Modelling *Zostera marina* restoration potential in Barnegat Bay New Jersey

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Principle Investigators:

Lead PI: **Peter Straub**, Professor

Richard Stockton College of New Jersey

101 Vera King Farris Drive

Galloway, NJ 08205, United States

Ph.: (609) 652-4556; Fax: (609) 626-5515

E-mail: peter.straub@stockton.edu

Co-PI: **Jessie C. Jarvis**, Senior Research Officer

Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER)

James Cook University - Cairns, 14-88 McGregor Road,

Smithfield, QLD 4878, Australia

Ph.: +61 (07) 4232-2028; Fax: +61 (07) 4781-5589

E-mail: Jessie.jarvis@jcu.edu.au

Co- PI: **Steven Evert**, Field Station Manager,

Richard Stockton College of New Jersey

101 Vera King Farris Drive

Galloway, NJ 08205, United States

Ph.: (609) 652-4486; Fax: (609) 748-0656

E-mail: steven.evert@stockton.edu

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Lead organization: Richard Stockton College of New Jersey (RSC)
Project Manager: P. Straub

INTRODUCTION

Seagrass populations have declined globally over the last several decades (Orth et al., 2006; Waycott et al., 2009; Short et al., 2011). Losses have been linked to coastal development (Short and Wyllie-Echeverria, 1996), eutrophication (Burkholder et al., 2007), and climate change (Short and Neckles, 1999). Within the Mid-Atlantic and Northeastern United States large-scale loss of the dominant seagrass species, *Zostera marina*, has been attributed to chronic declines in water quality compounded by extreme episodic stresses from short term events such as tropical storms or high water temperatures (Orth and Moore, 1983; Bintz et al. 2003; Moore and Jarvis, 2008; Costello and Kenworthy 2011). Loss of seagrasses, or submerged aquatic vegetation (SAV), from coastal habitats has significant impacts throughout the entire surrounding ecosystem due to the numerous ecosystem services provided by these populations (McGlathery et al. 2007; de Boer 2007). These include providing nursery and essential fish habitat and serving as a direct connection between benthic and pelagic habitats (Costanza et al. 1997; Orth et al. 2006, 2010; Heck et al. 2008).

In Barnegat Bay-Little Egg Harbour (BB-LEH), classified as a highly eutrophic system based on application of the National Oceanic and Atmospheric Administration's National Estuarine Eutrophication Assessment model (Kennish et al. 2007), *Z. marina* populations have declined significantly since 2004 with record lows recorded in 2010 (Fertig et al. 2013). Since the mid-1970s accelerated development in the BB-LEH watershed and atmospheric deposition from the overlying airshed has contributed greatly to the increasing eutrophication of the estuary (Kennish et al. 2007; Velinsky et al. 2010). The stress of eutrophication and associated reductions in light available as a bay-wide stressor is evident by the distinct and continued loss of *Z. marina* from the system throughout the 2000s and early 2010s (Fertig et al. 2014).

In response, the protection of the dominant seagrass species in BB, *Z. marina*, has been made a priority by both state (New Jersey Department of Environmental Protection) and federal agencies (Barnegat Bay Partnership, NJ Seagrant). Despite these efforts, *Z. marina* populations in BB-LEH have continued to decline (Kennish et al., 2007; Lathrop and Haag, 2011). Restoration

attempts in BB have increased in response to continued declines (Bolonga and Sinnema, 2012); however, efforts have not been done at the scale necessary to significantly increase *Z. marina* populations. In order to increase restoration efficiency, effectiveness, and success a better understanding of bed resiliency to perturbations, as well as loss and recovery processes within established seagrass beds is required (Duarte 2002; Orth et al. 2006).

Ecological models are useful tools in quantitative analysis of complex ecosystems such as SAV beds. Through models, the response of *Z. marina* to stressful environmental conditions such as low light, high nutrients, and high temperatures has been quantified under a variety of situations (Bach 1993; Aveytua-Alcázar et al., 2008). While these models provide insight into the effects of environmental stressors on *Z. marina* production, the capacity to accurately model population responses to stressful conditions is limited by focusing solely on vegetative reproduction and ignoring sexual reproduction (van Lent 1995). Recent research has shown that sexual reproduction plays a significant role in *Z. marina* bed recovery from large scale declines (Plus et al. 2003; Greve et al. 2005); therefore, a key component of the bed loss and recovery dynamic may be missing from *Z. marina* production models when sexual reproduction is excluded. The *Z. marina* model developed by Jarvis et al. (2014) is especially suited for application in areas marked by significant decline (i.e., BB-LEH) because it includes seed production, seed-bank density, seed viability, and germination. Information gathered from model simulations will provide a new approach for managers to assess areas for restoration or preservation of *Z. marina* in BB-LEH.

OBJECTIVES

The goal of this study was to refine and apply the model developed by Jarvis et al. (2014) to quantify SAV resiliency to perturbations through modelling loss and recovery processes within established SAV beds in BB-LEH.

The specific objectives for this project were to**:**

1. Refine and calibrate the model developed by Jarvis et al. (2014) to project the response of *Z. marina* beds in BB-LEH to stressful environmental conditions.

2. Use the calibrated model to quantify possible effects of reduced nutrient loading rates (i.e. present day, less 10%, less 30%) on seagrass survival of two existing *Z. marina* sites along a nutrient loading gradient in BB-LEH.
3. Use the calibrated model to determine suitability of three *Z. marina* sites along a nutrient loading gradient for restoration using the model and NJDEP comprehensive water quality data.

By focusing on interactions between SAV and their surrounding environment, the model described here may be developed into a tool to select suitable SAV restoration sites in BB-LEH as well as to quantify impacts of proposed water quality changes (i.e. reduction of watershed nutrient loading) on SAV abundance and persistence.

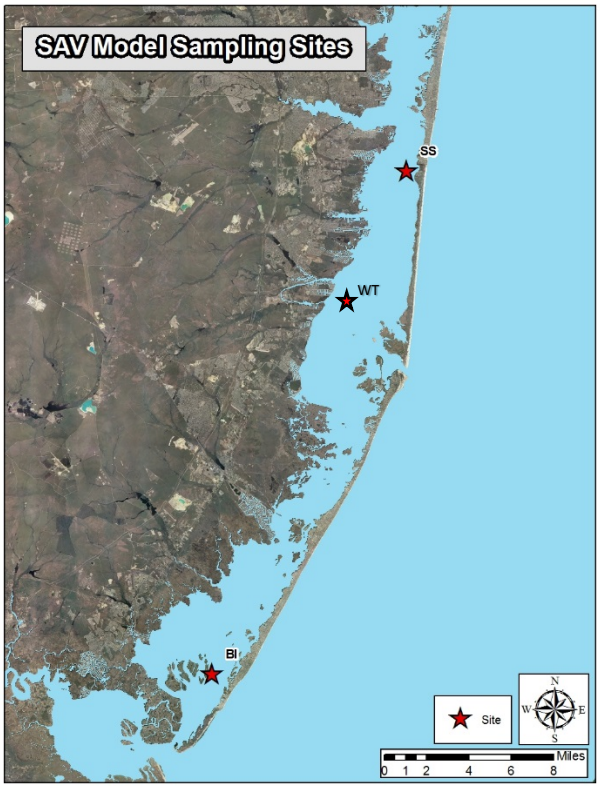

Figure 1. Map of sampling and modeling sites located in Little Egg Harbor (Barrel Island - BI) and Barnegat Bay (Waretown-WT, Seaside Park - SS).

METHODS

Direct abiotic and biotic measurements were collected from two sites in BB-LEH (Barrel Island – BI N 39.5561°, W 74.2727°; Seaside Park - SS N 39.7980°, W 74.0919°; Figure 1) to refine and apply the *Z. marina* model developed by Jarvis et al. (2014) to quantify loss and recovery processes within established SAV beds in the NJ Coastal Bays region. Sites were selected based on historical seagrass cover and the development of the surrounding area (Kennish et al., 2008). Abiotic and biotic data were collected independently at both sites from August 2012 – November 2013.

Sediment Characterization:

At both sites, five sediment cores (10.4 cm diameter by 10 cm depth) were collected monthly to quantify percent organic content and sediment exchangeable pore water nutrients (ammonia (NH_4 + NH_3), nitrite plus nitrate (NO_2 + NO_3), and orthophosphate phosphate (OPO_4)).

The upper 6 cm of the core was removed then subdivided in to 2 cm sections. Percent organic matter was determined by drying a sediment sub-section at 60°C until a constant dry weight (DW) was reached. Samples were then weighed, combusted at 500°C for 5 h, and weighed again. Percent organic matter was calculated as the difference in weights (Erftemeijer and Koch 2001).

Sediment exchangeable nutrients were extracted with a volume KCl (2 M) equal to twice the sediment volume, shaken on a rotary shaker for 1 h at room temperature, centrifuged 6 min at 1252 g, filtered (Gelman Supor, 0.45 µm), and frozen in sterile polypropylene centrifuge tubes until analysed for DIN ($NH_4^+ + NO_x$) and DIP (PO_4^{-3}) . NH_4^+ was determined by the technique of Zhang (1997), NO_x as per Zhang, Orntner and Fisher (1997) and DIP (PO_4^{-3}) as per Zimmermman and Keefe (1997), on a SEAL AA3 segmented flow nutrient auto analyser using SEAL autoanalyzer multitest applications MT-19 (Seal 2012a, 2012b, 2011). Since the SEAL method (SEAL, 2011) uses sodium dodecyl sulfate (SDS) as a surfactant, which is not compatible with high concentrations of KCL in the extract, the sediment phosphate preparation was modified in the following way. Sediment extracts were diluted 1:10 with 0.1 M SDS and centrifuged to remove the precipitate and excess KCL before running on the SEAL autoanalyzer. This modification was shown to have no effect on the detection of phosphate.

