentary environment, sediment type, depth, and salinity were used as inputs to the RSI (Eq. 1). Each parameter was reclassified independently to a suitability scale from 0.0–1.0, with 0 being unsuitable and 1 being suitable, producing a reclassified parameter-specific suitability (PSS). Parameters were constructed of both continuous and discrete data, and were transformed using a broken linear function or ordinal ranking, respectively (Fig. 3). After reclassification, a correlation analysis among the PSSs was performed to test for independence of parameters to evaluate whether correlation among parameters contributes any bias to the calculation of the RSI (Eq 1). To do so, a randomly generated set of points ($n = 10{,}000$) was created across the spatial extent of the index. The corresponding PSS values for each parameter were tabulated at each point for correlation analysis.

The resultant reclassified parameter-specific suitabilities (PSS_i) are then combined using a weighted geometric mean function (Eq 1) where w_i is the relative weight of importance of PSS_i, producing an RSI. This method is preferred because an overall suitability of a location is given a ranked value of 0 if any one parameter is found to be unsuitable. The RSI was evaluated across the 2-dimensional extent of the study area, displayed in Figure 1.

$$\mathrm{RSI} = \left(\prod_{i=1}^{n} \mathrm{PSS}_i^{wi} \right)^{1/n} \qquad (1)$$

The RSI model was constructed in the ModelBuilder Environment of ArcMAP. Data and results were maintained and analyzed in ArcGIS (ESRI ArcEditor version 9.3, Redlands, CA).

Parameter Selection

Reclassifications of the sedimentary environment are based on the likelihood that a reef structure in some sedimentary conditions

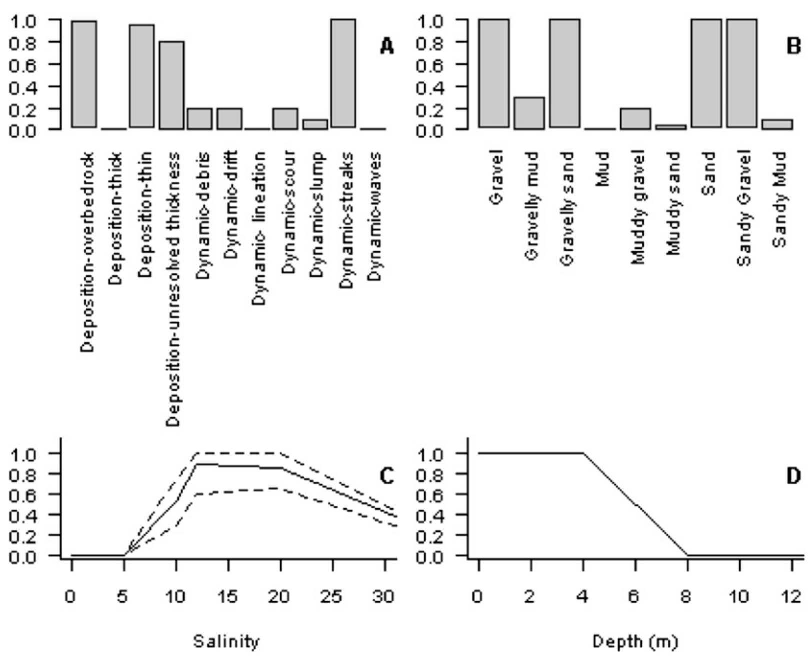

Figure 3. Parameter-specific suitability functions. (A, B) Nominal ranking functions converting categorical environmental data into suitability values. (C, D) Broken linear functions representing a continuous suitability function used to reclassify environmental data into suitability values. In (C), the salinity suitability function is presented as the center dark line. The proposed level of uncertainty around the definition of suitability is represented by dashed lines. The distribution of suitability values at break points were randomly generated from a beta distribution. Note the asymmetrical distribution at 10 psu resulting from truncation of suitability values at 1.0. In (D) the depth suitability function is represented.

will be subjected to heavy sedimentary deposition, which has been shown to limit the functionality of a reef structure (Powell et al. 1995, Grizzle et al. 2002). Whereas oysters can feed in turbid environments, they are less efficient and produce copious pseudofeces, which affects gill sorting (Urban and Kirchman 1992, Ward et al. 1998). Powers et al. (2009) reported the failure of several restored Eastern oyster reef structures due to burial of sediments and Lenihan (1999) found significantly higher mortalities of oysters along buried fringes of reef, compared with those found elevated and unburied. Additionally, Trimble et al. (2009) identifies unstable sediments as a potential limitation in restoration efforts of the Olympia oyster, *Ostrea lurida*, to west coast estuaries as well as high flow rates which can potentially transport shell material away from restoration sites. Flow rates have been shown to influence oyster populations through a number of mechanisms (Lenihan 1999). Settlement can be limited by high flow rates (Turner et al. 1994), whereas growth and survival of adults has been shown to increase with flow rate (Lenihan 1996). Predator-prey interactions can also be influenced by flow rate (Lenihan 1999). Ultimately the flow rate needs to be sufficient enough to provide a flux of particles to the reef structure yet not be of sufficient velocity near the bottom to cause removal or scouring of the reef material. Whereas water motion is required to deliver phytoplankton, oyster growth and likely feeding is inhibited at high flow speeds (Grizzle et al. 1992). Using this basic guideline, the categorical data representing the sedimentary environment are assessed and reclassified on a suitability scale.

