

FACTORS AFFECTING SURF ZONE PHYTOPLANKTON
PRODUCTION IN SOUTHEASTERN NORTH CAROLINA, USA

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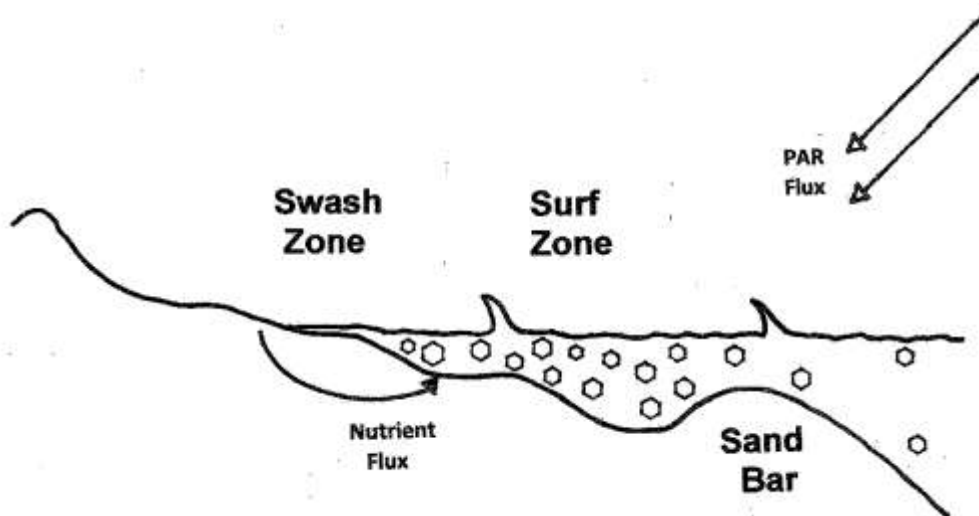
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Abstract: The biomass and productivity of primary producers in the surf zone of the ocean beach at Wrightsville Beach, North Carolina, USA, were measured during all seasons, along with environmental parameters and nutrient levels. Variation in biomass (chlorophyll *a*) was associated with temperature. Primary production (PP), measured by *in situ* 14-C incubations, was a function of chlorophyll *a*, tide height at the start of incubations, and rainfall in the preceding 24-hr period. Biomass-normalized production (P_B) was also a function of tide height and rainfall in the preceding 24-hr period. We interpreted these results as evidence of surf production 1) as combined contributions of phytoplankton and suspended benthic microalgae, which may confound application of simple P-E models to surf zone production, and 2) being regulated by nutrient source/supply fluctuations independently from other factors. Surf zone biomass and production levels are intermediate between relatively high estuarine values and much lower coastal ocean values. Surf zone production may represent an important trophic connection between these two important ecosystems.

Key Words: Phytoplankton; primary production; surf zone; chlorophyll *a*; beach

Graphical Abstract:



1. Introduction

The surf zones of ocean beaches were at one time thought to be relatively unproductive (Talbot et al., 1990). Dense accumulations of phytoplankton, typically diatoms, found exclusively in surf zones (Lewin & Mackas, 1972; Hewson et al., 2001; Rörig et al., 2004; Odebrecht et al., 2010), estimates of surf zone production (Campbell and Bate, 1987; Bate et al., 1990; du Preez and Campbell, 1996; Heymans and McLachlan, 1996), significant macrofaunal production in beach ecosystems (Lastra et al., 2006; Nel et al., 2014), and ecosystem models of surf zone communities (Campbell & Bate, 1988; Lercari et al., 2010) have changed that view and led to an appreciation that surf zones can support significant autochthonous production and important food chains (McLachlan and Brown, 2006).

Many studies of surf zone phytoplankton have generated impressive estimates of phytoplankton biomass, primary production, and biomass-specific production. Biomass estimates averaging $14.6 \text{ mg chl } a \text{ m}^{-3}$ (Campbell and Bate, 1988) and $\sim 36 \text{ mg chl } a \text{ m}^{-3}$ (Odebrecht et al., 2010) have been reported from South African and Brazilian beaches, respectively. Estimates of primary production from lab incubations and modeling include values of $480 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Campbell and Bate, 1988) and $1.2 \text{ to } 2.1 \text{ g C m}^{-2} \text{ d}^{-1}$ (Heymans and MacLachlan, 1996). Du Preez and Campbell (1996) reported biomass-specific production rates of up to $16 \text{ mg C (mg chl } a)^{-1} \text{ h}^{-1}$. These numbers are all quite high in comparison to most estimates of coastal ocean phytoplankton biomass and production, e.g., Yoder (1985); Cahoon and Cooke (1992). Most of the studies cited here, however, were conducted in surf zone habitats supporting extensive blooms of surf zone-specific diatoms, e.g., *Anaulus australis*, *Asterionellopsis glacialis* (Campbell et al., 1988; Odebrecht et al., 2010), which are apparently well-adapted to unique surf zone conditions and therefore competitive dominants in those habitats. Moreover, beaches supporting high accumulations of surf zone-specific diatoms also feature generally high nutrient availability (Campbell, 1996; Campbell and Bate, 1997; Rörig and Garcia, 2003; Odebrecht et al., 2010, 2014). These observations suggest that surf zones lacking specific dominant phytoplankton species with particular adaptations to life in the surf zone may be less impressively productive and more responsive to potentially limiting factors than in biologically distinctive surf zone communities.

