

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

J.K. Thompson^{a,b,*}, J.R. Koseff^b, S.G. Monismith^b, L.V. Lucas^{a,b}

^a *United States Geological Survey, 345 Middlefield Road, MS 496, Menlo Park, California, USA 94025*

^b *Stanford University, Department of Civil and Environmental Engineering, Terman Engineering Building, Stanford, California, USA 94305-4020*

Received 9 August 2006; received in revised form 1 December 2007; accepted 7 December 2007

Available online 31 December 2007

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.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Zoobenthos; Phytoplankton; Shellfish; Estuarine dynamics; Benthic grazing; USA; California; San Francisco Bay

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

* Corresponding author. United States Geological Survey, 345 Middlefield Road, MS 496, Menlo Park, California, USA 94025. Tel.: +1 650 329 4364; fax: +1 650 329 4327.

E-mail addresses: jthomps@usgs.gov (J.K. Thompson), koseff@stanford.edu (J.R. Koseff), monismith@stanford.edu (S.G. Monismith), llucas@usgs.gov (L.V. Lucas).

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 ≈ 15 m deep channel surrounded by expansive (≈ 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.

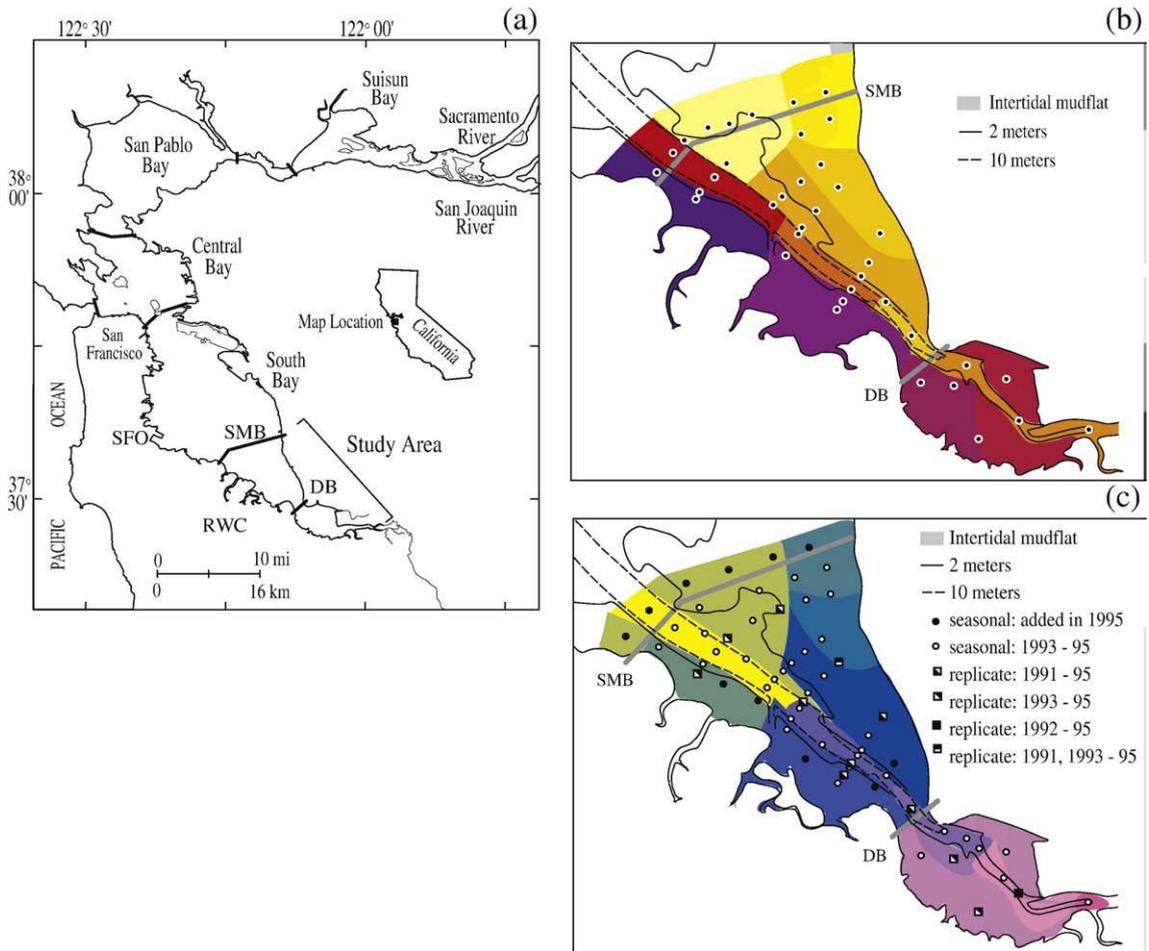


Fig. 1. Study location (SFO: San Francisco Airport; RWC: Redwood City; SMB: San Mateo Bridge; DB: Dumbarton Bridge) (a), station locations for water sampling (b) and for benthic samples (c) December 1990–January 1996. Shading in (b) and (c) represents station groupings used in analyses.

- Stratification will increase bloom magnitude in the channel and can result in localized blooms in the channel.

2. Field area and methods

2.1. General description of San Francisco Bay

San Francisco Bay (SFB) is the largest estuary on the Pacific coast of the United States and is surrounded by one of the major urban centers in the U.S. Most of SFB’s freshwater enters through the Sacramento and San Joaquin Rivers (Fig. 1a), which receive water from a watershed that includes 40% of the state of California (Conomos et al., 1985). Most tributaries entering SFB have some containment structure along their transit.

SFB is very shallow (average depth of 6 m at mean lower low water), has a Mediterranean climate, strong diurnal winds during the summer months, and semi-

diurnal tides. The climate, physiography, and tidal regime of SFB are discussed in Conomos et al. (1985). The bathymetric gradient is steep near the channel (Fig. 1) with greater than two-thirds of the surface area of SSFB ≤ 2 m. Herein we use the convention that

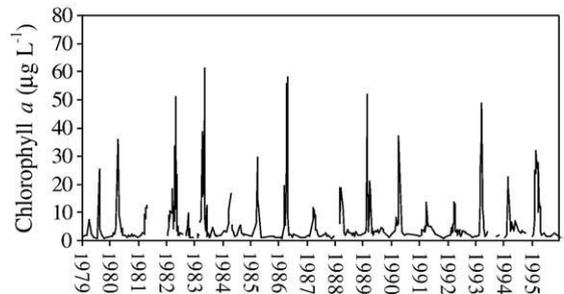


Fig. 2. Long-term chl *a* concentration at USGS Station 30 (between San Mateo and Dumbarton Bridges in Fig. 1). Data from <http://sfbay.wr.usgs.gov/access/wqdata>.

areas ≤ 2 m are shoal or shallow areas and those > 2 m are channel or deep areas.

Our study focused on the southern half of the South Bay and included the San Mateo Bridge area where the South Bay phytoplankton bloom usually peaks (Fig. 1a; Cloern, 1996). SSFB is of interest to resource managers as it is (1) the most urbanized area of the bay, with the cities of San Francisco and Oakland at its northern boundary and Silicon Valley at its southern boundary, (2) the portion of SFB with the lowest natural freshwater inflow, the largest wastewater inflow, and therefore the greatest potential for eutrophication, and (3) the site of a large (> 60 km²) ecosystem restoration program (South Bay Salt Pond Restoration Project) that will change the physiography and potentially the ecology of all of the South Bay (Fig. 1).

