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Benthic Microalgal Community Structure, Primary Productivity, and Fiddler Crab (*Leptuca pugilator*) Grazing in an Estuarine Salt Panne

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Abstract

Salt pannes are marsh features in the supratidal zone that are devoid of macrophytic vegetation. Although these habitats appear barren, benthic microalgae (BMA) inhabit the sediments and are potentially important primary producers. In addition, salt pannes are habitats for dense accumulations of sand fiddler crabs (*Leptuca pugilator*; Bosc 1802). The purpose of this study was to determine the temporal changes in BMA biomass, community composition, and net primary productivity (NPP) for a supratidal salt panne and quantify sand fiddler crab grazing on BMA. The impact of crab grazing on BMA abundance in surface sediments was determined by measuring chl *a* concentrations in ungrazed and grazed sediments. BMA biomass peaked to a high of 16 µg chl *a* g sediment^{-1} in June and July, suggesting growth in the spring followed by a small decline in the warmer summer months. The BMA community was primarily composed of benthic diatoms, with lesser amounts of cyanobacteria. NPP increased to a median of 0.51 mmol O_2 m^{-2} h^{-1} (6.12 mg C m^{-2} h^{-1}) in July. In comparison with other BMA habitats in this estuary, NPP and biomass for salt pannes was lower than the other 5 habitat types (tall and short *Spartina*, intertidal mud and sandflats, phytoplankton, and submerged sediments). Sand fiddler crabs do not appear to consume significant amounts of BMA during grazing in salt pannes. This first ever study of BMA NPP demonstrates that estuarine salt pannes are likely a small contributor to ecosystem NPP.

Keywords Microphytobenthos · Diatoms · ChemTax · Sandflat · South Carolina

Introduction

Salt pannes are a common habitat in vegetated salt marshes (Redfield 1972; Goudie 2013; Wilson et al. 2009, 2014). In southeastern US estuaries, these unvegetated features in the supratidal zone can result from the deposition of mats of *Spartina* wrack that eventually smother vegetation. Subsequent removal of the wrack by spring and storm tides leaves large sandy areas devoid of vegetation surrounded by dense stands of *Spartina* (Yapp et al. 1917; Miller and Egler 1950; Pethick 1974; Boston 1983). Infrequent flooding and high evaporation rates produce high porewater salinities that limit recolonization after the wrack is removed (Hoffman and Dawes 1997).

The spatiotemporal distributions of salt pannes in other areas have been determined using a combination of satellite, aerial, and drone imagery. In a Massachusetts salt marsh, pannes were distributed across the marsh platform and most abundant in the high marsh (Millette et al. 2010). Goudie (2013) found that pan density was higher on the west coast of England and Wales or at locations with a moderate tidal range and low sea level change. Pan density was also higher when creek density was low or on back barrier and drowned valley marshes with maximum pan size partly controlled by pan density (Goudie 2013). Li et al. (2020) documented salt pannes as a common feature in the North Inlet Estuary, South Carolina, especially following marsh dieback while Hoffman and Dawes (1997) report that salt pannes are common landward of the mangals and salt marshes of Florida.

Salt pannes are generally thought to have low productivity and little value to marsh ecosystems (Hoffman and Dawes 1997). However, this paradigm is based primarily on the absence of macrophytes and higher trophic levels.

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Benthic microalgae (BMA or microphytobenthos), inhabiting the upper few millimeters of sediments in salt pannes, are a potentially important contributor to primary production and an overlooked primary producer in these habitats. In addition, Ridd et al. (1997) suggest that salt pannes are locations for the outwelling of nutrients due to groundwater discharge and may subsidize primary production in adjacent vegetated areas. A variety of small macroinvertebrates inhabit salt pannes, including dense herds of sand fiddler crabs (*Leptuca pugilator*; Bosc 1802) (Montague 1980; Hoffman et al. 1984; Johnson et al. 2020). This species ranges from Massachusetts to the Gulf of Mexico and can be found throughout the intertidal zone (Dunn et al. 2023).

BMA are unicellular and filamentous algae, primarily benthic diatoms, inhabiting the surface of intertidal and subtidal sediments of coastal systems (Pomeroy 1959; Admiraal 1984; Sullivan and Moncreiff 1990; Underwood and Kromkamp 1999). Most of the diatoms are large motile pennates and uniquely different from phytoplankton species (Sullivan 1975). BMA provide a nutritious food source for estuarine food webs (Peterson and Howarth 1987; Sullivan and Moncreiff 1990), are an important component in biogeochemical cycles (Höpner and Wonneberger 1985; Paterson 1989; Rizzo 1990), and stabilize sediments (Holland et al. 1974; Madsen et al. 1993). As much as 30% of estuarine primary production can be attributed to BMA (Pinckney and Zingmark 1993a; Schreiber and Pennock 1995; Cahoon 1999; Gerbersdorf 2005; Ask et al. 2016). Aspects of estuarine BMA ecology are comprehensively summarized in reviews by Miller et al. (1996), MacIntyre et al. (1996), Cahoon (1999), Underwood and Kromkamp (1999), and Serôdio et al. (2020).

