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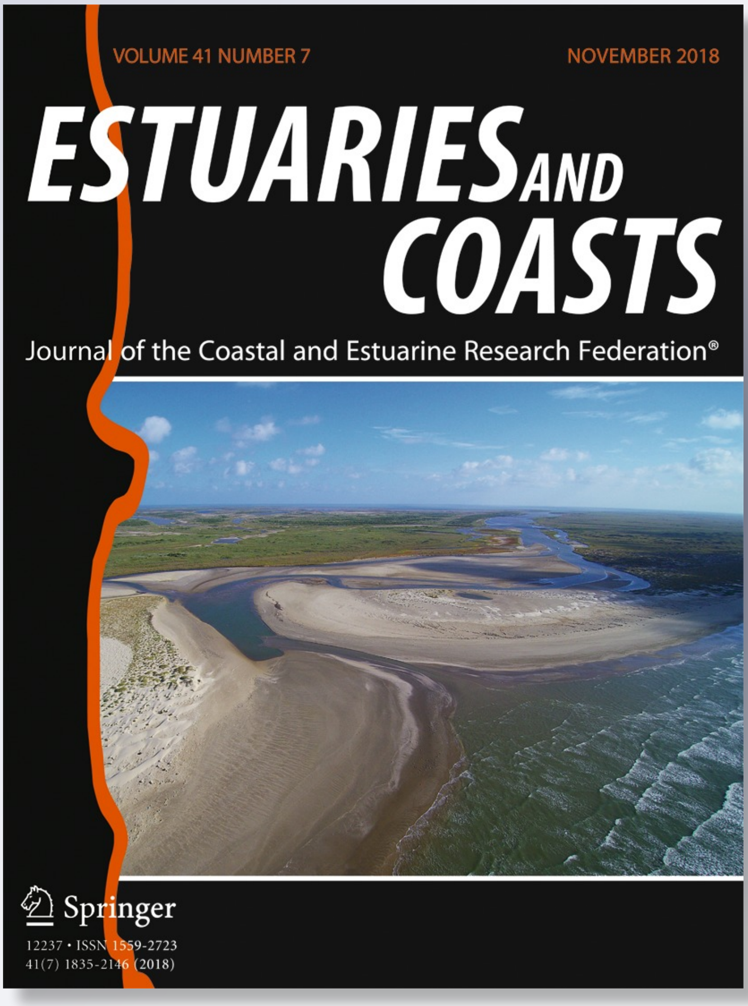

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A Mini-Review of the Contribution of Benthic Microalgae to the Ecology of the Continental Shelf in the South Atlantic Bight

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Abstract

Benthic microalgae (BMA) inhabit the upper few centimeters of shelf sediments. This review summarizes the current information on BMA communities in the South Atlantic Bight (SAB) region of the Southeastern US continental shelf to provide insights into the potential role of these communities in the trophodynamics and biogeochemical cycling in shelf waters. Benthic irradiance is generally 2–6% of surface irradiance in the SAB region, providing sufficient light to support BMA primary production over 80–90% of the shelf width. BMA biomass greatly exceeds that of integrated phytoplankton biomass in the overlying water column on an areal basis. The SAB appears to have lower BMA biomass, but higher production than most temperate continental shelves. Annual production estimates average 101 and 89 g C m^{-2} $year^{-1}$ for 5–20 and > 20 depth intervals, respectively. However, high variation in rates and biomass in time and space make comparisons between studies difficult. Submarine groundwater discharge (SGD) rather than the water column or in situ N regeneration from organic matter maybe the major "new" N source for BMA. The estimated supply of N (1.2 mmol N m^{-2} day^{-1}) by SGD closely approximates the rates needed to support BMA primary production (3.1 to 1.6 mmol N m^{-2} day^{-1}) in the sediments of the SAB. Identifying the source(s) of fixed N supporting the BMA community is essential for understanding the carbon dynamics and net ecosystem metabolism within the large area (76,000 km^2) of the continental shelf in the SAB as well other temperate shelves worldwide.

