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Study of photosynthetic productivity in the Northern Gulf of Mexico: Importance of diel cycles and light penetration

Yan Zhao [a,*], Antonietta Quigg [a,b]

[a] Department of Oceanography, Texas A&M University, College Station, TX 77843, USA
[b] Department of Marine Biology, Texas A&M University, Galveston Campus, Galveston, TX 77553, USA

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ABSTRACT

Based on ^{14}C uptake assays, in vivo chlorophyll (chl) *a* fluorescence and HPLC pigment analysis, phytoplankton photosynthetic physiology and productivity in 24-h diel cycles were characterized at three stations in April and August 2012 in the Northern Gulf of Mexico. The results indicated the sub-pycnocline primary production accounted for 5–48% of the total integrated primary production, emphasizing the important influence of euphotic zone in shallow coastal areas. During the diel cycles, chl *a*-specific light-saturated photosynthesis (P^B_{max}) as measured with photosynthesis versus irradiance curves (P–I) and the photoprotective pigment pool (diadinoxanthin, diatoxanthin, chl *a*) showed phytoplankton acclimation to be strongly influenced by water column structure (mixing versus stratification). Changes in chl *a* fluorescence and transformations between photoprotective pigments were most recognizable in surface samples. The dominate phytoplankton groups (diatoms and cyanobacteria in April and August respectively) also influenced the measured photosynthetic parameters. The Northern Gulf of Mexico is a typical coastal ecosystem with high variability of nutrients, light (intensity and attenuation) and mixing. Our study provided evidence that phytoplankton in this area are adapted to changing environmental conditions by means of fast responses as well as long-term photoacclimation strategies. Understanding the major drivers could help us to improve models involving the calculation of primary productivity, such as those focused towards understanding mechanisms controlling hypoxia.

1. Introduction

Phytoplankton dynamics are the outcome of nutrient availability, light conditions and physical mixing. The influence of light in diel rhythms on phytoplankton is observed in many aspects such as cell divisions, photosynthesis, chl *a* fluorescence and gene expression (Suzuki and Johnson, 2001; Ohi et al., 2005; John et al., 2012). Both laboratory and field studies have found that diel rhythms are predictable (Vaulot and Marie, 1999; Litaker et al., 2002; Bruyant et al., 2005; Brunet et al., 2008; Quigg et al., 2012; McInnes et al., 2014). Phytoplankton carbon fixation rates usually exhibit peak values early in the morning or around noon (Harding et al., 1981; Prézelin, 1992); without consideration of this variability errors in the calculation of total integrated primary production occur (Harding et al., 1981, 1982). For light reactions, chl *a* fluorescence parameters such as minimum fluorescence (F_0) and the maximum quantum yield of photosystem (PS) II (F_v/F_m) show quenching in the daytime caused by photoinhibition under excess light stress and recovery at night (Falkowski and Raven, 2007). Photoprotection involves an enzymatic-controlled epoxidation and de-epoxidation of pigment conversion, in order to dissipate extra energy as nonphotochemical quenching (NPQ) before the damage of light reaction centers (Falkowski and LaRoche, 1991). This process of pigment conversion was named the xanthophyll cycle (XC) (Long et al., 1994). In chromophyte algae, XC involves the transformation from diadinoxanthin (Dd) to diatoxanthin (Dt) (Lavaud et al., 2004; Falkowski and Raven, 2007). In cyanobacteria, photoprotection involves zeaxanthin and decoupling of phycobilisomes (Falkowski and Raven, 2007).

The diel "bio-clock" in phytoplankton shows variability in terms of frequencies and amplitudes in field studies. Physical mixing causes vertical movement of phytoplankton cells, which changes the irradiance experienced at different depths. Claustre et al. (1994) indicated the effect of mixing could diminish the difference in the proportion of Dt between day and night. At a 50 m deep coastal site with day–night alternations of thermal induced stratification and mixing, Brunet et al. (2008) found the sinusoidal diel patterns and exponential vertical patterns of Dt/ chl *a*, Dt/(Dt+Dd) (DES) and $\Delta F/F'_m$ (effective quantum yield of fluorescence). Doblin et al. (2011) found homogenous chl *a*

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[*] Corresponding author.
E-mail address: zhaoy@tamug.edu (Y. Zhao).

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fluorescence and photoprotective pigments within the mixed layer, but a lack of diel rhythm with carbon fixation rates in the Sub-Antarctic and Polar Front Zones.

As the largest river in the North America, the Mississippi River drains 40% of the area of the United States (Dagg et al., 2007). With the influence of riverine nutrients, the Northern Gulf of Mexico (NGOM) fuels high phytoplankton biomass and primary productivity, contributing to organic matter export and the complex food web. In the NGOM, the role of nutrients is frequently investigated, particularly along the Louisiana shelf (e.g., Quigg et al., 2011; Laurent et al., 2012; Turner and Rabalais, 2013), but the importance of light is less often examined (e.g., Lohrenz et al., 1994; Lehrter et al., 2009; Nunnally et al., 2014). John et al. (2012) found diel patterns of Rubisco (*rbcL*) mRNA and the chl *a*-specific light-saturated photosynthetic rate (P^B_{max}) in four different size classes of phytoplankton in the Mississippi and Orinoco River plumes, but did not consider the influence of hydrographic factors like mixing and depth on the amplitudes of the diel patterns.