Measurements of surf-zone nutrient availability and phytoplankton biomass are commonly made, though few studies of *in situ* primary production in these systems have been conducted and published. The physical challenges of sampling and working in surf zones certainly contribute to the general lack of *in situ* production estimates, as does the heterogeneous character of the habitat itself. The relatively few beaches that support dramatic accumulations of specially adapted surf-zone diatoms have been of particular interest, which may also contribute to a perception that beaches without such dramatic blooms may be less interesting and worthy of study. Nevertheless, observations of beach-associated food webs strongly suggest a non-trivial role for autochthonous production in the surf zone (Abreu et al., 2003; Bergamino et al., 2011; Lastra et al., 2006).

The study presented here examined surf zone primary production *in situ* at a beach in coastal North Carolina, USA (Wrightsville Beach, NC) during all seasons of the year in order to capture seasonal variability and evaluate various controlling factors. Previous studies of this beach community established that phytoplankton biomass and production in summer conditions was high in comparison to the neritic ocean community (Kahn and Cahoon, 2012), that some elements of the zooplankton community responded positively to elevated surf zone phytoplankton biomass in summer (Stull et al., 2015), and that beach meiofauna biomass was positively correlated to surf zone phytoplankton production (Cahoon, unpublished data). Consequently we expected to observe a strong seasonal signal in phytoplankton production in the surf zone, likely mediated by light and temperature effects.

2. Methods and Materials

2.1 Study Site

Our study site was located on the North Carolina shoreline approximately in the middle of Onslow Bay, a bight bounded by Capes Lookout and Fear and offshore by the Gulf Stream, friction from which sets up a counterclockwise circulation in Onslow Bay itself (Fig.1). River inputs to Onslow Bay are small (Atkinson and Menzel, 1985; Mallin et al., 2005); shelf break upwelling inputs of nutrients are generally limited to offshore waters of this broad (~80-130 km) continental shelf ecosystem (Yoder, 1985), so nearshore Onslow Bay is generally oligotrophic (average [DIN] < 0.5 μM), with phytoplankton biomass (average [Chl a] < 0.5 $\mu\text{g L}^{-1}$) and

production values (average: $27.4 \text{ mg C m}^{-2} \text{ h}^{-1}$) generally low on the spectrum for coastal ocean waters (Cahoon et al., 1990; Cahoon and Cooke, 1992; Mallin et al., 2005). The coastline is typified by low relief beaches on barrier islands with marsh and estuarine habitat inland and tidal inlets at varying intervals.

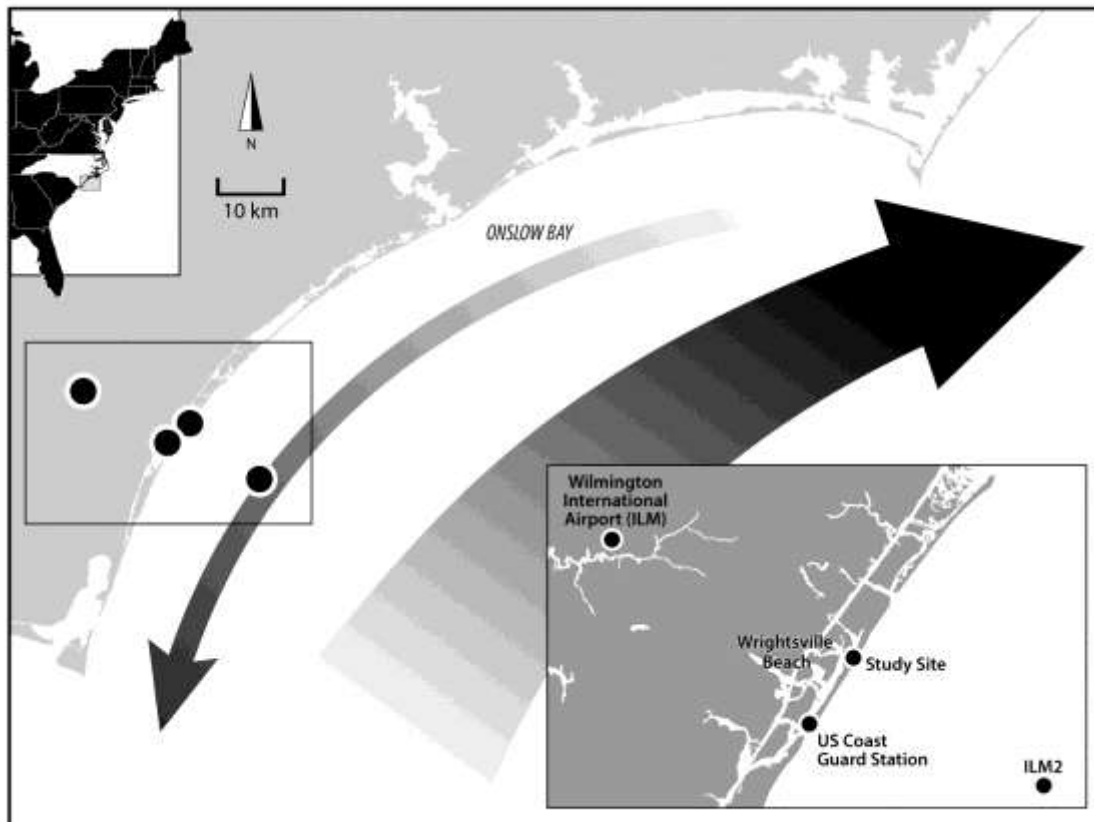


Fig. 1. Schematic of the study area showing general flow of the Gulf Stream offshore, the counter-flowing longshore current, and points from which data were obtained.