Sand fiddler crabs construct and occupy burrows in salt pannes (Montague 1980) and are commonly observed in highest abundance in mid- and high-marsh zones (Dunn et al. 2023). These crabs are primarily deposit feeders that graze on the upper few millimeters of sediment near burrows. Feeding by *L. pugilator* involves the collection of sand that is manipulated with mouth parts to extract food particles then discarded as small (ca. 1– 3 mm dia.), round feeding balls (Miller 1961; Montague 1980; Wolfrath 1992). Although several studies have reported the importance of fiddler crabs as consumers of BMA, the evidence is mostly circumstantial or correlational (Robertson and Newell 1982a, b; Ribeiro and Iribarne 2011; Johnson et al. 2020). A direct test of the BMA extraction from sediments during grazing would be to compare BMA abundance in feeding balls vs. nearby, undisturbed sediments. The difference in chl *a* abundance between grazed (i.e., feeding balls) and ungrazed (control) sediment would provide a direct measure of BMA consumption by grazing sand fiddler crabs.

Although many studies have reported the physical characteristics and geomorphological features that promote salt pan formation and maintenance, few studies have evaluated the ecological role of these habitats, especially in terms of primary production. Understanding the potential effects of sea level rise and loss of marsh habitat on ecosystem goods and services is critical for mitigation and restoration strategies. The purpose of this study was to quantify temporal changes in BMA biomass, community composition, and net primary productivity (NPP) during the spring and summer months for a supratidal salt panne and compare results to other representative habitat types in the North Inlet Estuary. The primary objective was to provide insights into the potential role of salt pannes in overall system primary production and their contribution to sand fiddler crab grazing on BMA abundance.

Materials and Methods

Study Site

North Inlet Estuary, South Carolina, USA, has an area of 33 km^2, is euhaline (salinity range of 25–40), and receives diffuse freshwater input (ca. 1–5 m^3 s^{-1}) as both groundwater discharge and surface runoff from a small (38 km^2) and relatively undeveloped watershed (Allen et al. 2014) (Fig. 1). Tides are semidiurnal with a range of 1.5 m. Tidal creeks are bordered by the saltmarsh cordgrass *Spartina alterniflora* (*Sporobolus alterniflorus*), and sediments are primarily muddy sand. Intertidal oyster (*Crassostrea virginica*) reefs and mudflats are common. Salt pannes are found as patches throughout the high intertidal area and along the margins of the estuary (Li et al. 2020).

The study location was a 2800 m^2 area (33.3234 N, 79.2083 W) that appeared to be representative of salt pannes in this estuary (Fig. 1). Like other salt pannes, this area is above mean high water (elevation > 1.4 m above mean low water) and only occasionally submerged during spring tides and storm events. This panne has persisted for at least the last decade and visible in satellite images (Goudie 2013; Li et al. 2020). The site is well-drained. Porewater salinities range from 30 to 90 and vary with duration since the last tidal inundation or rainfall (Dunn et al. 2023). The sediment was composed mostly of quartz sand (97% 0.50–0.063 µm dia.) with very little silt and clay (1% < 0.063 µm).

Samples and measurements were obtained from the study site on 5 occasions in May–September 2022. Sediment cores (10–30 cores, each 1.00 cm^2) for measurements of BMA photopigments were randomly collected at the sampling site; the upper 0.5 mm was sectioned, and the sample stored in 2-ml microfuge tubes. For BMA productivity measurements, 5–10 sediment cores (20 cm^2 × 15 cm) were randomly collected and returned to the laboratory for incubations within 2 h of collection.