Here, we examined diel patterns of primary productivity and photosynthetic physiology at a range of depths above and below the pycnocline, across the shelf at three stations, and during two very different time periods (April and August, 2012). Multiple techniques were used in our study, such as the ^{14}C method, Fluorescence Induction and Relaxation (FIRe) System and High Performance Liquid Chromatography (HPLC) pigments analysis, which were also common for the investigations in other field studies (Qian et al., 2003; Suggett et al., 2009a; Sylvan et al., 2011). Collectively this study provides information on the magnitude of productivity across a range of spatial and temporal scales.

2. Material and methods

2.1. Sample collections and hydrographic conditions

Two research cruises were conducted in April and August 2012 on the *R/V* Pelican. In each cruise, three 24 h stations along the 20 m isobath in the NGOM were studied (Fig. 1). Station A (29.07 °N, 89.93 °W) was in the Mississippi River plume while the other two stations were located further west on the Louisiana shelf area (B: 28.60 °N, 90.53 °W and C: 29.00 °N, 92.00 °W). A CTD rosette with 12 Niskin bottles and shipboard calibrated sensors was deployed overboard every 2 h to measure vertical hydrographic profiles such as temperature, salinity, chl *a* fluorescence and photosynthetically active radiation (PAR). Water samples were taken from four depths every 2 or 6 h and used to measure primary productivity (^{14}C method), chl *a* and pigment compositions and dissolved nutrient (N, P, Si) concentrations. The sampling intervals were dependent on the depth of the pycnocline, with two samples taken above and two below. We will refer to these as surface (sur), middle 1 (mid1), middle 2 (mid 2) and bottom (bot) respectively. The mixed layer depth (MLD) was defined by the depth of the maximum Brunt–Väisälä frequency (*N*) calculated using Eq. (1). The extinction coefficient (k_d) was calculated using Eq. (2), and the depth of euphotic zone (Z_{eu}) was calculated using Eq. (3).

$$N = \sqrt{-\frac{g}{\rho}\frac{\partial\rho(z)}{\partial z}}, \tag{1}$$

where ρ is the potential density, g is the local acceleration of gravity, z is the geometric height;

$$E_z = E_0 \exp^{-k_d z}, \tag{2}$$

where E_z is the solar irradiance at depth z, E_0 is the solar irradiance on the surface. In this study, we applied values at the surface and bottom to calculate k_d;

$$Z_{eu} = \ln(0.01)/-k_d, \tag{3}$$

when the calculated Z_{eu} exceeded the bottom depth, it was considered equal to the bottom depth.

2.2. Primary productivity measurements

Photosynthesis versus irradiance (*P–I*) curves were performed in a photosynthetron according to Lewis and Smith (1983) attached a water bath to maintain the in situ temperature. Aliquots of ^{14}C labeled seawater (1 mCi ml^{-1} $H^{14}CO_3{}^{-}$) were incubated at a range of PAR from 15 to 1800 μmol m^{-2} s^{-1}. Triplicate samples were treated with 5 ml Ecolume scintillation cocktail and 50 μl phenethylamine to determine the ‘total’ amount of ^{14}C added. Before the incubation, triplicate water samples were fixed with buffered formalin for ‘background’ values. Incubations were terminated with buffered formalin after 60 min in April and 45 min in August. Samples were acidified for 24 h to purge the unincorporated ^{14}C before counting with a Beckman LS 6500 liquid scintillation counter.

Photosynthetic parameters were calculated by fitting the *P–I* model of Platt et al. (1980) using Eq. (4) and the in situ primary productivity (PP) was calculated using Eq. (5).

$$P^B = P^B_{max}\left(1 - e^{-\alpha E/P^B_{max}}\right)e^{-\beta E/P^B_{max}}, \tag{4}$$

where P^B_{max} is the model estimated maximum production per unit chl *a*, α is the initial slope of the *P–I* curve, and E is the light exposure during incubation, β represents photoinhibition;

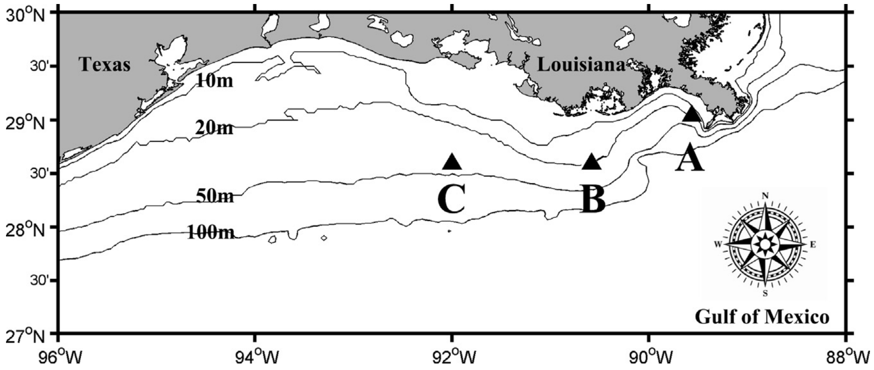

Fig. 1. Study area and bathymetry on the Texas–Louisiana shelf in northern Gulf of Mexico. The 10, 20, 50 and 100 m isobaths are shown. Locations of stations A, B and C which were sampled in April and August 2012 are offshore from the Mississippi and Atchafalaya Rivers respectively.