



# Algal Community Dynamics Within the Savannah River Estuary, Georgia Under Anthropogenic Stress

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## Abstract

Estuaries are naturally dynamic ecosystems mixing fresh and marine waters, while consistently varying in depth and discharge due to diurnal tide shifts. Anthropogenic alterations impacting the Savannah River are expected to change the hydrology of the ecosystem and effect algal community structure and composition. The Savannah Harbor Expansion Project began recently with the aim of widening and deepening the river by more than a meter. It is anticipated that tidal height, influx of salt water, and sedimentation rates will be affected, which will disturb algal communities upstream. Baseline data from the Savannah River mudflats were obtained in 2011 as part of a biodiversity assessment. Algal community indices were also examined and related to species alterations in the community. Living algal species were classified as freshwater, marine, or brackish in addition to planktonic, epipelagic, and epipsammic. Live diatoms were replaced by filamentous cyanobacteria representatives like *Phormidium* and green filamentous algae. There was a decrease in abundance of live chain-forming marine plankton species potentially due to sediment accumulation. Species richness within the diatom communities analyzed in clean material decreased (mean =  $40 \pm 6.6$  standard deviation to  $26 \pm 4.6$ ) and the 95% confidence interval narrowed when before and during dredging was compared. *Cymatosira belgica* Grunow remained as the dominant species with an average of 38% relative abundance at low tide and 33% relative abundance at high tide. With exposure to dredging and increased sediment deposition diatom communities showed significant change due to potential increase in turbidity and lower light availability.

**Keywords** Diatoms · Coastal algal communities · Savannah River · Coastal management

## Introduction

Estuaries are both ecologically and economically valuable, as they are very productive aquatic ecosystems (Barbier et al. 2011). Large human populations rely on these ecosystems for services and goods that are of critical importance today and in the future. Although coastal development is a worldwide concern, it is a particular concern for the Southeastern USA. Anthropogenic influence in coastal areas have been expanding

since at least the 1980s in order to accommodate increased industrial and urban development (Vernberg et al. 1992). With the increase in human population, these ecosystems are exposed to anthropogenic stress. Estuaries are sensitive to changes due to human pollution overlaying complex natural processes such as changes in tidal influences, freshwater flushing, climatic changes, and geomorphology (Barbier et al. 2011).

Microalgae are a diverse group of organisms considered to be reliable bioindicators due to their wide distribution, quick generation time, and distinct community structure-based response to specific habitats and conditions (Lavoie et al. 2008). Understanding algae within estuarine and river systems is primarily accomplished by analyzing benthic communities. The impacts of changes in estuarine and river systems are primarily investigated by analyzing changes in benthic algal communities; the phytoplankton community moves rapidly through the water column in response to river flow and tidal currents, and, therefore, has limited time to acclimate and reflect environmental changes (Bellinger and Sigeo 2010; Graham et al. 2009; Sawai 2001). However, since algae present a short life span, they can be used to document rapid

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environmental fluctuations. Within the turbid photic zone, benthic diatoms have temporary presence (Desrosiers et al. 2013).

Diatoms are the dominant algal group in exposed mud samples on the Savannah River. Mud samples found within littoral zones contain combinations of freshwater, marine, and brackish diatoms. The diatom community consists of epipelagic and epipsammic species; planktonic species can settle onto the coastal sediments (Manoylov and Dominy 2013; Stief et al. 2013) and alter trophic relationships with grazers. These particular algal communities thrive at the sediment-water interface, where light penetration is around 2–3 mm, with variable parameters such as pH, dissolved oxygen (DO), and nutrient levels (Miller et al. 1996).

The Army Corps of Engineers is leading a project known as the Savannah Harbor Expansion Project, which began in January of 2015. This project entails the widening and deepening of the river to accommodate larger vessels. The project has been approved by three other federal agencies: the Environmental Protection Agency, the US Fish and Wildlife Service, and the National Marine Fisheries Service (Corps of Engineers 2016). The project involves dredging an additional 1.5 m of the river, which will produce substantial economic benefits for the nation and state by enabling larger and more heavily loaded vessels to travel through the harbor with fewer tidal delays. The total project cost estimate is currently \$706 million and is expected to net more than \$174 million in annual benefits to the nation. The Corps have estimated 5 years for the construction to be completed. The Army Corps of Engineers has also conducted engineering and environmental studies to identify the serious environmental impacts that will be expected from the project. With the environmental disturbance of tidal height and increase of sedimentation, the epipelagic community is expected to be affected.

Data collected in the Savannah River Estuary in 2011 (Manoylov and Dominy 2013) was used as a baseline in order to elucidate changes in the algal community expected to accompany the changes in the physicochemical characteristics. In the present study, we hypothesized that planktonic marine algal species would dominate the community of primary producers in the estuary due to the expectation of an increased influx of marine water. Live diatom associations were expected to represent a lower proportion of the mudflat community, with a change towards a higher proportion of dead diatoms in the community as a result of the increased inflow of salt water, higher turbidity, and higher sedimentation rates accompanying the dredging and widening of the harbor. Species richness during low tide was significantly higher compared with high tide in 2011. The objectives of this study were to (1) identify algal communities within mud samples taken during high and low tide periods in the Savannah River Estuary, (2) evaluate changes in proportions of live and dead diatoms throughout 2016, and to (3) compare current data with previous baseline data from 2011 to determine the changes of the algal

communities due to current anthropogenic alternations within the Savannah River Estuary today.

## Materials and Methods

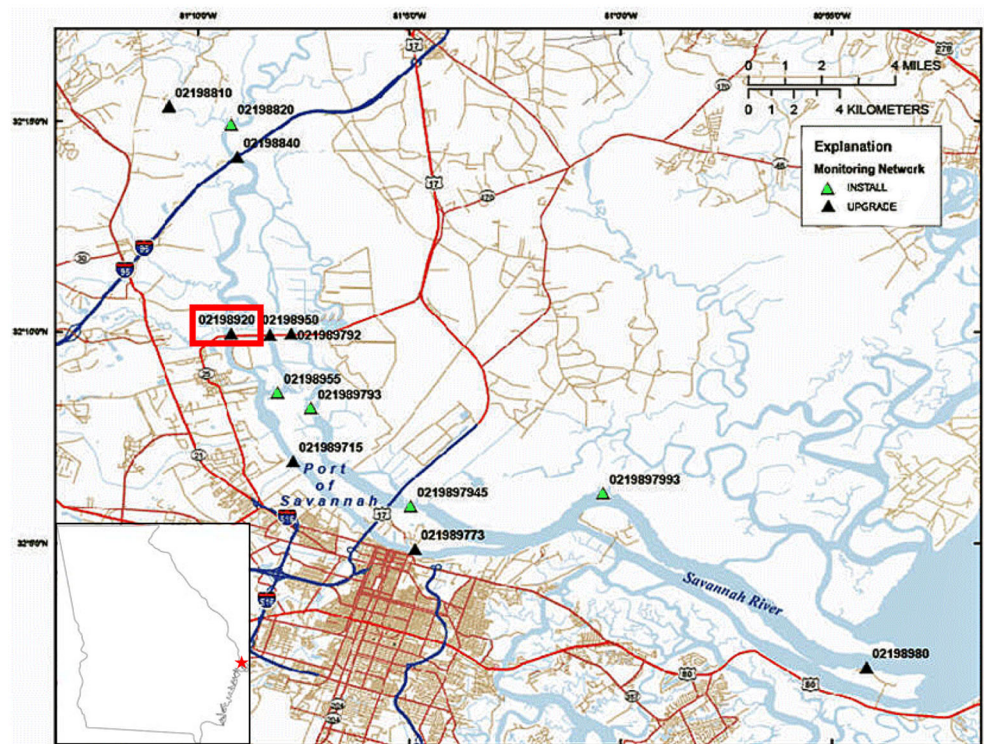
### Site Description

The sampling location was within the Savannah River Estuary at USGS site 02198920, located in Port Wentworth, Georgia (location lat 32° 09' 57" long 81° 09' 14"). The site is located approximately 31 km north of the mouth of the river. This area is tidally influenced, where freshwater from the river is continuously flowing towards the estuary with diurnal entrance of marine water moving inland during high tidal events. This location has long-term water parameter recordings measured by USGS. Data on the following parameters were accessed: water velocity, turbidity, and discharge from the USGS database (<https://waterdata.usgs.gov>). Velocity, total discharge, and precipitation data were unavailable from USGS during October 2016 (USGS 2016, Figs. 1 and 2).