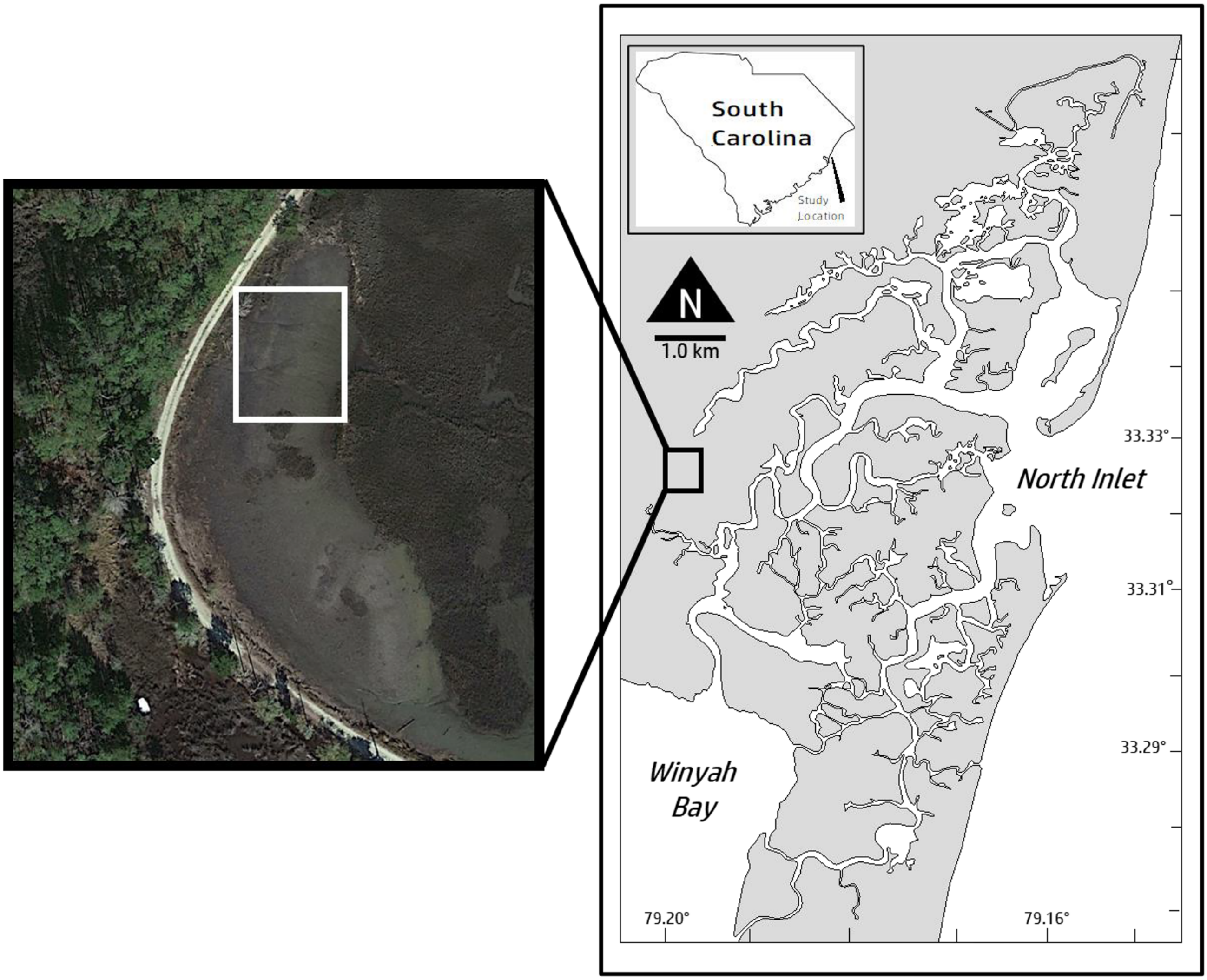


Fig. 1 Location map for the salt panne study site in North Inlet Estuary, SC

The impacts of sand fiddler crab grazing on BMA abundance in surface sediments were determined by measuring chl *a* concentrations in ungrazed and grazed sediments. Ungrazed areas were defined as "undisturbed" sandy areas, without evidence of crab burrowing or scraping, but within 1–2 m of crab burrows. The ungrazed surface sediment (undisturbed, control) was collected near crab burrows using a small spatula and carefully scraping the upper 2–5 mm of sediment. Fresh crab feeding balls (ca. 10–20) near fiddler crab burrows were gently collected with a spatula and placed in 2-ml microcentrifuge tubes. BMA biomass was normalized to sediment weight for comparisons of grazed and ungrazed sediments. Feeding balls were differentiated from sand balls produced during burrow construction based on size (feeding balls were much smaller) and color (sand balls were darker than feeding balls).

Photopigment Analysis

High-performance liquid chromatography (HPLC) was used to determine chemosystematic photosynthetic pigment concentrations (Roy et al. 2011). Sediment samples were lyophilized for 24 h at −50 °C, placed in 90% acetone (1 ml), and extracted at −20 °C for 18–20 h. Filtered extracts (0.45 μm, 250 μl) were injected into a Shimadzu 2050 HPLC equipped with a monomeric (Rainin Microsorb–MV, 0.46 × 10 cm, 3 μm) and a polymeric (Vydac 201TP54, 0.46 × 25 cm, 5 μm) reverse-phase C18 column in series. A nonlinear binary gradient of 80% methanol/20% 0.50 M ammonium acetate and 80% methanol/20% acetone was the mobile phase (Pinckney et al. 1996, 2001). Absorption spectra and chromatograms (440 ± 4 nm) were acquired using a photodiode array detector (PDA). Pigment peaks were identified by comparison of retention times and absorption spectra with pure carotenal and chlorophyll standards (DHI, Denmark). The synthetic carotenoid β-apo-8′-carotenal (Sigma) was used as an internal standard.

ChemTax (v. 1.95) was used to estimate the relative concentrations of major algal groups based on measured photopigment concentrations (Pinckney et al. 2001; Higgins et al. 2011). Total chlorophyll *a* (chl *a*) was partitioned into algal group abundances (e.g., diatoms, cyanobacteria, green algae). Samples were examined by qualitative microscopy to confirm algal groups included in the ChemTax analysis. The initial ratio matrix was derived from Lewitus et al. (2005), and the matrix randomization procedure with 60 simulations was used to minimize errors in algal group biomass resulting from inaccurate pigment ratio seed values (Higgins et al. 2011).