Primary production experiments were conducted *in situ* at Wrightsville Beach, NC ($34^{\circ}12'48.84''\text{N}$; $77^{\circ}47'17.05''\text{W}$) in close proximity to a fishing pier with meteorological instrumentation. The beach is moderately dissipative with an offshore bar/runnel/beach face structure, so that under normal conditions waves break at both the bar and beach face; we define the surf zone as the area within which breaking waves occur. Tidal range averages 1.3 m. This

section of Wrightsville Beach receives regular beach nourishment (addition of dredged sand to the beach face) typically every four years during the winter/early spring, most recently in 2014 (D. Piatkowski, US ACOE, pers. comm.). Nourishment material was obtained from a nearby inlet and closely matched native beach material, as required by regulation. No surf zone studies were conducted while beach nourishment activities took place; visible turbidity from nourishment activities typically persisted for less than 1 week after activity ended.

2.2 Primary Production

Primary production by surf zone phytoplankton was measured *in situ* following methods described by Kahn and Cahoon (2012). Briefly, a line 10 m long was strung between two anchoring devices deployed in the near-shore swash zone at depths of 0.3 to 0.5 m, with carabiners attached at 1 m intervals. Pairs of 250 ml polystyrene tissue culture flasks were filled with swash zone water, amended with 1-2 μCi ^{14}C - NaHCO_3 (MP Biomedicals), capped and attached to the carabiners. ‘Dark’ treatment flasks were amended with an aliquot of DCMU, which uncouples photosystems I and II and thereby blocks carbon fixation. Eight ‘light’ and four ‘dark’ flasks were deployed for two-hour mid-morning to noon incubations. The anchor-line-flask array was shifted as the tide changed water levels so that the flasks were kept in motion by wave action at a relatively constant depth range. Four separate swash zone water samples were collected at the start of each incubation for measurement of chlorophyll *a* (chl *a*) following Welschmeyer (1994). Upon retrieval, the ‘light’ flasks were amended with DCMU to stop further carbon fixation, and the samples returned to the laboratory. A 1 mL aliquot from each flask was removed for scintillation counting to determine total added isotope activity, then known volumes from each flask were filtered through Whatman GF/F (0.7 μm) or Millipore (0.45 μm) membrane filters, which were rinsed 3X with filtered seawater and placed in scintillation vials for counting. Primary production was calculated according to Parsons et al. (1984), using salinity of swash zone water measured with a YSI 85 meter to estimate total CO_2 . Primary production (PP) was expressed as $\text{mg C m}^{-3} \text{ hr}^{-1}$ and normalized to phytoplankton biomass (P_B) as $\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}$.

2.3 Related parameters

Phytoplankton and sediment-associated microalgal biomass in the surf zone were also measured in a prior 2-year study (2008-2010) at 4 locations at Wrightsville Beach. Nutrient concentrations of the water column and pore water, sediment-associated (=“benthic”) microalgal biomass, phytoplankton biomass, and responses of phytoplankton to nutrient enrichment in surf zone water samples were also measured as part of a graduate-level biological oceanography laboratory course during the spring semesters between 2012 and 2015. Analyses of ammonium, soluble reactive phosphate, and reactive silicate followed standard protocols (Koroleff, 1983; Parsons et al., 1984). Phytoplankton biomass was analyzed fluorometrically, as above; sediment microalgal biomass was analyzed fluorometrically as in McGee et al. (2008). Nutrient enrichment experiments were conducted as in Cahoon (2008), using a nutrient ‘deletion’ approach, in which combinations (all treatments replicated 4-6X) of macronutrients (N as nitrate, P as phosphate, and Si as silicate) were used to amend raw surf water, and growth rates calculated from changes in chl *a* compared to controls containing either all macronutrients or none. This approach allows identification of secondary limitation and co-limitation. Qualitative microscopic observations of the microflora were conducted at several times in conjunction with nutrient limitation experiments using epifluorescence microscopy. Surf zone water samples were incubated with acridine orange (AO) for 5-10 min, filtered through black membrane filters (Millipore, 0.45 μm pore size), rinsed with filtered sea water, and mounted with Cargille type FF immersion oil for slide viewing. Slides were examined on an Olympus BX60 epifluorescence microscope using blue excitation illumination and a digital photography system.

Additional relevant parameters were measured or sampled simultaneously with primary production incubations. Incident radiation at the study site was measured with a LiCor 192S 2π quantum PAR sensor interfaced with an LI-1000 data logger operating in log mode to record integrated PAR flux during the incubation period at 10 min intervals. Water temperature was measured with a YSI 85 meter shortly after incubations commenced. Observations of cloud cover, wind direction and speed, wave height, tide stage, and air temperature were also made during incubations. Data on tide heights (distance above mean low-low water) at the beginning of each incubation were obtained from a US Coast Guard tide gauge (#8658163) ~ 1.5 km from the study site (34°11’20.40 N; 77°48’43.49W). Data on significant wave height just offshore the study site were obtained from UNCW CORMP buoy ILM 2 (34° 08.400 N; 77° 42.900 W; http://www.cormp.org/query_mooring.php?mysta=ILM2) for each incubation day. Rainfall data

were obtained from the US NOAA-NESDIS station at Wilmington International Airport (GHCND: USW00013748) ~ 12.6 km WNW of the study site (34°16'32.35N; 77°54'39.90W).

2.4 Calculations and data analyses

Estimates of primary production and related variables were obtained from 18 field studies conducted between June 2012 and May 2013, supplemented by three data sets from the same location collected in July 2010 by Kahn and Cahoon (2012) and four data sets collected during field studies between February and April, 2015, for a total of 25 PP and P_B data sets used in the analyses presented here. Methods in each case were similar, particularly the *in situ* incubation approach to measuring surf zone phytoplankton production. Correlations among variables were initially explored using Principal Components Analysis, which was used to identify likely drivers for Chl *a*, PP and P_B . Specific hypotheses addressing factors having significant effects on Chl *a*, PP and P_B were then tested using multiple regression. All statistical analyses were performed using JMP Pro (SAS Institute).

