Suspended Algal Dynamics Across a Seagrass Meadow Landscape

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Abstract

Seagrasses are important foundation species in coastal ecosystems that facilitate primary production of themselves and macro-/microalgae and, through their water-baffling physical structure, encourage the accumulation of algal material in the system. However, the effect that seagrass meadows have on the vertical distribution of phytoplankton and suspended algal material and how that distribution changes seasonally and throughout the meadow landscape is largely unknown. To resolve this gap, I quantified suspended algal material in the water column across a seagrass meadow landscape in a temperate coastal lagoon. I collected samples stratified by depth at heights of 1, 5, 15, and 45 cm above the bottom at sites from which I calculated chlorophyll *a* and pheophytin concentrations. These sites were host to varying seagrass densities and differed in their distances from the meadow edge. I found that chlorophyll *a* concentrations were significantly higher in the bottom 1 cm of seagrass meadows than at other depths in the water column or at sites outside of the meadow. There was also a strong seasonal signal, with these concentrations most pronounced in late summer. This suggests a seasonal control of suspended algae concentration in the water column not reported in the literature. I found no significant relationship between chlorophyll *a* concentrations and seagrass density or distance from the meadow edge. Concentrations were instead dominated by the influence of habitat driven by seagrass presence/absence. These findings reveal spatial and temporal variation in suspended algal concentrations that likely exert controls on the secondary productivity of the diverse community of suspension feeding animals and adjacent bivalve aquaculture associated with this foundation species.

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Table of Contents

Abstract i

Acknowledgements ii

Table of Contents iii

List of Figures iv

1. Introduction 1

2. Methods 4
2.1 Study system 4
2.2 Water Sampling 5
2.3 Sample Processing 6

3. Results 8
3.1 Chlorophyll a Concentrations at Varying Depths..... 8
3.2 Pheophytin Concentrations at Varying Depths..... 9
3.3 Chlorophyll a concentrations and Distance from the Meadow Edge/Seagrass Density..... 13
3.4 Chlorophyll a and Pheophytins..... 11

4. Discussion 11
4.1 Relationship Between Chlorophyll a and Depth..... 11
4.2 Relationship Between Pheophytins and Depth 12
4.3 Relationship Between Chlorophyll a and Distance from the Meadow edge / Seagrass Density..... 13

References 14

List of Figures

Figure 1 Location of the study sites at the Virginia Coast Reserve. Sites are labeled with blue points. Green polygons show the South Bay and Ship Shoal seagrass meadows.......... 5

Figure 2 Shows the sampler used to collect water column samples at 1, 5, 15, and 45 cm from the bottom through the depicted ports. b) Shows the top of the sampler and the syringe used to pull samples up the plastic tubing in 60mL increments.......... 6

Figure 3 Height from the bottom (cm) vs. chlorophyll *a* concentration (µg/l) at sampling depths of 1, 5, 15, and 45 cm from the bottom. Panels represent one of seven sampling rounds. Each round contains the same amount of data with chlorophyll *a* concentration values at each depth averaged across eight sites from either inside (green) or outside (brown) of the meadow. Bars show standard error.......... 8

Figure 4 Height from the bottom (cm) vs. pheophytin concentration (µg/l) at sampling depths of 1, 5, 15, and 45 cm from the bottom. Panels represent one of seven sampling rounds. Each round contains the same amount of data with pheophytin concentration values at each depth averaged across eight sites from either inside (green) or outside (brown) of the meadow. Bars show standard error.......... 9

Figures 5&6 Each point shows the chlorophyll *a* concentration value of a single sample taken at 1, 5, 15, or 45 cm from the bottom at one of eight sites inside (green) or outside (brown) of the meadow. Panels represent one of seven sampling rounds. 5) Chlorophyll *a* concentration (µg/l) vs. distance from the meadow edge (m). Negative distance values represent distances into the meadow. 6) Chlorophyll *a* concentration (µg/l) vs. seagrass density (m^2).......... 10