2.2. Station locations

Water samples (Fig. 1b) were collected to measure phytoplankton biomass as chlorophyll *a* (chl *a*), salinity, and turbidity from December 1990 through January 1996 at monthly or smaller intervals. Water quality data collected in the channel by the U.S. Geological Survey (Hager, 1993, 1994, 1997; Hager and Schemel, 1999; and USGS: <http://sfbay.wr.usgs.gov/access/wqdata>) were used to augment this study and in most cases were collected on the same day and during the same tidal phase as the water samples collected during our study.

Benthic community samples were collected to examine the temporal and spatial distribution of the benthic bivalve filter-feeders (bivalves have been shown to be the dominant filter-feeders in SSFB, Schemel et al. (1988, 1990)). The benthos was sampled each month at 7 (4 shallow and 3 deep) stations from December 1990 through January 1996. Six additional stations (3 shallow, 3 deep) were sampled January 1993 through January 1996. Three replicate grabs were taken at each monthly station using a 0.05 m² van Veen grab. Three seasonal, spatially intensive benthic sampling studies with major emphasis on shallow water locations began in 1993 (one grab at each of 49 stations in 1993 and 1994 and at each of 59 stations in 1995, Fig. 1c). Seasonal studies were done (1) prior to or during the early stages of the spring bloom, (2) in mid-summer when there was no bloom, and (3) during the fall equinox.

2.3. Methods

2.3.1. Environmental data

Estimates for wind speed were based on data collected at Redwood City (RWC, Fig. 1) from April 1992 through

the end of the study (Schemel, 1995). Wind data prior to April 1992 were from the San Francisco Airport (SFO, Fig. 1, NOAA, 1991, 1992); as per Schemel (1995), wind velocities at SFO were halved to adjust for the lower wind velocities at RWC. Continuous near-surface and near-bottom water column measurements of temperature and salinity at the San Mateo and Dumbarton Bridges (Fig. 1a) were supplied by L. Schemel (USGS) and used, in conjunction with discrete CTD data taken during water sampling cruises, (<http://sfbay.wr.usgs.gov/access/wqdata>) to determine periods of persistent stratification in the deep channel.

2.3.2. Water column data

Surface water samples for chl *a* and salinity were taken at all stations during all years on a flooding tide. Although it was impossible to replicate conditions among the sampling periods due to the changing tidal velocities, the order of sampling and the tidal current direction were consistent. Chl *a* and phaeopigment concentrations were estimated with two techniques. All samples in 1991–1993 and a subset of samples in 1994–1995 were analyzed by the extracted spectrophotometric method. Samples were filtered and filters were frozen, ground in 90% acetone, extracted for 12–24 h at -10 °C and centrifuged; the extract was read on a Hewlett Packard 8452A diode array spectrophotometer. The extract was then acidified to measure phaeopigments (Riemann, 1978). Calculated concentrations of chl *a* and phaeopigments were based on the equations of Lorenzen (1967). Chl *a* concentrations were estimated in 1994 and 1995 by measuring *in vivo* fluorescence on a Turner Designs Model 10 fluorometer that had been calibrated for chl *a* using the samples measured by the spectrophotometric method.

Light attenuation coefficients (k_t) in 1991–1993 were estimated from Secchi depth (recorded to the nearest 0.1 m) based on the relationship $k_t = 1.4/\text{Secchi depth}$. Light attenuation coefficients were estimated from turbidity measurements and calculated suspended particulate matter (SPM) concentrations in 1994–1995; turbidity was measured with a Turner Designs Nephelometer and calibrated with at least 6 SPM samples. SPM was measured gravimetrically and corrected for salinity (Hager, 1993), and light attenuation was estimated using an empirical relationship derived by Cloern (1987): $k_t = 0.77 + (0.06 \times \text{SPM})$.

2.3.3. Benthic grazing estimates

Benthic samples were sieved through a 0.5 mm screen, preserved in 10% buffered formalin for no more than a week, transferred to 70% ethyl alcohol for storage, and stained with Rose Bengal before sorting.

All filter-feeding bivalve individuals [*Corbula* (formerly *Potamocorbula*) *amurensis*, *Venerupis japonica*, *Musculista senhousia*, *Mytilus* *c.f.* *edulis*, *Mya arenaria* and *Macoma petalum*] were removed from each sample and counted, and the longest length of each individual was measured. A size range (1.5 mm long and greater) of live animals was collected at each site during each month to calculate dry tissue weight for each size of animal. Animals were measured, dried at 60 °C (dry weight), weighed, ashed at 500 °C in a muffle furnace, and re-weighed (ash weight). A relationship between animal length and ash-free dry weight (AFDW = dry wt – ash wt) was then used to convert the measured animals from each benthic sample into biomass estimates for each species.

Bivalve community grazing rate estimates (BG) were based on bivalve biomass and species specific pumping rates (PR's) which were adjusted for a concentration boundary layer. Community PR's were based on published relationships: *C. amurensis*, 400 L/g AFDW/day (Cole et al., 1992); *V. japonica*, 200 L/g AFDW/day, (O'Riordan et al., 1993); *M. arenaria*, $PR = aw^b$, $a = 11.6$, $b = 0.7$, where w is tissue weight (Mohlenberg and Riisgard, 1979); and *M. edulis*, $PR = aw^b$, $a = 7.45$, $b = 0.66$ (Mohlenberg and Riisgard, 1979). Because there is no published relationship for *M. senhousia*, the *M. arenaria* PR relationship was used based on laboratory observations of excurrent siphon velocities for the two species. The PR for *M. petalum* (the least numerous bivalve) was based on a relationship for a congener, *Macoma nasuta* (Meyhofer, 1985), and may be an overestimate because *M. nasuta* frequently lives in higher velocity environments than *M. petalum* and may be better adapted for the filter-feeding mode than *M. petalum*. The PR relationships were chosen because they were from studies where bivalve sizes were similar to those seen in this study. PR was adjusted for seasonal changes in water temperature using coefficients (Q_{10}) from studies of *M. edulis*: Q_{10} of 2.2 at 5 °C, 1.2 at 10 °C, and 1 at 15°–20 °C (Winters, 1978).

Community pumping rates were converted to grazing rates by reducing PR to adjust for the presence of a concentration boundary layer. This adjustment was based on O'Riordan's (1995, Fig. 7b) refiltration relationship, $n_{\max} = 2.5/(s/d_0)$, where n_{\max} is the maximum refiltration proportion (ie the proportion of water previously filtered), s is the distance between siphon pairs, and d_0 is the diameter of the excurrent siphon. The diameter of the excurrent siphon was changed throughout each year to reflect the change in average size of animals as the year progressed, and the distance between siphon pairs was based on density of animals observed

in our benthic sampling assuming equidistant spacing within the 0.05 m² grab. The use of maximum refiltration proportion maximizes the effect of the concentration boundary layer resulting in a conservative grazing rate estimate. We assumed all bivalves grazed continuously.

