Do diatoms dominate benthic production in shallow systems? A case study from a mixed seagrass bed

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Scientific Significance Statement
Diatoms are ubiquitous members of macrophyte beds. They are part of the water column community and are found in the benthos, in the sediment and as epiphytes. It is recognized that assemblages in these coastal habitats are highly productive, yet diatom contribution to production has not been quantified directly. We disentangled contributions of diatoms from other producers in a seagrass bed by employing a diatom inhibitor and measuring community production and respiration. We found that the contribution of diatoms to benthic production in a seagrass habitat was substantial (71–83%). Diatom contribution in the water column and in an open sediment habitat was more variable (0–86%). Therefore, seagrasses allow for colonization of productive diatom assemblages. If contributions are similar among systems, this could represent a significant term in regional budgets that has been underestimated.

Abstract
We report an assessment for determining the contribution by diatoms to community productivity and respiration within a coastal benthic ecosystem with multiple autotrophs. During summer, cores of open sediment and seagrass habitat were collected from a lagoon within the Northern Gulf of Mexico. Cores were maintained in an outdoor mesocosm. Germanic acid, an inhibitor of diatom cell division, was added to half the cores and quantification of production and respiration was done. Inhibition of diatoms reduced benthic productivity within the seagrass habitat. 71–83% production attributable to diatoms and this contribution moved the benthic system into net autotrophy. Diatom contribution to production in other habitat-community components was more variable (varied from 0% to 86%). Findings underscore the ecological importance of diatoms as producers in seagrass beds, the role of seagrasses in maintaining productivity, and infer that diatoms may have similar contributions in other aquatic vegetated habitats.

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Associate editor: Daniel Conley

Author Contribution Statement: JK wrote the grant that financially supported this study. JK and JC formulated the research questions. JC, JK, TEC, LW, and MT designed the study approach. MT organized and collected data with assistance and guidance from LW and TEC. TEC analyzed data and lead manuscript preparation with input from all authors.

Data Availability Statement: All data and associated metadata are available through project 712667 (the biotic and abiotic controls on the Silicon cycle in the northern Gulf of Mexico at URLs: https://doi.org/10.26008/1912/bco-dmo.819932.1; https://doi.org/10.26008/1912/bco-dmo.819975.1) at the Biological & Chemical Oceanography Data Management Office.

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Diatoms play significant roles in carbon and silicon cycling and are responsible for up to 20% of global primary production (Nelson et al. 1995). Diatom contributions in continental shelf and deep-water systems are appreciated and to a lesser extent they are recognized in shallow coastal systems. Yet, diatoms are prominent in intertidal sediments (Cahoon 2002) where they migrate vertically and contribute to high primary production in macrophyte free areas (Guarini et al. 2000). Worldwide, diatoms grow on and add to primary production in kelp (Beltrones et al. 2016), maerl (Costa et al. 2014), mangrove (Hendrarto and Nitisuparjo 2011), and seagrass (Borowitzka et al. 2006) beds.

It is recognized that diatom assemblages in shallow coastal habitats are highly productive (Underwood and Kromkamp 1999, Guarini et al. 2000); however, contributions attributed to diatoms in macrophyte beds have yet to be quantified directly. Seagrass meadows are productive ecosystems and provide refuge for many organisms. Diatoms are ubiquitous in seagrass beds as epiphytes (Borowitzka et al. 2006), as plankton, and sediment microalgae (Daehnick et al. 1992). Other epiphytic micro- and macro-algae depend on seagrasses (Borowitzka et al. 2006). Algal components can account for 87% of total primary production (Moncreiff et al. 1992; Lebreton et al. 2009). In nutrient-enriched systems, phytoplankton or epiphytes frequently attain higher productivity rates than seagrasses (Coleman and Burkholder 1994), but group-specific contributions are not available. Microalgal biomass on seagrass leaves and sediment has accounted for 60% of total seagrass above-ground biomass (Lebreton et al. 2009). Most studies infer autotrophs contribution to ecosystem production from biomass (e.g., Lebreton et al. 2009). This oversight lies in difficulty of separating diatoms’ productivity signal among multiple autotrophs. To this end, some studies have used radioisotope $^{32}$Si (Ní Longphuirt et al. 2009). While a direct measurement, this isotope is expensive and regulated, and thus is limited for wide application. We demonstrate an approach, pioneered in plankton research (Lewin 1966), to disentangle contributions of diatoms from other producers.

