Impact of atypical ammonium concentrations on phytoplankton abundance and composition in fresh versus estuarine waters

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ABSTRACT: The impact of atypically high ammonium (NH_4^+) concentrations delivered via treated wastewater effluent on phytoplankton community composition was investigated in a tidal slough connected with Suisun Bay in the northern part of San Francisco Bay. Input of effluent to a downstream location resulted in NH_4^+ concentrations of (mean $\pm$ SD) $1021 \pm 380 \mu\text{mol l}^{-1}$, compared with $2.9 \pm 1 \mu\text{mol l}^{-1}$ at a site further upstream, and $4.8 \pm 1 \mu\text{mol l}^{-1}$ in Suisun Bay. Comparison of the diatom community at the downstream site in Pacheco Slough with that in Suisun Bay revealed a substantial overlap in species, including *Cyclotella scaldensis*, which dominated diatom species composition in both locations. The ratio of diatoms:other phytoplankton biomass ($\mu\text{mol}^3:\mu\text{mol}^3$) suggested that diatoms contributed a greater proportion of total phytoplankton community biomass at the downstream location (48.6 ± 87) versus in Suisun Bay (9.5 ± 1) or upstream (9.5 ± 8), and that diatoms can readily grow in the presence of NH_4^+ concentrations varying from 2 to $1350 \mu\text{mol l}^{-1}$. In the present investigation, species composition of the seeding population was found to be a more important predictor of final phytoplankton community composition than nutrient concentrations or ratios.

KEY WORDS: Phytoplankton · Ammonium · N:P ratio · $\text{NH}_4^+:\text{NO}_3^-$ ratio · Diatoms · Chlorophytes · San Francisco Estuary · Suisun Bay

INTRODUCTION

Compared with other estuaries in the United States, San Francisco Bay (SFB) on the Pacific Coast distinguishes itself by having exceptionally low phytoplankton productivity and biomass (Nixon 1988, Cloern 1999). The low productivity is generally attributed to light limitation (Cole & Cloern 1984, 1987, Alpine & Cloern 1988, Jassby et al. 2002), resulting from relatively high levels of sediments brought via the Sacramento River into the bay (Goodwin & Denton 1991, Ruhl & Schoellhamer 2004, Schoellhamer et al. 2012). Phytoplankton production and community structure are also controlled by high rates of benthic filter

feeding as well as high flushing rates and short water residence times (Carlton et al. 1990, Alpine & Cloern 1992, Lehman 1996, 2000, Jassby 2008). Both pose a greater threat to phytoplankton populations in the northern region (Suisun Bay) compared with the southern region (South Bay) of SFB due to a greater abundance of invasive clams and a closer proximity to the Sacramento River (Thompson et al. 2008, Cloern & Jassby 2012).

In addition to the aforementioned factors, it has recently been proposed that the concentration of ammonium (NH_4^+) in the wastewater effluent that flows into Suisun Bay impairs phytoplankton growth (Dugdale et al. 2007, Parker et al. 2012). Moreover,

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analyses of changes in nutrient concentrations and phytoplankton abundance using the cumulative sums of variability (CUSUM) statistic suggests that diatom abundance correlates positively with low dissolved N:P ratios and with NO_3^- being the dominant N source in the water column (Glibert 2010). Therefore, it has been hypothesized that the moderate increases in concentrations of NH_4^+ which have occurred over the past 2 decades in Suisun Bay may have affected diatoms disproportionately, potentially resulting in diatoms becoming outcompeted by cyanobacteria and flagellates (Glibert et al. 2011, but see also Cloern et al. 2012).