Figure 7 Square root of pheophytin concentration (µg/l) vs. square root of chlorophyll *a* concentration (µg/l). Points show raw data from individual samples taken at 1, 5, 15, or 45 cm from the bottom at one of eight sites inside or outside of the seagrass meadow across the entire sampling period. Gray bar shows the 95% confidence interval.. 11

Introduction

The fixation and flow of energy in the form of organic carbon is a fundamental process in ecology. Autochthonous carbon generated through primary production fuels ecosystem secondary production and contributes allochthonous carbon to cross-system energy flows. Both of these energy sources can be mediated by the presence of foundation species, those organisms whose structure or function define entire ecosystems by controlling ecological dynamics, stability, and processes (Dayton, 1972; Ellison et al., 2005). Foundation species are usually primary producers (fixing carbon) that also create habitat for epiphytic organisms (Angelini & Silliman, 2014) and alter the existing environment in ways that control fluxes of materials through the system (e.g., allochthonous carbon). The process of studying energy fixation and movement in ecosystems defined by foundation species is complicated due to the highly seasonal nature of many controlling factors.

Seagrass ecosystems are habitats created by one or several foundational seagrasses species (marine angiosperms) that contribute greatly to coastal primary production, sequestering significant amounts of carbon, modifying the physical environment, and facilitating high biodiversity (Bloomfield & Gillanders, 2005; Fourqurean et al., 2012; Macreadie et al., 2019; Reidenbach & Thomas, 2018; Waycott et al., 2009). Seagrass leaves serve as a substrate for large epiphytic algal and invertebrate communities and meadows alter water movement in a number of ways including increasing flow attenuation as water moves deeper into meadows and decreasing bed shear stress and wave height (Balata et al., 2007; Fonseca et al., 1982; Gambi et al., 1990; Reidenbach & Thomas, 2018). These hydrodynamic effects allow seagrass meadows to retain high quantities of seston by capturing incoming particles and reducing detrital and sediment resuspension (Duarte et al., 2013). Seagrass meadows are currently in decline due to global climate change caused increases in water temperature, making their study of immediate importance (Orth, Carruthers, et al., 2006; Waycott et al., 2009).

Through their effects on both autochthonous and allochthonous energy production, seagrass meadows influence phytoplankton and suspended macro-/microalgal particle concentrations and dynamics. Suspended material includes pelagic phytoplankton that are hydrodynamically transported into meadow ecosystems and benthic phytoplankton and fragmented epiphytic algae produced in meadows (Hondula & Pace, 2014; Kharlamenko et al., 2001; Moncreiff et al., 1992). These algal populations may be controlled by the herbivory by suspension feeders, water temperature, and possibly seagrass density (Bologna & Heck, 1999; de Wit et al., 2012; Irlandi et al., 1995; Lemmens et al., 1996; Moncreiff et al., 1992; Wall et al., 2008).

Studies by Irlandi & Peterson, (1991) and Judge et al., (1993) suggest that high suspended algal concentrations exist in meadows due to dampening of flow by seagrasses, increasing the deposition and retention of algal material. Judge et al., (1993) found that this effect occurs in the bottom 1 cm of seagrass meadows when compared to higher in the water column. However, these observations are not universal as the work of de Wit et al., (2012) show a lower level of suspended algae in seagrass meadows due depletion by bivalve feeding. In addition, suspended algal densities may decrease in meadows due to seagrass mediated decreases in water transport of algal sources from outside the habitat (Bologna & Heck, 1999; Irlandi et al., 1995). However, little work has been done to examine how these spatial dynamics vary seasonally. Studies like those conducted by Moncreiff et al., (1992) and Newell & Koch, (2004) have included some temporal analysis of suspended algae dynamics; however, their sampling timelines were short and contained long gaps between efforts.

