Restoration of the Hudson River Oyster: A physiological and spatial assessment of *Crassostrea virginica's* restoration potential in the Hudson River, NY

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Abstract of the Thesis

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The Hudson River was once home to abundant eastern oyster (*Crassostrea virginica*, (Gremlin 1791) populations which catered to an enormous fishery and supplied a number of vital ecological services to the estuary. Since this time, oysters have become depleted and the estuary's vitality has been compromised. Recognizing the current state of the Hudson, a comprehensive restoration plan has been implemented and targets the recovery of oysters and oyster reefs. To begin moving forward with these plans, a two year study investigating the physiological responses of the oyster to New York's Hudson River was made. The results have provided useful insights to the rivers potential for proposed large-scale restoration efforts. Results showed poor growth but potentially high survival of mature hatchery-reared oysters through the growing season. Observed recruitment of oysters is encouraging, signifying the system can still support the early stages of life. Still, there remains a number of potentially limiting conditions that will ultimately dictate the recovery efforts.

To best the chances of restoration of these reefs, a focus is needed in areas that provide conditions congenial to reef development. To begin identifying these areas, a spatial assessment of some basic environmental conditions across the lower Hudson was made. The result of this restoration suitability index show that much of the river is unsuitable for reef construction, though there remains a number of potentially ideal regions to focus on. Future work in this region should focus attention to these areas with the goal of elucidating the long term potential for restoring populations of oysters to this system.

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INTRODUCTION

The eastern oyster, *Crassostrea virginica* (Gremlin 1791), ranges from the Gulf of St. Lawrence to the Gulf of Mexico (Carriker and Gaffney, 1996). This species was historically abundant in mid-Atlantic estuaries such as the Hudson, Delaware and Chesapeake River basins, and played an important role in the natural and cultural histories of these regions. The Hudson River and surrounding bays have had an especially rich history tied to the oyster. Extensive populations were spread throughout the estuary contributing to an enormous fishery and an iconic culture of early New York City (Kurlansky, 2006, Kirby, 2004).

The coevolution of oysters and estuaries have led to the development of some impressive oyster adaptations (Shumway, 1996), but like many species, the oyster has not adapted well to the number of anthropogenic impacts that have become common to these Atlantic coastal estuaries. Its ability to survive harsh and inhospitable natural conditions within tidal estuaries has been hindered by overharvesting, pollution, habitat degradation and disease, which has driven the oyster to critically low population levels in many areas (Kirby, 2004, Rothschild et al., 1994, Kirby and Miller, 2005). This depletion has raised the awareness of their importance to the ecosystem and has made oysters a common restoration research target.

Aggregations of eastern oysters, in the form of reefs, provide structural habitat (Peterson et al., 2003), process nutrients (Dame and Libes, 1993), alter hydrodynamics, and supply a number of other ecosystem services to estuarine systems. These services are why oysters are considered to be a foundation species within these estuaries (Coen et al., 2007, Dame and Libes, 1993). The widespread reduction of oysters from the Hudson has removed much of this key habitat and has left oyster reef dependant species in jeopardy. Returning the oysters and oyster reefs to this system may encourage the recovery of a vast number of additional species promoting a healthier ecosystem.

The numerous benefits of a healthy oyster population have been recognized and oysters have been set as a restoration priority by an advisory committee responsible for the development of an ecological restoration plan in the Hudson River area (Bain, 2007). The creation of this restoration plan was initiated by the development of the Hudson-Raritan Estuary (HRE) Restoration Plan by the U.S. Congress and seeks to stimulate both the economic and ecological aspects of the region. Ecologically, the area is in dire straits. Returning this region to its former pristine state is simply unfeasible. A more achievable goal would be repairing crucial components of the system which may stimulate the recovery of a broad number of species of concern (Atlantic sturgeon, menhaden, American eel, etc.), along with their associated ecological benefits. This guiding principle was maintained during the planning process in developing several "Target Ecosystem Characteristics". These characteristics were chosen for their fulfillment of a specific niche within the ecosystem. Though the goal of the Hudson-Raritan Estuary Restoration Plan is system wide encompassing all resident species, this paper focuses on the eastern oyster, in terms of regional habitat suitability within the Hudson River.

This two-year study provides an initial assessment of the eastern oyster's physiological response to the system. The aim of the study is to identify the plausibility of large scale oyster restoration work within the Hudson River. By increasing our understanding of the physiological performance of oysters, we will have a better sense of current limitations within the system and can begin to gauge the future of oyster restoration within this system. Concurrently this study will validate the use of hatchery-sourced oysters in this region, which are often times used in restoration projects.

METHODS

Study Area

The Hudson River Estuary (HRE) system is a complex and heavily impacted urban estuary in southeastern New York. The system encompasses New York City, one of the largest metropolitan regions in the world, and is found in the middle of the vast coastal megalopolis that stretches from Boston to Washington D.C. (fig. 1). The HRE is a unique system in that it is made up by a number of river and bay systems that coalesce in a partly enclosed basin known as the Lower Bay. The Hudson River dominates the estuaries freshwater input as it flows in from the north, draining much of northern New York.

Our investigation focused on the lower Hudson River through a tidally-dominated region known locally as the Tappan Zee-Haverstraw Bay Region. The salinity regime in this lower portion of the Hudson is congenial for oyster restoration due to its potential to provide refuge from disease and predators as well as extend across the salinity range where oysters commonly thrive. These refuges occur in many estuaries and are thought to help sustain oyster populations through demanding epizootic events in systems of high disease pressure (Burreson and Calvo, 1996, Ford and Tripp, 1996). This section of river has historically supported oysters, both pre-colonial (Carbotte et al., 2004) and more recently, serving as a juvenile grow-out area for a local aquaculture company in the 1950's (Bromely, 1954).

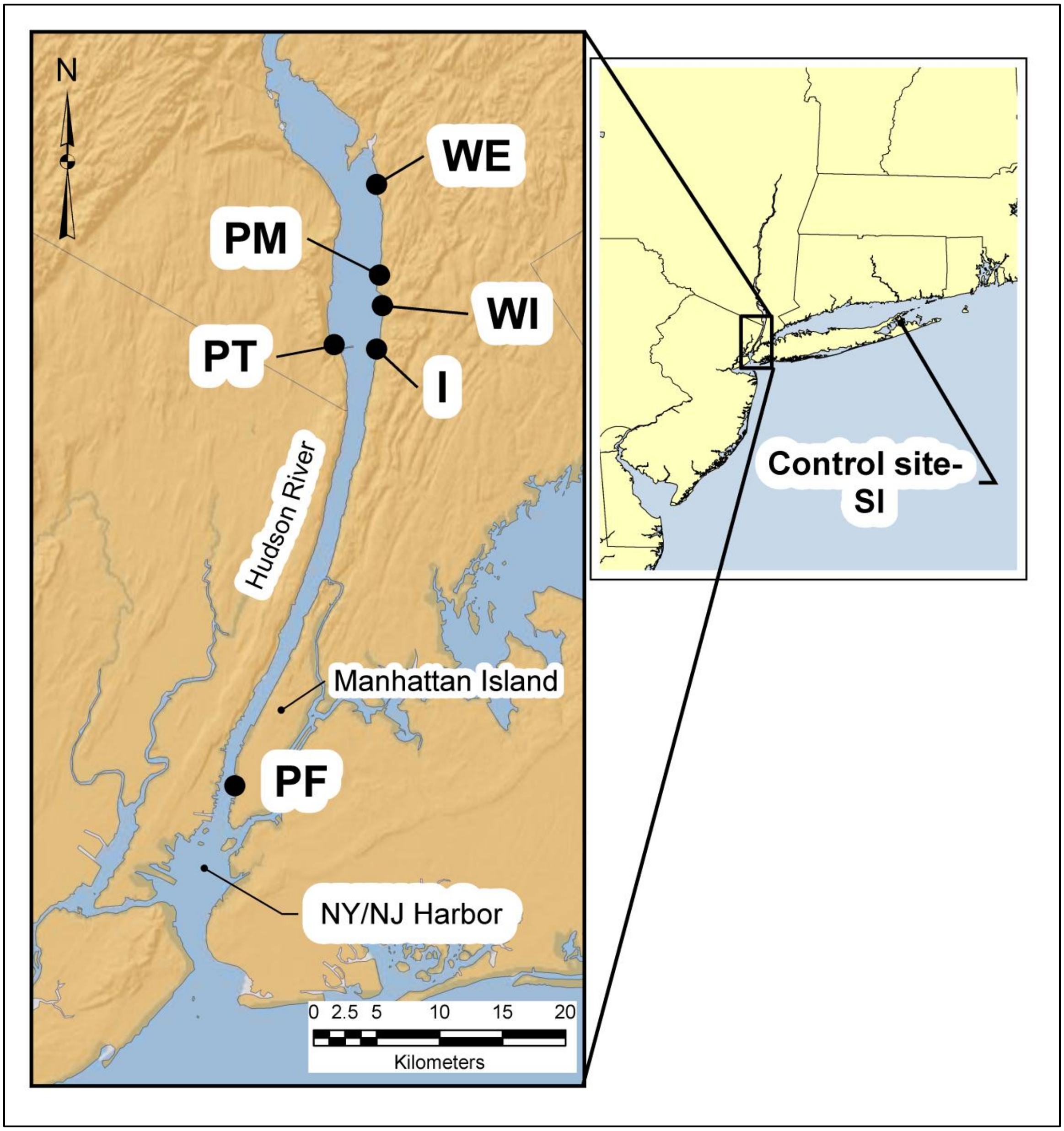

Figure 1- Hudson River Estuary study area, located in southeastern New York State; Study site locations within the river and SI- control site in an eastern Long Island coastal salt pond.

Site selection

During the first year of the study, six sites within the Hudson River were established in a longitudinal transect: five along the eastern shore of the river (fig.1, table 1), and one on the western shore in Piermont, NY. The localities ran from the north, in a salinity range that was suspected to be at the lower limits of oyster tolerance (WE), to the southern site in lower Manhattan Island (PF), which has more oceanic influence and salinities near the reported optima of oyster habitat. In the second year of the study the number of study sites was reduced to four river sites (PF, WE, WI, and I). A portion of the river south of the Tappan Zee region was omitted from our assessment due to logistics in field visits and issues of access. Control oysters were placed at a site in a relatively pristine area of eastern Long Island in a small tidally-flushed coastal salt-pond at the Mashomack Preserve on Shelter Island (SI). This area is known to support both natural and hatchery-reared oysters.

Table 1- Study site names, ID, and locations.

Site Name	Site ID	Latitude	Longitude
Westerly	WE	N 41° 09.521'	W 073° 52.321'
Philipse Manor	PM	N 41° 05.648'	W 073° 52.240'
Washington Irving	WI	N 41° 04.320'	W 073° 52.077'
Piermont	PT	N 41° 02.708'	W 073° 54.884'
Irvington	I	N 41° 02.463'	W 073° 52.450'
Pier 40	PF	N 40° 43.835'	W 074° 00.776
Shelter Island	SI	N 41° 02.832'	W 072° 18.020'

The study focused on three distinct groups of oysters within two age classes. During both years of the study (2008 and 2009), we used oysters that had been spawned in the previous summer, overwintered at the hatchery, and placed at the study sites in late spring. These oysters were sexually mature, and our inspection of a gonadal tissue smear, confirmed that nearly all individuals carried gametes at time of transplant. The second year (2009) of the study included an additional group of juvenile oysters (young of year, spawned that hatchery season) at each of the 3 remaining upriver study sites and at the control site. Oysters will be referred to by the year and age at which they entered the study, e.g. overwintered oysters placed in the field during 2008 will be referred to as 2008 mature. Mature oysters were kept in 6 mm mesh aquaculture bags which were enclosed in a 2-tiered wire cage and kept below mean low water level. Each study site included 2 cages for a total of 4 bags each containing 300 individuals. Juveniles were placed in 2 mm plastic mesh bags, at 500 per bag, 1 bag per site. All oysters were obtained from the Fishers Island Oyster Farm, Fishers Island, New York.

To collect both environmental and growth data during the season of highest growth, study sites were visited bi-weekly from initial deployment through early December. Visits were made to all sites within a one week period to minimize temporal variation in comparisons between sites. Water quality, mortality and shell growth were recorded during each site visit while condition index and tissue analysis was sampled monthly to avoid depletion of experimental oysters during the course of the study.

Water Quality

Basic water quality monitoring is important for identifying any limiting environmental conditions that may occur at our study sites as well as any correlates to oyster health. Water temperature was recorded at 15 minute intervals for all localities using TidBit® HOBO® temperature data loggers attached directly to the cage tops. Salinity, Dissolved oxygen concentration and saturation, were monitored biweekly using a handheld YSI model 85, during each site visit. Measurements were taken at surface, cage (1m) and bottom depth (10 cm from sediment).

Oysters feed on locally available suspended particles (Newell and Langdon, 1996). Chlorophyll *a* analysis was performed on water samples taken at the time of the site visit and used as a proxy for available food. Size fractionations were made at whole sea water (WSW), 2, 5, and 20 µm, allowing for an analysis of the abundances within each range of particle size. The extraction technique used was modified from Strickland and Parsons (1972).

Physiological Performance

Shell growth

Growth is a common indicator of physiological health. Valve size is an easy and effective way of measuring growth in oysters and is commonly used as a measure of biomass. Valve size was measured biweekly from a haphazard sampling of animals (n=20) from each aquaculture bag. Measurements were made on shell height (lip to hinge), shell length (lateral-dorsal measure), and shell width (left to right hinge) using digital calipers (accuracy 0.01mm). Change in the sample mean shell size was used as a surrogate to growth rate of the sampled population.

Condition Index/Tissue growth

Condition index is a relative measure of soft tissue mass to internal shell capacity. This ratio is useful as a proxy to track relative changes in tissue mass, which can be related to overall health and sexual development of an oyster (Lawrence and Scott, 1982, Crosby and Gale, 1990). Oysters exposed to unfavorable environmental conditions expend a higher proportion of their total energy in processes such as osmotic regulation or valve closure, and will subsequently have less invested towards tissue growth and reproduction relative to shell volume (Thompson et al., 1996).

