



Patterns in phytoplankton and benthic production on the shallow continental shelf in the northeastern Gulf of Mexico

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ARTICLE INFO

Keywords:

Dissolved oxygen

Benthic microalgae

Phytoplankton

Respiration

Northeastern Gulf of Mexico

ABSTRACT

Shallow continental shelves support productive pelagic and benthic communities. This study examined primary productivity at a shallow shelf region in the northeastern Gulf of Mexico focusing on the effect of light on water column and benthic productivity at water depths between 12 and 17 m. Measurements were made between November 2015 and September 2016. Dissolved oxygen fluxes were measured using benthic chambers with four different light levels and used to calculate gross primary production and respiration. Phytoplankton productivity was measured using ¹⁴C-uptake incubations in a laboratory photosynthetron. Organic matter production by benthic microalgae is substantial in this region of northeastern Gulf of Mexico with daily production rates ranging from 0.1 to 0.8 g C m⁻² d⁻¹ in this study. Maximum rates of phytoplankton production up to 2.7 g C m⁻² d⁻¹ occurred in spring. This peak productivity followed wind conditions favorable to upwelling and occurred when bottom water NO₃⁻ concentrations were 11 times greater than on any other sample date during the study. At these shallow depths, benthic microalgae made a significant contribution to total shelf production, averaging about 14% of total production. These results helped characterize benthic and water column production rates prior to planned habitat alterations caused by placement of numerous artificial reef structures in the region.

1. Introduction

Benthic microalgae make an important contribution to total primary production in estuarine, intertidal and shallow-water littoral environments when sufficient light reaches the sediment-water interface (Colijn and De Jonge, 1984; Cahoon and Cooke, 1992; MacIntyre et al., 1996; Grippo et al., 2009; Jahnke et al., 2000; Baustian et al., 2011; Baustian et al., 2013; Lehrter et al., 2014). Benthic microalgae support benthic as well as pelagic food webs. During summer months, benthic primary production on shallow continental shelves can contribute between 20 and 60% of total system primary production (Marinelli et al., 1998; Nelson et al., 1999; Jahnke et al., 2000; Allison et al., 2013; Lehrter et al., 2014). Benthic microalgae thus affect solute fluxes across the sediment-water interface (Sundbäck et al., 1991; Marinelli, 1992). Benthic regeneration of nutrients plays a key role in maintaining microphytobenthos and can support water column phytoplankton productivity (Hopkinson and Wetzel, 1982; Nelson et al., 1999; Lehrter et al., 2012). Major nutrient inputs to the shelf environments include

export from estuaries as surface water, via submarine groundwater discharge, sediment regeneration, and upwelling of nutrient rich water from the deeper oceanic waters. What little is known of nutrient cycling in the Gulf of Mexico sediments suggests that sandy, permeable sediments typical of the Florida shelf tend to have high rates of nutrient regeneration (Huettel et al., 2014).

Anthropogenic factors range from global pressure from climate change such as ocean acidification and rising temperatures to local activities such as placement of artificial reef structures throughout the area. Artificial reefs have become a popular means to enhance recreational fishing yet have the potential to fundamentally alter the benthic and pelagic ecosystems. As a means of remediating the effects of the Deepwater Horizon oil spill in 2010, funds from the National Resource Damage Assessment have been allocated for the deployment of thousands of artificial reefs on the Florida Shelf (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016), although the consequences of these deployments on water column and benthic processes are largely unknown. Thus, this study seeks to improve our

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<https://doi.org/10.1016/j.csr.2019.04.003>

Received 29 October 2018; Received in revised form 31 March 2019; Accepted 9 April 2019

Available online 18 April 2019

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understanding of the relative importance of phytoplankton and benthic microalgal production in an understudied region of the Florida Shelf prior to placement of numerous artificial reefs in the region. Such information is critical to understanding the antecedent conditions, which will be helpful in appropriately managing the region. Thus, this study provides crucial baseline information upon which future measurements may be compared.

2. Materials and methods

2.1. Study area

The study was conducted located in a shallow shelf region the northeastern Gulf of Mexico, near Pensacola Bay Estuary (FL, USA), thus is influenced by freshwater, turbidity, fluorescent dissolved organic matter, and nutrients from the estuary. In addition, deep waters upwelling from the DeSoto Canyon periodically intrude onto the shelf (Weisberg et al., 2005), resulting in characteristically higher nutrient and lower oxygen concentrations (Collard et al., 2000; Nowlin et al., 2000). Sediments in this region are dominated by quartz sands with relatively small contributions of fine-grained (silts, clays) sediment from local rivers (Schroeder and Wood, 2000). Nine sites located within a 6 km² area were examined between November 2015 to September 2016 (Fig. 1). Water depths ranged from 12 to 17 m. Water column phytoplankton photosynthesis and irradiance parameters were measured at all 9 sites on three dates: December 15, 2015, March 22, 2016, and July 20, 2016. Benthic flux measurements were made at 1 site per date on 13 dates between April and September 2016 (Supplemental Information Table 1). In addition, sediment samples were collected on 5 dates between November 11, 2015 and March 29, 2016. Benthic oxygen flux measurements and sediment characteristics could only be conducted when seas were less than 2 m for diver safety, thus they did not coincide with water column sampling.

2.2. Hydrographic data

A Sea-Bird 19 plus V2 CTD recorded profiles of water temperature, conductivity, pressure, fluorescent DOM, chlorophyll *a* fluorescence, and dissolved oxygen (DO) at each site. Irradiance measures ($\mu\text{E m}^{-2} \text{s}^{-1}$) were taken with a Li-Cor[®] Li 193 radiation sensor at the sea surface and at 0.5 m intervals to 3 m. Light profiles were measured in triplicate and used to calculate water column light attenuation coefficients (K_d) as:

$$K_d = \frac{\partial \ln(\text{Irradiance})}{\partial \text{depth}}$$

This assumes that light attenuation is constant throughout the water column. Light level at the sediment-water interface was calculated using the above formula based on K_d and water depth.

