

# Shallow water processes govern system-wide phytoplankton bloom dynamics: A field study

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## Abstract

Prior studies of the phytoplankton dynamics in South San Francisco Bay, California, USA have hypothesized that bivalve filter-feeders are responsible for the limited phytoplankton blooms in the system. This study was designed to examine the effects of benthic grazing and light attenuation on this shallow, turbid, and nutrient replete system. We found that grazing by shallow water bivalves was important in determining phytoplankton bloom occurrence throughout the system and that above a shallow water bivalve grazing threshold, phytoplankton biomass did not exceed bloom levels. Wind speed, used as a proxy for light attenuation in the shallow water, was similarly important in determining bloom development in the shallow water. Environmental conditions and benthic grazing in the deep water channel had a less discernible effect on system-wide phytoplankton blooms although persistent water column stratification did increase bloom magnitude. The shallow water bivalves, believed to be preyed upon by birds and fish that migrate through the system in fall and winter, disappear each year prior to the spring phytoplankton bloom. Because growth of the phytoplankton depends so strongly on shallow water processes, any change in the shallow-water benthic filter-feeders or their predators has great potential to change the phytoplankton bloom dynamics in this system.

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## 1. Introduction

There is an increasingly rich literature showing that phytoplankton biomass can be reduced and limited by benthic grazers in aquatic systems. There are relatively

few field studies that have examined how the spatial and temporal variability of grazers can influence phytoplankton population growth, although modeling studies have shown this to be an important factor (Lucas et al., 1999b; Pomeroy et al., 2006).

The detailed mechanisms of phytoplankton growth in the presence of benthic grazers and naturally varying environmental conditions are difficult to establish in field studies. Even when a large increase in the benthic grazing rate correlates with reduced phytoplankton biomass, as has been seen with invasive bivalve species (Cohen et al., 1984; Alpine and Cloern, 1992; Strayer

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et al., 1999), defining the interaction between bivalve filter-feeders and phytoplankton growth is frequently limited because the data are collected at inconsistent temporal and spatial scales. So, although we know the factors that are important for phytoplankton growth, we know less about how sensitive phytoplankton growth is to the interaction of environmental (e.g. light availability, transport) and biological (benthic grazing, zooplankton grazing) factors which are themselves highly variable.

We have learned from models by Herman (1993), Koseff et al. (1993), and Lucas et al. (1999a) that given a sufficiently high biomass of suspension feeders, the rate of vertical mixing and water depth are critical determinants in the successful development of a phytoplankton bloom. The Lucas et al. (1999b) and Cerco and Noel (2007) models have shown that transport between regions that have different phytoplankton growth rates is important in determining a phytoplankton bloom trajectory. Small scale temporal (e.g. monthly to seasonal) and spatial (e.g. 1–2 km) variability in benthic grazer biomass has not been used in most models partially due to lack of data; Cerco and Noel (2007) use field data to estimate the spatial distribution of oyster biomass but limit intra-annual variability in grazing to that generated by physiological responses to temperature changes. In shallow water systems with large intra-annual variability in bivalve biomass we need to understand how the spatial distribution, magnitude and seasonal cycles of benthic grazing rates affect phytoplankton growth relative to other limiting variables such as light availability. Because concurrent field studies of benthic grazer and phytoplankton biomass are limited, the goal of this study was to coincidentally measure phytoplankton biomass, benthic grazer biomass, dissolved nutrients, and turbidity at sufficiently fine temporal and spatial scales to further our understanding of the effect of grazing by benthic fauna on phytoplankton dynamics in shallow water systems.

A series of studies over the last 20 years has developed our current understanding of phytoplankton bloom dynamics in South San Francisco Bay (Fig. 1, SSFB). Phytoplankton ecology in SSFB has been described by Cloern (1996), and the long time series resulting from that work shows an annual spring phytoplankton bloom of varying length and magnitude (Fig. 2). This system has, when compared to other estuaries, relatively low net primary production ( $70\text{--}130\text{ g C m}^{-2}$ ) despite high concentrations of nutrients (Cloern et al., 1985; Cloern, 2001). Cloern (1982) was the first to suggest that the phytoplankton biomass in this system is at least partially

limited by grazing by benthic bivalves. There has not been, until this study, sufficient benthic grazer data to test his hypothesis.

The geomorphology of SSFB, with a narrow  $\approx 15$  m deep channel surrounded by expansive ( $\approx 2$  m deep) shoals, is important in the phytoplankton dynamics of the system. Two field studies (Cloern et al., 1985; Huzzey et al., 1990) reported a strong coherence between shallow water blooms and deep water blooms in SSFB and noted that, due to the high turbidity of the system, net phytoplankton growth rate was positive only in the shallows. Although turbidity in the shallow water is likely a result of wind resuspension, tidal currents are responsible for the transport of suspended sediment to the channel and along the axis of the system (Schoellhamer, 1996; Lacy et al. 1996). Therefore system-wide turbidity tends to peak during tidally active periods. Consistent with this observation, Cloern (1991) reported that the rate of observed phytoplankton biomass change was negatively correlated with tidal energy in this system, and thus that the spring bloom occurs around the period of the spring equinox. The lack of a similar bloom during the fall equinox, when tidal energy is also low, has not been explained.

Stratification in the channel can occur in winter and spring in SSFB and has been correlated with increased phytoplankton bloom magnitude in the channel (Cloern, 1984). Model results have helped explain how stratification increases bloom magnitude; stratification-induced isolation of phytoplankton in the upper water column, where light is abundant and bivalve grazers are remote leads to higher phytoplankton biomass growth rates in the channel (Cloern, 1984; Koseff et al., 1993). More recent model studies have shown that persistent (not tidally induced) stratification is most likely to produce a bloom, and should be able to produce localized blooms within deep channels (Lucas et al., 1998). Grazing by zooplankton in SSFB is poorly defined but believed to be a less significant determinant of phytoplankton biomass than light availability and grazing by benthic infauna (Cloern, 1982; Lucas et al., 1999a).

We propose to use field measurements described herein to test the following hypotheses, which are based on prior studies:

- Phytoplankton blooms start in the shallow water and spread throughout the system.
- Phytoplankton blooms are not limited by nutrient availability.
- Seasonal variability in benthic grazer biomass and shallow water turbidity controls the seasonality of phytoplankton blooms in SSFB.

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