Condition index (CI) was calculated as outlined by Lawrence and Scott (1982) and followed the equation:

$$\text{CI} = 100 \times \text{dry tissue mass (g)} / \text{internal shell capacity (mm}^3\text{)}$$

Dry tissue mass was determined by removing the soft tissue from the valves and drying at 70°C for seven days at which time it was weighed on an electronic balance with 0.001g accuracy. Whole live clean oysters were weighed prior to extraction of tissue to obtain a measure of internal shell capacity which was calculated gravimetrically under the assumption that the density of soft tissue is equal to that of the fluid enclosed within the valves (Crosby and Gale, 1990).

A haphazard sample (n=10) of oysters were drawn from each bag for measurement of dry tissue weight, shell size and volume and the calculation of condition index. Samples were collected on a monthly interval during the active growing season, between the months of April and December, and on a bimonthly interval during the dormant period, assumed to be while water temperatures are ≤5°C (Shumway, 1996). Samples were processed in the laboratory of Jeffrey Levinton in the Department of Ecology and Evolution, Stony Brook University.

Mortality

Survival was followed by making counts of oysters during each biweekly site visit. Overtly gaped or empty shells were counted as dead; fully closed solid-feeling oysters were classified as live. Mortality rates were calculated for each sampling interval for all oysters present during each site visit. From this a cumulative mortality rate was calculated. This assumes that live oysters removed for destructive sampling (disease and condition index) would have the same probability of survival as those oysters remaining. There was no evidence of mortality caused by predation and it is assumed to be insignificant in the survival assessment.

Disease

Diseases are an increasingly common problem facing oyster populations in many estuaries (Burreson and Calvo, 1996, Ford, 1996, Ford and Haskin, 1982, Ford and Tripp, 1996). An assessment of disease occurrence in this system would verify any potential challenges restored populations may face and help guide restoration strategies. Tests for the presence of two commonly occurring oyster parasites, *Perkinsus marinus*, the cause of Dermo disease, and *Haplosporidium nelsoni*, the cause of MSX, were performed in late summer when disease prevalence is generally at peak levels. Rectal and mantle tissue were assayed for presence of *Perkinsus marinus* using Ray’s standard fluid thioglycollate (RFTM) culture technique (Ray, 1952). Infection intensities were ranked according to the Mackin scale (Mackin, 1962) and a weighted prevalence was calculated by summing the intensity rankings and dividing by the total sample size. Soft tissue was sampled for infection by MSX using standard histopathology techniques and ranked following the procedures outlined by (Ford and Figueras, 1988). Assessments were made in the Marine Animal Disease Laboratory of Dr. Bassem Allam at the School of Marine and Atmospheric Sciences at Stony Brook University.

Recruitment

A basic survey of juvenile recruitment was performed in 2008 at the upriver sites and in 2009 at all sites. The aim of this survey was strictly to determine if there was an active larval pool in the system capable of recruiting to a natural substrate, not to quantify the recruitment potential. To do so, ¼ m^2 mesh (6mm mesh size) bags were filled with 1.0 L of loosely packed oyster shell and placed at each study site. These recruitment collectors were placed in the water in late July and retrieved in late October. Recruits were counted for each site and an estimated growth rate was calculated using the equation:

$$\text{Growth rate (mm/day)} = \text{Final shell height (mm)} / T_{\text{final}} - T_0$$

where T_0 is equal to the day the collectors were placed at each site and T_{final} the day they were removed. This yields a conservative estimate of growth rate by assuming recruited oysters settled on the collectors immediately after deployment. A mean growth rate was calculated for each site.

Analysis of data

Of primary interest in this study is the overall physiological performance differences between sites, including the changes through time at each locality within each year (i.e., comparative versus qualitative responses) and in order to form a general assessment of this region's potential for oyster restoration. To do so a 2-factor ANOVA was performed with the effects being locality and time (the start of the study and end of the growing season, at or around December 1st) for shell size and tissue weight. A Tukey test for means was used to identify significantly different ($p < 0.05$) means between sites and within sites through time (start and end of study period). Non-parametric analyses were performed on data with heterogeneous variance. Condition index was analyzed using a one-way ANOVA within each site to determine if there was a measurable change, increase or decrease, through time which could indicate spawning events or fluctuations of health associated with other environmental conditions. All analyses were preformed in JMP® 8.0.2 (SAS Institute, Cary, NC, USA 27513).

RESULTS

Environmental characteristics of study sites

Temperature

The temperatures observed through the course of the study were within the typical tolerances of oysters (Shumway, 1996). All sites reached temperatures of 25C^{o}, thought to be an important threshold for intense Dermo and MSX epizootics. Maximum temperatures occurred from late July to mid August and were the lowest in mid January (Fig. 2). Pier 40 (PF) in lower Manhattan, had lower summer maximum temperatures and higher minimum winter temperature compared to further up river, likely caused by the proximity to the open ocean. Overall temperature at all localities followed similar seasonal, daily and monthly trends between years.

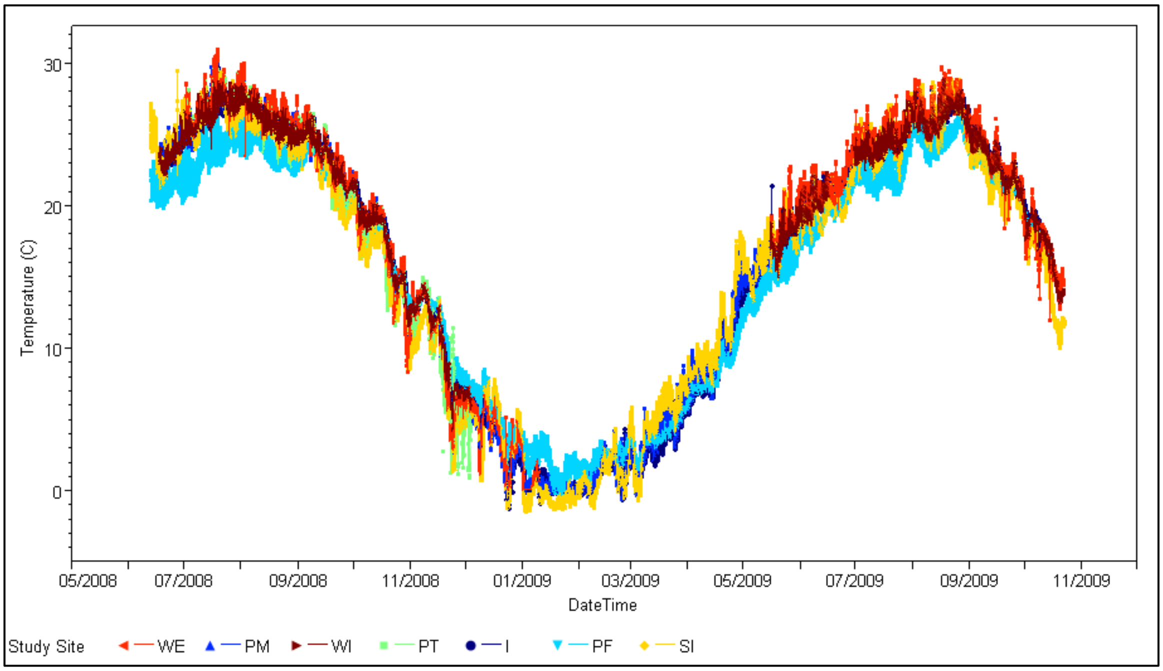

Figure 2- Mean daily temperature through study period at each study site.

The progression of seasonal temperature change did differ between field seasons. Maximum temperatures were higher (0.5 C^{o} mean increase across sites), occurred earlier (calendar day of maximum temperature ~20 days) and were present longer in 2008 than in 2009. Daily mean temperatures were above 25C^{o} for 70 days in 2008 and 47 days in 2009. This trend was observed at all sites within the study region.

Salinity

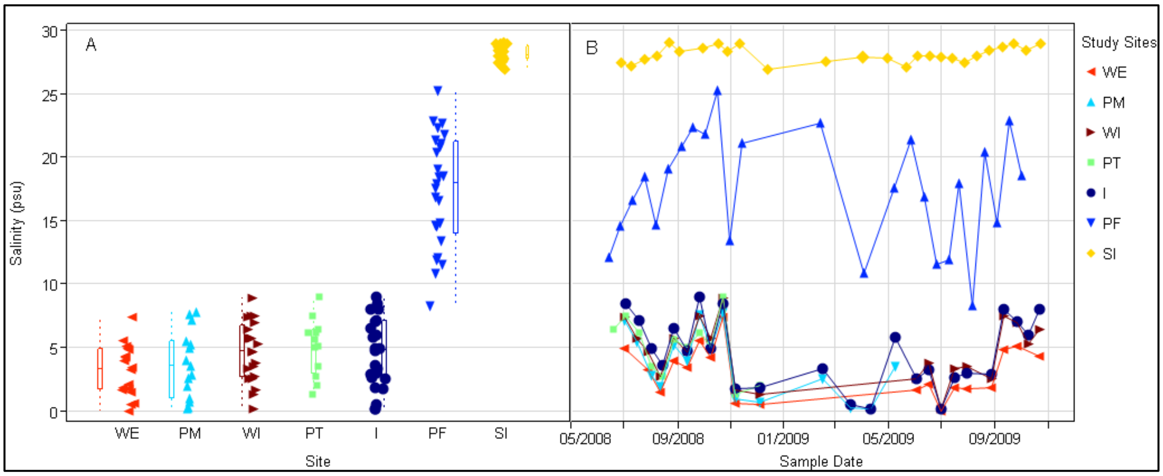

Figure 3- Observed salinity at cage depth (1m). A) Salinity distribution by site. Boxplots show mean, upper and lower quartiles; B) Salinity trends through time of study. 5 psu - Commonly regarded as lower threshold of oyster tolerances (Shumway, 1996).

A broad range of salinities were observed during the study and extended across the typical habitat range of the oyster (Shumway, 1996). Figure 3 shows the variation in the observed salinity between sites (fig. 3A) and between years for each site (fig. 3B). PF had the greatest variation in salinity, with heavy influence from both tides and river flow. SI experienced minimal salinity variation and was typically above 25 psu for the duration of the study. This site is dominated by oceanic tidal exchange, with relatively low and stable freshwater input. The upriver sites (WE, WI, PT, I, PM) had moderate variability, but ranged across the lower salinity tolerance of oysters (5 ppt) (Shumway, 1996). Upriver sites likely had a greater daily variance than PF and SI due to increased river influence during ebbing tides. It is unknown what effect this may have had on experimental oysters.

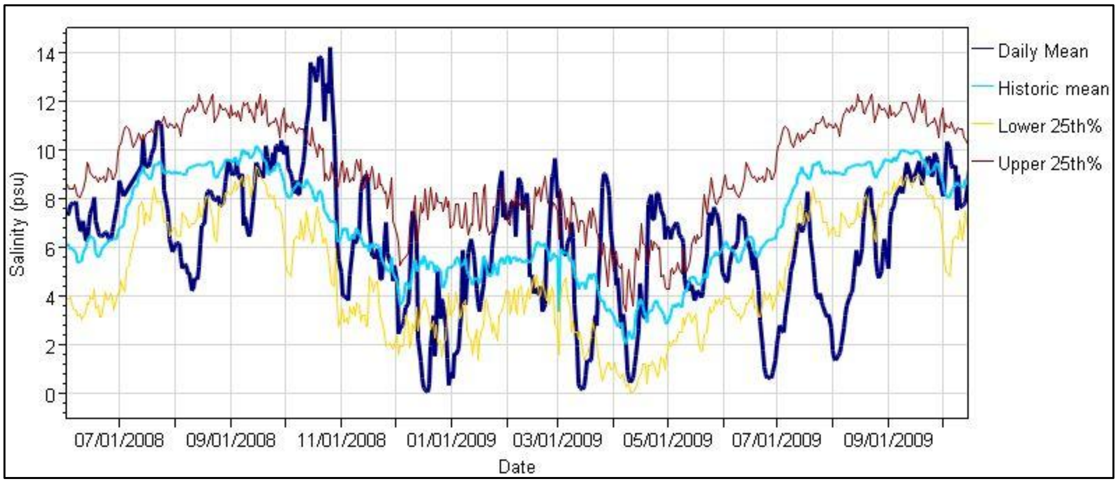

Figure 4- Hasting-on-Hudson USGS river gage data; Observed daily mean compared to historic mean. Upper and lower 25th% of historic salinity showing variability of the salinity of the river and the uncommonly low level of salinities observed during the 2008 and 2009 summers.

Salinity during the 2009 season was on average considerably lower for much of the study period in comparison to 2008. Salinities were consistently below the 5ppt threshold commonly thought to be a lower tolerance for oyster survival. Long term Hudson River gage data at Hastings-on-Hudson (USGS River gage station # 01376304) indicate that the 2008 and particularly 2009 summer seasons were below the historic mean salinity (fig. 4). This gage station is located ~2.5 km south of Irvington on the eastern shoreline.