2.3. Water column parameters

Surface and bottom water samples were collected at each site. All samples were kept on ice ($\sim 4^\circ\text{C}$) in the field and stored frozen (-20°C) in the laboratory until analysis. For chlorophyll *a*, water (100–500 ml) was filtered onto GF/F filters; the filtrate was retained and stored at -20°C for nutrient analyses, including ammonium (NH_4^+), nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$), and inorganic phosphate (DIP) as described below. During the cruises on December 15, 2015, March 22, 2016 and July 20, 2016, additional samples were collected for dissolved silica (DSi) analysis, and unfiltered samples were collected and preserved with sulfuric acid for Total Kjeldahl nitrogen (TKN) and Total Phosphorus (TP) analysis. On these dates, particulate carbon (PC) samples were also collected onto combusted (450°C 1 h) GF/F filters.

2.4. Phytoplankton productivity

Phytoplankton productivity experiments were conducted in the laboratory within 6 h of collection on December 15, 2015, March 22, 2016 and July 20, 2016. Samples were spiked with ^{14}C -bicarbonate ($59.2 \text{ mCi mmol}^{-1}$, $2 \mu\text{Ci ml}^{-1}$ final concentration), distributed into a series of vials (4 mL), and placed in a temperature-controlled photosynthetron, which exposed samples to varying light intensities (range: $0\text{--}240 \mu\text{mole quanta m}^{-2} \text{s}^{-1}$). After a 2 h incubation, samples were acidified with $100 \mu\text{l}$ of 20% HCl, shaken uncovered overnight at 150 rpm to remove excess ^{14}C -bicarbonate, and counted on a liquid scintillation counter (Neale et al., 1994). Light intensity at each vial position in the photosynthetron was measured with an irradiance sensor (QSL2101 Biospherical Instruments, San Diego, CA, USA).

The light-dependent carbon fixation measurements were used to estimate the experiment-wise photosynthetic parameters, and subsequently used to calculate integrated phytoplankton productivity at each study site with the formulation in Platt et al. (1990):

$$P = \int_{z=0}^H B_z * P_m^B \left(1 - e^{-\frac{\alpha^B I_z}{P_m^B}} \right) dz$$

where H is the depth of the water column, B_z is the chlorophyll *a* concentration at depth z based on chlorophyll *a* fluorescence profiles, α^B and P_m^B are the biomass-normalized photosynthetic parameters derived from the ^{14}C experiments, and I_z is irradiance at depth z . I_z was modeled based on measured K_d values and assumed light attenuation was constant throughout the water column. For the photosynthetic parameters, surface and bottom α^B and P_m^B parameters were averaged across the 9 sites and 3 sampling dates ($n = 27$) and applied to estimate phytoplankton productivity on all dates in which water column chlorophyll and light attenuation were measured.

2.5. Benthic productivity and respiration

Acrylic dome-shaped chambers were used for benthic incubation experiments (area = 0.212 m^2 , volume = 0.027 m^3 or 27 L). Light levels in individual domes were varied by adding layers of ordinary fiberglass window screen or opaque black polyethylene sheeting (dark chamber) to achieve 100% (light chamber), 50%, 25% and 0% (i.e. dark) of ambient light. Stirring was achieved by stirring cup paddle assembly (*sensu* wind anemometer) situated both outside and inside of the dome, connected by a spindle that transferred ambient external currents to the inside of the chamber. Chambers were fitted with sampling ports to allow sample water removal and replacement. During sampling, a total of only $\sim 120 \text{ ml}$ of water was removed from the chambers, thus dilution of chamber water was assumed negligible.

In the morning between 9 and 10 a.m., divers gently positioned benthic chambers on the bottom to minimize sediment resuspension and secured them to the bottom by covering the dome's external flange with sand. Chamber placement avoided visible polychaete burrows, tunicates, sand dollars or hard substrates. Chambers were allowed to stabilize for 10 min before initial (T_0) samples were taken. After $\sim 4 \text{ h}$, final time point samples (T_f) were taken. Water samples were collected into syringes and transported to the surface for processing on deck. For dissolved nutrients (NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, DIP) water was filtered through a 25-mm diameter Whatman[®] GF/F filter. For DO, samples were fixed with Winkler reagents (Strickland and Parsons, 1968) by injecting the reagents into the opening of the syringes used to collect the water samples. All oxygen and nutrient samples were processed shipboard within 15 min of collection.

Benthic primary productivity and respiration rates were determined as changes in DO concentration by Winkler titration (Carpenter, 1965). Titrations were performed at the laboratory within $\sim 6 \text{ h}$ of sample collection. Oxygen fluxes (FO_2 , $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$) were calculated as

taken within 2 m of the benthic chambers and the top 2 cm of sediment was processed for chlorophyll *a* analysis, water content, and C content. Chlorophyll *a* analyses (0.5 g sub-sample from sediment surface) were used to estimate microphytobenthic biomass. For C analysis, 10–15 g samples were processed by placing wet sediment in tared aluminum pans, then dried and ground. C content was measured on a Flash EA1112 elemental analyzer.