Water Quality Parameters:

Bottom water temperature (°C), salinity, chlorophyll a, (µg l^{-1}), and turbidity (NTU) was recorded at both BI and SS every 15 minutes during ice free periods from June 2012 to October 2013 with a Yellow Spring Instruments, Inc. model 6600 sonde deployed 4 cm above the sediment surface. Data sondes were housed in anti-fouling PVC pipes and managed according to the National Estuarine Research Reserve (NERR) Central Data Management Office (CDMO) protocols for the calibration, deployment, and QA/QC of collected data (Small et al. 2013). When data was not available at BI or SS water quality data from the Jacques Cousteau National Estuarine Research Reserve Buoy 126 (N 39.5079°, W 74.3385°); and United States Geological Survey (USGS) Station 1408167 (N 39.9157°, W 74.1094°) were used respectively (Appendix A). This is includes data collected from May to July 2012 prior to the establishment of the water quality monitoring stations in BI and SS and for periods of < 2 consecutive weeks due to sonde or probe failure. Total available photosynthetically active radiation (PAR µE m^{-2} s^{-1}) was also recorded every 15 minutes throughout the sampling period at both sites with a LI-COR, Inc. sensor (LI-190SA).

In addition, three replicated water samples were collected monthly throughout the duration of the study from each site and were filtered and analyzed for chlorophyll a (Strickland & Parsons, 1972) and total suspended solids (TSS). TSS was quantified from a well-mixed sample of known volume. The sample was filtered through a GF/F filter and the residue retained on the filter was dried to constant weight at 103–105°C and reported as mg TSS L^{-1}. Water samples were also filtered (Gelman Supor, 0.45 μm), and frozen until analyzed for NH_4^+ by the technique of Zhang (1997), NO_x as per Zhang, Orntner and Fisher (1997) and DIP (PO_4^{-3}) as per Zimmerman and Keefe (1997), on a SEAL AA3 segmented flow nutrient auto analyser using SEAL autoanalyzer multitest applications MT-19 (Seal 2012a, 2012b, 2011).

Seagrass biomass

Five *Z. marina* biomass cores (22 cm diameter, 10 cm depth) were randomly collected monthly from all sites. Samples were sieved (1.0 cm mesh box sieve) and washed clean of sediment in the field and all plant material was immediately transported back to the lab for processing on ice (Sidik et al., 2001). The samples were then separated by species and into vegetative or flowering shoots. Shoots covered in epiphytes were scraped with single edge razor blade held 90° to the leaf surface. The total number of shoots (vegetative and flowering) and the total number of seeds per flowering shoot in the sample were then counted. Following density measurements, the leaves were separated from the rhizome directly below the leaf sheath into aboveground and belowground biomass. All samples were dried in an air circulating oven at 50°C for a minimum of 24 hours. Each sample was then weighed a minimum of 3 times until the sample reached a constant dry weight (weight loss < 0.5 mg). Biomass is reported as g dry weight (DW) m^{-2}; (Duarte and Kirkman, 2001).

Macroalgal biomass

Five macroalgal biomass samples (0.25 m^2 quadrat) were randomly collected monthly from both sites. All algae samples were separated by species and rinsed with deionized water. Once identified, algae biomass was placed into the appropriate aluminum foil envelope (by species) and the weight recorded. All samples were dried in an air circulating oven at 50°C for a minimum of 24 hours. Each sample was then weighed a minimum of 3 times until the sample reached a constant dry weight (weight loss < 0.5 mg). Biomass is reported as g dry weight (DW) m^{-2}; (Sidik et al., 2001).

Epiphyte biomass

Fifteen individual *Z. marina* shoots were randomly selected from each site and transported back to the lab in plastic bags to determine epiphyte biomass (Kendrick and Lavery, 2001). Individual seagrass shoots were separated into individual leaves and rinsed with deionized water. Larger epiphytes were removed from the leaves by hand or with forceps. Each individual leaf was then scraped on both sides with a single edge razor blade held 90° to the leaf surface. The total number of leaves for each sample was counted and the leaf length and width were also recorded. All material scraped off of the leaves was rinsed into pre-weighed aluminium pans, weighed and then placed in an air circulating oven at 50°C for a minimum of 24 hours. Each sample was weighed a minimum of 3 times using the same scale or until the sample reached a constant dry weight (weight loss < 0.5 mg). Biomass was recorded as g Dry Weight (g DW) leaf area cm^{-2} (Kendrick and Lavery. 2001).

Seagrass seed bank density and viability

The maximum potential number of seeds produced at each site was calculated monthly as the product of the average number of seeds per reproductive shoot and the average number of reproductive shoots m^{-2} (van Lent and Verschuure 1994). At each site, five additional sediment cores (10.4 cm diameter by 10 cm depth) were collected to quantify total and viable sediment seed bank densities. All cores were wet-sieved (0.5 mm mesh) to separate the seeds from the rest of the samples. The seeds were then counted and stored overnight in ambient seawater at 4 °C. Viability of all collected seeds was tested using tetrazolium staining methods (Lakon, 1949; McFarland and Shafer, 2011). Seed embryos were removed from their seed coats and soaked in a 1% tetrazolium chloride solution for 24 h before examination on a dissecting scope at 10× magnification (Conacher et al. 1994). Seeds with a pink to brown stained cotyledon and axial hypocotyl were considered viable (Taylor 1957). The percentage of viable seeds retained within the sediment seed bank was quantified compared to the total number of seeds collected in the seed bank at each site.

Model Description:

Data from BI in 2012 was used to calibrate the *Z. marina* production model developed by Jarvis et al. (2014) for *Z. marina* populations in the Chesapeake Bay to BB-LEH (Figure 2) using the STELLA v:10 platform (ISEE Systems, Lebanon, NH). The initial model simulation period was run

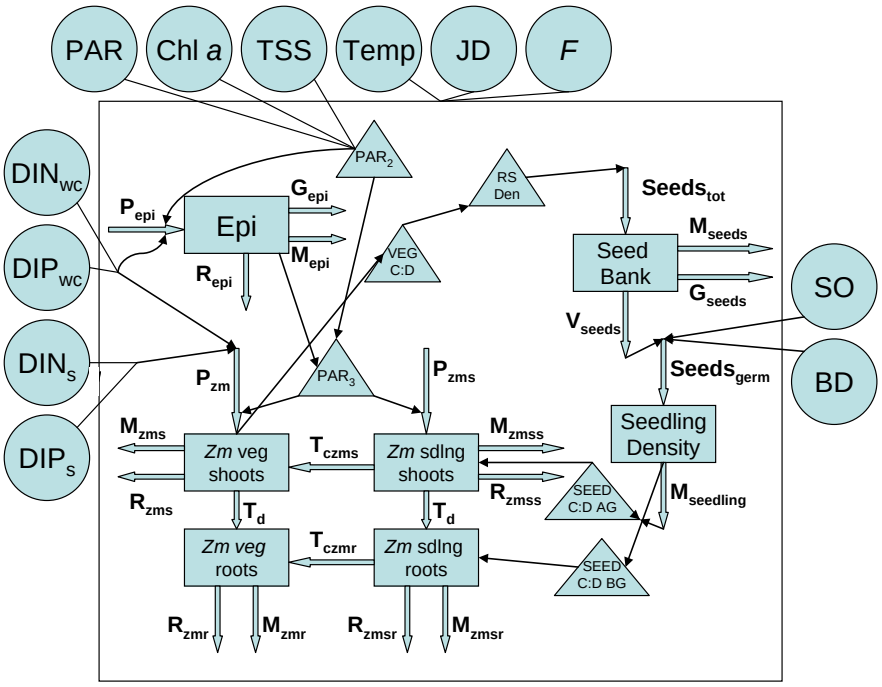

Figure 2. Conceptual diagram for *Zostera marina* production and sexual reproduction model. Circles = forcing functions, triangles = modifiers, squares = state variables, thick arrows = flows, and thin arrows = iterations. Temp, JD, and F affect multiple processes so are not connected to minimize diagram complexity**.**

for one year (May 1, 2012 through April 30, 2013) with a time step (dt) of 0.125 days. Governing equations for *Z. marina* vegetative and seedling shoot biomass are balanced between gains through photosynthesis and losses due to mortality, respiration and translocation to roots and rhizomes (Table 1). The state variable in the model includes epiphyte biomass (C_{epi}) and *Z. marina* vegetative shoot biomass (C_{zms}), vegetative root biomass (C_{zmr}), seed-bank density (Zm_{seed}); seedling density (Zm_{sd}); seedling shoot biomass (C_{zmss}), and seedling root biomass **(**C_{zmsr}). Forcing functions include water temperature (°C), photoperiod (F), photosynthetically active radiation (PAR, µE m^{-2} s^{-1}), water column chlorophyll *a* (µg l^{-1}), total suspended solids (mg l^{-1}), water column and sediment dissolved inorganic nitrogen (DIN_{WC}, DIN_S µmol l^{-1}), water column and sediment

dissolved inorganic phosphorus (DIP_{WC}, µmol l^{-1}), sediment hydrogen sulfide content (H_2S_s, µmol l^{-1}), sediment carbon content (SO, TOC, % organic), and seed burial depth (BD, cm).

The model was calibrated for BB-LEH using data from the literature and in situ measurements of water column, sediment, and *Z. marina* data collected at bi-weekly to monthly intervals from May 2012 to April 2013 at BI (Appendices A-C). During the calibration process the changes were made to shoot and root/rhizome mortality and respiration rates and flowering shoot densities after forcing functions were updated to represent local water quality and sediment conditions (Tables 2 and 3). This highlights the potential large scale utility of the model to sites throughout BB-LEH as it was flexible enough to reliably project above and below ground *Z. marina* biomass measures in both the Chesapeake and BB-LEH systems. The model was then verified using data from BI from April to October 2013. The model was not validated using the SS data due to the co-dominance of *Ruppia maritima* of the meadow (Appendix A). As the effects of multiple seagrass species are not accounted for in the model, the data for SS was used for model scenarios only and not for verification. Parameter values were left unchanged for verification, but forcing functions were updated to reflect the appropriate sites data (Appendices B-C). Comparisons were made between computed and observed values on a monthly average basis. Following validation, the model simulation was run for a minimum of three years to quantify impacts of scenarios on long-term bed persistence. The sensitivity of base model conditions to all parameter estimates and forcing functions was analyzed by sequentially varying values by ± 5, 10, and 20%.

