Climate anomalies generate an exceptional dinoflagellate bloom in San Francisco Bay

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[1] We describe a large dinoflagellate bloom, unprecedented in nearly three decades of observation, that developed in San Francisco Bay (SFB) during September 2004. SFB is highly enriched in nutrients but has low summer-autumn algal biomass because wind stress and tidally induced bottom stress produce a well mixed and light-limited pelagic habitat. The bloom coincided with calm winds and record high air temperatures that stratified the water column and suppressed mixing long enough for motile dinoflagellates to grow and accumulate in surface waters. This event-scale climate pattern, produced by an upper-atmosphere high-pressure anomaly off the U.S. west coast, followed a summer of weak coastal upwelling and high dinoflagellate biomass in coastal waters that apparently seeded the SFB bloom. This event suggests that some red tides are responses to changes in local physical dynamics that are driven by large-scale atmospheric processes and operate over both the event scale of biomass growth and the antecedent seasonal scale that shapes the bloom community. **Citation:** Cloern, J. E., T. S. Schraga, C. B. Lopez, N. Knowles, R. Grover Labiosa, and R. Dugdale (2005), Climate anomalies generate an exceptional dinoflagellate bloom in San Francisco Bay, *Geophys. Res. Lett.*, *32*, L14608, doi:10.1029/2005GL023321.

1. Introduction

[2] Phytoplankton primary production is the energy source that sustains pelagic food webs and drives variability in the cycling of key elements. Primary production is an unsteady process, varying at time scales from minutes to millennia as phytoplankton biomass and its turnover rate vary continuously. Much of this variability in the ocean is associated with phytoplankton blooms that are triggered by changes in physical dynamics, such as seasonal thermal stratification that initiates the North Atlantic spring bloom, and events that transport nutrient-rich deep water into the euphotic zone such as hurricanes [*Davis and Yan*, 2004] and upwelling.

[3] The ecological and biogeochemical significance of blooms depend strongly on the species composition of the community that grows [*Cloern*, 1996]: diatom production in upwelling systems fuels pelagic food webs supporting fisheries, whereas blooms of toxic flagellates suppress growth and reproduction of herbivores and endanger human consumers. Expanding programs of global surveillance suggest that the frequency of red tides and harmful algal blooms (HABs) is increasing in coastal ecosystems as a response to anthropogenic nutrient enrichment [*Hallegraeff*, 1993]. However, the conversion of land-derived nutrients into harmful-algal biomass is dependent upon a pelagic habitat that can sustain fast population growth. Fertilization of coastal ecosystems increases the potential for HAB development, but the realization of that potential is regulated by physical dynamics. HABs often develop when nutrient-rich waters become stratified, so their dynamics are tightly coupled to mixing dynamics driven by ocean-atmosphere interactions.

[4] Unresolved questions remain about the mechanisms and scales of linkage between physical dynamics and blooms [*Cullen et al.*, 2002]. For example, how do small-scale physical processes generate and maintain dense accumulations of phytoplankton cells in thin layers [*Dekshenieks et al.*, 2001]? What processes select the species that proliferate during algal blooms? If species composition is determined by "precedent and stochasticity" [*Reynolds et al.*, 2000], what are the time scales over which precedent conditions shape communities and their biomass? Coastal HABs are regulated by nutrient supply rate and climate-driven physical dynamics, but how will the accelerating human mobilization of nutrients interact with climate change to alter the frequency, severity and ecological impairments caused by harmful blooms?