There is regional information on benthic microalgal ecology and biogeochemistry of shallow systems in the Northern Gulf of Mexico (nGoM) (e.g., Stutes et al. 2006, Cebrian et al. 2011). Therefore, coastal shallow systems in nGoM represent an ideal location for disentangling contribution of diatoms to production in seagrass beds.

The purpose of this study was (1) to present an approach that allows for quantification of diatom metabolic contribution to community productivity in a macrophyte bed, and (2) elucidate role of diatoms in a mixed species seagrass bed located in nGoM. We hypothesized that diatoms would be significant contributors (~60%) to benthic production, based upon a previous study in nGoM where microalgae accounted for 60% and diatoms were prevalent (Moncreiff et al. 1992).

**Materials and methods**

**Field collection**

Cores (27 cm diameter, 14 cm depth) were collected from 50 m² area of seagrass bed at 1 m depth in Grand Bay (Alabama, United States, Supplementary Fig. 1). The site is in a shallow mesohaline embayment. It has muddy sediments and experiences salinity oscillations from riverine inputs and tidal forcing. The seagrasses *Ruppia maritima* and *Halodule wrightii* make-up the bed (see Antón et al. 2009 for further description). Macroalgae were not observed. Epiphytes were microscopic and were not quantified.

Three repeated experimental trials were done in summer months when productivity should be highest to characterize diatom contribution to productivity, test robustness of method, and capture variability related to environmental or compositional changes. Thirty-two cores were collected on: June 28, July 12, and July 26, 2017 for trials 1–3, respectively.

On each date, 16 cores were collected from seagrass habitat in pairs, within 2 m from one another. Another 16 cores were collected similarly but from open sediment (OS) habitat. Extracted, paired cores were placed upright side by side into an open-top plastic tub (49 $\times$ 33 $\times$ 42 cm) to produce eight tubs of each habitat.

**Mesocosm set-up**

Tubs were transported to Dauphin Island Sea Lab (~30-min drive) filled with seawater (to core depth of 16 cm) pumped from Mobile Bay (20 km, east of site) and arranged in four blocks within an outdoor mesocosm (Fig. 1). Each block contained two tubs of each habitat. Tubs were bubbled with air, surrounded by a flowing water bath, and covered with neutral density screen to mimic light at depth. After 2 days, a diatom-specific inhibitor (3 $\mu$M solution of germanic acid, i.e., Ge treatment) was randomly added to water, i.e., two tubs per block, one of each habitat type. Because tubs were separate, contamination of controls could not occur.

Germanium (Ge) at high Ge/Si ratios (>0.01) prevents formation of siliceous cell wall (Azam and Chisholm 1976). In mixed assemblages, negative net Ge effects on diatom biomass occur typically within 2 days (Scarratt et al. 2006; Brzezinski et al. 2011). We added 3 $\mu$M solution and allowed 2 days for Ge incorporation. Brzezinski et al. (2011) reported growth of diatom *Thalassiosira weissflogii* was arrested at [Ge] of 1.0 $\mu$M and concentrations up to 30 $\mu$M had no effect on nonsiliceous microalgal growth. Brown and green macroalgae showed metabolic inhibition at 42–96 $\mu$M concentration and, to reduce diatom competition with kelp, a concentration of 4.3–21.4 $\mu$M was recommended (Shea and Chopin 2007). Merrill and Gillingham (1991) recommended 0.4–1.7 $\mu$M Ge concentration. The dose, over the time scale we used, should not affect nonsiliceous algal photosynthesis, yet inhibit diatoms. Ge stocks were prepared based on the Nelson and Goering (1977) alkaline fusion method as adapted by Brzezinski et al. (2011).
Metabolism measurements