### Sample Collection and Field Equipment

Composite and mud samples were collected during May, August, October, and December in 2016 and physicochemical measurements were recorded on each collection date. Based on the findings from previous research, those sampling times accounted for seasonality in Georgia (Manoylov and Dominy 2013). Six samples were collected during each sampling event; three samples were taken during low tide from top 0 to 0.5 cm of surface sediment with water added to 150 mL in 207-mL Whirl-Paks® (Nasco, Fort Atkinson, WI) and three grab composite samples were taken at high tide. Habitat 1 (L1/H1) is heavily vegetated with grass and stabilized with large boulders. Habitat 2 (L2/H2) and Habitat 3 (L3/H3) are both exposed to boat ramps with surrounding grass (no large vegetation). Habitats were approximately 5 m apart. During low tide events, mud samples were collected by scraping the top 1 mm of the surface, which was exposed to sunlight. During high tide events, composite mud/water samples were taken at approximately the same location as the low tide samples. All samples were collected following the APHA standard protocol (APHA 1995). Physicochemical measurements of the water near the mud that was sampled were taken using an YSI 556 Multiprobe System (YSI Inc., Yellow Springs, Ohio) at the time of each collection to measure temperature, pH, specific conductance, and DO. All samples were transported to the lab on ice and preserved within 24 h of collection using formaldehyde (3% final concentration).

**Fig. 1** Map of study location, USGS site 02198920 in Port Wentworth, GA. (<https://ga.water.usgs.gov/projects/savannah-harbor/>)



**Algal and Diatom Assessment**

Preserved samples were analyzed for live algal cells, that is, cells containing intact chloroplasts, including algal colonies, filaments, diatom frustules, or unicellular algae. A Palmer Maloney counting chamber (Hausser Scientific, Horsham, Pennsylvania) was used followed by scanning flat slides with a known volume of sample depending on the amount of sedimentation. Flat slides and or Palmer Maloney counting chambers were scanned using a Leica DM5000 microscope equipped with differential interference contrast optics and

Leica DFC295 camera (Leica Microsystems, Wetzlar, Germany). At  $\times 400$  magnification, a minimum of 100 live natural algal units were enumerated including live diatoms and recording the number of dead diatoms. Taxa were identified to the lowest taxonomic unit possible.

Diatom analyses were performed on permanent mounting of diatom materials void of organic matter through chemical digestion. Subsamples were cleaned using a 2:1 ratio of nitric acid and a small concentration of potassium dichromate to catalyze the reaction. Samples were rinsed with deionized water for neutralization. Cleaned diatom samples were

**Fig. 2** Aerial view of study location with sampling areas (habitats) labeled and indicated by stars, USGS site 02198920 in Port Wentworth, GA (Source: GoogleMaps)



permanently mounted on microscope slides using Naphrax® (Brunel Microscopes Ltd., Chippenham, and Wiltshire, UK) mounting medium. A minimum of 300 valves were enumerated and identified under oil immersion at  $\times 1000$  magnification using a Leica Microscope and Imaging System (Leica Microsystems, Wetzlar, Germany). A scan of the slide was performed after enumeration until no new taxa were found per transect. Diatoms were identified to the lowest taxonomic level following Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Witkowski et al. (2000), Hofmann et al. (2011), and Cremer et al. (2007). Diatoms were classified as marine, freshwater, or brackish following published literature and algal databases (Akar and Sahin 2017; Barnum et al. 2000; Hendey 1964; Hustedt 1955; Laws 1988; Lopez-Fuerte et al. 2015; Lopez-Fuerte and Siqueiros-Beltrones 2016; Miho and Witkowski 2005; Patrick and Reimer 1966; Round et al. 1990; Tsoy and Moiseenko 2014; Vos and de Wolf 1994, Witkowski et al. 2000)

### Indices Calculated

The live algal community, including diatoms and other algal groups, was analyzed by calculating species richness (SR), Shannon Diversity ( $H'$ ), and evenness ( $J'$ ,  $J'$  refers to the proportions of each taxon in the total species abundance and was calculated as the ratio  $H'$  divided by natural logarithmic transformed species richness). Taxa from each triplicate (live and cleaned) were combined to calculate the final SR,  $H'$ , and  $J'$  for each sampling session during low tide and high tide events.

All community attributes were calculated using species abundance data. Dominant taxa were reported and taxonomically evaluated if their average relative abundance was more than 10%. Taxa that were identified to species level were classified as either planktonic, epipelagic, epipsammic, or epiphytic and either marine, brackish, or freshwater. Presence and absence taxa were used to compare similarities between habitats.

Average biomass between each habitat was calculated per sampling event during low and high tide events. Algal taxa that contributed  $> 10\%$  to the total biomass of the algal community and whose abundance was less than 2 standard deviations below the mean ( $\mu < 2\sigma$ ) were included. Average genera biovolume was calculated based on documented cell length, cell width, cell height, and cell diameter (depending on the shape) (Hillebrand et al. 1999). If measurements were not possible due to inability to observe and measure all dimensions per cell, estimated biovolume per taxon followed published data (Lowe and Pan 1996).

The Sørensen Similarity Index was used to assess the similarity of the diatom and algal communities found in the three habitats, and to test whether the samples could be pooled together. Sørensen Similarity Index compares the number of common species between samples. It takes into account the

presence and absence of species and is not biased by small sample sizes or relative proportions (Sørensen 1948). Due to the better account of common taxa, Sørensen was reported instead of Jaccard similarity coefficient (Jaccard 1912).

### Data Analyses

Kruskal-Wallis test (Systat 13, 2017 Systat Software, Inc.) was performed on all physicochemical water parameter data in 2011 and 2016 to assess comparisons between the two years and low vs high tide event. This includes data that was collected by USGS and data collected using YSI (velocity, discharge, conductivity, turbidity, temperature, DO, pH) as part of this study. Pearson correlation coefficient ( $r$ ) was performed on all physicochemical water parameter data and biological data to assess relationships between diatom taxa and water parameters. Patterns in frequency counts (such as species richness totals) were analyzed using chi-squared tests.

## Results

### Physicochemical Water Data

Water temperature during low and high tide events ranged from 13.6 to 28.9 °C, with August having the highest temperature and December having the lowest. Specific conductance during low tide events ranged from 186.3 to 293.0  $\mu\text{S}/\text{cm}$ , with December having the highest conductivity and August having the lowest. Conductivity during high tide events ranged from 2728.7 to 4544.3  $\mu\text{S}/\text{cm}$ , with May having the lowest conductivity and August having the highest. DO during low tide ranged from 5.98 to 9.7 mg/L. Dissolved oxygen during high tide ranged from 5.7 to 7.8 mg/L with October having the lowest DO and December having the highest. During low tide events, pH ranged from 6.7 to 8.2, and during high tide, pH ranged from 6.8 to 7.9, with December having the lowest pH and May having the highest (Table 1).

Without considering tide events, there was no difference in the comparison between 2011 and 2016 (Kruskal-Wallis test, velocity  $p = 0.83$ , discharge  $p = 0.91$ , and conductivity  $p = 0.06$ ). When comparing low and high tide events per year, statistical analysis showed significant differences for velocity (Kruskal-Wallis test,  $p = 0.02$ ), discharge ( $p = 0.001$ ), and conductivity ( $p = 0.01$ ) between 2011 and 2016 (Fig. 3). During 2016 only, between low and high tide events comparison, only discharge presented a significant value ( $p = 0.029$ ); velocity and conductivity did not differ at low and high tides ( $p = 0.06$  and  $p = 0.19$  respectively). Disregarding low and high water levels, there were no significant differences found between 2011 and 2016, but the reversal of flow at high tide, which leads to a negative discharge, was more significant in 2016 (Fig. 3).