Production Measurements

BMA net primary production (NPP) was determined on fresh samples using the procedure described by Berg et al. (1998). This method uses the steady-state dissolved O_2 concentration profile in sediment porewater and compares profile fits through statistical F-testing to determine the simplest O_2 production-consumption profile that reproduces the measured concentration profile. This procedure gives an estimate of O_2 fluxes (nmol O_2 cm^{-3} s^{-1}) that can be depth integrated to give units of mmol O_2 m^{-2} h^{-1} for each profile. Multiple profiles (3–5) were obtained to calculate a mean and standard deviation for NPP for each core sample.

Sediment O_2 concentrations were measured using Unisense oxygen microelectrodes (25-µm tip diameter) and the profiling function in the Unisense SensorTrace Suite software (Unisense A/S, Aarhus, Denmark). Automated vertical profiling (at 100-µm intervals) of dissolved O_2 concentrations in the porewater was accomplished with a computer-controlled motorized micromanipulator. Dissolved O_2 concentrations from the profiles were analyzed using the activity algorithm in the SensorTrace software (Berg et al. 1998) to calculate net O_2 production and consumption at each depth interval. For flux calculations, porosity was determined as the loss of water from the sediment sample after drying at 60° C and ranged from 0.4 to 0.6%. Dissolved O_2 production and consumption rates were integrated over the depth of the profile to determine total BMA NPP. Sediment cores were incubated at ambient air temperatures (ca. 32 °C), illuminated with a Schott (KL 2500 LED) fiber optic light (ca. 1,100 µmol photons m^{-2} s^{-1}), and allowed to reach steady state before measuring O_2 profiles. Preliminary photosynthesis vs. irradiance (P vs. E) experiments indicated that BMA NPP was maximal (P_{max}) at this irradiance (Pinckney and Zingmark 1993c). Measurements were obtained under subaerial conditions with a thin film of water on the sediment surface.

Results

Sediment cores for measurements of BMA chl *a* were normalized to dry sediment weight (µg chl *a* g dry sediment^{-1}) for each sample to allow intercomparisons with other studies. The weight normalized samples and areal estimates of chl *a* (µg chl *a* cm^{-2}) in the upper 0.5 cm of sediment for paired samples were analyzed using a linear regression (Fig. S1). Regression of the two variables yielded an adj. $r^2 = 0.91$ and the equation chl *a* (µg cm^{-2}) = 0.49(chl *a*, µg g dry sed^{-1}) + 1.85 ($n = 60$, $p < 0.001$). All measures of chl *a* concentrations below are based on sediment weight but can be converted to areal estimates using this equation.

Samples for BMA biomass were collected at the study site in May, June, July, and September 2022. Accessory photopigment concentrations were input into ChemTax to determine BMA community composition and relative abundances of algal groups (Fig. 2). The average RMS for the ChemTax analysis was 0.299. Three algal groups (diatoms, cyanobacteria, and green algae) comprised > 99% of the BMA community. Qualitative microscopy confirmed the presence of these three groups. Comparisons between dates were conducted using the non-parametric Kruskal–Wallis ANOVA and a Dunn's test ($p \leq 0.05$) for post hoc comparisons. Statistical results are indicated on the individual panels (Fig. 2). Green algae (chlorophytes and euglenophytes) were common in the early May samples, but near the limits of detection (0.05 µg chl *a*) on other dates. Diatoms were the most abundant group, with peak abundances in late June and early July. Cyanobacteria appeared to increase over the summer months and remained high in September. Chl *a* concentrations for the entire BMA community (total chl *a*) peaked in early July. The relative magnitude of the abundances of the different algal groups is illustrated in Fig. 3 using median values for each date, further showing the major contribution of diatoms relative to cyanobacteria and green algae.

Steady-state vertical profiles of the dissolved O_2 concentration in porewater were used to calculate net primary production (NPP) for benthic microalgae (Fig. 4). The sediment photic zone was typically limited to the upper 2–5 mm, and deeper sediments were anoxic. Unlike intertidal BMA, the salt panne BMA did not exhibit rhythmic vertical migration behavior. NPP measurements were obtained in May, June, and July 2022 and gradually increased over the summer along with increased variation in rates (Fig. 5). Median rates of NPP for May, June, and July were 0.13, 0.26, and 0.51 mmol O_2 m^{-2} h^{-1}, respectively. The minimum and maximum NPP for all dates combined were −0.574 (net oxygen consumption) and 2.89 mmol O_2 m^{-2} h^{-1}. Corresponding measurements of BMA chl *a* showed a similar pattern, with an increase from May to July. The median BMA biomass (µg