Two days after adding Ge solution, we quantified productivity and respiration from changes in oxygen content within 2–3 h incubations (usually terminating before daily solar maximum) of chambers and bottles following methods in Anton et al. (2009). A clear benthic chamber (15 × 15 × 15 cm) was pushed 3 cm into sediment for one core for each pair, and a dark chamber in the respective paired core (for 16 clear and 16 dark chambers, Fig. 1). Each chamber was paired with a corresponding clear or dark bottle filled with seawater from overlying water. Upon filling bottles, oxygen content was measured with a meter (HQ30d, Hach, Loveland, Colorado), and this was initial oxygen content for both chamber and bottle incubation.

After incubation, we measured final oxygen content in bottles and chambers. For chambers, we extracted water from mid-height using a 60 mL syringe attached to a tube, transferred water to an 80 mL tube, and measured with the meter.

To compare rates between treatments, net community productivity (NCP) and respiration were assessed in mg O₂ m⁻² h⁻¹ and mg O₂ L⁻¹ h⁻¹ for benthic and water-column (WC) communities, respectively. Equations were:

\[
WC\text{ NCP} = (F_{cb} - I_{cb}) t^{-1} \\
WC\text{ respiration} = (F_{db} - I_{db}) t^{-1} \\
Benthic\text{ NCP} = [(F_{cc} - I_{cc}) - (F_{cb} - I_{cb})] V t^{-1} A^{-1} \\
Benthic\text{ respiration} = [(F_{dc} - I_{dc}) - (F_{db} - I_{db})] V t^{-1} A^{-1}
\]

where capital letters are for initial (I) or final (F) oxygen content (mg L⁻¹) for clear (c) and dark (d) incubations (first letter in subscript) in chambers (c) or bottles (b) (second letter in subscript); t is incubation time (h), V is volume (L), and A is area (m²) of chamber. Gross primary productivity (GPP) was calculated as sum between NCP and absolute respiration for each tub.

To compare GPP between communities, control values were expressed in mg O₂ m⁻² h⁻¹ after WC metrics of NCP and respiration were integrated over a 1 m depth (×1000 L). System GPP was obtained by summing WC and benthic GPP.

Environmental measurements

Salinity and temperature were measured at time of oxygen measurements using the same meter. Surface photosynthetic
Table 1. Environmental conditions and producer biomass (mean ± SE) during each trial incubation for control and Ge added (+Ge) cores. Total dissolved nitrogen (TDN, μM), NO$_3^-$ + NO$_2^-$ (μM), germanic acid to silicic acid ration (Ge:Si) in treatments, seagrass biomass (dw g m$^{-2}$), Chl $a$ concentration in sediment (mg m$^{-2}$), integrated (∫) Chl $a$ concentration in the 1-m water column (mg m$^2$), Photosynthetic photon flux density (PPFD, Mol m$^{-2}$), salinity (psu), temperature (°C); $n$ = 4 for sediment and seagrass habitat, $n$ = 8 for all samples, $n$ = 2880 for PPFD.

