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SAND BOTTOM MICROALGAL PRODUCTION AND BENTHIC NUTRIENT FLUXES ON THE NORTHEASTERN GULF OF MEXICO NEARSHORE SHELF

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ABSTRACT: Benthic microalgal production on the continental shelves may be an important contributor to the overall productivity of offshore ecosystems. We used light and dark benthic chambers to measure *in situ* production, respiration, and benthic nutrient flux on the nearshore quartzite sands of the northeast Gulf of Mexico shelf. Net exchange of O_2 , NH_4^+ , $NO_3^- + NO_2^-$, PO_4^{3-} , and SiO_2 was measured in samples taken from chambers at depths of 15 to 16 m offshore of Pensacola, FL. Phytoplankton production and respiration in near-bottom water was determined in paired light/dark BOD bottles to correct chamber measurements for water column processes. Sediment chlorophyll *a* (Chl *a*) averaged 4.8 μg Chl *a*/g. Phytoplankton averaged 5.5 μg Chl *a*/L. Pheophytin:chlorophyll ratios for the sediment were near 1 indicating an actively growing algal community. Phytoplankton net production ranged from 0.6 to 2.8 $mg\ C/m^3/hr$. Benthic net production in three separate determinations was 17.7 ± 6.1 , 9.5 ± 2.9 , and $8.8 \pm 1.6\ mg\ C/m^2/hr$. Benthic respiration was 24.8 ± 0.7 , 30.8 ± 1.4 , and $11.3 \pm 0.3\ mg\ C/m^2/hr$, respectively. Benthic gross production was thus 42.5 ± 5.2 , 40.3 ± 1.2 , and $20.3 \pm 1.7\ mg\ C/m^2/hr$, respectively. Benthic nutrient fluxes were highly variable and generally low. Sediment uptake was observed for NH_4^+ and PO_4^{3-} throughout the study. $NO_3^- + NO_2^-$ and SiO_2 uptake was observed in 2004 with sediment release seen in 2005.

KEY WORDS: NPP, GPP, benthic chambers

INTRODUCTION

Benthic microalgae or the microphytobenthos are important primary producers in a wide variety of aquatic habitats including the nearshore continental shelf (Colijn and de Jonge 1984, Cahoon and Cooke 1992, Grippo et al. 2009, Jahnke et al. 2000). Cahoon and Cooke (1992) suggested that light and nutrient availability was sufficient to support benthic primary production beyond the North Carolina shelf break at 55 m depth, and Gattuso et al. 2006 showed that light availability is abundant in the coastal zone. Dynamics of offshore benthic community and phytoplankton production, respiration, algal biomass, and benthic nutrient fluxes have been examined in the northwestern Gulf of Mexico (GOM) impacted by the Mississippi River plume (Grippo et al. 2009, Baustian et al. 2011, Murrell and Lehrter 2011, Lehrter et al. 2012) but no reports are available for the sand bottom shelf of the Florida Panhandle Bight in the northeast GOM, an area extending about 240 km from Cape San Blas to Perdido Key.

Microphytobenthic communities are typically dominated by Bacillariophyceae (diatoms) encompassing various temperature, light, and salinity regimes. The contribution of benthic and epiphytic microalgae to shallow water ecosystem productivity has been well documented (Cahoon and Cooke 1992, Kang et al. 2003, Murrell et al. 2009), and supported by stable isotope tracer studies showing the importance of this production to benthic feeders (Sullivan and Moncreiff 1990, Kang et al. 2003). Some estimates have indicated benthic microflora production can equal or exceed phytoplankton production in the water column (Schreiber and Pennock 1995, Jahnke et al. 2000). However, relatively

few studies have attempted to measure deeper water benthic microalgal production *in situ*, owing to the logistical difficulties involved.

Core sampling has most often been employed to measure benthic microalgal production (Glud 2008), but this technique involves potential disruption of the sediment–water interface and isolation of sediment sample from advective exchanges through pore waters (Huettel and Rusch 2000) that attenuate natural conditions. *In situ* incubation allows production and respiration to occur under natural light regimes, ambient temperature conditions with intact sediment structure, and permits pore water advection. Net DO fluxes can be derived by transforming the change of DO concentration in the benthic chamber into areal estimates for the sediment surface.