[5] Ocean observing systems provide an empirical basis for building conceptual and numerical models to address these fundamental questions. Sustained observations capture anomalous events that can be exploited as natural experiments, and they provide context for understanding the significance of events and revealing their underlying mechanisms. Oceanographers are compiling libraries of event observations, building toward a synthetic understanding of the mechanisms of pelagic physical-biological coupling. Here we present observations of a large dinoflagellate bloom that developed in San Francisco Bay during a short-term anomaly of local climatic conditions following a seasonal-scale anomaly in coastal oceanographic conditions. This natural experiment suggests that some red tides
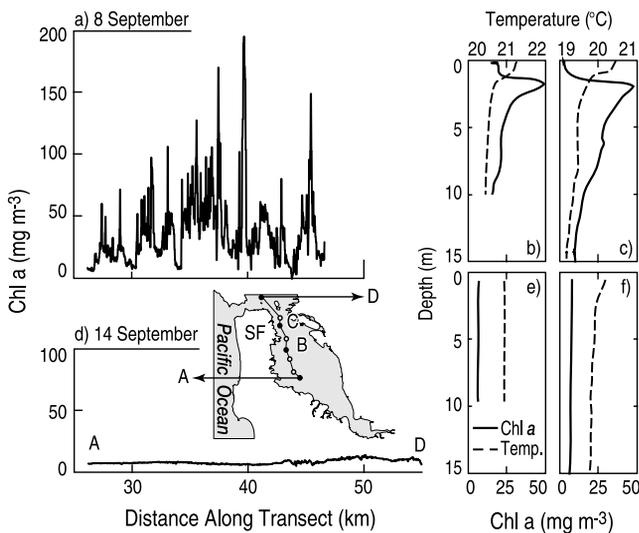
Figure 1. Horizontal distributions of near-surface chlorophyll *a* along transect *A-D* in San Francisco Bay during (a) 8 September and (d) 14 September 2004. Panels to the right show vertical distributions of temperature and Chl*a* at locations *B* and *C* on 8 September (b,c) and 14 September (e,f).

and HABs are responses to coupled effects of physical dynamics operating over multiple time scales, and that local-scale physical dynamics are driven by ocean-atmosphere processes operating over much larger spatial scales.

2. Data Sets

[6] The U.S. Geological Survey maintains a hydrographic sampling program in San Francisco Bay as a component of studies to understand how anthropogenic and natural forcings drive dynamics of coastal ecosystems. Horizontal variability of near-surface (upper $1-2$ m) phytoplankton biomass is measured using the proxy of chlorophyll fluorescence in water pumped from the bow intake of a research vessel as it follows a longitudinal transect (Figure 1d, inset). Vertical variability of salinity, temperature, dissolved oxygen and chlorophyll *a* (Chl*a*) are measured at fixed stations with a Seabird CTD, an oxygen electrode, and a Turner Designs Cyclops 7 fluorometer calibrated with discrete Chl*a* analyses [*Cloern and Dufford*, 2005]. Sampling has been done at least once monthly since 1978 (all data are available online: http://sfbay.wr.usgs.gov/access/wqdata).

[7] Air temperature and wind speed at San Francisco International Airport were obtained from NOAA's National Weather Service (http://www.wrh.noaa.gov/climate/index.php?wfo=mtr). Tidal current speeds were computed from harmonic analyses of long-term current-meter records from South San Francisco Bay [*Cheng and Gartner*, 1985]. Nutrient (nitrate, silicate) and Chl*a* concentrations were measured in surface samples collected at Tiburon along the northern shore of Central San Francisco Bay. Climatic and oceanographic data for the adjacent coastal Pacific Ocean were obtained from NOAA's National Data Buoy Center (http://www.nodc.noaa.gov) (buoy 46026, located

25 km west of San Francisco). We also used the Upwelling Index (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html) of wind-driven cross-shelf Ekman transport at 36N 122W, computed by NOAA's Pacific Fisheries Environmental Laboratory. NCEP/NCAR Reanalysis data were used to characterize atmospheric pressure and wind fields (http://www.cdc.noaa.gov/Composites/Day). MODIS (MODerate Resolution Imaging Spectroradiometer) local area coverage (LAC2, 1 km resolution) images of ocean surface temperature and Chl*a* were obtained from http://oceancolor.gsfc.nasa.gov and projected using a transverse mercator projection using NASA's SeaDAS (SeaWIFS Data Analysis System) program.