Table 1. Governing equations for (1) epiphyte biomass ($C_{epi;}$ g C m^{-2}); (2) *Z. marina* vegetative shoot biomass ($C_{zms;}$ g C m^{-2}); (3) *Z. marina* vegetative root/rhizome biomass ($C_{zmr;}$ g C m^{-2}); (4) *Z. marina* seed-bank density (Zm_{seeds}; seeds m^{-2}); and (5) *Z. marina* seedling density (Zm_{sd}; seedlings m^{-2}). Terms include P = production; M = mortality; G = grazing; R = respiration; T_d = translocation down; T_{czmss} = transfer of seedling biomass to vegetative shoot biomass; T_{czmsr} = transfer of seedling root/rhizome biomass to vegetative root/rhizome biomass; $Seeds_{germ}$ = germinated seeds; $Seeds_{prod}$ = total seeds produced; $Seeds_{via}$ = viable seeds; PR_{seeds} = seed predation; Zm_{sd} = germinated seedling density

Differential Equations	
(1)	$C_{epi} = C_{epi}\ (t\text{-}dt) + (P_{epi} - M_{epi} - G_{epi} - R_{epi}) * dt$
(2)	$C_{zms} = C_{zms}\ (t - dt) + (P_{zms} + T_{czmss} - M_{zms} - R_{zms} - T_d) * dt$
(3)	$C_{zmr} = C_{zmr}\ (t - dt) + (T_d + T_{czmsr} - M_{zmr} - R_{zmr}) * dt$

(4) $Zm_{seeds} = Zm_{seeds}\ (t - dt) + (Seeds_{prod} - M_{seeds} - PR_{seeds}) * Seeds_{via} * dt$

(5) $Zm_{sd} = Zm_{sd}\ (t - dt) + (Seeds_{germ} - M_{zmsd}) * dt$

intervals from May 2012 to April 2013 at BI. The parameter estimates for the main growth model are in Table 2 and for the sexual reproduction sub-model in Table 3. The model was then verified using data from BI from April to October 2013. The model was not validated using the SS data due to the co-dominance of *Ruppia maritima* of the meadow (Appendix A, Fig. 6). As the effects of multiple seagrass species are not accounted for in the model, the data for SS was used for model scenarios only and not for verification. Parameter values were left unchanged for verification, but forcing functions were updated to reflect the appropriate sites data. Comparisons were made between computed and observed values on a monthly average basis. Following validation, the model simulation was run for a minimum of three years to quantify impacts of scenarios on long-term bed persistence. The sensitivity of base model conditions to all parameter estimates and forcing functions was analyzed by sequentially varying values by ± 5, 10, and 20%.

Table 2. Parameter estimates for the *Z. marina* production model. References: 1 = calibration within the model; 2 = Buzzelli et al., 1999; 3 = Cerco and Moore, 2001; 4 = Madden and Kemp, 1996; 5 = Bach, 1993; 6 = Jarvis et al. 2014. Table modified from Jarvis et al. 2014.

Abbrev.	Description	Units	Value	Ref
BMR_{epi}	epiphyte basal metabolic rate	d^{-1}	0.047	2
JD	Julian Day	d^{-1}	0-365	
K_{gepi}	epiphyte grazing constant	d^{-1}	0.01	6
Khn_{epi}	epiphyte N half saturation constant	µmol N m^{-3}	1.79E-09	3

$Khns_{zm}$	*Z. marina* N half saturation constant sediment	µmol N m^{-3}	2.86E-09	3
$Khnw_{zm}$	*Z. marina* N half saturation constant water	µmol N m^{-3}	7.14E-10	3
Khp_{epi}	epiphyte P half saturation constant	µmol P m^{-3}	7.14E-11	3
$Khps_{zm}$	*Z. marina* P half saturation constant sediment	µmol P m^{-3}	7.14E-09	3, 4
$Khpw_{zm}$	*Z. marina* P half saturation constant water	µmol P m^{-3}	4.35E-10	3
$KPAR_{epi}$	epiphyte PAR half saturation constant	µE m^{-2} s^{-1}	90	4
$KPAR_{zm}$	*Z. marina* PAR half saturation constant	µE m^{-2} s^{-1}	57.5	3
KtB_{epi}	epiphyte respiration constant	°C	0.069	2
MR_{epi}	epiphyte mortality constant	d^{-1}	0.007	6
MR_{zmr}	*Z. marina* root mortality constant Jan - July	d^{-1}	0.0085	1
	Z. marina root mortality constant July - Dec	d^{-1}	0.031	1
MR_{zms}	*Z. marina* shoot mortality constant Jan - July	d^{-1}	0.002	1
	Z. marina shoot mortality constant July - Dec	d^{-1}	0.0032	1
RR_{zmr}	*Z. marina* root respiration at 20 °C	d^{-1}	0.00005	1
$Topt_{epi}$	epiphyte optimum temperature for production	°C	25	2
$Topt_{zm}$	*Z. marina* optimum temperature for production	°C	22.5	3
T_{zms}	*Z. marina* shoot to root transfer	unitless	0.3	3
WD	Water Depth	m	0.5	1
Θ_{zmr}	*Z. marina* root respiration constant	unitless	1.25	5

Table 3. Parameter estimates for the *Z. marina* reproduction model. References: 1 = Jarvis et al. 2014; 2 = Harwell, 2000; 3 = Fishman and Orth, 1996; 4 = Bintz and Nixon 2001. Table modified from Jarvis et al. 2014.

Abbrev	Description	Units	Value	Ref
MR_{seeds}	seeds mortality rate	d^{-1}	0.1	1
M_{zmsd}	*Z. marina* shoot mortality rate	unitless	0-1	4
PR_{seeds}	seeds predation rate	d^{-1}	0.33	3
$Seedling_{RD:C}$	*Z. marina* seedling density to roots conversion factor	g C $shoot^{-1}$	0.0384	1
$Seedling_{SD:C}$	*Z. marina* seedling density to shoots conversion factor	g C $shoot^{-1}$	0.0374	1
$Seeds_{sh}$	seeds per reproductive shoot	seeds $shoot^{-1}$	10	2
$Veg_{C:D}$	*Z. marina* shoot carbon to density	g C $shoot^{-1}$	0.0168	1
VR_{seeds}	seeds viability rate	d^{-1}	0.4	1
Zm_{rsf}	reproductive shoot density	unitless	0.03	n = 120 shoots

Model Scenarios:

Once the model was calibrated and verified, model scenarios were run at both SS and BI with reductions in nutrient loading rates (present day, less 10%, less 30%) to help quantify the possible impacts of water column nutrient reductions on BB-LEH seagrass survival and reestablishment. In addition, the model was run with water quality data, specifically chlorophyll a, turbidity, and water column temperatures, collected every 15 minutes as part of the NJDEP comprehensive ambient water quality monitoring network from three sites along a gradient of declining nutrient loading to determine the suitability of potential restoration sites. The first potential restoration site was SS and served as the site with most significant amount of nutrient loading due to the high population density in the area and relatively lower daily seawater exchange. The second potential restoration site, was located off the coast of Waretown, NJ near the Oyster Creek Channel (WT; NJDEP site ID BB07a) and served as the intermediate site due to the high population density and greater daily tidal exchange with the Atlantic Ocean. The final potential restoration site used the data collected as a part of this project at BI due to its location in a less populated area and greater connectivity with the Atlantic Ocean (Figure 1). The model scenarios were run with water quality data from May 2012 through December 2013 using light and sediment nutrient data from Seaside for SS and WT model runs, while BI used light and sediment data recorded at that site. Initial modelling conditions were set with 0 g *Z. marina* biomass, 0 g epiphyte biomass, and 0 g macroalgal biomass. Restoration scenarios were based on seed broadcasting methodology and each site was seeded with 50, 100, 250, or 500 seeds m^{-2} to

determine if initial seed densities impact overall restoration success. All modelling runs were run for a minimum of 3 years.

RESULTS

Model Calibration

The model captured the overall seasonal trends in above ground biomass and under typical conditions (i.e. ambient nutrient conditions) it produced repeatable annual biomass cycles with or without the inclusion of sexual reproduction (data not shown). Field estimates of biomass (reported as mean ± S.E.) in 2012 at BI ranged seasonally from 2.1 ± 1.9 g C m^{-2} to 39.7 ± 5.0g C m^{-2} while the model output ranged from 2.2 g C m^{-2} to 38.3 g C m^{-2} (Figure 3). The model consistently over-predicted *Z. marina* biomass between May to September 2012 with an average percent error of 52 ± 9% (Figure 3). However, the largest deviation occurred in October 2012 where the model error was 565% due to a significant over prediction of biomass in the model (14 g Cm^{-2}) compared to observed values (2.1 ± 2.0 g C m^{-2}).