Difficulties with calculating biomass from cell abundance or counting microalgae has led researchers to quantify benthic microalgal biomass using chlorophyll *a* (Chl *a*) (MacIntyre et al. 1996, Grippo et al. 2009). Cahoon et al. (1990) found that up to 80% of the Chl *a* in Onslow Bay, NC was associated with the sediment, and benthic Chl *a* almost always surpassed the value of integrated water column Chl *a*. Similar results from sandy sediments on Ship Shoal, offshore Louisiana, were found by Grippo et al. (2009). Total pheopigments (Pheo *a*) to Chl *a* ratios have been used as an indicator of the physiological state of the microalgal community, with higher values indicating a stressed or declining community while lower numbers suggest an actively growing community (Lorenzen 1967, Grippo et al. 2009).

Benthic chambers have also been used to obtain estimates

of *in situ* benthic nutrient fluxes in shallow coastal systems and estuaries (Fisher et al. 1982, Nicholson et al. 1999). Microbial breakdown of organic material in sediments results in nutrient regeneration and an outward flux to the overlying water column. Sediments may also take up nutrients from the water column, but net flux is generally outward to the water column (Hopkinson et al. 2001, Lehrter et al. 2012). Nutrient regeneration at the benthic boundary layer from microbial processing of sedimented organic matter and mineralization of benthic microalgae by grazers are significant in buffering and recycling water column nutrients (Fisher et al. 1982) which supports planktonic production (Rowe and Phoel 1992). This study used diver-tended *in situ* benthic chambers to estimate microphytobenthic production, total benthic respiration, and nutrient flux rates on the nearshore continental shelf of the northeastern GOM.

MATERIALS AND METHODS

Study Area

The northeastern GOM shelf sediments along the Florida Panhandle Bight are dominated by coarse quartzite sands. The study site was located about 11 km south southeast of the Pensacola Bay, FL pass (30.25°N and 87.25°W) in 15–16 m water depth (Table 1). Diurnal tides (one high water and one low water occur during a tidal day) exist in the region with a microtidal range of <1.0 m (Oey 1995). Minimal bottom currents were reported by SCUBA divers during the 3 reported sampling events: 3 September 2004, 10 September 2004, and 25 July 2005.

Hydrographic Data

A handheld YSI® Model 85 was used to record profiles of water temperature, salinity, and dissolved oxygen (DO) during incubations. Incubation periods (Table 1) traversed the solar zenith, typically from 0900 to 1600 h. Irradiance measures ($\mu\text{E}/\text{m}^2/\text{s}$) were taken every hour during incubations with a Li-Cor® LI-190SA radiation sensor at the sea surface and at 1 m intervals in vertical profiles of the water column to the seafloor, allowing for the calculation of percent transmission of photosynthetic active radiation (%PAR) and light extinction coefficients (k_d) as: $k_d = \ln(\text{surface irradiance}/\text{irradiance at depth})/\text{depth}$.

Ambient water samples near the bottom were collected using a Van Dorn bottle. Sub-samples for dissolved nutrients (NH_4^+ , NO_3^- , NO_2^- , PO_4^{3-} , SiO_2) were filtered through a 25 mm ashed (500°C for 1 h) Whatman® GF/F filter. Samples for pigment analysis were collected on 25 mm ashed GF/F filters, placed in foil envelopes, and analyzed by EPA Method 445.0 (US EPA 1992). All samples were kept on ice in the field and stored frozen (–80°C for pigments, –20°C for nutrients) until analysis.

Benthic Chambers

Replicate light and dark benthic chambers, 3 each, were constructed from clear acrylic domes of 0.26 m radius, 0.19

m height, covering an area of 0.212 m² with a volume of 0.027 m³ (Figure 1A). Dark chambers were covered with 0.15 mm black polyethylene sheeting (Film-Gard®) to block light (Figure 1B). Stirring devices were assembled with hemispherical plastic cups transferring ambient external current to internal acrylic stirring paddles (Figure 1A). Domes were fitted with two barbed hose fittings and silicone tubing, one to allow sample water to be removed by syringe and the other to allow replacement water to enter chambers. Replacement water dilution of chamber water was assumed to be negligible. Four samples were taken from each replicate dome at each time