Keywords Microphytobenthos · Diatom · Continental shelf · Biogeochemistry · Productivity · Phytoplankton

Introduction

Continental shelves serve as critical mixing zones and ecotones at the interface between land, atmosphere, and the deep ocean. These ecologically productive zones play a key role in nutrient and carbon cycling and provide economic resources that greatly exceed those in deeper water (e.g., Liu et al. 2010). Microalgae, both phytoplankton and in surficial sediments, are a major food source for benthic and planktonic food webs in these ecologically and globally important habitats (Marshall 1982; Cahoon and Tronzo 1992; Mallin et al. 1992; Blair et al. 1996). As the dominant primary producers in these habitats, microalgae provide essentially all the organic carbon supporting secondary production on the middle and outer shelf. The term benthic microalgae (BMA), also known as microphytobenthos, refers to microscopic, unicellular photoautotrophs that inhabit the upper centimeters of shelf sediments. Often overlooked in system production estimates, BMA are a major contributor to food webs and biogeochemistry in aquatic ecosystems (Sullivan and Moncrieff 1990; Kanaya et al. 2008; Christianen et al. 2017). Comprehensive reviews of the BMA ecology in shallow water and intertidal habitats are detailed in Admiraal (1984), MacIntyre et al. (1996), Miller et al. (1996), and Underwood and Kromkamp (1999). This review will focus on the permanently submerged habitats in waters deeper than 10 m on the continental shelf region in the Southeastern US.

Cahoon (1999) conducted a comprehensive review of the role of BMA in neritic systems that collated the results of 85 individual studies to provide a global estimate of annual BMA productivity (ca. 500 million tons C $year^{-1}$). The current review differs in that it provides a more detailed analysis of studies of the biomass and productivity of BMA within a defined region of the broad continental shelf off the southeastern US, compares BMA biomass and productivity with phytoplankton in the overlying water column, and suggests

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potential nutrient sources for BMA. The purpose of this review is to summarize current information on BMA communities in the South Atlantic Bight (SAB) region of the US continental shelf to provide insights into the potential major role of these communities in the trophodynamics and biogeochemical cycling in shelf waters. Since similar temperate continental shelves are found worldwide, the summary of information provided in this review has implications for other similar habitats. Due to the paucity of comprehensive, published studies on shelf BMA communities, this review includes speculations to highlight knowledge gaps and foster ideas for future research on trophodynamics and biogeochemical cycling on shallow continental shelves.

The South Atlantic Bight

The South Atlantic Bight (SAB) is representative of 70% of continental shelves around the world that are characterized by sandy surficial sediments (Emery 1968). Geographically, the SAB extends from Cape Hatteras, North Carolina to West Palm Beach, Florida, along the southeast coast of the continental US. The width of the SAB ranges from 40 to 140 km with an area of ca. 120,000 km^2 (46,000 mi^2) inside the 1000 m isobath (Fig. 1). The shelf portion of the SAB has an area of ca. 70,000 km^2 (29,000 mi^2). The area-weighted mean depth of the entire SAB shelf is 27 m (Jahnke et al. 2005), which is well within the euphotic zone for the benthos (Nelson et al. 1999; Gattuso et al. 2006; McGee et al. 2008).

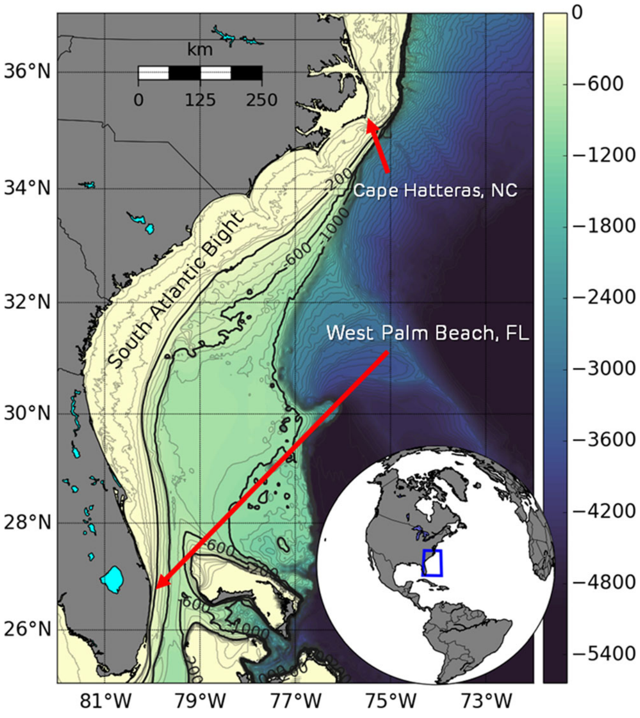

Fig. 1 Location map for the continental shelf region of the South Atlantic Bight (credit Douglas Cahl)