To address conflicting findings on the spatial dynamics of suspended algae, and the paucity of research on how those dynamics change seasonally, I conducted a five-month survey of suspended algae distributions across an extensive restored seagrass meadow landscape by collecting water samples at four depths in the water column and at sites located inside and outside of a meadow. This study addressed existing uncertainties by examining 1) how the vertical distribution of suspended algae varies with seagrass density and distance from the meadow edge and 2) how these dynamics vary seasonally. Overall, the research indicates that there is a significantly higher density of suspended algae at the bottom 1 cm of the water column in seagrass meadows in late summer, suggesting a hydrodynamically mediated accumulation of material near the benthos and a strong seasonal control on this vertical stratification.

Methods

2.1 Study System

I conducted field sampling at 16 sites in the Virginia Coast Reserve (VCR) on the Eastern Shore of the Delmarva peninsula: 8 inside and 8 outside of two restored seagrass meadows (Fig. 1). These meadows were reseeded with *Zostera marina* beginning in 2001 after a wasting disease and hurricane extirpated the grass from the area in the early 1930s4/29/22 10:48:00 AM (Orth, Luckenbach, et al., 2006). Inside-meadow sample collection took place at eight sites through South Bay, located 100 meters from VCR LTER long-term seagrass sampling sites and at varying distances from the meadow edge. This permitted the leveraging of long-term datasets alongside my data for subsequent analyses.

I established two bare-bottom transects of four sites each spaced 50m apart (Fig. 1), allowing me to capture effects driven by distance from meadow edge.

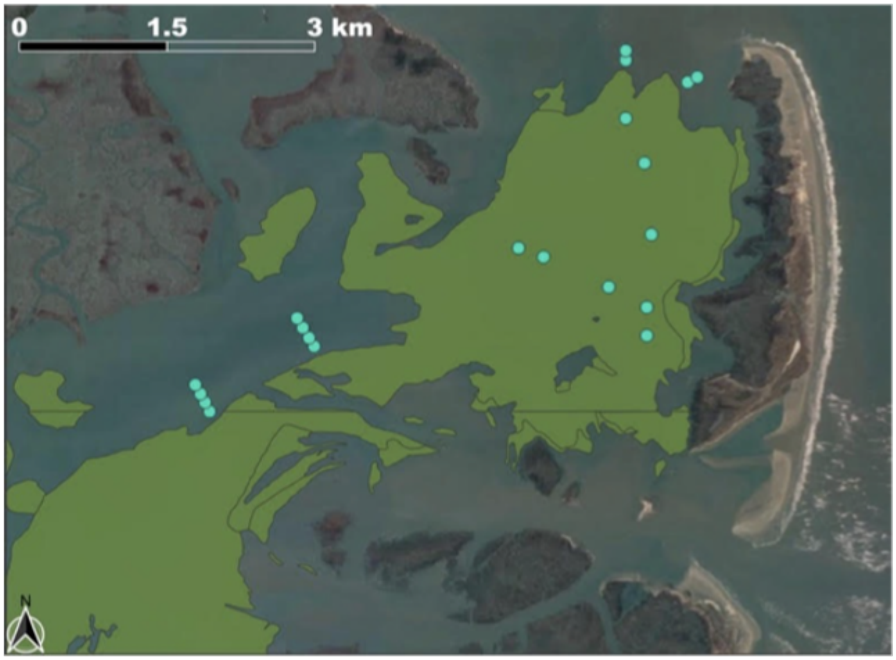


Figure 1. Location of the study sites at the Virginia Coast Reserve. Sites are labeled with blue points. Green polygons show the South Bay and Ship Shoal seagrass meadows.

2.2 Water Sampling

Weekly for 5 weeks in June to August of 2021, I collected water column samples at all 16 sites. I later reduced sampling to once a month in September and November to capture seasonal changes in chlorophyll *a* concentration. At each site, I collected samples using a water sampling device constructed of PVC piping, plastic tubing, and ports located at 1, 5, 15, and 45 cm from the base allowing for collection of water column samples at four depths while at the same site (Judge et al., 1993) (Fig. 2a). I collected the samples using three pulls with a 60 ml syringe leading to a total sample volume of 180 ml for each depth (Fig. 2b). At every site, I took one sample at each depth yielding a total of four samples per site per visit and 64 samples per week.