2.7. Analytical methods

NH_4^+ concentration was measured fluorometrically using an *o*-phthalaldehyde and borate buffer reagent (Holmes et al., 1999). DIP was analyzed using the ascorbic acid molybdate spectrophotometric method as in Parsons et al. (1984) on a 5-cm cell. $\text{NO}_3^- + \text{NO}_2^-$ were analyzed using cadmium reduction on a flow injection analyzer (EPA method 353.2) for samples collected on December 15, 2015, March 22, 2016 and July 20, 2016. The remaining samples collected during benthic chamber experiments were analyzed manually with a spectrophotometer using VCl_3 reduction and addition of sulfanilamide and N-1 naphthylethylenediamine dihydrochloride as in Schnetger and Lehnert (2014). Chlorophyll samples were extracted in 6 ml of 90% acetone overnight in a freezer (-20°C) and extract fluorescence was measured as in Welschmeyer (1994). TKN and TP were analyzed using U.S. EPA Method 351.2 and 365.4, respectively. Dissolved silica was analyzed by U.S. EPA Method 370.1 and C content was analyzed by U.S. EPA Method 440.0. Sediments were fumed with HCl prior to C content analysis to remove carbonate.

2.8. Statistics

Two factor ANOVAs were conducted to test whether α^B and P_m^B parameters were significantly different based on sampling date (December 15, 2015, March 22, 2016 and July 20, 2016) or depth layer (surface vs bottom). Correlation analysis among variables was conducted using R (R core team, 2018) with the non-parametric Spearman option given that the variables were not normally distributed. Statistical significance was evaluated at an experiment-wise error rate of $\alpha = 0.05$.

2.9. Other data sources

Additional data were acquired from internet sources to provide regional context for this study. First, daily water temperature data were acquired from NOAA's National Data Buoy Center (<http://www.ndbc.noaa.gov>) weather buoy (# 42012, Orange Beach Buoy) located approximately 28 km SW of our study area. Second, the USF Optical Oceanography Laboratory (<http://optics.marine.usf.edu>) provided weekly remote sensing estimates of temperature, chlorophyll *a* and K_d centered at a site located just outside of Pensacola Bay (OPC 01). In addition to the data coincident with our study, we compiled the fourteen-year record of the surface temperature data to create a weekly climatology. Third, data were included from station P1 (see Fig. 1), a site that was occupied repeatedly between January 2011 and June 2014 as part of a previous study, including water column chlorophyll *a*, dissolved nutrients, sediment chlorophyll *a*, and K_d (RA Snyder, https://data.gulfresearchinitiative.org/data-discovery;WHJeffrey_unpublished).

3. Results

3.1. Hydrographic conditions

Over the study, surface water temperature ranged from 14.7°C in January to 31.8°C in August (Fig. 2), while bottom water temperature had a narrower range from 17.7°C to 29.2°C , (SI Fig. 1). Surface waters became warmer than bottom waters starting in April 2016; temperature

trends were also consistent with nearby buoy and remote sensing data sources (Fig. 2).

Seasonal salinity variation was generally small, from 32 to 36 in bottom waters, but larger, from 17 to 35, in surface waters (SI Fig. 2). Periodic stratification occurred throughout the year at all sampling locations (Fig. 3). Higher chlorophyll fluorescence in bottom waters was regularly observed (Fig. 3), peaking at 8.1 mg m^{-3} in April 2016 at site AR5 (SI Fig. 3). Surface dissolved oxygen concentrations varied seasonally, with higher concentrations during winter, lower concentrations during spring and summer, and higher concentrations at the end of summer (Fig. 3). Dissolved oxygen in bottom waters was often undersaturated (SI Fig. 4) with the lowest value of 3.1 mg L^{-1} or 46% of saturation in July 2016 at AR3 (Fig. 3).

Nutrient concentrations were generally low, particularly in surface waters (Fig. 4). DIP was often at or below $0.20\text{ }\mu\text{mol L}^{-1}$. NH_4^+ concentrations were typically $< 3\text{ }\mu\text{mol L}^{-1}$ for both surface and bottom water except in February 2016 when concentrations peaked at $5.54\text{ }\mu\text{mol L}^{-1}$ in surface waters. Similarly, $\text{NO}_3^- + \text{NO}_2^-$ concentrations were usually below $2\text{ }\mu\text{mol L}^{-1}$. However, in March 2016, nutrient concentrations ($\text{NO}_3^- + \text{NO}_2^-$, NH_4^+ and DSi) were elevated in bottom water with nitrate concentrations above $6\text{ }\mu\text{mol L}^{-1}$ and DSi concentrations above $25\text{ }\mu\text{mol L}^{-1}$ (Fig. 4, DSi data not shown). TKN concentrations ranged between 7.1 and $40.1\text{ }\mu\text{mol L}^{-1}$, while TP was almost always below the detection limit of $3.2\text{ }\mu\text{mol L}^{-1}$ (data not shown). Dissolved nutrient concentrations were significantly correlated with each other ($p < 0.001$), with the strongest correlation between $\text{NO}_3^- + \text{NO}_2^-$ and DSi ($r = 0.81$, $p < 0.001$). DSi was also significantly negatively correlated with dissolved oxygen concentrations ($r = -0.63$, $p < 0.001$) (SI Table 2).

3.2. Phytoplankton biomass and productivity

Phytoplankton biomass as measured by chlorophyll *a* ranged from 0.1 to $12\text{ }\mu\text{g L}^{-1}$ (Fig. 4, Table 1). As with chlorophyll fluorescence (Fig. 3), extracted chlorophyll *a* concentrations were often higher in bottom waters than in surface waters. Light attenuation was generally low, averaging 0.38 m^{-1} (Table 1), but ranged between 0.12 and 0.95 m^{-1} . The range in α^B was from 0.026 to $0.130\text{ mg C (mg chl a)}^{-1} (\mu\text{mole quanta m}^{-2}\text{ s}^{-1})^{-1} (\text{h}^{-1})$ while P_m^B values ranged from 3.0 to $15.6\text{ mg C (mg chl a)}^{-1} \text{ h}^{-1}$ (Table 1). Both α^B and P_m^B were significantly higher in surface waters than bottom waters ($p = 0.05$). Neither parameter was significantly different by date ($p > 0.25$) nor was there a significant interaction between layer and date for either parameter ($p > 0.25$). We therefore used average surface and bottom α^B and P_m^B values for estimating primary productivity on all sampling dates (e.g. dates when benthic chamber incubations were conducted). Phytoplankton productivity was highest in the spring at $2.7\text{ g C m}^{-2} \text{ d}^{-1}$ and lowest in winter at $0.6\text{ g C m}^{-2} \text{ d}^{-1}$ (Fig. 5). Phytoplankton productivity was positively correlated with nitrate ($r = 0.30$, $p = 0.04$), ammonium ($r = 0.47$, $p = 0.001$) and silica concentration ($r = 0.37$, $p = 0.05$).

