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A biogeochemical model of phytoplankton productivity in an urban estuary: The importance of ammonium and freshwater flow

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ABSTRACT

Increased discharge of ammonium (NH_4) to the San Francisco Estuary (SFE), largely in treated domestic sewage effluent, has been linked to chronically food-limited conditions and to reduced fish abundance. Elevated chlorophyll concentrations at phytoplankton bloom levels are rarely observed if the ambient NH_4 concentrations are above 4 μmol L^{-1}—the NH_4 paradox. In both field samples and water held in enclosures for one week, an inverse relation was observed between NH_4 concentrations and nitrate (NO_3) uptake by phytoplankton, likely a result of inhibition of NO_3 uptake by NH_4. A simple model was constructed to examine the interaction between NH_4 and NO_3 inputs to the estuary, with varying freshwater river flow (hereafter termed flow) conditions. Sensitivity analyses were made and initial model parameters taken from an existing oceanic biogeochemistry model. Experiments were made with the model, and showed that initial NH_4 concentrations largely controlled the length of time to peak NO_3 uptake and NO_3 exhaustion. The model parameters were then tuned using observations from a set of enclosure experiments, and validated with results from a series of independent enclosure experiments with a variety of initial conditions. The model was run in three flow modes: (1) with no (zero) flow, (2) with flow, a fully mixed water column and a uniform light field, and (3) with flow, a fully mixed water column but with light attenuation and depth integrated values of N uptake. In the zero flow mode the model simulated enclosure experiments and when compared with enclosure results indicated the basic NH_4–NO_3 interactions to be correctly represented in the model. In the modes with flow, the model simulations reproduced a sharp transition from high phytoplankton productivity using both NO_3 and NH_4 to low productivity using only NH_4, simulating the historical effects of increasing NH_4 inputs to the SFE. With vertical integration to incorporate effects of irradiance, sharp boundaries at specific combinations of varying flow and NH_4 inputs were observed. The model could be embedded into three dimensional models of the SFE/Delta currently being implemented for management purposes such as regulating estuarine nutrients as required by the State of California and evaluating the effects of water management decisions on salmon and protected species of fish.

1. Introduction

In the urban San Francisco Estuary (SFE) a rapid decline of four fish species to low population levels suggests that some may be on the verge of extinction. The trend is known as the Pelagic Organism Decline (POD) and a search for the cause(s) has been in progress (e.g. Sommer et al., 2007). Studies have concluded that most levels of the food web above the primary producers are food limited (Müller-Solger et al., 2002; Kimmerer et al., 2005; Sobczak et al., 2005; Greene et al., 2011). The estuary has chronically low primary production (Kimmerer et al., 2012) near the bottom of estuaries listed in order of annual primary production (Boynton et al., 1982; Nixon, 1988). Suisun Bay in the northern SFE (Fig. 1) is a center of attention about the causes of the POD since it is where critical phases in the life cycle of one POD species occur. This species, the delta smelt (*Hypomesus transpacificus*), has been listed as endangered under the California Endangered Species Act since 2008.

Although the current debate on the cause(s) of the POD focuses on the period from 2000 to the present, the primary productivity of the SFE has been declining for more than three decades (Jassby et al., 2002) even though water transparency, previously shown to determine primary production in the SFE (Cole and Cloern, 1984), and nutrient loads have been increasing over the same period (Jassby, 2008). This situation with declining productivity and high nutrients has been termed oligotrophication by Nixon (1990). A trend of increasing chlorophyll in the Delta has occurred in the period 1996–2005, but not in Suisun Bay (Jassby, 2008).

Before 1980, Suisun Bay was characterized as a high chlorophyll ecosystem dominated by diatoms and large zooplankton (Ball and Arthur, 1979); it is now dominated by small phytoplankton,

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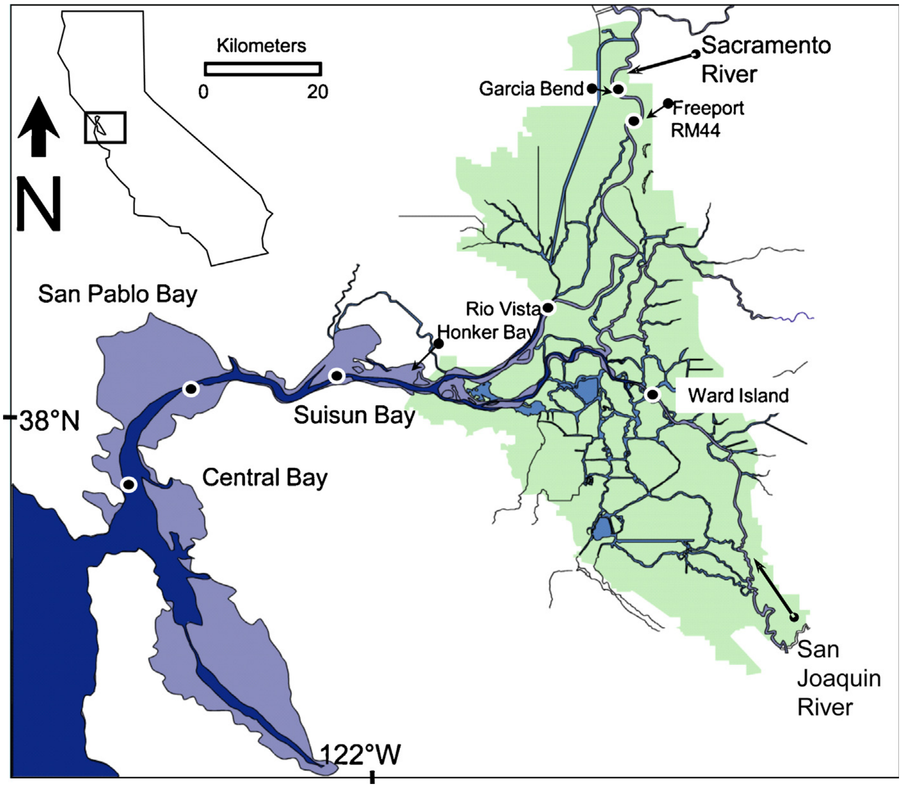

