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Potential export of unattached benthic macroalgae to the deep sea through wind-driven Langmuir circulation

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[1] Carbon export to the deep sea is conventionally attributed to the sinking of open ocean phytoplankton. Here, we report a Langmuir supercell event driven by high winds across the shallow Great Bahama Bank that organized benthic non-attached macroalgae, *Colpomenia sp.*, into visible windrows on the seafloor. Ocean color satellite imagery obtained before and after the windrows revealed a 588 km^2 patch that rapidly shifted from highly productive macroalgae to bare sand. We assess a number of possible fates for this macroalgae and contend that this event potentially transported negatively buoyant macroalgae to the deep Tongue of the Ocean in a pulsed export of $>7 \times 10^{10}$ g of carbon. This is equivalent to the daily carbon flux of phytoplankton biomass in the pelagic tropical North Atlantic and 0.2–0.8% of daily carbon flux from the global ocean. Coastal banks and bays are highly productive ecosystems that may contribute substantially to carbon export to the deep sea. **Citation:** Dierssen, H. M., R. C. Zimmerman, L. A. Drake, and D. J. Burdige (2009), Potential export of unattached benthic macroalgae to the deep sea through wind-driven Langmuir circulation, *Geophys. Res. Lett.*, *36*, L04602, doi:10.1029/2008GL036188.

1. Introduction

[2] Much of the past research on the fate of carbon in the world's oceans has focused on the vast pelagic regions and export of phytoplankton-associated biomass to the deep seafloor [*Laws et al.*, 2000]. Coastal regions, while covering far less area than the open ocean, contribute disproportionately to global budgets in terms of their productivity, elemental fluxes and biogeochemical cycles [*Borges*, 2005]. Moreover, the fate of carbon produced in coastal ecosystems has been difficult to constrain because of the limited knowledge of circulation and exchange processes between the shelf and coastal ocean [*Gattuso et al.*, 1998]. Here, we document a linkage between physical circulation (i.e., wind-driven Langmuir supercells [*Gargett et al.*, 2004]) and biological productivity on the shallow water platform of the Great Bahama Bank. We use ocean color satellite imagery obtained before and after this event to document the potential fate of this highly productive macroalgae and to elucidate the role of episodic events to the carbon cycle.

[3] This study was conducted on the Great Bahama Bank, a 75,000 km^2 region encompassing shallow, submerged carbonate banks, small islands, deep channels, and deep-water basins in the oligotrophic subtropical North Atlantic. The Bahama Banks influence the carbon cycle through carbonate production and accumulation [*Milliman et al.*, 1993], exchange of dissolved organic matter between the banks and the surrounding deep sea [*Otis et al.*, 2004], drawdown of CO_2 due to seagrass productivity [*Dierssen et al.*, 2003], and biologically mediated carbonate dissolution [*Burdige and Zimmerman*, 2002]. Much of the carbon fixed by the seagrass *Thalassia testudinum* living on the banks is recycled within the Banks leading to carbon dissolution and sequestration of carbon into the relatively stable bicarbonate pool of the ocean's surface layer [*Burdige et al.*, 2008].

[4] The macroalgae, *Colpomenia* sp., is considered to be an "ephemeral" opportunistic algae with a rapid growth rate that shows no photoinhibition at high light conditions [*Matta and Chapman*, 1991]. The species *Colpomenia sinuosa* possesses a heteromorphic life history alternating between erect and filamentous prostrate thalli [*Toste et al.*, 2003] and has been found as a minor constituent of turf algae associated with fore-reefs along the eastern edge of the Exumas [*Macintyre et al.*, 1996]. However, to our knowledge, mats of monospecific unattached *Colpomenia sp.* have not been reported in the literature for this region and little is known about the seafloor on the western Exumas. Over expansive "optically shallow" regions like the Bahamas Banks, the reflectance of light from the seafloor is dramatically visible from satellite sensors. Here, we use remote sensing assets to extend our observations in space and time and address the implications of this highly productive benthic macroalgae on the Bahama Banks and its potential transport due to wind-driven Langmuir circulation.