3.3. Sediment characteristics

The percentage of surface irradiance reaching the bottom was low in the winter of 2015 increasing in summer 2016 (Table 2). Sediment carbon content declined from winter to spring then increased in summer (Table 2). Water content was lowest in spring as was benthic chlorophyll *a* (Table 2). Benthic chlorophyll *a* was highest in summer, averaging $5.90 \pm 0.63\text{ }\mu\text{g chl a g}^{-1}$ (Table 2). Benthic chlorophyll *a* was negatively correlated with K_d ($r = -0.65$, $p = 0.001$) but positively correlated with water content ($r = 0.64$, $p = 0.004$), carbon content ($r = 0.77$, $p = 0.002$), and temperature ($r = 0.58$, $p = 0.002$).

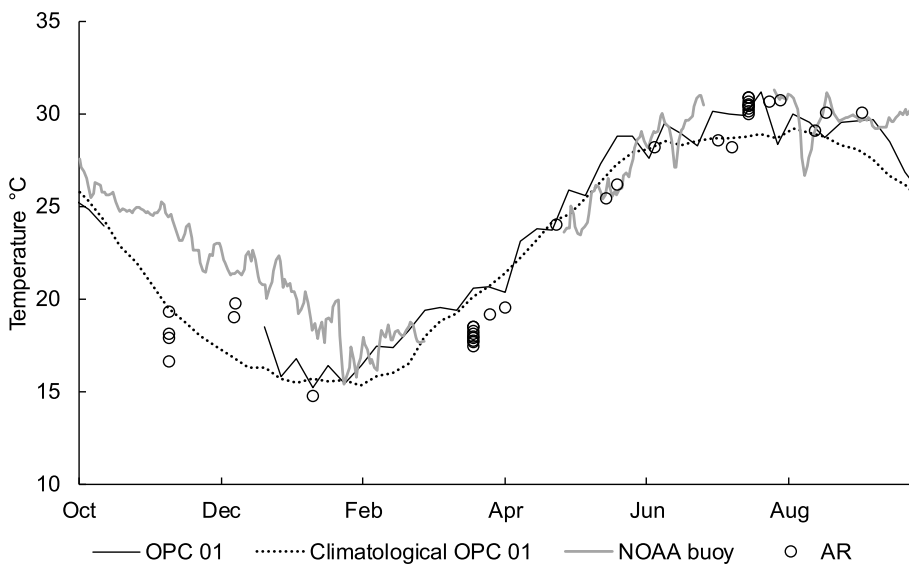


Fig. 2. Surface water temperature ($^{\circ}\text{C}$) at study sites (AR open symbols) compared to contemporaneous satellite (dark line) and buoy-based observations (grey line) and the long-term climatology from satellite observations (dotted line). Satellite data from University of South Florida's virtual buoy system (site OPC 01). Buoy observations from NOAA (site 42012 at Orange Beach, AL).

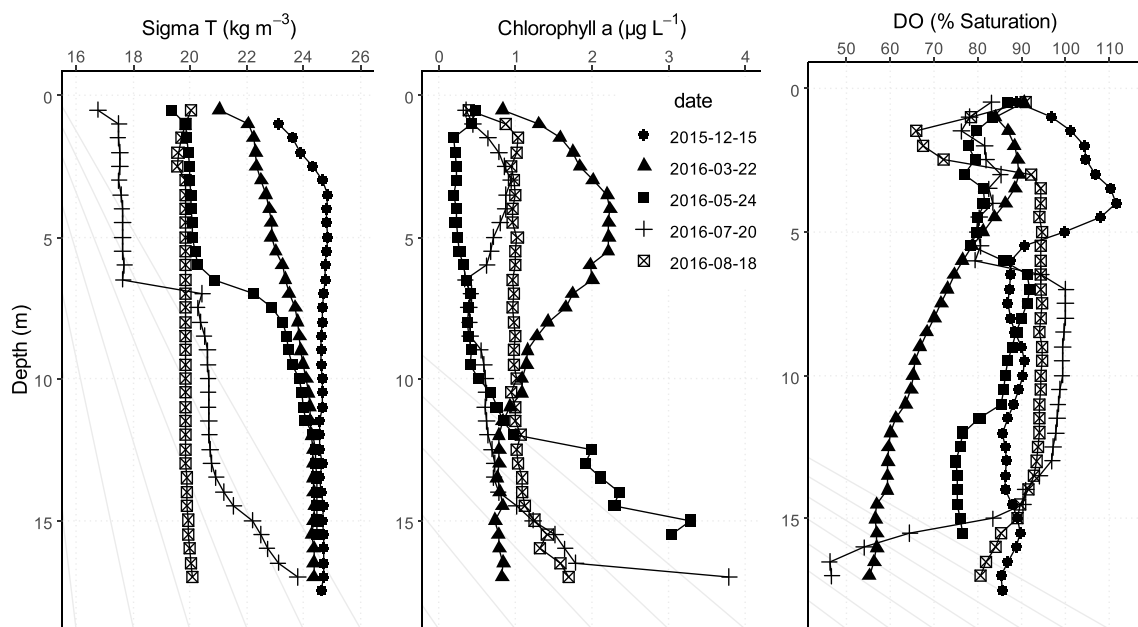


Fig. 3. Representative depth profiles of water column density, as sigma T (left panel), chlorophyll *a* (middle panel), and dissolved oxygen in percent saturation (right panel) at site AR3.