| Trial 1 | Open sediment habitat | Seagrass habitat | All samples |
|---------|-----------------------|------------------|-------------|
| 3 July 2017 | Control | +Ge | Control | +Ge | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| TDN | 58.6 | 2.9 | 66.5 | 6.1 | 59.7 | 2.5 | 68.5 | 7.1 | 63.3 | 3.5 |
| NO$_3^-$ + NO$_2^-$ | 0.9 | 0.2 | 1.3 | 0.8 | 0.8 | 0.2 | 1.0 | 0.5 | 1.0 | 0.5 |
| Ge:Si | — | — | 0.03 | 0.01 | — | — | 0.03 | 0.03 | — | — |
| Seagrass above-ground biomass | — | — | — | — | 0.4 | 0.2 | 0.9 | 0.3 | 0.7 | 0.2 |
| Seagrass below-ground biomass | — | — | — | — | 0.5 | 0.2 | 0.7 | 0.2 | 0.6 | 0.1 |
| Chl $a$ in sediment | 41.0 | 5.8 | 40.0 | 5.9 | 35.0 | 10.9 | 46.7 | 1.1 | 40.7 | 4.6 |
| ∫Chl $a$ in water column | 97.5 | 7.1 | 140.6 | 5.3 | 108.9 | 20.6 | 59.1 | 23.8 | 101.5 | 14.8 |
| Salinity | 7.9 | 0.5 | 8.3 | 0.5 | 9.1 | 0.7 | 8.0 | 0.5 | 8.3 | 0.4 |
| Temperature | 32.8 | 0.2 | 32.7 | 0.3 | 32.8 | 0.1 | 32.6 | 0.2 | 32.7 | 0.1 |
| PPFD | 224,723 | | | | |

| Trial 2 | Open sediment habitat | Seagrass habitat | All samples |
|---------|-----------------------|------------------|-------------|
| 17 July 2017 | Control | +Ge | Control | +Ge | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| TDN | 117.1 | 17.8 | 118.6 | 20.8 | 63.7 | 3.5 | 71.9 | 5.6 | 92.8 | 12.7 |
| NO$_3^-$ + NO$_2^-$ | 12.5 | 5.5 | 5.2 | 1.0 | 1.1 | 0.3 | 0.8 | 0.2 | 4.9 | 2.5 |
| Ge:Si | — | — | 0.04 | 0.01 | — | — | 0.04 | 0.001 | — | — |
| Seagrass above-ground biomass | — | — | — | — | 0.9 | 0.3 | 0.7 | 0.1 | 0.8 | 0.2 |
| Seagrass below-ground biomass | — | — | — | — | 0.8 | 0.2 | 0.7 | 0.1 | 0.7 | 0.1 |
| Chl $a$ in sediment | 26.7 | 6.7 | 24.0 | 5.7 | 34.8 | 7.1 | 35.6 | 8.2 | 30.3 | 4.8 |
| ∫Chl $a$ in water column | 107.9 | 34.9 | 35.5 | 10.4 | 30.3 | 11.2 | 27.1 | 10.6 | 50.2 | 17.5 |
| Salinity | 12.0 | 0.6 | 12.8 | 0.9 | 12.5 | 0.1 | 12.8 | 0.7 | 12.5 | 0.4 |
| Temperature | 30.1 | 0.2 | 30.0 | 0.2 | 30.2 | 0.1 | 30.3 | 0.2 | 30.1 | 0.1 |
| PPFD | 150,132 | | | | |

| Trial 3 | Open sediment habitat | Seagrass habitat | All samples |
|---------|-----------------------|------------------|-------------|
| 31 July 2017 | Control | Ge | Control | Ge | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| TDN | 77.4 | 14.6 | 108.8 | 18.9 | 59.2 | 5.3 | 72.5 | 8.1 | 79.5 | 10.5 |
| NO$_3^-$ + NO$_2^-$ | 1.7 | 0.7 | 2.9 | 0.9 | 0.5 | 0.1 | 0.8 | 0.1 | 1.5 | 0.5 |
| Ge:Si | — | — | 0.14 | 0.13 | — | — | 0.27 | 0.21 | — | — |
| Seagrass above-ground biomass | — | — | — | — | 1.5 | 0.3 | 0.4 | 0.1 | 0.9 | 0.3 |
| Seagrass below-ground biomass | — | — | — | — | 0.9 | 0.2 | 0.4 | 0.1 | 0.7 | 0.1 |
| Chl $a$ in sediment | 65.2 | 16.3 | 58.7 | 13.9 | 85.1 | 17.4 | 87.1 | 20.1 | 74.0 | 11.7 |
| ∫Chl $a$ in water column | 16.1 | 6.5 | 3.6 | 1.0 | 3.0 | 1.1 | 2.7 | 1.1 | 6.4 | 3.0 |
| Salinity | 26.7 | 1.1 | 24.2 | 0.6 | 24.4 | 1.1 | 23.5 | 1.2 | 25.1 | 0.7 |
| Temperature | 33.1 | 0.4 | 33.8 | 0.3 | 33.3 | 0.2 | 33.4 | 0.8 | 33.4 | 0.3 |
| PPFD | 278,250 | | | | |
active radiation (PAR) (from environmental station 30°15.075’ N, −88°04.670’ E Dauphin Island, Alabama; http://arcos.disl.org) was averaged over incubation duration and integrated over a 48 h-period prior to incubations (photosynthetic photon flux density, PPFD). 48 h reflects a short-term measure of light history.