The SAB shelf has a gentle slope (avg. < 1°) with occasional rocky outcrops that are limited to 1–2 m above the bottom (Uchupi 1968; Parker et al. 1983). High tidal amplitude (1–3 m) and a relatively shallow shelf (< 50 m) in the region provide vigorous mixing and transport with a homogeneous water column (Blanton et al. 2004; Savidge et al. 2010). Gulf Stream meanders produce periodic upwelling that results in eddy currents that penetrate the mid-shelf region of the SAB (Atkinson et al. 1985; Lee et al. 1991). Atmospheric forcing plays an important role controlling the shelf circulation and environmental conditions, especially during tropical storms (Atkinson et al. 1985; Warner et al. 2012). Near coastal waters (10–20 km offshore) form a southward-flowing frontal region that acts as a barrier to exchange with offshore waters (Blanton 1981). East of the coastal frontal zone, mid-shelf waters have a general net flow northward (Blanton 1981).

Sediments in the mid-shelf region of the SAB are composed of well-sorted, non-accumulating fine-to-medium-grained quartz sands with moderate amounts of heavy minerals and carbonate shell hash (Parker et al. 1983; Rao et al. 2008). Representative samples suggest that these sediments have a median grain size of 200–700 μm (Marinelli et al. 1998; Rao et al. 2008) and a high permeability, on the order of 5×10^{-11} cm^2 (Jahnke et al. 2005; Wilson et al. 2008). Porosity ranges from 30 to 40% (Rao et al. 2007). Sediment organic carbon (by weight) averages 0.05%, and organic nitrogen is very low at 0.005% (Marinelli et al. 1998; Rao et al. 2008). Jahnke et al. (2005) reported sediment total organic carbon (TOC) values of 0.057% for surface sediment and 0.008% in the top 3 cm. Thus, the highly permeable and porous SAB shelf sediments can be characterized as sandy with very low organic content.

Benthic Microalgae (BMA) in the SAB

The BMA community is composed primarily of pennate diatoms, with some attached to sand grains (epipsammic), some attached with stalks, some stacked chains, as well as motile (epipelic) species (Cahoon et al. 1990; Cahoon and Laws 1993; Cahoon 1999; Nelson et al. 1999). Centric diatoms may also be present, some presumably deposited from the phytoplankton (the so-called tychopelagic microalgae). Nelson et al. (1999) found diagnostic photosynthetic pigments (e.g., chlorophyll *b*, alloxanthin, 9′hexanoyloxyfucoxanthin, 9′butanoyloxyfucoxanthin, zeaxanthin) in sediments, suggesting that other minor components of the BMA community may include filamentous and unicellular cyanobacteria, prymnesiophytes, prasinophytes, cryptophytes, euglenophytes, chlorophytes, and possibly pelagophytes. Many of these species are typically pelagic and are likely deposited from the water column as well (Marshall 1982; Verity et al. 1993). Pennate diatoms are commonly found

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carpeting the surface of sediments, giving them a brown color and a fuzzy texture (Cahoon et al. 1990). McGee et al. (2008) identified 126 diatom species from 29 genera in Onslow Bay off North Carolina, with > 90% representing obligate benthic forms. The dominant genus was the epipsammic, monoraphid diatom *Cocconeis*. Other, less abundant genera were the diatoms *Amphora*, *Navicula*, *Nitzschia*, *Actinoptychus*, and *Diploneis* (Cahoon and Laws 1993; McGee et al. 2008).

