Resilience and positive feedbacks: Water quality management and eelgrass health in Great Bay Estuary, NH/ME

Technical Report

November 30th, 2024

Project Team:
Anna Mikulis, Chris Peter, Cory Riley, David Burdic,
Kalle Matso, Kelle Loughlin, Lynn Vaccaro, Miguel Leon, Thomas Gregory
Tom Lippmann, and William H. McDowell

The project team would like to thank the following people who reviewed drafts of this report:

Simon Courtenay, External Advisor, University of Waterloo
Lora Harris, External Advisor, University of Maryland
Jud Kenworthy, External Advisor, NOAA (emeritus)
Michael van den Heuvel, External Advisor, University of Prince Edward Island
Clifton Bell, Brown & Caldwell, consultant to MAAM*
Stacy Villanueva, Brown & Caldwell, consultant to MAAM*
Ted Diers, NH Department of Environmental Services
Harvey Pine, NH Department of Environmental Services
Ken Edwardson, NH Department of Environmental Services
Sally Soule, NH Department of Environmental Services
Nathan Chien, EPA Region 1

***MAAM refers to the Municipal Alliance for Adaptive Management**

This work was sponsored by the National Estuarine Research Reserve System Science Collaborative, which supports collaborative research that addresses coastal management problems important to the reserves. The Science Collaborative is funded by the National Oceanic and Atmospheric Administration and managed by the University of Michigan Water Center (NA19NOS4190058).

Abstract Summary

The Eelgrass Resilience Project was a three-year (2021-2024) collaborative science grant, funded by the National Estuarine Research Reserve (NERR) System Science Collaborative, that focused on linking science to management needs concerning eelgrass habitat loss in the Great Bay Estuary, NH/ME. Eelgrass habitat (acres) has decreased by 64% between 1996 and 2023. Yet, the response of eelgrass to water quality changes remains unclear, which makes eelgrass habitat management decisions uncertain. Given recent efforts in point source nitrogen loading reductions by wastewater treatment facilities in the watershed, this project sought to determine whether those reductions had demonstrable impacts on eelgrass in Great Bay Estuary. In other words, have recent (last decade) nitrogen loading reductions improved eelgrass health or resulted in positive feedbacks that enhance the resilience of eelgrass in Great Bay Estuary? This project combined hydrodynamics, biogeochemistry, and ecology to examine relationships between residence time, N loading, *in-situ* N processing, sediment dynamics, light availability, and eelgrass resilience. This report summarizes the motivations, methods, and results centered on both how eelgrass is affected by water quality and how eelgrass affects water quality in Great Bay Estuary. Our results are influenced by both abnormally wet years during our field seasons and by drastic loss of eelgrass throughout the Estuary in 2023.

Contents

Introduction

What is the Eelgrass Resilience Project?

The Eelgrass Resilience Project was a three-year (2021-2024) collaborative science grant, funded by the National Estuarine Research Reserve (NERR) System Science Collaborative, that focused on linking science to management needs concerning eelgrass habitat and loss in the Great Bay Estuary (Figure 1), located on the border of New Hampshire (NH) and Maine (Figure 2). Eelgrass habitat loss in Great Bay Estuary played an important role in the EPA establishing a Total Nitrogen General Permit that addresses both point and non-point sources of nitrogen (N). This Permit became effective in January of 2021 and will be up for renewal/modification by January 2026. The NH Department of Environmental Services and permitted municipalities are looking to their partners to provide the critical scientific insights needed to meet the new permit requirements and to consider management changes in the future. Gaps in understanding eelgrass response to water quality changes increases the uncertainty over which management tools would be best applied to protecting eelgrass. This project combined hydrodynamics, biogeochemistry, and ecology to examine relationships between residence time, N loading, *in-situ* N processing, sediment dynamics, light availability, and eelgrass resilience. A Project Advisory Committee (PAC) guided the last three years of transparent, iterative science to facilitate progress on the most challenging management issue for this estuary.

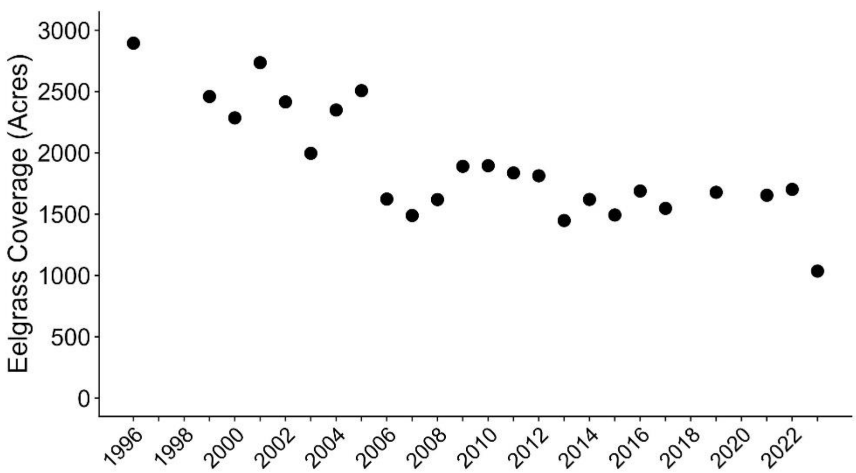

Figure 1. Annual eelgrass coverage in Great Bay Estuary between 1996 and 2023. Data source: Piscataqua Region Estuaries Partnership (PREP).

What is eelgrass?

Eelgrass (*Zostera marina)* is the dominant species of seagrass found in Great Bay Estuary. This flowering marine plant is circumglobally distributed across temperate coastal ecosystems. As a rooted plant, eelgrass grows underwater in both subtidal and intertidal regions of estuaries. Eelgrass extent becomes depth-limited as a function of light availability through the water column. The minimum light requirement of eelgrass for survival and growth ranges between 18.6%[1] and 22%[2,3] of light penetration through the water column. Mesocosm experiments in Great Bay Estuary demonstrated that eelgrass densities remained stable at 21% light availability.[3] Eelgrass resilience to light stress is a function of both the magnitude and duration of light reduction in estuaries.[4,5] When environmental conditions are optimum, eelgrass forms dense meadows that provide important ecosystem services, including carbon sequestration, nutrient uptake, substrate stabilization, and habitat provision for wildlife.[6,7]

Although eelgrass sometimes behaves as an annual plant, it is generally regarded as a perennial, meaning it persists year-to-year through both asexual (i.e. clonal growth) and sexual reproduction (seeds).[8] The combination of multiple reproductive strategies and wide tolerance of changing temperature and salinity conditions explains both the dominance and persistence of eelgrass throughout the northern hemisphere. Yet, eelgrass is an indicator of estuarine health as declines in its distribution usually signal detrimental change in water quality and environmental conditions within coastal ecosystems.[9,10] Eelgrass coverage in Great Bay Estuary has declined by 64% between 1996 and 2023, suggesting that estuarine conditions have been not conducive to the survival and recovery of this eelgrass to historic levels (Figure 1).

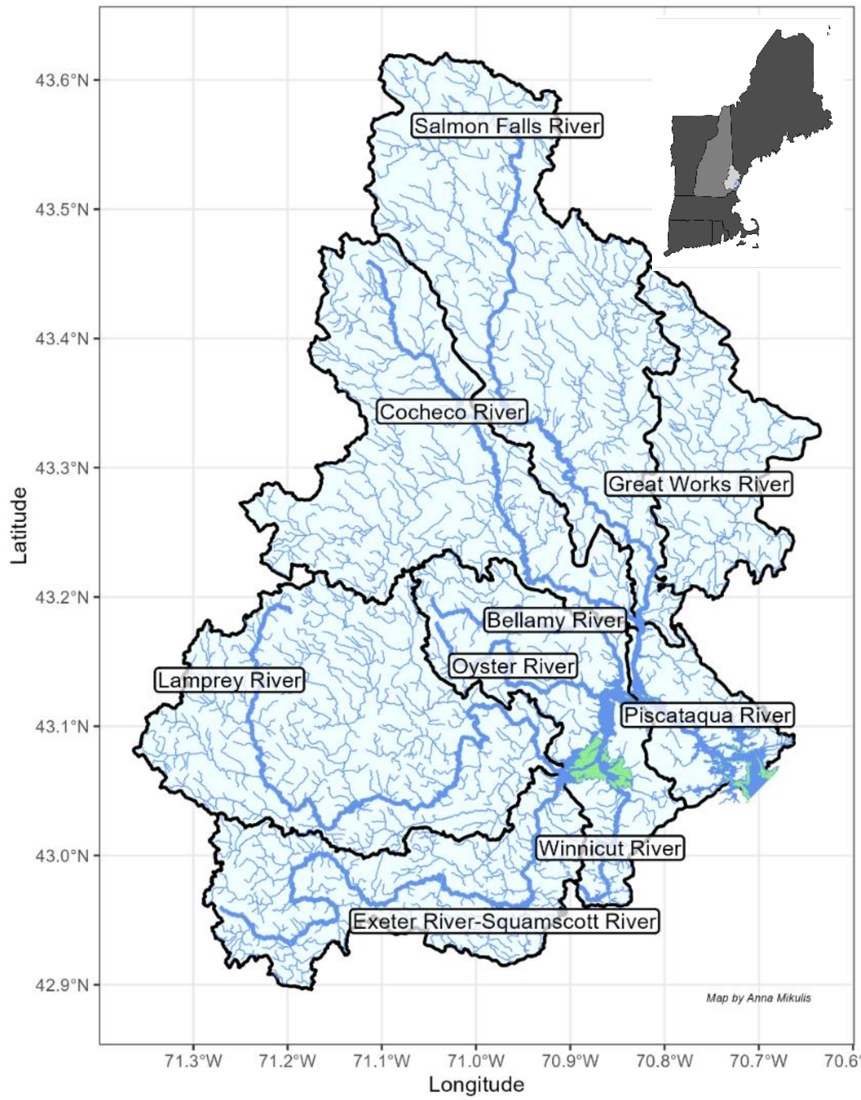

Figure 2. Map of Great Bay Estuary watershed highlighting the sub-watersheds (HUC10). Map inset shows the location of Great Bay Estuary within the New England region (light grey watershed). Green shows eelgrass coverage in 2021 (Data source: PREP).

What are stressors for eelgrass?

In Great Bay Estuary, eelgrass stressors are light availability, water quality, wasting disease, sulfide toxicity, herbivory, warming water temperatures, sea level rise, and human activity (e.g. boating, docks, dredging).[11] While there is a wide range of potential stressors to eelgrass meadows globally[10] and in Great Bay Estuary[11] specifically, this report focuses on stressors that were measured as part of the Eelgrass Resilience Project. We examined light availability as a stressor to eelgrass and water quality as a potential driver of light availability. The hydrodynamics of the estuary were also examined as both a stressor (i.e. shear stress) and driver of stressors (i.e. velocity, residence time) to eelgrass.

Light availability in an estuary is driven by four factors that prevent light from reaching the bottom of the estuary: water depth, colored dissolved organic matter (CDOM), total suspended solids (TSS), and phytoplankton (proxy measurement: chlorophyll-a).[12] CDOM and TSS inputs to the estuary can originate from watershed delivery, with watersheds comprised of high forest and wetland land cover often delivering more CDOM.[13,14] TSS can also be internally generated from resuspension within the estuary.[15–17] Nutrients, in particular N, are known to affect the light regime of eelgrass indirectly, by facilitating the growth of phytoplankton, epiphytes, and seaweed, reducing the light available to eelgrass.[15,18–20] The interaction between water quality and light availability is one of the largest driver-stressor relationships that negatively impact eelgrass meadows.[9,21–23]

Eelgrass loss can act as a positive feedback mechanism that can further decrease water quality and further increase eelgrass mortality. For example, the loss of eelgrass results in the loss of flow reduction by the canopy, which in turn reduces sediment trapping within meadows and increases resuspension and turbidity.[24,25] As turbidity increases, the reduction in light availability serves as a further stressor on the system. Eelgrass light requirements have been shown to increase as environmental conditions (water clarity, temperature, etc.) degrade in estuarine environments.[26]

How does eelgrass relate to water quality management?

The primary goal of this project was to better understand the stressors linked to eelgrass decline and to identify whether eelgrass habitats reduce water quality impairments such as elevated suspended sediment and nitrogen that can impact the persistence of eelgrass in estuaries. Eelgrass beds can be thought of as resilient when the reduction of water quality impairments within the bed is of sufficient magnitude to improve overall water quality. To achieve the goal of understanding the resilience of eelgrass habitats, it is important to leverage our understanding of stressor-response relationships to better inform future management actions. This goal also might provide relevant guidance on new regulatory requirements. In November 2020, US EPA released the “Great Bay Total Nitrogen General Permit, focused on reducing N loading from 12 New Hampshire communities with wastewater treatment facilities (WWTF) while also offering options for non-point source (NPS) controls of N inputs through an adaptative management approach. Great Bay Estuary is impacted by both point sources (accounting for 22% of total N loading, largely as inorganic N) and NPS, which account for 78% of N loading, mostly as dissolved organic N.[27] The low contribution of point sources to total nitrogen loading represents a significant reduction in point-source loads through WWTF technology upgrades since 2015. To incorporate progress made by the communities and changes observed in the estuary, the Permit lays out an adaptive management plan that calls out the need for exactly the activities proposed by this project. As these communities develop their adaptative management plans, they have worked closely with this project team in hopes of referencing this project to help achieve their goals. Finally, the current Permit is scheduled to expire in 2026 and the EPA has articulated that the Permit will be modified based on scientific analysis of changes to the Estuary over the coming years. Advanced understanding of the relationships between N, sediment dynamics, light, and eelgrass will directly inform the adaptive management requirements contained in the Permit.

What made this project "collaborative"?

A Project Advisory Committee (PAC) was formed to provide input to the project team at all stages of the project to ensure results were relevant, trusted, and useful within the current management context. We recruited representatives from 14 organizations to serve as local advisors, including individuals from the US Environmental Protection Agency, the NH Dept of Environmental Services, two non-profits (The Nature Conservancy and Conservation Law Foundation), six municipalities (Dover, Portsmouth, Rochester, Durham, Newfields and Exeter), and a consulting firm hired to represent an alliance of eight municipalities. In addition, the Piscataqua Region Estuaries Partnership (PREP) and Great Bay National Estuarine Research Reserve (GBNERR) served as both local advisors and members of the project's executive team. With separate funding, four external advisors joined all the PAC meetings to provide a synchronous peer review process throughout the project. These external advisors were drawn from academic institutions in the US and Canada and the National Oceanic Atmospheric Administration and were selected because they had direct experience studying eelgrass and water quality issues in estuaries. The advisors were viewed as being outside of the community and therefore possessing a high level of objectivity. Broadly, this group represented the management interests of state agencies and permitted municipalities regarding the Great Bay Total Nitrogen Permit and eelgrass habitat management.

The PAC met eight times over the course of the three-year project, including six workshop style meetings that lasted three hours or more, and a few optional office hours, field visits and small group consultations. During each of the PAC meetings, the project team provided updates on research plans and results, solicited feedback on specific questions that could guide the next steps and invited discussion about the current management and policy context. For each meeting, Advisors were given discussion prompts and slides to review in advance and they received a detailed meeting summary afterwards with an opportunity to add or refine comments.

The 3-year project versus historical analysis

This report focuses on the results of this 3-year National Science Collaborative project (2021 – 2023). This project utilized monitoring data provided by PREP and contributed new, discrete experiments and measurements that were not part of the regular monitoring program. From the earliest meetings with interested audiences, even before the proposal was submitted, the team heard a desire for an analysis of all the historical data on eelgrass and stressors to be combined with the 3-year project. While the project team agreed that this could be valuable, we chose to focus the limited project resources on novel experiments, models, and field samples that would help to provide insights into long-term trends. In addition, outside the scope of this project, PREP worked to prepare a preliminary analysis of historical data, which was presented to the PAC at the final project meeting on June 26, 2024. PREP will use the feedback and the extensive breakout group discussions to create a “PREP Eelgrass Resilience Report,” which will be published in 2025.

Questions we set out to answer (and new understanding we did not plan for)

Our proposal to the NERRS Science Collaborative posed this overarching question: Have recent (last decade) nitrogen loading reductions improved eelgrass health or resulted in positive feedbacks that enhance the resilience of eelgrass in Great Bay Estuary? This question recognizes that reductions alone may not manifest changes in eelgrass due to the interactions with other factors (e.g., water temperature, sediment, CDOM, extreme weather, etc.). This project also recognizes that time lags in estuarine ecosystems exist and thus eelgrass responses to nitrogen reductions may take time. To answer the overarching question, this project sought to address how eelgrass is both affected by and affects its physical environment. The two main research questions were:

1) Does eelgrass health vary spatially in response to variability in water residence time, bed shear stress, algae, epiphytes, and water quality?

2) Does nitrogen and/or sediment filtration (e.g. ecosystem services) vary along transects that span a gradient from unvegetated areas to areas vegetated with eelgrass?

Below, we share results of our work related to these questions and the sub-hypotheses that were posed. In addition, we will share additional discussion that we believe has bearing on the question of how managers can increase eelgrass and ecosystem health in the Great Bay Estuary. These additional discussion points are woven into the results for each hypothesis and will be further expanded upon in the So What Executive Summary.

***Note** The above questions were developed with the expectation that 2021 through 2023 would experience somewhat typical weather conditions. This did not turn out to be the case. In both 2021 and 2023, precipitation during the growing season was in the top four in terms of historically high precipitation for the period of record for eelgrass cover and annual rainfall data overlap (2003 – 2023) (Appendix I, Figure A1). The highest year in the last 20 years was 2006 (32.15 in of rainfall between May and August), the year of the Mother’s Day Flood. This unusual amount of rain during two of our three study years appears to have had a highly negative impact on eelgrass and transformed the project into a study of a struggling ecosystem rather than a recovering ecosystem, as initially envisioned.*

Methods

Hydrodynamic Model

We implemented a numerical model that computes the hydrodynamics for the Great Bay Estuary. The model implemented is the publicly available Regional Ocean Modeling System (ROMS)[28,29] available for download at https://www.myroms.org. The Great Bay model domain spans the mouth of the Piscataqua River and near-coastal ocean to the inland river mouths (including the Salmon Falls, Cocheco, Bellamy, Oyster, Lamprey, Squamscott, and Winnicut Rivers, and has horizontal spatial resolution of 33 m with 12 vertical layers. The bathymetric grid was obtained from a compilation of sources that include bathymetric soundings and LiDAR obtained by NOAA, USGS, USACE, and UNH.[30] Bottom boundary conditions for the Great Bay Estuary model were determined from a sensitivity analysis between model-predicted M2 tidal energy dissipation upstream and co-located observations obtained from acoustic Doppler current profilers (ADCPs) throughout the model domain.[30]

The model was driven at offshore ocean boundaries with 3 hour nowcasts produced by NOAA's Gulf of Maine Operation Forecast System (GOMOFS)[31] and includes wind-driven velocities, sea temperature, and salinity spanning the water column. Owing to the large 3 hour time intervals of the saved GOMOFS nowcasts, tidal forcing from the nowcasts were removed by filtering and only the subtidal forcing retained. Tidal forcing was then introduced using the Oregon State University Tide Prediction Software (OTPS)[32] Surface atmospheric boundary forcing across the entire domain is obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 reanalysis data, and includes surface wind stress, surface heat flux, precipitation, and barometric pressure. We have included bulk air-sea exchange parameterization[33–35] for cloud cover, net longwave radiation, surface air pressure, surface air relative humidity, rainfall, solar shortwave radiation, surface air temperature, and surface wind velocity.

Model runs were performed for 30-90 days for 2018, 2019, 2022, and 2023 encompassing the spring-neap tidal cycles with output saved at 15 minute intervals, and includes current velocities (at the surface, near-bed, and water column), surface water levels, bed shear stress, and temperature and salinity over the water column. The model runs from 2022 and 2023 are used to assess mean statistics for flows and bed stress that the estuary would encounter regularly on spring-neap tidal cycles. Although the details of the spring-neap tidal cycles vary on monthly intervals, the bulk statistics are very similar owing to the repeatability of tidal constituents over approximately 30 day intervals. Model runs were also performed during the field season summer months (June-August) of 2022 and 2023 and encompass in situ sampling days.

Saved model output was used to estimate the minimum, average, root-mean-square, and maximum shear stresses and depth-averaged flow velocities for any given eelgrass meadow with boundaries defined by annual eelgrass monitoring efforts led by PREP. Statistics were also obtained at the locations of the project sampling sites (interpolated spatially from neighboring model grid cell data). Particle tracking simulations were conducted using the saved velocity fields[36], with particle trajectories verified with surface GPS drifter experiments conducted in the estuary in 2022. Average residence time was determined for the eelgrass meadows, with residence time defined as the e-folding time scale or equivalently the time for 60.3% of randomly distributed particles to leave the meadow boundaries.