**Table 1** Physicochemical water data during low and high tide events at USGS site 02198920 in Port Wentworth, GA, during 2016 YSI measurements (average  $\pm$  standard error)

Tide event	Sampling event	Temperature (°C)	Conductivity ( $\mu$ S/cm)	DO (mg/L)	pH
Low	May	23.9 $\pm$ 0.12	186.3 $\pm$ 56.9	6.95 $\pm$ 0.28	8.2 $\pm$ 0.39
	August	28.9 $\pm$ 0.23	177.3 $\pm$ 7.21	6.75 $\pm$ 0.18	7.1 $\pm$ 0.16
	October	23.5 $\pm$ 0.27	244.0 $\pm$ 68.4	5.98 $\pm$ 0.39	7.0 $\pm$ 0.21
	December	13.6 $\pm$ 0.21	293 $\pm$ 20.6	9.7 $\pm$ 1.13	6.7 $\pm$ 0.07
High	May	23.6 $\pm$ .001	2728.7 $\pm$ 17.8	6.26 $\pm$ 0.36	7.9 $\pm$ 0.08
	August	28.9 $\pm$ 0.31	4544.3 $\pm$ 199.49	7.27 $\pm$ 0.16	7.8 $\pm$ 0.08
	October	22.1 $\pm$ 0.16	4078.0 $\pm$ 129.19	5.7 $\pm$ 0.21	7.0 $\pm$ 0.33
	December	13.79 $\pm$ 0.19	3978.7 $\pm$ 191.27	7.8 $\pm$ 0.52	6.8 $\pm$ 0.15

Pearson correlation coefficients were analyzed to show relationships between velocity, discharge, conductivity, and turbidity during 2016; where velocity and conductivity were used as independent variables. Discharge was positively correlated with velocity in 2016 ( $r=0.58$ ). In the current study, significant negative correlation was shown between discharge and conductivity with a value of  $-0.886$ . Pearson correlation coefficients were also analyzed to show relationships between physicochemical and biological data. Temperature had a negative correlation with DO ( $r=-0.532$ ) and green algal units ( $r=-0.552$ ), but had a positive correlation with pH ( $r=0.465$ ), cleaned SR ( $r=0.601$ ), cleaned H' ( $r=0.7$ ), and cleaned J' ( $r=0.521$ ). There was a positive correlation with pH and live SR ( $r=0.632$ ), cleaned SR ( $r=0.647$ ), and diatom units ( $r=0.501$ ). Live SR had a positive correlation with live H' ( $r=0.808$ ) and cleaned SR ( $r=0.563$ ), but a negative correlation with live J' ( $r=-0.503$ ). Cleaned SR had a positive correlation with cleaned H' ( $r=0.752$ ). Cleaned H' had a positive correlation with cleaned J' ( $r=0.848$ ) and a negative correlation with green algal units ( $r=-0.545$ ). Cleaned J' had a negative correlation with green algal units ( $r=-0.578$ ). Diatom units had a negative correlation with blue-green algal units ( $r=-0.944$ ) (Table 2).

### Algal Community Indices

The epipellic algal community was dominated by diatoms in all whole community analyses, followed by green filamentous algae. During low tide collections, live diatom proportion to all diatom frustules documented in whole community analyses was high for August, October, and December ( $62.4 \pm 4.5$ ,  $79.1 \pm 3.7$ , and  $65.4 \pm 6.1$  mean  $\pm$  SE respectively), with the exception of May  $23.97 \pm 1.6$ .

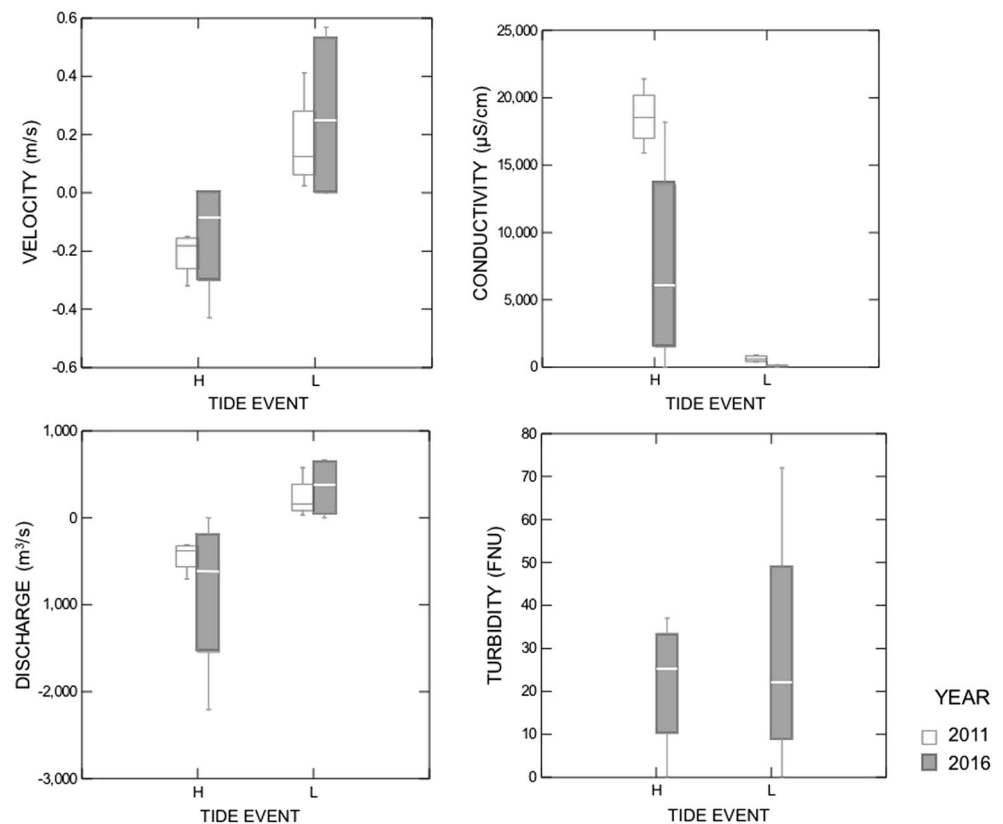
Species richness for live algal community units, during low tide, ranged from 7 to 23 between each habitat, with the lowest SR in Habitat 2 during May and the highest in Habitat 2 and 3 during October. Species richness during high tide ranged from 8 to 23, with the lowest SR in Habitat 1 during May and the lowest in Habitat 3 during October (Table S1). Shannon Diversity of live algal community units ranged from 1.71 to

2.68 during low tide, with Habitat 2 in August having the highest H' and Habitat 3 in October having the lowest H'. Shannon Diversity of live algal community units ranged from 1.94 to 2.51 during high tide, with Habitat 1 in May having the highest H' and Habitat 2 in October having the lowest H'. Overall, October had the lowest H' with all habitats taken into consideration with a diversity of 2.04 during low tide and May having the highest diversity with 2.78 during high tide. Evenness during low tide ranged from 0.71 to 0.95, with Habitat 1 in May having the highest J' and Habitat 2 in August having the highest J'. Evenness during high tide ranged from 0.76 to 0.94, with Habitat 3 in October having the highest J' and Habitat 3 in May having the lowest J' (Table S2). For total live algal community units, May had the highest SR with all habitats taken into consideration during low tide with 35 total taxa present. October had the lowest total SR with all habitats taken into consideration during low tide with 12 taxa present. Overall, October had the highest J' with all habitats taken into consideration with an evenness of 0.87 during high tide and May having the lowest J' with 0.74 during low tide (Table S2).

The dominant taxa contributing  $>10\%$  abundance for the total biomass included *Pleurosigma/Gyrosigma* spp., *Nitzschia* spp., *Tryblionella littoralis* (Grunow) D.G. Mann, *Skeletonema* spp., *Navicula* sp.1, *Navicula* sp.2., and Cyanobacteria filaments and *Nitzschia* spp. was the most consistent contributor with average biomass of  $3117\text{--}5333 \mu\text{m}^3$  throughout the year (except for May and August during low tide and May during high tide). Larger algal units, like *Pleurosigma/Gyrosigma* spp. contributed to more than  $9000 \mu\text{m}^3$  of biomass in May during low tide (Table 3).

Based on all algal community analyses, SR throughout the study ranged from 8 to 39 taxa. Habitats 1 and 3 had the highest total SR in May during high tide. Habitats 2 and 3 had the lowest total SR in October during low tide. Shared taxa ranged from 5 to 10, with Habitats 2 and 3 in August during high tide and Habitats 1 and 3 in December during high tide having lowest number of shared taxa. Habitats 2 and 3 in May during high tide had the highest number of shared taxa. Sørensen index ranged from 24 to 60% based on the presence/absence of species (Table S5).