3. Results

Primary production at Wrightsville Beach averaged 20.6 (sd=22.9) mg C m⁻³ h⁻¹ for an average phytoplankton biomass of 4.3 (sd=3.3) mg chl *a* m⁻³, yielding an average P_B value of 5.3 (sd=5.3) mg C (mg chl *a*)⁻¹ h⁻¹ (Table 1); assuming a 10 hour average production day, this yields daily production of ~200 mg C m⁻³ d⁻¹ and annual production of ~75 g C m⁻³ yr⁻¹. The data indicated a seasonal effect on both primary production and biomass-normalized production, with higher values occurring in summer months (Fig. 2). Chl *a* values reported in the primary production studies were not significantly different from site-averaged values obtained in the previous 2008-2010 study of phytoplankton biomass at Wrightsville Beach (1-way ANOVA, F=0.08, df=1,107, p=0.78). Phytoplankton concentrations for all data sets averaged 3.34 mg Chl *a* m⁻³ (s.d. = 0.91, n= 525), whereas sediment-associated microalgal biomass averaged 13.1 mg m⁻² (s.d. = 1.60, n=753) (Fig. 3).

| Parameter (unit) | Mean | sd | Range |
|--|-------|------|------------|
| Production (PP, mg C m ⁻³ h ⁻¹) | 20.64 | 22.9 | 0.48-74.5 |
| Biomass (chl <i>a</i> , mg m ⁻³) | 4.29 | 3.34 | 0.99-16.2 |
| Production/biomass (P _B , mg C (mg chl <i>a</i>) ⁻¹ h ⁻¹) | 5.27 | 5.33 | 0.18-20.2 |
| Temperature (°C) | 20.8 | 6.9 | 8.9-28.6 |
| Salinity (psu) | 34.5 | 1.14 | 31.7-36.1 |
| 1-day rain (cm) | 0.27 | 0.90 | 0-4.39 |
| 3-day rain (cm) | 1.46 | 2.03 | 0-7.09 |
| PAR (μmol m ⁻² sec ⁻¹) | 1605 | 499 | 440-2160 |
| Tide height (m above mllw) | 0.76 | 0.52 | -0.05-1.92 |
| Significant wave height (m) | 0.98 | 0.31 | 0.46-1.59 |

Table 1. Values of environmental and biological parameters during production incubations in the surf zone at Wrightsville Beach, NC, USA, July 2010 – May 2015; n=25.

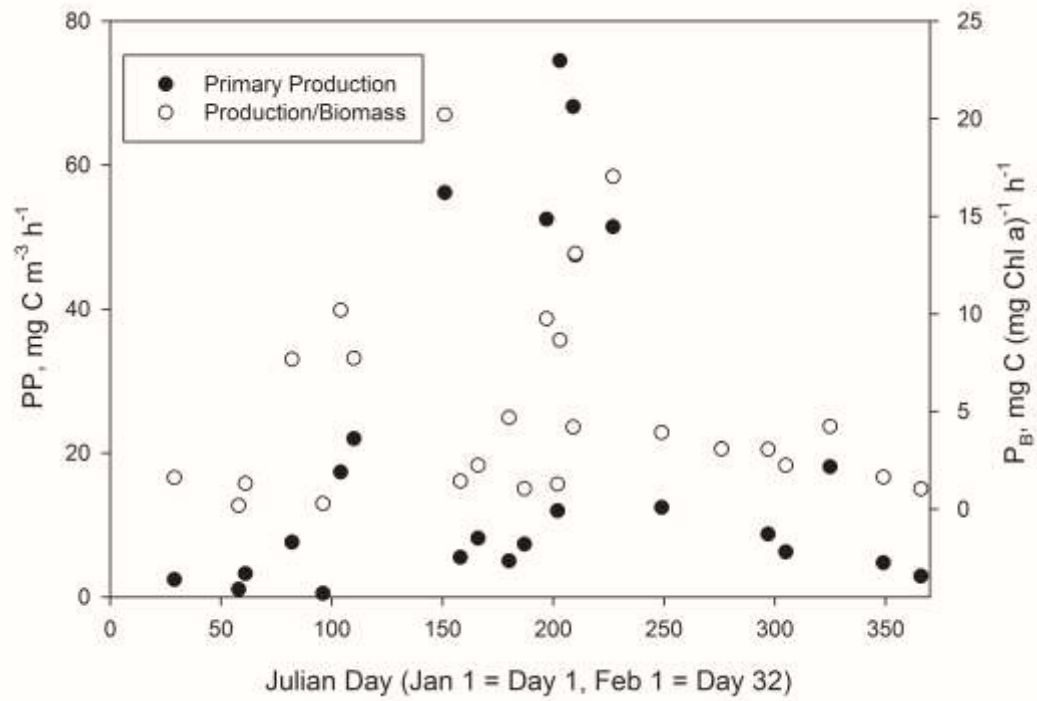


Fig. 2. Temporal pattern of primary production and biomass-normalized production at Wrightsville Beach, NC.