3.4. Benthic fluxes

Oxygen fluxes consistently increased with increasing light levels inside the chambers, ranging from -2053 to $+1692 \mu\text{mol m}^{-2} \text{h}^{-1}$ in spring and from -2664 to $+2199 \mu\text{mol m}^{-2} \text{h}^{-1}$ in summer (Fig. 6). Mean (\pm S.E.) net community productivity was $4466 \pm 4838 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $6641 \pm 2561 \mu\text{mol m}^{-2} \text{h}^{-1}$ in spring and summer, respectively. Respiration was also higher in summer ($-1533 \pm 281 \mu\text{mol m}^{-2} \text{h}^{-1}$) compared to the spring ($-1314 \pm 226 \mu\text{mol m}^{-2} \text{h}^{-1}$). Benthic gross primary productivity ranged from 47 to $355 \text{ mg C m}^{-2} \text{d}^{-1}$ (Fig. 5). Net community productivity was positively correlated with temperature ($r = 0.64$, $p = 0.02$). Respiration was negatively correlated with salinity ($r = -0.59$, $p = 0.035$). Gross benthic primary productivity was negatively correlated with phytoplankton primary productivity ($r = -0.79$, $p = 0.001$) and K_d ($r = -0.65$, $p = 0.02$).

4. Discussion

4.1. Factors influencing phytoplankton productivity

Environmental conditions observed during this study were similar to previous observations in the shallow northeastern Gulf of Mexico (Schroeder and Wood, 2000; Qian et al., 2003; Allison et al., 2013). The lower surface salinity coincided with freshwater inputs from nearby estuaries which promoted water column stratification and isolation of bottom water (Dzwonkowski et al. 2011, 2017). November and December 2015 were periods of significant freshwater input and more intense stratification was observed, with the difference between bottom and surface salinity exceeding 10 PSU at our study locations. These conditions were observed across the region along with higher phytoplankton biomass and primary production in nearshore waters compared to offshore (Dzwonkowski et al., 2017). This also coincided with a dinoflagellate bloom of *Karenia brevis*, which extended from the Florida panhandle to Mississippi coastal waters (Soto et al., 2018).

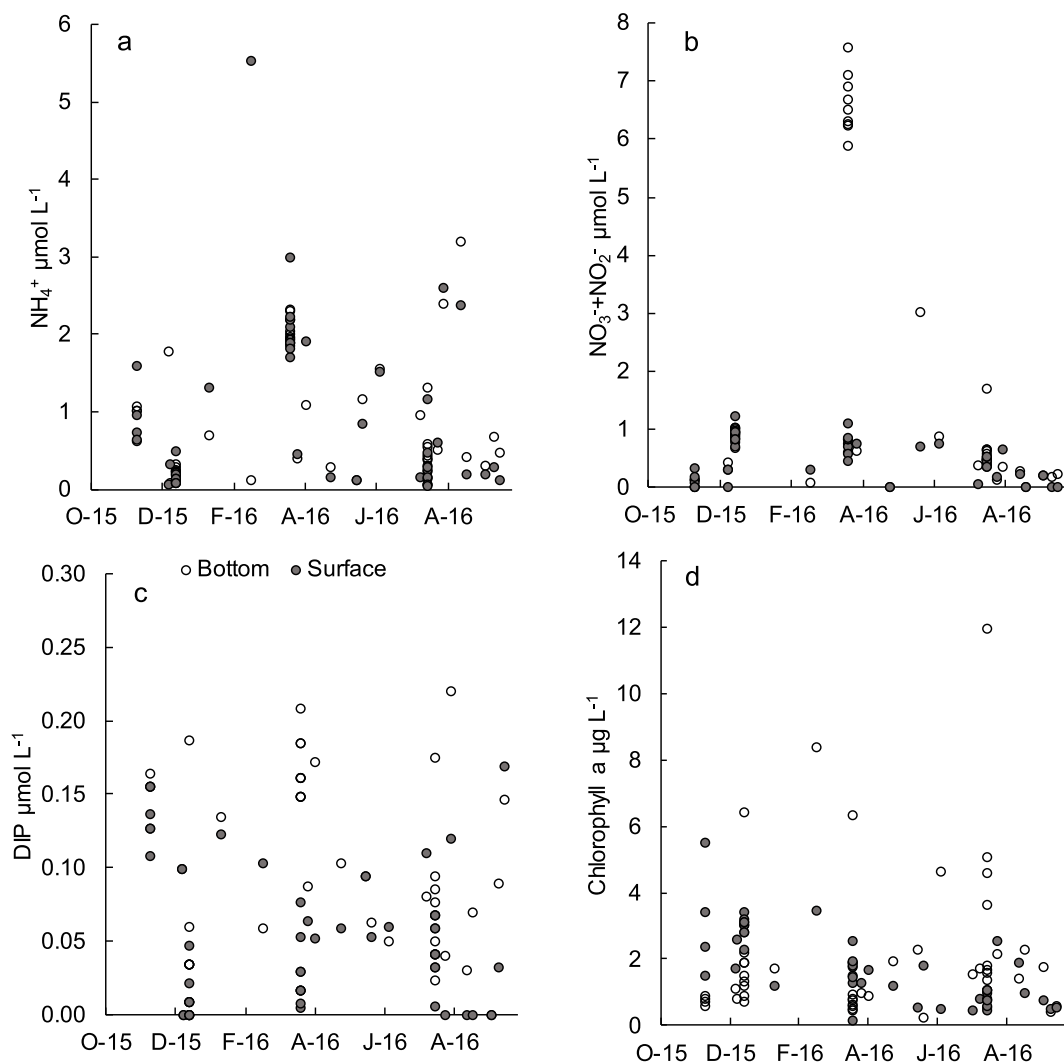


Fig. 4. Water column (a) NH_4^+ , (b) $\text{NO}_3^- + \text{NO}_2^-$, (c) DIP, and (d) chlorophyll *a* concentrations in surface (solid symbols) and bottom (open symbols) waters over study.