Particle tracking simulations were also conducted in reverse starting from the time that water samples were obtained and dating back 3 days. These simulations were used to estimate the time the sampled water parcels were in the meadow and exposed to eelgrass vegetation, as well as the approximate origin of the water parcels relative to the rivers that flowed into the estuary and the coastal ocean. These reverse particle trajectories allowed for assessment of the water particle paths leading up to the in situ field sampling.

Research Question 1: How does water quality affect eelgrass?

In 2021, 25 eelgrass meadow monitoring sites were established throughout Great Bay Estuary as part of a tiered monitoring program implemented by PREP (Figure 3).[37] These 25 Tier 2 sites were randomly selected from regions where eelgrass was present as of 2019.[38] Sites were sampled once every summer between June and August for eelgrass, seaweed (drift), epiphytes, and sediment characteristics as well as water quality. The Tier 2 monitoring program is on-going and is maintained separately from this three-year project.

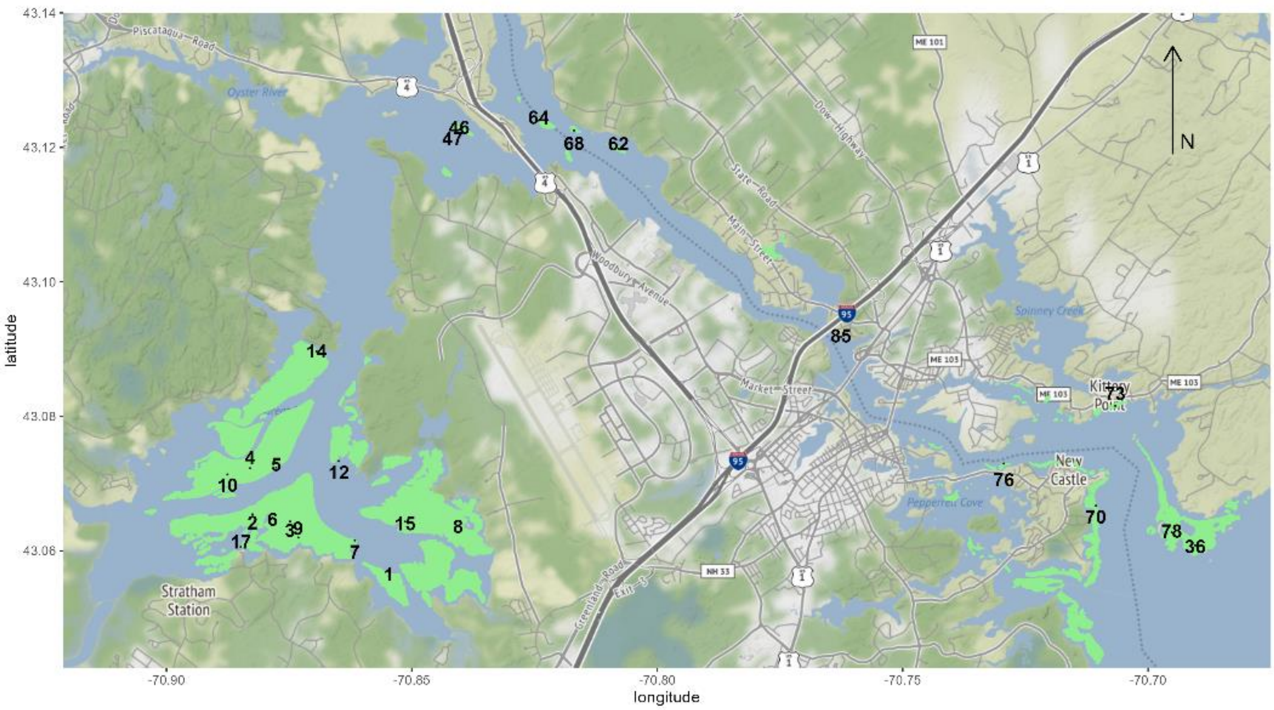

Figure 3. Map of Great Bay Estuary Tier 2 monitoring sites. Points and associated numbers indicate the site location and site number. Sites 1 through 17 are within Great Bay, Sites 46 through 62 are within Little Bay and the Piscataqua River, and sites 36 and 70 through 85 are within Portsmouth Harbor. Stations numbers are not sequential.

Eelgrass health metrics included biomass, shoot density, percent cover, and canopy height. Algal presence was measured as seaweed (red and green species) and epiphyte biomass within a quadrat. Detailed methodologies for how each metric is measured can be found in the Quality Assurance Project Plan (QAPP).[38] Although many eelgrass metrics were measured as part of this monitoring effort, we focused on eelgrass biomass (g dry weight/m^2) as a metric of eelgrass “health”; biomass measurements included both belowground and aboveground biomass. Eelgrass biomass was decided upon as the eelgrass “health” metric for this project due to its frequent use in the literature as the eelgrass response variable. Eelgrass metrics including biomass, shoot density, and percent cover usually both strongly and positively correlate with one another. This strong relationship means that stressor-response relationships using any of those three metrics usually yields the same result. The strong positive relationship between eelgrass percent cover and biomass in Great Bay Estuary has previously been demonstrated in other work.[39] Finally, eelgrass biomass measurements as part of this project encompassed both aboveground and belowground biomass, which means whole plant response to potential stressors is fully captured.

Water sampling occurred concurrent with Tier 2 eelgrass and seaweed sampling. Water was sampled at depth (within 0.5m of the substrate), within the eelgrass meadows, and care was taken not to disturb the sediment bed prior to the TSS sample collection. Additionally, light casts at select Tier 2 sites (time & weather permitting) were taken using a LI-COR 1500 datalogger, an underwater spherical quantum sensor, and a 2 pi quantum sensor for a land reference.[40] For days on which a water sample, but no light cast, were taken, Kd was estimated using a multiple linear regression with dissolved organic carbon (DOC) and TSS concentrations as the independent variables (Appendix I Figure A2). Water samples were analyzed at the UNH Water Quality Analysis Lab for TSS, nutrients, DOC, and sediment particulate N and carbon. Solute concentrations below instrument detection limits were set to one-half of the detection limit.

Research Question 2: How does eelgrass affect water quality?

A finer-scale field design was established in 2022 to measure rates of ecosystem services provided by eelgrass meadows. Three sampling flowpaths were established within Great Bay (Figure 4) based on 2021 eelgrass coverage, boat access, and output from the hydrodynamic model. Flowpaths were placed in locations where water parcels on the ebb tide moved from unvegetated regions of the bay into eelgrass meadows. By selecting sites in this way, a parcel of water could be followed as it moved across a gradient of unvegetated substrate into the eelgrass meadow. Each flowpath was established with four sampling sites (A through D), with the intention of sampling in order from A (unvegetated) to D (eelgrass meadow). Flowpath lengths varied based on how far into the meadow it took to reach at least 60% eelgrass coverage. Methodology details are provided here because the following measurements and experiments are not part of an ongoing monitoring program and therefore are not associated with a QAPP.

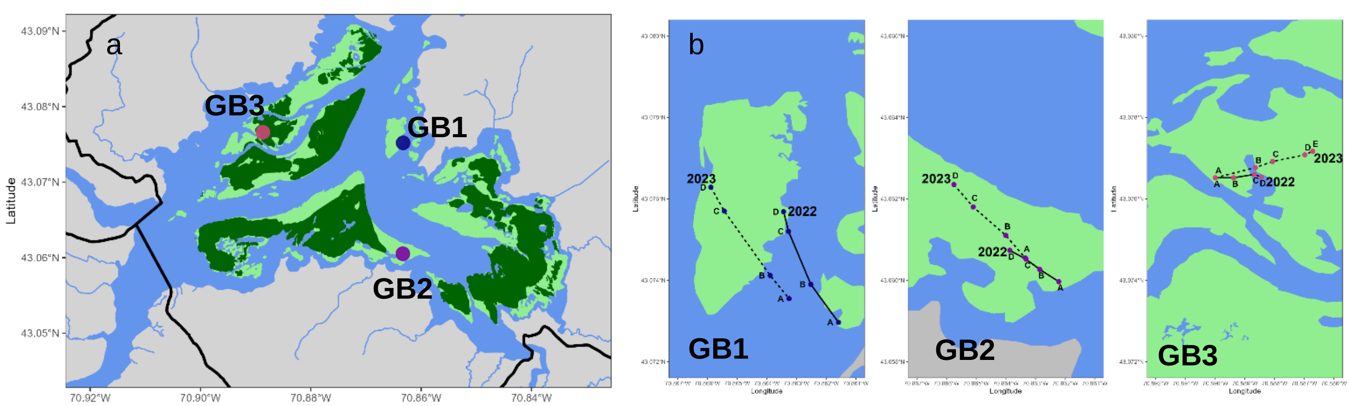

Figure 4. Map of Great Bay transect locations (a). Light and dark green indicates the 2022 and 2023 eelgrass coverage, respectively. Transects were shifted to be deeper in the eelgrass meadows between 2022 (solid line) and 2023 (dashed line) due to eelgrass meadow loss (b).

Each flowpath was sampled a total of three times each year in both 2022 and 2023 between June and August. Between 2022 and 2023 flowpath locations shifted slightly due to reduced eelgrass coverage in 2023. The flowpath lengths became longer in 2023 to reach a portion of the eelgrass meadow with at least 60% eelgrass coverage. Not all flowpaths in 2023 had eelgrass coverage more than 60% (quadrat average). Flowpath GB1 had complete eelgrass loss during the 2023 field season. Sampling protocols included methods for: water chemistry; sediment characteristics, eelgrass percent cover and density; eelgrass and seaweed growth; denitrification in sediments; and porewater nutrient levels. Biomass was estimated from percent cover estimates using the Tier 2 data from research question 1 (Appendix I, Figure A5). Each site (A through D) was sampled in sequential order for water chemistry. Water samples were approximately 0.5m from the bottom at each site. Two 1L HDPE acid-washed bottles were triple-rinsed and filled with unfiltered site water for analysis of TSS and chlorophyll-a analysis. A 60 mL HDPE acid-washed bottle was triple-rinsed with filtered site water using pre-combusted Whatman GF/F filters and filled for nutrient analysis. A YSI proDSS handheld was also deployed approximately 0.5 m above the bottom at each site to measure water temperature, pH, dissolved oxygen, specific conductance, and turbidity. Seaweed and eelgrass percent cover were visually assessed using four 0.25m^2 quadrats. Eelgrass density was measured in a 0.0625 m^2 quadrat placed within the larger 0.25 m^2 quadrat.

In addition to discrete water chemistry and eelgrass measurements, growth of seaweed and eelgrass was assessed both years in June. Seaweed growth rates were measured *in-situ* over a 9-12 day period using mesh cages attached to PVC stakes. A total of six cages, three holding red seaweed (*Graciliara sp.*) and three holding green seaweed (*Ulva lactuca*) were deployed 30 cm above the sediment bed at each of the transect sites (total of 72 cages across 12 sites). Cages were placed within 5m of the transect site GPS locations. Each cage was filled with 5-7g of damp algal biomass and closed with rubber bands and twist ties. Upon recovery of the cages, algae were rinsed in freshwater, cleaned of snail feces, damp dried with paper towels, and re-weighed. In 2023, the number of invertebrates found in the cage (amphipods, crabs, snails, etc.) were also tallied as a potential indicator of herbivory. The difference in mass over deployment time (days) was used to calculate a net growth rate. Eelgrass growth was assessed at sites C and D for each transect using the pin-method.[41] Approximately 12 eelgrass shoots were tagged with plastic flagging and a pin was used to punch a hole through the sheath. Plants were harvested 9-12 days later and pin hole shifts in each leaf were used to determine new growth. The seaweed and eelgrass samples were fully dried at 60°C and ground for CN analysis.

Denitrification rates were assessed using an isotope tracer and push-pull method adapted from salt-marsh work.[42] Six denitrification experiments were conducted in 2022 and 2023, for a total of 12 experiments over the two-year period. Of the 12 experiments, 6 were completed within eelgrass meadows (at the end of the transects) and the 6 were completed in bare sediment (start of the transects). Porewater from the site was amended with $^{15}NO_3^-$ and allowed to incubate for 20-30 minutes before extracting samples every 20-30 minutes for two hours. Samples were analyzed for dissolved $^{28}N_2$, $^{29}N_2$, $^{30}N_2$, and Argon gas using a Membrane Inlet Mass Spectrometry (MIMS). Raw MIMS values were corrected using lab standards and the change in 29- and 30-N_2 over the course of an experiment was used to calculate the rate of N_2 production using isotope pairing equations.[42,43]

Statistics & Calculations

Data were assessed for normality using measures of skewness and kurtosis, as well as Levene's test to assess homogeneity of variance. Variables that did not meet assumptions of normality were appropriately square-root or log-transformed based on whether variances or standard deviations, respectively, were proportional to the means. Assumptions of normality met following any data transformations, allowing for use of parametric statistics. Figure captions denote whether data shown have been transformed for statistical analysis. In instances where the linear regression was significant through the square-root transformed biomass data and the raw biomass data, the raw biomass data were presented for better interpretability. All statistics were done in R v4.3.2.[44] Exploratory univariate statistics were used to assess potential relationships between possible eelgrass stressors and eelgrass biomass, which served as the indicator of "eelgrass health". Multivariate statistics were explored as part of the PAC meetings, but the results from those analyses are not reported here due to a lack of clarity and interpretability. All the work presented in this report represents a three-year study window.

Results & Discussion: Research Question 1

How Does Water Quality Affect Eelgrass?

Hypothesis 1: Impact of Water Residence Time on Eelgrass Health

The relationship between eelgrass biomass and meadow residence time varied with spatial scale in Great Bay Estuary. Residence time is a measure of how long water remains in a given location before exiting. Here, residence time was estimated as the length of time a water parcel remains in an eelgrass meadow within Great Bay Estuary on an ebbing tide. Residence time is an important variable, because it influences whether and how eutrophication is expressed in estuarine ecosystems.[45] Traditionally, estuaries with shorter residence times will have healthier eelgrass meadows (i.e., higher biomass) and higher resilience to disturbance, due to improved water clarity and reduced algal light competition from high turnover of water.[21] Estuaries with longer residence times are typically associated with increased severity of eutrophication impacts.[18,45] Longer residence times allow for phytoplankton and seaweed blooms to persist, which can negatively affect eelgrass by decreasing light availability.[45] Alternatively, longer residence times would also allow more time for eelgrass to take up nutrients from the water column. From a management perspective, understanding the range of residence times helps to understand water quality patterns, which sub-watersheds might be most challenged and why.

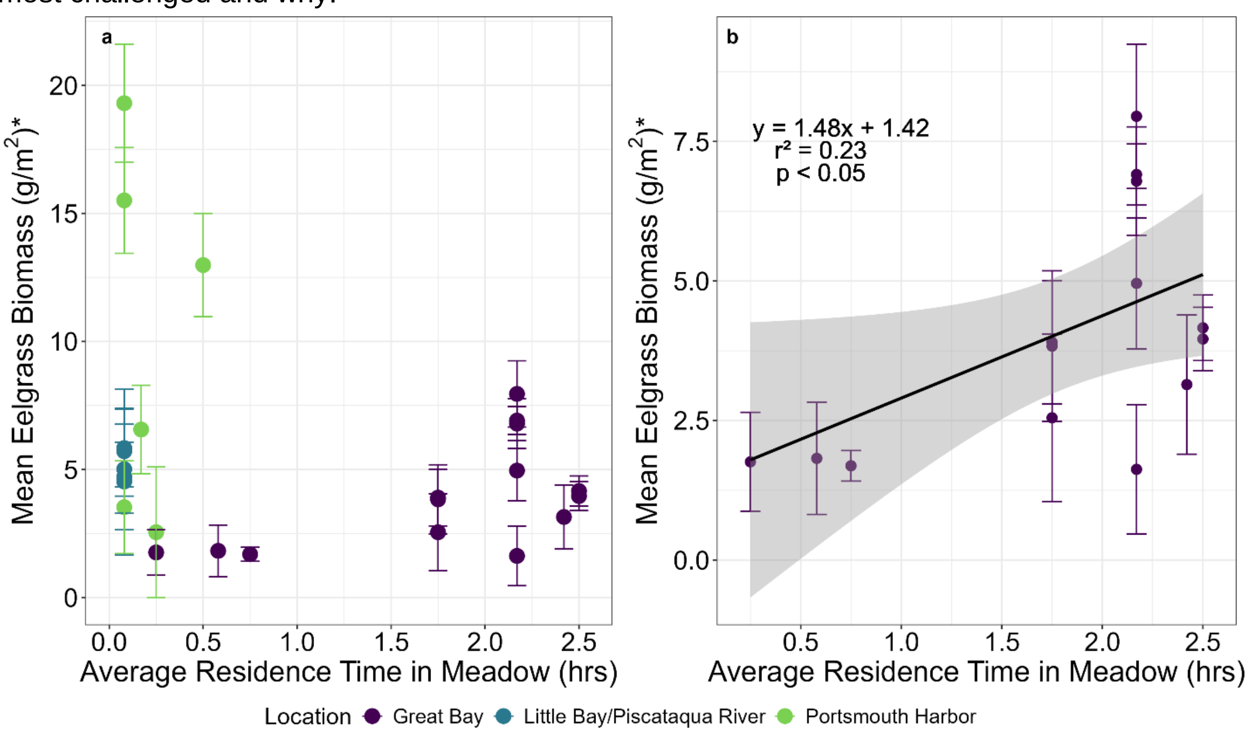

Figure 5. Estuary wide, the highest mean eelgrass biomass was found at sites with lower within-meadow water residence times (a). Looking only at Great Bay sites (b), mean eelgrass biomass increases with increasing within-meadow water residence times. Linear regression (b) reflects the line of best fit through the square-root transformed site means. Points are site means and standard error of the square-root transformed eelgrass biomass data.

Estuary wide, the highest eelgrass biomass is found in areas of lower average residence time (Figure 5a). The highest eelgrass biomass occurred in Portsmouth Harbor at sites with meadow residence times less than 30 minutes. In Great Bay, eelgrass biomass increased across Tier 2 sites as meadow-specific residence time increased (Figure 5b). The dichotomy between residence time and eelgrass biomass across spatial scales suggests that different mechanisms related to residence time and water quality may be simultaneously affecting eelgrass. Short residence times in Portsmouth Harbor, combined with lower average nitrogen concentrations (Figure 6, Figure 7), support the idea that rapid flushing may prevent phytoplankton and seaweed growth from outcompeting eelgrass for light. The low levels of chlorophyll-a , a proxy for phytoplankton, at Portsmouth Harbor sites supports this observation (Table 1).

Great Bay sites show the opposite pattern with long residence times, higher nitrogen concentrations, and lower eelgrass biomass (Table 1, Figure 6). The relationship between residence time and eelgrass biomass in Great Bay may be a function of location (Figure 8). The sites with the longest residence times and highest eelgrass biomass in Great Bay also happen to be on the eastern side of the Bay. Based on simulations of hydrodynamics developed for this project, Eastern Great Bay is less influenced by the river inputs of nitrogen, organic matter, and sediment from the Lamprey and Squamscott Rivers. To view these simulations, navigate to our Hydrodynamic Story Map. Other potential explanations for the pattern between residence time and eelgrass biomass in Great Bay include the relationship between sediment resuspension and residence time. In the Chesapeake Bay, long residence times provide more time for sediment to settle out and improve light availability.[20,46] Sediment-trapping by eelgrass meadows would increase light availability and support eelgrass growth.[46]

The empirical hydrodynamic data gathered as part of this project, including residence time and water parcel movement histories, has significantly changed the way scientists view Great Bay. Simulations based on new data visually illustrate how differently water moves in different areas of the Bay. As a result, at the final project meeting, the principal investigator of this project referred to Great Bay as resembling a river with the navigation channel as the river mainstem and the eelgrass flats as the "floodplain." (Personal communication, W. McDowell, June 26, 2024). Similarly, one of the project external advisors, after seeing the simulations, began referring to Great Bay as a "lagoonal estuary," because "there's this push and pull between clear inputs of new water through the deeper channels, but then the shallow banks of Great Bay act much more like an estuary with a very constricted outlet to the adjacent waterbody." (Personal communication, L. Harris, June 26, 2024). These observations suggest that better understanding of spatial variability in eelgrass stressors and health may provide important insights for management.

Previous work by Bilgili et al.[47] reported that particles starting in the heart of Great Bay spend between 5 and 20 days in the Great Bay before exiting. While this may be true for particles at the "heart" of Great Bay, this project indicated that particles coming in from the river mouths, depending on the tidal stage, could have residences times that last as long as 50 days indicating that the areas where eelgrass grows—away from the navigation channel—may be far more sensitive to riverine inputs (nutrients, sediments, organic matter) than previously thought.