Benthic irradiance (as photosynthetically available radiation, PAR) is generally 2–6% of surface irradiance in the SAB region, but values as high as 15% have been reported (Nelson et al. 1999; Jahnke et al. 2000). McGee et al. (2008) found diffuse attenuation coefficients for PAR (k_{PAR}) of 0.0497–0.046 m^{-1} while Cahoon et al. (1990) reported values ranging from 0.12 to 0.27 (based on secchi disk measurements) in shelf waters off North Carolina. Off the Georgia and North Florida shelf region, k_{PAR} ranged from 0.068 to 0.29 m^{-1} with a mean of 0.12 m^{-1} and 50% of the k_{PAR} values between 0.10 and 0.14 m^{-1} (Nelson et al. 1999). Nelson et al. (1999) calculated that there is sufficient light to support BMA primary production over a cross-shelf distance of up to 100–120 km or 80–90% of the shelf width in the central SAB. In Onslow Bay, NC, k_{PAR} ranged from 0.072 to 0.242 at shelf depths between 15 and 32 m (Cahoon and Cooke 1992). The minimum irradiance needed to support BMA production, based on 13 studies, ranges from 0.5 to 14 μmol photons m^{-2} s^{-1} depending on depth and location (Cahoon 1999). Cahoon (1999) concluded that BMA can grow at very low light intensities of 5–10 μmol photons m^{-2} s^{-1} and < 1% of the surface irradiance. Gattuso et al. (2006) use a value of 2.8 μmol photons m^{-2} s^{-1} as a global average for the minimum light requirement by BMA. In addition to the inherent optical properties of the water, storm events result in increased turbidity that limits benthic irradiance (Nelson et al. 1999; Warner et al. 2012). There are no published studies examining the effects of light spectral quality on photosynthesis and productivity or photoacclimation responses of shelf BMA. In summary, a large portion (> 90%) of the SAB shelf receives sufficient irradiance to support BMA photosynthesis and net production.

Most of the studies of BMA biomass in the SAB have focused on water depths < 40 m (Fig. 2). Several studies have clearly documented substantial abundances of photosynthetically competent BMA in SAB waters at depths exceeding 100 m (McGee et al. 2008). Abundances from 1 to 87 mg chl *a* m^{-2} have been recorded for shelf habitats, but the majority of measurements range between 10 and 40 mg chl *a* m^{-2} in water depths from 10 to 40 m. Although chl *a* measurements were obtained using a variety of methods (e.g., HPLC, fluorometry, spectrophotometry), variation between methods is small relative to the high spatial variability of BMA (Pinckney et al. 1994b). A compilation of several studies illustrates the variability in BMA biomass in the 10–40 m depth range (Fig. 2).

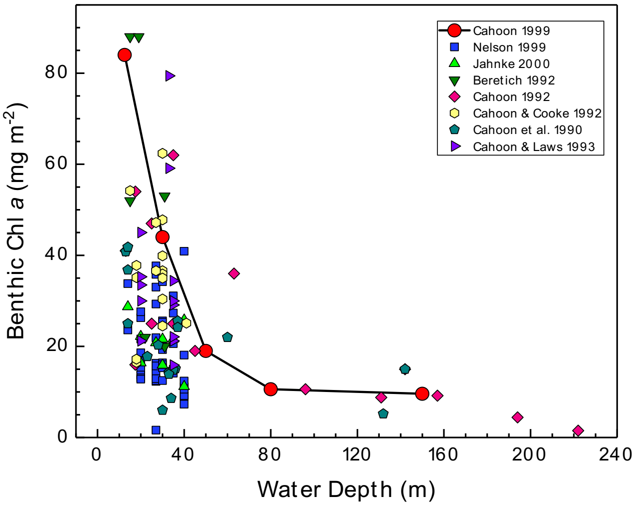

Fig. 2 BMA biomass (as chl *a*) as a function of water depth in the SAB. Data compiled from various sources are indicated in the legend. The curved line for Cahoon 1999 represents a global average for temperate shelves

Measureable BMA chl *a* has been found at 194 m depth, and there is a general decline in BMA chl *a* with depth (Cahoon 1999). This decline is likely due to a reduction in ambient irradiance associated with the attenuation of light by the water column. In his summary of shelf BMA studies worldwide, Cahoon (1999) estimated the average BMA chl *a* concentrations along a depth gradient (see curve in Fig. 2). Most of the measured chl *a* values for the SAB fall below this global average. Whether the SAB BMA biomass is below the global average or whether the trend line provided by Cahoon (1999) is an overestimate cannot be determined from existing data. However, given the large variation in measurements, this difference is not likely to be statistically significant. Therefore, BMA biomass (as chl *a*) exhibits relatively high abundance compared to phytoplankton and considerable spatial variability in the mid-shelf region of the SAB.