Reclassification of the data is essentially a comparative assessment with suitability values scaled to the relative suitability of each categorical datum. For instance, areas categorized as possessing thin deposits over bedrock are more suitable than areas categorized as possessing thick deposits, and will thus receive a higher suitability ranking. Reclassified suitability values are listed in Table 1, along with descriptions of data (Bell et al. 2006a, b) and spatial extent of each category.

The sediment type at a restoration site needs to be considered for two main reasons. First, an area containing fine sediments can be subjected to increased turbidity and suspended sediments during high river flow, tidal flow, or increased wave action (Rhoads and Young 1970). Increased turbidity has shown to significantly harm oyster eggs and larvae and has mixed impacts on adult and juvenile oysters (Shumway 1996). Marshall (1954) reported that reefs naturally occurred in areas of firm stable sediments.

Also, extra care would be needed during underwater monitoring activities; disturbing the surrounding sediments would create poor visibility during these activities. In general sediment grain size is positively correlated with suitability (Fig. 3b). Reclassified suitability values are listed in Table 1, along with descriptions of data and the spatial extent of each category.

Defining the suitability of water depth is based on the depths at which oysters can grow and the feasibility of successfully installing a reef structure into this system. Oysters have primarily been found to naturally occur in depths up to 4.0–5.0 m, although some areas have supported oysters up to 8.0 m (Eastern Oyster Biological Review Team 2007). Depth can influence oyster performance through a number of indirect processes. For instance, Lenihan (1999) found an increased oyster mortality, associated with reduced oxygen and poor food quality, along the bases of reefs placed in 6 m of water compared with reefs installed at 3 m. In addition to the biological considerations, the physical installation of reef material is increasingly difficult with water depths, and likely to become impractical at depths greater than 8 m owing to difficulties of installation and maintenance. Similarly, monitoring will likely be difficult as visibility at this depth will be limited. Using these guidelines depth suitability is defined as such: water depths less than or equal to 4 m are identified as suitable; suitability of water depths greater than 4 m decreases linearly to 8 m of depth above which is deemed unsuitable (Fig. 3c).

Numerous studies have focused attention on the salinity and temperature range that would optimize growth rates and spawning success (e.g., Shumway 1996). Though these studies have greatly enhanced the understanding of the physiology of the Eastern oyster there remains limited knowledge of performance at the physiological limits for salinity and temperature. A lower limit of 5 psu appears to be accepted as the limit for longer term survival of juveniles and adults (Shumway 1996 and references therein). Higher temperatures have been found to present a more stressful environment at very low salinities (La Peyre et al. 2003).

In the Hudson, *C. virginica* survive the winter in freshwater (Starke et al. unpublished data), but prolonged periods with salinities below 5 psu in late spring and summer result in varying levels of mortality, depending upon annual rainfall, which directly affects discharge and salinity variation, both seasonally and along the length of the Lower Hudson (Levinton et al. 2011). For this reason, our suitability index is based upon salinities from May-November, when water temperatures are high. The effect of low salinity stress and its variation with discharge and precipitation is most pronounced in the TZ-HB region. In years of low discharge, salinity is limiting toward the north of this region, but in high discharge years, salinity in spring and summer can cause extensive mortality for juveniles and adults even in the southern area of TZ-HB (Ralston et al. 2008, Levinton et al. 2011). These variations, including the predictably low salinity in the northern area and fluctuating salinity in the southern part of TZ-HB are incorporated in our model. More recently there has been interest on the influence of these extreme salinities and temperatures on the progression and outbreak of epizootics with particular concern for climate induced changes (Ford 1996, La Peyre et al. 2003, Ford and Chintala 2006, Ford and Smolowitz 2007).

Although temperature and salinity have a strong interactive effect on the physiological condition and survival of oysters the two parameters have contrasting properties within the river. Seasonal changes in temperature do not vary significantly through the study region (Levinton, unpublished data), and remains within the overall tolerances of oysters (Shumway 1996). An exception to this would be areas that may experience occasional exposure by extreme tides during the heat of summer or the freezing temperatures of winter. The overall stationarity of the temperature data limits its use in this type of analysis even though it still remains an important property of the river's environment. Conversely the salinity of the Hudson River ranges from fresh to oceanic with an oligohaline transition zone occurring in the (TZ-HB) area making it the critical biologically relevant variable in this spatial model. The interaction with temperature arises in spring and summer in years of high rainfall (Levinton et al. 2011).

Finding the optimum salinity within this system is an enormous challenge unto itself and we here present a suitability function (SSF) (Fig. 3d), based on results from a number of laboratory and field studies that examined the various influences of salinity

TABLE 1.

Reclassification of sedimentary environment and sediment type data.