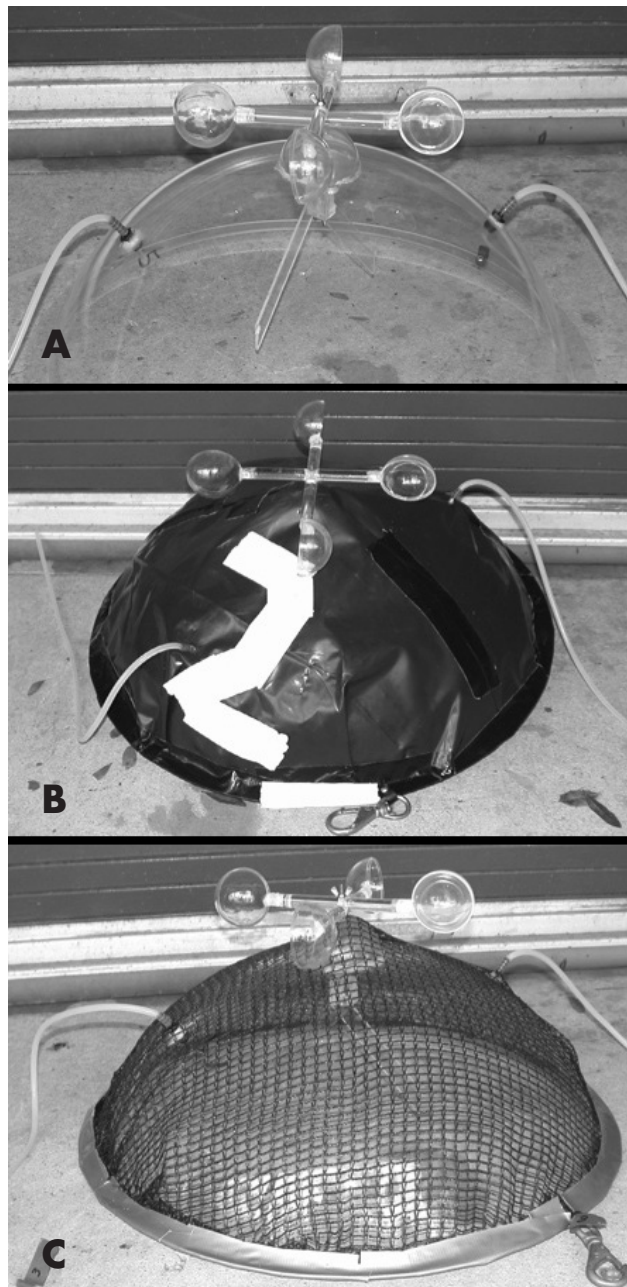


Figure 1. Light (A) and dark (B) benthic chambers with attached tubing for syringe sampling and current simulation device. Internal stirring paddles are visible in image (A). (C) Benthic chamber covered with shade cloth (30%) for the microphytobenthic response to variable irradiance compensation point estimation.

point (T_0 and T_x = post-incubation) for DO and dissolved nutrients (DN). On deck, samples in syringes were processed for nutrient analysis as described above or for Winkler titrations as described below.

Chambers were carefully lowered and positioned by divers on the bottom to avoid sediment resuspension; chamber placement avoided macrophytes, large polychaete burrows, tunicates, and hard substrates. The chambers were secured to the bottom by piling sand over the dome's 2 in. external flange. We assumed that negligible water exchange occurred between inside and outside of the domes during incubation. Chambers were allowed to stabilize for 10–15 min before initial (T_0) samples were taken. On deck, DO samples were fixed with Winkler reagents by inserting blunt ended needles into the opening of the sampling syringes. Samples were mixed by inverting, capped, and stored on ice for transport to the laboratory.

Chamber Production and Respiration

Benthic and planktonic primary production and respiration were determined as changes in DO concentration by Winkler titration of 50 mL syringe samples or 300 mL BOD bottles, respectively (Eaton et al. 2005). To obtain benthic community production and respiration, water contained under domes was corrected for near bottom plankton production and respiration. Replicate (3) light and dark BOD bottles were filled on deck with bottom water collected in Van Dorn bottles using tubing placed into the bottom of each BOD bottle; water was allowed to overflow before sealing. BOD bottles were returned to the bottom and incubated in a rack placed near the benthic chambers. Three additional samples were fixed shipboard with Winkler reagents at the start of the incubation period. At the end of the incubation period, syringe samples were taken from the domes, and BOD bottles were collected, and fixed on deck within 15 min of sampling. Winkler titrations were completed at the lab within 12 h of sample collection.