Decreasing diatom concentrations, whether due to clam filtration or changes in nutrients (concentrations, ratios, or forms), has become a serious issue in Suisun Bay as it is thought to be the root cause of a decrease in micro- and macrozooplankton abundance, leading to a general decline in the Suisun Bay–Delta ecosystem as a food resource for higher trophic levels (Kimmerer et al. 1994, Kimmerer 2002, Feyrer et al. 2003, Winder & Jassby 2011). For example, the decrease in zooplankton may be adversely affecting abundances of several species of pelagic fish that have been at historical lows since 2001 (Sommer et al. 2007, Glibert 2010). This acute decline in fish abundances has prompted considerable efforts on the part of resource management agencies to identify the causes in the hope of fostering recovery (Nobriga et al. 2005, Sommer et al. 2007). Identifying the key factors contributing to the fish decline has proven difficult, as many environmental changes have occurred leading up to the year 2001 and continuing into the present (Cloern & Jassby 2012). While regulating clam abundance or filtration rates is not easily accomplished, regulating the load of NH_4^+ discharged by local wastewater treatment plants into Suisun Bay is possible. Therefore, considerable efforts on the part of water quality managers has been expended on understanding how elevated concentrations of NH_4^+ may contribute to the decline of phytoplankton in general, and diatoms in particular (Jassby 2008).

The present study investigates the impact of atypically high NH_4^+ concentrations delivered via treated wastewater effluent on phytoplankton abundance and community composition in a tidal creek connected to Suisun Bay. This investigation arose fortuitously from the need to repair a discharge pipe that would ordinarily discharge effluent into the deepest part of Suisun Bay. Effluent was discharged into Pacheco Slough, a tidal slough connected to Suisun Bay, allowing close monitoring of the effect of high

levels of NH_4^+ in the effluent on phytoplankton abundance and community composition in a restricted volume of water. Moreover, the shallow depth and lower turbidity of the tidal slough compared with Suisun Bay avoided problems of light limitation on phytoplankton growth. This enabled us to focus solely on the effects of the effluent and to investigate whether (1) the phytoplankton community was of a different composition relative to Suisun Bay, potentially reflecting the increase in abundance of phytoplankton (e.g. flagellates, cyanobacteria) able to tolerate atypical NH_4^+ concentrations, high N:P and $\text{NH}_4^+:\text{NO}_3^-$ ratios, and (2) whether the proportion of diatoms was less in Pacheco Slough, indicating that diatoms at this location were more susceptible to inhibition of growth by NH_4^+ than other taxa, and if so, whether (3) the diatoms present were different than the species typically present in Suisun Bay. To answer these questions, we enumerated phytoplankton in the slough at regular intervals while the effluent was being discharged into it and compared the composition with that in Suisun Bay, as well as with a point upstream in the slough not impacted by effluent. Environmental parameters such as salinity, dissolved oxygen, pH, temperature, turbidity, and nutrient concentrations were also monitored.

MATERIALS AND METHODS

Treated wastewater effluent from the Central Contra Costa Sanitary District (CCCSD), a conventional secondary wastewater treatment plant located in Martinez, CA on the southern shore of Suisun Bay, is usually discharged through a deep-water outfall directly into Suisun Bay. Every 8 to 10 yr the CCCSD drains, inspects and repairs its outfall. During this time, the CCCSD discharges its treated effluent into a holding basin (hereafter the basin) that flows over into Pacheco Slough, which drains into Suisun Bay (Fig. 1).

Pacheco Slough is 5.5 km long and ranges in width from less than 15 m upstream to greater than 76 m near the entrance to Suisun Bay. Water depth in the Slough is regulated by tidal action and ranges from less than 0.6 m upstream to approximately 1.8 m near the entrance to Suisun Bay. Pacheco Slough receives surface water runoff from the Walnut Creek and Grayson Creek watersheds of Central Contra Costa County. Grayson Creek is about 12 km long and originates in the Briones Regional Park, and Walnut Creek is about 56 km long and originates in the San Ramon Valley. The discharge from the Walnut Creek

Fig. 1. Location of Pacheco Slough and USGS sampling stations in Suisun Bay. Inset with downstream, basin and upstream sites on Pacheco Slough as well as sampling site USGS7 at the entrance to the Slough

watershed is the larger of the 2. During the study period, the estimated inflow from Walnut Creek was about $132 \times 10^6 \text{ l d}^{-1}$; Grayson Creek contributed only a small portion of that flow.