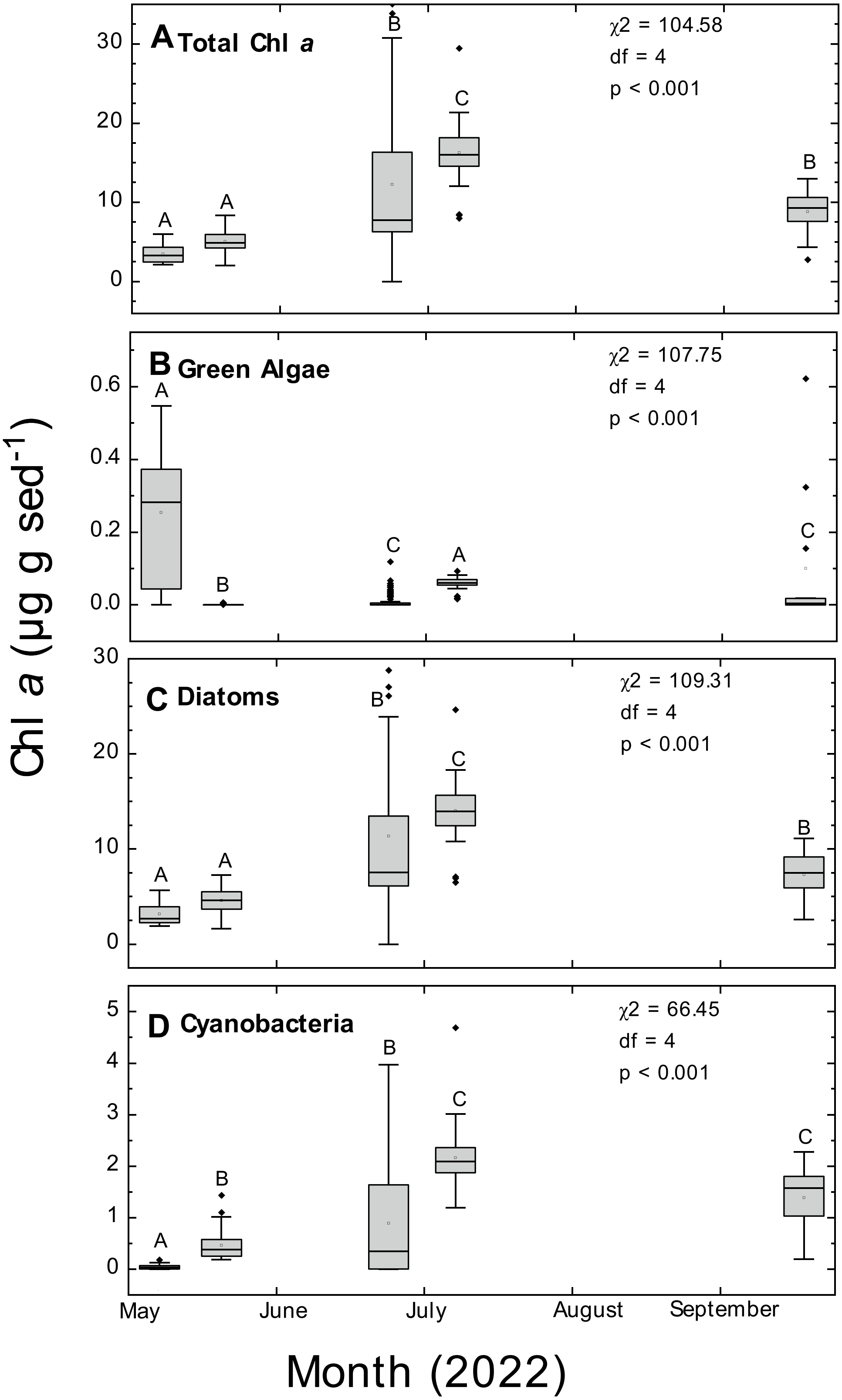


Fig. 2 Boxplots for total chl a (**A**), green algae (**B**), diatoms (**C**), and cyanobacteria (**D**) biomass and community composition. Boxes indicate the 25th and 75th percentiles; lines in the boxes show the median and points are the mean. The whiskers show the 5th and 95th percentiles and points outside the box are outliers. Results of a Kruskal–Wallis ANOVA are shown on each panel. Boxes that share the same letter were not significantly different ($p < 0.05$). Note the different *y*-axis scales

chl *a* g sediment^{-1}) for May, June, and July was 4.89, 7.88, and 16.00 and values ranged from 2.02 to 47.57. A scatterplot of paired BMA NPP vs. chl *a* shows a general trend of increasing NPP with an increase in biomass (Fig. S2), but the two variables were poorly correlated (Spearman correlation, $r = 0.55$, $p = 0.03$, $n = 15$).