Original Data Classification	Description of Data*	Reclassified Suitability Value	Rationale for Suitability Value	Coverage area (km^2)	Coverage area (% of total study area)
Sedimentary environment					
Deposition, over bedrock	Recent evidence of deposition, bedrock underneath thin drape	0.98	Structural support, thin deposits indicate low flow rates	0.004	0.002
Deposition, thick	Recent evidence of deposition, thick (>50 cm) usually transparent layer of sediment accumulation	0.00	Poor structural support, choking sedimentation rates probable	17.794	9.710
Deposition, thin	Recent evidence of deposition, thin (<50 cm) usually transparent layer of sediment accumulation	0.95	Structural support, lower energy	40.134	21.902
Deposition, unresolved thickness	Recent evidence of deposition, thickness unknown as a result of low backscatter	0.80	Lower energy, ground truthing needed to determine thickness of deposit,	4.847	2.645
Dynamic, debris	Erosional and depositional processes possible, debris flow deposits, scouring and sediment trails evident	0.20	Scouring indicates potentially high currents, debris may provide additional constraints	1.474	0.804
Dynamic, drift	Erosional and depositional processes possible, depositional in the lee of obstacles, scour along edges of obstacles	0.20	Scouring may occur around reef structure, offers structural support, moderate flow rate likely, obstacles may provide additional constraints	1.640	0.895
Dynamic, lineation	Erosional and depositional processes possible, parallel lineations of sediments	0.00	Lineations indicate high flow rates, shifting sediments	0.002	0.001
Dynamic, scour	Erosional and depositional processes possible, scouring generally found around obstacles	0.20	Scouring may occur around reef structure, offers structural support, moderate flow rate likely, obstacles may provide additional constraints	41.573	22.687
Dynamic, slump	Erosional and depositional processes possible, slumped sediments found along channel walls	0.10	Occurs along steep bottom types, not ideal for reef placement	0.022	0.012
Dynamic, streaks	Erosional and depositional processes possible, streaks evident but lack topographic relief	1.00	Moderate current flow, generally firm sediments present	0.459	0.251
Dynamic, waves	Erosional and depositional processes possible, migrating sand waves present	0.00	Sand waves evidence of very high flow rates, unsuitable for reefs	9.151	4.994
Erosion, bedrock	Bedrock exposed at surface, no deposition	1.00	Structural support, no sedimentation	0.051	0.028
Erosion, nondeposition	Areas that have no clear evidence of deposition	1.00	No deposition, characterized by firm sediments	36.751	20.055
Erosion, truncated	Truncated stratigraphy outcropped at sediment surface indicating erosional processes	0.90	Erosional processes evident of moderate flow rate, provides structural support	16.249	8.867
Unsurveyed	Areas unsurveyed	1.00	Unsurveyed areas may provide beneficial habitat characteristics, need to be verified	13.097	7.147

continued on next page

TABLE 1.

continued

Original Data Classification	Description of Data*	Reclassified Suitability Value	Rationale for Suitability Value	Coverage area (km^2)	Coverage area (% of total study area)
Sediment type					
Gravel	Gravel with <10% mud and <10% sand	1	Stable, low resuspended sediments, may provide substrate for oyster settlement	1.071	0.584
Gravelly mud	Mud with >10% gravel	0.3	Reduced stability, resuspended sediments problematic	0.523	0.285
Gravelly sand	Sand with >10% gravel	1	Stable, low probability of resuspended sediments	2.189	1.194
Mud	>90% mud (silt and clay)	0	High probability of suspended sediments, offers poor support to structure	72.258	39.431
Muddy gravel	Gravel with >10% mud	0.2	Reduced stability, resuspended sediments problematic	0.684	0.373
Muddy sand	Sand with >10% mud	0.05	Offers very little support, resuspended sediments problematic	16.090	8.781
Sand	Sand with <10% mud and <10% gravel	1	Stable, low resuspended sediments	16.844	9.192
Sandy gravel	Gravel with <10% sand and <10% mud	1	Stable, low resuspended sediments, may provide substrate for oyster settlement	0.430	0.235
Sandy mud	Mud with >10% sand	0.1	Reduced stability, resuspended sediments problematic	73.161	39.924

* Descriptions provided from Bell et al. (2006a, b).

on oyster physiology, biology, and ecology. A list of these findings, along with references, and their relevance to the definition of the suitability function is shown in Table 2.

Defining the SSF began by identifying salinities that are known to limit oyster growth and survival. A number of studies have identified specific physiological processes that become limiting below 5 psu, such as sexual development, feeding and growth (Shumway 1996). Salinities have also been shown to become limiting when greater than 40 psu (Shumway 1996). These salinity ranges (<5 psu and >40 psu) receive a suitability value of 0.0. Mann and Evans (2004) reported that populations often survive large-scale epizootics in salinity ranges between 6–12 psu, whereas Shumway (1996) reported an optimal salinity range of 10–20 psu. Dermo and MSX epizootics are generally confined to areas that have salinity values greater than 12 psu (Ford and Tripp 1996) and predators generally become increasingly common above 25 psu (White and Wilson 1996). Dermo and MSX disease, caused by the parasites *Perkinsus marinus* and *Haplosporidium nelsonii*, respectively, has been shown to control populations of oysters in many estuaries along the Atlantic (Ford and Chintala 2006, Ford and Smolowitz 2007). A number of studies have identified a positive correlation of salinity and temperature to the proliferation and virulence of the parasites causing Dermo and MSX (Ford and Tripp 1996, Lenihan et al. 1999). Confirmed presence of both Dermo and MSX within the Hudson (Medley 2010, Starke et al. unpublished) increases our concern over the placement of restoration activities to minimize the occurrence of epizootics. Accounting for these various influences a salinity of 12 psu was chosen as the optimal salinity, with slightly decreasing suitability with increasing salinity to 20 psu. Above 20 psu the suitability becomes increasingly limited by disease and predation and ultimately reaches a value of 0.0 at 40 psu. Salinities above 5 psu are increasingly suitable as low salinity stresses are alleviated. These limiting and optimal salinities form the baselines for the definition of the salinity suitability function.