In the summer of 2012, CCCSD shut down its outfall and directed its effluent into its holding basin, from where it overflowed into Pacheco Slough at an average rate of $148 \times 10^6 \text{ l d}^{-1}$. In addition to the basin, Pacheco Slough was sampled at 2 sites, one upstream from the basin overflow (hereafter upstream), and the other downstream of the overflow (hereafter downstream, Fig. 1). The downstream site was impacted by the effluent flow and tidal action, whereas the upstream site was not and therefore served as the control site. Surface samples were collected from all 3 sites on a weekly basis during slack, low-tide for chlorophyll *a* (chl *a*), dissolved inorganic nutrients (NH_4^+ , NO_3^- , phosphorus [P]), dissolved oxygen, pH, temperature, and phytoplankton community composition from 23 August through 11 October 2012 while

the basin was overflowing into the slough. The same parameters were also sampled in the effluent going into the basin.

Dissolved oxygen, pH and temperature were measured immediately after sample collection using a HQ 40d Multi Auto Analyzer (Hach). The analyzer was calibrated before each sampling event following Method 10360 (Hach Company 2011). Salinity was measured using Method 2520 B in Eaton et al. (2005). Turbidity was measured using Method 180.1 (US EPA 1983).

The concentration of chl *a* was determined according to Parsons et al. (1984). Briefly, water was collected in a high density polyethylene (HDPE) bottle wrapped in aluminum foil, placed on ice, and transported to the lab where it was filtered in duplicate onto 25 mm Whatman GF/F filters. Filters were extracted for 4 h in the dark at 4°C in 90 % acetone before being placed in a tissue grinder and macerated for 1 min at 500 rpm. Samples were transferred

to a centrifuge tube via several rinses of the tissue grinder. Following centrifugation, total sample volume was adjusted to 10 ml with 90% acetone, and chl *a* was measured fluorometrically using a Turner Fluorometer 10-AU (Turner Designs).

Samples for nutrient analysis were filtered through 0.7 µm pore size GF/F filters prior to analysis. No effort was made in the present study to separate the concentration of NH_4^+ from that of un-ionized ammonia (NH_3), which is toxic at relatively low concentrations (Källqvist & Svenson 2003). The concentration of ammonia as a fraction of the total ammonia pool ($\text{NH}_4^+ + \text{NH}_3$) is typically below 1% at pH 7 and below 2% at pH 8 (Collos & Harrison 2014), therefore of minor concern in the present investigation. Due to the wide range of NH_4^+ concentrations in the present investigation, 2 different methods for measurements were used to eliminate error due to non-linearity. Low concentrations of NH_4^+ were analyzed using the phenol hypochlorite colorimetric method (Solorzano 1969), and high concentrations of NH_4^+ were analyzed using the acidimetric Method 4500 NH_3 B.C (Eaton et al. 2005). NO_3^- was analyzed colorimetrically using Method 418.D (Eaton et al. 2005). Dissolved P was analyzed colorimetrically according to Parsons et al. (1984).

Samples for phytoplankton composition were preserved with 2 ml of Lugol's solution per 200 ml sample. Samples were filtered onto a 0.2 µm polycarbonate membrane (Nuclepore) and enumerated using a Leica DMLB compound microscope according to McNabb (1960) as described in Beaver et al. (2013). Briefly, at least 400 natural units (colonies, filaments, and unicells) were enumerated to the lowest possible taxonomic level from each sample. The abundance of common taxa was estimated by random field counts. Rare taxa were quantified by scanning a transect of the filter. In the case of rare, large taxa, half of the filter was scanned and counted at a lower magnification. Cell volumes (biovolumes) were estimated by applying the geometric shapes that most closely matched the cell shape (Hillebrand et al. 1999). Biovolume calculations were based on measurements of 10 organisms per taxon for each sample where possible. Mean biovolume values were computed for any sampling event that included duplicate samples. Biovolume data corrected for occurrence of large vacuoles was used as a surrogate for cell biomass (Strathmann 1967).