Table 1. Eelgrass and related ecosystem components by year and location in the Great Bay Estuary at Tier 2 sites. Values are medians (range, n) of untransformed dataset. NA indicates no data.

Year	Location	TSS (mg/L)	DOC (mg/L)	Chl *a* (μg/L)	Kd measured (1/m)	Kd estimated (1/m)	Seaweed Biomass (g/m^2)	Epiphyte Biomass (mg/cm^2)	Eelgrass Biomass (g/m^2)
2021	Great Bay	NA	5.5 (3.9, n=15)	25.8 (33.7, n=5)	NA	1.57 (1.14, n=15)	17 (116, n=15)	0.031 (0.49, n=15)	16 (139, n=15)
	Little Bay / Piscataqua River	NA	5.3 (6.35, n=4)	9.62 (6.1, n=3)	NA	1.53 (1.87, n=4)	7 (16, n=5)	0.056 (0.33, n=5)	35 (91, n=5)
	Portsmouth Harbor	NA	1.9 (0.36, n=2)	10.2 (0.3, n=2)	NA	0.51 (0.11, n=2)	13 (58, n=6)	0.0925 (0.29, n=6)	149 (262, n=6)
2022	Great Bay	25.8 (36.7, n=14)	2.4 (1.4, n=14)	NA	0.87 (0.36, n=4)	0.92 (1.12, n=14)	7.5 (28, n=14)	0.0695 (0.55, n=14)	24 (66, n=14)
	Little Bay / Piscataqua River	16.5 (7.6, n=5)	2.1 (0.69, n=5)	NA	0.4 (0, n=1)	0.65 (0.24, n=5)	4 (21, n=5)	0.625 (0.99, n=5)	16 (56, n=5)
	Portsmouth Harbor	10.9 (16.6, n=5)	1.4 (0.76, n=5)	NA	0.27 (0, n=1)	0.33 (0.31, n=5)	30 (134, n=5)	0.085 (1.18, n=5)	82 (540, n=5)
2023	Great Bay	17.3 (13.7,n=14)	5.4 (4.4, n=14)	11.4 (4.1, n=3)	1.49 (0.99, n=13)	1.58 (1.34, n=14)	1.5 (9.0, n=14)	0 (0.85, n=13)	5 (54, n=15)
	Little Bay / Piscataqua River	12.1 (5.5, n=5)	2.4 (0.77, n=5)	3.3 (2.0, n=2)	0.57 (0.24, n=5)	0.62 (0.31, n=5)	3 (12, n=5)	0 (12.0, n=5)	7 (71, n=5)
	Portsmouth Harbor	11.8 (7.2, n=6)	1.9 (0.60, n=6)	1.0 (0, n=1)	0.4 (0.31, n=6)	0.47 (0.17, n=6)	38 (115, n=6)	0 (0, n=6)	133 (362, n=6)

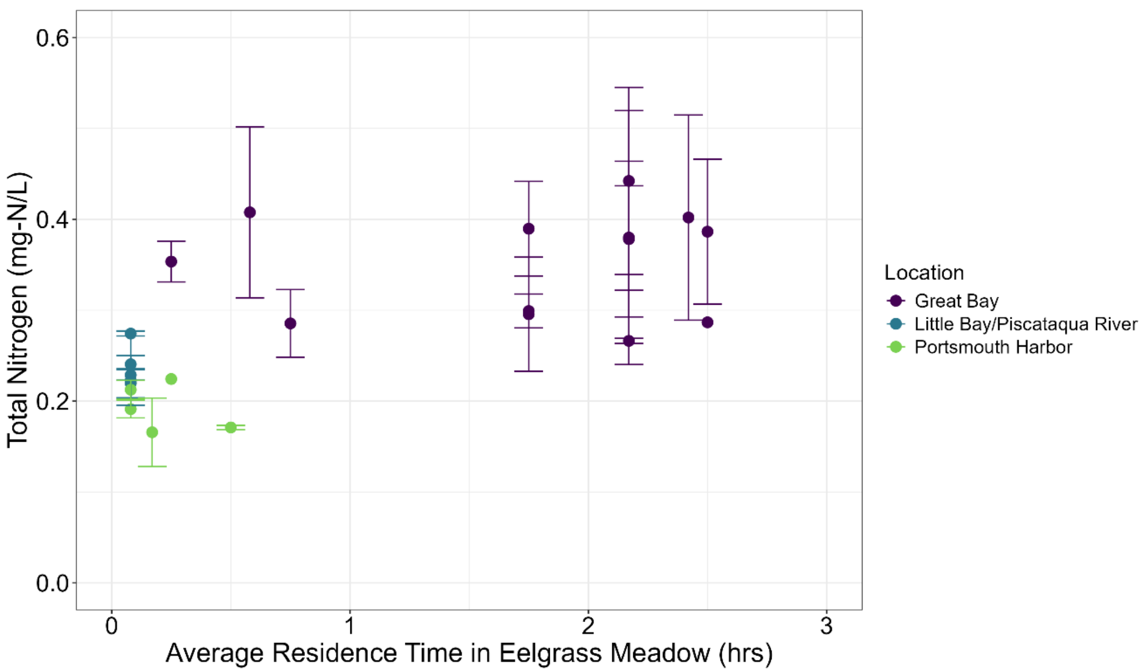

Figure 6. Plot of site-specific residence time versus concentration of total nitrogen. Points are mean and standard error of total nitrogen (n=2 per site) concentration at each Tier 2 sites. Total nitrogen was measured in 2022 and 2023 as the summation of total dissolved nitrogen and particulate nitrogen. Points without error bars had only one value for total nitrogen. Points are colored by relative location within the estuary.

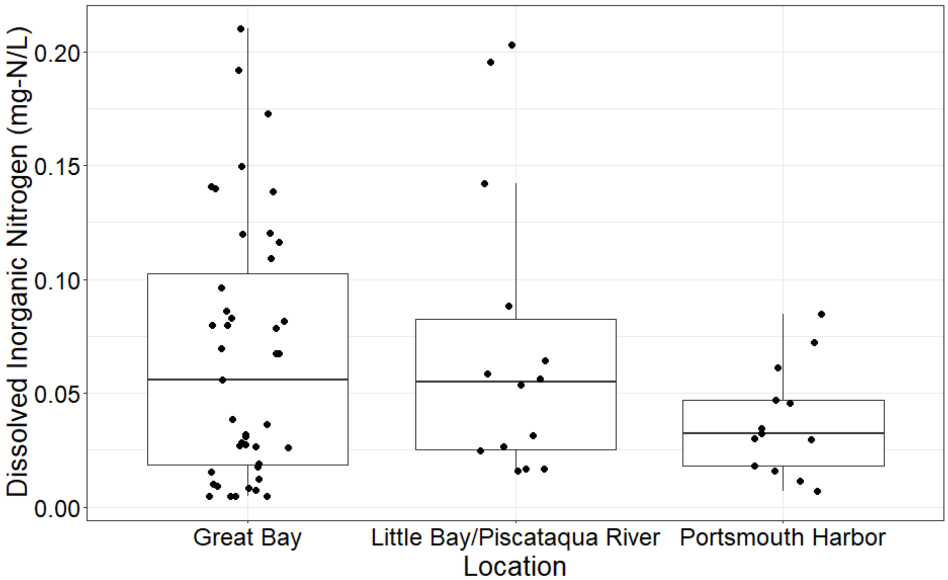

Figure 7. Concentration of dissolved inorganic nitrogen (DIN) in Tier 2 eelgrass sites, binned by location within the estuary. Box and whisker plot denotes median (line) and interquartile range (box). Points represent individual data points that went into each group.

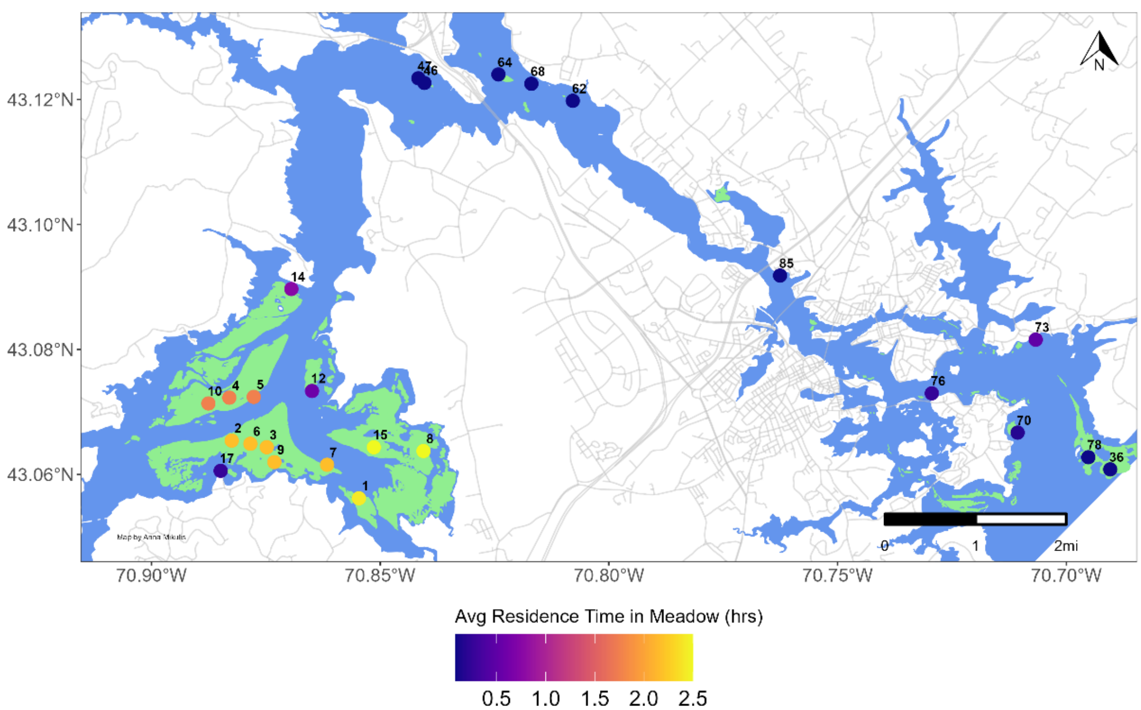

Figure 8. Map of within-meadow residence time at a given Tier 2 site for a water parcel on an ebbing tide.

Hypothesis 2: Impact of Shear Stress on Eelgrass Health

In estuaries, shear stress is the force created from water movement that consequently disturbs and moves sediment. Shear stress is important to eelgrass health due to its influence on sediment bed resuspension, erosion, and deposition within estuaries.[24,48] Higher values of shear stress are associated with higher resuspension rates of fine sediments, which reduce light availability for eelgrass meadows by bringing light scattering particles into the water column.[48–50] High shear stress also increases the movement of nutrients from the sediments into the water column.[49] This internal recycling of sediments and nutrients is often referred to as "internal loading" in contrast with sediment and nutrient inputs from the watershed, which is referred to as "external loading".[51,52] Although nutrients in the sediments may appear to be "new loading", the ultimate source — even if it was decades ago — may be from predominately terrestrial sources (both NPS and PS). Thus, both internal and external loading are impacted by human activities. Eelgrass has also been shown to affect shear stress by slowing water velocities and effectively reducing sediment resuspension rates.[53]

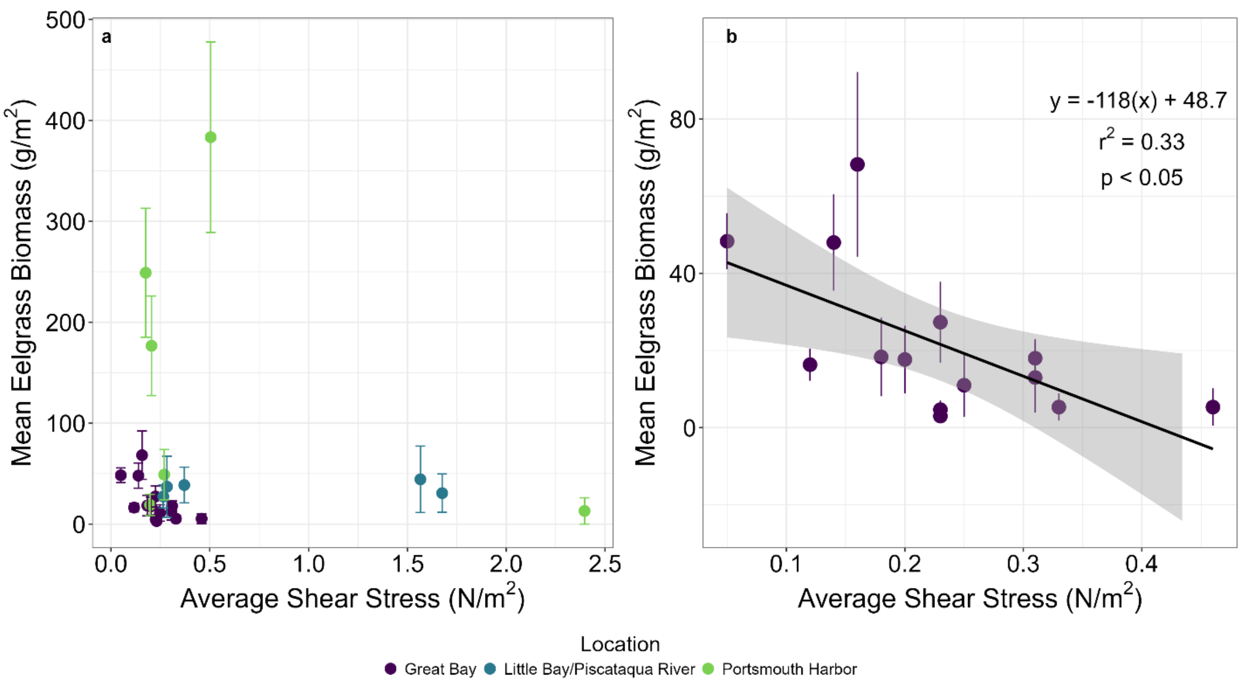

Figure 9. Mean eelgrass biomass does not vary with site average shear stress across the estuary (a). Looking only at Great Bay sites (b), mean eelgrass biomass decreases with increasing shear stress at Tier 2 sites. Points are three-year site means and standard error of the raw eelgrass biomass data. Linear regression (b) reflects the line of best fit through the site biomass means. Linear regression statistics are shown for the untransformed biomass data, as the linear regression was significant (p <0.05) for both raw and transformed biomass data.

Across the Great Bay Estuary Tier 2 sites, there was no clear relationship between average shear stress and the corresponding eelgrass biomass at a given Tier 2 site (Figure 9a). The highest eelgrass biomass values in Portsmouth Harbor correspond with lower shear stress values. In Great Bay, there is a significant decrease in eelgrass biomass as shear stress values increase (Figure 9b). In Great Bay Estuary, shear stress values above 0.35 N/m^2 are associated with erosion and resuspension of fine sediments.[49] Yet, this critical threshold for Great Bay Estuary is conservative, as sediment resuspension has been shown to occur at levels as low as

0.22 N/m^2.[49] Given this, it makes sense that eelgrass biomass decreases with increasing shear stress, due to the reduction in light availability from increased turbidity. With less available light, eelgrass growth would be reduced, resulting in less biomass. Reduction in eelgrass biomass can also be reflected in lower densities (i.e., a sparser meadow), which can increase flow turbulence and result in additional resuspension of sediment.[48,54] This may create a feedback loop where further sediment resuspension reduces light availability, making the eelgrass meadow more sparse, and leading to higher shear stress values. Finally, increased shear stress and resuspension are also recycling nutrients back into the water column, which could spur increased seaweed, epiphyte and phytoplankton production and further reduce light availability.[25]

Average shear stress in Great Bay Estuary ranged from 0.05 - 2.4 N/m^2 across Tier 2 sites. The highest shear stress values correspond to sites in the Piscataqua River and Portsmouth Harbor that had relatively low eelgrass biomass (below 50 g/m^2). Where shear stress is lower than 0.5 N/m^2, a wide range of eelgrass biomass was observed, including the highest biomass measurement of the three-year study period. Notably, the shear stress at the site with highest eelgrass biomass was greater than the critical threshold[49] for resuspension (0.35 N/m^2), which suggests that other factors may be interacting with shear stress to inform bed resilience, such as meadow size or differences in sediment grain size distribution. For instance, Portsmouth Harbor has less silt and clay in its sediment composition, which means there would be fewer fine particles to resuspend under high shear stress conditions (Table 2, Appendix I Figure A4).

Table 2. Mean and standard deviation grain size composition of Tier 2 sites, grouped by location. Means represent the average of all sites within a location between 2021 and 2023. Number of values for each location is shown in parenthesis.

Grain Size	Great Bay (42)	Little Bay/Piscataqua River (14)	Portsmouth Harbor (19)
% Gravel	1.6 ± 3.8	4.0 ± 5.8	8.9 ± 7.0
% Sand	51 ± 12	83 ± 5.3	84 ± 9.5
% Silt/Clay	48 ± 13	13 ± 7.6	7.2 ± 5.2

The shear stress results from this project add new understanding to how Great Bay Estuary functions, as previous work[49] had a narrower spatial scale for shear stress estimates. This project expanded the spatial and numerical range of shear stress estimates to include Portsmouth Harbor as well as Great Bay and specifically looked at sites with eelgrass present. It is important to note that while the shear stress estimates reported here are for eelgrass meadow locations, the hydrodynamic model did not explicitly include the impact of eelgrass presence on shear stress. Thus, shear stress values could be lower when the impact of eelgrass is accounted for.

Overall, shear-stress driven sediment resuspension is a concern in the Great Bay Estuary, particularly in the Great Bay where sediments are much finer due to the larger amount of silt and clay (Table 2). At Great Bay sites, shear stress ranged from 0.05 to 0.47 N/m^2. Three out of 14 sites in Great Bay had average shear stress values that exceeded the critical threshold for resuspension (0.35 N/m^2).[49] This has important implications for eelgrass health as sediment resuspension affects both estuarine light environment and nutrient recycling. For example, average TSS concentrations were consistently higher in Great Bay than Portsmouth Harbor in both 2022 and 2023 (Table 1), which could be related to the greater amount of fine sediments in

Great Bay being resuspended at lower shear stress values. Sediment resuspension in the estuary also has implications for both nitrogen and phosphate recycling. Dissolved inorganic nitrogen released due to resuspension during Tropical Storm Irene was a small fraction (~10%) of the total summer monthly dissolved inorganic nitrogen load for the year 2011.[49] However, for phosphorus, storm release was 65% of the summer phosphorus monthly riverine loading and exceeded the fall phosphorus monthly riverine loading.[49] While many estuarine studies focus on nitrogen as the limiting nutrient, any nutrient management approach needs to consider both nitrogen and phosphorus. In other words, eelgrass management is not as simple as just examining annual external (riverine) trends of nutrient or sediment loading.

For a visual guide to shear stress and hydrodynamics, please the StoryMap developed as part of this project.

Hypothesis 3: Impact of Algal Abundance (Seaweed, Epiphyte and Phytoplankton) on Eelgrass Health

Seaweed, epiphytes, and phytoplankton monitoring provides important insight into whether an estuary is showing signs of eutrophication (excessive loading of organic matter and nutrients).[55] Seaweed, epiphytes, and phytoplankton are important components of a healthy, well-functioning ecosystem. However, in high-nutrient (eutrophic) systems, they can become imbalanced, proliferate rapidly and have a negative effect on eelgrass (e.g., block light, enhance drag, alter sediment biogeochemistry). While phytoplankton can be assessed as part of light attenuation measures, seaweeds and epiphytes are not captured in those measurements. Yet, both seaweeds and epiphytes also block light, which impacts the ability of eelgrass to survive and grow.[3,56,57] Eelgrass has a higher light requirement than algae species, due to the metabolic demands of its relatively high biomass of non-photosynthetic tissue (e.g. root system structure).[58] The ability of eelgrass to access both water column and sediment nutrient pools due to its root system means that in nutrient-rich systems, light becomes a more important limiting factor to eelgrass growth.[58,59] In contrast, seaweeds, epiphytes, and phytoplankton need less light than eelgrass and experience maximum growth rates at higher water-column nutrient levels.[45,59,60]

In this three-year study, at both the estuary-wide (Figure 10) and Great Bay (Figure 11) scales, eelgrass biomass did not significantly correlate with any seaweed, epiphyte, or phytoplankton metric. A significant, but weak negative correlation was observed estuary wide between eelgrass percent cover and seaweed percent cover (r=-0.24, p=0.035, n=75). A significant but weak negative correlation was also observed estuary wide between eelgrass canopy height and seaweed percent cover (r=-0.23, p=0.046, n=73). If only Portsmouth Harbor sites are considered, then a significant and stronger, negative correlation is observed between eelgrass biomass and seaweed biomass (r=-0.60, p=0.006, n=17) (Figure 12). Also, for Little Bay/Piscataqua River, there is an almost significant positive relationship between eelgrass and seaweed biomass (Figure 12).