Dissolved Oxygen and Chlorophyll *a*

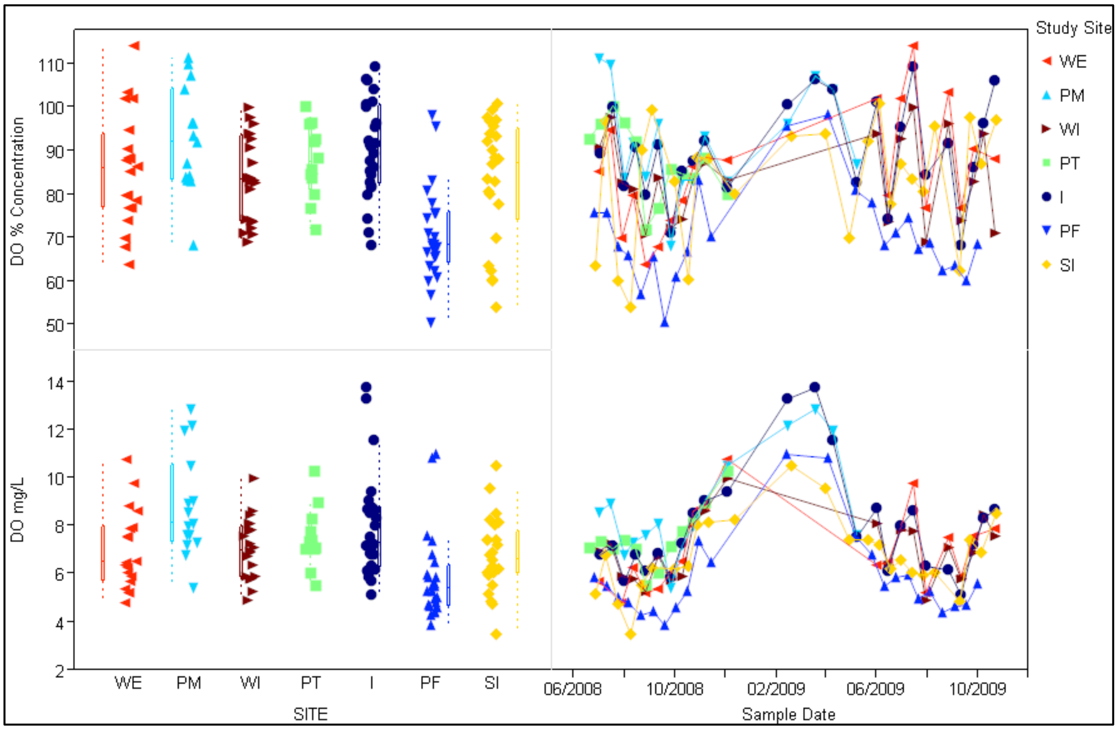

Figure 5- Observed dissolved oxygen concentration and saturation during study period. Seasonal trends and distributions by site.

Dissolved oxygen concentrations (fig.5) ranged from 3.5- 13.8 mg/L with PF having the lowest mean oxygen concentration (5.8 mg/L). Oxygen concentration and saturation fluctuated with season. Peak oxygen concentrations occurred in the late winter at the start of spring bloom conditions and were lowest during the late summer months of August and September, the warmest period of the year.

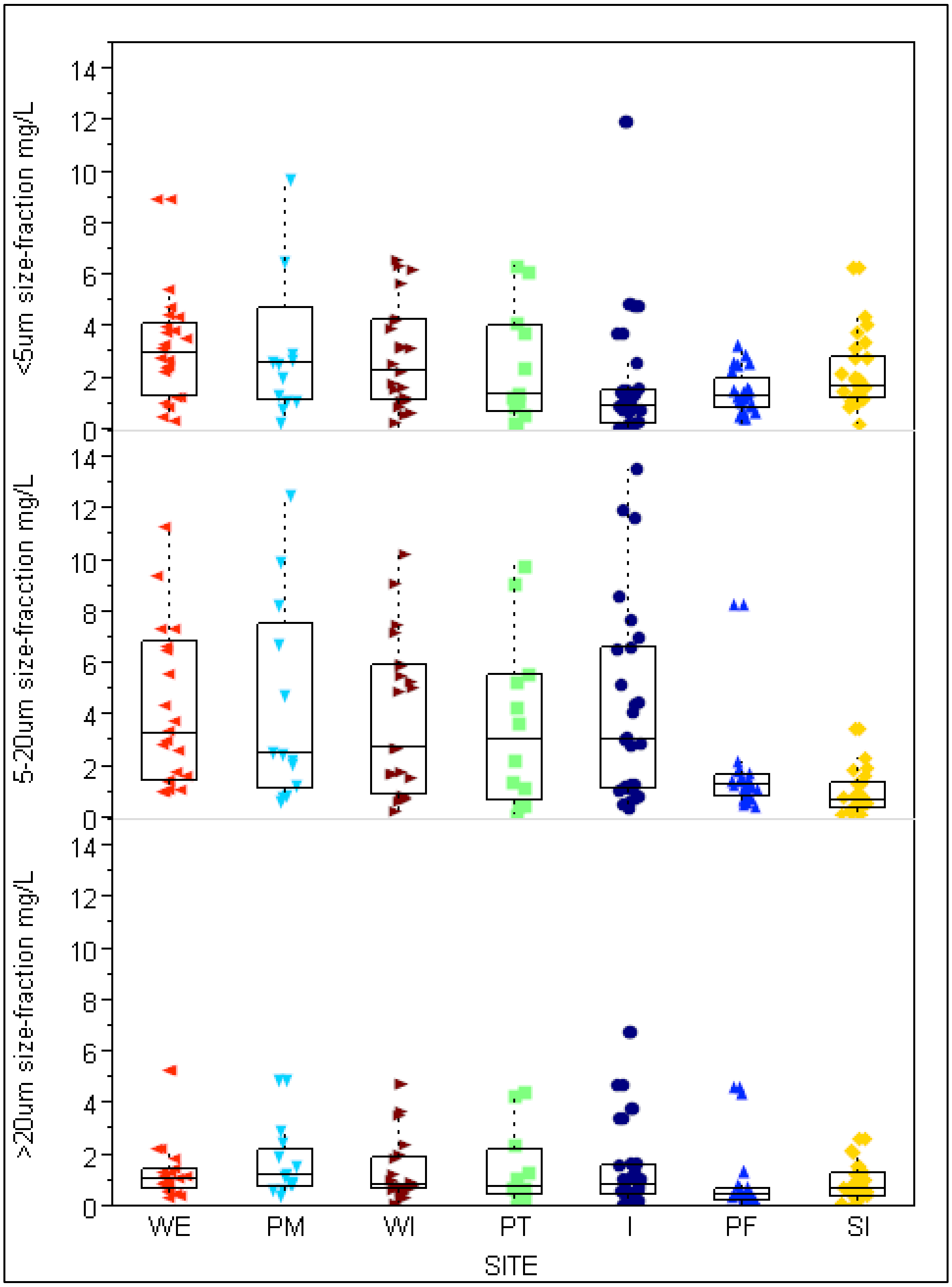

Figure 6- Boxplots of observed chlorophyll *a* concentrations by site and size fraction (>5µm, >20µm, 5-20 µm). Line found at mean value and box represents upper and lower quartile.

The major pattern evident in observed chlorophyll concentrations was the greater variance associated with the upriver sites, particularly in the 5-20µm size fraction (fig. 6). PF and SI had the least variation in chlorophyll *a* concentrations , 2.2 and 0.6, respectively, while the remaining sites ranged widely through the course of the year (mean variance of upriver sites = 12.6). Chlorophyll *a* found in the 5 µm to 20 µm fraction ranged between 41.7-55.1% of the total measured chlorophyll *a* concentration for river sites. SI had considerably less, with a mean of 20.5% of total chlorophyll *a* found in the 5 µm to 20 µm range.

Shell Growth

A strong correlation between shell height, shell length, and shell width existed (R^2= 0.75 to 0.86, $p<0.001$) for all sites through the course of the study. Shell height is therefore used as the indicator of shell growth. A single-factor ANOVA showed no significant difference in initial shell heights between oyster groups at the start of each study period. A 2-factor ANOVA testing the effect of location and sampling period (start and end of field season) showed that only SI, PF, and WI had significant growth. This significant change was observed in both 2008 and 2009. Table 2 provides a list of observed growth at each site along with measures of statistical significance of observed changes in mean shell height between the start and end of the study periods.

Table 2- Shell growth analysis- mean heights at start and end of season (mm) and percent change in height. Levels of significance between samples; *marginally significant reduction in mean shell height. [1] Complete mortality prior to end of study.

Site	Mean starting shell height (mm)	Shell height at end of season (mm)	% change in shell height	p-value
2008- Mature Oysters- Deployed June 16, 2008				
WE	52.10	50.90	-2.30	0.2875
PM	52.70	51.60	-2.09	0.2834
WI	51.00	59.80	17.25	<0.0001
PT	51.30	51.40	0.19	0.9574
I	53.50	51.60	-3.55	0.0866*
PF	50.00	59.90	19.80	<0.0001
SI	51.70	79.60	53.97	<0.0001
2009- Mature Oysters – Deployed May 14, 2009				
WE	40.3	[1]	NA	[1]
WI	40.1	44.5	10.97	<0.0001
I	39.7	37.7	-5.04	0.0492*
PF	41.1	55.9	36.01	<0.0001
SI	39.9	82.3	106.27	<0.0001
2009- Juvenile Oysters – Deployed July 23, 2009				
WE	11.6	[1]	NA	[1]
WI	11.9	21.3	78.99	<0.0001
I	12.2	20.3	66.39	<0.0001
SI	12.3	37.1	201.63	<0.0001

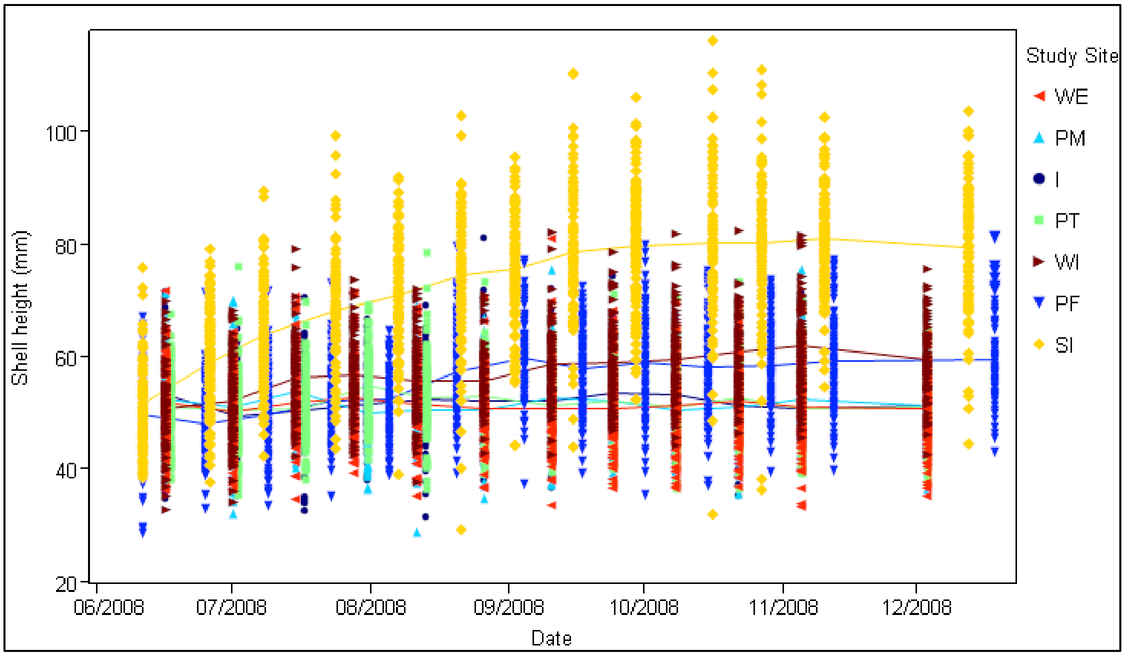

Figure 7- 2008 mature oyster shell growth, lines represent mean shell height.

Juvenile oysters placed at the upriver sites in 2009 showed much greater shell growth in comparison to both 2008 and 2009 mature oysters (fig 7-8, Table2). Oysters at upriver sites had a brief period of low growth soon after deployment which may indicate a period of adaptation to the low salinity environment. The largest difference in growth rate between the experimental and control site occurred within the first month after deployment, which could indicate a short pause in growth due to the shock of reduced salinity. It is difficult to quantify any potential legacy effects that this shock may have on subsequent health and development of these oysters as they mature and grow.

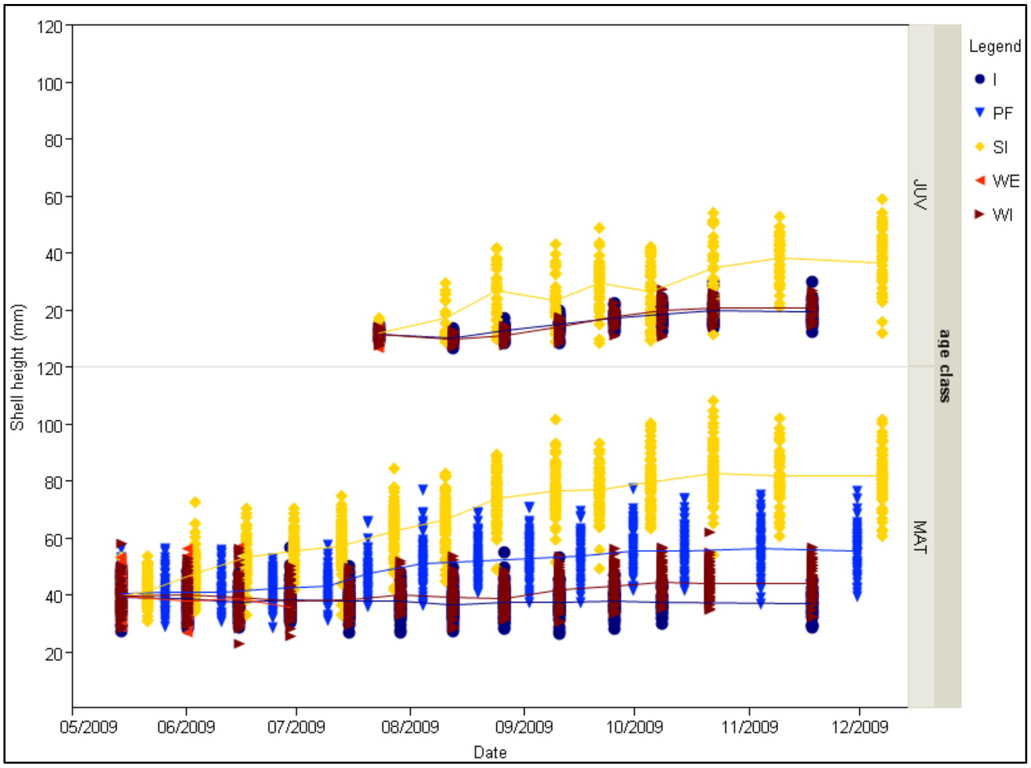

Figure 8- Mean shell size through time of juvenile (top) and mature (bottom plot) oysters, 2009.