Samples for phytoplankton enumeration, chl *a*, salinity, temperature, and turbidity were also collected on 17 September from United States Geological Survey (USGS) Stns USGS6, USGS7, USGS8, and

DWR-D7 in Suisun Bay using a zodiac boat (see Fig. 1 for locations). These samples were preserved and analyzed as described above. Data from Stns USGS6, USGS7, and USGS 8 were used as a point of comparison with the 3 sites sampled in the present study. The same data were measured at Stns USGS6, USGS7, USGS8, and DWR-D7 by the USGS on 11 September and are available online (<http://sfbay.wr.usgs.gov/access/wqdata>).

RESULTS

Effluent water discharged into the basin was characterized by low salinity and turbidity but very high dissolved nutrient concentrations (Table 1). NH_4^+ was the principal nitrogen source with an average concentration of $1931 \pm 118 \mu\text{mol l}^{-1}$, followed by NO_3^- with a concentration of $34 \pm 8 \mu\text{mol l}^{-1}$. The P concentration was $81 \pm 19 \mu\text{mol l}^{-1}$ (Table 1).

The basin had very similar water quality characteristics to the effluent water in terms of dissolved oxygen, pH, salinity, and turbidity (Tables 1 & 2). The upstream location was fairly similar to the basin with respect to salinity, but turbidity was lower (Table 2). The downstream location differed from the upstream location in 2 important ways. First, salinity was higher (3.6 ± 3.6 vs. 0.6 ± 0.05), and turbidity was an order of magnitude higher (27 ± 11 vs. 2 ± 0.5 nephelometric turbidity units [NTU]). The higher salinities and turbidities of the downstream location were indicative of the degree of mixing between Suisun Bay and Pacheco Slough water over the tidal cycle. In Suisun Bay, salinity was 11 ± 3 and turbidity was 26 ± 7 NTU (Table 2).

Chl *a* concentrations varied by an order of magnitude in the basin, from 40 to $400 \mu\text{g chl a l}^{-1}$ (Fig. 2A). Concentrations of chl *a* downstream were also variable but lower than in the basin, ranging from 5 to $120 \mu\text{g chl a l}^{-1}$ (Fig. 2A). Concentrations upstream were the lowest, and ranged from 1 to $5 \mu\text{g chl a l}^{-1}$.

Table 1. Effluent water-quality parameters (mean $\pm$ SD, $n = 47$)

Parameter	Concentration
Dissolved oxygen (mg l^{-1})	7.5 ± 1.7
pH	7.3 ± 0.1
Turbidity (NTU)	3.9 ± 1.1
Salinity	0.5 ± 0.03
NH_4^+ ($\mu\text{mol l}^{-1}$)	1931 ± 118
NO_3^- ($\mu\text{mol l}^{-1}$)	34 ± 8
P ($\mu\text{mol l}^{-1}$)	81 ± 19
N:P ratio (mol:mol)	24

Table 2. Basin, upstream, downstream and bay water-quality parameters (mean $\pm$ SD). DO: dissolved oxygen

Parameter	Basin (n = 11)	Upstream (n = 11)	Downstream (n = 11)	Suisun Bay (n = 3)
DO (mg l ⁻¹)	7.5 $\pm$ 1.7	6.2 $\pm$ 2	5.8 $\pm$ 2	8.8 $\pm$ 0.05
pH	7.6 $\pm$ 0.2	7.7 $\pm$ 0.2	7.6 $\pm$ 0.1	7.5 $\pm$ 0.06
Turbidity (NTU)	5.4 $\pm$ 1.7	2.0 $\pm$ 0.5	26.6 $\pm$ 11	25.5 $\pm$ 7
Salinity	0.5 $\pm$ 0.03	0.6 $\pm$ 0.05	3.6 $\pm$ 3.6	11 $\pm$ 3
Temperature (°C)	23 $\pm$ 2.3	20.5 $\pm$ 1.6	20.6 $\pm$ 2.3	19.3 $\pm$ 0.5

