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Long-term variations in primary production in a eutrophic sub-estuary: Contribution of short-term events

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ABSTRACT

We determined the role of events in generating short-term variability in production, how they contribute to interannual variability, and their relationship to variability in the determinants of production, primarily biomass and photo-physiological parameters. We examined residuals from the seasonal and spatial mean daily rate in a 20-year time series of primary production in a eutrophic sub-estuary of Chesapeake Bay. The seasonal and spatial means of production and residuals were based on natural log-transformed measurements of daily primary production calculated from measurements of light saturation curves of photosynthesis for 20 years at 6 stations on the Rhode River, Maryland (USA). The variance of the residuals was greater than that explained by the seasonal and spatial statistical model, so that the event scale was the largest single source of variance. Residuals were classified as events if they exceeded $\pm\ln(2)$, signifying a multiplier or divisor of 2 above or below the seasonal-spatial mean. Spatially, events were most frequent at the most upstream station affected by runoff from the local watershed, and temporally most frequent in spring at all stations. Principal component analysis (PCA) of monthly averaged residuals revealed 3 characteristic temporal modes of residual variance, the first of which was associated with variability in spring due to the occurrence of extremely large spring blooms or their complete absence. Interannual variation in annual production was correlated with the strength of expression of these modes. Production events were analyzed in relation to residuals in the determinants of productivity, i.e. phytoplankton chlorophyll biomass, B, the light-saturated photosynthetic maximum normalized to chlorophyll, P^B_{max}, the diffuse attenuation coefficient for light, and the depth integral of the dimensionless photosynthesis profile. Negatively correlated changes in B and P^B_{max} were the most common mode of variation among the determinants, and this mode dampened variations in production and were common in fall months. Positively correlated changes in B and P^B_{max} constituted the second most common mode of variation amongst determinants, and this mode was positively correlated with variations in production and were most common in spring months. The prevalence of the first mode in fall months modulated the impact of major named storms on primary production in this system.

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1. Introduction

Primary production by phytoplankton is an important process by which nutrients are assimilated and inorganic carbon converted to labile organic carbon in estuaries (Kemp et al., 1997). Phytoplankton production has important consequences for water quality (Malone et al., 1988), eutrophication (Nixon, 1995; Cloern, 2001), fisheries yield (Breitburg et al., 2009), and littoral vegetation (Krause-Jensen et al., 2008). Primary production by phytoplankton depends on the biomass of phytoplankton present, availability of light throughout the water column, and photo-physiological properties of the phytoplankton assemblage present (Cole and Cloern, 1984; Bouman et al., 2010). Each of these determinants—biomass (as chlorophyll-*a*, Cloern and Jassby, 2010), light attenuation (Moore et al. 2012), and parameters of the phytoplankton photosynthesis-irradiance (P-E) curve (Côté and Platt 1983; Canion et al., 2013)—is highly dynamic, displaying 2- to 3-fold variation over a time span of several days. Given this degree of variability in the determinants of production, it is to be expected that the resultant rate of primary production by phytoplankton itself would be similarly variable on scales not captured by regular seasonal patterns (Canion et al., 2013; Houliez et al., 2013).

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A significant barrier to understanding or predicting short term variability in production derives from the complex interrelationships amongst the determinants that may alternatively compensate or reinforce one another, and these may be expressed in highly site-specific ways. For example, flow events that deliver nutrients also increase stratification, thereby improving the light environment for phytoplankton and stimulating blooms (Loftus et al., 1972; Bouman et al., 2010). Alternatively flow may deliver high concentrations of particulate and dissolved light attenuating substances along with nutrients, that suppress primary production and limit the formation of blooms to their full potential (Ramus et al., 2003). Progress toward improved understanding and drawing generalizations must rely on data series of sufficient length to observe many such events, and an analytical procedure able to resolve the effects of different determinants independently.

In an analysis of a 20-year time series consisting of 3443 measurements of daily production, Gallegos (2014a,b) determined that primary production in the Rhode River subestuary of Chesapeake Bay was strongly seasonal with an average peak in summer, and that annual production varied by a factor of 2. However, interannual variability in annual phytoplankton production was not predictable from commonly used climate indices, although a qualitative classification of years based on spring bloom magnitude was a significant predictor of annual production. The Rhode River is a highly dynamic system, with much variability about the normal seasonal pattern capable of influencing annual totals that has not been systematically analyzed. For example, the spring freshets of the Susquehanna River may trigger extraordinary blooms of the dinoflagellate *Prorocentrum minimum* in some years (Tyler and Seliger, 1978; Gallegos and Jordan, 2002), or inhibit blooms by washout of phytoplankton biomass and delivery of turbidity in other years, depending on the amount and timing of flow (Gallegos et al., 1997, 2010). Here we analyze the residuals of that primary production series for the purpose of determining the role of major blooms (or their absence) and other short-term events in driving interannual variability in production, and to investigate how the determinants of production respond to particular perturbations to determine the overall response of the system. We begin with a basic statistical characterization of the residuals from the seasonal and spatial signal, and develop a procedure for partitioning the residual into contributions due to phytoplankton biomass, photo-physiological parameters, and light attenuation. Examination of the seasonal distributions in residuals revealed that patterns of variation among the determinants in spring combine to drive variations in production that are the main source of interannual variability, while those that occur in late summer-fall covary to dampen fluctuations in production.