Tissue growth and Condition index

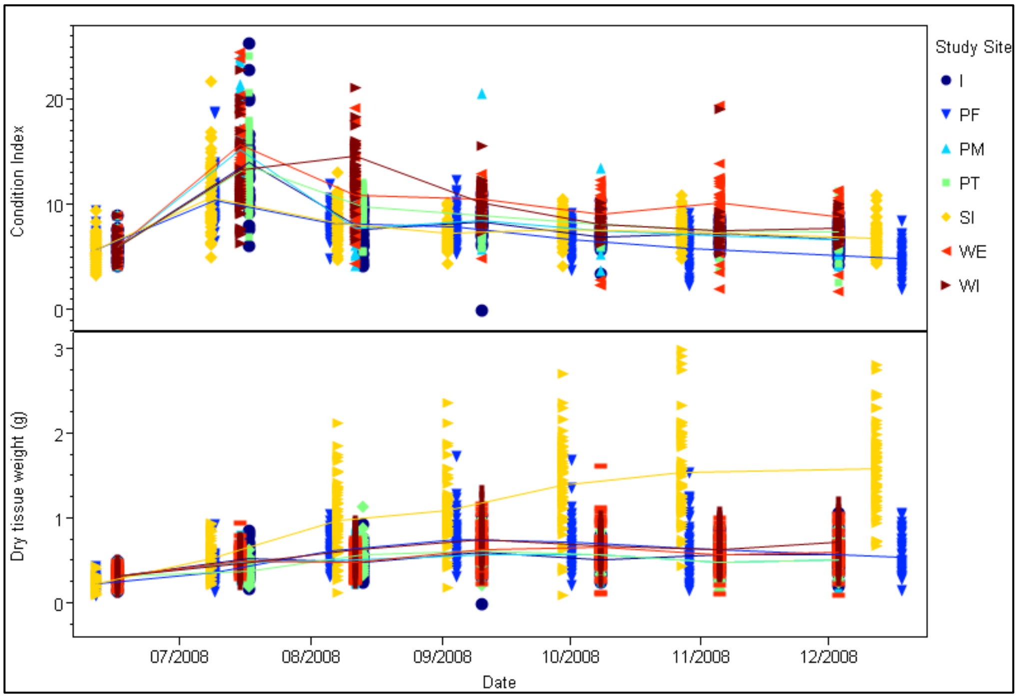

Figure 9 -2008 Grams dry tissue weight and calculated condition index.

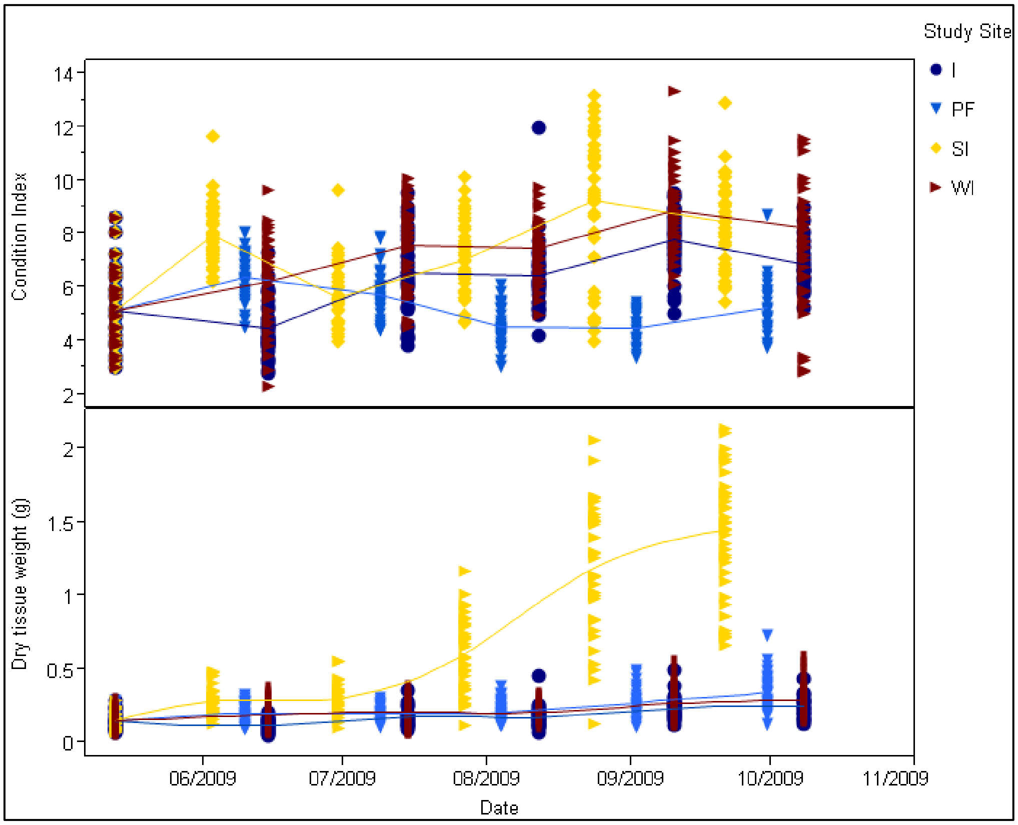

Figure 10- 2009 Grams dry tissue weight and calculated condition index.

Substantial changes in mean tissue weight of overwintered oysters were observed at all sites. Condition index (CI) followed similar trends between sites regardless of tissue weight. A quick increase in CI early in the study period was followed by a steady decrease over a period of time coincident with the typical spawning period for this region (Thompson et al., 1996). Less pronounced trends were evident in the second year of the study for mature oysters. Although all sites followed this general trend the timing and magnitude of these changes varied between sites.

Mortality

Mortality rates during 2008 ranged from less than 5% (sites, PM, I, WI) seasonal mortality (June- Dec) to as great as 36.2% and 42.7% for WE and PF, respectively. These large mortality events were temporally associated with a drop in salinity correlated with a high-river-discharge event (≤ 2 psu) at the northern-most Hudson River site (WE) and high disease prevalence (see below) at the southern-most Hudson River site along Manhattan's Pier 40 (fig. 11). Tappan Zee-Haverstraw Bay sites, except WE, had a higher survival rate at the start of the winter months than the control site SI, which was under a greater disease burden from Dermo. All sites, but PF and SI, were subjected to extremely harsh winter conditions (i.e. ice scour) presumed to result in the eventual and complete die-off of oysters during and following December 2008. These die-offs are thought to be strictly due to these circumstances and prevented further study of their responses the following spring.

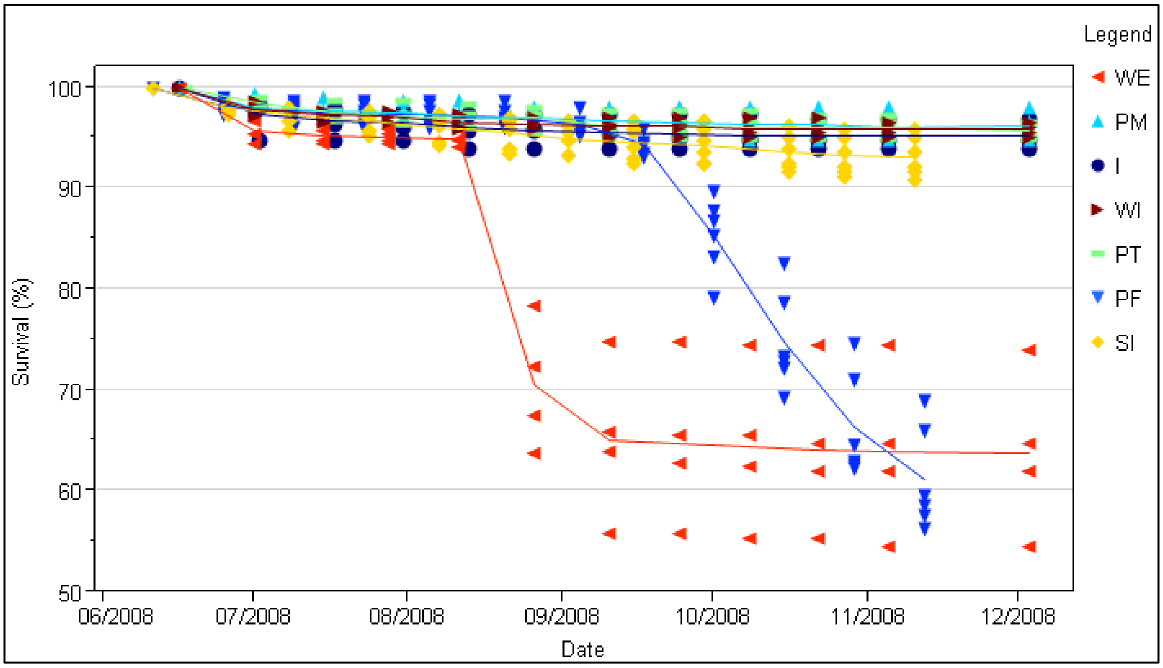

Figure 11- 2008 mortality trends, points represent replicate samples (each bag at each site); lines represent mean mortality at each site.

The second year of the study showed a range of mortalities at up-river sites at the start of the field season during a period of abnormally low salinities (fig. 12 and fig. 4). These mortality rates subsided as salinities returned to a more normal state.

Survival rates entering the winter months of 2009 increased with salinity from the total mortality at WE to 92.7% survival at PF. Oysters deployed in 2008 had an initially stronger survival rate going into the winter months than those in 2009.

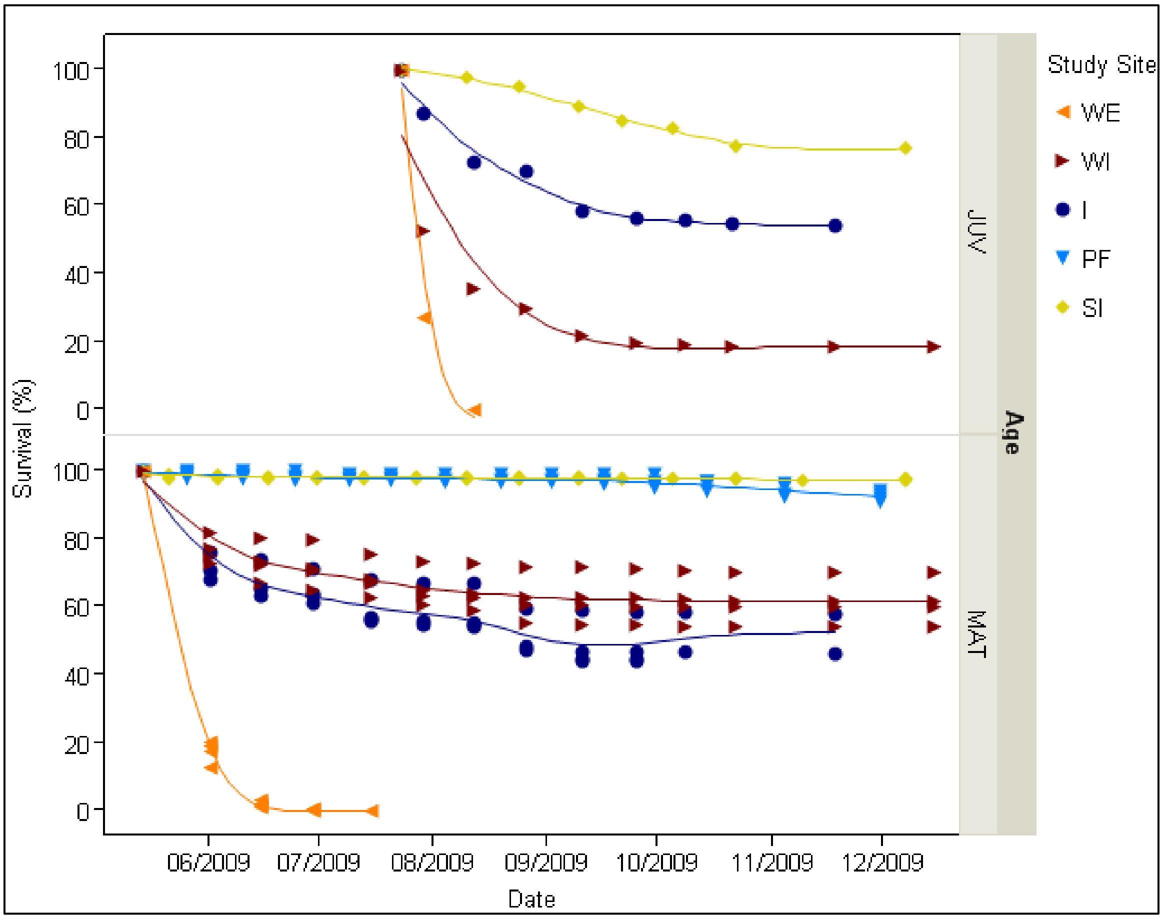

Figure 12- 2009 juvenile and mature oyster mortality trends.

Disease

Results from the RFTM tissue assay in September 2008 showed that no locality was free from disease; however, there was a distinct separation of prevalence rates between the low salinity study sites and the higher salinity PF and SI sites. Salinity correlated positively (r^2 0.72, $p<0.004$) with the prevalence of dermo (table 3), with the high salinity control site having a 50% occurrence of dermo. Upriver sites had considerably lower dermo prevalence compared to the saltier southern Hudson River (PF) and SI control sites. MSX was found at only PF in 2008.