3. Results and Discussion
3.1. An Exceptional Dinoflagellate Bloom

[8] On 8 September 2004 we observed patches of red water in South San Francisco Bay [*Cloern et al.*, 2005], and microscopic examination revealed high abundances (up to 400 cells ml^{-1}) of the large dinoflagellate *Akashiwo sanguinea* and smaller dinoflagellates including *Heterocapsa rotundata*, *Prorocentrum micans* and *Scrippsiella trochoidea*. Surface Chl*a* was extremely patchy, ranging from <1 to 195 mg m^{-3} (Figure 1a), and vertical profiles revealed thermal stratification and highest Chl*a* within the shallow thermocline (Figures 1b and 1c). We have never before observed a dinoflagellate bloom of this magnitude. In nearly three decades of sampling, our data have consistently shown low summer-autumn phytoplankton biomass: the 27-year mean August−October Chl*a* at stations B and C (Figure 1d) is <3 mg m^{-3}, and the previously recorded maximum August−October Chl*a* along transect A-D was 21 mg m^{-3}.

[9] The red tide dissipated by 14 September 2004 when transect-mean Chl*a* fell to 8.3 mg m^{-3} and the vertical gradients of temperature and Chl*a* disappeared or weakened (Figures 1d–1f). Lower biomass and vertical homogeneity were observed on 24 August 2004, prior to the red tide. Algal blooms are events of rapid biological production and associated biogeochemical change. We observed nitrate (but not silicate) removal by algal uptake (see Figure 2d), and supersaturated dissolved oxygen concentrations (maximum 10.7 mg l^{-1} = 142% saturation) along transect A-D, reflecting high primary productivity during this bloom. Although decomposition of *A. sanguinea* blooms has led to anoxia and mortalities of fish and cultured shellfish [*Kahru et al.*, 2004], there were no reports of oxygen depletion or animal mortalities in San Francisco Bay.

3.2. Event-Scale Climate Anomaly

[10] Red tides develop in high-nutrient, low-turbulence environments [*Margalef*, 1978]. Episodic thermal stratification can trigger these events in nutrient-rich coastal waters because density stratification suppresses turbulence and creates stable vertical gradients of light and nutrients that can be exploited by motile phytoplankton. Thin layers of high phytoplankton biomass occur under conditions of weak turbulence (Richardson number > 0.25 [*Dekshenieks et al.*, 2001]) when vertical migrations by fast-swimming species such as *A. sanguinea* can overcome vertical displacements by turbulent eddies. The vertical Chl*a*
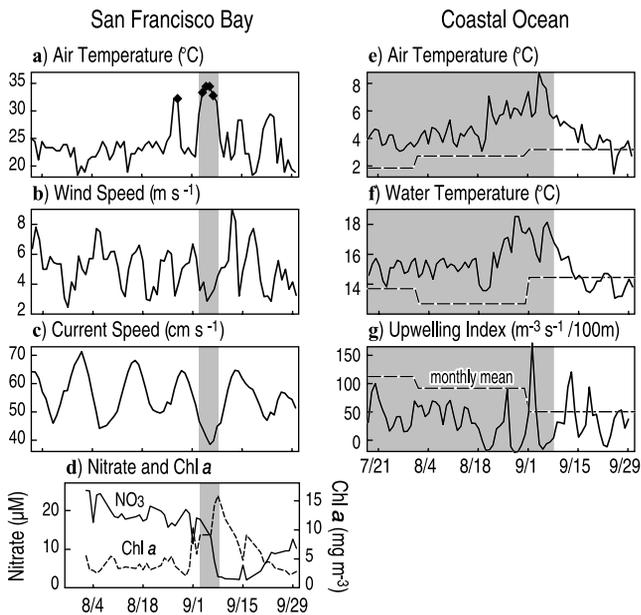
Figure 2. Time series (18 July–30 September 2004) of: (a) air temperature (diamonds denote dates of record high) and (b) wind speed at San Francisco Airport; (c) predicted maximum daily tidal current speed in South San Francisco Bay; and (d) near-surface Chl*a* and nitrate in San Francisco Bay at Tiburon; daily maximum (e) air and (f) surface water temperature in coastal waters adjacent to San Francisco Bay (dashed lines show monthly means from 1982–2001); and (g) the daily upwelling index at 36N 122W (dashed line shows monthly means from 1967–2004).

distributions measured here (Figures 1b and 1c) were probably ephemeral because diel migrations (downward at night and upward in morning) displace dinoflagellate layers over vertical distances of ∼10 m [*Pitcher et al.*, 1998].