**Fig. 3** Box plots that show variations of water parameters: velocity, conductivity, discharge, and turbidity (2016 only) between low and high tide events during 2011 and 2016 (data source USGS site 02198920 in Port Wentworth, GA)



Habitats were analyzed for similarities during both high and low tide events throughout the study using the Sørensen Similarity Index based on species presence/absence in cleaned preparations. Pair-wise comparisons were used to determine the relationships among total SR, shared SR, and the Sorensen Index. Total SR throughout the study ranged from 27 to 51 taxa, with Habitats 2 and 3 in August during low tide having the highest total SR and Habitats 2 and 3 in December during low tide having the lowest total SR. Shared taxa between habitats ranged from 6 to 25 taxa, with Habitats 1 and 3 in August during low tide having the lowest shared taxa and Habitats 1 and 3 in May during high tide having the highest shared taxa. Sørensen similarity indices based on species presence or absence ranged from 19 to 58% (Table S5).

Dominant live algal taxa in preserved subsamples during low and high tide events included *Cymatosira belgica* Grunow, *Nitzschia* spp., *Pleurosigma/Gyrosigma* spp., *Navicula* sp.2, *Navicula* sp.2, *Skeletonema* spp. (Plate 1), and filamentous cyanobacteria representatives. These taxa contributed to more than 10% of the total abundances with all habitats taken into consideration. *Nitzschia* spp. was present during each month and each tidal event, with the highest abundance of *Nitzschia* spp. in May during high tide with contributing 22% of the algal community (Table 4).

### Diatom Analyses

A total of 107 diatom taxa were identified in the cleaned algal preparations, 75 of which to the species level. Species richness during low tide ranged from 18 to 35, between each habitat, with Habitat 2 during December having the lowest SR and Habitat 2 during May having the highest SR. SR during high tide ranged from 19 to 34, between each habitat, with Habitat 2 during December having the lowest SR and Habitat 3 during May having the highest (Table S3). With data from all habitats combined, SR ranged from 37 to 65 with every habitat taken into consideration, with the low tide SR being lowest in December and highest in August (Table S4).

Shannon Diversity during low tide ranged from 1.98 to 2.65 between each habitat, with Habitat 2 during December having the lowest  $H'$  and Habitat 2 during August having the highest  $H'$ . Shannon Diversity during high tide ranged from 1.79 to 2.54 between each habitat, with Habitat 1 during December having the lowest  $H'$  and Habitat 1 in August having the highest (Table S3). Overall,  $H'$  ranged from 1.96 to 2.69 with every habitat taken into consideration, with December having the lowest  $H'$  during high tide and August having the highest  $H'$  during low tide (Table S4).

Evenness during low tide ranged from 0.64 to 0.76 between each habitat, with Habitat 3 having the lowest during August, Habitat 2 having the highest during the month of

**Table 2** Pearson Correlation Matrix of correlation of water parameters and biological data during 2016 (correlations that are significant at the 95% level are shown in boldface)

	Temperature	Conductivity	DO	pH	Live SR	Live H'	Live J'	Clean SR	Clean H'	Clean J'	Diatom	Green	Blue-Green
Temperature	1												
Conductivity	-0.023	1											
DO	<b>-0.532</b>	-0.153	1										
pH	0.465	0.049	-0.163	1									
Live SR	0.176	-0.101	0.051	<b>0.632</b>	1								
Live H'	0.27	0.009	0.066	0.417	<b>0.808</b>	1							
Live J'	0.186	0.113	-0.134	-0.398	<b>-0.503</b>	0.055	1						
Clean SR	<b>0.601</b>	-0.054	-0.287	<b>0.647</b>	<b>0.563</b>	0.494	-0.16	1					
Clean H'	<b>0.7*</b>	-0.128	-0.396	0.463	0.276	0.294	0.079	<b>0.752</b>	1				
Clean J'	<b>0.521</b>	-0.17	-0.338	0.164	-0.028	0.047	0.236	0.293	<b>0.848</b>	1			
Diatom	0.29	-0.003	-0.054	<b>0.501</b>	0.278	0.076	-0.37	0.238	0.141	0.022	1		
Green	<b>-0.552</b>	-0.049	0.435	-0.253	0.142	0.146	-0.135	-0.251	<b>-0.545</b>	<b>-0.578</b>	-0.261	1	
Blue-Green	-0.171	0.059	-0.155	-0.426	-0.327	-0.138	0.396	-0.187	0.002	0.143	<b>-0.944</b>	0.002	1

August, and Habitat 1 during the month of October. Evenness during high tide ranged from 0.56 to 0.76 between each habitat with Habitat 1 during December having the lowest J' and Habitat 1 during August having the highest (Table S3). Overall, J' ranged from 0.53 to 0.68 with every habitat taken into consideration, with December having the lowest J' during high tide and May having the highest J' during high tide (Table S4).

Comparison of clean diatom similarities between 2011 and 2016 differs significantly ( $\chi^2 = 5.94, df = 1; p = 0.015, Fig. 4$ ). When comparing 2011 and 2016, species richness decreased from  $40 \pm 6$  to  $26 \pm 5$  (mean  $\pm$  SE) and the 95% confidence interval narrowed from 35–45 to 24–28.

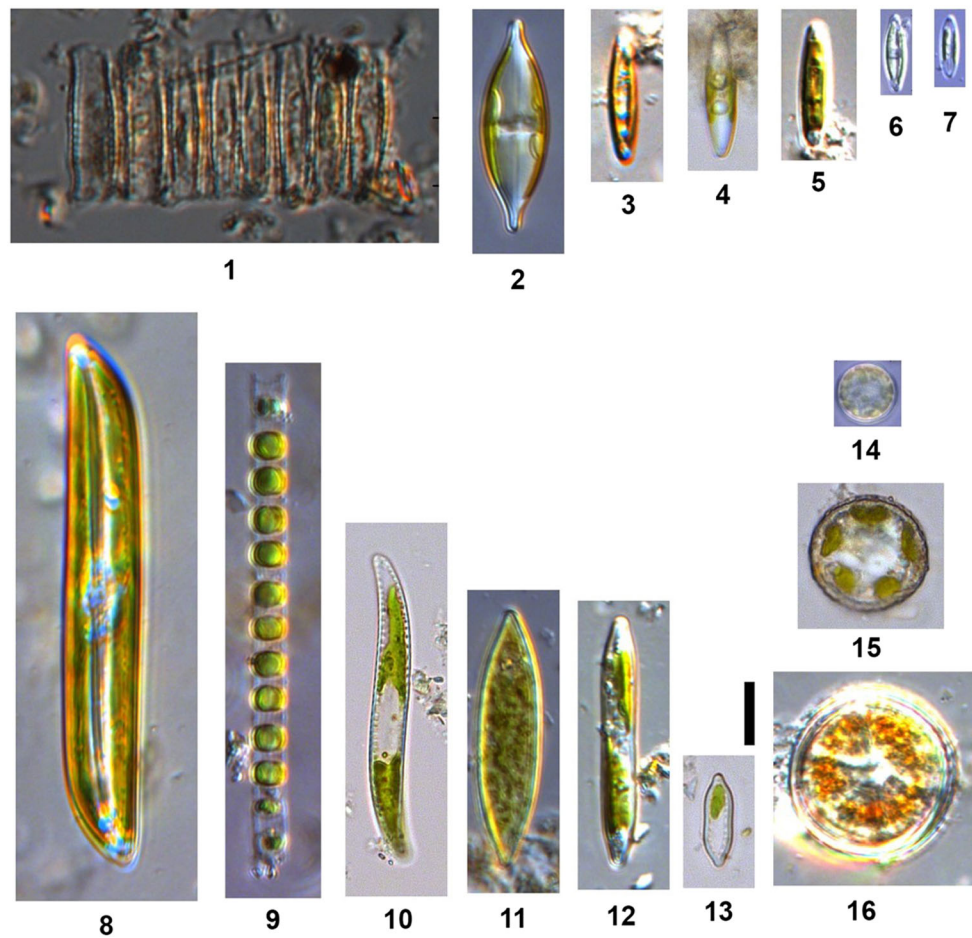
*Cymatosira belgica* Grunow, *Minidiscus* sp.1, *Shionodiscus oestrupii* (Ostenfeld) A.J. Alverson, S.-H. Kang and E.C. Theriot, *Nitzschia brevissima* Grunow, *Cymatosira lorenziana* Grunow, *Skeletonema costatum* (Greville) Cleve, and *Paralia sulcata* (Ehrenberg) Ehrenberg (Plate 2). These taxa each contributed to more than 5% (mean  $\pm$

standard error) of the total diatom community. *Cymatosira belgica* and *Minidiscus* spp. occurred in every sample during both low and high tide events throughout the study. *Cymatosira belgica* (Plate 2, 1–5) had the highest relative abundance with this species accounting for more than >29% in all samples (during both low and high tide events). *Minidiscus* spp. (Plate 2, 13–15) had a relative abundance of >10% during May (low and high tide) and December (low tide, Table 5).