The SSF is modeled after Van der Lee et. al.'s (2006) broken linear function method in which breakpoints are defined at critical salinity values as discussed above. The continuous SSF is defined through individual linear functions defined between each breakpoint (Fig. 3d) and forms the continuous definition of the salinity suitability that is used to reclassify the salinity data into salinity suitability.

Uncertainty and Error

Defining the SSF is open to subjective bias, particularly in defining the shape of the suitability function. A Monte Carlo routine was developed to better understand the influence that subjective bias may have in the process of reclassifying the suitability of salinity and thus the outputted value of the final RSI. The routine works by assigning a randomly drawn suitability value at each breakpoint (10, 12, 20 psu). Individual linear functions are then defined between each breakpoint to generate a continuous salinity suitability function (SSF_i) defining the suitability of the salinities found in the study area. The random values are drawn from a beta distribution (eq. 2) with, $\alpha = \beta = 1.5$, rescaled around the proposed mean suitability value and with a range proportional to the suspected level of uncertainty at that breakpoint. This newly created random function is then used to reclassify the suitability of the salinity within the study site. Multiple iterations ($n = 451$) of this routine, each generating a unique salinity suitability function, allowed for the calculation

TABLE 2.

Salinity impacts on oyster health and survival.

Salinity (psu)	Relevant Response	Reference
<2	Killing floods when greater than 2 wk duration	Soniat & Brody (1988)
<5	Gametogenesis, feeding and pumping impaired	Shumway (1996)
	Increased mortality in Hudson River study	J. Levinton (unpubl. data)
<9	Dermo intensity remains low	
10–28	Oysters optimum salinity range	Shumway (1996)
5–40	Tolerable salinity range of oysters	Shumway (1996)
6–12	Oysters found to survive epizootics	Mann & Evans (2004)
>12	Generally required for Dermo and MSX epizootics	Ford & Tripp (1996)
>15	Predators such as *Urosalpinx cinera,Eupleura caudate, Panopeus herbstiiCallinectes sapidus* become commonly found	White & Wilson (1996)
>25	High risk of epizootics from pathogens, including Dermo, MSX, juvenile oyster disease	Ford & Tripp (1996)

The threshold salinity values presented here were used in the creation of the salinity suitability function presented in Figure 2D.

TABLE 3.

Mean suitability and range of variation (uncertainty) of salinity reclassification function (Fig. 3 D).

Breakpoint Salinity Value (psu)	Mean Suitability Value	Range of Variation (min, max)
5	0.00	0
10	0.53	0.30, 0.74
12	0.89	0.60, 1.00
20	0.85	0.65, 1.00
40	0.00	0

of each cell's mean salinity suitability across the study region, as well the standard deviation. The standard deviation of a cells value across multiple model outputs provides a proxy for the relative amount of uncertainty associated with the model.

Table 3 outlines the breakpoints and associated beta distribution parameters used in generation of the random values around each breakpoint. Figure 3d shows the suitability function and the distribution of random values at each break point. The shape parameters for the beta distribution, $\alpha = \beta = 1.5$, provides a broad distribution around the mean suitability. Similar methods have been used in suitability models where subjective error may significantly influence model results (Van der Lee et al. 2006).

$$f(x;\alpha,\beta) = \frac{x^{\alpha-1}(1-x)^{\beta-1}}{\int_0^1 u^{\alpha-1}(1-u)^{\beta-1}du} \tag{2}$$

The calculation of the final RSI (Eq. 1) is also prone to subjective error in the weighting of the individual parameters, which can bias the output results of the model. To attempt to minimize this subjective uncertainty the analytic hierarchy process technique (AHP) (Saaty 1994) was used to optimize the appropriate weights for each parameter. This technique assists in decision making and has been adopted in other spatial multiple criteria decision analyses that require user input for weighting schemes (Banai 1993). The process begins with the construction of a preference or comparison matrix containing the parameters (PSS_i) within the analysis. A pair-wise ranking of the assumed importance that each parameter carries into the final suitability is then carried out between each combination of parameters. These ranked comparisons are then normalized and the weightings are calculated as the mean normalized Eigen value for each parameter. To gain an understanding of the sensitivity of the model's outputs to altered input weightings, two additional weighting scenarios were devised: One which gave equal weighting to all parameters ($w = 0.25$) and one in which salinity was the dominant parameter (salinity weight $= 0.85$, weight of other parameters, respectively $= 0.05$). Salinity was chosen as the dominant parameter due to the potentially high error inherent in the uncertainty of the original data and as well as error in the definition of the salinity suitability function. Each of the three weighting scenarios was run using the mean salinity suitability as well as the mean minus the standard deviation as the input $PSS_{salinity}$ for a total of six output scenarios. This provides an opportunity to evaluate the influences that uncertainty has in both the weighting process and the reclassification process of salinity in the final RSI output. Significant changes in the model's output with each weighting scenario would be a demonstration of model instability and would warrant an evaluation of the input parameters that are driving this variation of output values.

To analyze these changes in outputs with weighting scenarios, each RSI model output was standardized by dividing the RSI output by its respective maximum suitability value. This rescaling brought the range of each output between 1 and 0 and allowed for direct comparison of spatial changes between outputs (Legendre and Legendre 1998). The output of each scenario was separated into one of seven classes defined by break values at 25, 50, 75, 90, 95, 99 and 100% of the range of suitability values calculated. The total surface area (km^2) of each classification for each scenario was then calculated. This allowed for a comparison of the changes in area of suitability between output maps. The output of each weighting scenario is presented (Fig. 4) to allow for a visual comparison of spatial changes to areas selected as most suitable for restoration.