(a) **(b)**

Figure 2. a) Shows the sampler used to collect water column samples at 1, 5, 15, and 45 cm from the bottom through the depicted ports. b) Shows the top of the sampler and the syringe used to pull samples up the plastic tubing in 60mL increments.

I sampled the water column from an anchored boat after holding the device stationary in the water for 3 minutes to allow disturbed sediment to settle/flow away from the sampling device (Judge et al., 1993). Once collected, I stored the samples in a light-blocked cooler of ice to prevent any change in chlorophyll *a* concentration after collection. At each site I recorded the time, weather conditions, tide direction, wind direction, rough approximates of turbidity, and water depth.

2.3 Sample Processing

Sample processing was completed following the VCR LTER protocol based on the National Environmental Methods Index. Promptly upon return to the lab, I vacuum filtered the samples through Whatman glass fiber filters, after which I stored the filters in aluminum envelopes and froze them until they could be ground into a homogeneous mixture with 90% acetone. I then stored the samples in test tubes and froze them for 24 hours. After this freezing period, I condensed the filter material using a centrifuge and extracted 3 mL of each sample for colorimetric analysis using a spectrophotometer (665 and 750 nm). I calculated chlorophyll *a* and pheophytin concentrations using the following formulas.

Chl a = (26.7 (665o - 665a) * v)/(V* l)

Pheo = (26.7 ([1.77 x 665a] - 665o) * v)/(V* l)

Where:
665o = 665 - (750 - blank value) before acidification
665a = 665 - (750 - blank value) after acidification
v = volume of extract in ml
V = volume of water filtered in liters
l = pathlength of cuvette (1 cm)

Concentrations are in units of ug/L

Results

3.1 Chlorophyll a Concentrations at Varying Depths

I sought to describe the possible vertical stratification of suspended algal material in seagrass meadows, how that stratification varies with seagrass density and distance from the meadow edge, and how these concentrations vary seasonally. I found that there was a significantly higher concentration of chlorophyll *a* 1 cm above the sediment in seagrass meadows than at depths higher in the water column (Fig. 3). However, this did not become apparent until late summer (July-September) and no stratification in chlorophyll *a* concentrations existed in the bare sediment sites.