2. Methods

[5] This study was conducted on the Bahama Banks in March 2004 aboard the *R/V Walton Smith*. The Exumas stretch along the eastern arm of the Great Bahama Bank were water depths are less than 10 m and drop precipitously (>1000 m) on the east into the Exuma Sound and on the west into the Tongue of the Ocean [*Macintyre et al.*, 1996]. Physical and optical measurements were taken from a bio-optical package deployed from the ship and scuba divers conducted measurements and surveys of benthic constituents (e.g., seagrass, macroalgae) across stations along the western and eastern portions of the Great Bahama Bank. An *ac*-9 Plus package (WET Labs, Inc.) with a CTD (Sea-Bird Electronics 19) was deployed at each station and allowed to sample for 6 minutes at a fixed depth of 2–3 m below the sea surface. Above-surface radiance measurements were

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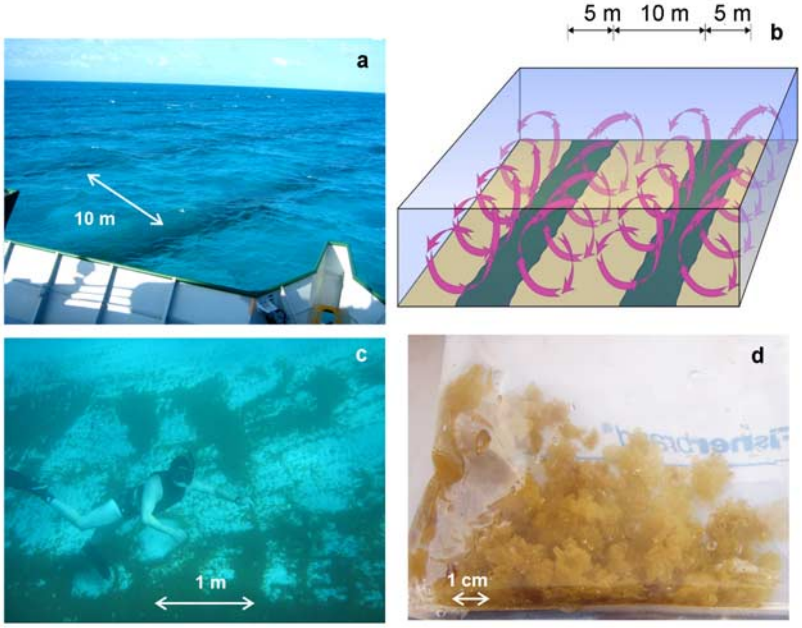

Figure 1. (a) Algal windrows observed from the ship as dark stripes on the seafloor. (b) Conceptual diagram of Langmuir supercells that serve to sweep ephemeral benthic algae into rows on the seafloor. (c) Clearing of the algae by the diver's (R. Zimmerman) left flipper illustrates the mobility of benthic algae along the seafloor. (d) Specimen of brown algae, *Colpomenia sp.*, collected from the windrow.

taken with the Field Spec Pro™ VNIR-NIR1 portable spectrometer system from Analytical Spectral Devices (ASD) to derive an estimate of spectral remote sensing reflectance, $R_{rs}(\lambda)$, the ratio of water-leaving radiance normalized to the plane irradiance incident on the sea surface. Detailed processing of the optical data is described by *Dierssen et al.* [2008] and given in the auxiliary material.[1]

[6] High resolution (1 km) Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua Level 1A Local Area Coverage (LAC) images were downloaded from the National Aeronautics and Space Administration (NASA) ocean color website for days coinciding with the field study. Atmospheric correction routines are not designed for optically shallow water and we applied an iterative scheme to first process the image using the multiple-scattering assumptions [*Dierssen et al.*, 2008]. Wind data at 10-m height from the Nassau International Airport (780730, MYNN) were obtained from the National Oceanic and Atmospheric Administration National Environmental Satellite, Data, and Information Service, National Climatic Data Center.