A final summary suitability map was constructed by overlaying the outputs of the weighting scenarios and calculating a mean and standard deviation from the mean at each cell, across the entire output range of RSI. This provides an assessment of the spatial suitability across the region, along with associated uncertainty of the model's output due to errors of uncertainty associated with the weighting process and defining the salinity suitability in this system. A low standard deviation will be found

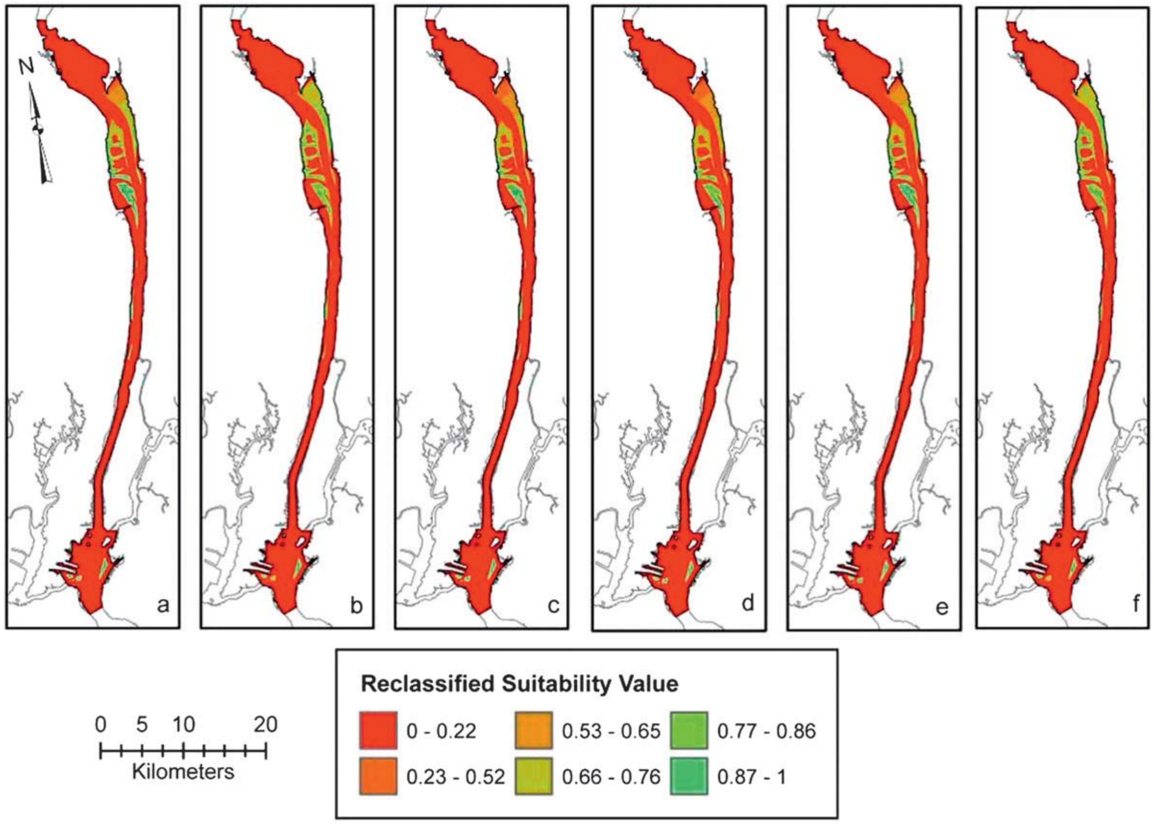

Figure 4. RSI weighting scenario outputs. a) Analytic hierarchy process (AHP) weighting scenario/mean salinity suitability. b) Even weighting scenario/mean salinity suitability. c) Salinity dominant/mean salinity suitability. d) AHP weighting scenario/mean minus uncertainty in salinity suitability. e) Even weighting scenario/mean minus uncertainty in salinity suitability. f) Salinity dominant/mean minus uncertainty in salinity suitability.

in areas that have results that are stable, regardless of the parameter weightings. Conversely, a high standard deviation will be found in areas that have a range of suitability values dependent on the weighting scenario used. Although simplistic, this technique provides insight into the appropriate selection of areas not only found suitable under a predetermined weighting scenario, but found to be preferentially suitable under a variety of weighting scenarios.

RESULTS

Calculation of parameter-specific suitability maps (Fig. 5) showed a number of limiting environmental conditions throughout the river system. Salinity suitability diminished in the northern section of the wide, shallow Tappan Zee–Haverstraw Bay (TZ-HB) region of the river, with a peak in suitability just to the south of the Piermont Pier (location in Figure 1). The south end of the (TZ-HB) area has high variance in the suitability of the salinity (Fig. 5e) as this correlates with the zone near an important salinity threshold for oysters (10–12 psu). Depth suitability is predominately high in the Tappan Zee–Haverstraw section and portions of the New York Harbor area. The depth suitability is reduced to near zero for much of the narrow, midsection of the river. The sediment type and sedimentary environment data have a similar spatial pattern, as the two data are physically associated to one another; though the suitability values are not strongly correlated between parameters (Table 4). Furthermore, parametric and nonparametric (Pearson product-moment correlation coefficient and Spearman's rank correlation coefficient) correlation analyses between the PSS parameters show no strong dependence between parameters (Table 4; $|r| \leq 0.37$; $|\rho| \leq 0.36$, $P < 0.0001$).