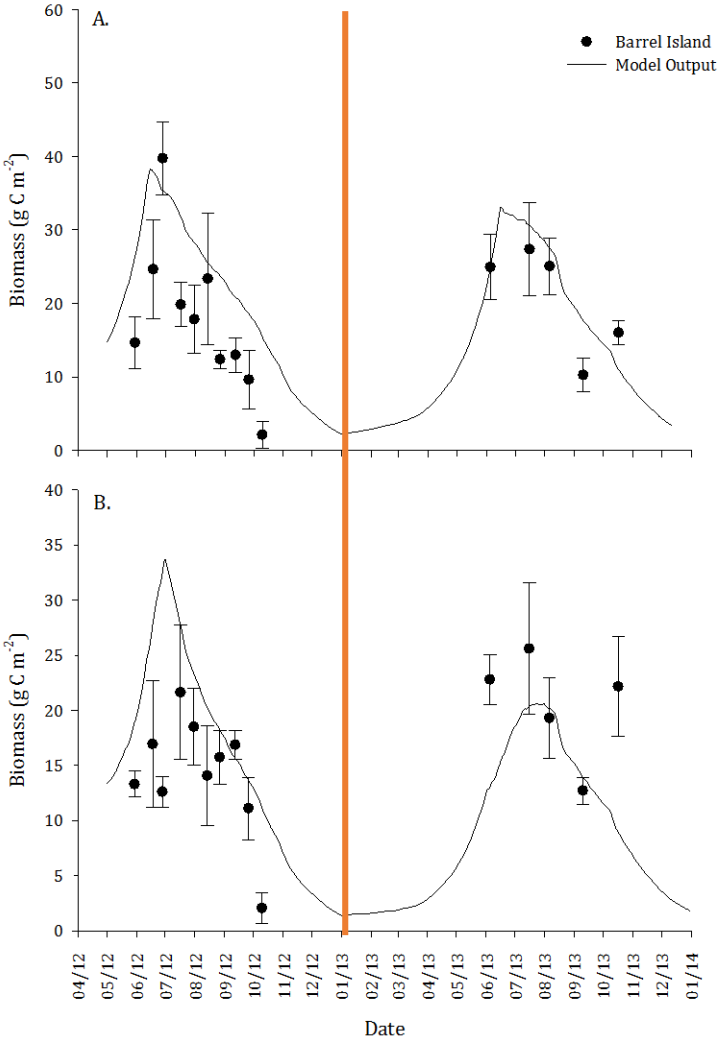

Figure 3. Calibration and verification data of *Zostera marina* above-ground (A) and below-ground (B) biomass model (black line) with observed BI data (circles). Observed data are given in monthly means ± SE. The orange line denotes separation between calibration and verification datasets.

Below ground biomass was also consistently over-predicted by the model, but to a smaller extent than above ground biomass. Observed belowground biomass at BI ranged from 2.1 ± 1.4 g C m^{-2} to 21.6 ± 6.1 g C m^{-2} while modeled values were similar and ranged from 1.4 g C m^{-2} to 33.7 g C m^{-2} (Figure 3). As with

aboveground biomass, the model over-predicted belowground biomass values throughout the calibration period as percent error from August to September averaged 27 ± 5 % and 81% in October. During model calibration both above and below ground biomass respiration, mortality and carbon translocation constants were altered systematically by increasing and decreasing all factors individually and combined to reduce the biomass error. The smallest error corresponded to the literature values reported in Table 2.

In 2012 observed total seed bank density varied seasonally and ranged from 8 ± 8 seeds m^{-2} to 71 ± 25 seeds m^{-2} with viable seeds found only in May, July and August (Table 4). The model significantly over-predicted germinable seed densities of 2,682 seeds m^{-2}. Maximum viable seedbank densities predicted by the model were also greater than observed values. Only 4% of *Z. marina* seeds were viable in July and August 2012 (3 ± 0 seeds m^{-2}) with no other seeds observed in the ambient seed bank during this time period. In the calibration model maximum viable seed bank densities of 71 seeds m^{-2} were produced in 2012.

Table 4. *Zostera marina* total and viable seed bank density at BI. Values are means ± SE.

Date	Total Seed Density (m^{-2})	Viable Seed Density (m^{-2})
05/18/12	31 ± 18	4 ± 4
06/18/12	55 ± 23	0 ± 0
07/31/12	31 ± 18	3 ± 0
08/14/12	71 ± 25	3 ± 0
08/27/12	34 ± 15	0 ± 0
10/10/12	8 ± 8	0 ± 0
11/12/12	31 ± 14	0 ± 0
12/13/12	39 ± 15	0 ± 0
01/04/13	39 ± 15	0 ± 0
03/11/13	102 ± 38	0 ± 0
05/06/13	118 ± 26	0 ± 0
05/22/13	31 ± 14	0 ± 0
06/08/13	16 ± 11	0 ± 0
07/16/13	118 ± 35	2 ± 2
09/03/13	0 ± 0	0 ± 0
10/17/13	16 ± 11	0 ± 0

Model Verification

The model accurately predicted above and below ground biomass values in BI *Zostera marina* beds in 2013 (Figure 3). Similar to the base model runs, the verification runs were the most accurate in describing above and below ground biomass between May and September in 2013 and significantly over-predicted biomass in October. As with above ground biomass, the model over predicted below ground biomass throughout the verification period.

Similar to the base model runs, the model over-predicted maximum total seed bank densities at 2,587 seeds m^{-2} compared to ambient maximum seed bank densities of 118 ± 26 seeds m^{-2} (Table 4). Maximum viable seed-bank densities predicted by the model were also greater than observed values. Viable seeds were only found in the ambient sediment seed-bank in BI in July 2013 with mean densities of 2 ± 2 seeds m^{-2} (Table 4). In the verification model runs 69 seeds m^{-2} were produced in 2013.

Sensitivity Analyses

Parameter Effects

Epiphyte biomass was most sensitive to changes in respiration and least responsive to grazing and mortality (Table 5). Z*ostera marina* above ground biomass was also most sensitive to changes in production while both above and below ground biomass were sensitive to shoot to root translocation and mortality rates. Seedbank densities were more sensitive to factors that influenced seed production (total shoot carbon to density ratio, reproductive shoot densities) rather than seed density (i.e. predation, mortality, and viability). Once in the seed-bank, seed germination was highly sensitive to the number of viable seeds and seedlings. Overall seed germination was more sensitive to increasing than decreasing seed viability while the effects of seed mortality were similar across analyses (Table 5).

Forcing Functions

All state variables were sensitive to changes in temperature and total available light (Table 6). *Zostera marina* state variables were more sensitive to decreases compared to increases in water temperature. Effects of reductions in total available light (PAR_1) as it entered the water column on all state variables seemed to be driven by total suspended solids concentrations rather

than chlorophyll *a.* Seed-bank density was the most sensitive to increased total suspended solid concentrations in the water column and to changes in light after it was reduced by both water column light attenuation factors and by epiphytic growth on *Z. marina* blades (PAR_3; Table 6).

Table 5. Minimum sensitivity simulation (± 5, 10, 20 %) for model parameters which resulted in significant variation (≥ 10 %) of state variables relative to base model concentrations. Non-significant values are denoted with (--).

State Variable	Parameter	Min % Change
Epiphytes	PR_{epi}	± 5
	P_{max}	± 5
	K_{gepi}	--
	MR_{epi}	--
	BMR_{epi}	± 5
	KtB_{epi}	± 10
Z. marina shoots	PR_{zm}	± 5
	P_{max}	± 5
	T_{czms}	--
	MR_{zms}	± 5
	R_{zms}	--
	T_d	+ 5
Z. marina Root/Rhizome	T_d	± 10
	T_{czmsr}	--
	MR_{zmr}	± 10
	RR_{zmr}	--
	R_{zmr}	--
Seed-bank	$Veg_{D:C}$	±10
	Fs_{den}	±10
	MR_{seeds}	--
	PR_{seeds}	--
	VR_{seeds}	--
Seed Germination	V_{seeds}	± 5
	M_{sd}	± 5

Table 6. Minimum sensitivity simulation (± 5, 10, 20 %) for model parameters which resulted in significant variation (≥ 10 %) of forcing functions relative to base model concentrations. Non-significant values are denoted with (--).

Forcing Function	Parameter	% Change
Temperature	Epi	± 5
	Zm Shoots	-10
	Zm Roots	-10
	Seed-bank	+ 5
	Seed Germination	±5
PAR_1	Epi	± 5
	Zm Shoots	± 10
	Zm Roots	± 10
	Seed-bank	+ 10
	Seed Germination	+ 10
PAR_2	Epi	± 5
	Zm Shoots	± 10
	Zm Roots	± 10
	Seed-bank	± 10
	Seed Germination	± 10
PAR_3	Epi	± 5
	Zm Shoots	+ 5
	Zm Roots	+ 5
	Seed-bank	+ 10
	Seed Germination	+ 5
Chlorophyll *a*	Epi	--
	Zm Shoots	--
	Zm Roots	--
	Seed-bank	--
	Seed Germination	
TSS	Epi	- 5
	Zm Shoots	-10
	Zm Roots	± 20
	Seed-bank	± 20
	Seed Germination	± 20

Model Scenarios

Nutrient Reductions

For both the low nutrient (BI) and high nutrient (SS) scenarios reductions of water column and sediment nutrients up to 30% below ambient conditions resulted in no change in above or