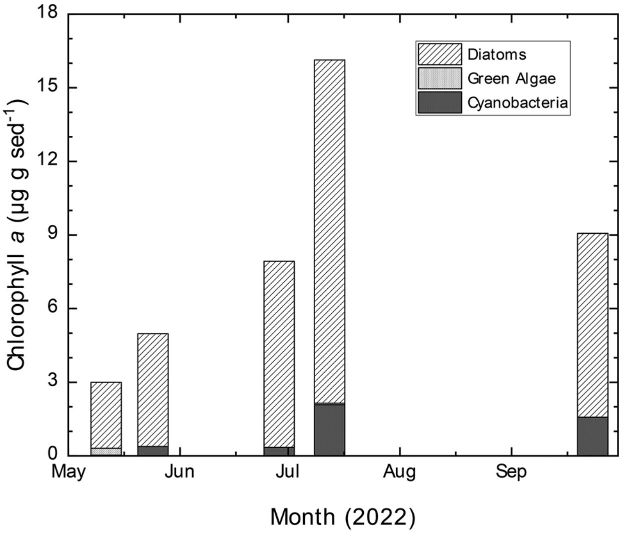


Fig. 3 Stacked bar chart showing the proportions BMA community components. Median values were used for each sampling date

Estimates of salt panne BMA NPP and biomass were compared with those for other habitat types in North Inlet Estuary to evaluate the panne contributions relative to other habitats (Fig. 6). NPP and biomass for salt pannes were lower than the other 5 habitat types. The mean BMA NPP and biomass for the salt panne for May to July was 0.36 mmol O_2 m^{-2} h^{-1} ($\pm$0.06 SE) and 53.8 mg chl *a* m^{-2} ($\pm$3.3 SE), respectively. In contrast, similar intertidal sandflats (0–1.4 m above mean low water) have an NPP that is ca. 8 times higher, while BMA biomass is only 1.5 times higher than measured in the salt panne. Salt pannes are similar in appearance to intertidal sandflats in terms of sediment grain size and absence of macrophytes but receive daily tidal inundation. These results suggest that periodic tidal flushing may enhance BMA NPP.

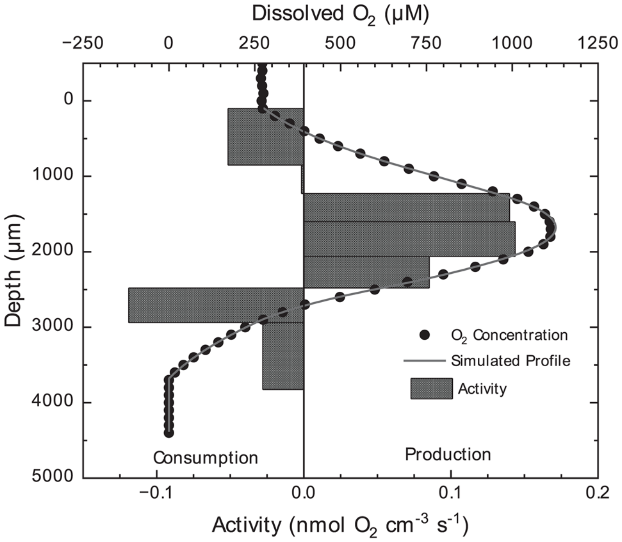


Fig. 4 Representative vertical profile of oxygen concentration, the fitted profile, and calculated activities for the different depth intervals

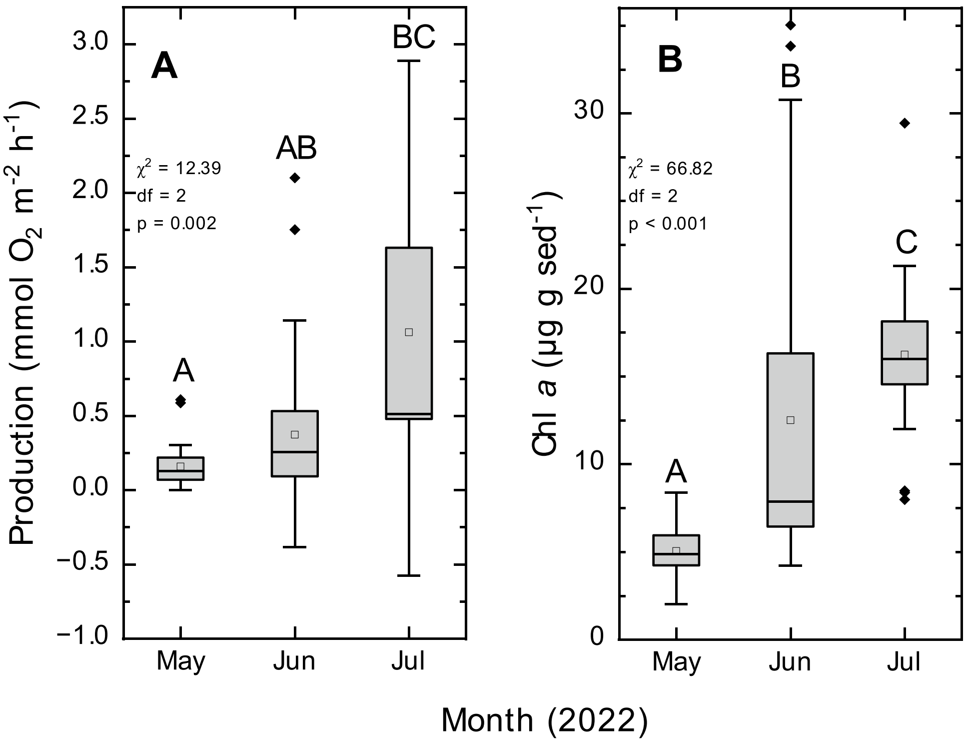
The impacts of sand fiddler crab grazing on BMA abundance were determined comparing the chl *a* content in nearby surface sediments with the content in crab-feeding balls (Fig. 7). The results of a two-way ANOVA indicated a significant difference in chl *a* abundance between all 3 dates ($F_{2,95} = 31.64$, $p < 0.001$, Bonferroni $p < 0.05$) but no difference between grazed and ungrazed sediments ($F_{1,95} = 2.11$, $p = 0.15$). The interaction of the two factors was not significant ($F_{2,95} = 0.17$, $p = 0.84$).