[7] *Colpomenia* thalli were collected by divers and incubated in clear glass water-jacketed incubation chambers (5 ml volume). Temperature inside the chambers was maintained at 22°C and electrode drift measured in chambers filled with air-saturated seawater prior to the addition of each algal sample. Algal respiration was measured in the dark using air-saturated seawater. The light-saturated rate of photosynthesis (P_{m}) was measured by exposing each sample to approximately 600 μmol m^{-2} s^{-1} of white light. Photosynthesis-saturating irradiances were provided by a fiber optic light source using a variable intensity incandescent lamp (Dolan-Jenner Industries, Incl. Fiber-Lite Series 180), and incubation irradiance was measured using a factory-calibrated quantum irradiance meter (Biospherical Instruments Inc. QSL-100). Dry weight of the samples was measured using a Despatch drying oven set at 65°C. Taxonomic identification was provided post-cruise on preserved samples by Brian Lapointe, (Harbor Branch Oceanographic Institution). Net primary productivity was estimated assuming photosynthesis for 10 h d^{-1} and a photosynthetic quotient (O_2:CO_2) of 1.1 following the procedure outlined by *Vaudrey* [2007] using a C:N ratio published for *Colpomenia* of 24:1 [*Atkinson and Smith*, 1983].

[8] Assumptions used to estimate the potential carbon export of macroalgae are provided in Table 1. The area of the cleared patch was estimated from satellite imagery and the density of macroalgae along the seafloor was estimated from in situ diver observations (as shown in Figure 1c). Density of negatively-buoyant *Colpomenia* was conservatively assumed to equal the measured density of the water (1025 kg m^{-3}). Macroalgal dry weight was assumed to be 10% of fresh weight. Carbon content of 24% came from *Colpomenia sinuosa* from N. Queensland [*Atkinson and Smith*, 1983].

3. Results and Discussion

[9] On 19 March 2004, we observed long, alternating stripes of dark and light rows running NE to SW in shallow water (~5 m depth) on the eastern arm of the Great Bahama Bank between the Exuma Archipelago and the Tongue of the Ocean (24°14.083′N, 76°43.953′W, Figures 1a and 1b)

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[1] Auxiliary materials are available in the HTML. doi:10.1029/2008GL036188.

Table 1. Estimated Carbon Content Within the Macroalgal Rows Associated With Potential Langmuir Transport

Description	Value	Units	Reference
A) Areal extent of windrow export	588	km^2	Estimated from satellite imagery (Figure 2c)
B) Areal extent of algal rows only	196	km^2	33% of total in A (Figure 1b)
C) Areal extent of *Colpomenia* within rows	98	km^2	Assume ∼50% algal coverage per row (Figure 1c)
D) Thickness of *Colpomenia* on seafloor	3–10	cm	Visually estimated by divers
E) Volume of *Colpomenia*	0.003–0.01	km^3	C × D
F) Density of *Colpomenia*	1025	$kg\ m^{-3}$	conservatively assume negatively-buoyant algae has the same density as seawater (measured)
G) Fresh weight of *Colpomenia*	$3 \times 10^9 – 1 \times 10^{10}$	kg fw	F × E
H) Dry weight of *Colpomenia*	$3 \times 10^{11} – 1 \times 10^{12}$	g dw	Assume 10% of G
I) Total carbon biomass in patch	$7 \times 10^{10} – 2 \times 10^{11}$	g C	Assume 24% of H

while aboard the *R/V Walton Smith*. We photographed and collected samples of the dark windrows that formed along the seafloor, which were comprised exclusively of *Colpomenia* sp., a brown alga of the division Phaeophyceae (Figures 1c and 1d). The *Colpomenia* sp. was unattached to the seafloor and could be lifted off the bottom with the slightest water disturbance. The distribution of this macroalga within a windrow is illustrated in underwater photograph (Figure 1c) and its unattached nature and slightly negative buoyancy can be observed in the patch cleared by the gentle motion of the diver's left flipper.

[10] The benthic *Colpomenia* sp. windrows ran parallel to the prevailing wind direction and perpendicular to the wave-induced sand ripples on the seafloor. This type of ordered pattern, commonly observed with wind-induced Langmuir circulation at the sea surface, is characteristic of Langmuir "supercells" reaching the full depth of the water column [*Gargett and Wells*, 2007]. At the benthic interface, the supercells organized *Colpomenia* sp. into rows far into the horizon. The negatively-buoyant thalli accumulated at the bottom convergence zone of the Langmuir cell in a layer approximately 3–10 cm in thickness with no coincident resuspension into the overlying water column. The windrows measured approximately 5 m wide, separated by 10 m of bare sand. Hence, the width of the windrows corresponded to the water depth (5 m) and the distance between the rows corresponded to double the water depth (10 m) — dimensions consistent with shallow water Langmuir cells reaching the full depth of the water column (Figure 1b) [*Gargett et al.*, 2004].