**Seagrass biomass and Chl a concentration**

At end of incubation, seagrass above- and below-ground biomass were separated, dried, and weighed. To measure chlorophyll a (Chl a) concentration in water-column, 100 mL of water from each clear chamber was filtered through 47 mm Whatman glass fiber filter. Filtered water was analyzed for total dissolved nitrogen (TDN) and nitrate+nitrite (NO₃⁻ + NO₂⁻) colorimetrically using Skalar autoanalyzer (Dzwonkowski et al. 2017), and for dissolved silicic acid (Si[OH]₄) using a manual colorimetric method (Krause et al. 2009). A 3-cm diameter core was used to collect sediment from each chamber and Chl a concentration was quantified from top centimeter. For WC and sediments, Chl a was extracted using 90%

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**Fig. 2.** Benthic community gross primary productivity (GPP), respiration, and net community productivity (NCP) (mean ± SE, n = 4) with (control = C) and without (+Ge) diatom metabolic activity within the seagrass (left) and the open sediment (right) habitats on three trial dates (July 3, 17, and 31). In the seagrass habitat, NCP and GPP were significantly (p < 0.05) lower without diatom metabolic activity. The text in the upper corner of panels and above bars shows the results of pairwise comparisons within and between treatments, respectively, when two-way ANOVA results (see Table 2) indicated significance. No other statistical differences were found.
acetone and concentration determined by fluorometry following non-acidiﬁcation method (Welschmeyer 1994).

**Statistical analyses**

Data are expressed as mean ± standard error (SE) and were tested for normality and homogeneity of variance using Shapiro–Wilk’s and Levene’s test, respectively. Data that did not meet parametric requirements were transformed. When data could not be transformed to meet requirements, a two-way ANOVA was applied, and statistical alpha adjusted to <0.01 to avoid false discovery. A series of two-way ANOVAs with trial and treatment as ﬁxed factors were used to test for differences in environment and producer biomass in both habitats and were used to test for differences in rates with and without diatom metabolism. Tukey’s test identiﬁed pairwise differences when a main effect was found. Differences in rates were attributed to diatom metabolism and percent contribution to GPP was calculated based off mean GPP for each trial (n = 4) with Ge rate as a proportion of control rate, expressed as a change from 100%.

### Results

#### Environmental measurements

Overall salinity was 8.3 ± 0.4, 12.5 ± 0.4, 25.1 ± 0.7 psu for trials 1 through 3 (Table 1). Indeed, salinity signiﬁcantly increased from trial 1 to 3 in seagrass cores. For OS, within treatments, salinity signiﬁcantly increased from trial 1 to 3 (Supplementary Table 1). PPFD (not tested) was similar prior to trial 1 and 3, but lower for trial 2 (Table 1). PAR (mean ± SD) was 1345.0 ± 234.7, 855.7 ± 212.1, and 1610.4 ± 127.6 μmol m−2 s−1 for trials 1 through 3. Temperature reﬂected PAR and differed between trials. TDN and NO3− + NO2− differed between trials in OS cores. Within seagrass cores, TDN was greater in control than Ge treatment (68.5 ± 7.1 vs 59.7 ± 2.5 μM). Ge:Si ratio (mol:mol) reﬂected variation in Si(OH)4 concentration (Table 1).