Diatoms with lower than 10% relative abundance that were identified throughout the study included *Luticola* cf. *australomutica* Van de Vijver, *Luticola similis* Levkov, Metzeltin and A. Pavlov, *Luticola* cf. *pseudoimbricata* Levkov, Metzeltin and A. Pavlov, *Achnantheidium exiguum* (Grunow) Gzarnecki, *Eunotia pectinalis* var. *undulata* (Ralfs) Rabenhorst, *Eunotia* cf. *lapponica* Grunow, *Delphineis surirella* (Ehrenberg) G.W. Andrews, *Cymbella helvetica* Kutzing, *Biddulphia alternans* (Bailey) Van Heurck, *Diploneis bombus* (Ehrenberg) Ehrenberg,

**Table 3** Average values of algal biomass ( $\mu\text{m}^3$ ) that contributed to >10% of the total abundance during low and high tide events during 2016 (average  $\pm$  standard error)

Tide event	Taxa	May	August	October	December
Low	<i>Pleurosigma/Gyrosigma</i> spp.	9100 $\pm$ 2407.6	–	–	–
	<i>Navicula</i> sp.1	–	3000 $\pm$ 661.4	–	5166.6 $\pm$ 712.0
	<i>Navicula</i> sp.2	–	–	1767 $\pm$ 348.0	2667 $\pm$ 416.7
	<i>Nitzschia</i> spp.	–	–	3033 $\pm$ 210.3	3033 $\pm$ 154.3
	<i>Skeletonema</i> spp.	–	2340 $\pm$ 90	–	4590 $\pm$ 679.5
	<i>Centric</i> spp.	–	–	1257 $\pm$ 156.2	–
High	Cyanobacteria filaments	–	–	3148 $\pm$ 714.7	–
	<i>Tryblionella littoralis</i>	2167 $\pm$ 440.9	–	2533 $\pm$ 480.7	–
	<i>Navicula</i> sp.1	–	–	–	5280 $\pm$ 1258.2
	<i>Nitzschia</i> spp.	–	3383 $\pm$ 308.7	3117 $\pm$ 113.3	5333 $\pm$ 352.8



**Plate 1** “Live” dominant diatom taxa within mud samples from the Savannah River Estuary at USGS site 02198920 during 2016. (1) *Cymatosira belgica* Grunow (chain) visible connection between neighboring frustules in the central part of the valves and not with the poles; (2) *Navicula* sp.1; (3–7) counted as *Navicula* sp.2; (8) *Gyrosigma* sp.1; (9)

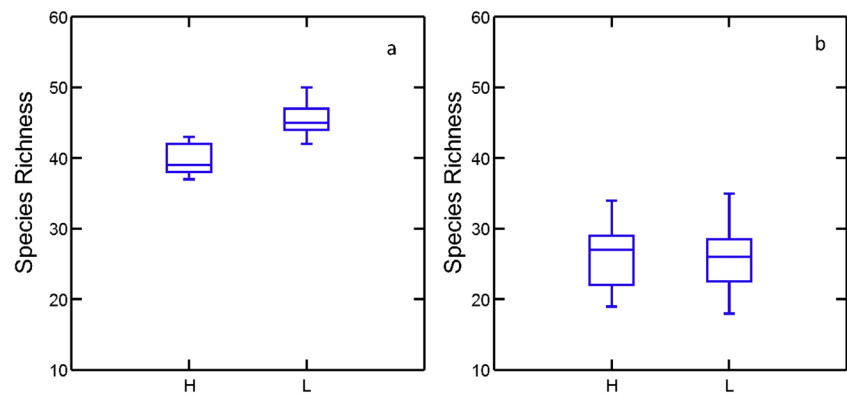
*Skeletonema* spp.; (10, 12) counted as *Nitzschia* spp.; (11) counted as Pennate spp.; (13) *Nitzschia brevissima* Grunow; (14) counted as Centric spp.; (15) *Thalassiosira* spp.; (16) *Actinopterychus senarius* Ehrenberg. Scale bar = 10  $\mu$ m

**Table 4** Average percent relative abundance of dominant live algal taxa (whole community analyses) during low and high tide events at USGS site 02198920 during 2016. Dominant taxa were determined if they were more than 10% of the given sample based on natural unit counts (average  $\pm$  standard error)

Tide event	Taxa	May	August	October	December
Low	<i>Cymatosira belgica</i>	29.6 $\pm$ 17.6	16 $\pm$ 1.73	22 $\pm$ 4.2	16 $\pm$ 1
	<i>Nitzschia</i> spp.	20 $\pm$ 7	11 $\pm$ 1.5	17.3 $\pm$ 1.2	17.3 $\pm$ 0.8
	Centric spp.	10.6 $\pm$ 6.7	–	19.3 $\pm$ 2.4	–
	<i>Pleurosigma</i> / <i>Gyrosigma</i> spp.	10 $\pm$ 2.6	–	–	–
	<i>Navicula</i> sp.1	–	12 $\pm$ 2.6	–	20.6 $\pm$ 2.8
	<i>Navicula</i> sp.2	–	10 $\pm$ 5.3	17.6 $\pm$ 3.5	10.7 $\pm$ 1.7
	<i>Skeletonema</i> spp.	–	–	–	17 $\pm$ 2.5
High	<i>Cymatosira belgica</i>	–	19.6 $\pm$ 0.7	20 $\pm$ 3.5	13 $\pm$ 6.6
	<i>Nitzschia</i> spp.	22 $\pm$ 9.1	19.3 $\pm$ 1.7	18.3 $\pm$ 0.6	13.3 $\pm$ 0.9
	Centric spp.	11 $\pm$ 5.5	14 $\pm$ 1.2	14 $\pm$ 0.6	–
	<i>Navicula</i> sp.1	–	–	12.7 $\pm$ 6.7	21 $\pm$ 5
	<i>Navicula</i> sp.2	–	11.6 $\pm$ 1.7	–	11 $\pm$ 2.1
	<i>Skeletonema</i> spp.	–	–	–	11.6 $\pm$ 6.1
	Filamentous Cyanobacteria spp.	–	–	10.6 $\pm$ 2.2	–



**Fig. 4** Change in diatom species richness (“Clean” diatoms) during high (H) and low (L) tide events during 2011 (a) and 2016 (b). Boxes extend from 25th to 75th percentiles and the central line shows median species richness for the entire sampling period



*Diploneis weissflogii* (A.W.F. Schmidt) Cleve, *Diploneis cf. caffra* (M.H. Giffen) Witkowski, Lange-Bertalot and Metzeltin, *Neodelphineis pelagica* Takano, and *Pinnularia subcapitata* W. Gregory (Plate 3).

Diatoms that were identified to species level were categorized as marine, freshwater, or brackish based on published literature and AlgaeBase (2018, Table S6). A total of 44% of species were classified as marine species, 37% species were classified as freshwater species. Diatoms were classified as 15% as brackish species, 4% were unclassified. Out of the diatoms that were identified to species level, 32% were classified as planktonic, 8% were classified as epipsammic, and 28% were classified as epipellic. Other taxa were classified as a combination epiphytic, epipellic, epipsammic, or planktonic, contributing < 31% of the total classified diatoms. Diatom species, that contributed to > 2% of the total diatom community, were classified as planktonic average 75.1% (range 69 to 84%) or benthic 14% (range 9 to 22%).