The lack of strong relationships between eelgrass biomass and seaweed, epiphyte, or phytoplankton metrics was unexpected. The effects of eutrophication on eelgrass meadows are well documented in estuarine ecosystems, with increased algal competition resulting in reduced eelgrass presence.[18,61] The lack of a relationship between eelgrass biomass and the algal competitors in Great Bay Estuary and Great Bay specifically may imply a lack of impact on eelgrass, but this is left unclear from this three-year project. With significant eelgrass loss in 2023, the 2021-2023 eelgrass biomass dataset represents a narrow range of potential eelgrass health and does not include higher values observed in earlier monitoring years. For example, mean eelgrass biomass at SeagrassNet monitoring sites in Great Bay ranged from 4 to 189 g/m^2 (mean 77 g/m^2 across the three transects) in 2020.[62] In comparison, eelgrass biomass in Great Bay for Tier 2 ranged from 0 to 140 g/m^2 (mean 23 g/m^2) across three field seasons (2021 through 2023). It is important to note that the wide range for Tier 2 is driven by one site with a biomass of 140 g/m^2 (Site 6 in 2021). The range for Great Bay sites without that outlier is 0 to 66 g/m^2. This suggests that the first three years of Tier 2 monitoring has captured the lower end of potential eelgrass biomass in the system, which affects our ability to interpret linear relationships with observed algal biomass. This range of eelgrass biomass is also likely to be significantly lower than earlier years in which eelgrass extent (Figure 1) was much greater. In other words, the confirmation of statistical relationships (or lack thereof) often requires a wide range in the response variable (eelgrass health), which did not occur due to two out of the three study years with low eelgrass biomass. It may well be that algae and epiphytes have negative impacts on eelgrass but this is only seen at high eelgrass densities which did not occur in our study.

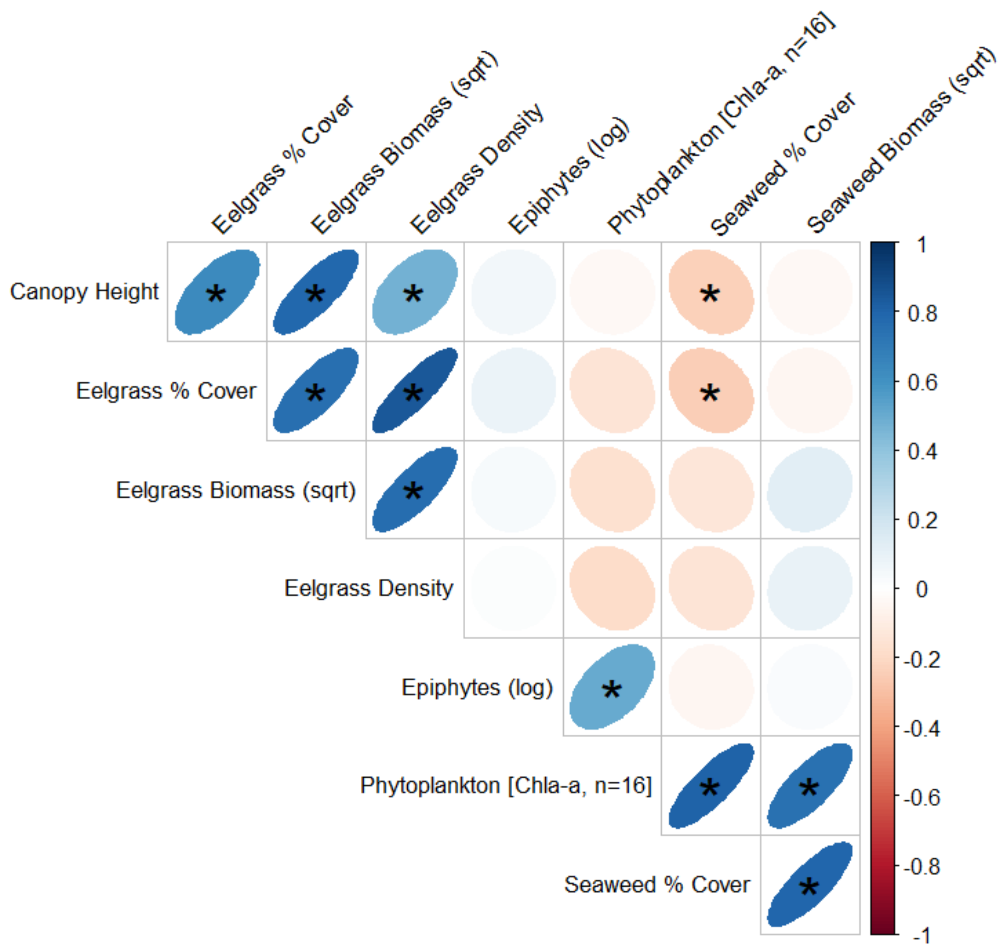

Figure 10. Correlation heat map of eelgrass, seaweed, phytoplankton, and epiphyte metrics for the estuary-wide dataset. Data transformations to meet assumptions of normality are denoted in parentheses of a given variable. Blue ellipses indicate strong positive correlations and red ellipses indicate strong negative correlations. Color ramp on the right indicates range of correlation coefficients (r) and corresponds to ellipse colors. Asterisks indicate significance at the 0.05 threshold.

The loss of eelgrass across multiple sites in 2023 may have resulted in lower values of epiphyte and seaweed biomass. Epiphytes grow on the surface of eelgrass blades. Thus, epiphytes can only be measured if eelgrass is present at a site. Moreover, in Great Bay, sites with no eelgrass often also had no seaweed in 2023, suggesting that seaweed remains in the system when it is caught within eelgrass meadows as frequently observed in field sampling. In this regard, much of the seaweed that is present may not originate in the Great Bay, but instead be transported with the tide from other parts of the estuary and retained by the seagrass itself. Under these conditions, seaweed is not necessarily displacing seagrass so much as co-occurring with it.

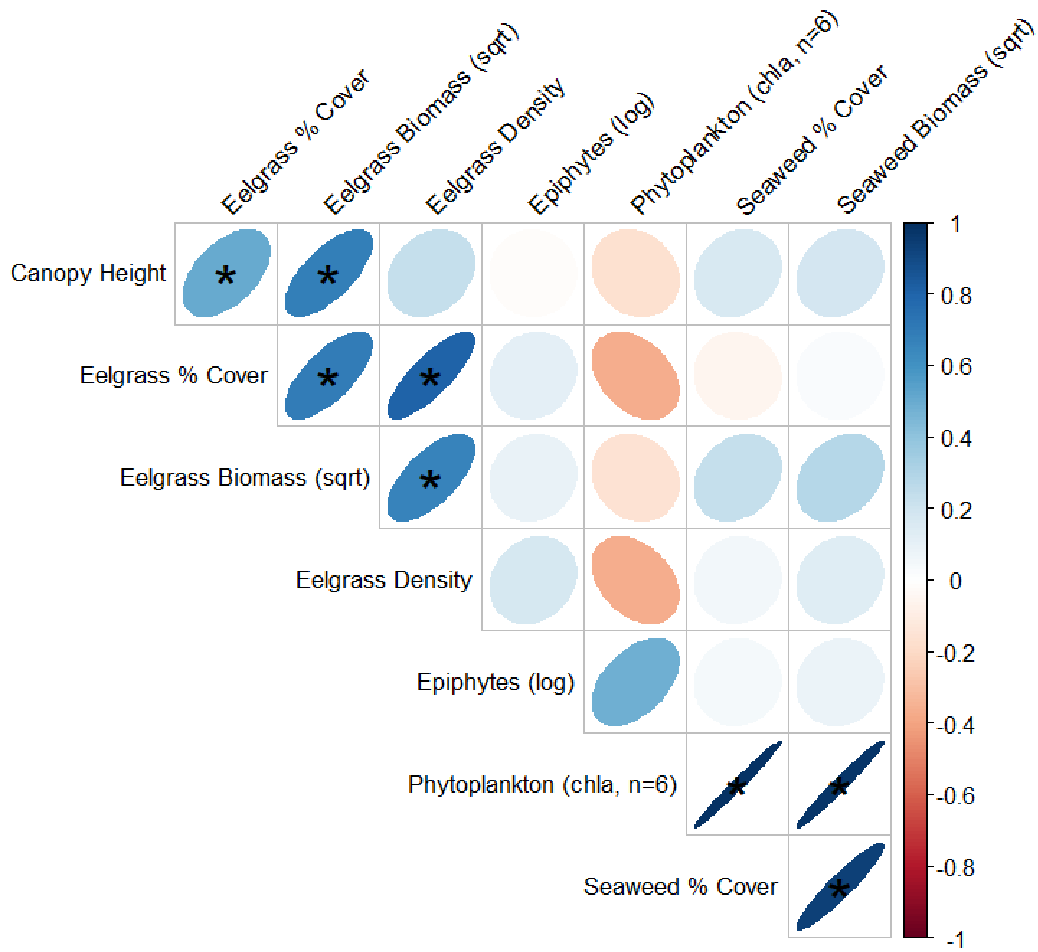

Figure 11. Correlation heat map of eelgrass, seaweed, phytoplankton, and epiphyte metrics for the Great Bay Tier 2 sites. Data transformations to meet assumptions of normality are denoted in parentheses of a given variable. Blue ellipses indicate strong positive correlations and red ellipses indicate strong negative correlations. Color ramp on the right indicates range of correlation coefficients (r) and corresponds to ellipse colors. Asterisks indicate significance at the 0.05 threshold.

Additionally, the summers of 2021 and 2023 had record rainfall (Figure 13), which may have reduced primary productivity of eelgrass, seaweed, epiphytes, and phytoplankton due to limited light availability. Other factors, including stress from low salinity, could also have had an impact. In 2023, median eelgrass, seaweed, and epiphyte biomass was lower compared to 2022 and 2021 for Great Bay (Table 1), while Portsmouth Harbor saw similar amounts of biomass across years (Table 1). Concurrently 2021 and 2023 median Kd estimates for Great Bay were 1.57 and 1.58, respectively (Table 1), while Portsmouth Habor median Kd values were 0.51 and 0.47 in 2021 and 2023. Given this context, the lack of relationship between eelgrass and algae is less surprising as monitoring efforts would have measured primary productivity at its lowest (particularly in Great Bay) rather than its highest potential.

In addition to correlations with eelgrass health covered above, two questions are relevant to address here. First, there has been a debate about whether seaweed is broadly a direct cause of seagrass loss or, alternatively another symptom of eutrophication that does not directly cause eelgrass loss. In this project, both eelgrass and seaweed seem to have experienced lower biomass levels than in previous years, suggesting that poor light conditions are affecting seaweeds as well as eelgrass. In addition, as noted above, when eelgrass is less abundant, there is less structure for seaweed to be trapped by. Table 1 indicates that 2023 had very low levels of seaweed in Great Bay, but seaweed was more abundant in Portsmouth Harbor where there was less light attenuation. Second, most of the seaweed biomass levels were less than 50 g/m^2. These levels of seaweed biomass are not as high as the levels seen in many other studies of eutrophic estuaries[45], which can have consistent biomass over 200 g/m^2. Currently, seaweed levels are not high enough to indicate that it is an important stress factor for eelgrass, although it could have been in previous years. More years of monitoring are required to make a definitive statement about seaweed as a stressor for eelgrass.

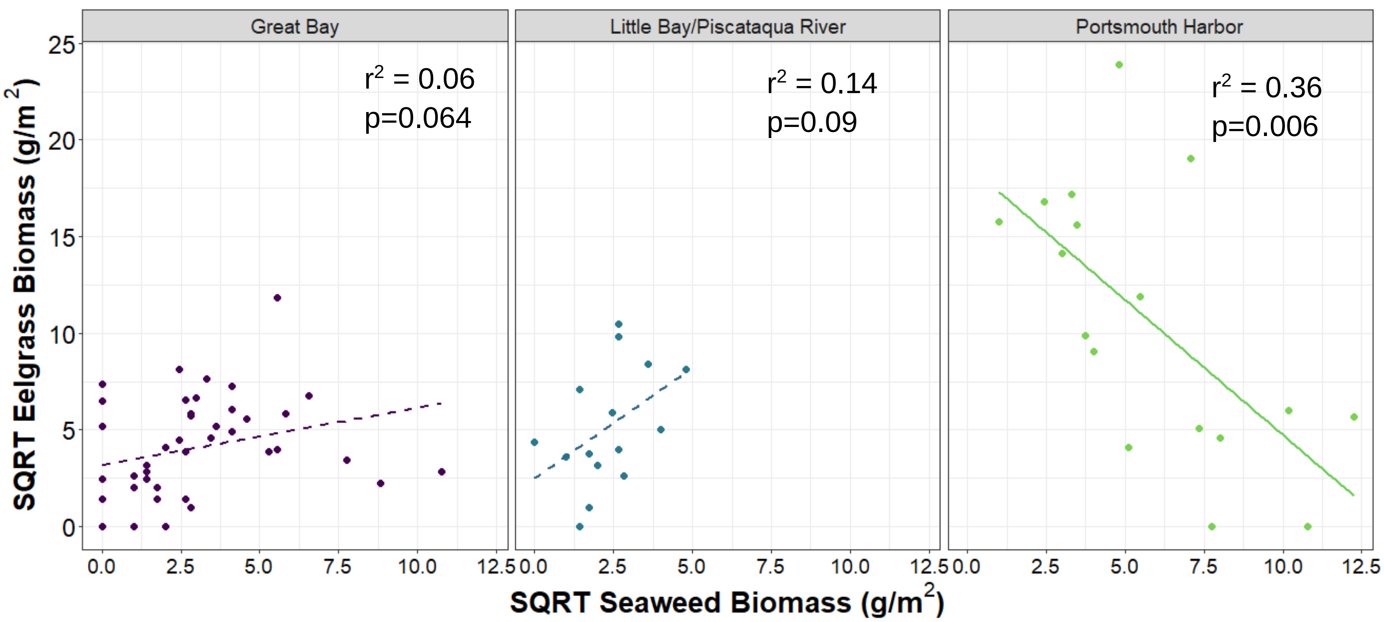

Figure 12. Relationship between square-root transformed seaweed biomass and square-root transformed eelgrass biomass, separated by location with Great Bay Estuary. Solid lines indicate significant linear regression ($p<0.05$) and dashed lines indicate almost-significant linear regressions ($0.05 < p < 0.1$). Linear regression statistics shown for transformed data. Adjusted r^2 values are shown.

Chlorophyll-a results from this project (Table 1) show that chlorophyll-a is usually low to moderate at most locations but can be high in Great Bay some years. In 2021, chlorophyll-a levels were low to moderate in most of the Estuary, but the highest values measured during this project were in Great Bay. In contrast, in 2023, median levels of chlorophyll-a only exceeded 5 ug/l in Great Bay and were much lower than in 2021 (Table 1). A seasonal median chlorophyll-a value of less than or equal to 15 ug/L has been cited as a habitat indicator for the growth and survival submerged aquatic vegetation (i.e. eelgrass).[63] Only the Great Bay in 2023 exceeded this value, and most chlorophyll-a medians were in the single digits (Table 1). This indicates that phytoplankton levels are not highly problematic in all regions or years, but in 2021 they were high enough to contribute to light problems for eelgrass in Great Bay. One way to consider this is that, for years when conditions are good to medium for eelgrass growth, and light penetration is greater, phytoplankton will have a higher probability of blocking light to eelgrass. In contrast, during years of particularly poor water quality, even plankton levels can be suppressed. Seen this way, the current argument for nutrient reductions is supported, because it will be critical for eelgrass to rebound as strongly as possible during the less rainy years. Particularly in Great Bay, where the eelgrass population depends on seeds each year for meadow maintenance, maximizing expansion in “good” years will be essential for maintaining viable eelgrass beds (unpublished data, Cynthia Hays).

The range of values for epiphytes was between 0.0 and over 1.0 mg/cm^2. As noted above, when there is little eelgrass, there is less opportunity for epiphytic growth. Nevertheless, in 2021 and 2022, eelgrass may have been affected by epiphytes, as values less than 1.0 mg/cm^2 can block significant amounts of light to the photosynthesizing parts of the plant, inhibiting their ability to gain energy from sunlight.[64,65] In contrast, in 2023, epiphytes were at very low levels, perhaps suppressed by rainy conditions, although both eelgrass and seaweed seem to have been more abundant in Portsmouth Harbor in 2023, which is difficult to explain.

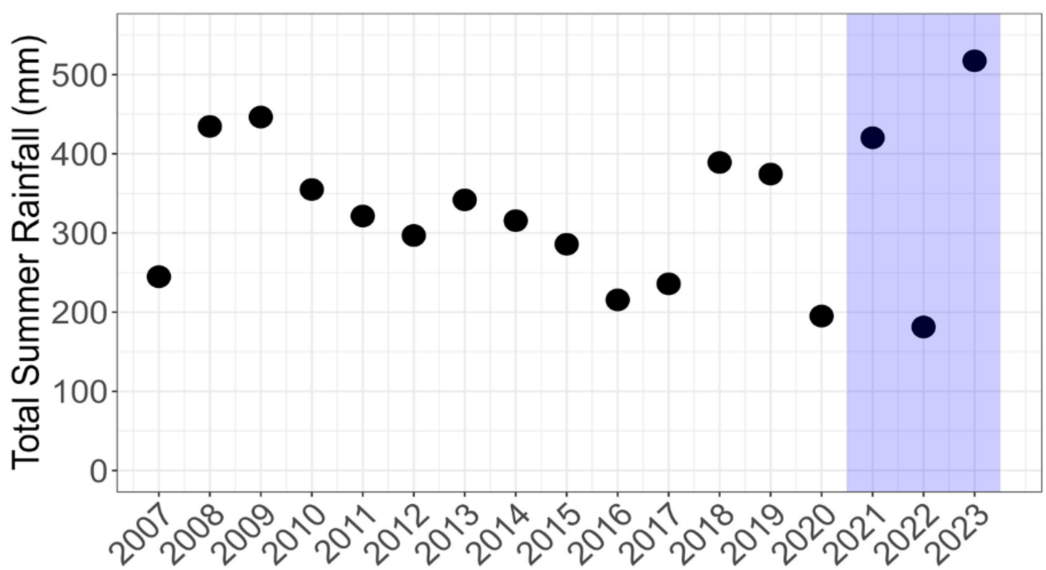

Figure 13. Total summer rainfall (June – August) of each calendar year between 2007 and 2023.Data sourced from the U.S. Climate Reference Network (CRN; GHCND: USW00054795; NH Durham 2 SSW) using the Durham, NH location. Hourly precipitation values (NOAA National Centers for Environmental Information) were summed by month and then by year and season. The blue region indicates the three summers of field work represented in this report.

Hypothesis 4: Impact of Water Column Nitrogen Concentrations on Eelgrass Health

Water column nitrogen concentrations are relevant to eelgrass health because they represent one of the compartments in the nitrogen cycle. Other compartments include plants like eelgrass and algae, microbes, and the sediments. These are all places where nitrogen is stored and changes forms from organic to inorganic and back to organic form or is converted relatively inert nitrogen gas and rejoins the atmosphere. Interpretation of nitrogen concentrations should be done with caution, because nitrogen, especially the dissolved inorganic forms, are taken up by primary producers quickly (less than hours in some cases). In contrast, organic nitrogen can take weeks and even months to break down and become available to primary producers. Mesocosm work in Great Bay Estuary has shown that increased nitrogen concentrations have the potential to indirectly reduce eelgrass biomass through stimulation of algal blooms that subsequently reduce light availability.[3] In this regard, the relations of eelgrass and light attenuation with algal components (addressed in other sections) are more direct indications of stressor via eutrophication.