2. Methods

2.1. Site description

The Rhode River (Maryland, USA, 38° 52′ N, 76° 31′ W) is a shallow, eutrophic subestuary on the western shore of Chesapeake Bay. A site map showing station locations is given in Gallegos (2014a). The main local source of freshwater and inorganic P (Jordan et al., 1991) to the Rhode River is Muddy Creek, an intermittent stream draining a 2378 ha watershed that is dominated by forest (57%) and grassland (24%). Spring flow of the Susquehanna River, which is the main freshwater source to upper Chesapeake Bay, supplies the major input of nitrate to the system. This nitrate source enters at the mouth of the subestuary, and exceeds the supply from Muddy Creek (Jordan et al., 1991). Primary production of the Rhode River is strongly seasonal with a minimum in late winter and maximum in July (Gallegos, 2014a). Annual production varies from 152 to 612 (average 328) g C m^{-2} (Gallegos, 2014b).

2.2. Field and laboratory methods

Six stations from 1.4 km down estuary (weather permitting) to 5.2 km up estuary of the mouth were sampled at approximately weekly to biweekly intervals from 1990 to 2009. Station names are designated by their distance (km) from the mouth, positive up estuary. Sampling commenced as early as the first week in January to as late as early April, depending on ice conditions and availability of boats. For this analysis we restricted the data to measurements made between March and December in order to have an even distribution of residuals throughout the series. A more complete description of field protocols and instrumentation is given in Gallegos (2012, 2014a). Briefly, water samples were collected using a 2-L Labline™ Teflon™ sampler. From the boat vertical profiles of temperature, salinity, and photosynthetically available radiation (PAR, 400–700 nm) were measured. Diffuse attenuation coefficients for downwelling PAR, K_d, were calculated from linear regression of the log-transformed irradiance with depth. A vertically averaged sample for was collected estimation of water column integrated biomass (B) as chlorophyll-*a*. A sample for measurement of photosynthesis-irradiance (P-E) parameters was collected at the depth of disappearance of the top of the sampler (i.e. the Secchi depth) in order to sample at a roughly consistent optical depth.

On 3 occasions (February, May, and August) in 1990 we sampled daily for 6–10 days to determine sub-sampling variability. Within these intensive sampling periods and an additional occasion in 1991 we sampled one station (Stn. 3.8) multiple times (2–4) during one day to further unpack the variance aliased by our routine sampling. Data from these intensive sampling periods are reported in the online Supplemental Material, along with an assessment of the effect of less frequent, i.e. monthly, sampling on estimates of annual production.

P-E curves were measured by ^{14}C uptake using the "photosynthetron" procedure (Lewis and Smith, 1983). 1-ml samples were incubated for 1 h at a range of 24 light intensities supplied by a Westinghouse metal halide lamp with variable intensities achieved by position and nickel screens. Measurements were fit to the hyperbolic tangent function of Jassby and Platt (1976),

$$P^B = P^B_{\max} \tanh\left(\frac{\alpha^B E}{P^B_{\max}}\right) + R^B \quad (1)$$

where P^B (mg C mg^{-1} Chl*a* h^{-1}) is the rate of ^{14}C uptake normalized to the concentration of chlorophyll *a* in the discrete-depth sample used for P-E measurements, $P^B_{\max}$ is the maximal rate of normalized ^{14}C uptake at light saturation, α^B is the initial slope of the linear portion of the curve, and the intercept, R^B, is included to prevent bias in the estimation of α^B. Photoinhibition was relatively uncommon (10.6% of samples). When it was observed, we estimated α^B, β^B, and P^B_s in Eq. (1) of Platt et al. (1980) and calculated $P^B_{\max}$ according to their Eq. (4), but inhibition was ignored in the calculation of depth-integrated daily production. Photosynthesis of Rhode River assemblages is also sensitive to inhibition by solar UV (Banaszak and Neale, 2001) which typically lowers integrated water column production, midday, by 15–20% (Neale, 2001).

2.3. Data analysis

Daily primary production, $P_{H,T}$, integrated over depth of the water column, H, and photoperiod was calculated by the formalism of Platt and Sathyendranath (1993) with minor adjustments for