Overall disease prevalence in 2009 was reduced in almost all sites. The upriver sites had no dermo or MSX disease present. Only PF had slightly higher dermo prevalence in 2009, but no MSX was present. The positive relationship between salinity and dermo prevalence existed in 2009 as well.

Table 3- Dermo disease prevalence of 2008/2009 mature oysters sampled in the fall of each year - Sites are ordered by descending mean salinity. [1] WE had no live oysters remaining at the time of disease testing. [2] No oysters deployed at PT or PM in 2009.

Site	Site ID	Prevalence of Dermo disease 2008/2009	Weighted prevalence of Dermo disease 2008/2009	Prevalence of MSX 2008/2009	Weighted Prevalence of MSX 2008/2009
Westerly	**WE**	3.33 / NA[1]	0.02 / NA[1]	0.0 / NA[1]	0.0 / NA[1]
Philipse Manor	**PM**	13.33 / NA[2]	0.18 / NA[2]	0.0 / NA[2]	0.0 / NA[2]
Washington Irving	**WI**	6.67 / 0.0	0.03 / 0.0	0.0 / 0.0	0.0 / 0.0
Piermont	**PT**	16.67 / NA[2]	0.08 / NA[2]	0.0 / NA[2]	0.0 / NA[2]
Irvington	**I**	10.00 / 0.0	0.05 / 0.0	0.0 / 0.0	0.0 / 0.0
Pier 40	**PF**	3.33 / 13.3	0.13 / 0.20	70.0 / 0.0	1.90 / 0.0
Shelter Island	**SI**	50.00 / 26.67	0.92 / 0.25	0.0 / 0.0	0.0 / 0.0

Recruitment

In 2008, analysis of the oyster shell settling substrate showed a varying abundance of settled oysters with increasing abundances from northern sites towards southern sites (fig. 13).

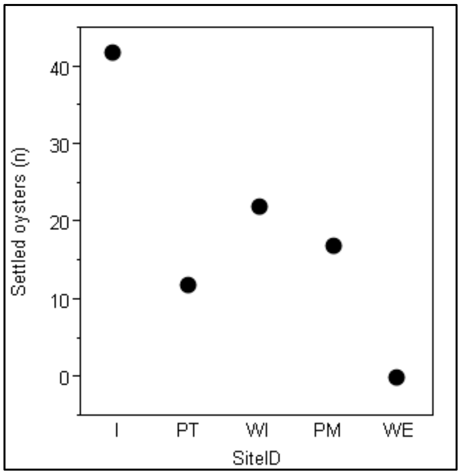

Figure 13- 2008 Observed recruitment at upriver sites.

Recruited oysters exhibited rapid growth, in comparison to both mature and juvenile oysters within respective sites, during the short period of settlement bag deployment (80 days). Washington Irving (WI) had the fastest growth rate, at nearly 1.5mm/week. The northern most site, WE, had zero recruited oysters but an abundant set of zebra mussels attached to the settlement bag. This fresh /brackish water, invasive mussel demonstrates an inverse distribution with an increased abundance occurring in the northern localities, further indication of the extremely low salinity conditions during this study.

Table 4- 2008- Recruitment of oysters to settlement bags. [1] WI shell height significantly greater than other sites p=0.0049.

Site:	mean shell height (mm)	Mean shell growth (mm/day)	Settled zebra mussels (n)
Westerly	-	-	96
Philipse Manor	21.04	0.24	7
Washington Irving	23.17 [1]	0.27	8
Piermont	17.61	0.20	9
Irvington	19.43	0.22	0

A similar survey in 2009 found only 2 oysters settled at the upriver sites, both occurring at I, between July 24th and October 8th and 3 oysters at Pier 40. Growth rates were similar to those measured in 2008. Zebra mussels were again common to the north with reduced recruitment to the south.

DISCUSSION

This study provides a preliminary investigation of important physiological and population health parameters of eastern oysters contributing to an assessment of restoration potential in the lower Hudson River region. Briefly, experimental oysters placed in the Hudson River showed the ability to maintain the development of reproductive tissue after deployment, but lacked significant shell growth that is crucial for development of reef communities. Yet, survival was impressively high under typical salinity conditions, and with what larval source was available, recruitment and ensuing growth can possibly be robust. These responses varied with latitude within the river and it seemed likely that salinity will ultimately dictate the geographic range of restored populations. The conclusions drawn from this assessment should be limited to the oyster stocks that were used in the study, but nonetheless can help guide restoration activities and further our understanding of restoration ecology for this area.

Previous reviews of bivalve health incorporated a measure of condition index (CI) (Volety, 2008, Wilson et al., 2005, Doall et al., 2008) to assess the animal's response to the environmental conditions. The condition index assessment provided little evidence that any of these sites were limiting in healthy growing conditions, while there was a clear difference in tissue growth between sites. This highlights the importance of using multiple metrics to measure oyster health. A peak in condition index followed immediately by a decline in CI and observed gametes are indications that spawning had occurred. This was evident at all localities in both years but total reproductive output will likely vary with tissue weight between sites (Thompson et al., 1996). Tissue growth and thus condition index may also be limited by the size of the oyster's shell yielding a high condition index even while health maybe suboptimal. It has not been established if the fertile condition of the oysters at time of deployment contributed to their evident spawning. Fertilization and larval recruitment would need to be investigated further to determine any limitations during these life stages.

Reduced growth cannot be ascribed to a lack of available particles to feed upon as the system does not seem to be limited in quantity of food resources. Size fractionated chlorophyll *a* analysis shows that a large portion of the total chlorophyll occurs in the size range (>5 µm) that oysters can readily capture while feeding (Newell and Jordan, 1983). However, it is not known whether the measured chlorophyll species are nutritionally sufficient for oysters, which may explain the meager growth. Studies of digestion and absorption efficiency of oysters on various algal species show that some chlorophyte species are poorly utilized by oysters (Langdon and Newell, 1996).

Mature oysters within the river had very poor shell growth in relation to the control site. Even if statistically significant, the shell growth was small in magnitude and would not contribute to a sustainable shell budget. Juvenile oysters had comparatively higher growth rates than mature oysters, but still trailed behind the growth rates observed at the control site. This raises an interesting question whether there is a high energetic cost associated with maintaining gametes by mature oysters which leads to a reallocation of resources put towards reproduction over shell growth during strenuous ambient conditions.

It is likely that the low salinities of the river caused the meager growth of experimental oysters. Oysters lack cellular regulation of osmotic pressures (Shumway, 1996), and exposure to rapidly or constantly changing salinities can cause osmotic stress. Although they can mitigate some of this stress through valve closure, basic physiological functions will be hindered (Shumway, 1996). Clearly some of the observed mortalities in the river are owing to low salinity stress, acute salinity shock or a combination of both. Oysters may be more sensitive to the rate of the salinity change not the magnitude of change (Shumway, 1996, La Peyre et al., 2003), both of which can be quite high in this river system. Despite the poor growth and stressful environment, low salinity conditions were not always destructive.

The lower salinities to the north provided a refuge from disease, evident in the disease prevalence data, with no disease presence north of PF in 2009 and light infection intensities in 2008. Although pathogens existed at all but one site in 2008, the intensity of infections were quite low and likely not to lead to any large scale mortalities. Interestingly, the MSX pathogen only occurred at PF where a low *Perkinsus marinus* prevalence was also observed. This presence by MSX may explain some of the poor growth compared to SI. Spatial patterns of disease prevalence in the Hudson River follow trends similar to other estuaries which experience occurrence of these oyster diseases (Powell et al., 2008, Ford and Smolowitz, 2007, Albright et al., 2007). These similarities may assist in the understanding and management of epizootics within the Hudson River.

The growth rates observed in settled oysters challenges the stance that oyster shell growth is limited within the river. The overall mean growth rate, 0.24mm/day, is near that reported for oysters in other estuaries along the Atlantic coast (Shumway, 1996). Although the larval source is unknown it also demonstrates that the system can support spawning, fertilization, settlement and subsequent growth. An investigation of these settled oysters is needed to determine if there has been adaptation to this dynamic system allowing for this vigorous growth, and if so, are these native populations prone to the same sorts of disease pressures as oysters used in this study. Understanding these population parameters will elucidate the potential for using these populations in restoration work and can gauge the sustainability of restored populations into the future.

Experimental oysters showed a range of physiological responses between sites and years which raise important and potentially challenging questions about pursuing restoration work within this system. Though much of the variance in the physiological responses may be through a simple association with the salinity gradient found along our study transect of sites along the Lower Hudson, the oyster's physiological responses reveal a range of tradeoffs associated with this gradient. These tradeoffs, between individual growth and survival from disease, foster a unique and challenging ecological dilemma for those in support of returning large populations of oysters to this region.

The return of Hudson River oyster reefs depends on a positive net balance in shell supply. The growth of an individual oyster contributes to the reef by accreting its shell mass while taphonomic and depositional processes reduce reef structure. Though high survival rates, as seen at many sites in 2008, leads to increased shell accumulation (Powell et al., 2006, Powell and Klinck, 2007) it will ultimately need to be determined if the reduced shell growth of these oysters can provide enough shell mass to meet the needs of this shell budget. Understanding this aspect of oyster population biology can help determine if reef restoration would be sustainable in the long term. Current modeling efforts can be modified and applied in this area to elucidate the minimum growth and survival parameters that are needed to meet this shell budget.

The dynamic nature of the river with its constantly shifting salinity regime has made it difficult to fully assess the long term potential of recovering these oyster populations, yet there is evidence supporting short term recovery. This assessment also highlights the importance of the selection of life stage of the restoration "starting stock" along with the timing and methods of deploying these animals. Upriver sites showed promising survival during the first year of the study under more typical, though still below mean, salinity ranges. Year two of the study showed that periods of low salinities will be a limitation to survival in that area, and will control the distribution of populations on a longer time scale. Much of these observed salinities can be related to summer rainfall in 2009 being especially high, over 20 cm in July alone at Albany, New York. Determining the frequency of events such as seen in 2009 will help estimate the probability of developing a sustainable population in these upper areas of the river.

Temperature patterns may also be important to the restoration potential of the river. Variations in the timing and magnitude of the observed peak temperatures in 2008 and 2009 indicate the system may have a high annual variance in the way temperatures progresses through the season e.g. a slow increase in temperature versus a prolonged increase. These changes in the temperature regime may lead to high variance associated with the timing and the intensity of a spawning event or disease outbreak, which can lead to population instability due to changes in annual recruitment and disease prevalence year to year. It should be noted that all sites in each year attained a peak temperature between 20^{o}C and 30^{o}C which is thought to be a critical temperature zone for the initiation of many important reproductive processes (Shumway, 1996), while staying below the purported threshold for intense epizootic events (25^{o}C) (Ford and Tripp, 1996).

Although the Tappan Zee region showed little promise for productive oyster growth by emplaced oysters, prolonged survival due to low disease prevalence, reports of locally adapted populations and possibly ideal hydrologic conditions make this region a potentially important component in the process of recovering oysters to the Hudson River. Though a number of questions remain to be answered about this regions ability to host oyster populations, the results of this assessment provide a foundation upon which future restoration research can develop. Further investigation is needed to verify the claims of natural populations within the Tappan Zee area and to recognize any potential adaptations to this regions environment that may be useful in restoration efforts. An assessment of the possible benefits and drawbacks to using hatchery reared oysters, particularly relating to issues of diversity and physiological tradeoffs, can assist in identifying appropriate brood stock for use in restoration. Chapter two of this thesis will provide a physical assessment of the restoration potential within the Lower Hudson and New York Harbor region.

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Chapter 2

A spatial assessment of *Crassostrea virginica's* restoration potential within the Hudson River, NY

INTRODUCTION

My assessment of physiological performance of oysters within the Hudson River system (Chapter 1) has highlighted two main points of interest relating to oyster restoration. Growth of hatchery-reared oysters is limited in the Hudson, yet I have found that high survival can occur within a low salinity, disease refuge. Also, there are signs of restoration potential, as evidenced by quick growth in new recruits and growth of juveniles from hatcheries (Chapter 1). Successful oyster restoration will of course depend on maximizing population growth, possibly by utilizing locally adapted founder brood stock, sheltering them from disease and focusing on locations that have the needed habitat characteristics (e.g. substrate availability, hydrodynamics, food availability that support populations) for natural expansion and sustainability. It is the purpose of this chapter to create a map identifying areas with characteristics suitable for oyster reef restoration within the lower Hudson system (fig. 14).