Net benthic primary production (NBPP, mg C/m²/h) was calculated from DO concentration changes in light and dark chambers using the formula for non-standard sample volumes (Strickland and Parsons 1972):

$$\text{NBPP} = (([\text{DO}]_{t_x} - [\text{DO}]_{t_0}) * V * 12) / (\text{PQ} * H * A),$$

where: $[\text{DO}]_{t_x}$ = dissolved oxygen concentration in mmol/L at the end of incubation; $[\text{DO}]_{t_0}$ = dissolved oxygen concentration in mmol/L at the beginning of incubation; V = volume of benthic chamber in liters; 12 = atomic weight of carbon; PQ = photosynthetic quotient (mol O₂ evolved / mol C fixed), 1.2 is recommended (Strickland and Parsons, 1972); H = incubation time in h; and A = area under the benthic chamber in m².

Benthic respiration was also determined using this equation with the exception that a respiration quotient (RQ) of 1.0 was used in place of the PQ, as recommended by Strickland and Parson (1972).

Student's t -test was performed to determine if initial DO concentrations were significantly different from post incubation measures. Confidence intervals (95%) were determined for benthic flux data in order to establish if a flux was significantly different from zero.

Algal Biomass

Chlorophyll analyses were conducted on sediment samples (collection techniques described in Allison 2006) and on filtered water samples to represent microphytobenthic and phytoplankton biomass, respectively. Samples were extracted in 8–10 mL of 90% acetone with probe sonication and held overnight at -20°C . Extracts were measured for their fluorescence on a Perkin Elmer[®] LS45 luminescence spectrometer according to the methods of Dandonneau and Neveux (2002), beginning at excitation wavelengths of 406 nm. Emission (fluorescence) wavelengths for detection of Chl *a* were between 666 and 668 nm, for Chl *c* at 630 nm, and for Pheo *a* from 646 to 656 nm. Pheophytin *a* was quantified by acidifying the stock Chl *a* (Sigma[®]) standard according to the methods of Welschmeyer (1994). Chl *c* was quantified using standard material extracted from reference Cryptophyceae (DHI Water and Environment[®]). Pigment concentrations in acetone extracts were normalized to dry weight for sediments and to volume for water samples.

Nutrient Analyses

All samples for nutrient analysis (SiO₂, PO₄⁻³, NH₄⁺, NO₃⁻ + NO₂⁻) were analyzed using standard methods (US EPA 1993) on a Bran-Luebbe[®] AutoAnalyzer 3. Benthic nutrient fluxes were calculated from nutrient results as in Rowe and Phoel (1992): Flux = [(Initial Conc. - Final Conc.) * Vol.] / (Time * Surface Area), expressed in mmol/m²/d.

Irradiance Curve for Benthic Production

A separate experiment was conducted on 25 July 2005 to measure the microphytobenthic response to variable irradiance allowing compensation point estimations ($P/R = 0$). Benthic chambers were covered with a commercial (Greenhouse Mega Store[®]) shade cloth with 30% and 60% shading density ($n = 3$ each; Figure 1C). Irradiance intensity for each treatment was recorded by a Li-Cor[®] light meter and plotted against the measured benthic production. Samples were collected and processed for DO flux calculations as described above.

RESULTS

Bottom water salinity was similar on all sampling dates, ranging from 33–36 (Table 1). Bottom water temperature ranged from 26–30°C (Table 1). DO on the bottom was lowest (3.23 mg/L) on 25 July 2005 (Table 1). YSI[®] temperature and salinity profiles indicated that the water column was well-mixed on 3 September 2004, and stratified on the other 2 dates (data not shown). Percent surface PAR at the bottom averaged $7.5 \pm 0.01\%$ (mean \pm sd) with a range of 1.9–10.5%. Based on surface irradiance values, mean light

TABLE 1. Summary of sampling dates, incubation times, daylight hours, depth, physicochemical properties and the light extinction coefficient (kd) from PAR attenuation with depth from each experiment.

Date	Incubation Duration (h)	Total Daylight (h) ¹	DO (mg/L)	Salinity	Temp (°C)	Light Extinction (kd/m)	Depth (m)
3 Sep 04	4	12.7	8.95	33.1	30.3	0.17	15
10 Sep 04	3.5	12.5	5.08	35.6	26.6	0.16	16
25 Jul 05	5	13.8	3.23	34.2	26.9	0.19	15

¹taken from: http://aa.usno.navy.mil/data/docs/Dur_OneYear.php/

intensities reaching the bottom for the three incubations were 7.3, 4.8, and 8.0 $\mu\text{E}/\text{m}^2/\text{s}$, chronologically. The mean k_d value for the site was $0.17 \pm 0.01/\text{m}$ and ranged from 0.16–0.19/m for all experiments (Table 1). Divers noted good visibility on the bottom for both 2004 experiments and reduced visibility, presence of planktonic jellyfish, and a more disturbed bottom topography for the 2005 experiment.