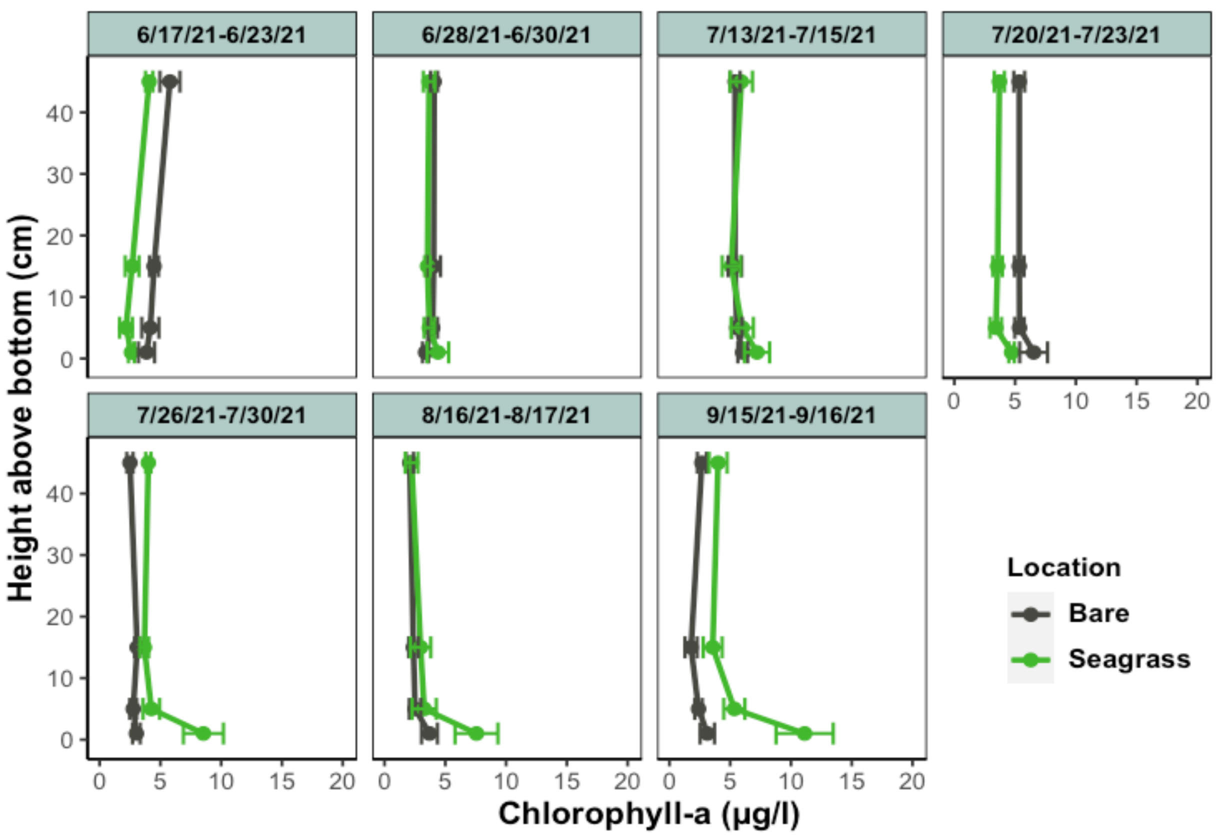


Figure 3. Height from the bottom (cm) vs. chlorophyll *a* concentration (µg/l) at sampling depths of 1, 5, 15, and 45 cm from the bottom. Panels represent one of seven sampling rounds. Each round contains the same amount of data with chlorophyll *a* concentration values at each depth averaged across eight sites from either inside (green) or outside (brown) of the meadow. Bars show standard error.

3.2 Pheophytin Concentrations at Varying Depths

At the end of the sampling season, there was a significantly higher concentration of pheophytins at the bottom of the water column (1 cm above bottom) in seagrass meadows that I did not see duplicated in the bare sites (Fig. 4). The trend was most apparent in late July and mid-September. However, this in-meadow stratification was not as consistent or obvious as that seen in the chlorophyll *a* samples and the concentrations of pheophytins inside and outside of the meadow were mostly very similar.