Discussion

High intertidal salt pannes are a common feature in most estuaries of the southeastern US (Redfield 1972; Goudie 2013; Wilson et al. 2009, 2014) and North Inlet Estuary, SC (Li et al. 2020). However, data on BMA NPP, biomass, and community composition for these habitats are sparse and rarely incorporate changes over time. In this study, we followed BMA biomass, community composition, and NPP during late spring and summer months (May–September 2022) for a salt panne in North Inlet Estuary. BMA biomass (as total chl *a*) peaked to a high of 16 µg g dry sed^{-1} in June and July, suggesting growth in the spring. The BMA community was primarily composed of benthic diatoms, with much lesser amounts of cyanobacteria. Green algae (chlorophytes and euglenophytes) were only present in significant abundance in May. BMA NPP increased to a median of 0.51 mmol O_2 m^{-2} h^{-1} in July. For comparisons with other studies, NPP can be converted to carbon (C) units using the equation mmol $O_2 \times 12 =$ mg C (assuming a photosynthetic quotient of 1) (Grant 1986). Thus, the median salt panne BMA NPP would be approximately 6.12 mg C m^{-2} h^{-1}. Assuming an average of 10 h of sunlight per day and a constant NPP, a very liberal estimate of BMA annual NPP would be 22 g C m^{-2} year^{-1}.

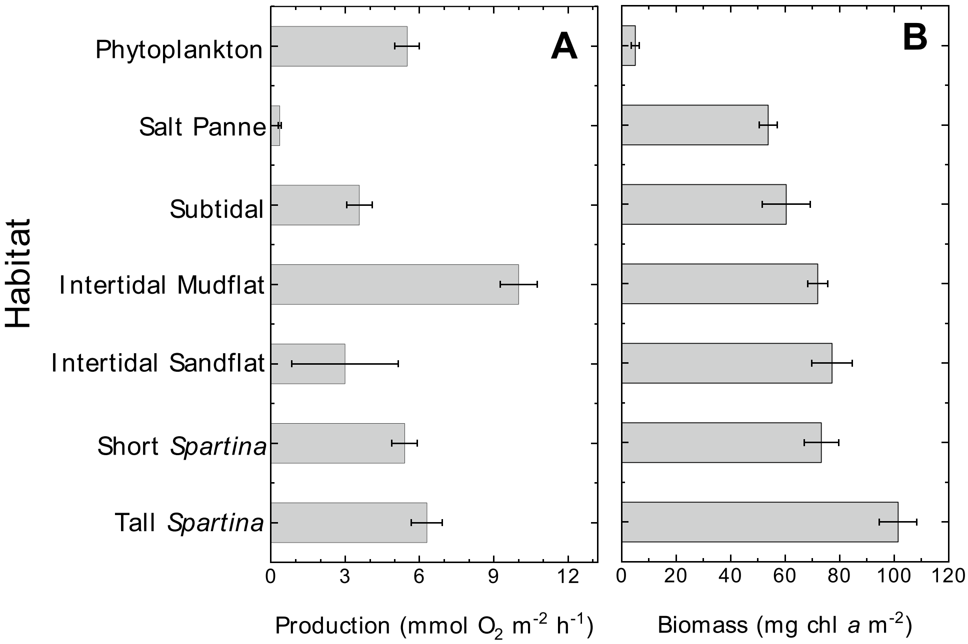
In comparison with other habitat types, BMA biomass and productivity in this salt panne were low. BMA community composition also differed from nearby areas, with a higher contribution of cyanobacteria in salt pannes relative to intertidal habitats. High temperatures, high porewater salinities, and sandy sediments may favor the growth of cyanobacteria in salt pannes (Paerl et al. 2000; Paerl and Huisman 2008) relative to other intertidal habitats. However, benthic diatoms were the major BMA community components in all habitat types in this estuary. High benthic diatom abundance is a common feature for salt marsh estuaries (Sullivan 1975; Cahoon 1999; Underwood and Kromkamp 1999).