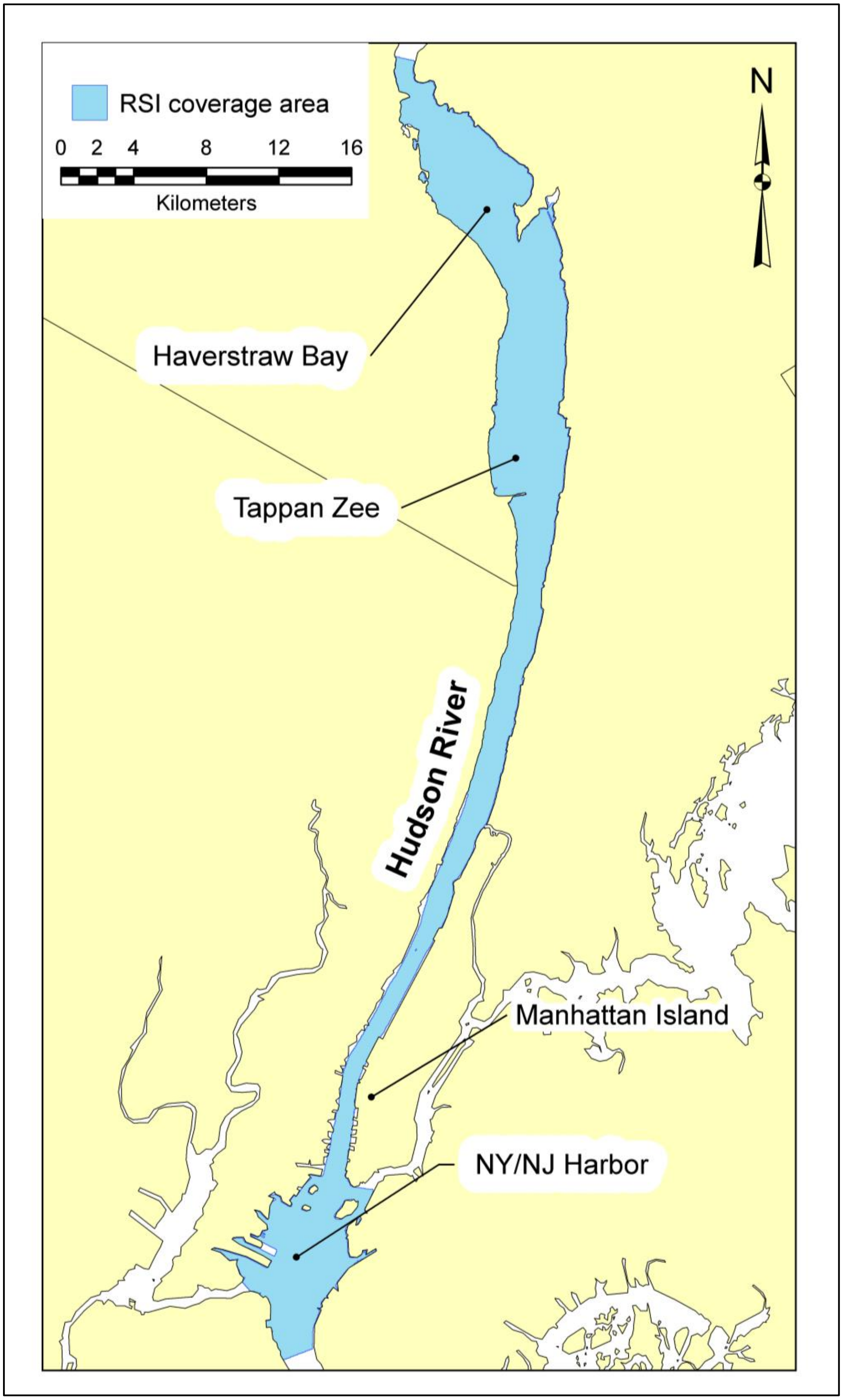

Figure 14- Study location; Hudson River Haverstraw Bay-Tappan Zee- NY/NJ Harbor.

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 would typically be provided among the shells of prior oyster generations, both live individuals and remnant valves, in the form of a reef structure. Although the Hudson River currently provides some localized appropriate substrate, in relic oyster reefs, shell hash, rock, and gravelly sediments; it is likely that this substrate lacks the 3-dimensional structure and/or exists in areas physiologically unsuitable for natural recovery. Alleviating this limitation, by enhancing substrate and habitat, is a reasonable place to begin restoration efforts.

Habitat enhancement, by way of substrate addition (shell hash and/or man-made 3-d structures), is a common approach to oyster restoration projects (Powers et al., 2009, Schulte et al., 2009, Brumbaugh and Coen, 2009) and is considered crucial to the recovery of oysters in systems that have become substrate limited. Observed recruitment and vigorous growth on suspended shell bags (Results section, chpt.1) along with frequent anecdotal reports of oyster settlement on a variety of other surfaces (i.e. mooring chains, docks, and ropes) indicate some spawning populations in the Tappan Zee 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.

The estuary's lack of oyster reef structure was specifically highlighted as problematic and has become a main focus in restoration planning, with the ambitious goal of restoring 500 acres to the Hudson-Raritan Estuary by 2012 (Bain, 2007). To achieve these goals there needs to be an enormous investment of resources to the study and development of restoration strategy in this system. Fortunately there have been many efforts of oyster restoration along the Atlantic coast which can contribute to our understanding of how best to tackle restoration within the Hudson.

There have been a number of oyster restoration projects that have had some demonstrated measures of success using reef enhancement and construction techniques. These successes have generally coincided with reef morphology and construction methods (Powers et al., 2009, Nestlerode et al., 2007, Schulte et al., 2009, Gregalis et al., 2008), with reef height seeming to be the vital component to their respective achievements. To increase the chances of successful restoration within the Hudson River, there should be an effort to mimic these past efforts, as well as establishing of these efforts in an appropriate manner. Locating these restoration efforts is a cautious undertaking, as 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 have sufficient physical properties for reef construction and maintenance.

Restoration Suitability Index

Habitat suitability indexes are a commonly used tool by resource managers in conservation and restoration planning (Barnes et al., 2007, van Katwijk et al., 2000, Vincenzi et al., 2006). They are frequently built using a spatial correlation analysis between presence/absence or abundance data and known environmental conditions found within the study area to efficiently assess the species "potential" range. 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 range. With diminished populations, such as the oyster 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 method, this index aims to spatially identify areas that have characteristics that fit well with reef creation and enhancement practices, not to identify currently suitable habitat. 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, Barnes et al., 2007, Vincenzi et al., 2006), with a focus on some basic habitat requirements for a successful reef restoration project.

Briefly, the model operates by organizing spatially explicit environmental data into grid-based datasets (10-meter x 10-meter cell size) which are then independently reclassified on a suitability scale and combined to form a continuous map of spatially referenced restoration suitability. The structure of this model and the associated outputs are purely qualitative and do not act as an assessment of the region's capacity to restore reef systems, but rather to identify specific areas that are potentially good candidates for implementing reef construction. As our understanding of oyster physiology, disease dynamics, the physical nature of the Hudson River, and the interaction of all these improve, we will better understand the system's capacity to host restored oyster populations.

METHODS

Environmental Habitat Characteristics

A number of important abiotic and biotic environmental habitat characteristics are essential to the successful construction, maintenance and persistence of oyster reef 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 focuses on two distinct criteria while making the suitability assessment, the ability of a location to support the installation and maintenance of a constructed reef and the area's potential for successful oyster population growth.

Reef installation physical environment

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 hinder the performance and reduce the life of the installed reef and should be avoided. Tidal and other bottom currents often interact with muddy sediments and cause resuspension, which inhibits suspension feeding (Rhoads and Young, 1970).

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 in promoting survival. Emplacement of these structures in the very active Hudson River can be difficult and potentially dangerous. Post-deployment 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 piling in shallow shoreward areas each winter. Oyster reef structures would therefore need to be fitted between an ideal near-shore deployment and monitoring depth and depths to deep to have appropriate conditions of relatively low near-bottom turbidity.

Data acquisition - Sediment type/sedimentary environment/bathymetry

The physical-environmental data for this study was obtained from the NYSDEC GIS Clearinghouse (http://www.nysgis.state.ny.us/index.cfm (Bell et al., Bell et al., 2006b, Ladd, 2008)) and was gathered as part of a 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, sub-bottom profiling, multi-beam bathymetry, sediment cores and grabs (Nitsche et al., 2007, Nitsche et al., 2004). The original sedimentary environment and sediment type data were converted from polygon shape file format to raster format (10-meter cell size) and depth was resampled to a 10-meter cell size for consistency of data inputs. Figure 15 A-C displays these data as thematic maps.

Salinity-Temperature

Salinity and temperature are important environmental factors that influence the health and distribution of the eastern oyster, which control the species range and distribution within an estuary (Shumway, 1996). A variety of physiological and biological processes, feeding, spawning and disease and predator interactions are influenced by salinity and temperature (Shumway, 1996). Like many estuarine species the oyster has a remarkable tolerance for drastic changes in both temperature and salinity, allowing them to survive the often harsh conditions of an estuary. Though an oyster is able to withstand these stresses in short exposures, like all species, they have an optimal salinity and temperature range in which they grow and survive best.

Numerous studies have focused attention towards salinity and temperature while looking to optimize things such as growth rates and timing of spawning, primarily for application in a hatchery setting. Though these studies have greatly enhanced the understanding of the physiology of the eastern oyster there remains limited knowledge of performance at the ends of these optima. 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 and Smolowitz, 2007, Ford and Chintala, 2006, Ford and Tripp, 1996, La Peyre et al., 2003).

Dermo and MSX disease, caused by the haplosporidium parasite *Perkinsus marinus* and *Haplosporidium nelsonii*, respectively, has been shown to control populations of oysters in many estuaries along the Atlantic (Ford and Smolowitz, 2007, Ford and Chintala, 2006). 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). Similar trends were evident in disease prevalence data presented in chapter 1. Confirmed presence of both Dermo and MSX (Chapter 1, pg.19) within the Hudson increases our concern over the placement of restoration activities to minimize the occurrence of epizootics.

Salinity and temperature influence growth as well. Oyster growth rates generally will increase when approaching optimum temperature and salinity. Low salinity conditions provoke oysters to allocate more resources towards the mediation of osmotic shock than for assimilation and tissue growth (Shumway, 1996). Complicating matters it appears that the response to this shock is temperature dependant, with higher temperatures presenting a more stressful environment (La Peyre et al., 2003).

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. Temperature does not vary significantly, biologically speaking, through the study region, 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 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 Tappan Zee and Haverstraw Bay area making it the critical biologically relevant variable in this spatial model.

Salinity data acquisition

The Hudson River is an active system that ranges from a well-mixed estuary, during periods of low river flow and high tidal amplitude, to a highly stratified estuary, in periods of high river flow and low tidal amplitude (Geyer and Chant, 2006). The river's dynamic nature makes it difficult to monitor and categorize salinities through the study region. To generate a simplified, yet reasonably accurate picture of the salinity regime through this area data generated from a 2-dimensional hydrodynamic model was used (Ralston et al., 2008, Ralston and 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 (Mar 1 to Nov 1), the time in which oysters are most sensitive to salinity (Shumway, 1996). The model's output of basin-wide daily mean bottom salinity was then averaged over the model's extended time period (1918-2005) for each model station point through the study area. Mean bottom salinities were then interpolated using the geostatistical process of kriging (Legendre and Legendre, 1998) to produce a continuous coverage of salinity values across the study area. This data is presented in figure 15D. Although the geostatistical model output poorly reflects the cross-basin salinity distribution observed in real-time latitudinal salinity measures, it mimics the source data (a basin wide average) well and provides a reasonable estimate of long-term salinity averages across the region.

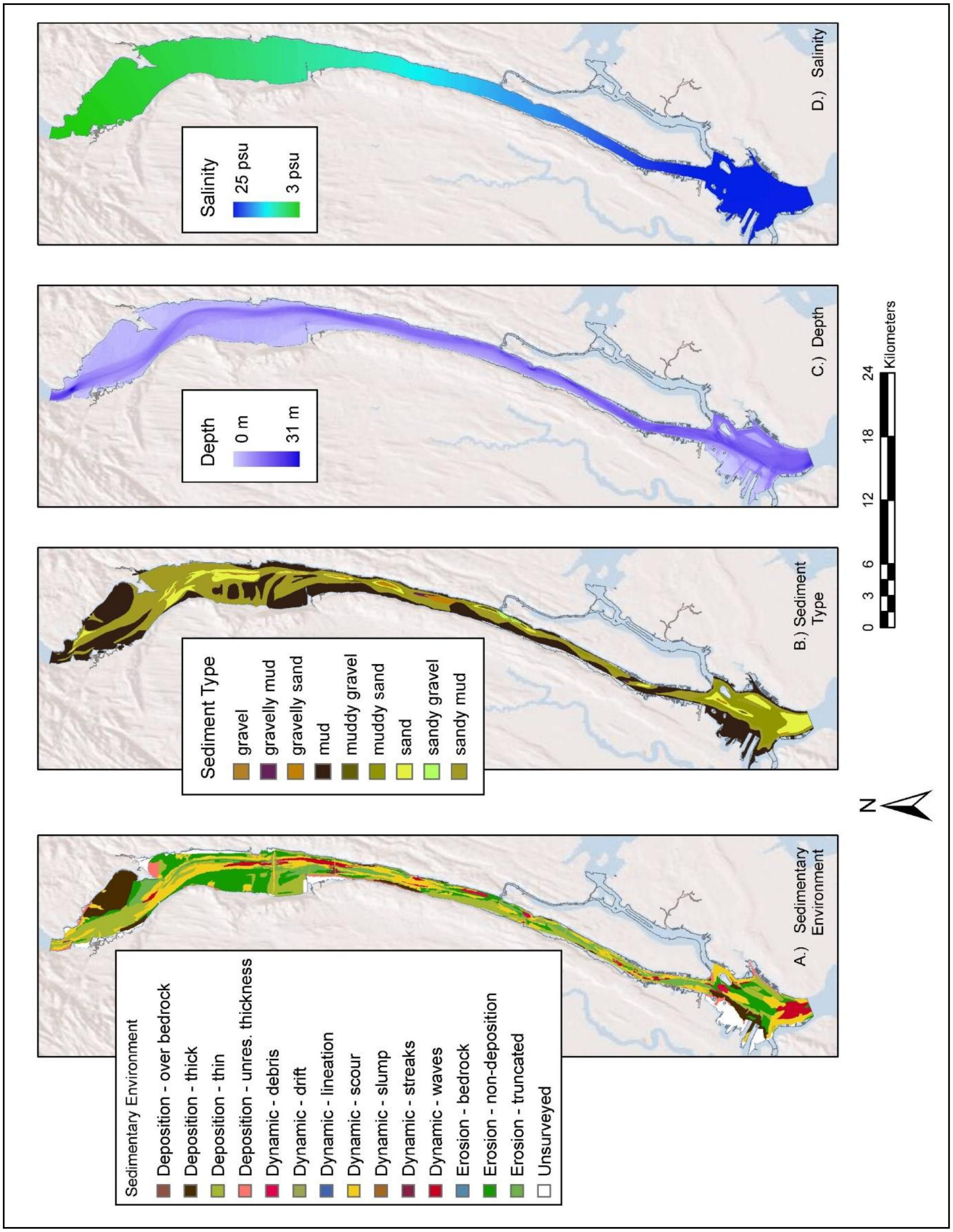

Figure 15-GIS maps of input environmental habitat characteristics. A-C) Data obtained from NYSDEC GIS Clearinghouse (Bell et al., 2006a, Bell et al., 2006b, Ladd, 2008); D) Estimated salinity coverage interpolated from long-term longitudinal salinity data.