3. Results

3.1. Environmental conditions

The study period encompassed some of the largest variations in freshwater flow seen in this system. A drought, which began in 1987, continued through the first two years of the study (1991–1992, Fig. 3a) and ended with moderate freshwater flow in 1993. This was followed by one of the driest years on record (1994) and a 100 year flood event in 1995. The wettest years resulted in periods of persistent vertical stratification (persisting for >24 h) coincident with periods of maximum freshwater flow and low tidal velocity (Fig. 3a, b and d). No persistent stratification occurred in the dry years.

Turbidity was examined as a function of wind speed and tidal velocity during the spring bloom period (February through April, Cloern, 1996). The highest sustained wind speeds were seen in 1991 and 1995 (Fig. 3c). The summer wind speeds were significantly lower in 1991 than in any of the other years, and the late summer–fall wind speeds were on average higher for longer periods of time in 1994 than during the other years (Fig. 3c). Seasonal patterns and magnitudes of the maximum daily tidal speed (tidal currents supplied by R. Cheng, USGS, numerical model results) were similar for all years with the following exceptions: maximum tidal velocities were lower during the annual lowest tidal velocity periods in 1993 (i.e. the spring and fall equinoxes, Fig. 3d), highest during the spring equinox in 1994, and highest during the fall equinox in 1995 (Fig. 3d). During the 5-year study, light attenuation estimates (k_t) during very high wind and spring tide conditions ranged from near 40 m⁻¹ in the shoals to near 20 m⁻¹ in the channel. Similar tidal conditions and low to moderate wind speeds produced k_t values that were about one quarter of these values. Low to moderate winds and neap tides resulted in k_t values of about half of those seen during spring tides. Yearly median k_t values measured during spring bloom periods ranged from 1–6 m⁻¹ in the shoals and 1–4 m⁻¹ in the channel areas.

3.2. Phytoplankton biomass

Phytoplankton blooms (defined for SFB as chl *a* concentrations >10 µg L⁻¹ by J.E. Cloern, 1982)

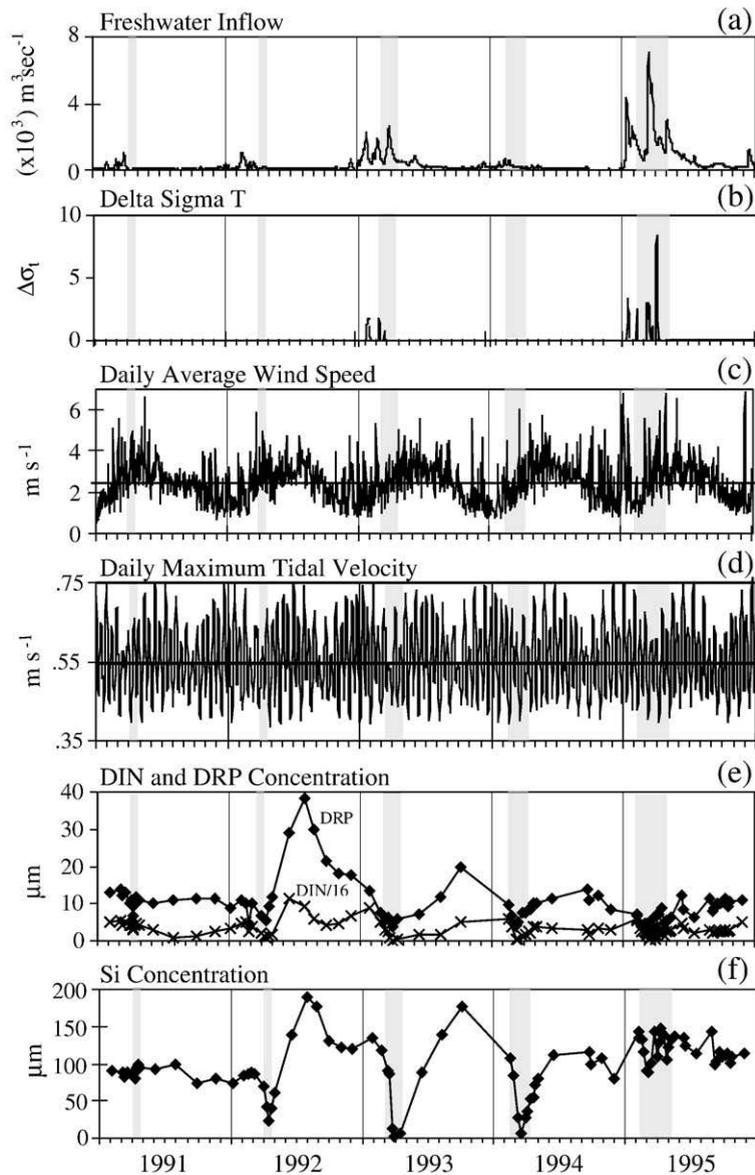


Fig. 3. Environmental conditions during period of study. (a) freshwater inflow from tributaries (Delta outflow), (b) persistent (>24 h) density stratification parameter ($\Delta\sigma_t$), (c) daily average wind speed, (d) maximum daily RMS tidal velocity, (e) dissolved reactive phosphate and inorganic nitrogen (normalized to Redfield ratio) in channel, and (f) dissolved silica concentration in channel. Highlighted areas show bloom periods.

occurred in all five years of the study but with varying magnitudes and durations (Fig. 4). The 1991 and 1992 blooms were some of the smallest magnitude blooms ($15\text{--}20 \mu\text{g L}^{-1}$) seen in almost 20 years of data collected by the USGS in SSFB (Fig. 2). During the wet years of this study, chl *a* concentrations ($70\text{--}90 \mu\text{g L}^{-1}$ in 1993 and 1995) were larger than the 20 year average. Phytoplankton blooms lasted for about 2 weeks in 1991 and 1992 and for 6 weeks or longer in 1993–1995 (Fig. 4). The bloom in 1995 was longer (10 weeks) than

average. Chl *a* concentrations were higher during the non-spring bloom period in 1994 than in other years. For any one year, bloom timing was consistent among the channel stations, although bloom magnitude was higher in the southernmost channel (Fig. 4d) than in the northern channel (Fig. 4a–c).