[11] Although San Francisco Bay has high nutrient concentrations, summer-autumn blooms are rare because inputs of turbulent kinetic energy from wind stress and tidal currents overcome buoyancy inputs from surface heating and prevent stratification. Blooms do occur in spring when density gradients from runoff-induced salinity stratification are strong enough to resist mixing forces. Continuous mixing between a shallow photic zone and deeper aphotic zone constrains phytoplankton growth by light limitation and increases mortality by delivering phytoplankton cells to benthic suspension feeders, so San Francisco Bay is typically a well mixed high-nutrient/low-chlorophyll marine system during summer and autumn [*Cloern*, 1996]. The anomalous thermal stratification and red tide observed on 8 September coincided with 4 consecutive days of record high air temperature and weak winds coupled with a low-energy neap tide (Figures 2a–2c). This local weather event was caused by an upper-level high-pressure anomaly off the U.S. west coast and a strong ridge over California (Figure 3a). This pressure pattern is associated with convergence aloft that caused airmass subsidence, higher temperatures, and stagnant surface conditions. Thermal stratification in the Bay broke down, and the red tide

dissipated when the atmospheric ridge pattern weakened, local winds increased, and tidal currents accelerated during the neap-spring transition (Figures 2b and 2c). These observations illustrate fast biological and biogeochemical responses to an event of changing physical dynamics in a coastal ecosystem.

3.3. Antecedent Seasonal-Scale Climate Anomaly

[12] Phytoplankton biomass in San Francisco Bay is usually dominated by diatoms, which thrive in high-nutrient, high-turbulence environments [*Margalef*, 1978] such as tidal estuaries and upwelling systems. However, dinoflagellates contributed 88–95% of biomass (cellular biovolume) in samples collected on 8 September, and this biomass was dominated by *Akashiwo sanguinea*. Red tides and HABs are often dominated by single species, but the selective processes are often difficult to establish. Antecedent oceanographic conditions give strong clues about why this species dominated the San Francisco Bay red tide.

[13] *Akashiwo sanguinea* (= *Gymnodinium splendens*) forms dense, patchy blooms in the Eastern Pacific, from California to Peru [*Dugdale et al.*, 1977]. It occurs only in the seaward regions of San Francisco Bay [*Cloern and Dufford*, 2005], suggesting that it is an allochthonous species produced in the coastal ocean and transported into the Bay by density-driven currents or tidal dispersion. This species typically occurs in autumn, when equatorward winds diminish or reverse and the central California coastal ocean switches from a diatom-producing upwelling system to a warm, stratified system with onshore or weak offshore transport that favors growth of picoplankton and dinoflagellates. However, weak upwelling occurred early in 2004. The Coastal Upwelling Index, which represents offshore surface transport due to alongshore wind stress, was much smaller than average during July and August (Figure 2g). Persistent weak upwelling allowed warming of the coastal ocean, particularly during the last two weeks of August (Figure 2f) when the Upwelling Index approached
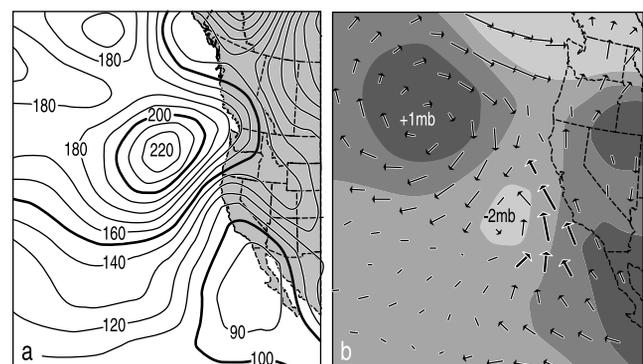