The major primary producers in the SAB are phytoplankton (Marshall 1982; McClain et al. 1988; Verity et al. 1993) and BMA (Cahoon and Cooke 1992; Cahoon 1999; Jahnke et al. 2000). Phytoplankton distributions in the SAB have been characterized in several studies (e.g., Bishop et al. 1980; Marshall 1982; Yoder et al. 1987; McClain et al. 1988; Verity et al. 1993; Martins and Pelegrí 2006) which show that biomass decreases with distance offshore but is relatively constant along the longitudinal axis of the SAB. Phytoplankton concentrations typically range from 2.2 mg chl *a* m^{-3} in nearshore waters to 0.8 mg chl *a* m^{-3} in the mid-shelf region (Yoder et al. 1987; McClain et al. 1988; Martins and Pelegrí 2006). Upwelling of nutrient-rich deep water along the shelf edge produces periodic phytoplankton blooms (Atkinson et al. 1985; Lee et al. 1991).

BMA biomass may exceed phytoplankton biomass (on an areal basis) in the SAB by a factor of 4 to 6 (Cahoon and

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Cooke 1992; Nelson et al. 1999). A comparison of three studies that simultaneously measured BMA and phytoplankton chl *a* in the SAB shows that, in almost all cases, BMA biomass greatly exceeds that of integrated phytoplankton biomass in the overlying water column on an areal basis (Fig. 3). These collective results clearly illustrate that more than half of the microalgal biomass on the SAB shelf is associated with the benthos. The implication is that studies neglecting the contribution of BMA to the biogeochemistry and trophodynamics on the SAB shelf are missing a major part of the story.

Most studies of BMA primary productivity in the SAB have been limited to the 10–40 m depth range and exhibit a wide variation in magnitude (Fig. 4). Annual benthic production for SAB BMA at 27 m depth on the Georgia shelf ranged from 10.8 to 64 g C m^{-2} $year^{-1}$ (Jahnke et al. 2000). Cahoon and Cooke (1992) reported BMA production rates of 24.9 mg C m^{-2} h^{-1} in Onslow Bay while Cahoon (1999) estimated that the global average shelf BMA production in the 5–20 m depth range in temperate regions was 62 g C m^{-2} $year^{-1}$. Seasonal variations in rates and the specific times when measurements were obtained make it difficult to draw comparisons between the different studies. Estimates of integrated annual phytoplankton production range from 90 to 248 g C m^{-2} $year^{-1}$ for the SAB (Cahoon and Cooke 1992; Menzel 1993; Jahnke et al. 2005). Unfortunately, all of the BMA production studies employed benthic chambers to measure dissolved gas fluxes (dissolved O_2) and estimate net and gross BMA community primary productivity. Benthic chambers are known to create artifacts due to alterations in porewater flow in permeable sediments and may provide inaccurate estimates of BMA production (Archer and Devol 1992; Tengberg et al. 2005; Huettel et al. 2014). Eddy covariance measurements may offer more accurate estimates of in situ BMA photosynthetic rates and primary productivity than traditional chamber methods (Berg et al. 2003, 2007, 2016). The available data do not show an expected decrease in BMA productivity with water depth. The reasons for this paradox are unknown but could be related to spatial variations in biomass, photoacclimation state, species differences, seasonality, water clarity, or even, methodological artifacts.

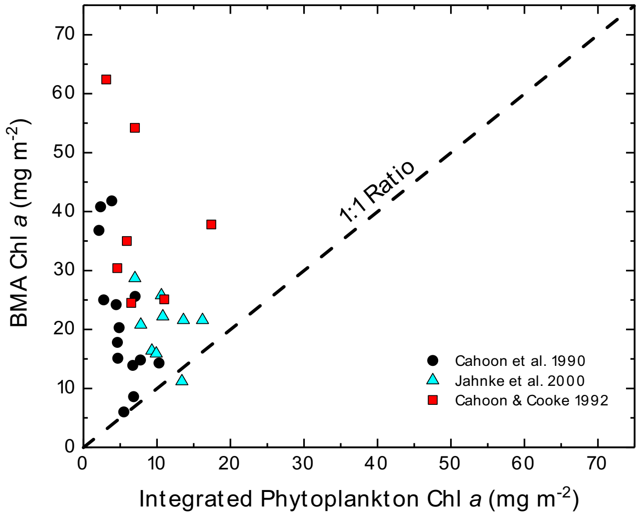

Fig. 3 BMA biomass vs. phytoplankton biomass (as chl *a*) in the overlying water column for various locations in the SAB. Data compiled from various sources are indicated in the legend