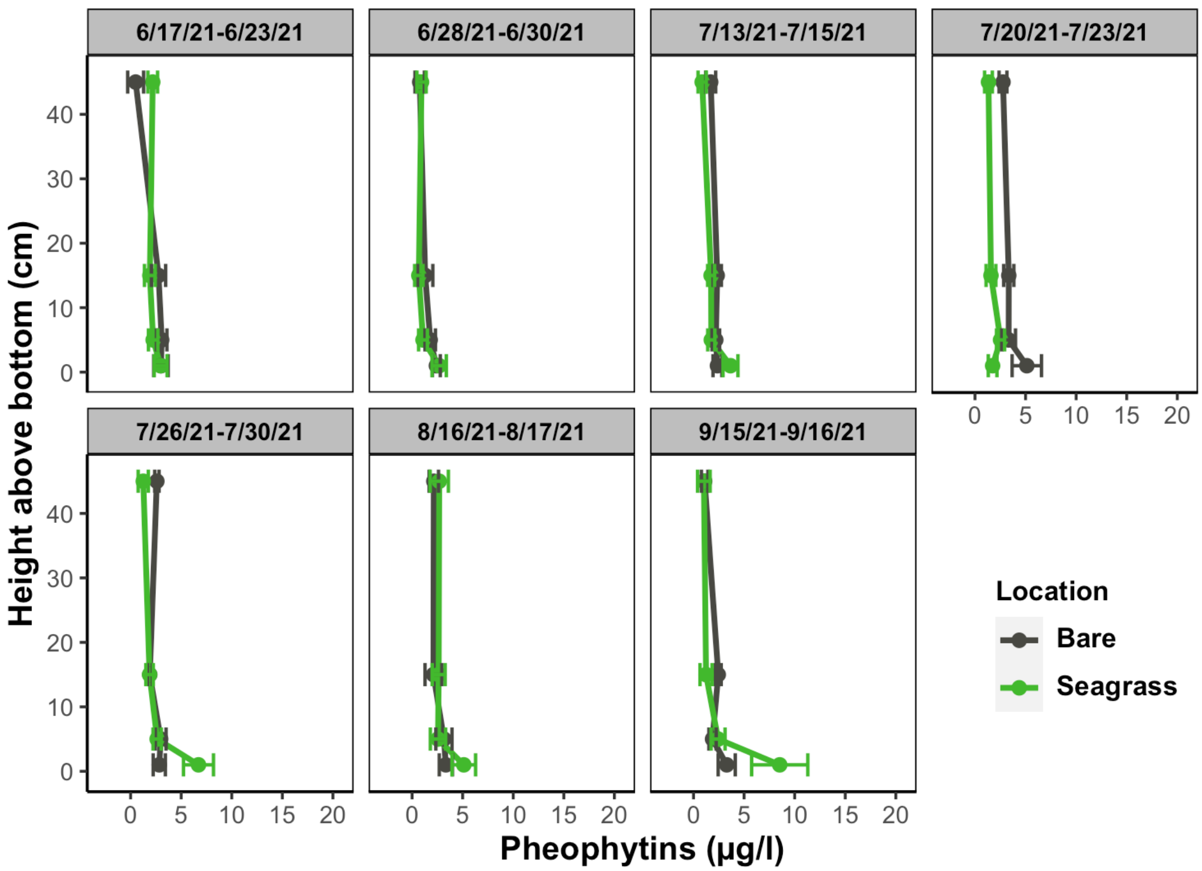
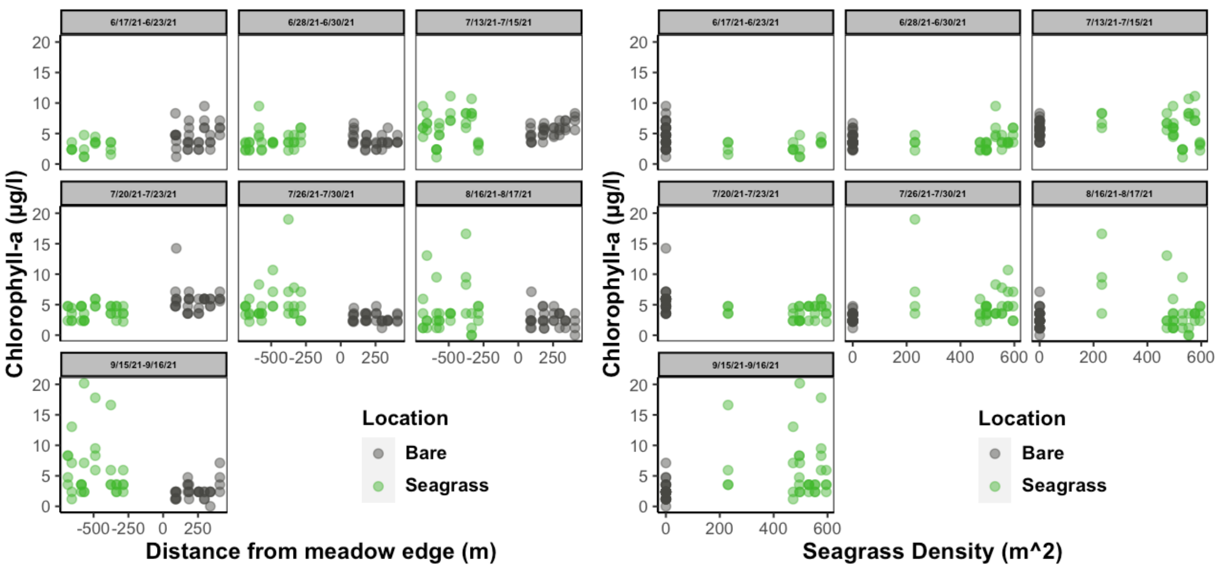