Spring phytoplankton biomass first increased on the shoals, with the initial increase occurring on the northeastern shoal for most years (Figs. 4a and 5a). Chl *a* concentration was generally higher on the shoals than

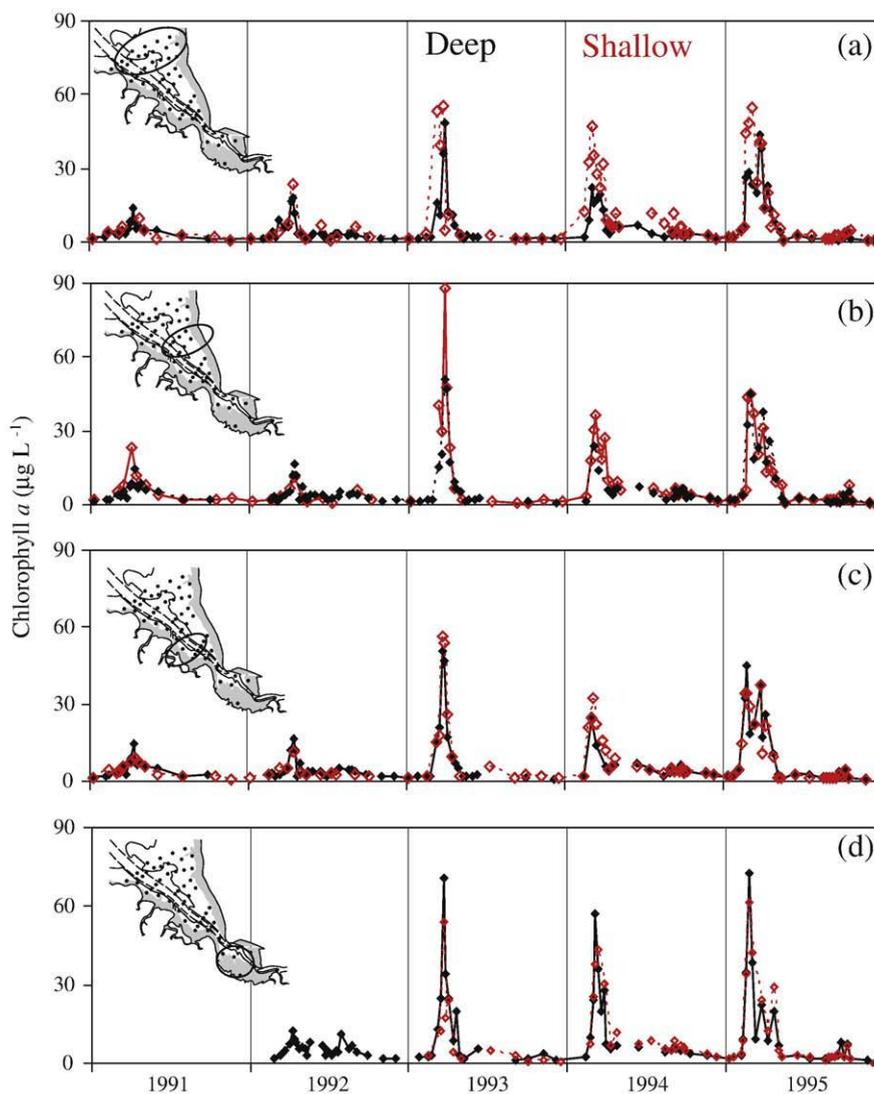


Fig. 4. Chl *a* concentrations at four channel and four shoal locations. Inset maps show position of stations used for each location.

in the adjacent deep channel, and more frequently higher on the eastern shoals (Fig. 4a and b) than on the narrower western shoals (Fig. 4c) in the regions north of Dumbarton Bridge (see also Fig. 5). The differences between shoal and channel chl *a* concentration were greatest along the northern transect, particularly during the early stages of the bloom (Fig. 4a). There were no system-wide phytoplankton blooms during other seasons of the year, although local summer and fall increases in chl *a* concentrations were observed on the shoals in 1994 (Figs. 4a and 5b).

Dissolved nutrients in SSFB (Hager, 1993, 1994; Hager and Schemel, 1996; Hager, 1997; Hager and Schemel, 1999) were high during most of the year as previously noted in other studies of SSFB; wastewater

treatment plants are the major source of dissolved reactive phosphorus and dissolved inorganic nitrogen. DIN concentrations approached zero for very short periods in 1993–1995 in the channel (Fig. 3e) and shallow water (not shown), as did Si (Fig. 3f) in 1993 and 1994.

3.3. Benthic grazing

There was little coherence in benthic grazing rates among years for any site or between channel locations and their adjacent shoal locations (Fig. 6), but there were some consistent trends. Benthic grazing rates generally peaked in summer or fall at all locations except in 1994. Grazing rates in the shoals (BGS) declined to near zero each winter except in 1994 and remained low through

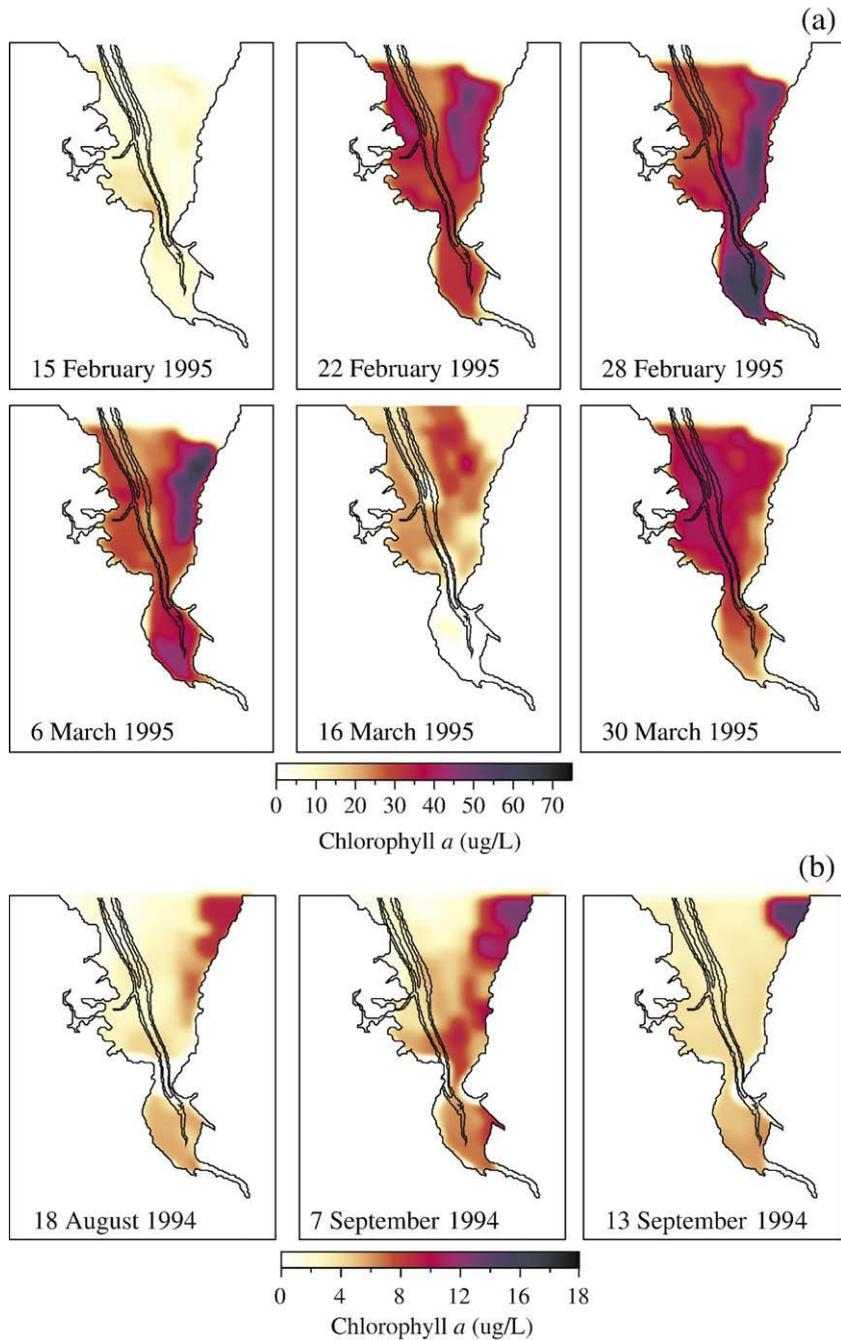


Fig. 5. Chl *a* concentration distribution in (a) spring 1995 and (b) fall 1994. Plots generated in SPYGLASS (Version 3.0, MAC).