Bottom water nutrient concentrations varied 6-fold among sample dates. The highest concentrations of dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) occurred in 2005. DIN was mostly NH_4^+ ranging from 51%–84% of DIN. For dissolved inorganic phosphorous ($\text{DIP} = \text{PO}_4^{3-}$), concentrations varied from 0.06–0.25 μM , being greatest on 10 September 2004 (Table 2). Bottom water SiO_2 concentrations were similar on all sample dates, ranging from 4.07–5.36 μM (Table 2).

The largest DIN fluxes were measured in 2004 experiments (Table 3). Sediment DIN uptake was observed in all experiments except in light domes on 3 September 2004. On the other dates, DIN uptake in light domes was twice as high as dark domes. DIN flux was dominated by NH_4^+ for all experimental treatments. Release of $\text{NO}_3^- + \text{NO}_2^-$ from sediments occurred in both light and dark domes in 2005, with

TABLE 2. Ambient bottom water dissolved nutrient concentrations for each experiment. All concentrations are expressed as μM . DIN = dissolved inorganic nitrogen; DIP = dissolved inorganic phosphorous; SiO_2 = dissolved silica.

Date	DIN	$\text{NO}_3^- + \text{NO}_2^-$	NH_4^+	DIP	SiO_2
3 Sep 04	3.60	0.59	3.01	0.16	5.16
10 Sep 04	2.16	0.59	1.58	0.25	4.07
25 Jul 05	12.37	6.13	6.24	0.06	5.36

dark domes releasing twice as much as light domes. However, the largest sediment release was in light chambers on 3 September 2004 (Table 3). PO_4^{3-} was released from sediments on 3 September 2004 and sediment uptake observed on the other 2 dates with $-7.5 \mu\text{mol}/\text{m}^2/\text{h}$ on 10 September 2004 as the largest PO_4^{3-} flux measured. Sediment uptake of SiO_2 occurred on 10 September 2004 with dark dome

measures twice as high as light domes. Sediment release of SiO_2 happened on 25 July 2005, also with dark incubations twice as high as light domes (Table 3).

Plankton net production was greatest (2.8 mg C/ m^3/h) on 3 September 2004 and nearly identical on 25 July 2005 (Table 4). On 10 September 2004, net plankton production (0.74 ± 0.2 mg C/ m^3/h) and respiration (1.01 ± 0.1 mg C/ m^3/h) were

much lower resulting in the lowest recorded GPP (Table 4). Plankton respiration was greatest (3.58 ± 0.4 mg C/ m^3/h) on 3 September 2004 which was 3.5 times more than the experiment the following week (Table 4). Phytoplankton biomass, as chlorophyll, was less abundant during 2004 incubations than in 2005 (Table 5). Pheo *a* always exceeded Chl *a* in both sediment and phytoplankton samples (Table 5). The Chl *a* : Pheo *a* ratio was similar for both phytoplankton and sediments with an overall range of 0.60–0.77. Sediment Chl *c* estimates were between 12–15% of Chl *a* values while phytoplankton Chl *c* estimates were slightly higher, between 15–25%, indicating only a small presence of the Bacillariophyceae.

Net benthic production was greatest on 3 September 2004 (17.7 ± 6.1 mg C/ m^2/h). The value obtained 10 September 2004 was nearly half, and was similar to the value obtained the following year (25 July 2005; 8.8 ± 1.6 mg C/ m^2/h) (Table 4). Net benthic production for all experiments in the study period ranged from 6.6–23.8 mg C/ m^2/h . Benthic respiration ranged from 10.8–38.6 mg C/ m^2/h , was the largest on 10 September 2004 (30.8 ± 1.4 mg C/ m^2/h), slightly less on 3 September 2004 (24.8 ± 0.7 mg C/ m^2/h), and less than half the following year on 25 July 2005 (11.3 ± 0.3 mg C/ m^2/h). GPP always exceeded benthic respiration and was almost equal on the 2004 events (42.5 ± 5.2 and 40.3 ± 1.2 mg C/ m^2/h for experiments 1 and 2, respectively) which were double that of 25 July 2005 (20.3 ± 1.7 mg C/ m^2/h) (Table 4).