Figure 3. (a) Mean 1000 mb geopotential heights, composited for 4–7 September 2004, and showing a strong ridge over California during the record warming and dinoflagellate bloom in San Francisco Bay; (b) 20–30 August 2004 composite pressure and surface anomalies, showing southerly wind anomaly responsible for weak upwelling near California's coast.
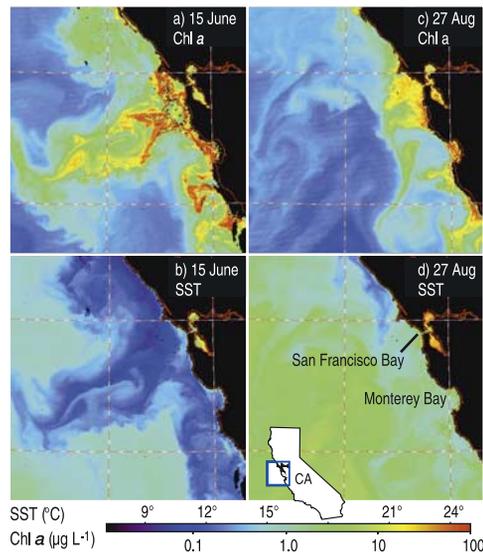
Figure 4. MODIS chlorophyll *a* (top) and surface temperature (bottom) images for 15 June (strong upwelling, left) and 27 August 2004 (weak upwelling, right).

zero. The early seasonal relaxation of upwelling was associated with a contraction of the East Pacific High, creating a local low-pressure anomaly and a southerly geostrophic wind anomaly off the California coast. This low-pressure anomaly was especially pronounced from 20–30 August (Figure 3b) when the coastal air and surface ocean warmed further.

[14] Summer 2004 produced the weakest August-mean upwelling index (at 36N) since records began in 1946. We speculate that weakened offshore flows, coupled with surface warming, promoted growth of dinoflagellates in the adjacent California Current System before the red tide developed inside San Francisco Bay. Satellite imagery is consistent with this speculation, revealing high surface temperatures and high phytoplankton biomass in the near-shore coastal ocean during late August (Figures 4c and 4d), compared to the typical summer upwelling state of low nearshore surface temperature and offshore transport of cold, chlorophyll-rich water within filaments (Figures 4a and 4b). Dinoflagellate-dominated brown tides occurred in Monterey Bay during the 2004 summer of weak upwelling (note the high Chl*a* there on 27 August, Figure 4c), and *Akashiwo sanguinea* was common in Monterey Bay during late August (M.W. Silver, unpublished data, 2005). We also observed *Akashiwo sanguinea* in San Francisco Bay on 24 August. Dinoflagellates accumulate near the coast during relaxation of upwelling in other eastern-boundary current systems [*Pitcher et al.*, 1998], and these 'pelagic seed banks' can inoculate nearshore habitats and lead to local blooms [*Smayda*, 2002]. Weak upwelling conditions were associated with blooms of vertically migrating dinoflagellates, including *Gonyaulax* sp. and *Gymnodinium* sp., in coastal Baja California waters [*Walsh et al.*, 1974]. Water column NO_3 was entirely consumed by these populations during their daily migrations to the surface regions. It seems likely that these same processes led to

the lowest NO_3 concentrations observed in Central Bay near Tiburon Figure 2d.

[15] The exceptional red tide in San Francisco Bay was apparently a coupled response to a short-term weather anomaly that produced an opportunity for rapid population growth, preceded by a seasonal-scale coastal anomaly that generated a seed stock of *Akashiwo sanguinea* to exploit this opportunity. Blooms are dominated by species that either sustain high net growth rates or have large inocula [*Reynolds et al.*, 2000], and these two selective processes can operate over different time scales.