#### Seagrass biomass and Chl a concentration

Above-ground biomass reﬂected patchy nature in the bed and varied as a function of treatment and trial (Table 1, Supplementary Table 1). At trial 3, controls contained greater biomass than Ge treatment (1.5 ± 0.3 vs. 0.4 ± 0.1 dry weight [dw] g m−2) and within controls, biomass was greater at trial 3 than trial 1 (0.4 ± 0.2 dw g m−2). Below-ground biomass was not found to differ. Chl a concentration within seagrass sediments was highest in trial 3. In OS, it was greater in trial 3 than trial 2. In seagrass habitat, integrated (∫)Chl a concentration in 1 m water was greatest at trial 1 and it decreased for each trial. Yet, within OS it varied as a function of treatment and trial.

#### Metabolism measurements

**GPP from different community-habitats**

Mean (± SE) system-GPP (GPP in mg O2 m−2 h−1) within seagrass habitat was 446.6 ± 130.8, 306.5 ± 105.7, and
Comparison of Ge and control treatments

Benthic community—seagrass habitat

In all three trials, there was significantly reduced GPP and NCP (both in mg O₂ m⁻² h⁻¹), when diatoms were inhibited compared to controls (Fig. 2, Table 2). Mean GPP ranged from 184.5 to 232.0 in control and 33.2 to 57.2 in Ge treatment. Mean NCP was −44.3 to −38.6 when diatoms were inhibited as opposed 9.2 to 122.0 observed in controls. There was no
difference in benthic community respiration with or without diatoms inhibited.

**Benthic community—OS Habitat**

Ge addition did little to alter GPP, NCP, and respiration in trial 1 and 2 (Fig. 2 and Table 2). On trial 3: (1) GPP was higher than controls of previous trials (GPP controls = 24.3 ± 17.4, 0 ± 0, 137.1 ± 21.4 mg O₂ m⁻² h⁻¹ for trials 1 through 3) (2) NCP was positive as opposed to earlier trials, and (3) there was higher GPP and NCP in control than in Ge treatment. There was no statistical difference in benthic respiration with or without diatoms inhibited.

**WC community—seagrass habitat**

In trial 1 and 2, rates in Ge and control treatment did not differ from one another (Fig. 3 and Table 2). On trial 3, GPP and NCP (in mg O₂ L⁻¹ h⁻¹) were more than x3 greater in control cores (GPP = 1.37 ± 0.3, NCP = 1.16 ± 0.4) than from previous trials (trials 1 and 2: GPP = 0.44 ± 0.16, 0.20 ± 0.08; NCP = 0.32 ± 0.18, 0.13 ± 0.14) and from rates in Ge treatment (3rd trial GPP = 0.28 ± 0.05, NCP = 0.01 ± 0.02). GPP and NCP in Ge treatment of trial 3 remained within range of previous trials. Respiration did not statistically differ between control and Ge treatment.

**WC community—OS habitat**

There were no differences in rates between control and Ge treatments (Fig. 3, Table 2). Respiration was not detected in timeframe of incubation for trial 2, control treatment.

**Percent contribution of diatom metabolism to GPP**

In seagrass habitat, diatom metabolism contributed 75.4, 70.9, and 83.3% to benthic-GPP and 0, 0, and 79.9% to WC-GPP for trials 1 through 3. In OS habitat, diatoms contributed 0, 0, and 85.7% to benthic-GPP for trials 1 through 3 and there was no detected (p > 0.05) contribution to WC-GPP.

**Discussion**

Results emphasize the ecological and biogeochemical importance of diatoms to a seagrass bed ecosystem and utility of this approach in benthic studies to quantify taxon-specific contribution to production. Diatoms contributed up to 85.7% to benthic production, and 80% to WC production. The magnitude of diatom benthic production pushed seagrass habitat into net autotrophy, as without diatoms this habitat during study conditions was net heterotrophic (Fig. 2). This result is due to: (1) elevated community respiration in seagrass habitat, (2) large contribution of diatoms to GPP, and (3) lack of significant diatom contribution to community respiration. This finding underscores the role of epiphytes and microphytobenthos in supporting secondary production in a seagrass bed (Mateo et al. 2006).