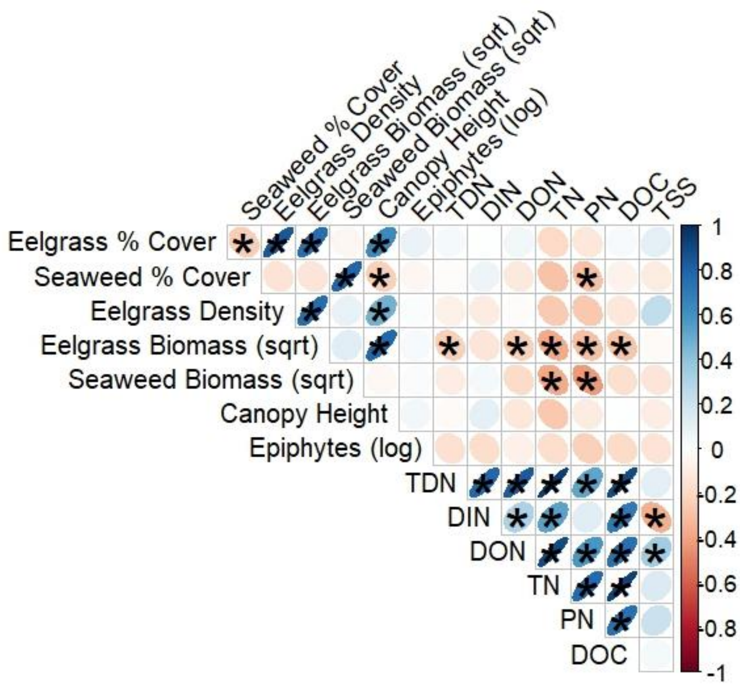

Figure 14. Correlation heat map of eelgrass, seaweed, epiphytes, and water chemistry metrics for the estuary-wide Tier 2 dataset. Data transformations to meet assumptions of normality are denoted in parentheses of a given variable. Blue ellipses indicate strong positive correlations and red ellipses indicate strong negative correlations. Asterisks indicate significance at the 0.05 threshold.

In this study, across the estuary, strong negative correlations were observed between multiple types of nitrogen concentrations, including total nitrogen (TN), particulate nitrogen (PN), total dissolved nitrogen (TDN), and dissolved organic nitrogen (DON), and eelgrass biomass (Figure 14). Those correlations did not hold up when only Great Bay data were examined (Figure 15), suggesting that the Portsmouth sites were driving the estuary-wide correlations.

The significant, negative correlation between DON and eelgrass biomass (Figure 16b), was also is driven by the Portsmouth Harbor sites. The relationship between DON and eelgrass biomass, though weak, suggests that light is a stressor in the system. Since DON is part of the larger dissolved organic matter (DOM) pool, DON concentrations in Great Bay Estuary could contribute to light attenuation. Water quality monitoring in Massachusetts estuaries has shown that healthy eelgrass meadows typically have total nitrogen concentrations below 0.34 – 0.37 mg/L, with degraded meadows having twice that amount of TN.[66] While TN concentrations greater than 0.40 mg/L were measured at most sites in Great Bay in 2023 (Figure 16), there was no significant relationship between TN and eelgrass biomass in Great Bay only sites. The negative correlation observed between TN and eelgrass biomass estuary wide (Figure 16) was driven by the low values of TN and high values of biomass at the Portsmouth Harbor sites. Also, given the relative poor health of Great Bay eelgrass overall (measured as low coverage, Figure 1 and low biomass (Table 1), within Great Bay relationships likely more difficult to detect due to very low variation in the response variable, eelgrass biomass, and over the study time frame.

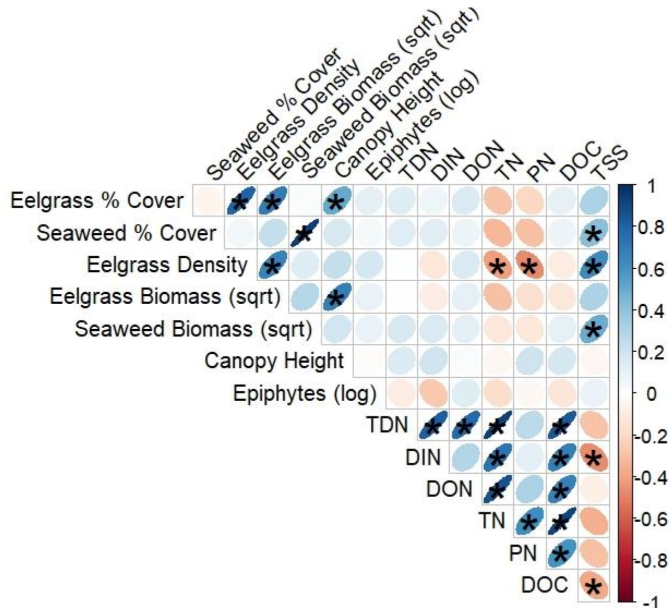

Figure 15. Correlation heat map of eelgrass, seaweed, epiphytes, and water chemistry metrics for Great Bay only. Data transformations to meet assumptions of normality are denoted in parentheses of a given variable. Blue ellipses indicate strong positive correlations and red ellipses indicate strong negative correlations. Asterisks indicate significance at the 0.05 threshold.

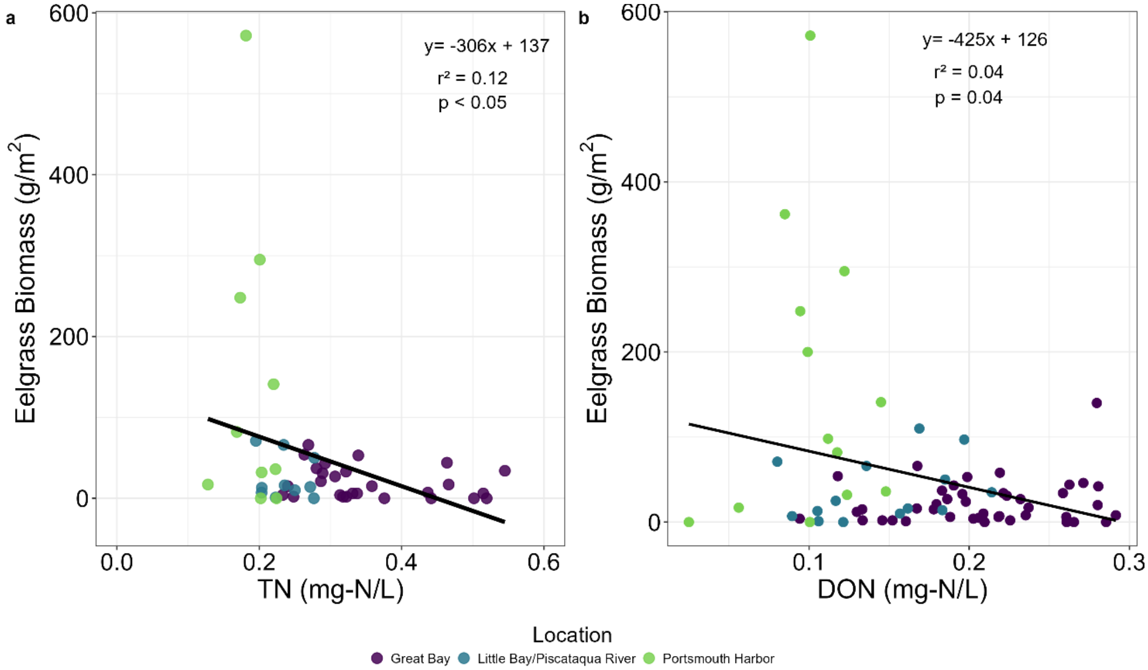

Figure 16. A negative correlation was observed between eelgrass biomass and total nitrogen (TN) concentrations (a) in Great Bay Estuary and between eelgrass biomass and dissolved organic nitrogen (DON) concentrations (b). Points are colored by relative location. Untransformed eelgrass biomass is shown, along with regression equation. Coefficients of determination (and p values) are from linear regression through square-root transformed data.

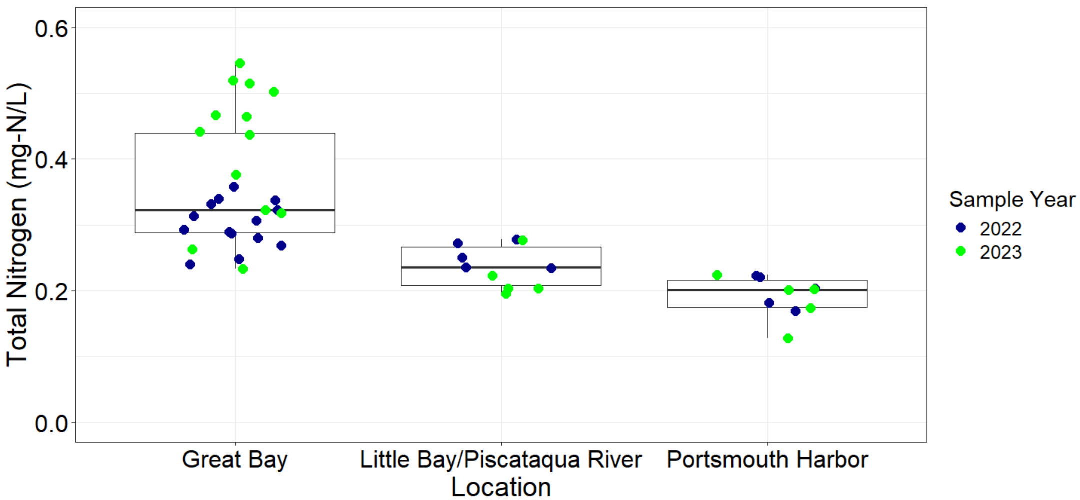

Figure 17. Concentration of total nitrogen within eelgrass meadows at Tier 2 sites in 2022 and 2023. Total nitrogen could not be calculated in 2021 due to lack of particulate nitrogen data. Points are colored by sample year.

Hypothesis 5: Impact of Light Attenuation on Eelgrass Health

Light attenuation (Kd) is a measure of water clarity: how much light is extinguished between the surface and deeper water. Therefore, as light attenuation increases, water clarity decreases. Light attenuation is of interest because, when eelgrass declines and ecosystems begin to struggle due to excessive loading of organic matter (i.e., eutrophication), light attenuation often but not always increases. Light attenuation measures the amount of light extant at different depths in the water column, and most directly reflects levels of total suspended solids (TSS), phytoplankton (chl-a), and colored dissolved organic matter (CDOM). However, as noted in the previous section on algae, light attenuation measurements will not capture changes in seaweed abundance nor epiphytes and these would be the prominent responses in areas that are "well flushed," such as Portsmouth Harbor and the navigation channel in Great Bay[22]. This is why it is critical that light attenuation measurements also occur in areas where eelgrass is growing and not just in the channels.

Estuary wide, eelgrass biomass is negatively correlated with light attenuation (Kd) (r^2=0.07, p=0.01), meaning that as light attenuation increased (i.e., light availability decreased), there was less eelgrass biomass (Figure 18). This finding is consistent with other work that has shown the role of light availability in controlling seagrass distribution and extent.[17,67,68] The maximum colonization depth of seagrasses linearly decreases with increasing light attenuation (Kd), indicating that estuaries with higher Kd values will have shallower eelgrass extent.[67] Tier 2 sites in Portsmouth Harbor had the lowest values of Kd (best water clarity), ranging between 0.25 and 0.6, and the deepest meadows, ranging from 1.5 to 4.8m at mean tide level. The high eelgrass biomass observed in Portsmouth Harbor, combined with the low Kd values, indicates that sufficient light is reaching the bottom of these deep meadows.

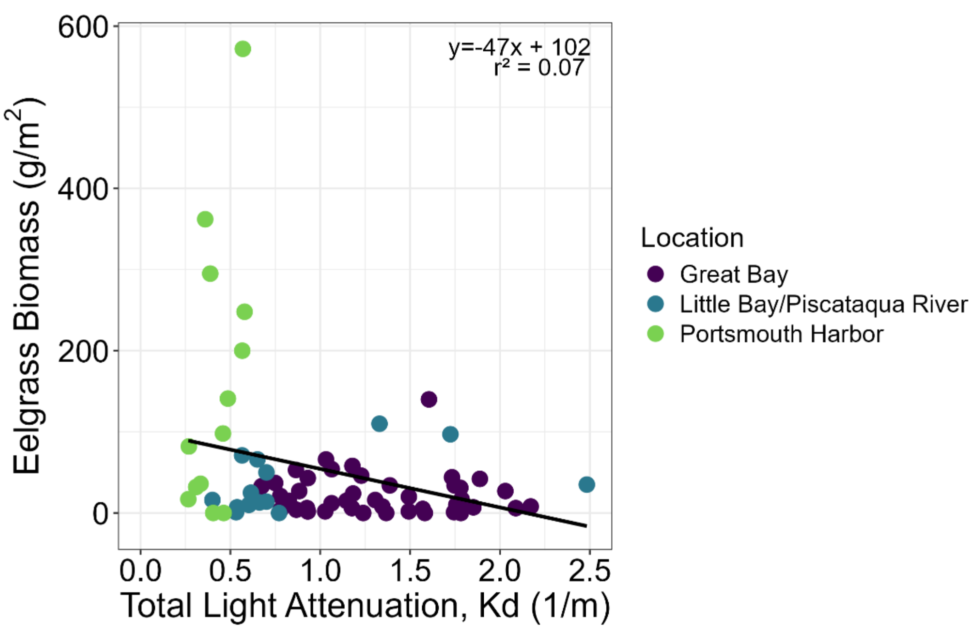

Figure 18. Light attenuation (Kd), measured on the day that eelgrass biomass samples were collected, versus eelgrass biomass at Tier 2 sites. Points are colored by location within the estuary. Data includes both measured Kd and predicted Kd.

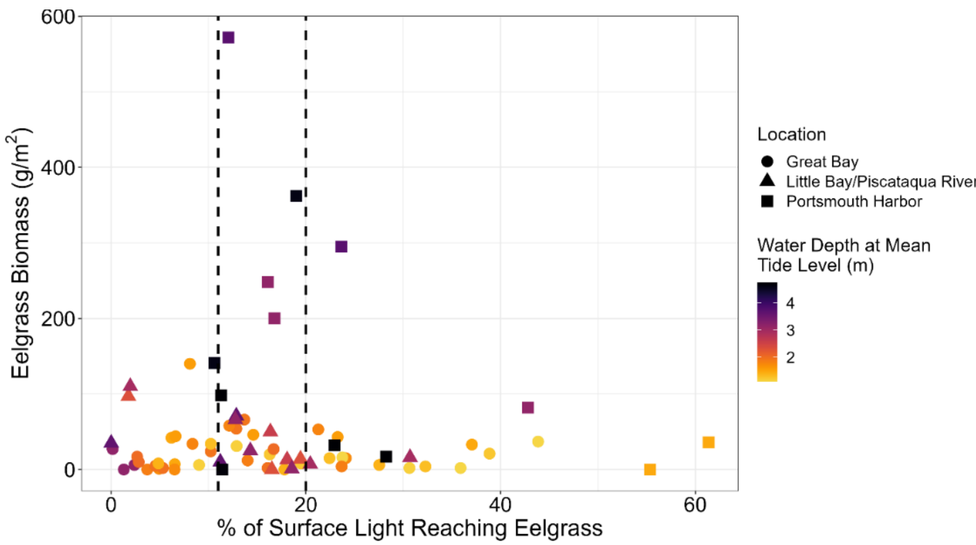

Figure 19. Relative amount of surface light that reaches eelgrass versus eelgrass biomass at all Tier 2 locations between 2021 and 2023. Points are colored by average water depth at mean tide level (m) and shapes denote relative location within the estuary. Vertical dashed lines indicate the reported minimum eelgrass light requirement range from the literature.[2,67]

In contrast with Portsmouth Harbor, Great Bay had the highest values of Kd and the lowest values for eelgrass biomass, suggesting poor water clarity may be reducing light availability to the shallow meadows (Table 1). This is also reflected in the Kd values for Great Bay, where most sites exceed values over 1.0, the threshold recommended for Great Bay eelgrass (Figure 18).[69] When light is assessed as a percentage of surface light that reaches the bottom, 35 out of 43 Great Bay samples had less than the minimum light required for eelgrass survival (22%) (Figure 19).[2,67] Seagrasses have higher light requirements at higher temperatures, suggesting that poor water clarity during the summer could create a stressor interaction between temperature and light availability[70–72]. This interaction between light availability and temperature will only become more important as water temperatures continue to rise.

TSS, and therefore light attenuation was greater in 2023 than 2022 (Table 1). In Great Bay, this corresponded with a decrease in biomass throughout the Bay. In the Piscataqua River and Portsmouth Harbor, however, eelgrass biomass seemed to increase in 2023 despite lower light. While surprising, it is important to note that light levels in 2023 were still adequate enough for eelgrass growth according to the NH DES study from 2009.[69] In this model, Kd must be lower than 0.75, 0.6 and 0.5, respectively, for Great Bay, Piscataqua River and Portsmouth Harbor. Table 1 indicates that only Great Bay is receiving less light than is required for eelgrass habitat maintenance, which agrees with the empirical relationship between Kd and eelgrass biomass in 2022 and 2023.

The lack of correlation between Kd and eelgrass biomass in Great Bay sites is surprising due to the observed poor water clarity during our sampling periods. The fact that SAV losses have occurred in both shallow and deep areas is additional evidence that factors other than light (e.g., shear stress, sediment quality, herbivory) partially control SAV distribution. However, these results should be interpreted with caution as light availability can be highly variable in an estuary. The light cast data presented here represents 17 unique sampling days during the

2022 and 2023 field seasons. Light casts on a given day may not represent average light availability throughout the growing season and provide information on the duration and frequency of low-light events over the course of the growing season. In addition, there may be a time lag between the occurrence of stressful light conditions and a measurable response in eelgrass biomass.

Hypothesis 6: Impact of Individual Light Attenuation Components on Eelgrass Health

This report has already detailed why light is a critical factor to study in estuarine ecosystems. It is important to go beyond identifying that light is a problem and also focus on what water column constituents are most affecting light availability to eelgrass. The three constituents that mainly attenuate light are CDOM, phytoplankton (chl-a) and total suspended solids (TSS). Because these constituents are often examined in the context of nutrient management, it is important to point out that both TSS and CDOM can be affected by nutrient-driven processes, although not to the same extent as phytoplankton. TSS contains not only inorganic particulate matter—mostly sediment—but also any organic matter that is retained by a 0.7 µm filter, such as most phytoplankton. (For context, many phytoplankton are larger than 1.5 µm.) The proportion of plankton in TSS can vary from less than 5% to 50%.[73] For example, in the York River Estuary in Virginia, the majority of TSS particles were comprised of between 20 and 30% organic matter.[73] CDOM also incorporates nitrogen since CDOM refers to colored or “chromophoric” dissolved organic matter, which includes nitrogen as a constituent of the organic molecules that are colored.

In general, examining the different light attenuators is relevant for managers considering different pollution reduction options, from stormwater management to septic tank optimization to wastewater treatment plant reductions. For example, if TSS is by far having the highest impact and phytoplankton levels are relatively low, this would suggest a different response than if both TSS and phytoplankton were moderately high. CDOM is a different case, because the negative impact of CDOM on eelgrass may vary based on its origin. CDOM tends to only attenuate light in the shorter wavelength portion of the light spectrum. In contrast, plankton and TSS attenuate light across the entire portion of the spectrum that is relevant for eelgrass.

Individual light attenuation components did not show strong relationships with eelgrass biomass across the Estuary nor in Great Bay specifically, except for dissolved organic carbon (DOC) estuary wide (Figure 20). Variability in concentrations of DOC explained 7% of the variability in eelgrass biomass across Tier 2 sites (Figure 20c). This relationship may be driven by the high biomass and low DOC in Portsmouth Harbor. DOC can be used as a proxy for colored dissolved organic matter (CDOM), which is the light absorbing portion of the organic matter pool.[74] The DOC and eelgrass relationship is not surprising, given that CDOM in Great Bay has previously comprised roughly 30% of total light attenuation.[75] The lack of relationship between TSS and eelgrass biomass is surprising, as the contribution of TSS to total light attenuation in sediment-driven systems is well documented.[20] There may not have been a clear relationship between TSS and eelgrass biomass for several reasons, including a limited dataset (2022-2023 only for TSS) and differing comparison scales. TSS can be highly variable during baseflow and storm conditions, which means that a set of discrete grab sample for TSS may not provide a true measure of overall TSS impacts on light availability over the growing season for eelgrass.

While the data do not show a relationship between TSS and eelgrass health, the TSS values shown in Figure 17 are certainly high enough to be of concern. In general, values over 15 mg/L are often regarded as being challenging for eelgrass, although none of the three light attenuating constituents should be considered in a vacuum; in other words, the impact on eelgrass is found in the combination of all three. Figure 20 shows that the highest biomass eelgrass occurred where TSS values were lower in Portsmouth Harbor. Table 1 illustrates that TSS levels are consistently higher as one proceeds upstream, with the lowest levels in Portsmouth Harbor. As noted earlier, Portsmouth Harbor differs from Great Bay in many other ways, including temperature, sediment organic matter, and water column nitrogen concentrations.

The same can be said for phytoplankton data. In 2021, chl-a values were high enough to be of concern throughout the estuary and quite high (median of 25.8 µg/L) in Great Bay. In 2023, levels were much lower overall with the highest values (median of 6.38 µg/L) in Great Bay. Dissolved organic carbon (DOC), a proxy for CDOM, was regularly lowest at Portsmouth Harbor and highest at Great Bay (Table 1).