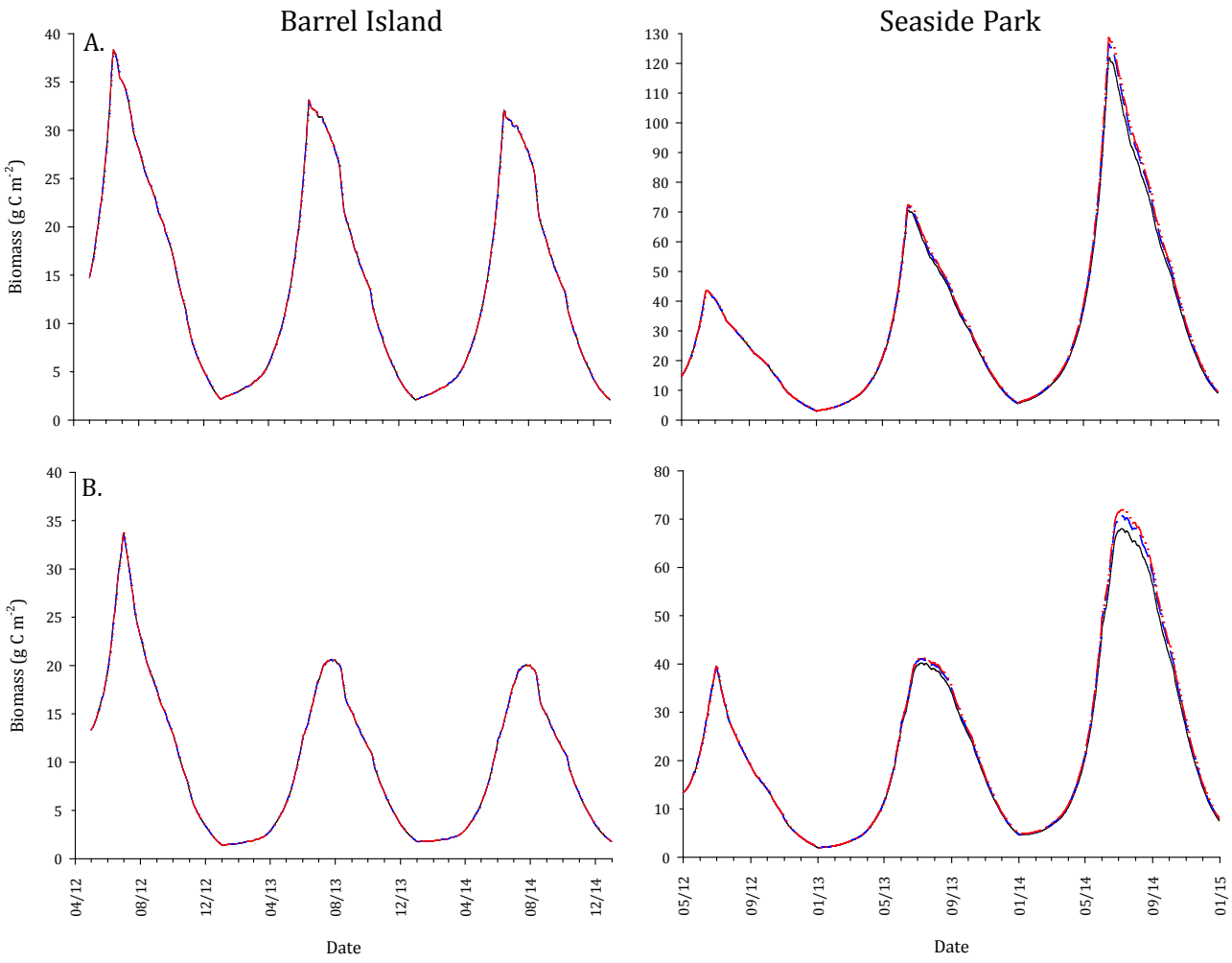

Figure 4. Above (A) and below (B) ground biomass for *Zostera marina* shoots in BI and SS respectively. Biomass values are given under modeled ambient nutrient conditions (black line), ambient -10% (blue dashed) and ambient -30% (red dot-dashed lines) conditions. Observed data are given in daily means of modelled data.

below ground biomass (Figure 4.). Above ground biomass increased to a greater extent in SS compared to BI regardless of nutrient scenario. Below ground biomass responded similarly to above-ground biomass with no significant change in biomass with reductions in nutrients (Figure 4). Maximum total and viable seed densities were similar across treatments with no significant effect of nutrient reduction projected in any scenario (Table 7).

Restoration Site Selection

Seagrass became established at all three sites selected as potential *Z. marina* restoration locations in all model projections (Figure 5). However, there was variation in biomass between sites and seed density treatments, with the greatest above (max = 70.4 g C m^{-2}) and below ground (max = 44.8 g C m^{-2}) biomass projected for WT under ambient water quality conditions using 500 seeds m^{-2} as initial seed densities. Maximum *Z. marina* above ground (max = 49.8 g C m^{-2}) and below ground biomass was 34-36% lower at SS compared to WT. BI scenarios supported the lowest above ground (max = 20.3 g C m^{-2}) and below ground biomass (max = 13.6 g C m^{-2}) with values 59-84% less than WT and SS. Despite the large range in maximum above and below ground biomass values, all biomass projections were within the range observed for mid-Atlantic *Z. marina* populations (Jarvis et al. 2012, Fertig et al. 2013).

Initial seed densities also affected projected above and below ground biomass values. The greatest biomass projections occurred in scenarios with initial seed densities of 500 seeds m^{-2} across all sites (Figure 5). For SS both maximum above and below ground biomass values were similar (<10% difference) for the 50, 100 and 250 seeds m^{-2} treatments. When initial seed densities were increased from 50 – 250 seeds m^{-2} to 500 seeds m^{-2} maximum above ground biomass increased from 22 – 25% and below ground biomass increased from 44-108%. Although projections using 500 seeds m^{-2} were also greatest for both WT and BI there was more variation between lower density treatments. For example, maximum *Z. marina* biomass in WT increased between 18-28% when seed densities were increased from 50 to 250 and 100 seeds m^{-2} and unexpectedly decreased by 7% when seed densities were increased from 100 to 250 seeds m^{-2}. Similar trends were observed in *Z. marina* below ground biomass at this site (Figure 4). At BI projections resulted in <30% change in *Z. marina* maximum above and below ground biomass between the two low (50 and 100 seeds m^{-2}) and between the two high (250 and 500 seeds m^{-2})

treatments. However, large variations were observed in both the above ground (53 – 105 %) and below ground biomass (51-90%) between the low and high initial seed density treatments.

Total and viable seed bank densities were only quantified during the third year of the model scenario due to the delay in seed production by perennial *Z. marina* shoots until their second year of growth. Both total and viable maximum seed densities varied <25% between all scenarios (Table 7). BI was projected to produce the second largest viable and total seed densities; however, there was larger variation between treatments (3-105%) and the greatest densities occurred in the 500 seeds m^{-2} projections. Projected maximum viable and total seed densities also varied to a large extent between WT seed density treatments (8 – 170%). As with both Seaside and BI projections maximum viable and total seed bank densities were produced when the model was initiated with 500 seeds m^{-2} (Table 7).

Table 7. Maximum total and viable *Z. marina* seed densities projected for all nutrient (A) and restoration (B) scenarios.

A. Site		**Ambient**	**Amb - 10%**	**Amb - 30%**
Viable				
Seaside Park		580	598	608
Barrel Island		230	230	230
Total				
Seaside Park		22,467	23,240	23,590
Barrel Island		8,940	8,940	8,940
B. Site	**50 seeds m^{-2}**	**100 seeds m^{-2}**	**250 seeds m^{-2}**	**500 seeds m^{-2}**
Viable				
Seaside Park	181	177	179	221
Waretown	40	51	47	108
Barrel Island	68	66	104	136
Total				
Seaside Park	7,031	6,848	6,932	8,585
Waretown	1,552	1,988	1,836	4,188
Barrel Island	2,654	2,578	4,053	5,286

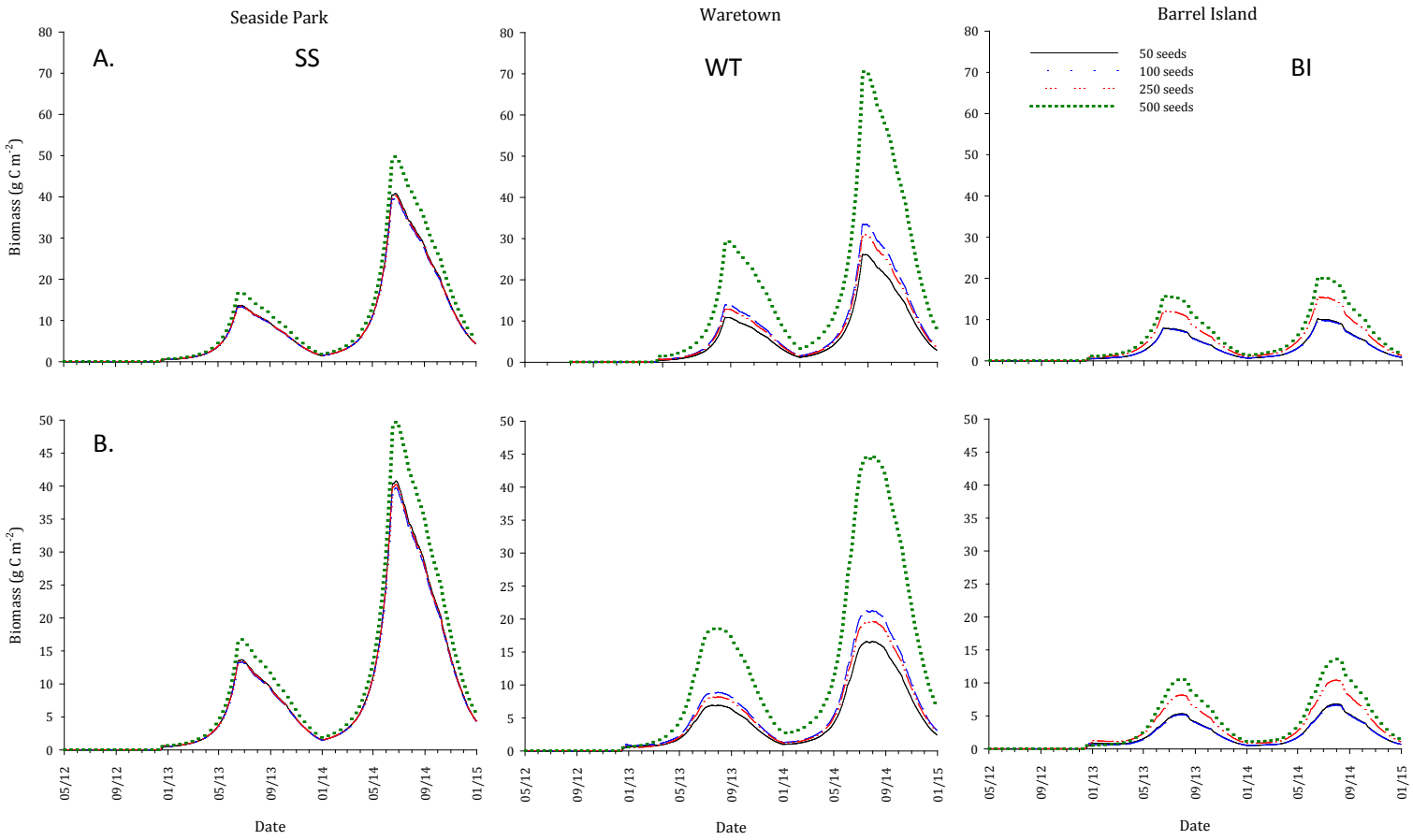

Figure 5. Above ground (A) and below ground biomass (B) for potential restoration sites at SS, WT and BI locations for 2012 – 2014 with 50 seeds m^{-2} (black solid line), 100 seeds m^{-2} (blue dashed line), 250 seeds m^{-2} (red short dashed and dotted line) and 500 seeds m^{-2} (green dotted line).