early spring ($BGS \leq 0.5 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$). Although benthic grazing in the channels (BGC) also declined in winter at least some channel locations maintained grazing rates in excess of $1 \text{ m}^{-3} \text{ m}^{-2} \text{ d}^{-1}$ during most winters and springs. Highest grazing rates generally occurred in the channel, and maximum grazing rates were observed in the southern extreme embayment (e.g. $BGC > 50 \text{ m}^3$

$\text{m}^{-2} \text{ d}^{-1}$ in spring 1994). Bivalve recruitment and growth was unique in 1994 (Thompson, 1999). Bivalves that recruited in the northern shoals and at the southern extreme stations in fall 1993 persisted through spring 1994. Bivalves failed to recruit in the spring of 1994 at all locations. Some recruits appeared in the southern extreme channel in summer 1994, but declined by

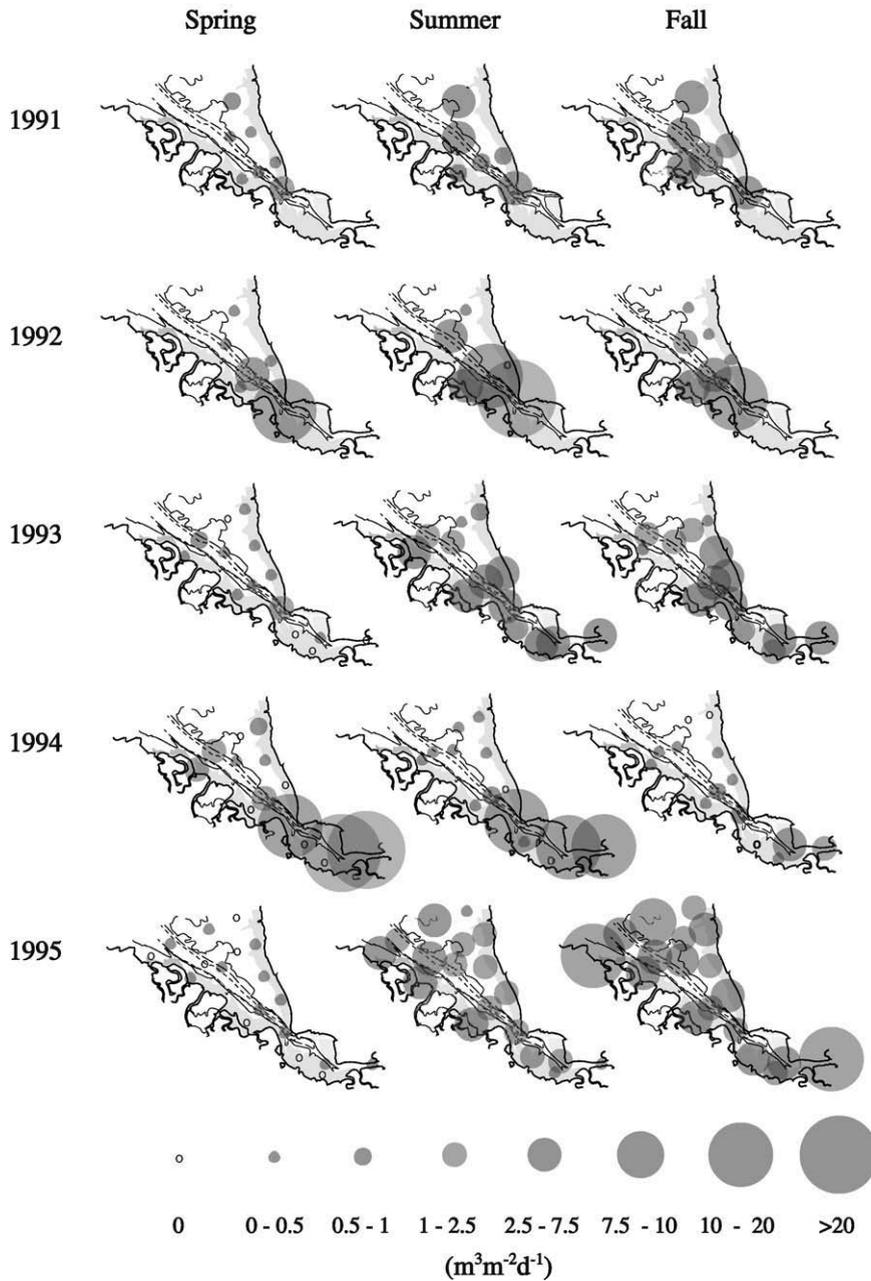


Fig. 6. Bivalve grazing rates prior to spring bloom, in mid-summer, and in fall for all years of study. Each data point in 1993–1995 represents multiple stations in each region as shown in Fig. 1c.

winter 1995 (Fig. 6). Thus, by early spring 1995, there were very few bivalves present in SSFB during the initiation of the spring phytoplankton bloom.

4. Discussion

Phytoplankton blooms appeared first in the shallow water and later in the deep regions (Figs. 4 and 5),

consistent with our hypothesis that blooms start in the shallow water and spread. Given the low DIN and Si concentrations that were occasionally measured, we must reconsider our hypothesis that nutrients do not limit the phytoplankton in SSFB. Due to our lack of knowledge on benthic and water column nutrient regeneration rates we can not conclusively state that nutrients were limiting phytoplankton growth during this

study, but it is apparent that this issue warrants future study in this system.

Spring blooms began in the shoals, coincident with low shallow water benthic grazing rates, high nutrients and, as will be shown below, relatively high light availability. Grazing rates of shallow water bivalves (BGS) were $\leq 0.5 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ immediately preceding shallow water blooms and, with only two exceptions, deep water blooms as well (Fig. 7a and c). The two outlying data points in Fig. 7c occurred in 1995 at the end of a period of intense stratification, during which time the phytoplankton may have been produced locally within the channel and thus less affected by BGS. This was the only instance during our 5-year study a possible channel-produced phytoplankton bloom attributable to persistent stratification (as posited by Lucas et al., 1998) was observed. The numerous instances of low chl *a* when BGS was less than $0.5 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ (Fig. 7a and c) were due to phytoplankton growth limitation by factors such as light or possibly nutrient limitation (discussed below). Plots of chl *a* with deep water grazing rates (BGC) do not reveal a BGC bloom threshold within the range of values observed (Fig. 7b and d), although there appears to be a decreasing trend in maximum chl *a* concentration with increasing BGC.

Thus as hypothesized, phytoplankton blooms first appeared in the shoals during periods when benthic grazing rates were too small to control phytoplankton

biomass. BGS appeared to limit the occurrence of blooms in both shallow and deep water. There was no evidence that BGC could limit bloom occurrence within the values of BGC observed, although BGC may be able to reduce the magnitude of phytoplankton biomass.