Benthic production response to irradiance was measured on 25 July 2005 and showed a linear ($r = 0.99$) relation-

ship for the replicate clear dome and domes covered with shade cloth (Figure 2). The bottom irradiance of 134 $\mu\text{E}/\text{m}^2/\text{s}$ represented 8% transmission of surface irradiance. Irradiance under the shade cloths was 42.3 and 24.8 $\mu\text{E}/\text{m}^2/\text{s}$, respectively for the 2 treatments (30 and 60% shade) representing 2.5 and 1.5% transmission of surface irradiance. The compensation irradiance, or point of zero net community

TABLE 3. Average benthic flux of dissolved nutrients ($\mu\text{mol}/\text{m}^2/\text{h}$) from light and dark chambers ($n=3$ each) measured in situ for each experiment. Negative values denote uptake by sediments. * = significantly different from zero; DIN = dissolved inorganic nitrogen; $\text{NO}_3^- + \text{NO}_2^-$ = nitrate + nitrite; NH_4^+ = ammonia; PO_4^{3-} = dissolved inorganic phosphorous; SiO_2 = dissolved silica.

Date	Dome	DIN	$\text{NO}_3^- + \text{NO}_2^-$	NH_4^+	PO_4^{3-}	SiO_2
3 Sep 04	Light	197.6 \pm 24.6*	21.2 \pm 5.1*	176.4 \pm 19.5*	4.1 \pm 3.1	49.1 \pm 23.4*
3 Sep 04	Dark	-277.1 \pm 299.2	-0.3 \pm 0.6	-276.8 \pm 299.4	3.6 \pm 2.3	-144.6 \pm 99.5
10 Sep 04	Light	-322.3 \pm 94.7*	-9.5 \pm 4.4*	-312.8 \pm 95.6*	-5.5 \pm 0.4*	-86.6 \pm 24.3*
10 Sep 04	Dark	-118.8 \pm 74.2	-6.5 \pm 0.8*	-114.0 \pm 76.5	-7.5 \pm 1.4*	-154.3 \pm 6.9*
25 Jul 05	Light	-86.7 \pm 22.3	8.6 \pm 2.4	-95.3 \pm 33.8*	-0.7 \pm 0.2*	113.4 \pm 37.2*
25 Jul 05	Dark	-40.2 \pm 11.4*	15.6 \pm 2.7	-55.8 \pm 17.2*	-0.1 \pm 0.1	226.8 \pm 24.6*

TABLE 4. Summary data on the net production of the benthos and plankton (NPP) measured in light domes and BOD bottles, respectively. Benthic and planktonic respiration (RESP) measured in dark domes and BOD bottles, respectively. Gross production (GPP) is the total of NPP and RESP for all experiments. Hourly means are mean \pm sd. P/R values are instantaneous measures and are not indicative of overall net community P/R for the shelf.

Date	BENTHOS $\text{mg C}/\text{m}^2/\text{h}$				PLANKTON $\text{mg C}/\text{m}^3/\text{h}$		
	NPP	RESP	GPP	P/R ratio	NPP	RESP	GPP
3 Sep 04	11.6	25.7	37.3	1.5	2.8	3.8	6.6
3 Sep 04	23.8	23.9	47.7	2.0	--	3.3	6.1
Mean	17.7 \pm 6.1	24.8 \pm 0.7	42.5 \pm 5.2	--	--	3.5 \pm 0.4	6.4 \pm 0.4
10 Sep 04	12.5	29	41.5	1.4	0.6	0.9	1.7
10 Sep 04	6.6	32.6	39.2	1.2	0.9	1.1	2.0
Mean	9.5 \pm 2.9	30.8 \pm 1.4	40.3 \pm 1.2	--	0.7 \pm 0.2	1.0 \pm 0.1	1.7 \pm 0.3
25 Jul 05	10.4	11.7	22.1	1.9	2.8	1.2	4.0
25 Jul 05	7.2	11.5	18.7	1.6	--	2.6	5.4
25 Jul 05	--	10.8	--	--	--	2.2	5.0
Mean	8.8 \pm 1.6	11.3 \pm 0.3	20.3 \pm 1.7	--	--	2.0 \pm 0.7	4.8 \pm 0.7