[11] This event coincided with highest maximum sustained wind speeds (18 $m\ s^{-1}$) recorded for the month of March 2004 in Nassau, approximately 100 km to the northwest. Mean wind speed recorded by the *R/V Walton Smith* during the period was ∼8.2 $m\ s^{-1}$ with a predominant wind direction from the NE (31.5° true). The wind speed (u, $m\ s^{-1}$) necessary to create Langmuir supercells of 5-m depth in homogenous fully developed seas can be estimated by:

$$u \approx 73.53\, d\, N \tag{1}$$

where d, is the depth of penetration for Langmuir circulation and N is the Brunt-Väisala (buoyancy) frequency [*Gargett et al.*, 2004; *Li and Garrett*, 1997]. For a wind speed of 8.2 m s^{-1}, Langmuir cells of 5.3 m could be created from waters with a buoyancy frequency $<0.021\ s^{-1}$. We arrived at the station after the windrows were fully established and were unable to measure N prior to Langmuir cell penetration. However, buoyancy frequency measured at a neighboring Bahamian station was 0.011 s^{-1} in the top 1–2 m, well below this threshold.

[12] Langmuir supercells can suspend sediments and transport the resuspended particles offshore by inducing turbulence along the highly sheared oscillatory "wave" that serves to lift sediment grains from the seafloor into the water column [*Gargett et al.*, 2004]. Visual observations and measured optical properties of the water column during the windrow episode revealed little scattering from suspended matter. Sediment along the Exumas consists of composite grains or clumps (e.g., grapestone or ooilitic sands) that are much larger (mean diameter = 800 μm) than the fine aragonite muds from the region of the Great Bahama Bank west of Andros Island (mean diameter = 382 μm) [*Winland and Matthews*, 1974]. The latter area is prone to whitings, events in which kilometer-sized regions appear milky white from the suspension of extremely fine-grained sediment in the water column [*Shinn et al.*, 1989]. Higher critical water velocity is required to resuspend larger sands (e.g., ∼25 $cm\ s^{-1}$) compared to finer aragonite muds (e.g., 18–20 $cm\ s^{-1}$) [*Vanoni*, 1974]. We contend that bottom shear associated with Langmuir supercells was sufficient to sweep unattached benthic macroalgae into rows and potentially transport algal biomass in "jets" parallel to the wind direction, but not great enough to resuspend the coarse sediment particles found in this region [*Dierssen et al.*, 2008].

[13] Productivity of the *Colpomenia* in these windrows appears to rival the most productive ecosystems known. Gross photosynthesis was 2.2 ± 0.2 $\mu mol\ O_2\ min^{-1}\ g\ dw^{-1}$, respiration was 0.5 ± 0.1 $\mu mol\ O_2\ min^{-1}\ g\ dw^{-1}$ and net area-specific primary productivity (NPP) of 5 $cm\ m^{-2}$ thick stripes of *Colpomenia* assuming 10 $h\ d^{-1}$ photosynthesis and 24 $h\ d^{-1}$ respiration was equivalent to 30 $g\ C\ m^{-2}\ d^{-1}$. The frequency and duration of macroalgal blooms has yet to be quantified on these Banks, but the availability of phosphorous, rather than nitrogen, may limit primary production of macroalgae in these carbonate-rich tropical waters [*Lapointe et al.*, 1992]. If such blooms occur only one month each year, the annual NPP of 922 $g\ C\ m^{-2}\ y^{-1}$ dwarfs the productivity of marine phytoplankton blooms (130 $g\ C\ m^{-2}\ y^{-1}$) and rivals the productivity of terrestrial forests, seagrass meadows, and mangroves (130, 400, 817, 1000 $g\ C\ m^{-2}\ y^{-1}$, respectively) [*Mateo et al.*, 2006].