## Discussion

### Interactions Between Algae, Fine Sediment Load, and Salinity

With the Savannah Harbor Expansion Project currently underway, an increased fine sediment load throughout the ecosystem was documented. Turbulence caused by tides will push excess sediment upstream, causing increased turbidity. As diatoms are photosynthetic, they depend on light availability. In lotic systems, diatoms can experience either deposition or suspension. Diatoms that are suspended in the mixed water column (planktonic) have a better adaptive ability to dominate in the photic zone, due to the turbulence driven by wind, currents, and morphology of the river (Diehl 2002). Diatoms that are deposited can also be affected by increased turbidity. Depending on where diatoms settle, light availability may significantly decrease, especially if buried. For motile diatoms, burial from fine sediment load may not be an issue as they can move through sediment to reach the surface where

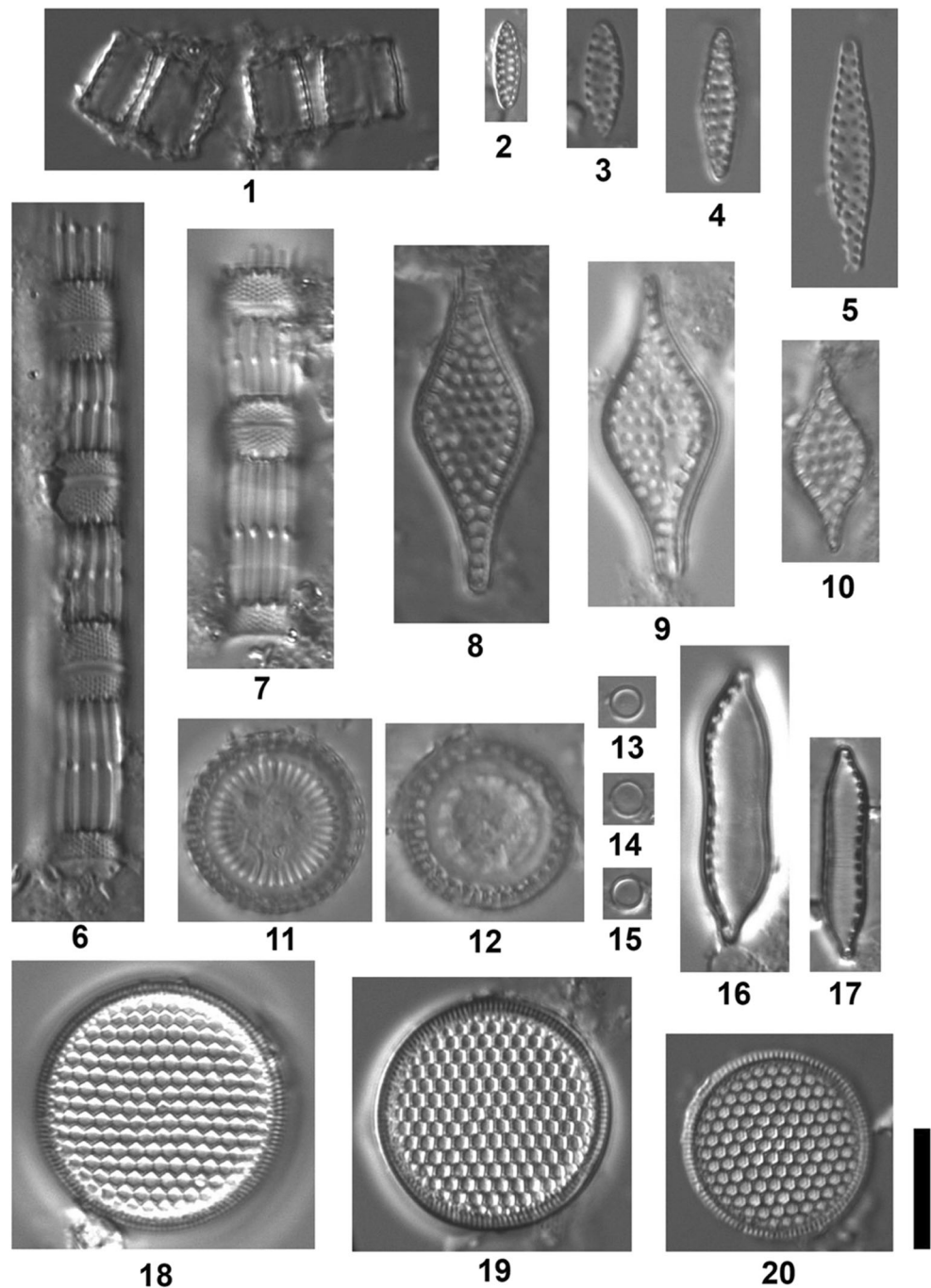
light is available, while non-motile diatoms do not have the ability to move (Harper 1976).

*Nitzschia* spp., *Pleurosigma/Gyrosigma* spp., *Navicula* spp., and *Navicula* sp.2 are classified as epipellic or epipsammic and were reported as live dominant taxa during both low and high tide events. Their survival during these events provides evidence that these species were capable of moving upward in the sediment to the surface or are re-deposited with new sediment. *Cymatosira belgica* and *Skeletonema* spp. (in clean material we confirmed only *S. constatum*, but live material morphology was inconclusive) were reported in the live taxa during low and high tide events and are classified as planktonic diatoms. Cyanobacteria filaments were also documented in the dominant live algal taxa. Their survival is most likely due to their outer mucilage, which protects filaments from attaching particles and allows them to tolerate systems that are highly turbid with suspended sediment. Periodic sediment loading stimulated production of mucilage aiding coagulation of filamentous cyanobacteria in clay-dominated environments (Avnimelech et al. 1982; Soballe and Threlkeld 1988). This defense mechanism gives filaments an opportunity to glide towards better light availability. Similar response was reported by Burkholder (1992) in a phytoplankton lentic community dominated by mucilaginous cyanobacteria and dinoflagellates.

Salinity is one of the main contributors in regulating metabolic activities in primary producers, such as carbon concentration mechanisms in aid of photosynthesis (Clement et al. 2017) and nutrient exchange (Admiraal et al. 1982), although high salinity can be detrimental (Liska et al. 2004). Microalgae differ in their adaptability to salinity based on their tolerance (Rao et al. 2007). A study by Admiraal and Peletier (1980a) determined that estuarine diatoms had a wide range of salinity tolerances (2–45%), demonstrating that salinity had little effect on the diatom’s photosynthetic processes. Although, salinity did not have a direct effect on the diatom’s photosynthetic abilities, it appeared to influence competitive interactions between taxa.

Many algal groups contribute to the overall productivity of estuaries, including diatoms, cyanobacteria, and

**Plate 2** “Clean” dominant diatoms within mud samples from the Savannah River Estuary at USGS site 02198920 during 2016 at  $\times 100$  magnification. (1–5) *Cymatosira belgica* Grunow; (1) Chain; (2–5) separated frustules; (6–7) *Skeletonema costatum* (Greville) Cleve; (8–10) *Cymatosira lorenziana* Grunow; (11–12) *Paralia sulcata* (Ehrenberg) Cleve; (13–15) *Minidiscus* sp.1; (16–17) *Nitzschia brevissima* Grunow; (18–20) *Shionodiscus oestrupii* (Ostenfeld) A.J. Alverson, S.-H. Kang, and E.C. Theriot. Scale bar = 10  $\mu\text{m}$



green algae. With the variable hydraulic dynamics of estuaries, it is expected to see a diverse range of algal groups inhabiting the ecosystem. Specific conductance recorded during 2016 did not exceed more than 4544  $\mu\text{S}/\text{cm}$  (in August during high tide), which would define the Savannah River Estuary at USGS site 02198920 as a brackish environment. This research would suggest that some diatom species originally described as freshwater or marine taxa show high competitive abilities in brackish environments.

### High vs. Low Tide Events: Community Analyses

Of the variables that were measured, pH was the most important environmental factor correlating with live diatom species richness (Table 2). May samples had the highest species richness (35) and pH (7.9–8.2) during the study. It is suggested by Schneider et al. (2013) that pH gradients interfere with nutrient indices and patterns of taxon richness. Diatoms prefer close to neutral pH level, whereas green algae are highly abundant in a pH of more than 8 (Smol and Stoermer 2010).