Figure 4. Height from the bottom (cm) vs. pheophytin concentration (µg/l) at sampling depths of 1, 5, 15, and 45 cm from the bottom. Panels represent one of seven sampling rounds. Each round contains the same amount of data with pheophytin concentration values at each depth averaged across eight sites from either inside (green) or outside (brown) of the meadow. Bars show standard error.

3.3 Chlorophyll a concentrations and Distance from the Meadow Edge / Seagrass Density

I found no relationship between chlorophyll *a* concentration and the sampling distance from the meadow edge in either the sites inside or outside of the meadow (Fig. 5). In addition, there was no relationship between chlorophyll *a* concentration and seagrass density inside of the meadow (Fig. 6). However, Figures 5 and 6 do highlight the seasonal change of increasing chlorophyll *a* concentration in the meadow.



(a) **(b)**

Figures 5 & 6. Each point shows the chlorophyll *a* concentration value of a single sample taken at 1, 5, 15, or 45 cm from the bottom at one of eight sites inside (green) or outside (brown) of the meadow. Panels represent one of seven sampling rounds. 5) Chlorophyll *a* concentration (µg/l) vs. distance from the meadow edge (m). Negative distance values represent distances into the meadow. 6) Chlorophyll *a* concentration (µg/l) vs. seagrass density (m^2).

3.4 Chlorophyll a and Pheophytins

Lastly, I found no relationship between chlorophyll *a* and pheophytin concentrations (P = 0.x, $R^2 = 0.04$) (Fig. 7).

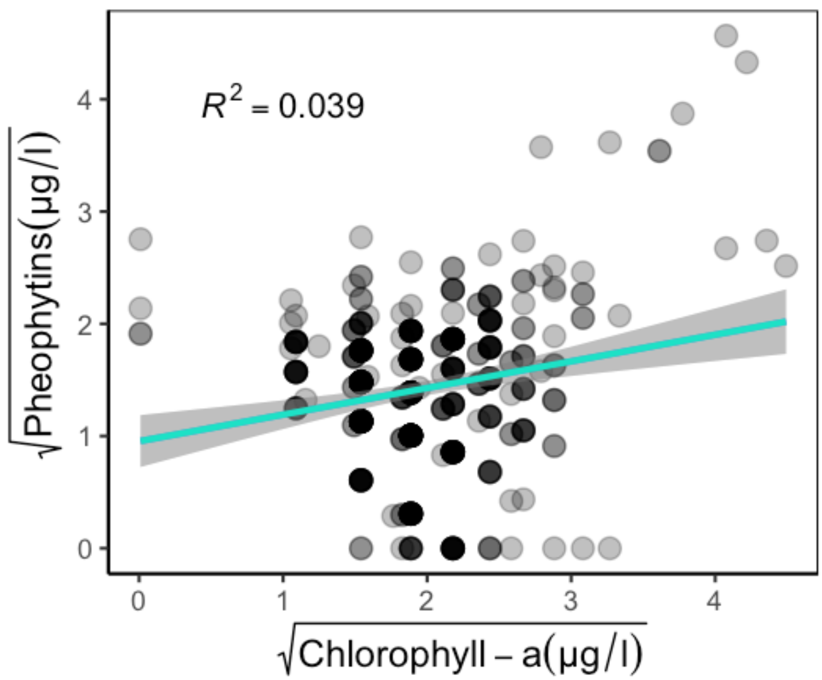


Figure 7. Square root of pheophytin concentration (μg/l) vs. square root of chlorophyll *a* concentration (μg/l). Points show raw data from individual samples taken at 1, 5, 15, or 45 cm from the bottom at one of eight sites inside or outside of the seagrass meadow across the entire sampling period. Gray bar shows the 95% confidence interval.