DISCUSSION

The model presented here reproduced the general observed trends in above and below ground *Zostera marina* biomass in Barnegat Bay – Little Egg Harbor in 2012 – 2013. Given adequate water quality (total suspended solids, chlorophyll *a*, total available light), sediment (% organic content), and nutrient data (water column and sediment DIN, DIP) the model calibrated here was shown to accurately project both the magnitude and seasonality of *Z. marina* above and below ground biomass growth in this system. The potential of the model to be used as a research/management tool in BB-LEH was illustrated by both the nutrient reduction and restoration site selection scenarios. As SAV populations continue to decline in BB-LEH (Fertig et al. 2013) the ability to determine where (based on site suitability) and when (based on response to reductions in nutrient loading) *Z. marina* restoration can be more effectively conducted in BB-LEH is critical to increase the resilience and response of these beds to stressful environmental conditions.

Model Performance

The *Z. marina* model developed for the York River in the Chesapeake Bay by Jarvis et al. (2014) was refined and calibrated to project the response of *Z. marina* beds in BB-LEH to stressful environmental conditions with minimal change to the original model. Interestingly the model consistently under-predicted above and below ground biomass in Chesapeake Bay *Z. marina* populations during the second half of the growing season (August – October; Jarvis et al. 2014). However, in BB-LEH the model over-predicted *Z. marina* biomass during this same time period. This may be attributed to a reduction in temperature limitation in *Z. marina* growth in BB-LEH compared to Chesapeake Bay where large scale declines in *Z. marina* populations have been attributed to temperatures exceeding 30°C in both 2005 and 2010 (Moore and Jarvis 2008; Moore et al. 2013). Finally, in both applications the model predicted total seed bank densities (Chesapeake Bay 50 – 25,500 seeds m^{-2}; BB-LEH 50 – 23,590 seeds m^{-2}) which were higher than observed seed bank values but within the range reported for *Z. marina* populations (0 – 25,746 seeds m^{-2}; Harwell and Orth, 2002; Morita et al., 2007; Lee et al., 2007). For many plant populations the seed-bank density is not a direct reflection of yearly seed production as seeds are lost to dispersal, predation and mortality (Baskin and Baskin, 1998). While both mortality and predation are considered in our model, currently, the model does not account for the loss of seeds

through dispersal of flowering shoots. As *Z. marina* seeds can disperse up to 20-300 km away from their source bed (Harwell and Orth, 2002) this is a potential source of seeds which may significantly impact the level of resilience provided by the seed bank and requires further investigation. In addition the discrepancy between model predicted seed-bank values and observed values may be explained by the non-homogeneous development of reproductive shoots (Harwell and Rhode, 2007) and the patchy distribution of local seeds within established Z. marina beds (Harwell and Orth, 2002). The model described here does not have a spatial component, therefore the patchy distribution of seeds described for ambient seed banks was not taken into account and all seeds were easily accounted for, possibly resulting in the greater predicted seed-bank densities.

Nutrient Reductions

Reductions of water column and sediment nutrient concentrations up to 30 % below ambient conditions unexpectedly did not result in increased *Z. marina* above or below ground biomass in any model scenarios (Figure 4). Eutrophic conditions are associated with SAV loss in BB-LEH (Fertig et al. 2013; Fertig et al. 2014). However loss is not observed through direct negative effects of excess nutrient concentrations, but rather through indirect negative effects due to greater benthic macroalgal (Hauxwell et al. 2001; Kennish et al. 2007) or phytoplankton (McGlathery et al. 2007) biomass which limits the amount of available light for SAV growth and survival or through the production of metabolic by-products like anoxia and sulphides (Thompson et al. 2012). The lack of effect in model scenarios presented here were due in part to the lack of large scale macroalgal or phytoplankton blooms in either SS or BI in 2012 – 2013. While benthic macroalgae was observed at both BI and SS during this study, a portion of the macroalgal biomass was only observed as it was moving quickly through both sites (Jarvis personal obs). As quantifying the duration of impact from the mobile macroalgae was beyond the scope of this research, the model could not be calibrated with a macroalgal component and indirect effects could not be measured.

Restoration Scenarios

Successful restoration of *Z. marina* in lagoonal systems like BB-LEH have been documented in areas where a lack of propagule supply was the main limiting factor (Orth et al. 2012).

However, in areas where additional stressors such as episodic low light and high water temperatures occur, successful large scale restoration of *Z. marina* can be limited by poor site selection (Fonseca et al. 1998; Shafer and Bergstrom, 2010). While all sites selected as potential restoration sites for *Z. marina* in BB-LEH supported the establishment and growth of SAV populations, modelled *Z. marina* above and below ground biomass was greater at WT compared to both SS and BI sites regardless of the number of seeds used to initiate recovery (Figure 5). The greater light availability due to lower turbidity and chlorophyll *a* concentrations indicate that restoration site selection which focuses on those sites where light availability is greatest may result in short term restoration success (Appendix B and C). Maximization of SAV biomass in a short period of time may result in a greater change for long term survival of the restoration site as the establishment of a seagrass meadow creates a positive feed-back loop where local water quality conditions, including light availability, improve as the meadow expands (Orth et al. 2012). Due to the light limitations associated with the indirect effects of eutrophication, maximizing potential restoration success by selecting sites which are projected to produce large amounts of *Z. marina* biomass quickly may be a potential restoration strategy within BB-LEH.

In addition to site selection the method of restoration can have significant effects on long-term site survival (Shafer and Bergstrom, 2010). In a comparison of restoration methods for *Z. marina* populations in the Patuxent and Potomac Rivers in the Chesapeake Bay found that the most cost effective method for this species was the use of seeds with either direct injection into the sediment or via broadcasting (Golden et al. 2010). Similar to field restoration trials, the number of seeds was not found to have a significant impact on *Z. marina* germination and initial seedling establishment (Orth et al. 2003). However, greater maximum above and below ground biomass projections were made for all sites when initial seed densities were 500 seeds m^{-2}. Greater seed numbers may help offset effects of predation, mortality and loss of seed viability over time and the production of large numbers of seeds to ensure survival is a strategy utilized by *Z. marina* populations exposed to stressful conditions (Robertson & Mann 1984; Santamaría-Gallegos et al. 2000; van; Lent & Verschuure 1994; Jarvis et al. 2012). Ultimately the combination of restoration at sites with good water quality and seed densities of at least 500 seeds m^{-2} are projected to result in the greatest restoration success in BB-LEH.

Model Limitations

The model presented here reproduced the general observed trends in above and below ground *Zostera marina* biomass in BB-LEH in 2012-2013; however, it does have several limitations. One of the greatest percent errors in base model calibration occurred due to a significant overestimate of fall *Z. marina* production which may be attributed to the use of constant rates for translocation of carbon from *Z. marina* above ground to below ground biomass. The lack of above ground production due to temperatures > 25 °C (Marsh et al., 1986, Nejrup and Pederson, 2008, Hosokawa et al., 2009; Höffle et al., 2010) may inhibit carbon translocation to below ground biomass; however, the exact relationship is unknown so translocation was held constant throughout all model runs. In addition carbon storage in the rhizomes has been shown to help balance increased carbon demands when photosynthesis is limited but respiration is increased (Moore et al. 1996) indicating that carbon may flow both to and from the roots and rhizomes. Defining the seasonality of the relationships between temperature and the rate and direction of carbon translocation in *Z. marina* plants is necessary to increase the accuracy of the model.

As discussed by Jarvis et al. (2014) there were several limitations on the accuracy of sexual reproductive output in the model resulting in overestimation of total and viable seed bank densities. The areas that are primarily lacking in the BB-LEH application of the model include the lack of change in mortality, grazing and viability rates over time. While the impacts of grazers on *Z. marina* seed dispersal and burial have recently been described for grazers including infauna, fish, and turtles (Sumoski and Orth 2012; Blackburn and Orth 2013) the impacts of grazers on mortality and germination rates are not well defined (Fishman and Orth 1994). In addition, while the long-term persistence of Mid-Atlantic *Z. marina* seeds was found to be <6 months in the sediment (Jarvis et al 2014) factors that affect the short-term changes in viability over time are not well understood. As the relationship between environmental factors, grazing pressures, mortality rates and seed bank viability is not well defined, this remains a limitation of the model.