The major factors controlling light availability in SSFB include large, sustained freshwater flow events (relevant only in April 1995 for this study), wind wave resuspension of bottom sediments in the shoals, and transport of suspended sediment into and along the channels during spring tides (Schoellhamer, 1996; Lacy et al., 1996). Thus we expected wind speed and tidal current speed to be good proxies for turbidity in the shallow and deep water respectively. We compared average maximum wind speed against the observed rate of phytoplankton biomass change ($\Delta B/\Delta t = (\text{Chl}_{t+1} - \text{Chl}_t)/(\text{JD}_{t+1} - \text{JD}_t)$, where *B* is phytoplankton biomass, *t* is time, Chl is chl *a* concentration, and JD is julian day as defined by Cloern, 1996). Seven days was chosen as the averaging period for the wind speed because the lowest chl *a* values prior to bloom initiation were $\approx 1 \mu\text{g L}^{-1}$ and a conservative net growth rate for phytoplankton in the shoals of SSFB in early to mid spring ($0.1\text{--}0.5 \text{ d}^{-1}$, Cloern et al., 1985) results in bloom concentrations in about 7–10 days. Observed rate of phytoplankton biomass change was calculated for the 7–10 days preceding the bloom through the end of the bloom.

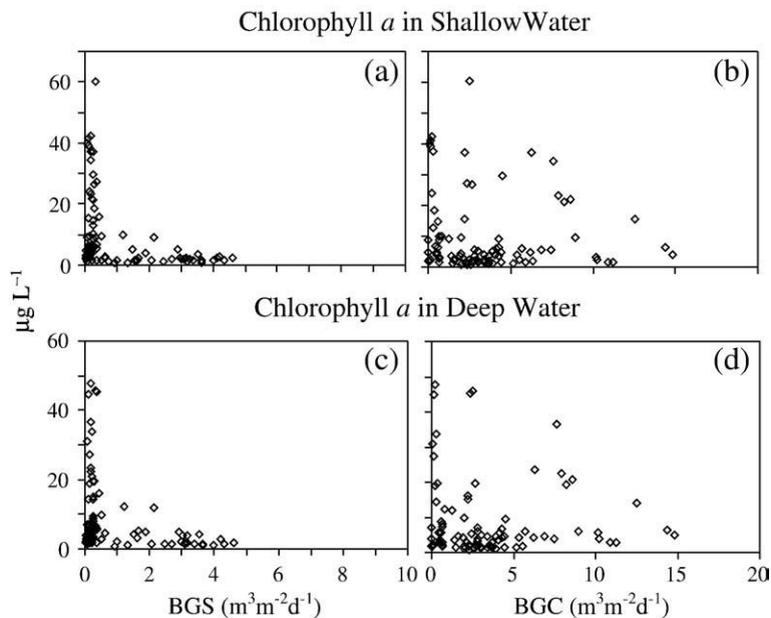


Fig. 7. Average chl *a* concentration plotted with preceding 2 week average benthic bivalve grazing rate for each water sample date: (a) shallow water chl *a* vs grazing by shallow water bivalves, (b) shallow water chl *a* vs grazing by deep water bivalves, (c) deep water chl *a* vs grazing by shallow water bivalves, (d) deep water chl *a* vs grazing by deep water bivalves.

A relationship does not exist between average maximum wind speed and net rate of phytoplankton biomass change in the shoals when all points are considered (Fig. 8). However, a regression of the data points for which neither benthic grazing nor nutrients on the shoals (shoal DIN < 1 μM) were potentially limiting (Fig. 8, open symbols) shows a significant ($p < 0.05$) relationship, with 30% of the variability in phytoplankton biomass change accounted for by wind speed. There appears to have been an average wind threshold speed of $\approx 2.5 \text{ m s}^{-1}$ for the environmental conditions observed during our study, below which phytoplankton biomass in the shoals grew and above which it did not. There is no relationship between average wind speed and channel phytoplankton biomass change (not shown), even for periods when neither grazing nor nutrients were potentially limiting. Thus wind appears to be an important factor in determining turbidity levels that can limit phytoplankton biomass growth in the shoals, but is less or not important in the channel.

If channel turbidity is mostly advected from the shoals, we might expect a negative relationship between tidal velocity and phytoplankton biomass in the channel, but not necessarily with phytoplankton biomass in the shoals. Consistent with Cloern (1991), we found a negative relationship between rate of deep water phytoplankton biomass change during bloom periods and the average antecedent (7 day) tidal current speed; phytoplankton change becomes negative when tidal current speed $\approx 0.55 \text{ m s}^{-1}$. A similar analysis combining data from this study with data collected in the early 1980s (Cloern, pers. comm.) did not reveal a relationship between rate of shallow water phytoplankton biomass change and tidal current speed. Therefore turbidity in the channel that can limit phytoplankton biomass

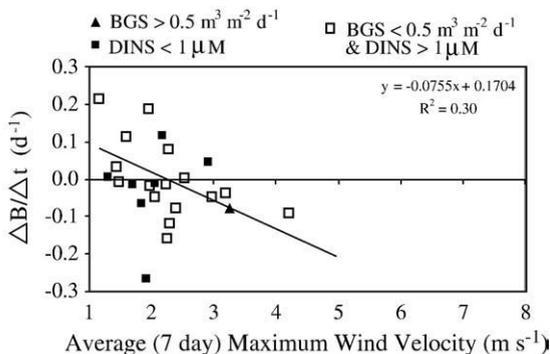


Fig. 8. Net average rate of phytoplankton biomass change as a function of antecedent maximum daily wind speed (7 day) in shallow water. Regression line shown for periods when DIN was high and BGS was below the threshold (open symbols).

growth in the channel is determined either by turbidity produced non-locally and advected to the channel during higher tidal current periods or by turbidity produced by the tidal currents in the channel.

Based on the observations of Cloern et al. (1985), we did not expect phytoplankton blooms to be generated in the channel because of the low net growth rate of the phytoplankton in the channel. Despite lower turbidity in the deep water than in the shallow water, we observed lower phytoplankton biomass, and a delayed bloom period, in the channel relative to the shoals. Our observations are consistent with the hypothesis that phytoplankton in a well-mixed channel spend more time in aphotic conditions than do phytoplankton in a well-mixed shoal in turbid systems such as SSFB.

We also observed that phytoplankton biomass was highest in shoal regions furthest from the channel (e.g. in the northeastern shoal, Figs. 4 and 5), and that phytoplankton biomass on the narrowest (western) shoal was very similar to phytoplankton biomass levels in the nearest channel region. The spatial differences in phytoplankton biomass on the shoals were likely the result of varying timescales for transport of shoal water into the channel (the timescale for lateral transport is proportional to the square of the mixing distance if transport is diffusive and proportional to the mixing distance itself if transport is advective). The summer and fall phytoplankton bloom in 1994 demonstrated the effect of varying transport time scales in combination with mostly aphotic channel conditions. Despite extremely low BGS and BGC throughout most of the system, we observed only small magnitude increases in chl *a* concentration (Fig. 6), with small phytoplankton blooms being isolated to the eastern shoal (Figs. 4 and 5b). Average wind speed for summer and fall 1994 was the highest of our 5-year study, and met or exceeded our spring wind speed threshold ($\approx 2.5 \text{ m s}^{-1}$) for shoal phytoplankton growth (Fig. 3c). Thus, it is likely that high turbidity was the primary factor limiting phytoplankton growth on the shoals. Channel chl *a* concentration was then limited by the relatively low chl *a* concentrations being transported from the shoals to the channel where local light availability further limited the phytoplankton biomass growth.