(Fig. 2A). Despite vigorous phytoplankton growth, a high rate of effluent inflow to the basin prevented nutrients from becoming depleted; NH_4^+ concentrations varied from 1671 to 2000 $\mu\text{mol l}^{-1}$ (Fig. 2B). Concentrations downstream varied from 150 (at the end of the time course) to 1350 $\mu\text{mol l}^{-1}$ (Fig. 2B). Upstream, NH_4^+ concentrations varied from 1 to 5 $\mu\text{mol l}^{-1}$ (Fig. 2B). Concentrations of NO_3^- were greatest downstream, varying from 12 to >80 $\mu\text{mol l}^{-1}$, followed by the upstream location at 31 to 50 $\mu\text{mol l}^{-1}$, and the basin where concentrations ranged between 5 and 30 $\mu\text{mol l}^{-1}$ (Fig. 2C). Concentrations of P were greatest in the basin at 25 to 52 $\mu\text{mol l}^{-1}$, followed by downstream at 6 to 38 $\mu\text{mol l}^{-1}$, while upstream concentrations ranged from 2 to 5 $\mu\text{mol l}^{-1}$, similar to the NH_4^+ concentrations (Fig. 2D). At all 3 sites, chl *a* concentrations were much lower than that which

would be predicted based on nutrient concentrations (Fig. 2).

The basin phytoplankton community evidenced biomass maxima occurring on 5 and 18 September and 5 October (Fig. 2A). The basin phytoplankton biomass maximum was dominated by chlorophytes on 5 September, giving way to a community dominated by euglenophytes on 18 September and back to chlorophytes on 5 October (Fig. 3A). While chloro-

phytes and euglenophytes dominated the community composition based on biomass, they also dominated based on numerical abundance (Fig. 3B). In contrast to the basin, phytoplankton community composition based on biomass was dominated by diatoms at the downstream location (Fig. 3C). Although cryptophytes (and to a lesser degree, chlorophytes) became numerically important towards the end of the time course, contributing nearly 70% of phytoplankton community abundance on the last sampling day (Fig. 3D), they contributed $<10\%$ to phytoplankton community composition on a biomass basis (Fig. 3C). Similar to the downstream community, the upstream phytoplankton community biomass was dominated by diatoms, with the exception of 9 October when biomass was co-dominated by diatoms and chlorophytes (Fig. 3E). Chlorophytes, cryptophytes, and to

Fig. 2. Time course of (A) chl *a*, (B) NH_4^+ , (C) NO_3^- , and (D) phosphorus concentration in the basin, downstream, and upstream

Fig. 3. Percent biomass and percent abundance of phytoplankton taxa over time in (A,B) the basin, (C,D) downstream, and (E,F) upstream. Dates are mm/dd/yy

a lesser degree cyanobacteria, comprised a much greater share of community composition based on abundance compared with biomass at the upstream location (Fig. 3E,F).

Changes in phytoplankton species composition in the basin were driven by a succession of 3 different genera (Fig. 4). The maximum on 5 September was dominated by the chlorophyte *Sphaerocystis* sp., the maximum on 18 September was co-dominated by the euglenophytes *Lepocinclis tripteris* and *Phacus* sp., while the maximum on 5 October was dominated by the chlorophyte *Gloeococcus minor* (Fig. 4A–C). Downstream, peaks in chl *a* occurred on 5 and 14 September and 9 October and were dominated by the centric diatoms *Cyclotella* sp., *Cyclotella scaldensis*, and a mixed diatom–cryptophyte *Rhodomonas* sp. community, respectively (Fig. 5A–C). Upstream, peaks in chl *a* biomass (3.4, 2.6, and 4.8 $\mu\text{g chl } a \text{ l}^{-1}$)

occurred on 23 August, 14 September, and 5 October, and were dominated by a chlorophyte from the Volvocales order, co-dominated by the diatoms *Nitzschia* spp. and *Fragilaria* spp., and *Navicula vanhoeffenii* and *Cocconeis placentula*, respectively (Fig. 6A–C).

