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Factors affecting surf zone phytoplankton production in Southeastern North Carolina, USA



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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.

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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 and 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 and 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 mg chl *a* m⁻³ (Campbell and Bate, 1988) and ~36 mg chl *a* 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 g C m⁻² yr⁻¹.

(Campbell and Bate, 1988) and 1.2–2.1 g C m⁻² d⁻¹ (Heymans and McLachlan, 1996). du Preez and Campbell (1996) reported biomass-specific production rates of up to 16 mg C (mg chl a)⁻¹ 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 zonespecific 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

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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 beachassociated 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 near-shore Onslow Bay is generally oligotrophic (average [DIN]< 0.5 μ M), with phytoplankton biomass (average [Chl a] < 0.5 μ g L⁻¹) and production values (average: 27.4 mg C m⁻² 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.

Primary production experiments were conducted *in situ* at Wrightsville Beach, NC (34°12′48.84″N; 77°47′17.05″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 0.3-0.5 m, with carabiners attached at 1 m intervals. Pairs of 250 ml polystyrene tissue culture flasks were filled with swash zone water, amended with $1-2 \mu Ci^{14}C$ -NaHCO₃ (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 2-h 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 um) or Millipore (0.45 um) membrane filters, which were rinsed $3 \times$ 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 m to estimate total CO₂. Primary production (PP) was expressed as mg C m^{-3} hr^{-1} and normalized to phytoplankton biomass (P_B) as mg C $(mg chl a)^{-1} h^{-1}$.

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, sedimentassociated (="benthic") microalgal biomass, phytoplankton biomass, and responses of phytoplankton to nutrient enrichment in surf zone water samples were also measured as part of a graduatelevel 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 colimitation. 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

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