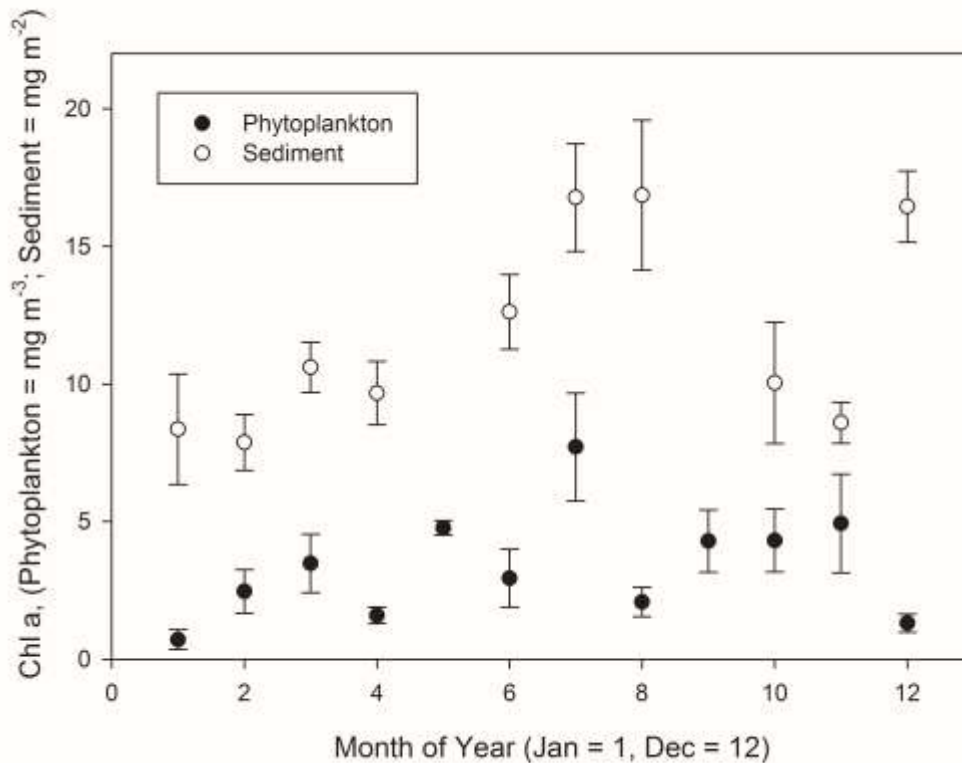


Fig. 3. Seasonal variation of phytoplankton and sediment-associated microalgal biomass at Wrightsville Beach, NC.

Long-term (1-week) nutrient limitation experiments identified statistically significant primary limitation by nitrogen and secondary limitation by silicate for surf-zone phytoplankton in February and April 2012, February 2013, February 2014, and co-limitation by N, P, and Si in February 2015 and February and September 2016. Pore water nutrient levels measured in 2013 were higher than levels in surf zone water (1-way ANOVA: NH_4^+ : $F=43.8$, $df=1,75$, $p<0.0001$; PO_4^{3-} : $F=6.60$, $df=1,72$, $p=0.012$; SiO_3^{2-} : $F=183$, $df=1,72$, $p<0.0001$; Table 2a, b). Nutrient concentrations were never below detection limits in these samples.

The relatively high coefficients of variation ($sd/mean$) in the biological parameters, Chl a , PP, and P_B (Table 1), indicated the likelihood that one or more environmental parameters drove phytoplankton biomass and production. Consequently, the relationships among the biological and environmental parameters were examined using principle components analysis (PCA). Eigenvalues for the first three principal components (PC, eigenvector values >1) in each analysis indicated potentially interesting effects of each independent variable on overall variance (Table

3). PC1 was driven primarily by PP and temperature. PC 2 was driven by 1-day and 3-day rainfall and incident PAR. PC3 was driven primarily by Chl *a*, significant wave height, and P_B.

| Date (m/d/y) | [NH ₄ ⁺] | [PO ₄ ³⁻] | [SiO ₃ ²⁻] |
|--------------|---------------------------------|----------------------------------|-----------------------------------|
| 1/16/13 | 2.05 [7.68] 7 | 0.20 [0.38] 9 | 2.44 [1.10] 6 |
| 2/4/13 | 0.11 [0] 3 | - | 1.31 [0.05] 4 |
| 4/10/13 | 1.40 [0.34] 12 | 1.51 [1.24] 12 | 0.18 [0.24] 12 |
| (high tide) | | | |
| 4/17/13 | 1.27 [0.49] 12 | 0.31 [0.23] 12 | 1.17 [0.19] 12 |
| (low tide) | | | |
| 4/24/13 | 1.18 [0.51] 6 | 0.68 [0.17] 6 | 1.92 [0.08] 6 |
| 2/5/14 | 1.31 [0.61] 8 | 1.68 [1.29] 8 | 2.30 [0.88] 8 |
| 1/23/15 | 1.51 [0.31] 10 | 0.27 [0.19] 11 | 4.60 [1.13] 12 |
| Overall: | 1.37 [1.29]58 | 0.76 [0.59]58 | 2.02 [0.55]60 |

Table 2a. Nutrient (uM) data (**mean** [sd] n) from surf zone waters at Wrightsville Beach, NC, USA, 2012-2015. Missing value was not measured at respective sampling time.

| Date (m/d/y) | [NH ₄ ⁺] | [PO ₄ ³⁻] | [SiO ₃ ²⁻] |
|--------------|---------------------------------|----------------------------------|-----------------------------------|
| 1/16/13 | 6.61 [0.88] 11 | 1.86 [1.04] 9 | 4.88 [0.90] 8 |
| 1/30/13 | 7.68 [2.76] 6 | 1.14 [0.73] 6 | 10.4 [3.88] 6 |
| 2/6/13 | 5.16 [2.48] 6 | 0.53 [0.16] 6 | 8.62 [0.89] 6 |
| 2/13/13 | 4.74 [0.79] 6 | 0.97 [0.20] 6 | 7.21 [2.35] 6 |
| 4/24/13 | 3.66 [1.18] 3 | 10.5 [7.37] 3 | 6.70 [1.26] 3 |
| Overall: | 5.91 [1.54]32 | 2.14 [1.27]30 | 7.47 [1.85]29 |