Our findings are congruent to production reported for regional *H. wrightii* beds. Moncreiff et al. (1992) found within a *H. wrightii* bed epiphytic algae were dominant primary producers, accounting for 60% of total benthic primary production. Given reported abundance of diatoms on seagrass leaves, our result that epiphytic and sediment diatom contribution was dominant (71–83% of GPP in seagrass habitat) is consistent with previous findings (Moncreiff et al. 1992). However, in our study system (at time of sampling) the WC was most productive, followed by benthos with seagrass and in OS.

If quantitative contribution of epiphytic and sediment diatoms is similar among systems, this may represent a significant term in marine productivity budgets (Nelson et al. 1995) that is underestimated. In global review, Cahoon (2002) estimated that global benthic microalgal production represented ~1% of marine primary production, but this did not specifically include epiphytes. Microphytobenthos production can be significant regionally (Guarini et al. 2000; Ní Longphuirt et al. 2007). Epiphytic and sediment microalgae may play a similar role, considering diatoms colonize substrate in variety of habitats in many regions (temperate, Ní Longphuirt et al. 2007; subtropical, this study; polar, Amsler et al. 2019).

Seagrass and other macrophytes have biogenic structures that can decrease stress (e.g., reduce inhibitory irradiance) and provide matrices where organisms find refuge (Heck and Orth 1980). Studies have tied foundational species to increased biodiversity and subsequent maintenance of ecosystem services, such as production (e.g., Boyer et al. 2009). Our results concur with these cited roles. High diatom productivity has been related to one or several productive species or ideal environmental conditions with few limitations (MacIntyre et al. 1996; Virta et al. 2019). Despite variation in producer biomass and in bed environment, diatoms had consistent and high contributions to benthic production. Diatom contribution to WC productivity was also more substantial surrounding seagrasses (80%) than above OS (0%).

Environmental drivers could affect assemblages differently. Influxes of seawater could bring new assemblages and/or alter production. The increase in productivity within OS benthic and WC at trial 3 coincided with elevated salinity and changes in Chl a concentration. These changes are difficult to interpret given the lack of context (e.g., plankton composition, nutrients) for elevated salinity water in preceding days. Future studies should explore the relationship between diatom contribution and environmental variability and the role of biodiversity (e.g., species densities of seagrasses and microalgae).

The inhibitor Ge can disentangle contributions of diatoms from other producers to system production. To better understand coastal benthic ecosystems, future investigations should apply this technique. Open-ocean studies have used Ge concentrations up to 86 µM (Scarratt et al. 2006). Our quantitative estimates could be conservative, given lower Ge concentration used and significantly higher Si(OH)₄ concentrations (~60 µM) quantified in this region may have not completely arrested diatom production. Additionally, diatom contribution could have...
been underestimated in this study because of removal by herbivores. Future studies could disentangle contributions of epiphytic diatoms from those in sediment by isolating leaves and using Ge additions. Beyond these manipulations, inter- and intra-seasonal variation data are needed to estimate diatom contribution to annual production and to better constrain fate of carbon.

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Acknowledgments

We would like to thank two anonymous reviewers who provided comments and edits to improve the quality of this manuscript. We also thank Sarah Schmid, Josh Goff, Emory Wellman, William Dobbins, Aaron Macy, Alex Marquez, Jeremey Marquez for assisting with field and laboratory work. We thank Hunter King, Laura Linn, and Sydney Acton for technical and analytical support, and Ruth Carmichael for organization of the Research Experience for Undergraduate program (OCE 1358873) at the Dauphin Island Sea Lab. This research was supported by the National Science Foundation (OCE 1558957, JWK). Authors declare no conflicts of interest.

Submitted 05 July 2019
Revised 15 August 2020
Accepted 17 August 2020