By spring, stratification was much less evident. During March 2016, high nutrient concentrations were observed in bottom waters, particularly $\text{NO}_3^- + \text{NO}_2^-$, NH_4^+ and DSI, which were between 2 and 11 times greater than bottom water concentrations in other months. The source of these elevated nutrients was likely due to upwelling of deep waters from the head of DeSoto canyon, which is located ~100 km southeast of our study location. Incidence of upwelling in the study region has been observed previously (Collard et al., 2000; Nowlin et al., 2000; Weisberg et al., 2005; Nguyen, 2014), as well as on the nearby Alabama-Mississippi shelf (Dzwonkowski and Park, 2012; Dzwonkowski et al., 2015). During the current study, the NOAA weather buoy recorded northwest winds for 2 days prior to sampling, presumably creating conditions favorable to upwelling, and water

levels at Pensacola station showed a drop in low frequency water level (<https://tidesandcurrents.noaa.gov/Pensacola>, FL - Station ID: 8729840), conditions consistent with strong offshore transport of surface waters promoting coastal upwelling in the region (Dzwonkowski and Park, 2012; Dzwonkowski et al., 2015). Current velocity and temperature data from the nearby FOCAL (Fisheries Oceanography of Coastal Alabama) site also were consistent with coastal upwelling during this same time period (B Dzwonkowski, pers.comm.). Phytoplankton primary productivity peaked during March 2016, perhaps in response to prior upwelling of nutrient-rich waters from DeSoto Canyon. While the significant correlation observed between phytoplankton primary productivity and nutrients is consistent with this hypothesis, further studies are needed to more directly establish this

Table 1

Water column parameters used for calculating phytoplankton primary productivity, including light attenuation coefficient (K_d), phytoplankton biomass (as chlorophyll *a*), physiological α^B and P_m^B in surface and bottom water column layers. Mean \pm S.E.

Date	Depth layer	$K_d \text{ m}^{-1}$	Chlorophyll <i>a</i> mg m^{-3}	$\alpha^B \text{ mg C (mg chl a)}^{-1} (\mu\text{mole quanta m}^{-2} \text{s}^{-1})^{-1} (\text{h}^{-1})$	$P_m^B \text{ mg C (mg chl a)}^{-1} (\text{h}^{-1})$
12/15/2015	Surface	0.35 ± 0.01	2.97 ± 0.10	0.026 ± 0.002	3.2 ± 0.3
	Bottom		2.00 ± 0.57	0.041 ± 0.009	3.9 ± 0.8
3/22/2016	Surface	0.39 ± 0.04	1.59 ± 0.25	0.072 ± 0.006	8.3 ± 0.8
	Bottom		1.43 ± 0.63	0.046 ± 0.012	5.3 ± 1.1
7/20/2016	Surface	0.40 ± 0.04	0.77 ± 0.07	0.115 ± 0.250	16.3 ± 3.8
	Bottom		3.64 ± 1.15	0.033 ± 0.007	5.0 ± 1.0

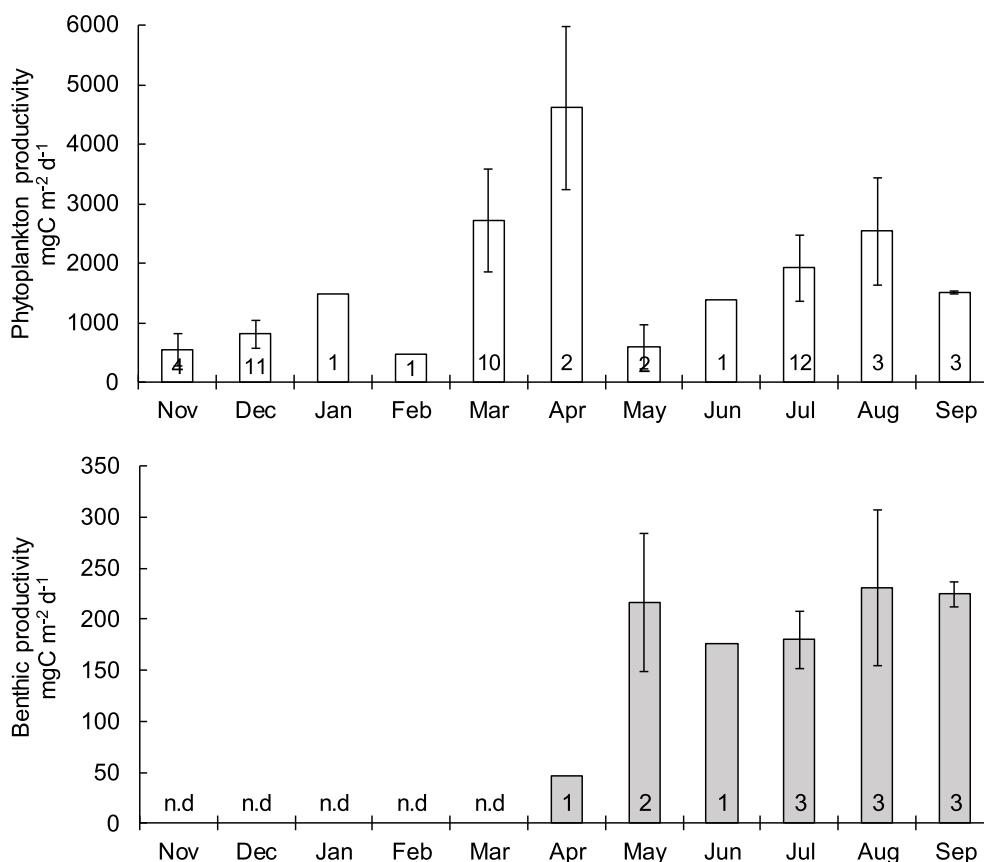


Fig. 5. Phytoplankton (top panel) and benthic (bottom panel) gross primary productivity over study. Mean ± S.E. with n.d. (no data). Number label is the number of stations used to estimate productivity per month. Note the change in scale between top and bottom panel.

connection.