Table 2b. Pore water nutrient (uM) and sediment Chl *a* (mg m⁻²) data (**mean** [sd] n) from the surf zone at Wrightsville Beach, NC, USA, 2013.

| | <u>PC 1</u> | <u>PC2</u> | <u>PC3</u> |
|-------------------------|-------------|------------|------------|
| <u>Eigenvalues:</u> | 3.27 | 1.89 | 1.51 |
| <u>Eigenvectors</u> | | | |
| Chl <i>a</i> | 0.29 | -0.10 | 0.50 |
| PP | 0.48 | 0.09 | -0.07 |
| P _B | 0.33 | 0.23 | -0.46 |
| Salinity | 0.33 | 0.18 | 0.40 |
| Temperature | 0.45 | 0.07 | 0.27 |
| 1-day rain | 0.14 | 0.60 | -0.02 |
| 3-day rain | -0.20 | 0.54 | 0.12 |
| PAR | 0.29 | -0.43 | -0.05 |
| Tide height | -0.28 | 0.19 | 0.27 |
| Significant wave height | -0.22 | -0.11 | 0.45 |

Table 3. PCA results for Chl *a* (mg m⁻³), PP (mg C m⁻³ h⁻¹), P_B (mg C (mg chl *a*)⁻¹ h⁻¹) and environmental parameters at Wrightsville Beach, NC, USA.

A biplot of PC 1 and PC2, the correlation matrix from PCA and subsequent pair-wise correlation analyses revealed potentially significant cause-effect relationships among Chl *a*, PP, or P_B and several environmental parameters (Fig. 4; Table 4). These relationships were further explored by stepwise multiple regression, in which non-significant independent variables were removed from the model until only significant (p<0.05) variables remained and R²_{Adj} was maximized. Results of these regressions were:

$$(1) \text{ Chl } a = 0.23(\text{Temp}); F = 6.98, df = 1,23, p = 0.0146; R^2_{\text{Adj}} = 0.20$$

$$(2) \text{ PP} = 2.89(\text{Chl } a) + 9.70(\text{1-Day Rain}) - 4.83(\text{Tide Height}); \text{ overall } F = 6.43, df = 4,19, p = 0.002, R^2_{\text{Adj}} = 0.49$$

$$(3) \text{ P}_B = 8.11 + 2.30(\text{1-Day Rain}) - 1.38(\text{Tide Height}); \text{ overall } F = 4.40, df = 2,22, p = 0.025, R^2_{\text{Adj}} = 0.22$$

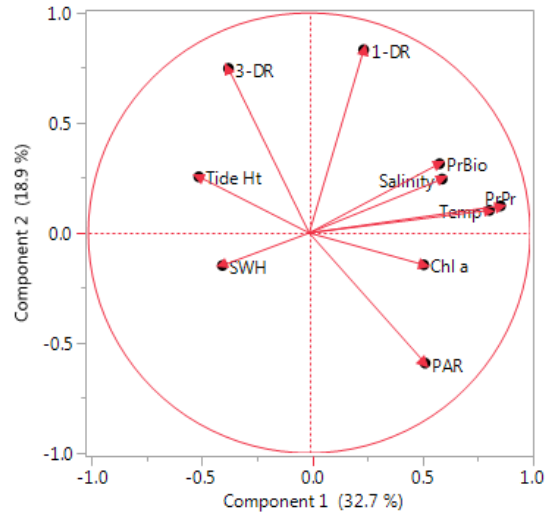


Fig. 4. Biplot of PC1 and PC2 from Principle Components Analysis of surf zone parameters. Chl *a* = phytoplankton biomass, PAR = ambient light flux, PrBio = biomass-normalized production (PB), PrPr = primary production, SWH = significant wave height, Temp = temperature, Tide Ht = tide height (vs. mean low-low water) at incubation start, 1-DR = 1-day rain, 3DR = cumulative rainfall 3 days prior to incubation start.

| Parameter | Chl <i>a</i> | PP | P _B |
|--------------|--------------------|--------------------|----------------|
| Salinity | 0.33, n.s. | 0.36, n.s. | 0.11, n.s. |
| Chl <i>a</i> | - | 0.52, 8.59; 0.0075 | - |
| Temp. | 0.48, 6.98; 0.0146 | 0.56, 10.4; 0.0037 | 0.31, n.s. |
| 1-day rain | 0.03, n.s. | 0.23, n.s. | 0.31, n.s. |
| 3-day rain | 0.08, n.s. | -0.11, n.s. | 0.02, n.s. |
| PAR | 0.22, n.s. | 0.38, 9.87; 0.0046 | 0.16, n.s. |
| Tide height | 0.15, n.s. | -0.41, 4.72; 0.04 | -0.37, n.s. |
| SWH | 0.08, n.s. | -0.26, n.s. | -0.30, n.s. |

Table 4. Pair-wise Pearson's correlation coefficients and statistics for Chl *a*, PP and P_B vs. environmental parameters at Wrightsville Beach, NC, USA. Values are r, F; p; (all df = 1,23); n.s. = not significant, p ≥ 0.05.

Chl *a* (phytoplankton biomass) was weakly but significantly driven by increasing temperature, with generally higher biomass in the summer months; the Y-intercept was not significant. PP was, not surprisingly, a function of Chl *a* (and therefore higher in summer months as well); inclusion of PAR in the regression yielded the highest R²_{Adj} value, but the effect of PAR itself was not significant (P=0.061), nor was the Y-intercept. Both PP and P_B responded positively to rainfall on the day immediately preceding each incubation (1-day rain), and were inversely

related to tide height at the beginning of *in situ* incubations. In contrast, neither primary production nor biomass-normalized production responded significantly to temperature, PAR, or other measured environmental parameters.