In summary, the data from this 3-year period indicate that all three light attenuating components are important factors in blocking light and may be negatively impacting eelgrass health. Therefore, all three factors should likely be considered regarding pollution reduction and other management actions.

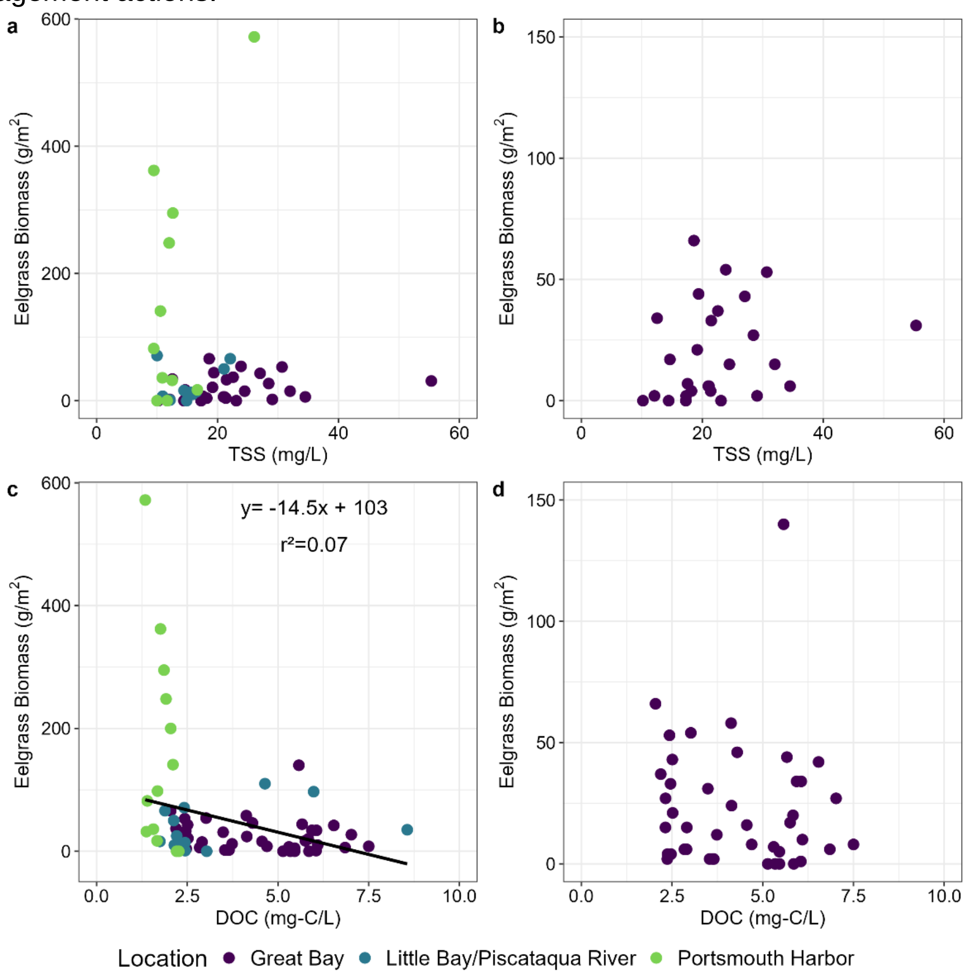

Figure 20. Comparison of eelgrass biomass to individual light attenuating components, including total suspended solids (TSS) at the estuary-wide (a) and Great Bay (b) scale and dissolved organic carbon (DOC) concentrations at the estuary wide (c) and Great Bay (d) scale. Total suspended solids were not measured in 2021, resulting in less data points (a and b). Points are color coded by relative location within the estuary. Lines represent significant linear regression relationships (p< 0.05).

Results and Discussion: Research Question 2

How does eelgrass affect water quality?

Hypothesis 1: Nitrogen/TSS concentrations along an eelgrass gradient

When this project was conceived, many on the project team expected that recent reductions in nitrogen from wastewater treatment plants would have some demonstrably beneficial impact on eelgrass. If that were the case, a natural question would be: *How will we judge whether continued nitrogen reductions would be beneficial to eelgrass?* To help with that question, we wanted to document how eelgrass health affected its environment along a gradient. By answering that question, we might be able to better predict future scenarios regarding eelgrass, nitrogen, and sediments. During this three year study, two of the years were abnormally rainy. Coinciding at the same time, there were significant decreases in eelgrass acreage across the Estuary. This set of field circumstances changed the inferences that we can draw from Question 2. Rather than being a study of how a recovering eelgrass habitat filters nitrogen and sediment, it became a study of how an eelgrass habitat in poor condition functions with regard to nitrogen and sediment filtration.

In this study, concentrations of dissolved inorganic nitrogen (DIN) in the surface water—i.e., the water between the sediment surface and the air/water interface—did not consistently decrease with increasing distance into the eelgrass meadow flowpaths (Figure 21). Flowpaths fluctuated between net uptake of DIN (negative flux) and net release of DIN (positive flux) (Figure 22), with the median DIN fluxes centering around zero, indicating no change. Flowpath GB3 had the largest range in DIN fluxes, from a net uptake of 38 mg N m^{-2} $hour^{-1}$ to a net release of 79 mg N m^{-2} $hour^{-1}$. The variability in net uptake or release across flowpaths is not

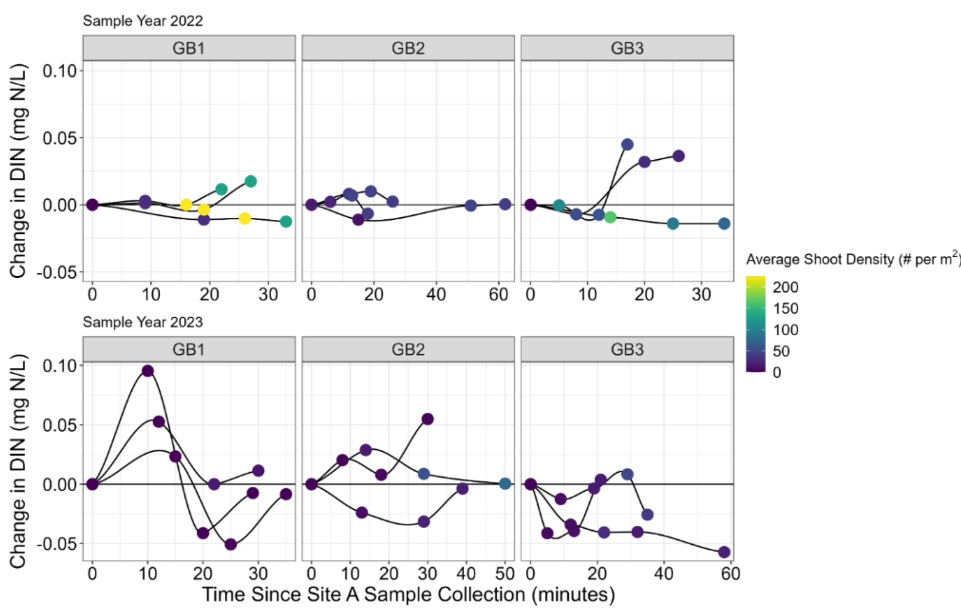

Figure 21. Change in dissolved inorganic nitrogen concentrations (DIN) over time, relative to the starting concentration at the beginning of each flowpath sampling event. Each line represents one sampling day along each flowpath. Each panel represents one of the three sampling transects (GB1, GB2, GB3) in 2022 (top) and 2022 (bottom). Points are colored according to average eelgrass shoot density at each site to represent the gradient of mudflat to eelgrass meadow. Points greater than zero indicate an increase in DIN and points less than zero indicate a decrease in DIN, relative to starting concentration. GB1 in 2023 has complete eelgrass loss along the flowpath.

surprising, since the eelgrass loss in 2023 could have increased the DIN flux back into the water column from decomposition of plant material.[64,65] Interpretation of the fate of DIN is limited by comparison of surface water concentrations along the flowpaths. The role of additional primary producers, including seaweed and phytoplankton, is uncertain. They may be contributing to both DIN uptake and release, especially given that both seaweed and phytoplankton take up nitrogen at faster rates than eelgrass under light limiting conditions.[59] For instance, leaf uptake of DIN has been measured via benthic flux chambers, with an average growing season rate of 3.3 mg DIN m^{-2} $hour^{-1}$.[65] Mean rates of nitrogen uptake along the flowpaths ranged from 2.9 to 38 mg N m^{-2} $hour^{-1}$, suggesting that additional uptake by seaweed and phytoplankton could explain why observed DIN uptake rates are higher than eelgrass-only estimates from the literature.

Concentrations of total suspended solids (TSS) did not consistently decrease with increasing distance into the eelgrass meadows (Figure 23). In 2022, there was minimal change in TSS across flowpaths, apart from one sampling date at GB1, where concentrations decreased along the flowpath with increasing eelgrass shoot density. In 2023, eelgrass loss throughout the estuary resulted in flowpaths with little to no eelgrass. TSS concentrations often increased in 2023 along the flowpaths, indicating a lack of sediment retention/trapping with the loss of eelgrass meadows in 2023 relative to 2022.[24,76]

Sediment accretion is a well-documented ecosystem service provided by eelgrass meadows, as their canopies reduce the velocity of currents and allow particles to settle out.[77–79] This ecosystem service is usually quantified through experimental sediment traps, whereas this work attempted to demonstrate sediment trapping by quantifying changes in TSS within the water column. The difference in methodology is one possible explanation for the lack of a decrease in TSS across the flowpaths in Great Bay. Yet, the striking difference in TSS behavior between 2022 and 2023 demonstrates the loss of an ecosystem service, with increasing TSS along those flowpaths with little to no eelgrass in 2023 (Figure 23).

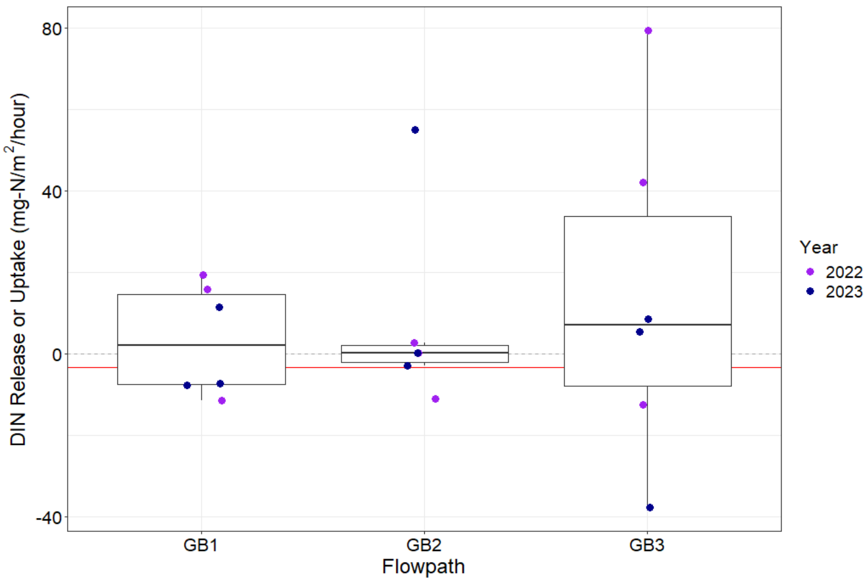

Figure 22. Rate of DIN uptake or release along each flowpath and sampling day (points). Rate of change calculated as the difference in DIN concentration between the start and end of the flowpath divided by the time (hours) to sample the entire transect length. Rates were scaled from volume to area by multiplying by a depth constant of 0.5m. Positive values indicate a net release of DIN (i.e. more DIN at the end of the flowpath than at the start) and negative values indicate a net uptake of DIN (i.e. less DIN at the end of the flowpath than at the start). The red line denotes a reported literature rate of 3.3mg DIN m^{-2} $hour^{-1}$.[65]

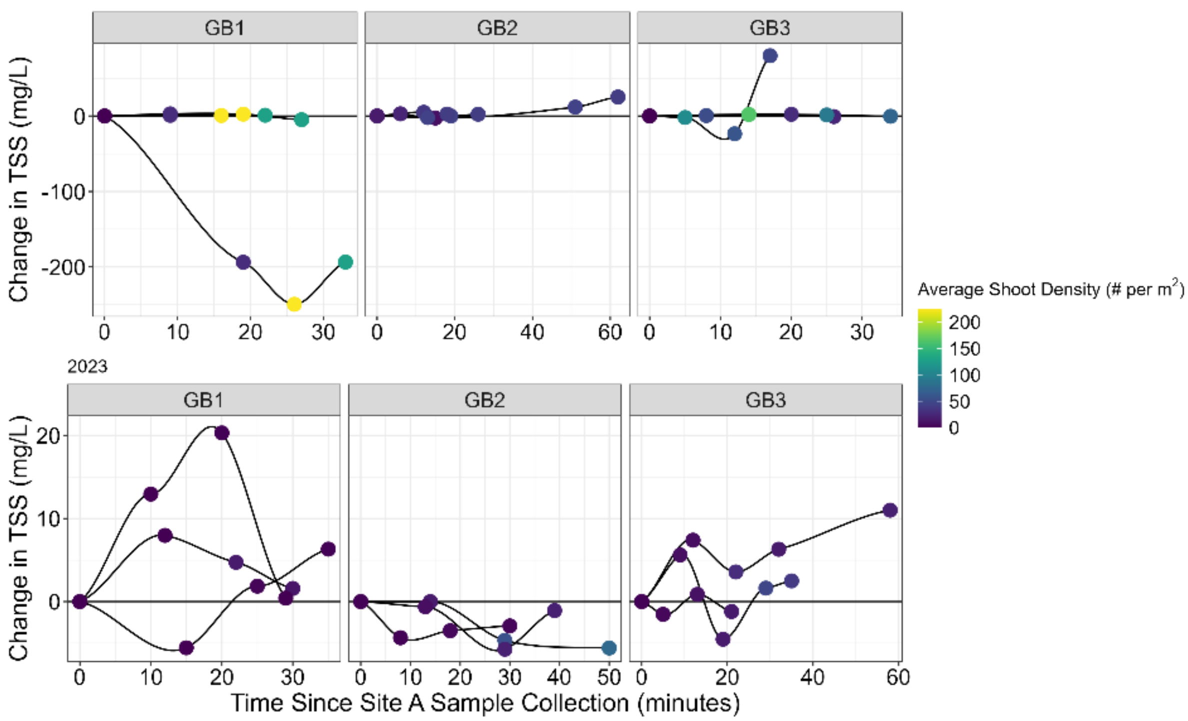

Figure 23. Change in total suspended solids (TSS) over time, relative to the starting concentration at the beginning of each flowpath sampling event. Each line represents one sampling day along each flowpath. Each panel represents one of the three sampling transects (GB1, GB2, GB3) in 2022 (top) and 2022 (bottom). Points are colored according to average eelgrass shoot density at each site to represent the gradient of mudflat to eelgrass meadow. Points greater than zero indicate an increase in TSS and points less than zero indicate a decrease in TSS, relative to starting concentration. GB1 in 2023 has complete eelgrass loss along the flowpath.

Hypothesis 2: N filter processes and residence time

As noted earlier in the report, residence time—how long water remains in particular portions of the estuary—is important because it determines how long critical ecosystem services (i.e. nitrogen cycling) have to occur. In this study, it was hypothesized processes that take up dissolved inorganic forms of nitrogen (i.e. denitrification and/or assimilation) would increase in rate with increasing eelgrass meadow water residence time. In part, this is due to longer residence times allowing sufficient time for plants to cycle nitrogen or for anoxia to develop and promote denitrification proceed.

Nitrogen uptake by eelgrass did not significantly vary with meadow residence time (Figure 24). Mean rates varied from 7.8 to 14.6 mg-N per m^2 per day across the three flowpaths (and the three residence time bins). Nitrogen uptake by red seaweed (*Graciliaria sp.*) also did not vary significantly across meadow residence times (Figure 25), but uptake by green seaweed (*Ulva lactuca)* was significantly higher at GB3 with a residence time of 0.92 hours. Overall, we expected higher rates of nitrogen uptake by primary producers with increased within-meadow residence times due to the ecosystem service of water quality improvement by eelgrass meadows. With longer residence times, it was hypothesized that primary producers would have more time and capacity to efficiently remove nitrogen from the water column and/or sediment bed and recycle it into plant biomass. This ecosystem service is occurring in Great Bay, though at reduced rates, as indicated by our measured rates of nitrogen uptake.

The median denitrification rate was 2.7x higher in the bare sites (n=3) compared to the eelgrass meadow sites (n=3) (Figure 26). Median values were compared due to the high influence of outliers on mean rates in both the bare and eelgrass experiments. Rates of denitrification were higher in Great Bay Estuary than in Chesapeake Bay eelgrass meadows, a surprising finding given that the density of eelgrass in Great Bay was half that of the restored Chesapeake meadows.[80] Eelgrass meadows support denitrification through the contribution of oxygen and carbon to the sediment bed, which enables the production of nitrate and subsequent reduction to N_2 gas.[80] For example, eelgrass meadows in the Chesapeake Bay had denitrification rates that were 4x greater than bare site comparisons.[80] Thus, we expected higher denitrification rates in healthy meadows. As eelgrass continues to decline in Great Bay, the loss of oxygen and carbon inputs to the sediment bed should ultimately reduce the denitrification capacity of the system. The higher denitrification rates in bare sediment in Great Bay highlights the loss of the eelgrass influence on sediment biogeochemical dynamics. Yet, it is surprising that rates across both bare and vegetated sites remain higher than those reported in the Chesapeake. The lack of trend between meadow residence time and denitrification rate is not surprising due to the small number of data points available (n=6) (Figure 27).

Potential explanations include differences in both sediment and porewater characteristics across the two systems (Table 3). Great Bay sediments have greater carbon availability across both habitat types, measured as both percent organic matter and percent carbon in the sediments, than Chesapeake sediments. Higher carbon availability and the detectable amounts of nitrate in Great Bay sediments suggest sufficient inputs for denitrification to occur, regardless of habitat type.

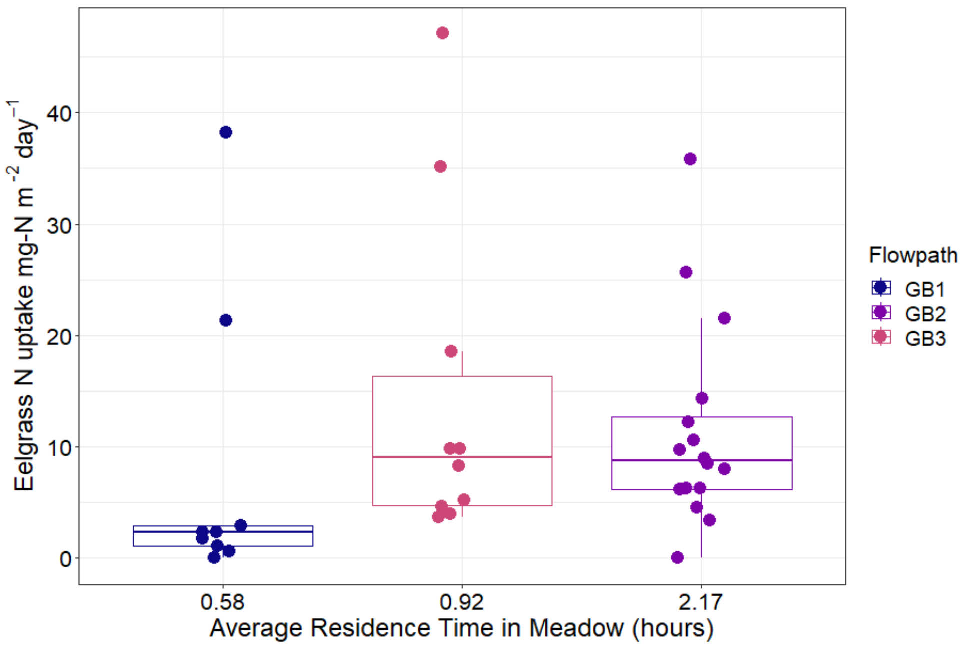

Figure 24. Eelgrass nitrogen uptake rates from flowpaths as a function of average within meadow residence time. Each point represents nitrogen uptake by one plant sample. N uptake was estimated using eelgrass growth (pin method) and percent nitrogen content from new growth.