Figure 4 presents the output RSI for each weighting scenario using both mean salinity suitability and mean suitability minus the uncertainty, to provide a conservative measure. The spatial distribution of areas selected as potential restoration sites remains unchanged between weighting scenarios. Though this is largely driven by the distribution of parameters found to be unsuitable, bringing the RSI to zero independent of the weightings used, the output remains valid in identifying areas that are have no local environmental characteristics that will be limiting to reef restoration. The areas that have been excluded by a limiting environmental characteristic are shown in black in Figure 6a. The comparison between the outputs of the weighting scenarios show that the salinity-dominated weighting scenario provides the most conservative result. The uncertainty associated with the salinity suitability has little influence in the final output.

The weighting scenarios and surface area comparisons are presented in Table 5. Much of the region is identified as unsuitable for oyster reef restoration. Less than 25 km^2 was classified in the top 5% (>95% suitability class) in overall suitability from a total area of 1830.6 km^2. Such numbers are useful but require a specific geographic context, especially for areas with maximum suitability. These areas are predominately found in

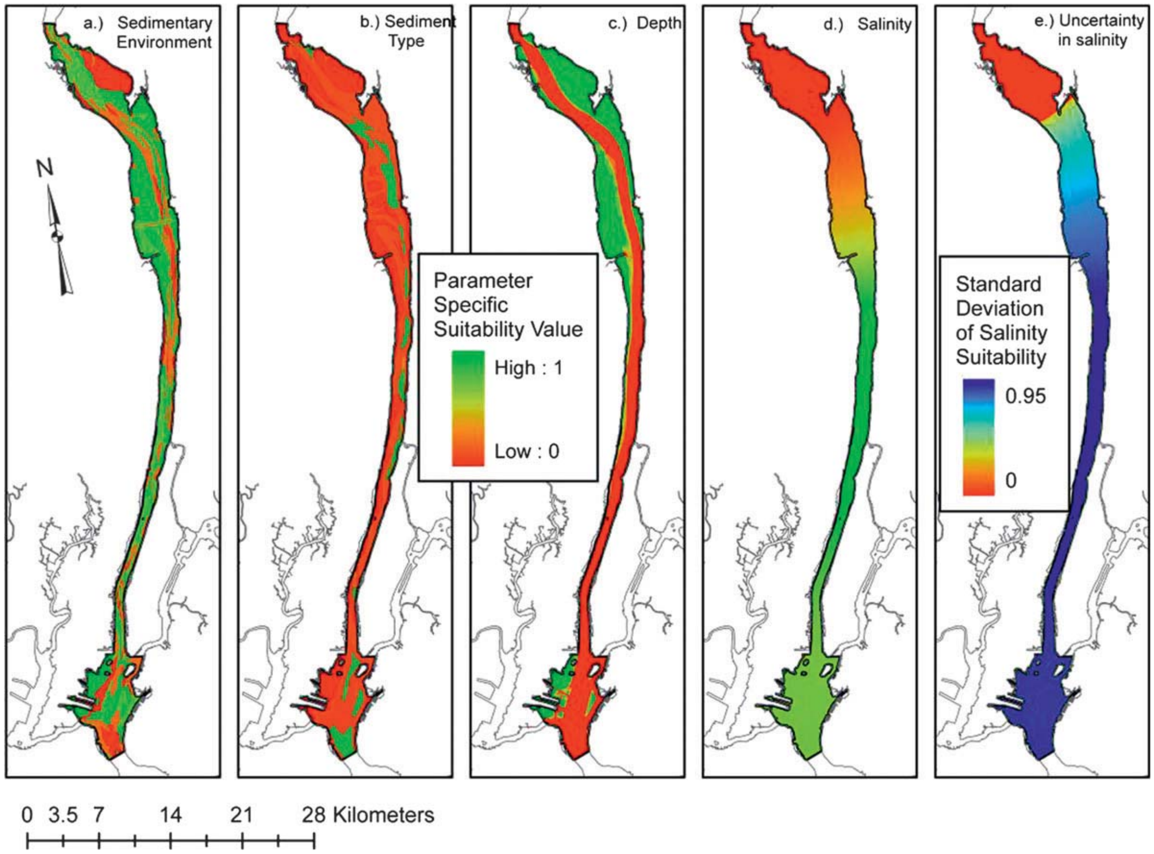

Figure 5. Reclassified parameter specific suitability maps. a-d) Maps show the spatial distribution of suitability for each environmental characteristic of interest. Areas of red are considered unsuitable; areas of green are suitable. d) The salinity suitability map is calculated from the mean of a set of randomly generated suitability maps to provide an estimate of the overall suitability despite the uncertainty in the salinity data and the reclassification process. e) Map of salinity suitability uncertainty, by way of a calculated standard deviation. Areas of red are prone to increased error in suitability reclassification; a more conservative approach should be taken when calculating RSI in these areas.

the harbor area, south of the ''Battery'', and along the edges of the main river channel through the narrow section of river to the north of Manhattan Island. Within the (TZ-HB) area, 35.7% (13.45 km^2) of the total area is ranked in the upper 10% of overall suitability value. This area however is very significant as it has at present little danger of oyster disease, as evidenced by

TABLE 4.