Fig. 5 Box plots of BMA production (**A**) and biomass (**B**). See Fig. 2 for boxplot descriptions. The results of a Kruskal–Wallis ANOVA are shown in each panel. Boxes that share the same letter were not significantly different ($p < 0.05$)



The ratio of NPP to BMA biomass can be used as relative indicator of turnover time for BMA in the different habitat types. Compared to other major habitats in the estuary, BMA turnover is much slower in salt pannes than in similar intertidal sandflats, beneath *Spartina*, or on unvegetated intertidal mudflats (Pinckney et al. 2003). The low turnover indicates that consumption and losses of BMA are much lower in salt pannes than other estuarine habitats. Our results suggest that sand fiddler crabs do not consume significant amounts of BMA during grazing in salt pannes. Although some studies report significant BMA consumption by fiddler crabs (Montague 1980; Johnson et al. 2020), others have shown that sand fiddler crabs are grazing primarily on detritus, microheterotrophs, meiofauna, ciliates, segmented worms, and bacteria (Montague 1980; Robertson and Newell 1982a, b; Hoffman

Fig. 6 Comparison of BMA production (**A**) and biomass (**B**) for different habitat types in North Inlet Estuary. Data for habitat types was derived from this study and Pinckney and Zingmark (1993b). Values are the mean ± 1 SE



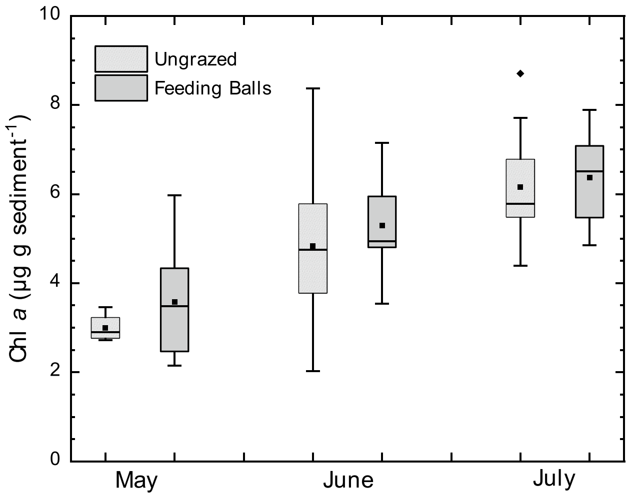


Fig. 7 Boxplots comparing chl *a* abundance in ungrazed sediments vs. fiddler crab feeding balls. See Fig. 2 for boxplot descriptions

et al. 1984; Dye and Lasiak 1986). Similarly, Ribeiro and Iribarne (2011) report that fiddler crabs have a low impact on BMA abundance. One speculation is that BMA are a food source for micrograzers and bacteria that are then consumed by fiddler crabs. The results of this study show that fiddler crabs may not have a direct impact on BMA in *Spartina*-dominated marshes. However, these burrowing crabs may facilitate salt panne recolonization by plants (Beheshti et al. 2022). Bioturbation by fiddler crabs may have indirect effects on BMA growth and abundance by reworking surface sediments to expose buried BMA (Wilson et al. 2012; Xie et al. 2022).

In this study, the BMA abundances in “ungrazed” sediments were compared to crab balls. In reality, the ungrazed sediments may have been grazed at some point prior to collection and are not truly “ungrazed.” However, the “undisturbed” sediment represents the available food source, whether previously grazed, for fiddler crabs. Thus, a comparison of BMA abundances in the discarded crab balls and surrounding sediments provides a useful measure of grazing effects.

This research was conducted over 5 late spring and summer months at a single location in North Inlet Estuary. Extrapolating the results to assess the annual BMA contribution to other salt pannes in this estuary or other estuaries is a limitation of this study. However, the measurements were well-replicated within the study site. This study examined only one salt panne area within North Inlet estuary and may not be representative of all salt pannes in the estuary, especially those at different elevations. Future studies should focus on quantifying the spatial variability in BMA biomass, NPP, and crab grazing among pannes in this estuary and between estuaries, especially those where panne formation is not driven by *Spartina* wrack dynamics.

The results of this study demonstrate that estuarine salt pannes are likely a small contributor to ecosystem NPP. However, these habitats are not “barren” areas and are an important component and contributor to ecosystem processes (Hope et al. 2020). Furthermore, they serve as foraging and burrowing areas for sand fiddler crabs (Montague 1980; Hoffman et al. 1984; Johnson et al. 2020; Dunn et al. 2023). Sea level rise due to warming temperatures and global climate change may also have a negative effect on the abundance, structure, and function of estuarine salt pannes (Linhoss and Underwood 2016). Similarly, sediment starvation of coastlines produced by river dredging and damming may have negative effects at least comparable to the accelerating sea-level rise (Mariotti and Fagherazzi 2013). The effects of the loss of salt pannes on marsh ecosystem processes are unknown but could result in habitat loss for some microbenthic grazers, alterations in biogeochemical cycling, and contributions of microbial/meiofaunal processes (Ridd et al. 1997). In addition, salt pannes may be an important source of “blue carbon” due to their low turnover times (Ward et al. 2021). Future research should further explore the role of salt pannes in biogeochemical cycling and microbial trophodynamics.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-023-01208-8.

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Data Availability Data for this study are available from the author upon request.

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