Relationships between seedling growth and survival and surrounding environmental conditions are not well defined. There is some evidence that seedlings respond similarly to temperature limitations when compared to established *Z. marina* plants (Bintz and Nixon, 2001; Abe et al., 2008) and may be more resilient to stress from anoxia (Raun and Borum 2013); however, there is little other information available on *Z. marina* seedlings or the effects of changes in habitat conditions on seedling growth and survival. Information on seedling physiology would

enable parameterization of a separate seedling sub-model to track seedlings in their first year of growth likely increasing the overall accuracy of the model.

In order to more accurately predict the response of SAV populations to potential management scenarios the indirect effects of benthic and epiphytic macroalgae need to be quantified. The relationships between environmental drivers and changes in macroalgal biomass over time within BB-LEH need to be defined before they can be incorporated into the model. Finally as *Z. marina* populations continue to decline and populations of other SAV species, including *Ruppia maritima*, increase the model should be expanded to incorporate inter-species interactions. Both the inclusion of indirect effects and the incorporation of multiple SAV species would likely increase the overall accuracy and applicability of the model.

Conclusions

The results presented here highlight a new research/management tool that can be used to help select sites suitable for *Z. marina* restoration. The model described here can be used to help determine where (based on site suitability) and when (based on response to changes in water quality conditions) *Z. marina* restoration can be most effectively conducted in BB-LEH. In addition, by quantifying impacts of environmental stressors on *Z. marina* persistence and recovery, the results from this study when paired with future model simulations will help improve understanding of the condition, ecology, and threats coastal stressors (e.g., water quality) and long term health of SAV beds within the BB-LEH ecosystem**.**

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Appendix A.

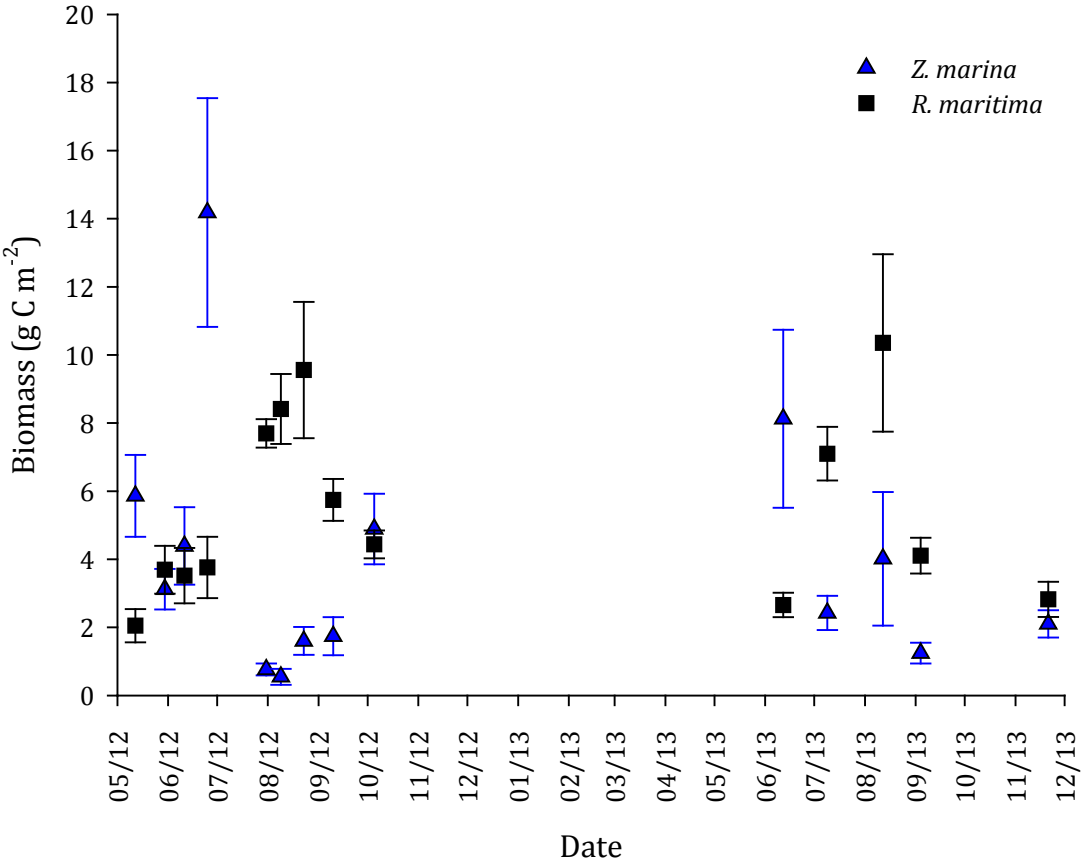

Figure 6. Above ground biomass for *Z. marina* (blue triangles) and *R. maritima* (black squares) at SS in 2012 and 2013.

Appendix B.

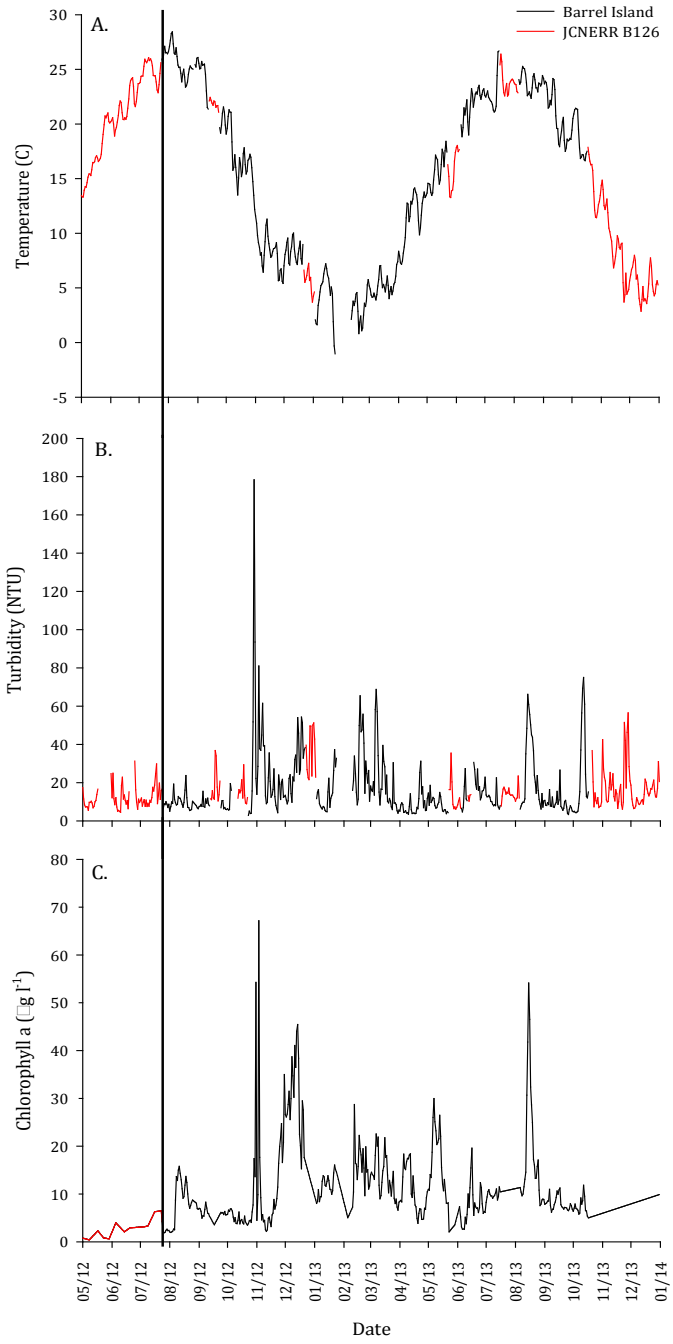

Figure 7. Sources of water temperature (A), turbidity (B) and chlorophyll *a* (C) for model scenarios model calibration and verification. Black lines are data collected as part of this project at BI while red lines denote secondary source data collected by the Jacques Cousteau National Estuarine Research Reserve at Buoy 126. Vertical black line denotes establishment of continuous monitoring station at BI.