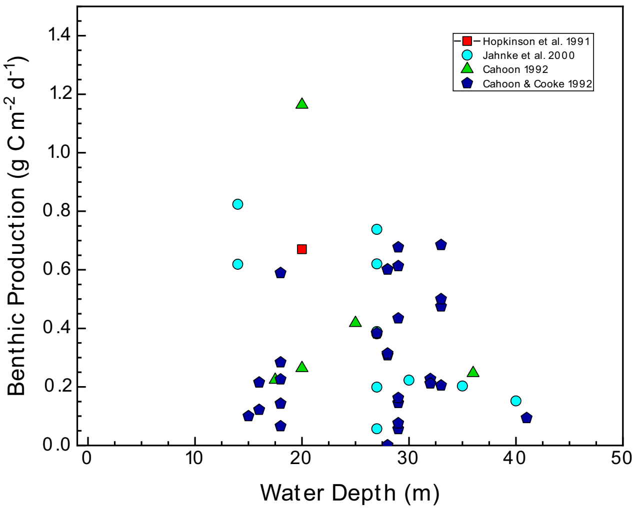

Fig. 4 BMA primary production as a function of water depth in the SAB. Data compiled from various sources are indicated in the legend

Grazing of BMA

The euphotic zone in the sediments penetrates only a few millimeters, limiting photosynthesis and primary productivity to the upper layers of the sediment (Fenchel and Straarup 1971; Pinckney and Zingmark 1993; Ploug et al. 1993; Kuhl et al. 1994). BMA biomass accumulates within this layer, producing a highly concentrated food source for grazers. Essentially, the total amount of phytoplankton biomass in the water column is compressed and concentrated in a layer of BMA biomass only a few millimeters thick, creating an algal carpet analogous to agricultural fields in terrestrial environments. This dense BMA layer provides an easily accessible, highly nutritious food source for microalgal grazers. Surficial sediments in the euphotic zone on the continental shelf offer rich foraging areas for microalgal herbivores.

Small, motile polychaetes are the most abundant macrofauna in the sands of SAB mid-to-outer shelf while meiofauna are common within sediments and are likely grazers on the BMA (Tenore 1985; Nelson et al. 1999). Demersal zooplankton, which are taxonomically distinct from holozooplankton, likely consume BMA when they are in the sediments. Cahoon and Tronzo (1992) found demersal zooplankton abundances as high as 6×10^4 individuals m^{-2} in Onslow Bay. These abundances were comparable in number to holozooplankton.

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Typical members of the demersal zooplankton were harpacticoid and cyclopoid copepods, copepod nauplii, nematodes, cumaceans, gammarid amphipods, and mysids (Cahoon and Tronzo 1990, 1992). Demersal zooplankton typically emerge from the sediments into the water column at night. Thus demersal zooplankton provide a potential trophic transfer mechanism wherein BMA productivity may be transferred to holozooplankton and nektonic food webs on the shelf.

Nutrient Sources for BMA

Conceptual models for nutrient cycling in the benthos in sandy shelf sediments were established nearly 20 years ago (Marinelli et al. 1998; Jahnke et al. 2000, 2005; Boudreau and Jørgensen 2001; Burdige 2006), and these models persist today (Huettel et al. 2014). The concentrations of organic matter and inorganic nutrients in the water column of the SAB are typically very low (NO_3^-, NH_4^+, PO_4^{3-}; all < 1 μM) (Bishop et al. 1980; Verity et al. 1993). Likewise, nutrient concentrations in sandy shelf sediments are generally low, which suggests that remineralization rates and porewater concentrations of fixed N (nitrate and ammonium) should be slow and low, respectively (Rao et al. 2007). In a simulation model of BMA production and biomass in sandy, permeable shelf sediments, Darrow (2008) could not account for the observed concentrations of BMA biomass based on nutrient (N and P) supply from the water column, suggesting a significant supply of inorganic nutrients from the benthos are necessary to support BMA communities. Jahnke et al. (2005) and Marinelli et al. (1998) reported high concentrations of porewater NH_4^+ in the upper sediment layers of the South Atlantic Bight (SAB) and postulated that these high concentrations were supported by extremely high rates of remineralization (2.45 mmol N m^{-2} day^{-1}). Marinelli et al. (1998) reported that denitrification was not an important process in these sediments, and Rao et al. (2008) found very low nitrification rates. In addition, Rao et al. (2008) demonstrated that sediments were N-limited, suggesting the sediments were not replete with fixed N. Therefore, the measured high concentrations of NH_4^+ are difficult to explain in the absence of a significant source of organic matter remineralization and NH_4^+ for surface sediments. Note that water column concentrations of NO_3^- and NH_4^+ are near the limits of detection and not a likely source for the high porewater NH_4^+ (Bishop et al. 1980; Verity et al. 1993). Thus, the supply of nutrients necessary to support the observed BMA abundances and productivity cannot be easily explained based on remineralization processes within the sediments or from the overlying water column. Furthermore, BMA may control the flux of nutrients between the sediment and the water column and are usually a sink for fixed N and orthophosphate (Sundbäck et al. 2004).