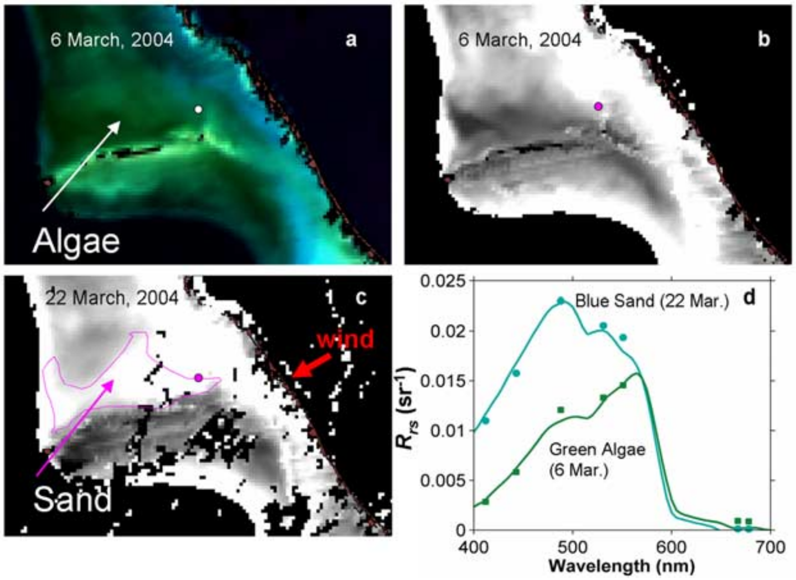

Figure 2. (a) Pseudo true color MODIS Aqua satellite imagery (6 March 2004) of the lower Exumas, Bahamas prior to windrow observation (white dot) showing presence of green algae across the Banks. Spectrally-classified images showing (b) predominantly algae (gray) from 6 March compared to (c) a bare sand patch extending 588 km^2 (outlined in maroon) with the characteristics of sand (white). Black regions represent gaps in the imagery due to cloud cover. (d) Mean spectral remote sensing reflectance, R_{rs}, from available visible MODIS Aqua channels with the patch illustrate shift from green algae (squares) to blue sand (dots).

[14] The fate of these drifting windrows of benthic macroalgae is not known, but can be inferred from remote sensing imagery. Satellite imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua sensor revealed the entire Exumas shelf region to be covered with green algal matter prior to the windrow event (6 March 2004, Figures 2a and 2b). Imagery 3 days after the windrow observation (22 March 2004) revealed a total loss of green matter from a 588 km^2 patch (Figure 2c). Retrieved remote sensing reflectance (R_{rs}) from the patch region peaked in the green region of the visible spectrum (555–580 nm) prior to the windrows and in the blue region of the spectrum (490 nm) afterwards (Figure 2d). A spectral shift from green- to blue-dominated R_{rs} is consistent with a shift from net primary producers, such as seagrass and macroalgae, to bare carbonate sand characteristic of this region [*Dierssen et al.*, 2003].

[15] The green patch visible in the imagery extended westward from the location of the observed windrows towards unsampled portions of the Exumas. We contend that the green matter in the imagery is comprised primarily of the same macroalgae observed in the field, but briefly address several other benthic constituents known to occur on the Bahama Banks that may generate similarly-colored reflectance. Seagrass beds also produce a green-peaked R_{rs} spectrum, but seagrass beds were not found this far west on the Exumas and tend to be much more stable over time [*Dierssen et al.*, 2003]. 'Grapestone' sediments contain microalgae [*Winland and Matthews*, 1974] that also appear green from space, but the sediments sampled at the windrow station were much whiter in color (see Figure 1c) than grapestone sediment. Moreover, the lack of coincident sediment resuspension suggests that bottom turbulence from the Langmuir cells was not sufficient to mobilize large-grained sediment and provides circumstantial evidence that the majority of the patch was not comprised of grapestone. Hence, we conclude that the cleared patch primarily consisted of highly mobile, concentrated mats of *Colpomenia* sp. (Figure 1c).