Fig. 1. Map of San Francisco Estuary/Delta California showing Suisun, San Pablo and Central Bays, and sampling locations along the Sacramento and San Joaquin rivers.

small zooplankton (Glibert et al., 2011) and low primary production (Kimmerer et al., 2012). High summer chlorophyll concentrations in Suisun Bay declined to low levels in 1987. Additionally spring blooms were not observed in Suisun Bay (Dugdale et al., 2012). The invasive Asian overbite clam (*Potamocorbula amurensis*) appeared in substantial numbers at that time and is considered the primary reason for the crash in phytoplankton biomass (Alpine and Cloern, 1992). However clam populations are low in spring (Greene et al., 2011) and grazing is insufficient to explain the lack of spring blooms. Nutrients had been neglected as a factor in regulation of primary production in the SFE as N, Si and P were all in excess of requirements throughout the year (Jassby et al., 2002). However, the decline in chlorophyll in Suisun Bay (in all seasons) began at about the same time as NH_4 discharge and concentrations began to increase rapidly in the Sacramento River the main water source for Suisun Bay (Glibert et al., 2011), the result of both increases in urban populations and agricultural use of nitrogen fertilizers (Jassby, 2008). In 1984 there were 5.2 tons NH_4-N day^{-1} added to the Sacramento River at Freeport from municipal waste (Schemel and Hager, 1986); additional natural/agricultural NH_4 in the Sacramento River was less than or equal to half of the effluent input. Today, discharge of NH_4 at Freeport is about 15 tons NH_4-N per day (Jassby, 2008).

A growing body of evidence points to NH_4 inputs of anthropogenic origin as a driving factor in the decline and eventual collapse of the primary productivity of the northern SFE and in particular of Suisun Bay (e.g. Dugdale et al., 2007; Glibert et al., 2011; Dugdale et al., 2012). Measurements of dissolved inorganic N (DIN) uptake by phytoplankton using incubations with $^{15}NO_3$ and $^{15}NH_4$ as tracers have indicated that nutrients in SFE are important in determining phytoplankton productivity (Wilkerson et al., 2006; Dugdale et al., 2007, 2012; Parker et al., 2012a,b). NO_3 is rarely used in the SFE/Delta as a consequence of suppression of NO_3 uptake by NH_4, with phytoplankton blooms occurring in the SFE only when NH_4 concentrations declined to low levels (Wilkerson et al., 2006; Dugdale et al., 2007). NO_3 uptake is essential for high productivity rates and phytoplankton bloom occurrence as NO_3 is the largest reservoir of DIN in the SFE (Wilkerson et al., 2006; Dugdale et al., 2012). Decreased phytoplankton growth rates and reduced carbon fixation (primary production) occurred when the algae were using NH_4 compared to NO_3 (Wilkerson et al., 2006; Parker et al., 2012a). When chlorophyll concentrations and NO_3 uptake rates were plotted against NH_4 concentration, a threshold of about 4 μmol L^{-1} NH_4 appeared to delineate the level at which suppression of NO_3 uptake occurred. Below this concentration, NO_3 uptake was enabled and occurred even more rapidly when NH_4 concentrations decreased to ~1 μmol L^{-1} accompanied by a rapid increase in chlorophyll (Dugdale et al., 2007).

To understand the sequence of events involved in the NH_4 response by phytoplankton, to use in simulation models, experiments were made with water from Central San Francisco Bay that was enclosed and incubated under natural light. The phytoplankton response in the enclosed water followed the pattern shown in Fig. 2 (taken from Dugdale et al., 2007) that has been repeatedly observed (e.g. Parker et al., 2012a). First NH_4 concentrations decreased and then NO_3 concentrations decreased rapidly to zero within four days (Fig. 2a and b) (Dugdale et al., 2007). During this four day cycle, the biomass-specific NO_3 uptake rate (VNO_3) increased to a peak at Day 2 or 3 and then declined rapidly as NO_3 was depleted (Fig. 2c). The biomass-specific NH_4 uptake rate (VNH_4) remained relatively unchanged or decreased (Fig. 2d). Chlorophyll accumulation (Fig. 2e) occurred as NO_3 was drawn down. This rapid use of NO_3 observed in SFE water is virtually identical to that observed in newly upwelled ocean water (Wilkerson and Dugdale, 1987; Dugdale et al., 2006) and incorporated into a productivity model that included acceleration or "shift up" of NO_3 uptake rates (Dugdale et al., 1990). The essential feature of this shift-up model is that the biomass specific NO_3 uptake rate, VNO_3 (equivalent to a nitrogen-based growth rate) increases at a rate proportional to the ambient NO_3 concentration. Since NO_3 is usually