The surf zone microflora consisted of a diverse array of taxa that included small centric and pennate diatoms, dinoflagellates, cyanobacteria, and other very small forms that could not be identified using epifluorescence microscopy. Nutrient enrichment experiments, especially when nitrogen and silicate were provided, yielded assemblages dominated by small centric diatoms, including the genera *Skeletonema*, *Chaetoceros*, and *Thalassiosira*, as well as several pennate forms (Fig. 5).

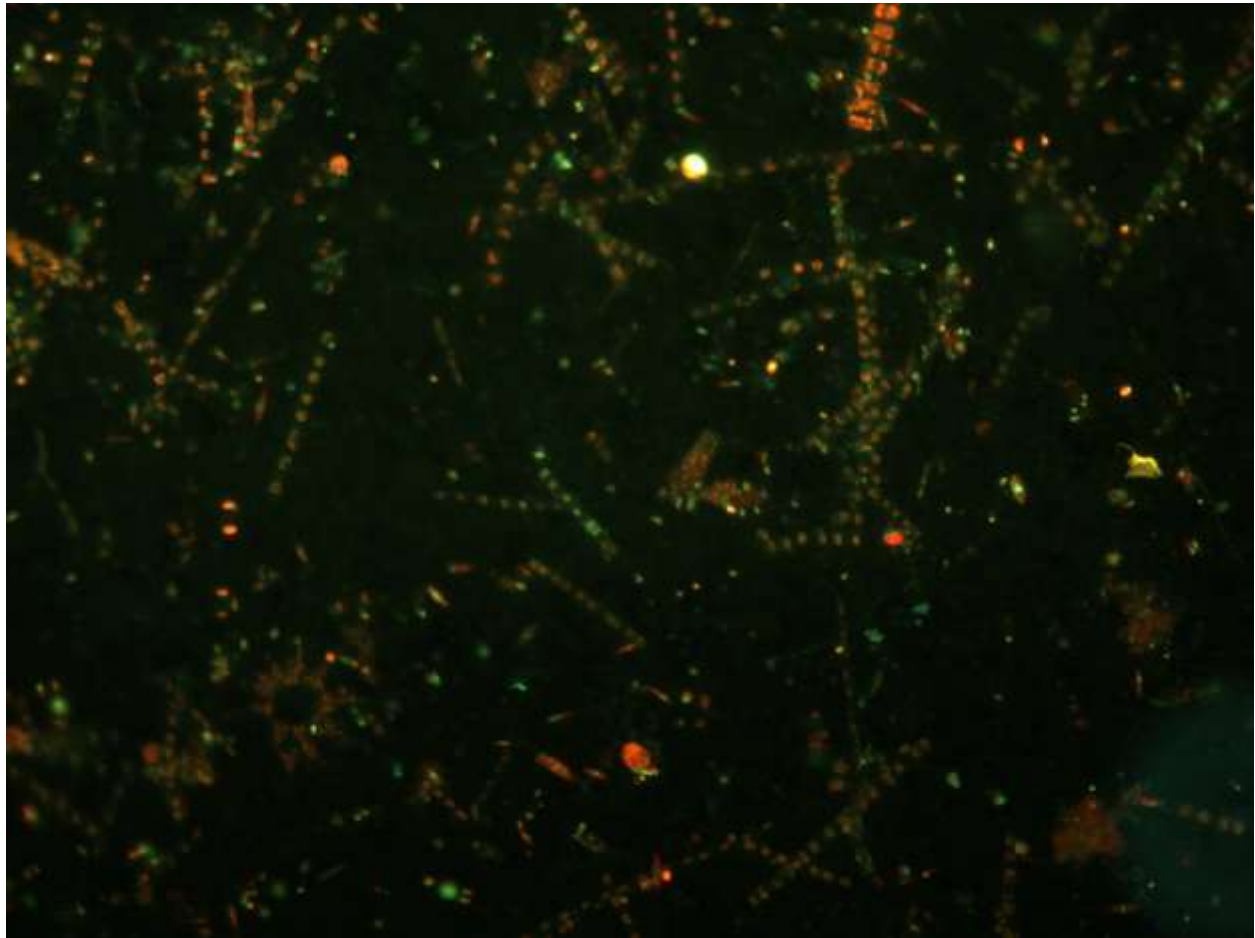


Fig. 5. Epifluorescence photomicrograph of surf zone phytoplankton illustrating representative forms grown in nutrient-replete conditions. Note abundant chain-forming and single pennate diatoms.

4. Discussion

The only significant driver of phytoplankton biomass (chl *a*) in the surf zone detected in these analyses was temperature, although the effect was not strong. A variety of temperature-related mechanisms might be advanced, including enhanced growth rates of surf zone microflora, enhanced nutrient recycling in the surf zone, higher silicate solubility at warmer temperatures (Iler, 1979; potentially relieving silicate limitation by diatoms), but these are not mutually exclusive. We hypothesize that surf zone phytoplankton assemblages may adapt to seasonal variation in temperature to some degree, which might weaken a temperature effect on biomass, as might seasonality in grazer effects (Stull et al., 2015). Although temperature was not significantly associated with PP, the significant effect of chl *a* on PP could include a temperature-mediated effect.