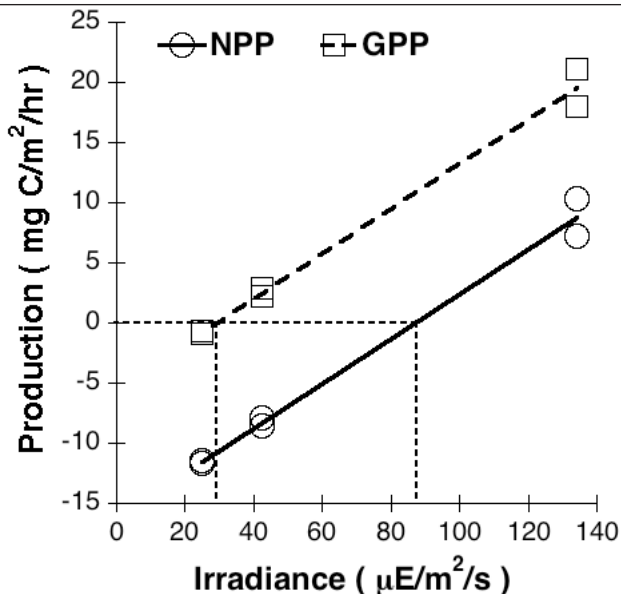


Figure 2. Benthic net (NPP) and gross (GPP) community production response to irradiance intensity during a single experiment on 25 July 2005. The least squares regression model slope is 0.186 ± 0.01 , $r^2 = 0.989$. Dotted lines indicate the point of zero net and gross community production, respectively.

production, estimated from regression analysis of benthic chamber production versus irradiance was $87 \mu\text{E}/\text{m}^2/\text{s}$, or 5.2 % of surface irradiance (Figure 2). GPP was zero at $29 \text{ mE}/\text{m}^2/\text{s}$.

DISCUSSION

The majority of continental shelves in the world are shallow enough that the benthos is included in the photic zone (Gattuso et al. 2006). With distance away from coastal enrichment sources, water column turbidity decreases which increases light penetration. Increasing depth with distance may be offset by lower k_d values with distance offshore so that the potential for benthic primary production exists for much of the continental shelf ecosystem. This was certainly the case for this study of the nearshore shelf of the Florida Panhandle Bight, providing the first estimates of benthic community production, respiration, and benthic nutrient fluxes on the nearshore continental shelf of the northeastern GOM.

One major advantage of the benthic chamber method is that the area of sediment enclosed by chambers can be large, minimizing the effect of micro-heterogeneity. Theoretically, *in situ* benthic chambers should give the most accurate estimate of fluxes, because chambers include the effects of diffusion and incorporate the exchange across the sediment-water interface created by bioturbation. Diver deployment of simple benthic chambers can be a major disadvantage when considering weather, water depth, water temperature, wind speed, current velocity, water visibility, bottom time limitations, and risk to personnel. In order for benthic chamber experiments to properly estimate benthic primary production, one must assume that all samples are taken from homogeneous, well-mixed chamber water (Glud 2008, Lehrter et al. 2012). The stirring rate inside the chamber should mimic the ambient near bottom water flow to avoid build up of concentration gradients that would inhibit diffusive fluxes and cause uneven sampling.

In our observations, elevated bottom water N and low P

TABLE 5. Summary of the mean (\pm sd) and range of photopigment values for sediment ($\mu\text{g/g DW}$) and phytoplankton ($\mu\text{g/L}$). Pheophytin *a* is the main chlorophyll *a* degradation product.

	Chl <i>a</i>	Chl <i>c</i>	Pheo <i>a</i>	Chl <i>a</i> : Pheo <i>a</i>
Sediments				
10 Sep 04	4.77 \pm 0.84	0.63 \pm 0.12	6.81 \pm 1.26	0.69 \pm 0.01
Range	2.46 - 8.71	0.31 - 1.17	3.41 - 12.79	0.64 - 0.77
Phytoplankton				
25 Jul 05	5.48 \pm 1.24	1.37 \pm 0.40	8.30 \pm 2.38	0.68 \pm 0.04
Range	3.45 - 7.74	0.82 - 2.14	4.87 - 12.87	0.60 - 0.71
03 Sep 04	0.71 \pm 0.06	0.10 \pm 0.02	0.85 \pm 0.14	0.83 \pm 0.12
Range	0.64 - 0.77	0.07 - 0.14	0.67 - 1.12	0.70 - 0.91