**Table 5** Average percent relative abundance of dominant diatom species (diatom analyses) during low and high tide events at USGS site 02198920 during 2016. Dominant diatoms are reported if they were more than 5% in a single sampling event (average  $\pm$  standard error)

Tide event	Taxa	May	August	October	December
Low	<i>Cymatosira belgica</i>	41.2 $\pm$ 1.5	41.6 $\pm$ 3.5	28.2 $\pm$ 1.9	43.8 $\pm$ 1.7
	<i>Minidiscus</i> spp.	10.7 $\pm$ 1.4	7.6 $\pm$ 1.1	7.7 $\pm$ 2.4	12.0 $\pm$ 1.3
	<i>Thalassiosira oestrupii</i>	6.5 $\pm$ 1.1	–	4.6 $\pm$ 0.7	–
	<i>Nitzschia brevissima</i>	6.0 $\pm$ 0.8	–	–	–
	<i>Cymatosira lorenziana</i>	–	5.0 $\pm$ 0.9	–	10.2 $\pm$ 2.4
	<i>Paralia sulcata</i>	–	–	4.5 $\pm$ 1.1	–
	<i>Skeletonema costatum</i>	–	–	–	5.8 $\pm$ 0.6
High	<i>Cymatosira belgica</i>	35 $\pm$ 1.6	30.5 $\pm$ 3.8	29.7 $\pm$ 1.0	37.5 $\pm$ 2.0
	<i>Minidiscus</i> spp.	13.8 $\pm$ 2.1	5.9 $\pm$ 0.1	7.7 $\pm$ 1.9	8.7 $\pm$ 2.2
	<i>Nitzschia brevissima</i>	6.9 $\pm$ 0.6	–	–	–
	<i>Cymatosira lorenziana</i>	–	–	–	5.9 $\pm$ 1.2
	<i>Skeletonema costatum</i>	6.1 $\pm$ 0.9	–	–	–

According to a study by Brock (1973), blue-green algae cannot survive in a pH lower than 4. In 2011, pH at the location stayed close to 7 and for all sampling events in 2011, diatoms dominated the algal community in the Savannah River estuary location and average live-to-dead ratio of diatoms was at 82% (Dominy 2012). In 2016, pH in May was above 8, but without nutrient estimations in this study and especially in the month of May, it is difficult to explain the low proportions of live diatoms observed during this month (<24%). But the higher more alkaline pH levels in the current study do suggest higher nutrient levels (USGS 2016), potentially also inferred by the documented increase in physiologically active cyanobacteria and green filaments. In May 2016, the lower diatom live-to-dead ratio was driven by the increase in empty diatom frustules potentially washed downstream with spring influx of sediment particles with higher freshwater discharge. A study by Wilson and Holmes (1981) suggests that, for diatoms in estuarine sediments in Mugu Lagoon, California, the percentage of dead diatoms can be large. The ratios of living to dead diatoms vary between different sediment habitats and the ratios of live species richness and diversity are lower than the ratios of dead diatoms. Even with the large number of parameters affecting the diatom community within estuaries, the results of the present study are consistent with those of Wilson and Holmes (1981).

The majority of live taxa were only identified to genus level in 2016, but morphological differentiation to the lowest taxonomic unit was attempted and photosynthetic activity for marine chain diatoms was confirmed. Without identification to the lowest taxonomic level, it is not possible to classify diatoms as marine, freshwater, or brackish. But understanding the proportions of genus based on ecological preferences and live algal units is still important, as they are a representation of the overall health of the benthic community. Studying live diatoms is difficult and rarely documented, which is one of the major contributions of this study. Biomass correlates with the size of the algal cells within a unit. *Skeletonema* spp. biomass was double in December compared with August collection, which differs from reports in the literature, where chain length

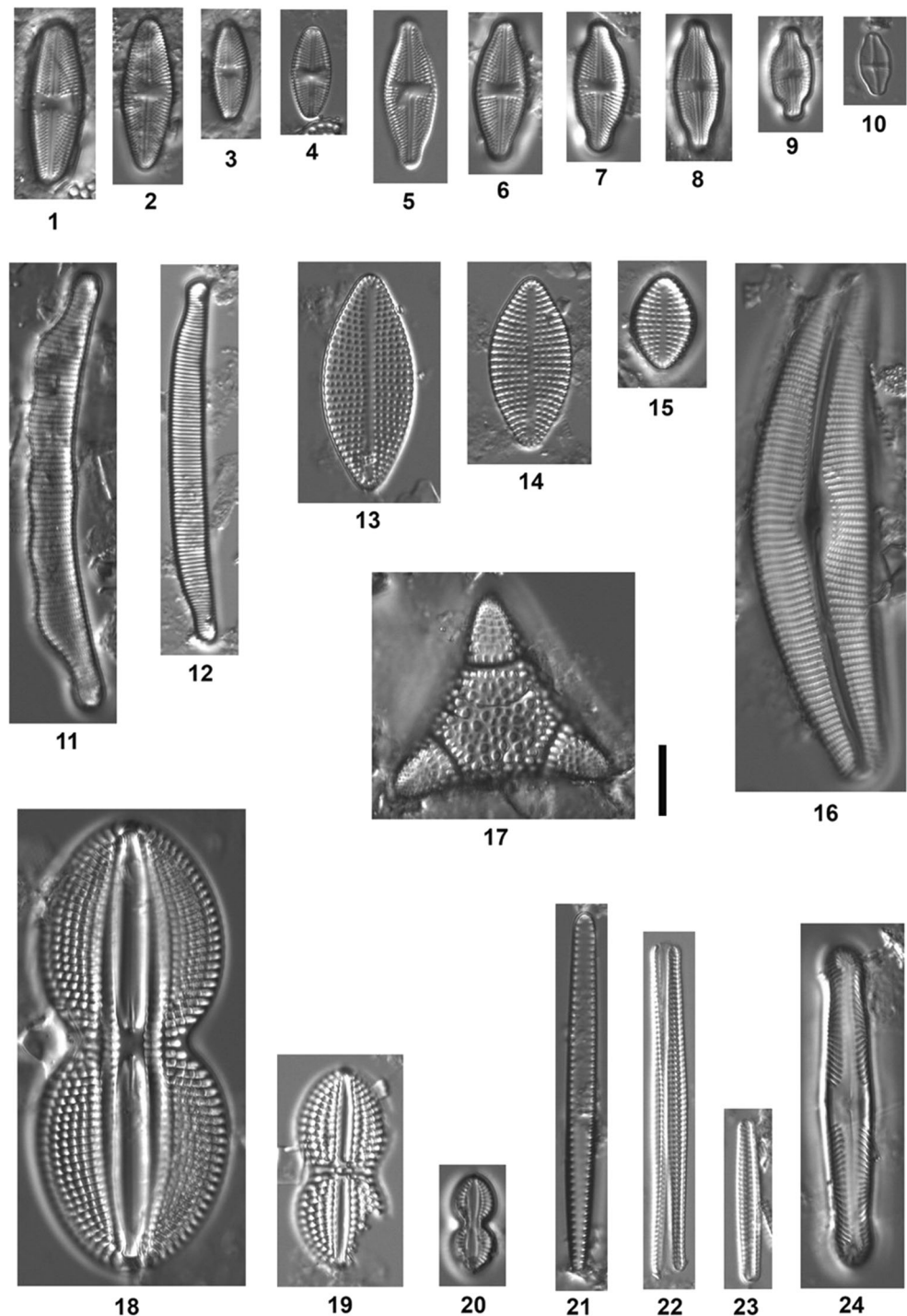
and growth rate of *Skeletonema costatum* increased in higher temperature and nutrient availability (Takabayashi et al. 2006). Species with larger cells/frustules like representatives of *Pleurosigma*, *Gyrosigma* (sigmoid motile diatoms), and *Mougeotia* sp.1 (filamentous green algae) did not have high relative abundances.

Sørensen Similarity Index indicated significantly higher heterogeneity within the 2011 clean diatom analyses (range of similarity indices 6 to 36%) compared with habitat similarity calculations for clean diatoms in 2016 (Table S5), where similarity range was 19 to 59%. Live algal community similarities are provided for future comparison. Distribution patterns of diatoms are difficult to conclude due to the many variables interacting within the community, such as salinity and nutrient fluctuations, stream flow velocity, and turbidity (Admiraal and Peletier 1980b). Several studies have shown no consistent patterns in biodiversity in relation to salinity and nutrients (Sullivan and Daiber 1975; Sullivan 1975; Sullivan 1978). Benthic diatoms were consistently lower in relative abundance during high tide events with the exception of May. Overall, there was an increase in abundance of planktonic diatoms from May 2016 to December 2016. Given the significance of velocity, discharge, and conductivity, this study suggests that natural processes are bringing in more planktonic and marine species from the Atlantic Ocean.