Parametric and nonparametric correlation matrix among PSS parameters.

r / ρ	Depth	Salinity	Sedimentary Environment	Sediment Type
Depth	1	–0.3746	0.2345	–0.3024
		–0.3646	0.2826	–0.3187
Salinity	–0.3746	1	0.0330	0.0424
	–0.3646		0.0447	0.0245
Sedimentary environment	0.2345	0.0330	1	–0.1769
	0.2826	0.0447		–0.0282
Sediment Type	–0.3024	0.0424	–0.1769	1
	–0.3187	0.0245	–0.0182	

n = 10,000 spatially random sample points; all relationships highly significant ($P < 0.0001$).

recent analyses (Levinton, unpublished data). The remaining suitable areas are found along the edges of the main channel through the narrow portion of the river between the Tappan Zee–Haverstraw Bay region and the NY/NJ Harbor area.

Figure 6 presents an overall summary of the suitability across the region. The mean of the various RSI output identifies a range of suitability values across the study area, from 0–0.98 (Fig. 6a) and a level of confidence in the models output (Fig. 6b). Areas that consistently rank highest in suitability, possessing a high mean and a low standard deviation, should be identified as target restoration locations.

DISCUSSION

This assessment provides a simple but telling picture of the Hudson River's potential to accommodate reef restoration activities. The model results indicate that a majority (75.9%) of the suitable restoration areas (those found in the >75% suitability class) are found in the wide, shallow areas of the TZ-HB region of the river. Though the ''most'' suitable area (upper 5% overall suitability) is found in the Harbor area, south of Manhattan Island because of higher salinities, the extensive areas in the TZ-HB region of the river have additional potentially important habitat characteristics related to substratum and depth.

TABLE 5.

Weighting scenarios and spatial coverage of suitability classes.

Weighting Scenario		Weights				Area (km^2) by Suitability Class						
		Salinity	Sediment Type	Sedimentary Environment	Depth	<25%	26–50%	50–75%	76–90%	90–95%	95–99%	>99%
Mean salinity suitability	AHP	0.6676	0.725	0.725	0.1874	1533.7	13.2	100.1	136.9	30.9	15.5	0.3
	Even weighting	0.25	0.25	0.25	0.25	1533.5	0.2	86.3	199.5	0.9	8.2	1.9
	Salinity dominant	0.85	0.05	0.05	0.05	1534.8	29.8	116.1	103.7	25.3	18.5	2.4
Mean salinity suitability less uncertainty in salinity suitability	AHP	0.6676	0.725	0.725	0.1874	1533.8	14.7	107.1	137.4	21.5	15.8	0.3
	Even weighting	0.25	0.25	0.25	0.25	1533.5	0.2	90.8	195.0	0.9	8.2	1.9
	Salinity dominant	0.85	0.05	0.05	0.05	1534.9	32.5	122.0	99.4	16.9	22.5	2.4

AHP, Analytic Hierarchy Process, a decision making method used in generating weighting of each parameter.

The TZ-HB area's oligohaline salinity regime can provide refuge from disease and predation reducing mortality rates and increasing the potential persistence of populations (Levinton et al. 2011). The circulation within the bay may also distribute larvae in a manner that would benefit regional metapopulation development, an important component to overall population health. We have observed spat recruitment in all but the northernmost part of TZ-HB (Starke et al. unpublished data). The large areas of existing suitable substrate (shell hash from relict reefs and gravel) in relatively shallow water may also allow for natural expansion of reef communities post restoration. As source-sink dynamics are important to the survival of a reef community it would be preferable to focus attention to the question of how and where larvae would be transported prior to finalizing the location of restoration sites. Such considerations have been incorporated in recent models of oyster and other invertebrate metapopulations (Epifanio and Garvine 2001, North et al. 2008, Lipcius et al. 2008).

An important potential limitation to restoration in the (TZ-HB) area may be the dynamic salinity regime present there. Drastic seasonal, monthly and even daily salinity fluctuations are common through this region, and have been shown to influence oyster survival (Levinton et al. 2011). Though this model attempts to capture the overall influence of the average spring and summer salinity on the region's suitability for restoration it fails to address the potential limitations presented by the rate and magnitude of salinity changes (i.e., variance and range of salinity observed at a location), especially in years of extreme precipitation and discharge in spring and summer. Data of this type are limited as is the influences of these changes on oyster physiology and biology in the field, but an extreme event was described by Levinton et al. (2011) during a high discharge season in 2009. There also is potential that geographical patterns in the river's salinity structure could be changing, especially with further human impacts such as dredging and regional climate shifts on decadal and larger time scales (Najjar et al. 2010, Levinton et al. 2011). Even in past decades, hindcast models (Ralston et al. 2008, Levinton et al. 2011) suggest that all of the TZ-HB region for years at a time may have been unsuitable for oysters because of low salinity. Levinton et al. (2011) point out that incorporation of climate change models may eliminate TZ-HB as a likely place for restoration, which would eliminate an important refuge area from disease if precipitation and discharge were to increase in spring and summer.

The depth of much of the Lower Hudson south of Tappan Zee limits habitat suitability and it is likely that river and tidal currents would further reduce the restoration suitability there. New York Harbor is among the busiest ports in the world, heavy boat traffic and near continuous maintenance dredging will challenge any work in this area. Dredging through the harbor area may impact sediment dynamics and thus the potential suitability for restoration. The salinity regime in this region leaves oysters more vulnerable to potential disease epizootics, which may be further enhanced by the water quality associated with the heavy urban influence of the Harbor. Further investigation of these chosen areas is needed to ultimately decide the feasibility of working there.