Model Construction

Restoration Suitability Index

Environmental parameters represent sedimentary environment, sediment type, depth, and salinity, were used as inputs to the RSI. Each parameter was independently reclassified to a suitability scale from 0.0 to 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 (figure 16- results section). After reclassification, a correlation analysis among the PSS's was performed to test for independence of parameters and ensure minimal bias that may result during calculation of the RSI (eq.1). To do so a randomly generated set of points (n=10,000) were created across the spatial extent of the index. The corresponding PSS values were then tabulated at each point for correlation analysis.

The resultant reclassified parameter-specific suitabilities are then combined using a weighted geometric mean function (eq. 1) where w_i is the relative weight ($0 \leq w_i \leq 1$; $\sum_1^i w = 1$) of importance of PSS_i, producing a restoration suitability index (RSI). This method is preferred in that an overall suitability of a location will be ranked a value of zero 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 13.

Eq. 1

$$RSI = \left(\prod_{i=1}^{n} PSS_i^{\,w_i} \right)^{\frac{1}{n}}$$

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

Parameter Specific Suitability

Sedimentary Environment

Reclassifications of the sedimentary environment are based on the likelihood that a reef structure will be subjected to heavy depositional sedimentary processes, which has been shown to limit the functionality of a structure (Powell et al., 1995, Grizzle et al., 2002). 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 found along buried fringes of reef compared to those found elevated and unburied. Additionally, Trimble et al. (2009) identifies unstable sediments as a potential limitation in restoration efforts of the Olympia oyster 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, while growth and survival of adults has been shown to increase with flow rate, predator-prey interaction 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 swift enough to cause removal or scouring of the reef material. 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 a relative suitability of each categorical data. 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 5, along with descriptions of data and spatial extent of each category.

Sediment Type

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 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 16B). Reclassified suitability values are listed in table 5, along with descriptions of data and the spatial extent of each category.

Table 5- 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, chocking 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 due to low back-scatter	0.80	Lower energy, ground truthing needed to determine thickness of deposits,	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

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 (continued)					
Erosion-Bedrock	Bedrock exposed at surface, no deposition	1.00	Structural support, no sedimentation	0.051	0.028
Erosion- Non-deposition	Areas that have no clear evidence of deposition	1.00	No deposition, characterized by firm sediments	36.751	20.055
Erosion-Truncated	Truncated startigraphy 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	Unsuryved areas may provide beneficial habitat characteristics need to be verified	13.097	7.147
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

Depth

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 to 5.0 meters, although some areas have supported oysters up to 8.0 meters (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 meters of water compared to reefs installed at 3 meters. In addition to the biological considerations, the physical installation of reef material is increasingly difficult with water depths, and likely to become quite tedious at depths greater than 8 meters. 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 meters are identified as suitable; suitability of water depths greater than 4 meters decreases linearly to 8 meters of depth above which is deemed unsuitable (fig. 16C).

Salinity

As discussed above, the eastern oyster has an optimal salinity for growth and survival from disease. Finding this optimum salinity within this system is an enormous challenge unto itself and will be merely outlined in this work by way of a suitability function (fig. 16D). The creation of this salinity suitability function (SSF) is based on results from a number of lab and field studies that examined the various influences of salinity on oyster physiology, biology, and ecology. A list of these findings, along with references, and their relevance to the definition of the suitability function are shown in table 6.

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, while 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). 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.

Table 6. Salinity impacts on oyster health and survival. The threshold salinity values presented here were used in the creation of the salinity suitability function (SSF) presented in fig.15D.

Salinity (psu):	Relevant Response:	Reference:
<2	Killing floods when greater than 2 weeks duration	(Soniat and Brody, 1988)
<5	Gametogenesis, feeding and pumping impaired Increased mortality in Hudson River study	(Shumway, 1996) previous chapter
<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 and Evans, 2004)
>12	Generally required for dermo and MSX epizootics	(Ford and Tripp, 1996)
>15	Predators become commonly found; *Urosalpinx cinera, Eupleura caudate, Panopeus herbstii, Callinectes sapidus*	(White and Wilson, 1996)
>25	High risk of epizootics from pathogens, including Dermo, MSX, Juvenile oyster disease	(Ford and Tripp, 1996)

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. 16D) and forms the continuous definition of the salinity suitability that is used to reclassify the salinity data into salinity suitability.

Uncertainty in Defining the Salinity Suitability

Defining the SSF is open to subjective bias. 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 output of the RSI. The routine works by randomly drawing a suitability value, from a rescaled beta distribution, at each breakpoint. Then constructing an individual linear function defined between each breakpoint, which creates a continuous function of suitability (SSF_i) throughout the range of salinity. This newly created random function is then used to reclassify the suitability of the salinity within the study site. The shape parameters for the beta distribution, $\alpha = \beta = 1.5$, provides a distribution with ample variation throughout the range. Scaling of the distribution is equal to the proposed level of uncertainty at each breakpoint. Table 7 outlines the breakpoints and associated beta distribution parameters used in generation of the random values around each breakpoint. Figure 16D shows the suitability function and the distribution of random values at each break point. Multiple iterations (n=451) of this routine each generating a unique salinity suitability function, allowed for the calculation of each cell's mean salinity suitability across the study region, as well as the level of uncertainty in suitability, by way of a calculated standard deviation.

Table 7- Mean suitability and range of variation (Uncertainty) of salinity reclassification function (fig. 15E).

Break point- 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

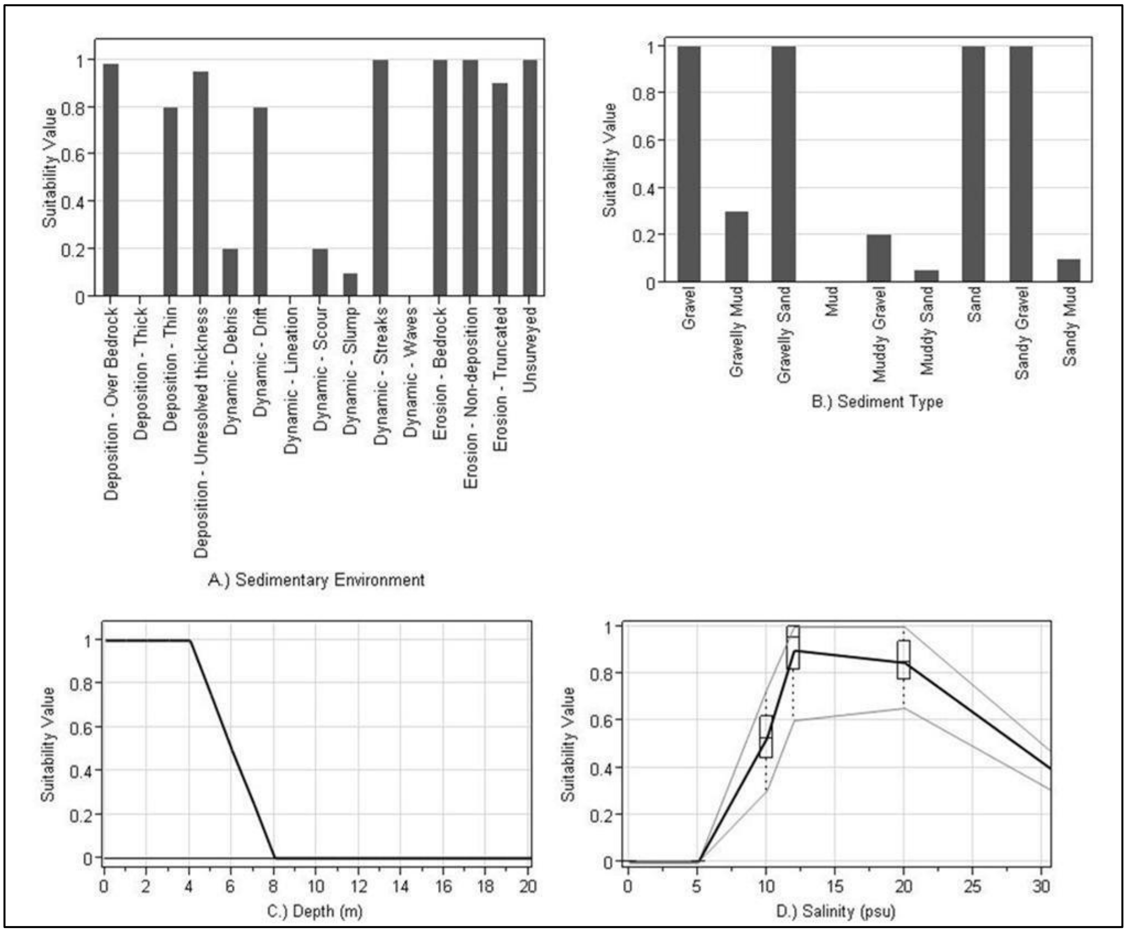

Figure 16- Parameter Specific Suitability (PSS) functions. A-B) Nominal ranking functions converting categorical environmental data into suitability values. C-D) Broken linear functions representing a continuous suitability function used to reclassify environmental data into suitability values. D) Salinity Suitability Function (SSF) center dark line, proposed level of uncertainty around definition of suitability represented by light gray lines and box plots at break points. Distribution of suitability values at break points were randomly generated from a beta distribution. Note asymmetrical distribution at 10 psu due to truncation of suitability values at 1.0.

Subjective Uncertainty

The weighting of parameters during the calculation of the RSI (eq. 1) is prone to subjective error, which can bias the results of the model. To attempt to minimize this subjective uncertainty the analytic hierarchy process technique (AHP) (Saaty, 1994) was used to determine the appropriate weights for each parameter. This technique assists in decision making and has been adopted in many 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 importance 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 models 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 dominate parameter (salinity weight = 0.85, others weight = 0.05). Salinity was chosen as the dominate parameter due to the potentially high error inherent in the uncertainty of the original data and as well as error in the salinity suitability function. Each of the three weighting scenarios were ran 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 variance.

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 (figure 18) 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 RSI extent. 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.

RESULTS

Calculation of parameter-specific suitability maps (fig. 17) showed a number of limiting environmental conditions throughout the river system. Salinity suitability diminished in the northern section of the wide, shallow Tappan Zee region of the river, with a peak in suitability just to the south of the Piermont Pier. The south end of the Tappan Zee area has high variance in the suitability of the salinity (fig. 17E) 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 section and portions of the lower Harbor area. The depth suitability is reduced to near zero for much of the narrow, mid-section of the river. The sediment type and sedimentary environment data have similar spatial patterns, as the two are physically similar; though the two have distinct suitability coverage's and lack significant correlation (table 8). Parametric and non-parametric (Pearson product-moment correlation coefficient and Spearman's rank correlation coefficient) correlation analyses between PSS parameters show no strong dependence between parameters (Table 1; $| r | \leq 0.37$; $| \rho | \leq 0.36$, $p<0.0001$).

Table 8- Parameteric and non-parametric correlation matrix among PSS parameters; n=10,000 spatially random sample points, all relationships highly significant (p<0.0001).

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

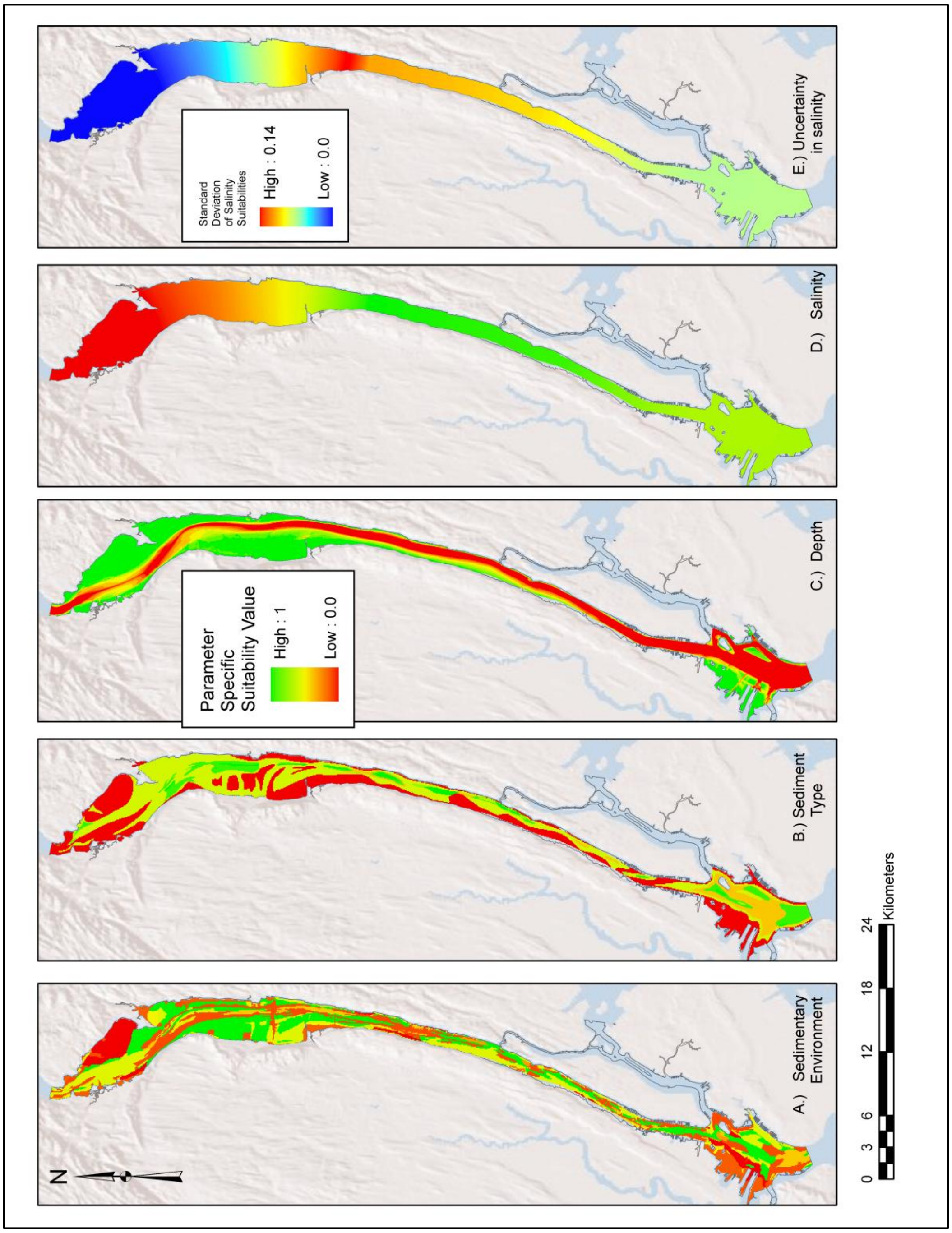

Figure 17- Reclassified parameter specific suitability maps. A-D) Maps show the spatial distribution of suitability for each environmental characteristic of interest. Areas in red are considered unsuitable; green areas are suitable. D) The salinity suitability map is calculated from the mean of a set 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. Dark areas are prone to increased error in suitability reclassification; a more conservative approach should be taken when calculating RSI in these areas.