Salinity stratification during summer was similar to that observed in spring, between 2 and 7 PSU. In contrast to spring, bottom water dissolved oxygen concentrations during summer were much lower, reaching a minimum of 3.1 mg L⁻¹ or 46% saturation. While hypoxia has been reported in this region (Collard et al., 2000; Dzwonkowski et al., 2017), it is uncommon compared to the Louisiana-Texas Shelf in the northwestern Gulf of Mexico (Schroeder and Wood, 2000; Rabalais et al., 2001; Murrell et al., 2013).

Our estimates of phytoplankton productivity ranged from 0.6 to 4.6 g C m⁻² d⁻¹ and were consistent with other studies performed in shallow coastal environments (Table 3). For example, phytoplankton productivity on the Louisiana shelf ranged from 0.23 to 3.8 g C m⁻² d⁻¹ (Lohrenz et al., 1994, 1997; Lehrter et al., 2009; Zhao and Quigg, 2015). The highest rates observed in this study were also similar to other nutrient rich environments such as the Amazon River Plume (Smith and Demaster, 1996) and Hong Kong waters during summer when nutrient inputs, chlorophyll *a* and temperature were high (Ho et al., 2010). Conversely, primary productivity in a temperate coastal embayment was lower based on a moderate nutrient loading and a high nutrient uptake (Glé et al., 2008).

4.2. Role of benthos in total system productivity

In the coastal zone, benthic microalgae are strongly dependent on ambient light available to support primary productivity (Colijn and De Jonge, 1984; Cahoon and Cooke, 1992; Grippo et al., 2009; Jahnke et al., 2000). This study area in shallow northeastern Gulf of Mexico is a relatively high light environment with the percent surface irradiance at the sediment-water interface ranging from 0.89 ± 0.24% to 4.70 ± 1.00% (Table 2). This is sufficient to support benthic microalgae and associated primary productivity on these sandy sediments. Biomass of benthic microalgae were similar to other studies (MacIntyre et al., 1996; Cahoon et al., 1999; Allison et al., 2013). The results from our benthic oxygen fluxes supported this expectation of significant productivity, demonstrating a consistent positive response to light (Fig. 6). Summer net community production and respiration rates from Allison et al. (2013) were comparable to our summer data. Ranges of benthic productivity, respiration and GPP in this study were also comparable to values in nearby Pensacola Bay (Murrell et al., 2009), and those from Onslow Bay, NC (Cahoon and Cooke, 1992). Benthic gross primary productivity which ranged from 0.05 to 0.35 g C m⁻² d⁻¹ was somewhat lower than Allison et al. (2013). In Onslow Bay on the sandy North Carolina continental shelf (water depths of 15–41 m),

Table 2

Seasonal averages of benthic characteristics including percent of surface irradiance reaching sediment-water interface, sediment water content, carbon content and chlorophyll *a* concentration. Mean + S.E.

Season	Surface irradiance (percent)	Water content (percent)	Carbon Content (percent)	Chlorophyll <i>a</i> (µg g ⁻¹)
Winter 2015	0.89 + 0.24	21.5 + 1.2	0.16 + 0.08	2.49 + 0.23
Spring 2016	1.14 + 0.36	14.2 + 1.1	0.09 + 0.01	1.92 + 0.22
Summer 2016	4.70 + 1.00	21.9 + 0.6	0.26 + 0.04	5.90 + 0.63

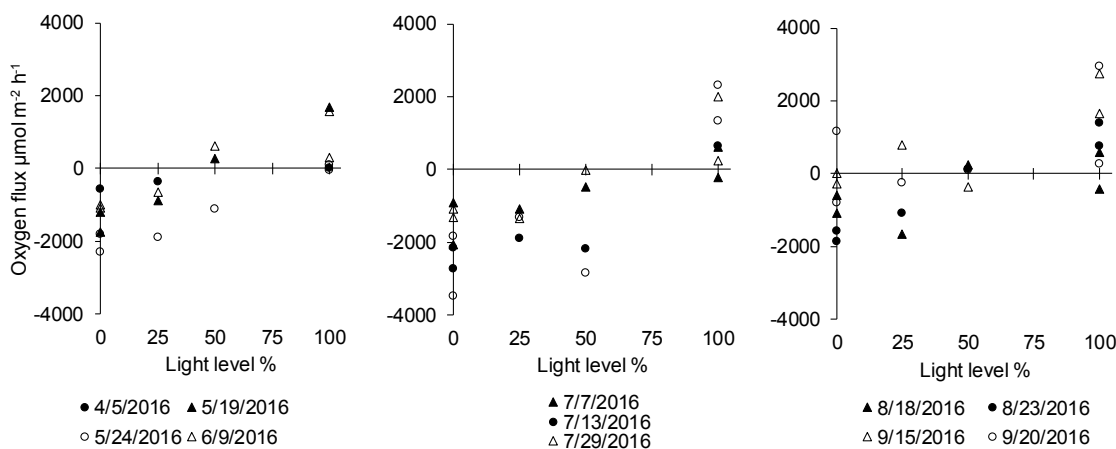


Fig. 6. Benthic oxygen flux as a function of percentage of full ambient irradiance.

gross benthic microalgal productivity averaged $0.3 \text{ g C m}^{-2} \text{ d}^{-1}$ (Cahoon and Cooke, 1992). On the South Atlantic Bight shelf, Jahnke et al. (2000) and Nelson et al. (1999) reported gross benthic primary productivity rates averaging $0.4 \pm 0.3 \text{ g C m}^{-2} \text{ d}^{-1}$.