4. Conclusions

[16] Red tides and HAB's are often studied at a local geographic scale and the event time scale, but observations presented here illustrate the importance of broadening this perspective. Blooms are shaped by changing physical dynamics over multiple time scales, and we highlight event-scale processes that determine the timing and rate of biomass buildup and antecedent processes operating over longer time scales that can shape the bloom community. Bloom-regulating physical dynamics described here are driven by atmospheric processes that vary over multiple spatial scales, from the local winds and heat flux that set up stratification inside San Francisco Bay to the ocean-basin scale atmospheric processes that produce variability in wind-driven coastal circulation. Meeting the challenges to resolve human vs. natural influences on HABs and to forecast coastal-ecosystem responses to global change will require consideration of the full spectrum of spatial and temporal variability through which atmospheric and physical dynamics regulate phytoplankton biomass and community composition.

References

Cheng, R. T., and J. W. Gartner (1985), Harmonic analysis of tides and tidal currents in south San Francisco Bay, California, *Estuarine Coastal Shelf Sci.*, *21*, 57–74.

Cloern, J. E. (1996), Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California, *Rev. Geophys.*, *34*, 127–168.

Cloern, J. E., and R. Dufford (2005), Phytoplankton community ecology: Principles applied in San Francisco Bay, *Mar. Ecol. Prog. Ser.*, *285*, 11–28.

Cloern, J. E., T. S. Schraga, and C. Burns Lopez (2005), Heat wave brings an unprecedented red tide to San Francisco Bay, *Eos Trans. AGU*, *86*(7), 66.

Cullen, J. J., P. J. S. Franks, D. M. Karl, and A. Longhurst (2002), Physical influences on marine ecosystem dynamics, in *The Sea*, vol. 12, edited by A. R. Robins, J. J. McCarthy, and B. J. Rothschild, pp. 297–335, John Wiley, Hoboken, N. J.

Davis, A., and X.-H. Yan (2004), Hurricane forcing on chlorophyll-a concentration off the northeast coast of the U.S., *Geophys. Res. Lett.*, *31*, L17304, doi:10.1029/2004GL020668.

Dekshenieks, M., P. L. Donaghay, J. M. Sullivan, J. E. B. Rines, T. R. Osborn, and M. S. Twardowski (2001), Temporal and spatial occurrences of thin phytoplankton layers in relation to physical processes, *Mar. Ecol. Prog. Ser.*, *223*, 61–71.

Dugdale, R. C., J. J. Goering, R. T. Barber, R. L. Smith, and T. T. Packard (1977), Denitrification and hydrogen sulfide in the Peru upwelling region during 1976, *Deep Sea Res.*, *24*, 601–608.

Hallegraeff, G. M. (1993), A review of harmful algal blooms and their apparent global increase, *Phycologia*, *32*, 79–99.

Kahru, M., B. G. Mitchell, A. Diaz, and M. Miura (2004), MODIS detects a devastating algal bloom in Paracas Bay, Peru, *Eos Trans. AGU*, *85*(45), 465.

Margalef, R. (1978), Life-forms of phytoplankton as survival alternatives in an unstable environment, *Oceanol. Acta*, *1*, 493–509.

Pitcher, G. C., A. J. Boyd, D. A. Horstman, and B. A. Mitchell-Innes (1998), Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system, *Mar. Ecol. Prog. Ser.*, *172*, 253–264.

Reynolds, C., M. Dokulil, and J. Padisák (2000), Understanding the assembly of phytoplankton in relation to the trophic spectrum: Where are we now?, *Hydrobiologia*, *424*, 147–152.

Smayda, T. J. (2002), Turbulence, watermass stratification and harmful algal blooms: An alternative view and frontal zones as "pelagic seed banks," *Harmful Algae*, *1*, 95–112.

Walsh, J. J., J. C. Kelley, T. F. Whitledge, and J. J. MacIsaac (1974), Spin-up of the Baja California upwelling system, *Limnol. Oceanogr.*, *19*, 553–572.

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