To investigate whether the NH_4^+ tolerant diatom species in Pacheco Slough were unique, we compared the composition of the diatom communities at the downstream and upstream location in Pacheco Slough with that in Suisun Bay at Stns USGS6, USGS7, USGS8 and DWR-D7 on 17 September 2012.

Of the 25 diatom species identified in Suisun Bay, and the 29 species identified at the downstream location in Pacheco Slough, 9 species overlapped (Table 3). These included *Actinocyclus* sp., *Aulacoseira* sp., *Cyclotella* sp., *C. scaldensis*, *Cocconeis placentula*, *Nitzschia* sp., *Thalassiosira* spp., *T. eccentrica* and

Fig. 4. Phytoplankton species composition during 3 separate biomass maxima in the basin occurring on (A) 5 September, (B) 18 September, and (C) 5 October 2012. Black bars: diatoms; grey bars: chlorophytes; stippled bars: cryptophytes; white bars: cyanobacteria; light grey bars: euglenophytes

Tryblionella debilis. Of the overlapping species, *Aulacoseira* sp., *Actinocyclus* sp., *C. scaldensis*, *Thalassiosira* sp., *T. eccentrica* and *Tryblionella* sp. did not occur in measurable abundance upstream or in the basin. Two of the overlapping species, *C. placentula* and *Cyclotella* spp., were present at the upstream station (possibly also a *Nitzschia* sp.). The genera *Stephanodiscus* and *Pleurosigma* commonly occurred in the Suisun Bay samples but did not occur in Pacheco Slough or in the basin (Table 3).

Of the 28 diatom species identified at the upstream site, 9 overlapped with the downstream site. These included, as mentioned, *Cyclotella* sp. and *C. placentula*, and *Bacillaria paxillifer*, *Geissleria decussis*, *Gomphonema parvulum*, *Nitzschia* spp., *Nitzschia archibaldii*, *N. palea* and *Rhoicosphenia abbreviata*. Of these, *G. parvulum* and *N. palea* also occurred in the basin (Table 3). Several diatom species present at the upstream site were not present in the basin, downstream, or in Suisun Bay. These included *Amphora minutissima*, *Fragilaria capucina*, *F. crotonensis*, *Pleurosira laevis* and *Stephanocyclus meneghiniana* (Table 3).

The chlorophyll concentration in Suisun Bay was only $2.8 \pm 0.7 \mu\text{g l}^{-1}$, and with above-normal incursions of Suisun Bay water coinciding with the spring tides, the downstream community evidenced biomass minima on 11 September and 11 October (Figs. 2 & 7). On these dates, low-chlorophyll Suisun Bay water pushed the community growing at the downstream location further upstream; the chl *a* concentration downstream was restored the following sampling event when the tide started to retreat (Figs. 2 & 7).

Mean chl *a* and NH_4^+ concentrations were greatest in the basin, followed by the downstream site, with Suisun Bay and the upstream site 30 to 80 times lower (Fig. 8A,B). Similarly, mean P concentrations were 5 to 9 times greater at the basin and downstream sites compared with Suisun Bay and the upstream site (Fig. 8A). In contrast, the mean NO_3^- concentration was greater at the downstream site ($59 \pm 27 \mu\text{mol l}^{-1}$) compared with the basin ($39 \pm 7 \mu\text{mol l}^{-1}$), Suisun Bay ($28.8 \pm 0.5 \mu\text{mol l}^{-1}$), or upstream ($21 \pm 7 \mu\text{mol l}^{-1}$).

This could potentially be because residence times at the downstream location were long enough for NO_3^- to accumulate from these sources, or NO_3^- could have been produced at the downstream location by nitrifying bacteria. Using the geometric mean specific nitrification rate (0.162 d^{-1}) to calculate $\mu\text{mol NO}_3^- \text{ l}^{-1}$ produced per $\mu\text{mol NH}_4^+ \text{ l}^{-1} \text{ d}^{-1}$ according to Yool et al. (2007), we obtained a potential production of $165 \pm 61 \mu\text{mol NO}_3^- \text{ l}^{-1} \text{ d}^{-1}$ at the downstream location, which could explain the higher concentrations observed there.