## Taxonomy and Species Diversity

*Cymatosira belgica* and *Minidiscus* spp. remained dominant diatoms in the Savannah River Estuary in 2011 and 2016. Although dominant in cleaned material, *Minidiscus* spp. was not documented as a live unit due to its small size (diameter < 5  $\mu$ m). This small size suggests that *Minidiscus* spp. would be a small contributor to the overall community. *Cymatosira belgica* is a marine planktonic chain-forming diatom consistently present in both live and cleaned material, but also had little contribution to biomass. *Cymatosira belgica* is often classified as a marine benthic diatom (Hustedt 1955; Hendey 1964; Laws 1988) as it is often found as a single cell.

**Plate 3** “Clean” diatoms that were present within mud samples from the Savannah River Estuary to show diversity at USGS site 02198920 during 2016 at  $\times 100$  magnification. (1) *Luticola* cf. *australomutica* Van de Vijver; (2) *Luticola similis* Levkov, Metzeltin, and A. Pavlov; (3) *Luticola* cf. *pseudoimbricata* Levkov, Metzeltin, and A. Pavlov; (4) *Luticola* sp.1; (5–7) *Luticola* sp.2; (8) *Luticola* sp.3; (9) *Luticola* sp.4; (10) *Achnanthyidium exiguum* (Grunow) Gzamecki; (11) *Eumotia pectinalis* var. *undulata* (Ralfs) Rabenhorst; (12) *Eumotia* cf. *lapponica* Grunow; (13–15) *Delphineis surirella* (Ehrenberg) G.W. Andrews; (16) *Cymbella proxima* Reimer; (17) *Biddulphia alternans* (Bailey) Van Heurck; (18) *Diploneis bombus* (Ehrenberg) Ehrenberg; (19) *Diploneis weissflogii* (A.W.F. Schmidt) Cleve; (20) *Diploneis* cf. *caffra* (M.H. Giffen) Witkowski, Lange-Bertalot, and Metzeltin; (21) *Thalassionema nitzschioides* (Grunow) Mereschkowsky; (22–23) *Neodelphineis pelagica* Takano; (24) *Pinnularia subcapitata* W. Gregory. Scale bar = 10  $\mu\text{m}$



However, in many cases, it has also been associated as a tychoplanktonic (Villac et al. 2013) or marine littoral diatom species (Vos and de Wolf 1994) when grown in chains. This study documented both single frustules and diatoms in chains as physiologically active; such adaptations may enable *C. belgica* to exploit both benthic and pelagic environments.

Decline in clean diatom species richness between the two years was at a lower rate (Fig. 4). Clean frustules could have

represented dead diatoms. Species richness stayed relatively similar through seasons in 2011 and 2016, with the exception of summer. In 2016, summer sampling in the current study species richness more than doubled to 65 diatom species (Table 6), which differed from the previous study, where Dominy (2012) found that species richness was lower in summer months. Potentially, this was due to the advantages of smaller diatoms that were more efficient at harvesting light

**Table 6** Diatom community indices for mud samples at low tide events at USGS site 02198920 during 2011 and 2016; SR, species richness; H', Shannon Diversity; J', evenness (2011 data derived from Dominy Thesis, 2012)

Season	2011			2016		
	SR	H'	J'	SR	H'	J'
Spring	29	2.50	0.74	41	2.41	0.65
Summer	26	1.60	0.49	65	2.69	0.64
Fall	37	2.50	0.70	43	2.48	0.66
Winter	40	2.70	0.73	37	2.15	0.60

and reproduction (Litchman et al. 2006). In the current study, higher diversity may be caused by higher temperatures and higher light availability, since all algae growth is enhanced by higher temperatures (Admiraal and Peletier 1980a). Summer months naturally have an extended amount of sunlight compared with winter months.

### Dynamics Within the Estuarine System

The Savannah River Estuary is characterized by its unique and dynamic hydrology and complex habitats. Organisms in the system are adapted to the continuous river flow and daily tidal events. In a 24-h and 50-min span, two high tides and two low tides occur. It takes approximately 6 h and 12 min for low tide to reach high tide and vice versa (NOAA 2017). The natural velocity, discharge, and salinity influxes created rapid and temporary changes in the lotic system. But with the implementation of the Savannah Harbor Expansion Project, this study shows that water parameters have changed compared with 2011 (before dredging). From May 2016 to December 2016, overall conductivity during high tide has decreased and has significantly changed compared with sampling during 2011 ( $p$  value < 0.05, Fig. 3). Variations between YSI and USGS values could have been caused by the location of the probes. USGS probes are located near the center of the river, whereas the YSI probe was placed on the perimeter of the river due to easier accessibility. The center of the river naturally has higher velocity, which could affect overall temperature, pH, DO, and specific conductance readings.

Tidal resuspension is a significant factor in determining the spatial distribution of algae. The process affects the horizontal distribution of both benthic and planktonic algae by causing shoreward transport of the cells to the mudflats, where extensive number of empty frustules are deposited (Baillie and Welsh 1980; Facca and Sfriso 2007). With high tide submerging the intertidal zone, this gives the opportunity for epipelagic and epipsammic diatoms to become suspended in the water column. But, this also allows for planktonic diatoms to be deposited in a benthic environment. The phenomenon of tidal resuspension could also have an effect on the distribution of dead diatoms.

Inconsistent tidal processes like flow, velocity, and discharge, potentially due to precipitation, could have influenced the high percentage of dead diatoms during the month of May.

Cyanobacteria abundances increased during the month of October with an average species composition of 10.6% during high tide and contributing to more than 10% of biomass during both low and high tide events. Samples in October were taken 3 days after Hurricane Matthew hit Savannah, GA. Our site had receded flooding at the time of collection. Although the storm pulse from Hurricane Matthew had to be significant, 2016 was a year marked by high rainfall (Paerl et al. 2018), and Matthew was reported to constitute about 10% of the annual total flow in the Southeast. It is suggested by Paerl et al. (2000, 2018) that individual strong storms in the southeast can influence aquatic microbial communities with increase in discharge. Algal community could have been exposure to high conductivity water as a result of storm surge. Microbial organisms can easily be washed out or buried during periods of increased flow. Additionally, the sampling site is a close large industrial complex with retention ponds with visible algal growth and possible discharge of particles could have altered the community in October. The reported October increase in cyanobacteria in this southeastern estuarine system differs from the expectations of high temperature and low salinity increase reported for other estuarine systems (Carstensen et al. 2015).

Change in salinity can cause algal community alteration; lower salinity associated with strong tropical storms lead to cyanobacteria surge in the tidal James River (Filippino et al. 2016). Dissolved oxygen levels during the month of October were the lowest levels documented for the study (5.70–5.98 mg/L). Rapid declines in DO levels can affect algal communities, as it was previously observed that cyanobacteria abundance increased in the lower Neuse River estuary after Hurricane Irene (Paerl et al. 2014). Cyanobacteria filaments thrive in low-oxygen environments, due to their evolutionary history and can therefore outcompete other algal groups for nutrients (Voorhies et al. 2012).

### Conclusion

This study analyzed changes within the algal community as the Savannah Harbor Expansion project started. Samples were taken 4 months after the start of construction, which could have been too short of a period after the beginning of alteration. It is suggested that sediment fauna is slow to respond to environmental changes because of the stability of the benthic habitat (Baillie and Welsh 1980). Also, due to the continuous river flow and daily tidal events, this environment has already been constantly mixing freshwater and marine water, creating a high-energy brackish environment. The few observed significant trends, such as between the algal communities and water parameters, may be due to this type of high energy environment.

However, dredging, pollution, and other anthropogenic changes may have provided additional stress, resulting in the observed trends of decreasing diatom species richness and an increase of the abundance in high-nutrient tolerance filamentous algae. The research in 2011 was used for coarse comparison and evaluation of changes in the same habitat. This research will be continued by analyzing the post effects of the dredging of the Savannah Harbor to observe how the algal community will recover or change over the years to come. With depletion of biodiversity and ecosystem services degradation of estuaries and coastal seas due to anthropogenic alteration (Lotze et al. 2006), taxonomic work on primary producers from the economically important Savannah River will remain relevant. Algal ecology understanding required species-level population studies (Stevenson et al. 1996); this research is one of the few studies on the ecology of benthic diatoms in the Southeastern USA. Accounting for the limitation of sampling as a single location, this research contributes to the species-specific ecology of diatoms in high energy systems. Microscopic primary producers show remarkable resilience to large-scale changes in sedimentation, flow, turbidity, and light availability.

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