In their conceptual models, Jahnke et al. (2005) and Marinelli et al. (1998) suggested that the nutrients and carbon supporting the high rates of remineralization are supplied by rapid flushing of seawater 5–8 cm below the sediment–water interface, driven by the interaction of bottom layer currents with seafloor topography. This type of flushing, termed hydrodynamic exchange (Wilson et al. 2016), is still considered the major source of dissolved and particulate nutrients to the benthos in sandy continental shelves around the world (Huettel et al. 2014). This hydrodynamic exchange in the surficial layers also facilitates the "pumping" of deeper groundwater to the surface sediments and may supply nutrients dissolved in the submarine groundwater (Huettel et al. 2014). Concentrations and fluxes of nutrients can also be controlled through porewater pumping by infauna and the rate of denitrification (Marinelli 1992; Burdige 2006; Huettel et al. 2014). However, observations of the mid-shelf SAB suggest the absence of high densities of burrowing infauna.

Another possible explanation for the reported high NH_4^+ concentrations in surficial sediments is through groundwater inputs of NH_4^+ rather than the extremely high remineralization rates (2.45 mmol N m^{-2} day^{-1}) postulated by Marinelli et al. (1998) and Jahnke et al. (2005). They also reported very low NO_3^- concentrations, which would be consistent with groundwater NH_4^+ input (which has high concentrations of NH_4^+ relative to NO_3^- in the SAB; Moore 1999) into surface layers of sediment. Thus, groundwater rather than the water column or in situ N regeneration from organic matter may be the major "new" N source for BMA.

Support for the groundwater source of fixed N supporting BMA production rests on evidence that has been building for more than 20 years but has only recently been independently confirmed. Moore (1996) reported significant enrichment in ^{226}Ra in coastal waters of the SAB and suggested that the source of this enrichment was brackish to saline groundwater discharging through the seafloor. Moore (2010b) estimated that this saline discharge may be as much as *three times* the volume of river discharge in the SAB, with rates averaging 2.1×10^{14} l $year^{-1}$ for the entire shelf. Moore (1999) reported groundwater nutrient concentrations that ranged from 33 to 182 μM for combined nitrate and ammonium (NO_3^- and NH_4^+) while phosphate ($PO4_3^-$) concentrations ranged from 0.1 to 8.5 μM in the SAB. Spatial variations in geological strata and outcroppings undoubtedly result in local variations in input rates of SGD. In addition to nutrients, submarine groundwater discharge (SGD) carries metals, carbon, and bacteria to coastal waters around the globe (Taniguchi et al. 2002; Burnett et al. 2006; Moore 2010a). Therefore, substantial indirect evidence suggests that much of the BMA biomass and production on the SAB shelf could be attributed to inputs of NH_4^+ rich SGD. Verification of this possible nutrient source is a topic well-worthy of further exploration.

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Other known sources of new nutrients to the waters of the SAB shelf include Gulf Stream frontal eddies that result in intrusions of cold, deep, nutrient rich (ca. 10 μM nitrate) waters onto the bottom waters of the shelf (Lee and Atkinson 1983; Lee et al. 1991). These intrusions may extend into the shallow (< 20 m) regions of the shelf and result in a significant, but infrequent source of nutrients for shelf BMA.

Comparison with Temperate Shelves Worldwide

Published data for BMA biomass and production for the SAB were compiled for comparison with similar measures for continental shelves in the temperate region of the world's oceans. The review by Cahoon (1999) summarized the available information BMA on temperate shelves to provide global estimates of their contribution and provides an invaluable resource for comparisons with BMA in the SAB. BMA biomass in the SAB appears to be lower than the global average for most depth zones (Table 1). In terms of primary production, BMA production in the SAB is nearly 50% higher than the global averages for temperate shelves (Table 1). However, the high variability in the measurements for the SAB as well as estimates for worldwide temperate shelves prevents the demonstration of statistically significant differences.