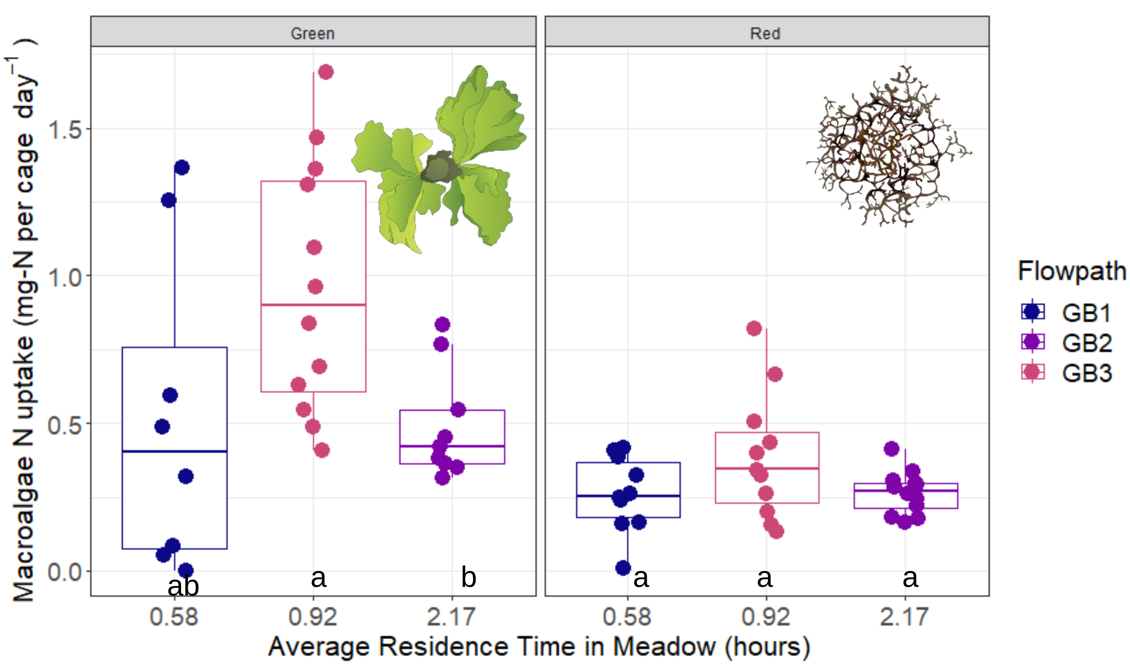

Figure 25. Seaweed nitrogen uptake rates from in-situ cage experiments. Green seaweed (left) had higher nitrogen uptake than red seaweed (right). Green seaweed had significantly higher nitrogen uptake at 1 hour residence time compared to the 2 hour residence time (ANOVA, $p < 0.05$, post-hoc Tukey test). There was no significant difference in red seaweed nitrogen uptake relative to residence time within the eelgrass meadows (ANOVA, $p > 0.05$). Plot includes cages at the mudflat sites (site A) that are not within the meadow.

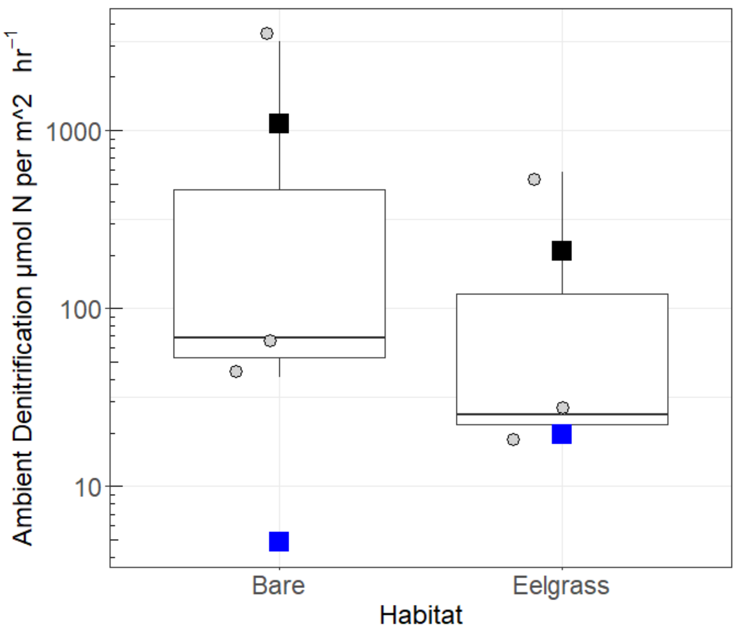

Figure 26. .Ambient denitrification rates across bare and eelgrass sites. Grey circles denote individual experiments. Lines represent the median and box shows the interquartile range. Black squares denote means from this study (n = 3) and blue squares denote mean denitrification rates from coastal Virgina eelgrass and bare sites.[80,81]

Table 3. Comparison of sediment and porewater characteristics in the South Bay, VA[80,81] and Great Bay during denitrification experiments. Values are mean and standard deviation. BDL indicates below-detection-limit.

	South Bay			Great Bay	
	Seagrass	**Bare**	**Cleared Seagrass**	**Seagrass**	**Bare**
Organic Matter %	2.53 ± 0.74	1.39 ± 0.21	2.00 ± 0.44	4.23 ± 1.2	4.18 ± 2.5
%C	0.57 ± 0.13	0.42 ± 0.16	0.47 ± 0.10	2.10 ± 0.65	1.9 ± 1.2
%N	0.04 ± 0.01	0.02 ± 0.002	0.03 ± 0.01	0.20 ± 0.06	0.19 ± 0.12
Bulk Density	1.45 ± 0.15	1.46 ± 0.36	1.29 ± 0.12	0.68 ± 0.18	0.78 ± 0.33
Sediment Temp (C)	29 ± 1.4	29.0	NA	21.0	20.7
Porewater Nitrate (µM)	BDL	BDL	BDL	4.5 ± 2.2	4.9 ± 3.3
Porewater Ammonium (µM)	10.1 ± 5.2	56.5 ± 15.1	154.6	213 ± 171*	192 ± 140*

**Values from 2021 pilot study in Great Bay*

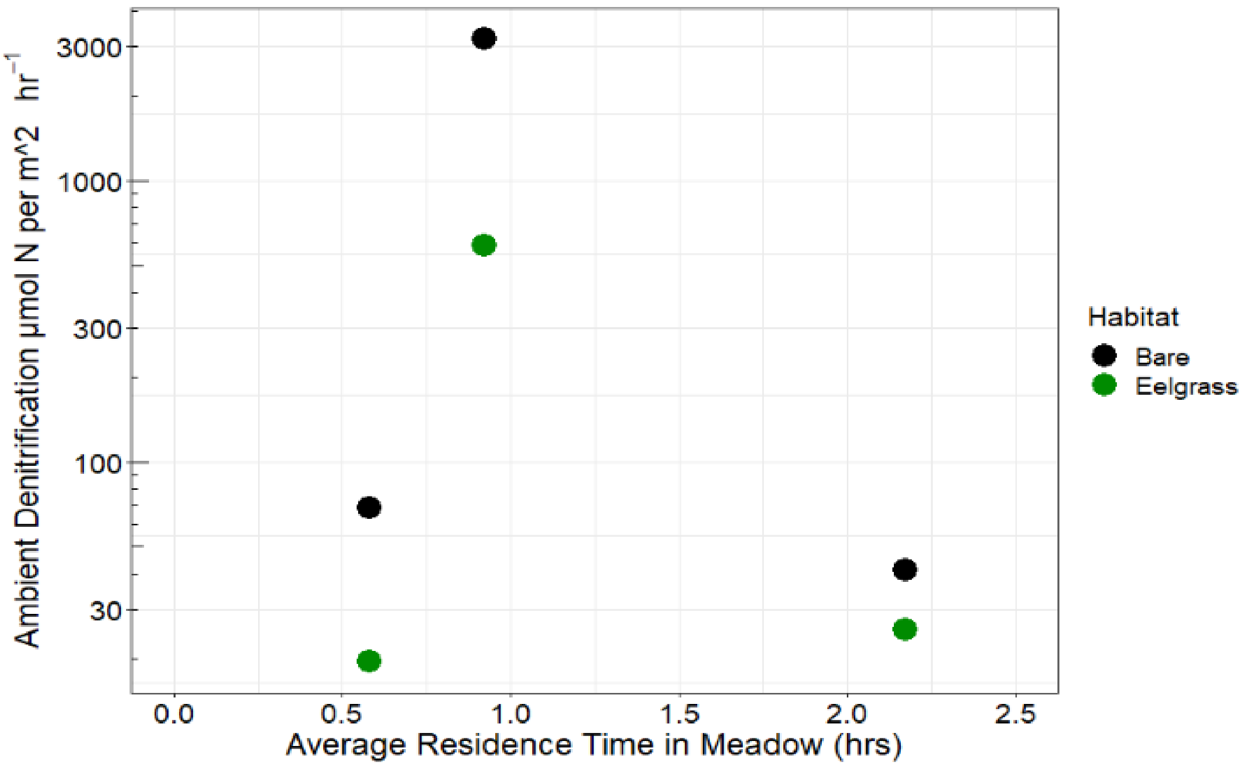

Figure 27. Ambient denitrification rates as a function of eelgrass meadow residence time. Points are colored by habitat where each denitrification experiment took place.

Hypothesis 3: Nitrogen filter processes and water parcels of different origin

Based on the difference in watershed-delivered nitrogen loads[27], we hypothesized that the eelgrass meadow nitrogen cycling rates would vary depending on the source of water they typically received. For instance, the Lamprey River has the highest non-point source nitrogen load to Great Bay, compared to the Squamscott and the Winnicut, in part due to its larger watershed size.[27] Mean non-point source total nitrogen loads between 2017 and 2020 were 9x greater from the Lamprey than the Winnicut River.[27] Part of our hypothesis was that eelgrass meadows receiving mostly Lamprey River water may not need to be as efficient in their nitrogen uptake as meadows receiving mostly Winnicut River water.

However, in this study, eelgrass nitrogen uptake did not significantly vary as a function of river water source (Figure 28). The usual caveats apply; both the low number of replications and the poor health of eelgrass could have confounded results. In addition, it may have been unrealistic to expect to detect differences in areas that are relatively close to each other. In the future, a similar experiment could be done comparing Great Bay sites with sites from the Piscataqua River and/or Portsmouth Harbor.

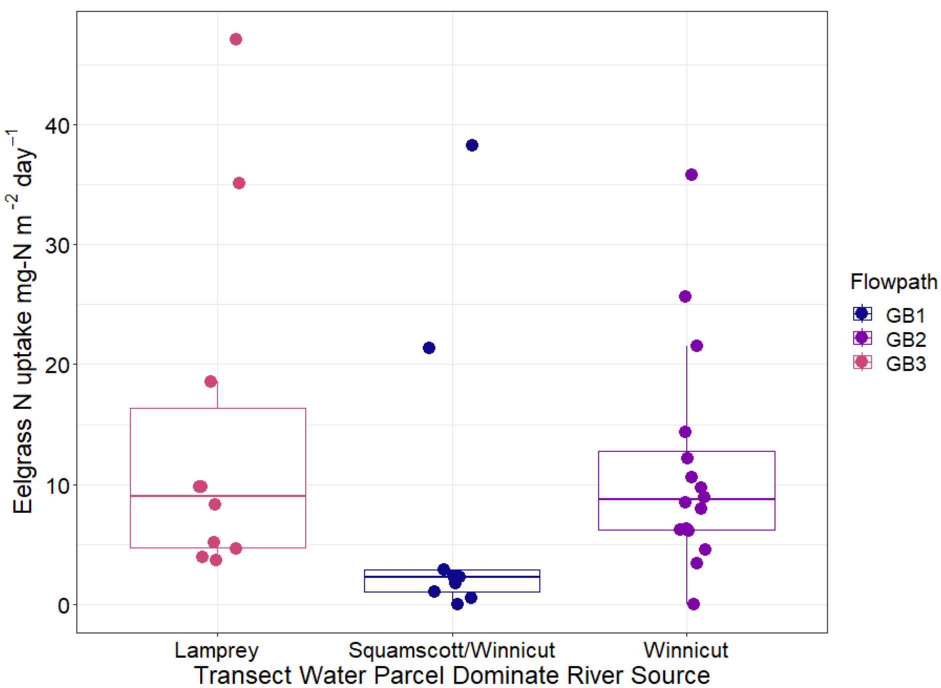

Figure 28. Eelgrass nitrogen uptake rates as a function of dominate water source

Hypothesis 4: Eelgrass health and nitrogen filter processes

In this study, eelgrass biomass did not exhibit a clear pattern with increasing eelgrass nitrogen uptake (Figure 29). Once again this is surprising, given that others have shown positive correlations between aboveground eelgrass biomass and DIN net uptake.[65] Eelgrass meadows are regarded as dissolved nitrogen sinks, but the balance between uptake and loss from eelgrass leaves results in a lack of nitrogen accumulation in leaves.[65] The lack of accumulation, which reflects a nitrogen use efficiency, may explain why this project did not see a strong relationship between uptake and biomass. Additionally, the methodology used in this study cannot account for translocation of nitrogen within the plant. Thus, the uptake rates could include both new nitrogen taken up by the plant and nitrogen translocated from other parts of the plant. As noted throughout this report, the very low eelgrass biomass values were unanticipated and make it more difficult to discern relationships. For example, in previous years, Figure 29 could very well have had eelgrass that was 100 g/m^2, rather than topping out at less than 15g/m^2.

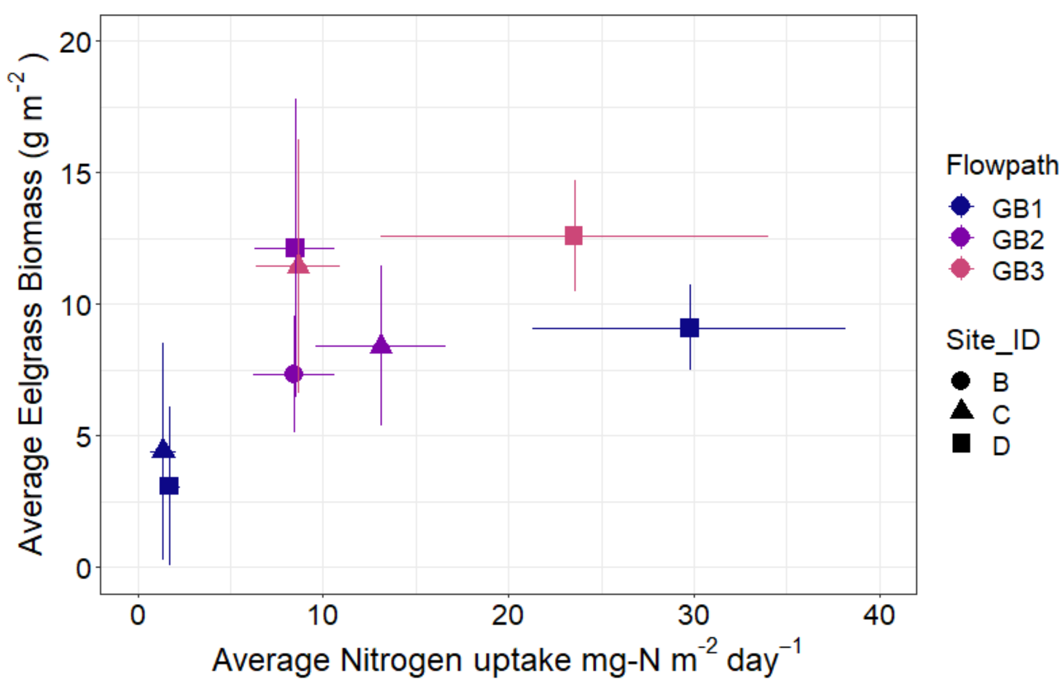

Figure 29. Average nitrogen uptake by eelgrass versus average eelgrass biomass at each flowpath and site. Points are means, lines are standard error. Sites within the eelgrass meadow (B through D) are shown.

References

1. Dennison, W. C. *et al.* Assessing Water Quality with Submersed Aquatic Vegetation. *BioScience* **43**, 86–94 (1993).
2. Environmental Protection Agency. *Ambient Water Quality Criteria for Dissolved Oxygen, Water Clarity and Chlorophyll a for the Chesapeake Bay and Its Tidal Tributaries*. https://cdn.ioos.noaa.gov/media/2017/12/ambient_water_quality_criteria.pdf (2003).
3. Short, F., Burdick, D. M. & Kaldy, J. E. Mesocosm experiments quantify the effects of eutrophication on eelgrass, Zostera marina. *Limnology and Oceanography* **40**, 740–749 (1995).
4. Biber, P. D., Kenworthy, W. J. & Paerl, H. W. Experimental analysis of the response and recovery of Zostera marina (L.) and Halodule wrightii (Ascher.) to repeated light-limitation stress. *Journal of Experimental Marine Biology and Ecology* **369**, 110–117 (2009).
5. Wong, M. C., Vercaemer, B. M. & Griffiths, G. Response and Recovery of Eelgrass (Zostera marina) to Chronic and Episodic Light Disturbance. *Estuaries and Coasts* **44**, 312–324 (2021).
6. Hemminga, M. & Duarte, C. M. *Seagrass Ecology*. (Cambridge University Press, Cambridge, 2000). doi:10.1017/CBO9780511525551.
7. Orth, R. J. & Heck, K. The Dynamics of Seagrass Ecosystems: History, Past Accomplishments, and Future Prospects. *Estuaries and Coasts* **46**, 1653–1676 (2023).
8. den Hartog, C. *The Sea-Grasses of the World*. https://pdf.usaid.gov/pdf_docs/PNAAM467.pdf (1977).
9. Orth, R. J. *et al.* A Global Crisis for Seagrass Ecosystems. *BioScience* **56**, 987–996 (2006).
10. Waycott, M. *et al.* Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* **106**, 12377–12381 (2009).
11. Burdick, D. *et al. A Case for Restoration and Recovery of Zostera Marina L. in the Great Bay Estuary*. 28 https://www.greatbay.org/wp-content/uploads/2020/05/Seagrass-White-Paper-FINAL-May-8-2020.pdf (2020).
12. Kirk, J. *Light and Photosynthesis in Aquatic Ecosystems*. (Cambridge University Press, Cambridge, 1983).
13. Branco, A. B. & Kremer, J. N. The Relative Importance of Chlorophyll and Colored Dissolved Organic Matter (CDOM) to the Prediction of the Diffuse Attenuation Coefficient in Shallow Estuaries. *Estuaries* **28**, 643–652 (2005).
14. Le, C. *et al.* Relation between inherent optical properties and land use and land cover across Gulf Coast estuaries. *Limnology and Oceanography* **60**, 920–933 (2015).
15. Ganju, N. K., Miselis, J. L. & Aretxabaleta, A. L. Physical and biogeochemical controls on light attenuation in a eutrophic, back-barrier estuary. *Biogeosciences* **11**, 7193–7205 (2014).
16. Ganju, N. K., Schoellhamer, D. H., Warner, J. C., Barad, M. F. & Schladow, S. G. Tidal oscillation of sediment between a river and a bay: a conceptual model. *Estuarine, Coastal and Shelf Science* **60**, 81–90 (2004).
17. Ralph, P. J., Durako, M. J., Enríquez, S., Collier, C. J. & Doblin, M. A. Impact of light limitation on seagrasses. *Journal of Experimental Marine Biology and Ecology* **350**, 176–193 (2007).
18. Bricker, S. B. *et al.* Effects of nutrient enrichment in the nation's estuaries: A decade of change. *Harmful algae* **8**, 21–32 (2008).
19. van der Heide, T. *et al.* Positive Feedbacks in Seagrass Ecosystems: Implications for Success in Conservation and Restoration. *Ecosystems* **10**, 1311–1322 (2007).
20. Adams, M. P. *et al.* Feedback between sediment and light for seagrass: Where is it important? *Limnology and Oceanography* **61**, 1937–1955 (2016).
21. Valiela, I. *et al.* Nitrogen Loading from Coastal Watersheds to Receiving Estuaries: New Method and Application. *Ecological Applications* **7**, 358–380 (1997).
22. Latimer, J. S. & Rego, S. A. Empirical relationship between eelgrass extent and predicted watershed-derived nitrogen loading for shallow New England estuaries. *Estuarine, Coastal and Shelf Science* **90**, 231–240 (2010).
23. Short, F. & Burdick, D. M. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* **19**, 730–739 (1996).
24. Hansen, J. C. R. & Reidenbach, M. A. Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. *Marine Ecology Progress Series* **448**, 271–288 (2012).