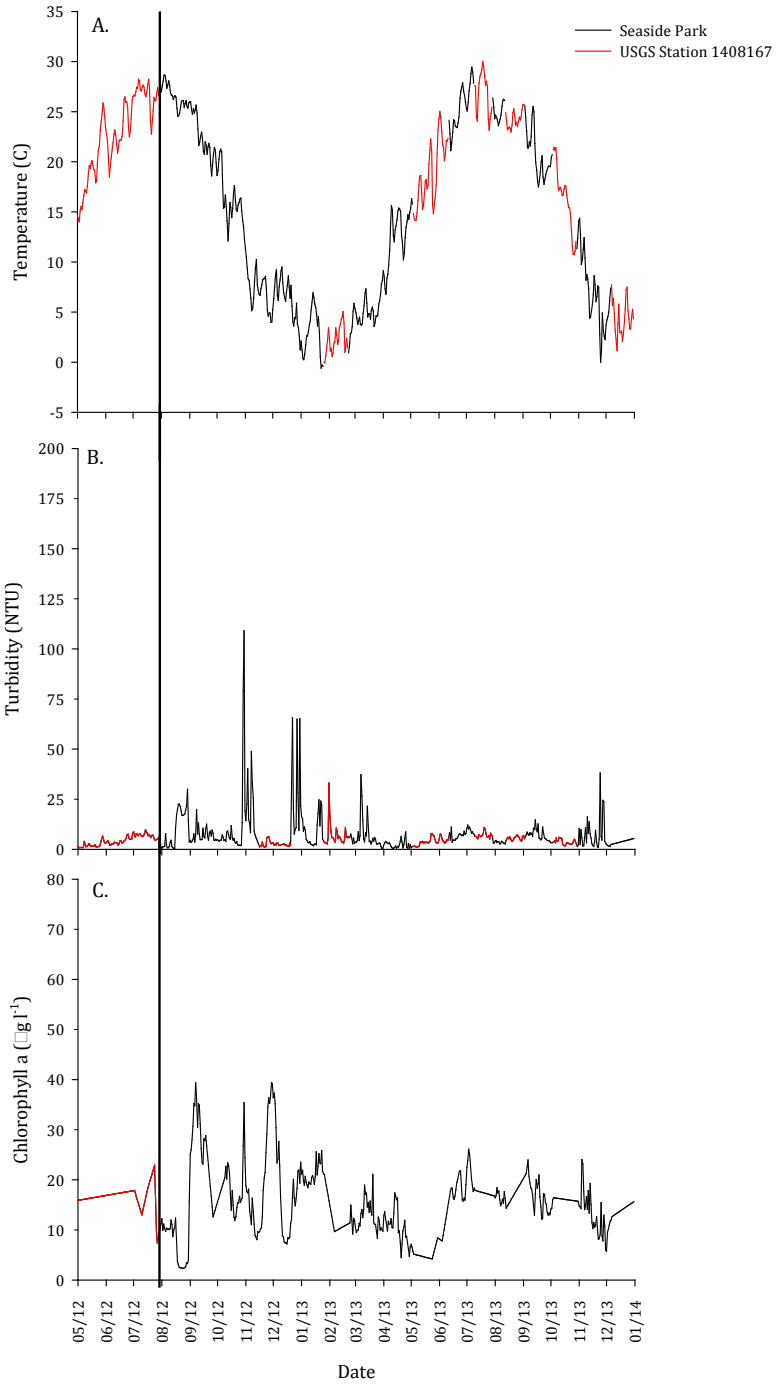

Figure 8. Sources of water temperature (A), turbidity (B) and chlorophyll *a* (C) for model scenarios using SS data. Black lines are data collected as part of this project at SS while red lines denote secondary source data collected by the USGS Station 1408167. Vertical black line denotes establishment of continuous monitoring station at SS.

Appendix C.

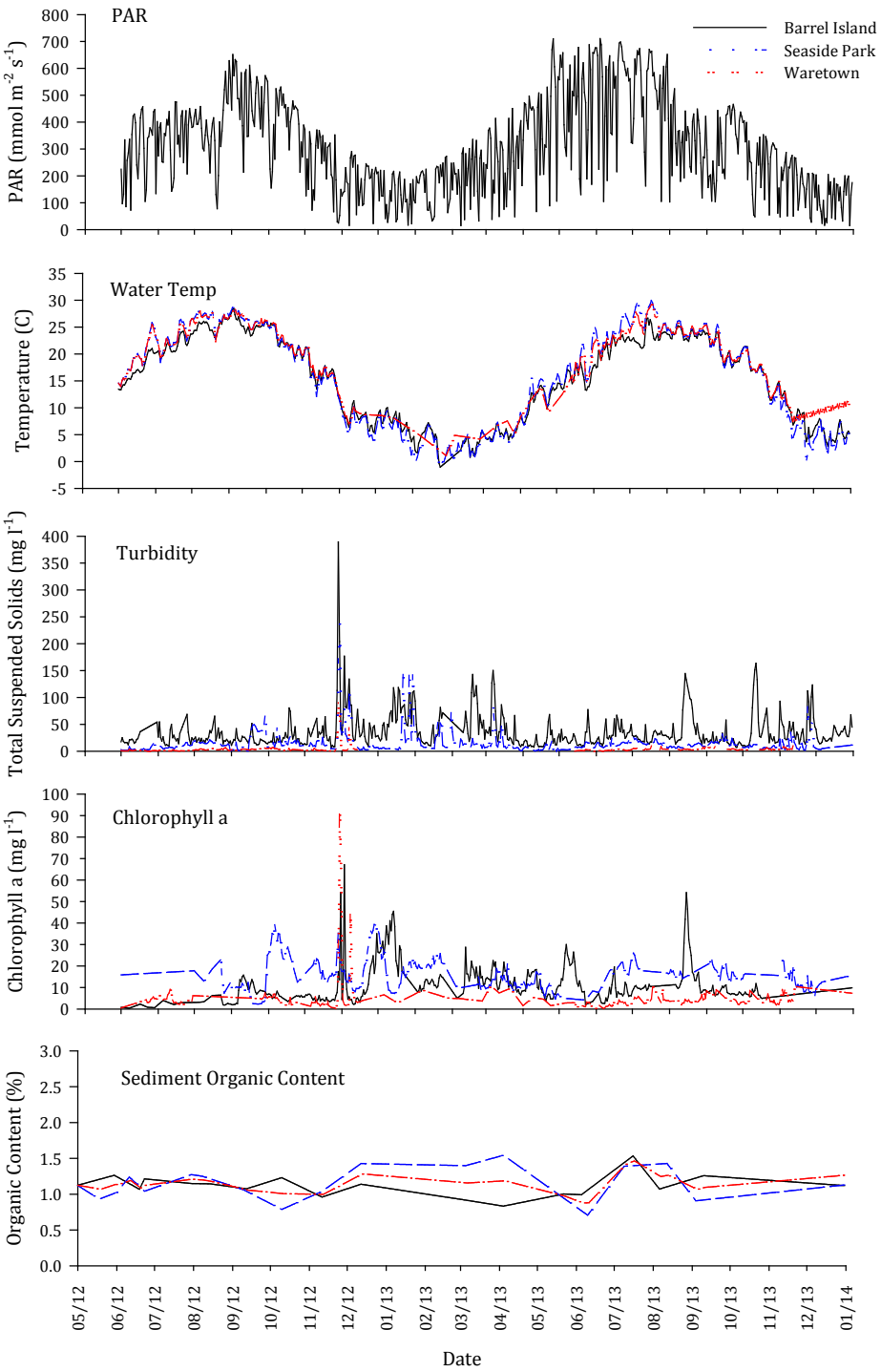

Figure 9. Forcing functions for BI (solid black line), Seaside (blue dashed line) and WT (red dash dot line) for 2012 – 2014.

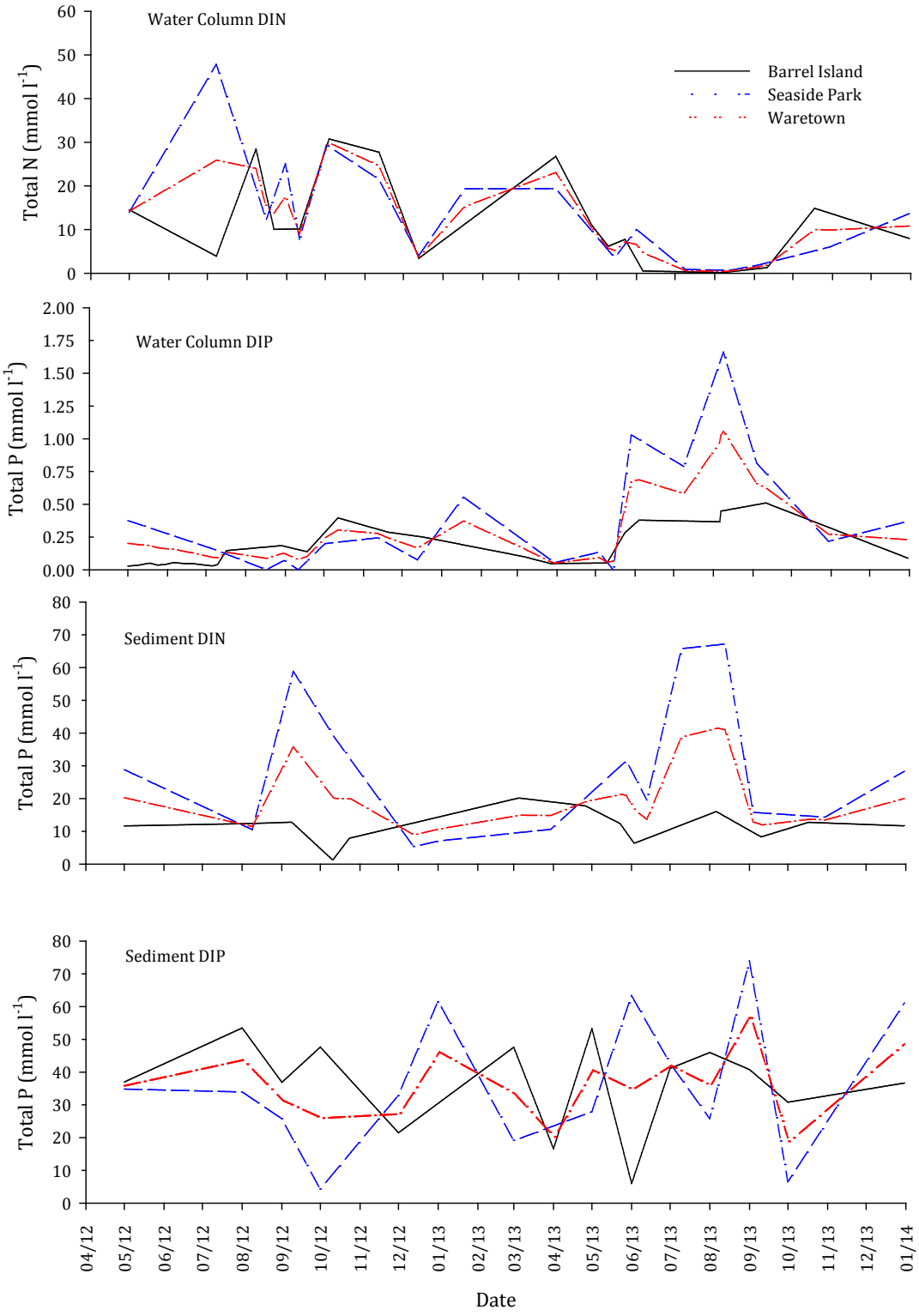

Figure 10. Water column and sediment nutrients for BI (solid black line), Seaside (blue dashed line) and WT (red dash dot line) for 2012 – 2014.