Average daily gross production by benthic microalgae during spring and summer averaged $0.4 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$ compared to $2.3 \pm 0.8 \text{ g C m}^{-2} \text{ d}^{-1}$ by phytoplankton over the same period. Thus, the benthos represented about 14% of total system production. We used the Redfield ratio of C:O₂ of 106:138 for this conversion ($PQ = 1.3$). If we used a photosynthetic quotient of 1:1, as is commonly done, then the benthos would represent 17% of total system production. While two different techniques (O₂ and ¹⁴C) were used to estimate primary productivity, the results were consistent with other studies using both techniques. In nearby Pensacola Bay, benthic production represented 14% of the total (Murrell et al., 2009) and can reach up to 32% in other estuaries (Moncreiff et al., 1992; Schreiber and Pennock, 1995). Periodic high chlorophyll *a* concentrations near the bottom in euphotic environments may be from resuspension of benthic microalgae, settlement of surface phytoplankton or net growth of phytoplankton in the bottom layer stimulated by benthic nutrient regeneration. Both water depth and light attenuation exert an important control on the light available the microphytobenthos.

The observed negative correlations between benthic and phytoplankton gross primary production and between benthic chlorophyll *a* and *K_d* are consistent with a seasonal switch between high water column and low benthic productivity in the spring to lower water column and higher benthic productivity in the summer. Further research on benthic productivity would help establish whether this apparent seasonal pattern is consistent interannually and would further elucidate the factors controlling both water column and benthic processes. For example, nutrients supplied from the estuaries, submarine groundwater discharge, upwelling, and benthic regeneration may be important, although their contributions to benthic production in our

region are unknown.

4.3. Conclusions

Results presented herein represent important baseline information for a region that faces myriad anthropogenic stressors, such as hypoxia, oil spills, and habitat alteration. Regional habitat alteration can include habitat damage due to fishing activities or ocean acidification, as well as the creation of artificial reefs. Artificial reef deployment causes the conversion of sandy bottoms to hard bottom communities and is increasing in the northeastern Gulf of Mexico. The most recent increases are occurring as National Resource Damage Assessment money is being used to compensate for lost fishing activity following the Deepwater Horizon oil spill in 2010 (Deepwater Horizon Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). From a fisheries perspective, sandy bottoms are often perceived as barren environments, although more recent studies highlight their importance for fisheries (Kritzer et al., 2016; Cahoon, 2017). However, this study shows that they are a source of significant primary productivity in this region.

Author roles

JMC, WFP and WHJ designed the study. FC, JMC, and WHP conducted field work. WHJ, MEH, FC and JMC conducted and supervised laboratory analyses. FC, JMC, WHJ, and MCM analyzed data. FC and JMC wrote the paper with input from all co-authors.

Acknowledgements

This project was paid for [in part] with federal funding from the Department of the Treasury under the Resources and Ecosystems Sustainability, Tourist Opportunities, and Revived Economies of the

Table 3

Phytoplankton characteristics measured in this study and from various literature sources. Ranges are reported.

Site	Chlorophyll <i>a</i> mg m ⁻³	α^B	P_{max}^B	Phytoplankton productivity g C m ⁻² d ⁻¹	Reference
Northeastern Gulf of Mexico	0.77 to 3.64	0.025 to 0.125	3.0 to 15.6	0.6 to 4.6	This study
LA shelf (USA)	1.4 to 5.9 ^a	0.015 to 0.055	4.0 to 8.7	0.47 to 1.75	Lehrter et al. (2009)
LA shelf (USA)		0.018 to 0.055	5.4 to 23	0.28 to 3.8	Lohrenz et al., (1994), (1997)
LA shelf (USA)		0.009 to 0.033	1.8 to 13	0.23 to 2.28	Zhao and Quigg (2015)
Amazon River plume (Brasil)	0.12 to 11.3 ^a			0.2 to 8.16	Smith and Demaster (1996)
Hong Kong waters	< 1 to 34 ^a			0.2 to 25	Ho et al. (2010)
Blanes Bay (Spain)	0.02 to 3.4	0.001 to 0.045	0.49 to 14.81	3.12	Gasol et al. (2016)
Arcachon Bay (France)				0.28	Glé et al. (2008)

^a Surface water samples.

Gulf Coast States Act of 2012 (RESTORE 529 Act). Funding source had no involvement in study design, collection, analysis and interpretation of data or writing of the report. We thank Fritz Scharer, Joe Moss, Rachel Capps, Amy Brower, Gary Baine, Matt Davis, Stewart Hood, Ryan Lavoie, Christina Toms, Jeff Eble, Nine Henriksen, Kendra Brooks, Sarah Friedl, Miaya Glaback, Steve Garner, Joe Tarnecki, Sean Kelly and the crew of the Total Package, and Douglas Hammock and the crew of the H2O Below for their assistance in the field. Jeremy Bosso, Katherine Haynes, Chelsea Barfield, Whitney Brentana, and Porsha Hernandez assisted in the laboratory. The views expressed here are solely those of the authors, thus do not necessarily reflect the views or policies of the US EPA. Mention of trade names or commercial products does not constitute endorsement by the authors or the US EPA.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.csr.2019.04.003>.

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