4.1. A new understanding of phytoplankton dynamics in SSFB

Our hypotheses were mostly confirmed by this study. Local blooms developed in the shallow water when benthic grazing and light availability were below a threshold value. These shoal blooms spread and were

followed by system-wide blooms in spring of all years studied. No BGC threshold appeared to exist as it did for BGS, and BGC was, at most, subservient to the grazing effects of shallow water bivalves. Stratification increased the phytoplankton bloom magnitude and appeared to be responsible for one brief channel-derived increase in phytoplankton biomass. The limitation of phytoplankton biomass by nutrients is an unanswered hypothesis and deserves more study.

The criticality of shallow water processes in phytoplankton dynamics is relevant to our understanding of the SFB ecosystem and to other shallow, turbid tidal systems. Small changes in primary production in these inherently low productivity systems can alter their trophic dynamics and ultimately their trophic state, as has been seen in northern SFB (Kimmerer et al., 2002; Thompson, 2005). In shallow systems such as SSFB, where nutrients are usually replete, small changes in the biomass or seasonality of filter-feeders could change a low productivity system into an even lower productivity system or may initiate the harmful effects of eutrophication.

Although Cloern had shown in 1982 that grazing by benthic bivalves was an important factor in phytoplankton bloom development, we were surprised in this study by the critical importance of the seasonal cycle of the bivalves to SSFB phytoplankton bloom dynamics. The annual disappearance of the bivalves in the shoals sets the potential for a bloom each spring. Thus the mechanisms for the disappearance of the bivalves and for the timing of bivalve recruitment are critically important in our understanding of phytoplankton dynamics in this system. We believe the annual disappearance of bivalves in the SSFB shoals during winter is due to predation by fall migratory birds and fish (Alpin, 1967 and personal observation by J. Thompson) since neither the condition nor the growth rate of the individuals show signs of stress (Thompson, 1999). As in other autochthonous systems, the dynamics of secondary producers in SSFB are ultimately controlled by the primary producers (Jassby et al., 1993). Reproduction in both zooplankton (Kimmerer, 2004) and *Corbula amurensis* (Parchaso and Thompson, 2002) is triggered by increases in phytoplankton biomass in this system. The response of the benthos to the spring phytoplankton bloom can be dramatic, as in 1995 when bivalves that settled in the shoals at the beginning of the bloom grew sufficiently to control the shoal phytoplankton biomass within 6 weeks.

One of the reasons why benthic bivalves can so effectively control phytoplankton biomass in many systems is that they are “always” present to some degree. Bivalves’ long lives (relative to zooplankton)

and large size allow them to survive periods of low food availability and to respond immediately to any increase in phytoplankton biomass. We know of no other system where the bivalves are so effectively removed from the zone of phytoplankton growth each year, thereby allowing the annual phytoplankton bloom to develop. Richman and Lovvorn (2004) and Poulton et al. (2004) have reported large reductions in *Corbula* at half of their shallow water study sites in northern SFB following the fall bird migration, so we may find that the phytoplankton dependence on bivalve seasonal patterns extends into north SFB. Future studies may find the SSFB pattern of interdependence between migratory bird predation and phytoplankton dynamics is common in shallow estuaries located along migratory bird flyways.

The tight connection between shallow water bivalves and their predators means that the temporal and spatial distributions of top predators, such as birds and demersal fish, are likely to be key parameters defining the variability of primary production between years in SSFB. Thus any changes to prey or predators, both of which are possible in this estuary with an extensive history of non-indigenous species invasions (Cohen and Carlton, 1995, 1998), could result in large ecosystem changes.

Acknowledgements

J.K.T. received support for this study from the USGS Toxic Substances Hydrology Program. L.V.L., J.R.K., and S.G.M. wish to acknowledge the support of the NSF Division of Biological Oceanography through grant number OCE-9504081, as well as the Josephine De Karman Foundation, NASA, and the EPA, through grant number CE00960502. The field work would not have been possible without the careful guidance of Francis Parchaso at the USGS and the assistance by numerous students from Stanford University and University of San Francisco. Jim Cloern of the USGS took part in numerous discussions and generously offered services and data. Ralph Cheng and Jeff Gartner of the USGS kindly provided tidal current data. J.K.T. performed this work as part of her dissertation research at Stanford University.

References

- Alpin, J.A., 1967. Biological survey of San Francisco Bay 1963–1966. Report 67-4. California Department of Fish and Game, Marine Resources Operations Laboratory.
- Alpine, A.E., Cloern, J.E., 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37 (5), 946–955.
- Cerco, C.F., Noel, M.R., 2007. Can oyster restoration reverse cultural eutrophication in Chesapeake Bay? *Estuaries and Coasts* 30 (2), 331–343.