Estimation of Supply and Demand

The available data allow the calculation of some very coarse estimates of N supply by SGD and N demand by shelf BMA production. SGD inputs onto shelf waters average 2.1×10^{14} l year^{-1} for a shelf area of ca. 76,000 km^2 (Moore 2010a, b). Assuming constant flow rates over 365 days, the SGD rate can be converted to 7.7 l m^{-2} day^{-1}. Using the higher and lower estimates (101 and 54 g C m^{-2} year^{-1}) for BMA production from Table 1 and dividing by 365, the daily rates of BMA production are estimated to range from 276 to 148 mg C m^{-2} day^{-1}. Using a diatom C:N molar ratio of 7.5 (Hillebrand and Sommer 2003; Montani et al. 2003), converting production to molar units (23.0 and 12.3 mmol C m^{-2} day^{-1}) and applying the C:N ratio result in an N requirement of 3.1 and 1.6 mmol N m^{-2} day^{-1}. Assuming a SGD of 7.7 l m^{-2} day^{-1} and an N (nitrate + ammonium) concentration of 150 μmol l^{-1} (Moore 1999), the N supply via SGD can be estimated at 1.2 mmol N m^{-2} day^{-1}. Thus, the supply of N (1.2 mmol N m^{-2} day^{-1}) closely approximates the rates needed to support BMA primary production (3.1 to 1.6 mmol N m^{-2} day^{-1}) in the sediments of the SAB. Concentrations of combined N in the water column are generally lower than 1 μM, except during bottom water intrusions, and could not support the estimated BMA primary production. Unfortunately, there have been no measurements of the potential contribution of benthic cyanobacterial nitrogen fixation in these sediments. Thus, their contribution to the N budget is unknown but could be significant given the low N concentrations in overlying waters. These rough estimates demonstrate that SGD inputs of N could be the major source of N fueling BMA production in the SAB.

Ecosystem Implications of BMA Production

The current paradigm is that the SAB shelf is a net heterotrophic ecosystem, based on high plankton respiration values (Hopkinson 1985) relative to primary production (Smith and Hollibaugh 1993). Cai et al. (2003) and Hopkinson et al.

Table 1 Comparison of annual estimates of benthic microalgal biomass (as chl *a*) and primary production for temperate continental shelves and the South Atlantic Bight. *SD* is ± 1 standard deviation and *N* is the sample size. Data for temperate shelves was obtained from Cahoon (1999). South Atlantic Bight data were compiled from the following: Cahoon et al. (1990), Hopkinson et al. (1991), Cahoon (1999), Nelson et al. (1999), Jahnke et al. (2000), Beretich (1992), Cahoon and Cooke (1992), and Cahoon and Laws (1993)

	Temperate shelves			South Atlantic Bight		
Depth range (m)	Mean biomass (mg chl *a* m^{-2})	*SD*	*N*	Mean biomass (mg chl *a* m^{-2})	*SD*	*N*
5–20	84	204	17	35.7	23.8	34
20–40	44	24	18	27.3	16.8	70
40–60	19		1	17.2	9.2	14
60–100	10.6		1	19.1	14.7	3
100–200	9.6	43	4	8.6	4.8	8
	Mean production (g C m^{-2} year^{-1})			Mean production (g C m^{-2} year^{-1})		
5–20	62	116	12	101	129	20
> 20	54	29	4	89	74	33

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(1991) suggested that inputs of allochthonous organic matter supported the high planktonic respiration rates. However, if benthic autotrophic production (Jahnke et al. 2000) is added to the values reported by Smith and Hollibaugh (1993), the shelf ecosystem may be much closer to metabolic balance (i.e., P:$R = 1$) (Jahnke et al. 2005). The degree of coupling between benthic and planktonic trophic pathways has not been explored for the SAB, making it difficult to quantify net ecosystem processes. One possibility is that the benthos and water column may function as uncoupled systems, further complicating assessments of net ecosystem metabolism. Understanding the source of fixed N supporting the BMA community is essential for understanding the carbon dynamics and net ecosystem metabolism within the large area (76,000 km^2 or 29,000 mi^2) of the continental shelf in the SAB as well other temperate shelves worldwide.

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