Discussion

4.1 Relationship Between Chlorophyll a and Depth

I found a vertical stratification of suspended algae (chlorophyll *a*) within seagrass meadows not present in neighboring bare sediment habitats (Fig. 3). The significantly higher concentration of algal matter in the bottom 1 cm of seagrass meadows is likely facilitated by close proximity to macroalgal biomass coupled with decreased water flux and bead shear stresses within meadows (Reidenbach & Thomas, 2018). The stratification only became significant in late summer, likely explained by considering the seasonality of seagrass macroalgae; micro- and macroalgae, many of which are benthic, reach peak biomass in June-July and then experience a collapse during which macroalgae may experience higher degrees of decomposition, dissolution, and fragmentation through the grazing of "shredding" invertebrates (Anderson et al., 2010; McGlathery, 2001). Those fragments would then contribute to the chlorophyll *a* density near the benthos in seagrass meadows beginning around the time when we saw increases in concentration as 1 cm and 5 cm above the bottom. In addition, in late summer after the macroalgal collapse and seasonal die-off of seagrass, benthic microalgae become the most important contributors to ecosystem production in seagrass meadows (McGlathery et al., 2001). This provides another potential source of chlorophyll *a* at the 1 cm level that has a seasonal cycle matching that of the vertical stratification I documented. Lastly, phytoplankton populations also increase in late summer and, through hydrologically mediated sinking, may contribute to seasonal stratification (McGlathery et al., 2001).

4.2 Relationship Between Pheophytins and Depth

I also found a small increase in pheophytin concentration in only the seagrass meadow sites in late summer (Fig. 4). The same hydrological forces explain this accumulation as those that facilitate a high density of chlorophyll *a* near the benthos in meadows (Reidenbach & Thomas, 2018). The seasonality of chlorophyll *a* concentrations may be linked to the annual increase in seagrass density, peaking in June (Rheuban et al., 2014). As seagrass density increases, water flows through the meadow decrease and more material can be trapped over time including deteriorating macroalgae and organic matter from the ecosystem as a whole. I also saw no relationship between chlorophyll *a* and pheophytin concentration within seagrass meadows

(Fig. 7). This supports my methodological assumption that sediment was not being sucked up into my water column samples due to disturbance caused by the water sampling device.

4.3 Relationship Between Chlorophyll a and Distance from the Meadow edge / Seagrass Density

No significant relationship appeared between chlorophyll *a* concentration and distance from the meadow edge, nor seagrass density (Fig. 5 & 6). Water flow into the meadow decreases at such a rapid rate that my scale of observation may not have been large enough to measure any edge effects of the meadow on chlorophyll *a* concentration (Fonseca et al., 1982). In addition, there was little variation in seagrass density between my sampling sites in the meadow which may account for the lack of relationship between seagrass density and chlorophyll *a* concentration. Any continuation of this work should include examining seagrass meadow edge effects on a smaller scale and seagrass density effects using sites with higher density variability

This study was novel in its finding of a seasonal change in vertical stratification of chlorophyll *a* in seagrass meadows not previously reported in the literature. In addition, my findings demonstrate that autochthonous primary production and allochthonous carbon sources into seagrass meadows more than compensate for any depletion of suspended algal matter due to bivalve filtration near the benthos. These findings lend new insight into the effect of seagrass meadows on suspended algae and the temporal dynamics of food availability for suspension feeders, such as bivalves, in these systems (Judge et al., 1993). This, in turn, could be leveraged to maximize bivalve aquaculture production, an important source of income for many coastal communities including those on the Eastern Shore of Virginia.

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