- Cloern, J.E., 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Marine Ecology Progress Series* 9, 191–202.
- Cloern, J.E., 1984. Temporal dynamics and ecological significance of salinity stratification in an estuary (south San Francisco Bay, USA). *Oceanologica Acta* 7, 137–141.
- Cloern, J.E., 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Continental Shelf Research* 7 (11/12), 1367–1381.
- Cloern, J.E., 1991. Tidal stirring and phytoplankton bloom dynamics in an estuary. *Journal of Marine Research* 49, 203–221.
- Cloern, J.E., 1996. Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* 34 (2), 127–168.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210, 223–253.
- Cloern, J.E., Cole, B.E., Wong, R.L.J., Alpine, A.E., 1985. Temporal dynamics of estuarine phytoplankton: a case study of San Francisco Bay. *Hydrobiologia* 129, 153–176.
- Cohen, A.N., Carlton, J.T., 1995. Nonindigenous Aquatic Species in a United States Estuary: A Case Study of the Biological Invasions of the San Francisco Bay and Delta. U.S. Fish and Wildlife Service, Washington, D.C.
- Cohen, A.N., Carlton, J.T., 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279, 555–558.
- Cohen, R.R.H., Dresler, P.V., Phillips, E.J.P., Cory, R.L., 1984. The effect of Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnology and Oceanography* 29, 170–180.
- Cole, B.E., Thompson, J.K., Cloern, J.E., 1992. Measurement of filtration rates by infaunal bivalves in a recirculating flume. *Marine Biology* 113, 219–225.
- Conomos, T.J., Smith, R.E., Gartner, J.W., 1985. Environmental setting of San Francisco Bay. *Hydrobiologia* 129, 1–12.
- Hager, S.W., 1993. Dissolved nutrient and suspended particulate matter data for the San Francisco Bay estuary, California, October 1988 through September 1991. Technical Report 93-57. United States Geological Survey, Menlo Park, California.
- Hager, S.W., 1994. Dissolved nutrient and suspended particulate matter data for the San Francisco Bay estuary, California, October 1991 through November 1993. Technical Report 94-471. United States Geological Survey, Menlo Park, California.
- Hager, S.W., 1997. Dissolved nutrient data for the San Francisco Bay estuary, California, February through November 1994. Technical Report 97-17. United States Geological Survey, Menlo Park, California.
- Hager, S.W., Schemel, L.E., 1996. Dissolved inorganic nitrogen, phosphorus and silicon in South San Francisco Bay. I. Major factors affecting distributions. In: Hollibaugh, J.T. (Ed.), *San Francisco Bay: The Ecosystem*. Pacific Division of the American Association for the Advancement of Science, San Francisco, California, pp. 189–216.
- Hager, S.W., Schemel, L.E., 1999. Dissolved nutrient data for the San Francisco Bay estuary, California, January through November 1995. Technical Report 97-359. United States Geological Survey, Menlo Park, California.
- Herman, P.M.J., 1993. A set of models to investigate the role of benthic suspension feeders in estuarine ecosystems. In: Dame, R.F. (Ed.), *Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*. Springer-Verlag, pp. 421–454.
- Huzzey, L.M., Cloern, J.E., Powell, T.M., 1990. Episodic changes in lateral transport and phytoplankton distribution in South San Francisco Bay. *Limnology and Oceanography* 35 (2), 472–478.
- Jassby, A.D., Cloern, J.E., Powell, T.M., 1993. Organic carbon sources and sinks in San Francisco Bay: variability induced by river flow. *Marine Ecology Progress Series* 95, 39–54.
- Kimmerer, W.J., 2004. Open-water processes of the San Francisco Estuary: from physical forcing to biological responses. *San Francisco Estuary and Watershed Science* 2 (Article 1).
- Kimmerer, W.J., Burau, J.R., Bennett, W.A., 2002. Persistence of tidally-oriented vertical migration by zooplankton in a temperate estuary. *Estuaries* 25 (3), 359–371.
- Koseff, J.R., Holen, J.K., Monismith, S.G., Cloern, J.E., 1993. Coupled effects of vertical mixing and benthic grazing on phytoplankton populations in shallow, turbid estuaries. *Journal of Marine Research* 51, 843–868.
- Lacy, J.R., Schoellhamer, D.H., Burau, J.R., 1996. Suspended-solids flux at a shallow-water site in South San Francisco Bay, California. *Proceedings of the North American Water and Environment Congress*. American Society of Civil Engineers, New York, New York.
- Lorenzen, C.J., 1967. Determination of chlorophyll *a* and phaeopigments: spectrophotometric equations. *Limnology and Oceanography* 12, 343–346.
- Lucas, L.V., Cloern, J.E., Koseff, J.R., Monismith, S.G., Thompson, J.K., 1998. Does the Sverdrup critical depth model explain bloom dynamics in estuaries? *Journal of Marine Research* 56, 375–415.
- Lucas, L.V., Koseff, J.R., Cloern, J.E., Monismith, S.G., Thompson, J.K., 1999a. Processes governing phytoplankton blooms in estuaries. I: the local production-loss balance. *Marine Ecology Progress Series* 187, 1–15.
- Lucas, L.V., Koseff, J.R., Monismith, S.G., Cloern, J.E., Thompson, J.K., 1999b. Processes governing phytoplankton blooms in estuaries. II: the role of horizontal transport. *Marine Ecology Progress Series* 187, 17–30.
- Meyhofer, E., 1985. Comparative pumping rates in suspension-feeding bivalves. *Marine Biology* 85, 137–142.
- Mohlenberg, F., Riisgard, H.U., 1979. Filtration rate, using a new indirect technique, in thirteen species of suspension-feeding bivalves. *Marine Biology* 54, 143–147.
- O’Riordan, C.A., Monismith, S.G., Koseff, J.R., 1993. A study of concentration boundary layer formation over a bed of model bivalves. *Limnology and Oceanography* 38 (8), 1712–1729.
- O’Riordan, C.A., Monismith, S.G., Koseff, J.R., 1995. The effect of bivalve ecurrent jet dynamics on mass transfer in a benthic boundary layer. *Limnology and Oceanography* 40 (2), 330–344.
- Parchaso, F., Thompson, J.K., 2002. Influence of hydrologic processes on reproduction of the introduced bivalve *Potamocorbula amurensis* in Northern San Francisco Bay, California. *Pacific Science* 56 (3), 329–345.
- Pomeroy, L.R., D’Elia, C.F., Schaffner, L.C., 2006. Limits to top-down control of phytoplankton by oysters in Chesapeake Bay. *Marine Ecology Progress Series* 325, 301–309.
- Poultou, V.K., Lovvorn, J.R., Takekawa, J.Y., 2004. Spatial and overwinter changes in clam populations of San Pablo Bay, a semiarid estuary with highly variable freshwater inflow. *Estuarine Coastal and Shelf Science* 59 (3), 459–473.
- Richman, S.E., Lovvorn, J.R., 2004. Relative foraging value to Lesser Scaup ducks of native and exotic clams from San Francisco Bay. *Ecological Applications* 14 (4), 1217–1232.
- Riemann, B., 1978. Carotenoid interference in spectrophotometric determination of chlorophyll degradation products from natural populations of phytoplankton. *Limnology and Oceanography* 23, 1059–1066.
- Schemel, L.E., 1995. Supporting data for hydrologic studies in San Francisco Bay, California: meteorological measurements at the Port of Redwood City during 1992–1994. Open-File Report 95–327. United States Geological Survey, Menlo Park, California.

- Schemel, L.E., Ota, A.Y., Harmon, J.G., Shay, J.M., Adorador, R.N., 1988. Benthic Macrofauna and Ancillary Data for San Francisco Bay, California, March to November 1987. U.S. Geological Survey. Open-File Report 88-192.
- Schemel, L.E., Ota, A.Y., Harmon, J.G., Shay, J.M., Adorador, R.N., 1990. Benthic Macrofauna and Ancillary Data for San Francisco Bay, California, January to November 1988. U.S. Geological Survey. Open-File Report 89-596.
- Schoellhamer, D.H., 1996. Factors affecting suspended-solids concentrations in South San Francisco Bay, California. *Journal of Geophysical Research* 101 (C5), 12087–12095.
- Strayer, D.L., Caraco, N.F., Cole, J.J., Findlay, S., Pace, M.L., 1999. Transformation of freshwater ecosystem by bivalves. *Bioscience* 49, 19–27.
- Thompson, J.K., 1999. The effect of infaunal bivalve grazing on phytoplankton bloom development in South San Francisco Bay. Ph.D. Thesis, Department of Civil and Environmental Engineering, Stanford University, Stanford, California.
- Thompson, J.K., 2005. One estuary, one invasion, two responses: phytoplankton and benthic community dynamics determine the effect of an estuarine invasive suspension-feeder. In: Dame, R.F., Olenin, S. (Eds.), *The Comparative roles of Suspension-Feeders in Ecosystems*. Springer, pp. 291–316.
- Winters, J.W., 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* 13, 1–33.