Figure 18 presents the output RSI for each weighting scenario using both mean salinity suitability and mean suitability minus the uncertainty. 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 red in figure 19A. A comparison between the outputs of the various weighting scenarios show that the salinity dominate weighting scenario provides the most conservative results. The uncertainty associated with the salinity suitability has little influence in the final output.

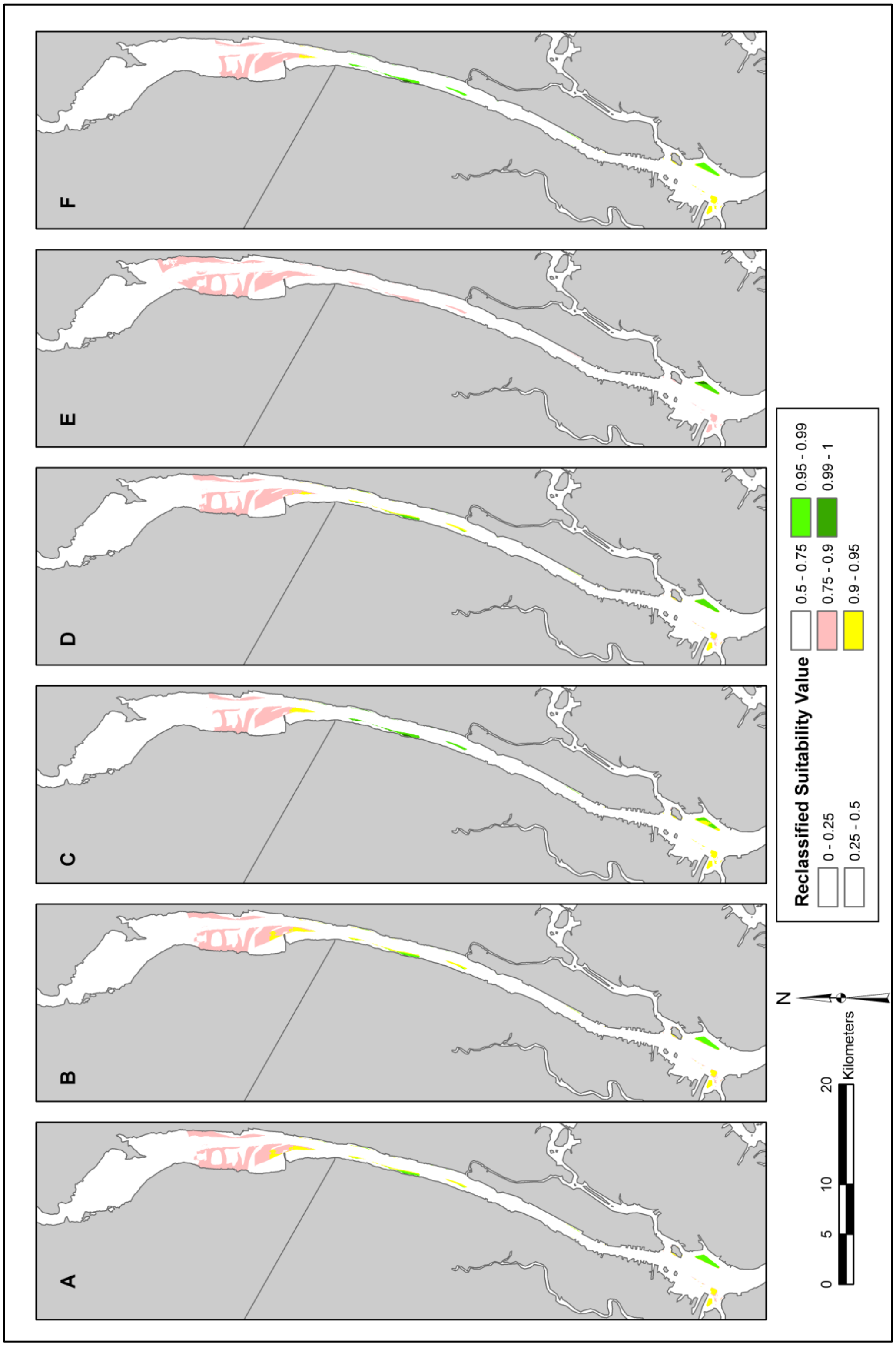

Figure 18- RSI weighting scenario outputs. A) AHP weighting scenario/mean salinity suitability. B) Even weighting scenario/ mean salinity suitability. C) Salinity dominant/ mean salinity suitability. D) AHP weighting scenario/ mean minus uncertainty in salinity suitability. E) Even weighting scenario/mean minus uncertainty in salinity suitability. F) Salinity dominant/ mean minus uncertainty in salinity suitability.

The weighting scenarios and surface area comparisons are presented in table 9. Much of the region is determined to be 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. These areas are predominately found in 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 Tappan Zee area, 35.7% (13.45 km^2) of the total area is ranked in the upper 10% of overall suitability value. The remaining suitable areas are found along the edges of the main channel through the narrow portion of the river between the Tappan Zee region and the NY/NJ Harbor area.

Table 9- Weighting scenarios and spatial coverage of suitability classes.

		Weights:				**Area (km^2) by suitability class**						
	Weighting scenario:	**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 dominate	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 minus 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 dominate	0.85	0.05	0.05	0.05	1534.9	32.5	122.0	99.4	16.9	22.5	2.4

Figure 19 present 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 to 0.98 (fig. 19A) and a level of confidence in the models output (fig. 19B). Areas that consistently rank highest in suitability, possessing a high mean and a low standard deviation, should be identified as target restoration locations.

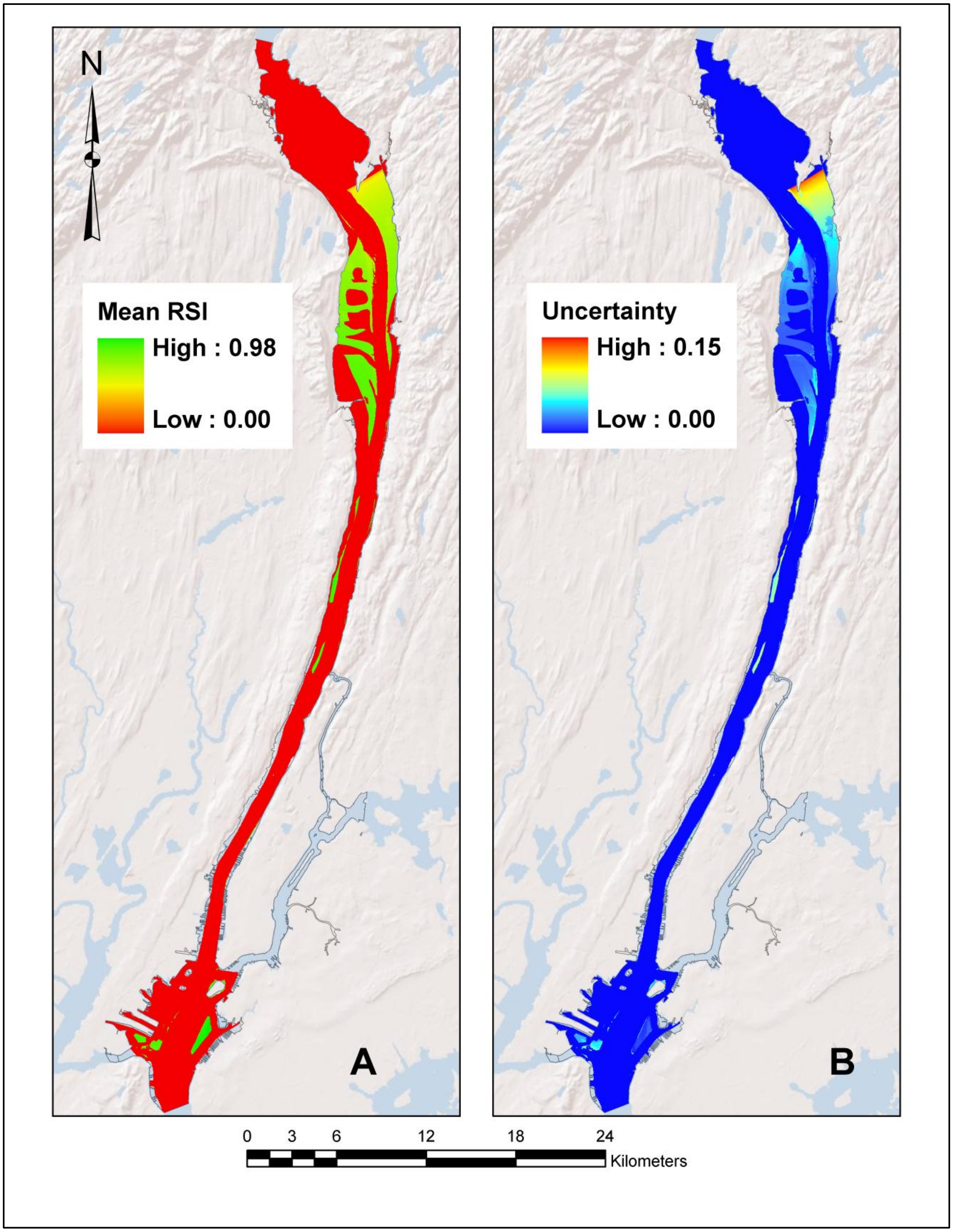

Figure 19- Summary RSI output; A) Mean RSI output of all weighting scenarios. B) Uncertainty in final RSI output.

DISCUSSION

This assessment provides a simple but telling picture of the Hudson River's potential to accommodate reef restoration activities. The models result indicates 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 Tappan Zee region of the river. Though the "most" suitable area (upper 5% overall suitability) is found in the Harbor area, south of Manhattan Island. The extensive areas in the Tappan Zee region of the river may coincide with additional potentially important habitat characteristics. These characteristics have not been included in this index due to availability or spatial extent, but may still be pivotal to the successful restoration of eastern oyster reefs to the Hudson River estuary.

The area's oligohaline salinity regime can provide refuge from disease and predation reducing mortality rates and increasing the potential persistence of populations. 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. The large areas of existing suitable substrate (shell hash from relic 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.

An important potential limitation to restoration in the Tappan Zee 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 as presented in Chapter 1. Though this model attempts to capture the overall influence of salinity (i.e. mean 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). Data of this type are limited as is the influences of these changes on oyster physiology and biology. There also is potential that the patterns of these changes in the river's salinity structure could be changing, especially with regional climate changes and the role that local weather plays in the systems salinity composition or by dredging activities increasing tidal influence in salinity.

Much of the southern river sections depth limits the suitability and it's 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 (as seen in this area in 2008, chp 1) 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 Tappan Zee area coincides with vast expanses of relic oyster reefs (Carbotte et al., 2004), indicating that this area has, at least historically, provided the needed hydrodynamics 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 well 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 section that went unevaluated. Limited 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 winter months or issues with shoreline usage. Regardless, these areas may still provide a substantial areal coverage, potentially as much as 23km^2, and should not be excluded from consideration for restoration efforts.

This model’s simplicity provides an estimation of suitability across the Hudson River area. The output of this index can be used as a basemap of restoration planning of the eastern oyster in the Hudson River. The suitable areas defined here will provide an adequate salinity and preferred environmental qualities to facilitate reef restoration work. The locations can begin as sites for work 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 restoration potential of the Hudson River, and bring these results from a qualitative to a quantitative assessment. Regardless, restoration work should continue to take a careful approach while working towards restoration of oyster communities.

CONCLUSIONS

The physiological and 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 such wide disciplines. Restoration practitioners will need to be mindful of population genetics and demography, as well as community and functional ecologies when pursuing restoration in the Hudson River area. These assessments presented here have shown that a tradeoff exists between growth and disease related mortalities, which will influence population development and sustainability. These tradeoffs may be enhanced in hatchery-reared oysters; increasing the importance of understanding population genetics and acknowledging the potential founder effects of using these individuals in stimulating populations. Understanding the nuances of these tradeoffs will assist in identifying suitable conditions for maximizing population growth and thus besting the potential for restoration of this lost resource. Any reef restoration efforts will be further limited to areas that have suitable environmental conditions for reef community construction and development. These areas have been identified in this spatial assessment and can be further scrutinized for additional limitations as restoration plans move forward.

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