25. Gacia, E. & Duarte, C. M. Sediment Retention by a Mediterranean Posidonia oceanica Meadow: The Balance between Deposition and Resuspension. *Estuarine, Coastal and Shelf Science* **52**, 505–514 (2001).
26. Kenworthy, W. J., Gallegos, C. L., Costello, C., Field, D. & di Carlo, G. Dependence of eelgrass (Zostera marina) light requirements on sediment organic matter in Massachusetts coastal bays: Implications for remediation and restoration. *Marine Pollution Bulletin* **83**, 446–457 (2014).
27. Piscataqua Region Estuaries Partnership. *State of Our Estuaries 2023*. https://scholars.unh.edu/prep/467 (2023).
28. Shchepetkin, A. F. & McWilliams, J. C. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling* **9**, 347–404 (2005).
29. Haidvogel, D. B. *et al.* Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. *Journal of Computational Physics* **227**, 3595–3624 (2008).
30. Cook, S. E., Lippmann, T. C. & Irish, J. D. Modeling nonlinear tidal evolution in an energetic estuary. *Ocean Modelling* **136**, 13–27 (2019).
31. Yang, Z. *et al. NOAA'S Gulf of Maine Operational Forecast System (GOMOFS): Model Development and Hindcast Skill Assessment*. 44 (2019).
32. Egbert, G. D. & Erofeeva, S. Y. Efficient Inverse Modeling of Barotropic Ocean Tides. (2002).
33. Liu, W. T., Katsaros, K. B. & Businger, J. A. Bulk Parameterization of Air-Sea Exchanges of Heat and Water Vapor Including the Molecular Constraints at the Interface. (1979).
34. Fairall, C. *et al.* Cool-skin and warm-layer effects on sea surface temperature. *J. Geophys. Res.* **101**, 1295–1308 (1996).
35. Fairall, C. W., Bradley, E. F., Rogers, D. P., Edson, J. B. & Young, G. S. Bulk parameterization of air-sea fluxes for Tropical Ocean-Global Atmosphere Coupled-Ocean Atmosphere Response Experiment. *Journal of Geophysical Research: Oceans* **101**, 3747–3764 (1996).
36. Choi, J.-G. *et al.* Physical forces determine the annual bloom intensity of the giant jellyfish Nemopilema nomurai off the coast of Korea. *Regional Studies in Marine Science* **24**, 55–65 (2018).
37. Neckles, H. A., Kopp, B. S., Peterson, B. J. & Pooler, P. S. Integrating Scales of Seagrass Monitoring to Meet Conservation Needs. *Estuaries and Coasts* **35**, 23–46 (2012).
38. Matso, K., Mattera, T., Burdick, D. & Gregory, T. Great Bay Estuary Tier 2 Seagrass/Seaweed Monitoring Program 2021 Quality Assurance Project Plan. (2021).
39. Burdick, D. *et al.* Seaweed Monitoring in the Great Bay Estuary: 2019 Annual Report. *PREP Reports & Publications* (2020).
40. Matso, K., Mattera, T., Martin, L., Gregory, T. & Gruen, N. Great Bay Estuary Tier 2 Seagrass/Seaweed Monitoring Program 2023-2027 Quality Assurance Project Plan. (2023).
41. Short, F. & Coles, R. G. *Global Seagrass Research Methods*. (Elsevier, 2001).
42. Aoki, L. R. & McGlathery, K. J. Push-pull incubation method reveals the importance of denitrification and dissimilatory nitrate reduction to ammonium in seagrass root zone. *Limnology and Oceanography: Methods* **15**, 766–781 (2017).
43. Nielsen, L. P. Denitrification in sediment determined from nitrogen isotope pairing. *FEMS Microbiology Letters* **86**, 357–362 (1992).
44. R Core Team. R: A Language and Environment for Statistical Computing. (2023).
45. Valiela, I. *et al.* Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* **42**, 1105–1118 (1997).
46. Adams, M. P. *et al.* Water residence time controls the feedback between seagrass, sediment and light: Implications for restoration. *Advances in Water Resources* **117**, 14–26 (2018).
47. Bilgili, A., Proehl, J., Lynch, D., Smith, K. & Swift, M. Estuary/ocean exchange and tidal mixing in a Gulf of Maine Estuary: a Lagrangian modeling study. *Estuarine, Coastal and Shelf Science* **65**, 607–624 (2005).
48. Marin-Diaz, B., Bouma, T. J. & Infantes, E. Role of eelgrass on bed-load transport and sediment resuspension under oscillatory flow. *Limnology and Oceanography* **65**, 426–436 (2020).
49. Wengrove, M., Foster, D., Kalnejais, L., Percuoco, V. P. & Lippmann, T. Field and laboratory observations of bed stress and associated nutrient release in a tidal estuary. *Estuarine, Coastal and Shelf Science* **161**, 11–24 (2015).

50. Lawson, S. E., Wiberg, P. L., McGlathery, K. J. & Fugate, D. C. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuaries and Coasts: J ERF* **30**, 102–112 (2007).
51. Percuoco, V. P., Kalnejais, L. H. & Officer, L. V. Nutrient release from the sediments of the Great Bay Estuary, N.H. USA. *Estuarine, Coastal and Shelf Science* **161**, 76–87 (2015).
52. Lillebø, A. I. *et al.* Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. *Estuarine, Coastal and Shelf Science* **65**, 697–707 (2005).
53. Contti Neto, N., Pomeroy, A., Lowe, R. & Ghisalberti, M. Seagrass Meadows Reduce Wind-Wave Driven Sediment Resuspension in a Sheltered Environment. *Frontiers in Marine Science* **8**, (2022).
54. Lefebvre, A., Thompson, C. E. L. & Amos, C. L. Influence of Zostera marina canopies on unidirectional flow, hydraulic roughness and sediment movement. *Continental Shelf Research* **30**, 1783–1794 (2010).
55. Nixon, S. W. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia* **41**, 199–219 (1995).
56. McGlathery, K. Macroalgal Blooms Contribute to the Decline of Seagrass in Nutrient-Enriched Coastal Waters. *Journal of Phycology* **37**, 453–456 (2001).
57. Williams, S. L. & Ruckelshaus, M. H. Effects of Nitrogen Availability and Herbivory on Eelgrass (Zostera Marina) and Epiphytes. *Ecology* **74**, 904–918 (1993).
58. Sand-Jensen, K. & Borum, J. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic botany* **41**, 137–175 (1991).
59. Duarte, C. M. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* **41**, 87–112 (1995).
60. McGlathery, K., Sundbäck, K. & Anderson, I. Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. *Mar. Ecol. Prog. Ser.* **348**, 1–18 (2007).
61. Sand-Jensen, K. Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany* **3**, 55–63 (1977).
62. Matso, K. *et al.* SeagrassNet Monitoring in the Great Bay Estuary, NH/ME Field Season 2020. *PREP Reports & Publications* (2022).
63. Batiuk, R.A. *et al. Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis.* https://d18lev1ok5leia.cloudfront.net/chesapeakebay/documents/Submerged_Aquatic_Vegetation_Water_Qaulity_and_Habitat-Based_Requirements_and_Restoration_Targets_2000.pdf (2000).
64. Hemminga, M., Harrison, P. G. & Lent, F. van. The balance of nutrient losses and gains in seagrass meadows. *Marine Ecology Progress Series* **71**, 85–96 (1991).
65. Risgaard-Petersen, N. *et al.* Nitrogen balance of a temperate eelgrass Zostera marina bed. *Marine Ecology Progress Series* **174**, 281–291 (1998).
66. Benson, J. L., Schlezinger, D. & Howes, B. L. Relationship between nitrogen concentration, light, and Zostera marina habitat quality and survival in southeastern Massachusetts estuaries. *Journal of Environmental Management* **131**, 129–137 (2013).
67. Duarte, C. M. Seagrass depth limits. *Aquatic Botany* **40**, 363–377 (1991).
68. Dennison, W. C. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* **27**, 15–26 (1987).
69. Trowbridge, P. *Numeric Nutrient Criteria for the Great Bay Estuary*. 120 https://www.des.nh.gov/sites/g/files/ehbemt341/files/documents/r-wd-09-12.pdf (2009).
70. Bulthuis, D. A. Effects of temperature on photosynthesis and growth of seagrasses. *Aquatic Botany* **27**, 27–40 (1987).
71. Moore, K. A., Wetzel, R. L. & Orth, R. J. Seasonal pulses of turbidity and their relations to eelgrass (Zostera marina L.) survival in an estuary. *Journal of Experimental Marine Biology and Ecology* **215**, 115–134 (1997).
72. Moore, K. A. Influence of Seagrasses on Water Quality in Shallow Regions of the Lower Chesapeake Bay. *Journal of Coastal Research* 162–178 (2004).
73. Fall, K. A., Friedrichs, C. T., Massey, G. M., Bowers, D. G. & Smith, S. J. The Importance of Organic Content to Fractal Floc Properties in Estuarine Surface Waters: Insights From Video, LISST, and Pump Sampling. *Journal of Geophysical Research: Oceans* **126**, e2020JC016787 (2021).

74. Harvey, E. T., Kratzer, S. & Andersson, A. Relationships between colored dissolved organic matter and dissolved organic carbon in different coastal gradients of the Baltic Sea. *Ambio* **44**, 392–401 (2015).
75. Morrison, J. R., Gregory, T. K., Pe'eri, S., McDowell, W. & Trowbridge, P. *Using Moored Arrays and Hyperspectral Aerial Imagery to Develop Nutrient Criteria for New Hampshire's Estuaries*. 65 https://ccom.unh.edu/sites/default/files/publications/Morrison_2010_Report_Using_Moored_Arrays_and_Hyperspecral_Areial_Imagery_to_Develop_Nutrient_Criteria_NH_Estuaries.pdf (2008).
76. Van Der Heide, T., Van Nes, E. H., Van Katwijk, M. M., Olff, H. & Smolders, A. J. P. Positive Feedbacks in Seagrass Ecosystems – Evidence from Large-Scale Empirical Data. *PLoS ONE* **6**, e16504 (2011).
77. Gacia, E., Granata, T. C. & Duarte, C. M. An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. *Aquatic Botany* **65**, 255–268 (1999).
78. Fonseca, M. S. & Kenworthy, W. J. Effects of current on photosynthesis and distribution of seagrasses. *Aquatic Botany* **27**, 59–78 (1987).
79. de Boer, W. F. Seagrass–sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. *Hydrobiologia* **591**, 5–24 (2007).
80. Aoki, L. R. & McGlathery, K. J. Restoration enhances denitrification and DNRA in subsurface sediments of Zostera marina seagrass meadows. *Marine Ecology Progress Series* **602**, 87–102 (2018).
81. Aoki, L. R., McGlathery, K. J. & Oreska, M. P. J. Seagrass restoration reestablishes the coastal nitrogen filter through enhanced burial. *Limnology and Oceanography* **65**, 1–12 (2020).

Appendix I

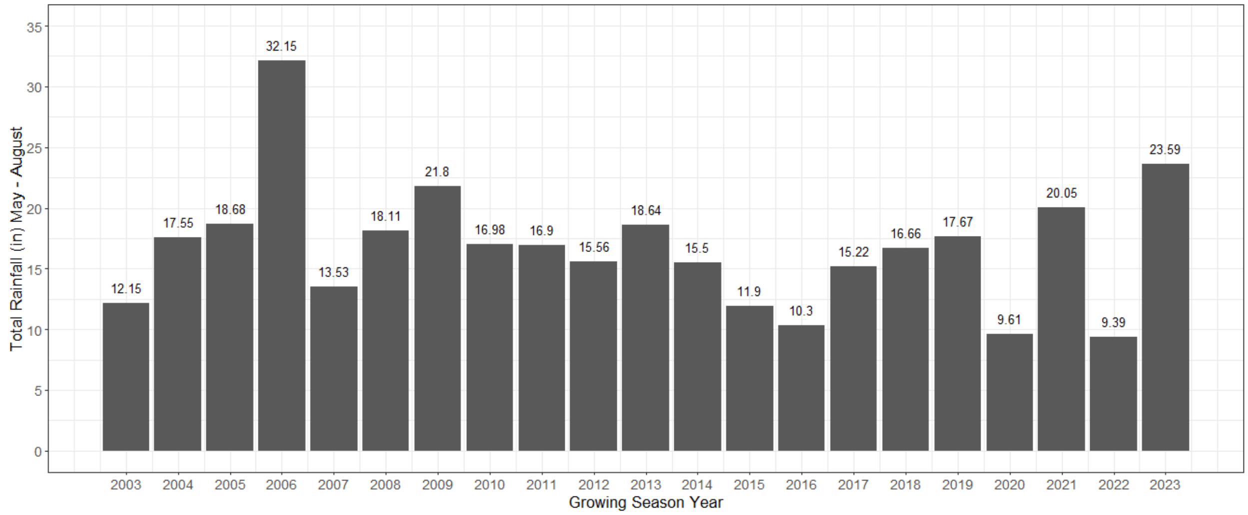

Figure A1. Total rainfall between May and August of each year. Text above bars gives the summed total for each growing season. Data source: NOAA hourly precipitation data for Durham SSW station (https://www.ncei.noaa.gov/pub/data/uscrn/products/houlry02/)

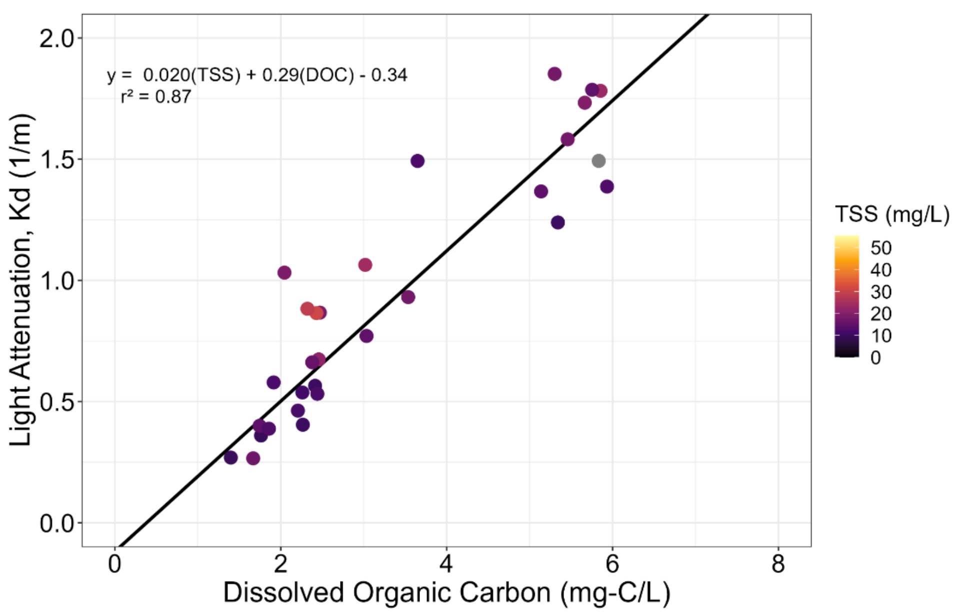

Figure A2. Relationship between measured dissolved organic carbon (x axis) and total suspended solids (color ramp) and individual light casts taken the same day. A total of 30 paired light attenuation measurements and water samples were used to build the predictive model.

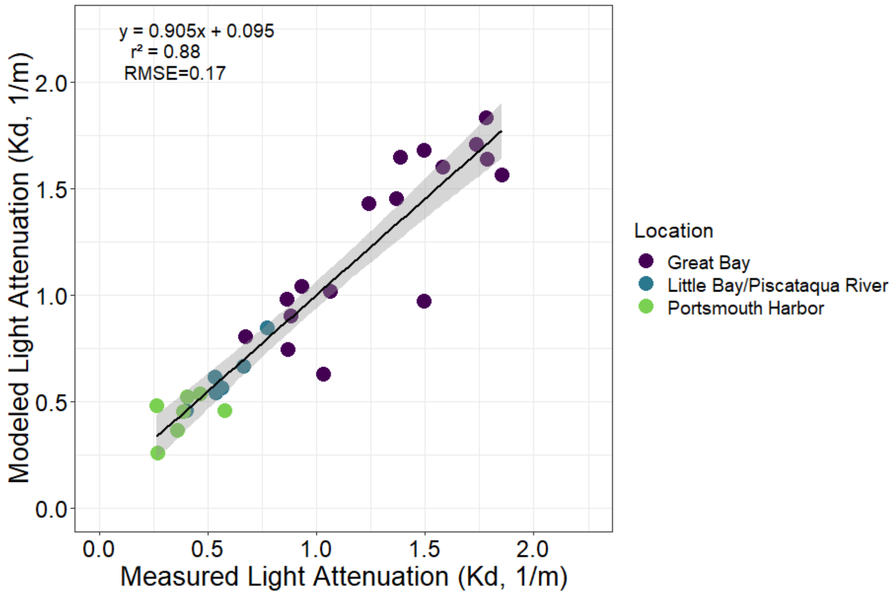

Figure A3.The linear model to predict Kd (Figure A2) was tested against measured Kd values and exhibited good fit.

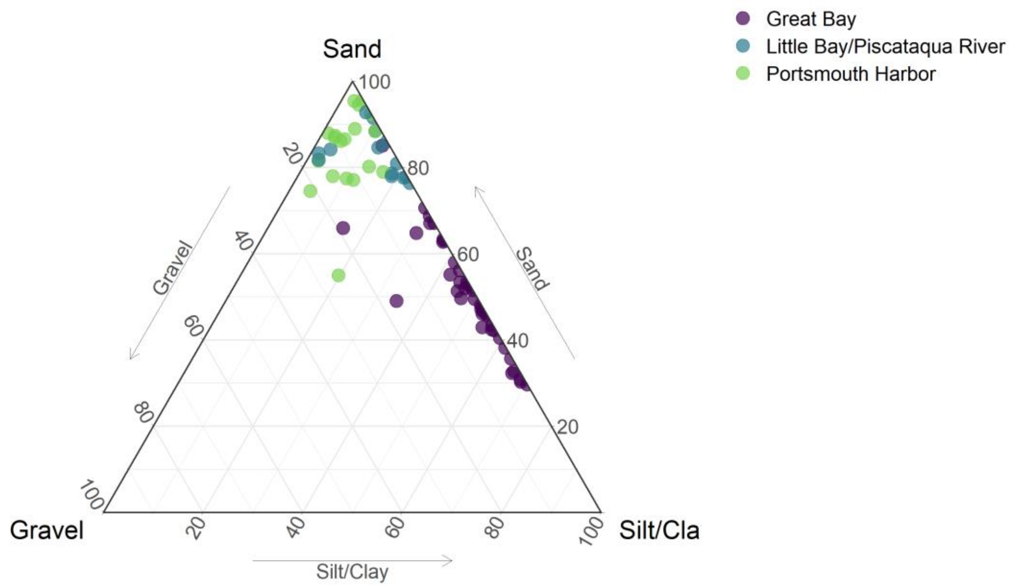

Figure A4. Ternary plot of grain size distribution of Tier 2 sites. Each point represents a year and site (total of 25 sites measured once each year for three years). Points are colored by location within the estuary. Grain sizes are expressed as a percentage.

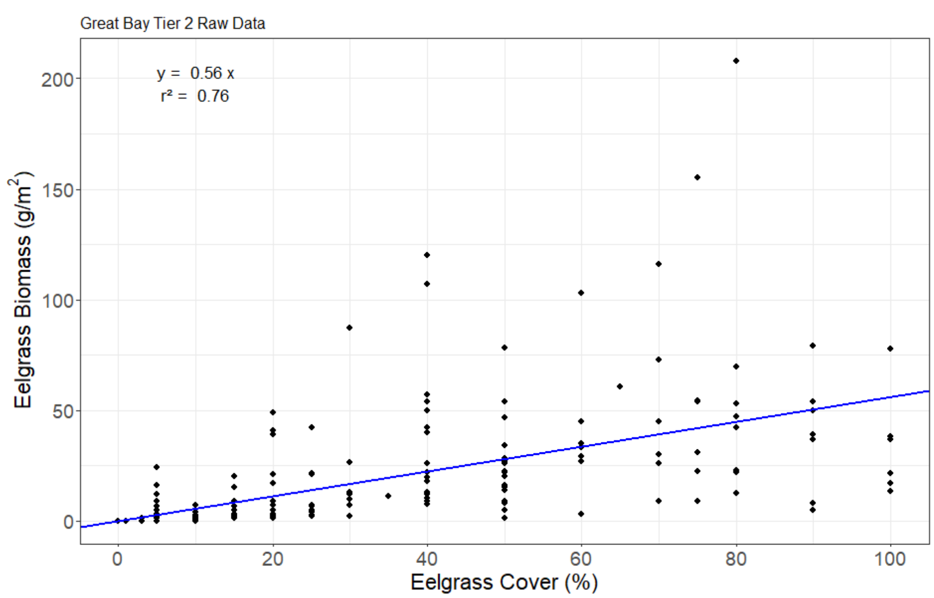

Figure A5. Eelgrass percent cover plotted against eelgrass biomass at Great Bay Tier 2 sites (site numbers 1-17 only) across 2021, 2022, and 2023. A significant ($p<0.05$) linear regression was found with the equation and r^2 shown on the plot.