concentrations in 2005 compared to 2004 (see Table 2), may suggest that production was P-limited. The range of PO_4^{-3} flux in this study was much less in both directions (-8 to $+4$ $\mu\text{mol/m}^2/\text{h}$) than the range (-0.03 to $+0.50$ $\text{mmol/m}^2/\text{h}$) reported by Hopkinson et al. (2001) in offshore waters of Massachusetts Bay, but more similar to the range (-1.5 to $+9.6$ $\mu\text{mol/m}^2/\text{h}$) reported in Reay et al. (1995) from the nearshore Delmarva Peninsula. Sediment release (in 2005 only) of SiO_2 was less than the range reported (1.8–14.1 $\text{mmol/m}^2/\text{h}$) for the offshore waters of Massachusetts Bay (Hopkinson et al. 2001). Hopkinson et al. (2001) did not report any findings of sediment uptake for SiO_2 as was observed in the current investigation on 10 September 2004. Jahnke et al. (2000) reported a SiO_2 release from southeastern U.S. continental shelf sediments, but concentration changes in chamber water of NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, and PO_4^{-3} were not significant. The highest SiO_2 release in the current study (227 $\mu\text{mol/m}^2/\text{h}$) was comparable to the high value (219 $\mu\text{mol/m}^2/\text{h}$) seen by Marinelli et al. (1998) for the South Atlantic Bight.

Marinelli et al. (1998) and Murrell et al. (2009) in Pensacola Bay found that nutrient fluxes in light versus dark chambers were highly variable and did not follow a regular shallow water pattern of increased efflux in the dark and decreased efflux in the light, similar to our experience. This pattern was true for SiO_2 regardless of flux direction. The opposite was found for NH_4^+ and DIN fluxes with increased concentrations in light chambers. The range of NH_4^+ flux in this study was greater in both directions than the range reported (-13.9 to $+59.5$ $\mu\text{mol/m}^2/\text{h}$) for the nearshore Georgia shelf (Marinelli et al. 1998). NH_4^+ was predominantly taken up by sediments, which was contrary to the findings of Reay et al. (1995).

Reduced respiration rates and GPP on 25 July 2005 may

have been the result of reduced visibility and disturbed bottom as reported by divers and not by % PAR reduction with cloud cover, as the k_d value for that sampling event was similar to those from the previous year. Although GPP was reduced by half in that incubation, net benthic production was nearly identical to 10 September 2004. Benthic production was also 2 times greater on the first experiment with less respiration than the second experiment one week later. Increased respiration on 10 September 2004 made up the difference when comparing the similar GPP estimates of the 2004 experiments. Re-

duced ambient oxygen concentrations on the bottom on 25 July 2005 may explain the reduced production observed on that date.

The range of net benthic production, respiration, and GPP in this study was comparable to values of the nearshore study sites in Onslow Bay, NC (Cahoon and Cooke 1992). Average hourly respiration rates obtained by Cahoon and Cooke (1992), 18.2 $\text{mg C/m}^2/\text{h}$, are comparable to the 2004 data and slightly higher than 2005. Estimates in this study were much greater than values of benthic production (1.8–8.5 $\text{mg C/m}^2/\text{h}$) and respiration (0.6–6.5 $\text{mg C/m}^2/\text{h}$) reported for tropical marine sediments (Bunt et al. 1972).

Patchy distribution of benthic microalgae can lead to a 2–to 10–fold difference in biomass estimates over a distance of a few centimeters (Colijn and de Jonge 1984). Thus, a wide range can be expected when estimating sediment microalgal processes. Sediment Chl *a* values in the current investigation were comparable to the shallow sands of the Swan–Canning estuary, Australia which ranged between 2–20 $\mu\text{g Chl a/g}$ (Masini and McComb 2001), and slightly higher than the LCS studies of Lehrter et al. (2012) and Baustian et al. (2011) reporting maximum values of 2 $\mu\text{g/g}$.

Photopigments (Chl *a*, Chl *c*) and the primary degradation product (Pheo *a*) followed similar trends and showed similar variation in all experiments. Chl *a* : Pheo *a* ratios were similar for the water column and benthos, and values near 1 for all samples indicate an actively growing assemblage. Benthic diatoms were visually observed in sediment grab samples from the continental shelf further offshore (30 km) of Pensacola, FL at a depth of 67 m (Allison, unpublished data), indicating the potential for benthic autotrophic production to occur over broad areas on the northeastern GOM continental shelf.

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