The significant effects of tidal height on surf zone production and biomass-normalized production, in that lower tidal heights at the start of incubations corresponded to higher PP and P_B values, suggest interesting interactions that bear further examination. One hypothesis is that re-suspended benthic microalgae are relatively more abundant in surf zone water at low tide, and that photo-adaptation to relatively lower light levels than water column phytoplankton allows them to support higher PP and P_B when suspended into the better-illuminated water column. Benthic microalgal biomass can be important in the shallow surf zone at Wrightsville Beach on an areal basis (Fig. 3), similar to findings by Speybroeck et al. (2008) elsewhere. Microscopic observations of surf zone water samples revealed the presence of pennate, benthic diatoms, indicating re-suspension effects in the surf zone (Fig. 5). Benthic microalgal photo-adaptation to lower light levels and their ability to respond positively to increased light availability across a wide range of values are well documented (Barranguet et al., 1998; Hartig et al., 1998; Cahoon, 1999; Cahoon, 2006; Gattuso et al., 2006; Jesus et al., 2009). Consequently, we cannot rule out that two somewhat distinct surf zone microfloras, phytoplankton and benthic microalgae, play complementary roles in supporting enhanced biomass and production in the surf zone compared to deeper waters offshore. If so, the application of P-I (or P-E) relationships derived from phytoplankton may inadequately predict responses of the surf zone flora to PAR flux variations, which may also explain our inability to detect a statistically significant PAR effect on PP and P_B .

values in this study. Thus, relationships among Chl *a*, PP, and P_B may be a more complex function of multiple, moderately related processes than has previously been assumed.

The significant, positive effects of 1-day rainfall on PP and PB suggest that rainwater may pump pore water through the highly permeable beach and thereby enhance nutrient fluxes into the nearshore zone. Our observations of pore water nutrients (Table 2b) and other studies of beach nutrient dynamics (Campbell and Bate, 1996, 1997; Avery et al., 2008) support this inference. Questions remain about the magnitude of this effect vs. other nutrient supply mechanisms, such as estuarine outwelling and *in situ* regeneration, but the rainfall effects suggest the overall importance of nutrient supply in regulating surf zone production.

Phytoplankton biomass concentrations and primary production rates in the surf zone at Wrightsville Beach, NC, USA, were generally lower than values reported from other analyses of surf zone ecosystems, e.g., 14.6 mg chl *a* m⁻³ (Campbell and Bate, 1988) and 1.2 to 2.1 g C m⁻² d⁻¹ (Heymans and MacLachlan, 1996), but several qualifications attach to those observations. First, in large part owing to the logistic challenges inherent in such measurements (Clark et al., 2009, 2010), there are very few published reports of actual *in situ* measurements of surf zone production, e.g., Steele and Baird (1968, although technically not an open beach study). Most analyses have relied on measures of biomass, light availability, and temperature to model production using P-I relationships (Bate et al., 1990; Campbell and Bate, 1988; Heymans and MacLachlan, 1996; Lercari et al., 2010; Vassallo et al., 2012). Second, many studies of surf zone phytoplankton in other coastal regions have been prompted by observations of unusually high biomasses of distinctive surf-zone microflora, typically diatoms adapted to surf zone conditions (Talbot and Bate, 1988, 1989; Talbot et al., 1990), which experience high nutrient availability from onshore or upwelling-associated inputs to the nearshore zone (Campbell and Bate, 1997; Odebrecht et al., 1995, 2014; Rörig and Garcia, 2003). Consequently, the surf zone production values reported here are consistent with the more modest phytoplankton biomass observed as well, and likely reflect the lower nutrient availability typical of Onslow Bay waters (Atkinson, 1985). P_B values obtained in this study indicate a moderately active surf zone phytoplankton population, consistent with the photo-physiological assessments reported from this surf zone community by Kahn and Cahoon (2012) and elsewhere (Campbell et al., 1988).

Comparisons of this surf zone community with unusual surf zone phytoplankton communities elsewhere, however, are less insightful than comparisons with biomass and

production of adjoining phytoplankton communities in the coastal ecosystem. The surf zone community connects with estuarine communities via tidal flows through inlets and longshore currents, and with continental shelf waters via various transport mechanisms, including wind effects, longshore transport, and whole-shelf scale circulation (Fig. 1). Phytoplankton biomass and production in the surf zone measured in this study are generally lower than in nearby estuarine habitats (Williams and Murdoch, 1966; Boyer et al., 1993; Litaker et al., 1993; Paerl et al., 2007), but are significantly higher than values reported from offshore Onslow Bay waters (Cahoon and Cooke, 1992; Mallin et al., 2005), a pattern noted elsewhere in the world ocean (Rörig and Garcia, 2003). We are aware of no studies of phytoplankton biomass and production in the nearshore zone just offshore of the surf zone itself, but visual observations of ocean color suggest that the most productive waters lie within 100-200 m of the beach. Thus, the surf zone may be described as a relatively narrow band of coastal water with relatively high phytoplankton biomass and production compared to adjacent offshore waters.

Relatively high phytoplankton biomass and production in the spatially-restricted surf zone indicate two ecologically important features. First, this productivity likely plays a role in supporting higher trophic level organisms in the nearshore zone, a role that has been explored in other regions (Lastra et al., 2006; Lercari et al., 2010). Stull et al. (2015) found that increased surf zone phytoplankton biomass in the warm season corresponded with higher numbers of planktonic larvae of invertebrate taxa common in both estuarine and coastal waters. Surf zone zooplankton are in turn important to planktivores (Delancey, 1989; du Preez et al., 1990). Second, along coastlines with extensive sandy beaches transected by inlets, surf-zone primary producers provide connectivity between estuaries and offshore habitats (Nel et al., 2014). Watt-Pringle and Strydom (2003) and Cowley et al. (2010) reported finding estuarine-dependent post-flexion fish larvae in the surf zone. Beyst et al. (2001) offered a similar community connectivity argument about surf zones on the Belgian coast. Thus the primary productivity of surf zones may complement and support the nursery function of estuaries and the dispersal function of longshore transport. Along much of the U.S. Southeast Coast, surf zone habitats may therefore be important to many fishery species.

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