[16] The algal biomass within the patch disappeared due to grazing or senescence on the Banks or was transported from the shallow Banks. In intertidal zones with a high abundance of grazers (herbivorous snails, urchins), short-lived opportunistic macroalgae, like *Colpomenia*, are consumed with high efficiency [*Valiela*, 1995]. Such macrograzers, however, were not evident to divers in these oligotrophic, subtidal waters (see Figure 1c). Amphipods and isopods are also important grazers of macroalgae, but the densities required to consume 500 g dw m^{-2} (see Table 1) within 3 days would have been unreasonable (>40,000 ind m^{-2}), even at maximal grazing rates (4 mg dw ind^{-1} d^{-1}) [*Hauxwell et al.*, 1998]. Senescence and disintegration of the macroalgal thalli is also possible [*Schaffelke and Klumpp*, 1997], but collected material was visibly intact and metabolic rates were healthy (Photosynthesis:Respiration >4.7). Moreover, rapid disintegration of the entire biomass within a 3-day period is unlikely. Transport of algal matter along the Banks orthogonal to the wind would require a transport mechanism other than Langmuir circulation and was not observed as enhanced "greenness" in the imagery to the north and south of the cleared patch (Figures 2b and 2c). Intensified near-bottom currents from Langmuir supercells would provide net along-wind transport of material [*Tejada-Martinez and Grosch*, 2007] consistent with the west-northwesterly location of the patch and westward transport of material from the Exuma Banks.

[17] Therefore, we contend that much of the *Colpomenia* sp. was transported off the Banks and into the oligotrophic

Tongue of the Ocean, a deep oceanic trench in the Bahamas separating the islands of Andros and New Providence (Figure 2c). Here, the bathymetry drops rapidly from the shallow Exumas platform ($\sim$5 m) to over 1,800 m, and the negatively buoyant *Colpomenia* sp. should have descended rapidly to the seafloor without considerable water column grazing or remineralization. Episodic, rapid sinking by large particles is a major pathway by which organic matter reaches the seafloor [*Valiela*, 1995]. For example, cm-scale organic marine snow sinks at rates upwards of 100 m day^{-1} [*Alldredge and Gotschalk*, 1988]. Actual sinking rates for these irregularly-shaped negatively-buoyant macroalgae are difficult to model, but estimates using a semi-empirically derived version of Stokes Law for fecal pellets [*Komar et al.*, 1981] indicate that sinking rates can be upwards of 1000 m d^{-1} depending on the assumed particle density and length scales.

[18] The amount of carbon within this one patch amounts to roughly 0.7–2 $\times$ 10^{11} g C depending on the thickness of *Colpomenia* sp. distributed throughout the patch (Table 1). If a majority of this carbon reached the deep seafloor, it would be equivalent to the daily carbon flux due to sinking phytoplankton biomass from the entire subtropical North Atlantic [*McGillicuddy et al.*, 2007], or about 0.2 to 0.8% of the daily carbon export from the global ocean. Estimates of carbon export indicate that phytoplankton across all the world's oceans contribute about 11.1 Gt y^{-1} or 3 $\times$ 10^{13} g C d^{-1} [*Laws et al.*, 2000]. Extrapolated spatially over other carbonate banks and temporally throughout the year, episodic wind-driven transport of biomass from such shallow water carbon "incubators" to the deep sea may therefore represent an important missing component of the global carbon cycle. More interdisciplinary research is needed to measure the production and transport capabilities of Langmuir supercells directly and the implications on the formation and fate of algal matter on these Banks, including direct measurements of these episodic carbon fluxes to the seafloor.

[19] **Acknowledgments.** We acknowledge Lynn McMasters (Moss Landing Marine Laboratories) for the Langmuir schematic, Brian Lapointe (Harbor Branch Oceanographic Institution) for macroalgae taxonomy, the *R/V Walton Smith* crew, the Exuma Land and Sea Park, Christopher Buonassissi for image processing, Hans Dam and Grace Chang for helpful comments, and the NASA Ocean Biology Processing Group for the production and distribution of the ocean color data. Financial support was provided by the Chemical Oceanography Program of the National Science Foundation (D.J.B. and R.C.Z.), the NASA Ocean Biology and Biogeochemistry (H.M.D. and R.C.Z.).

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