Validation of this Restoration Suitability Index model will be difficult until restoration reefs have been installed and monitored. Regardless, there are encouraging indicators that this index provides accurate site selection criteria for oyster restoration. The large area to the west of the river channel in the (TZ-HB) area coincides with vast expanses of relict oyster reefs, indicating that this area has, at least historically, provided the needed hydrodynamics (Carbotte et al. 2004), and substrate for reef development. In addition, these areas were also more recently selected as "grow-out" areas by a large oyster aquaculture company based in New York (Bromely 1954). Surveys of these grow-out beds outline large areas to the east of the channel, as well, along the shoreline extending through the same areas found suitable by this RSI. Bromely (1954) reported that these areas were selected by the experienced oyster growers due to a number of suitable habitat characteristics present at these locations. The large area to the south of Manhattan Island and west of Brooklyn was recently selected for a small scale oyster reef "demonstration" project. Preliminary results indicate that oysters have survived, although intermittently, in this area (B. Chezar, personal communication).

Although this index assesses a large portion of the Hudson River, there remains a relatively large area within the lower river and Harbor that was not scored for suitability. Limited habitat quality data availability along the shoreline prevented a full assessment of these regions. Much of these areas may likely be limited in suitability due to the potential of ice scour during

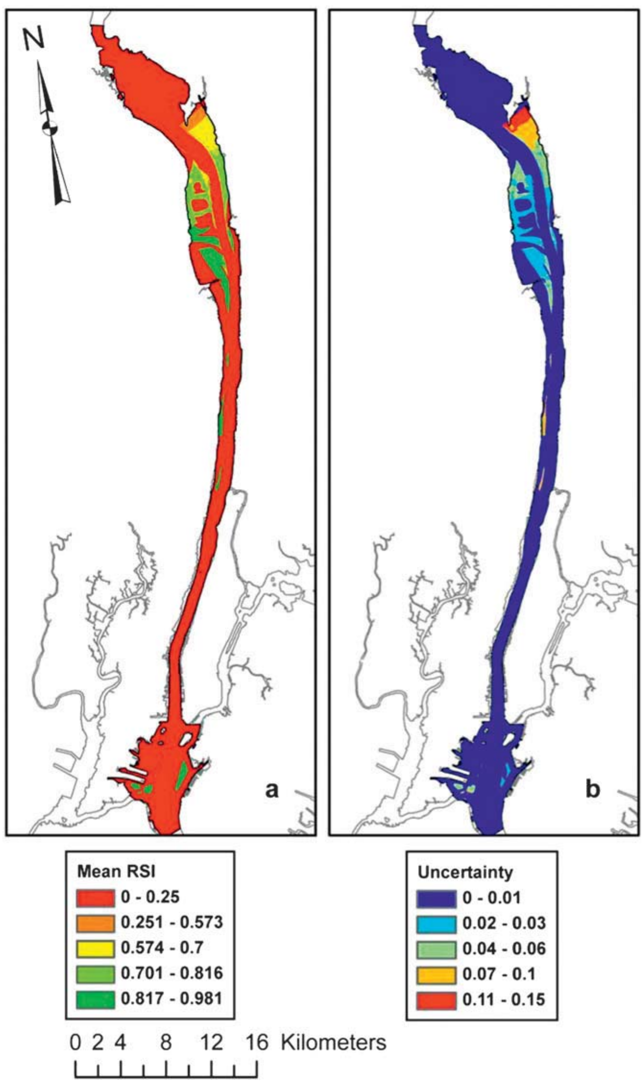

Figure 6. Summary RSI output; a) Mean RSI output of all weighting scenarios. b) Uncertainty in final RSI output. Areas of low uncertainty and high RSI are preferential for focused restoration activities.

winter months or issues with shoreline usage. Regardless, these areas may still provide a substantial areal coverage, potentially as much as 23 km^2, and should not be excluded from consideration for restoration efforts.

This simplistic model provides an estimation of restoration suitability across the Hudson River area. The output of this index is best used as a basemap of restoration planning of the Eastern oyster in the Hudson River. The locations defined here can begin as sites for initial research of oyster restoration such as oyster settlement surveys useful in identify genetic diversity, recruitment patterns, and growth studies of potentially adapted natural populations to be used as founder brood stocks. Understanding these types of population parameters at these locations can provide powerful insight to the restoration potential of the Hudson River, and begin moving from a qualitative assessment to a quantitative measure of restoration success. The model can also provide a means to forecast the restoration and habitat suitability of the river under altered salinity distributions due to regional climate changes and/or human-altered hydrology regimes. Using this tool, restoration practioners may best their chances of restoration success by selecting locations that provide stable salinities under altered scenarios. Regardless, restoration work should continue to take a careful approach whereas working towards restoration of oyster communities.

This spatial assessment of the restoration potential of the Eastern oyster to the Hudson River reveals the difficulties of restoring a species to an area long devoid of populations. It also highlights the many considerations that need to go into restoration planning and why the science of restoration ecology encompasses a broad set of disciplines. Restoration practitioners will need to be mindful of population genetics and demography, community and functional ecologies, as well as the physical and geological environments when pursuing restoration in the Hudson River region.

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