Despite high potential NO_3^- production rates and concentrations, the mean dissolved N:P ratio was largely driven by the high NH_4^+ concentration in the basin and downstream, averaging 58 ± 14 and 65 ± 60 , respectively. In Suisun Bay and upstream, where

NO_3^- was the dominant N source, the N:P ratio was 6.9 ± 0.6 and 11 ± 2 , respectively (Fig. 8A). Consistent with the switch from NH_4^+ to NO_3^- as the dominant N source, the $\text{NH}_4^+ : \text{NO}_3^-$ ratio was 122 ± 115 and 26 ± 32 in the basin and downstream, respectively, versus 0.16 ± 0.03 and 0.08 ± 0.03 in Suisun Bay and upstream, respectively (Fig. 8A). In the basin, chlorophytes were most abundant, whereas diatoms were most abundant downstream, in Suisun Bay, and upstream (Fig. 8B). Cyanobacteria were approximately the same at all 3 sites. The ratio of diatom biomass to the biomass of chlorophytes + euglenophytes + cyanobacteria + cryptophytes (i.e. diatoms:others) was 0.02 ± 0.02 in the basin, 48 ± 87 downstream, 9.5 ± 1 in Suisun and 9.5 ± 8 upstream (Fig. 8B). The large ratio of diatoms:others at the downstream site, and the large variability in this ratio, was driven by a large increase in the ratio of diatom:others biomass at the beginning of the time course (data not shown).

DISCUSSION

Phytoplankton biomass at the downstream location in Pacheco Slough ($59 \pm 37 \mu\text{g chl a l}^{-1}$) was 30-fold greater than the Suisun Bay ($2.8 \pm 0.7 \mu\text{g chl a l}^{-1}$) or the upstream ($2.1 \pm 1 \mu\text{g chl a l}^{-1}$) end-members, suggesting that the basin overflow into the Slough either delivered a great deal of phytoplankton biomass to this location, or that the nutrients delivered via the wastewater effluent resulted in promoting the growth of the phytoplankton already present at this location. Analysis of phytoplankton community composition at the downstream site compared with Suisun Bay demonstrated that the latter was true. The analysis also demonstrated that high concentrations of NH_4^+ do not lead to a community that is substantially different from the seed community. Diatoms, as a fraction of total community composition, increased dramatically lead by the centric diatom *Cyclotella* *scaldensis*. This species, together with diatoms such as *Thalassiosira* *eccentrica*, *Thalassiosira* sp., *Actinocyclus* sp., and *Aulacoseira* sp. were present at relatively high abundances in Suisun Bay at the time of the study. Moreover, these species were either not present, or present in low concentrations at the upstream site in Pacheco Slough or in the basin.

Fig. 5. Phytoplankton species composition during 3 separate biomass maxima occurring downstream on (A) 5 September, (B) 14 September, and (C) 9 October 2012. Black bars: diatoms; grey bars: chlorophytes; stippled bars: cryptophytes; light grey bars: euglenophytes

Fig. 6. Phytoplankton species composition during 3 separate biomass maxima occurring upstream on (A) 23 August, (B) 14 September, and (C) 5 October 2012. Black bars: diatoms; grey bars: chlorophytes; stippled bars: cryptophytes; white bars: cyanobacteria; light grey bars: euglenophytes

These results suggest that a seed population advected with the tide into Pacheco Slough from Suisun Bay was responsible for the high phytoplankton biomass observed there. Several interesting conclusions can be drawn from this observation. One is that estuarine diatoms that typically grow in the range of 0 to 20 $\mu\text{mol l}^{-1}$ NH_4^+ can easily grow at concentrations approaching 1350 $\mu\text{mol l}^{-1}$. Another is that the high NH_4^+ conditions favored diatoms over

other phytoplankton species, demonstrating that diatoms are not more susceptible to inhibition of growth by NH_4^+ than other taxa. Thirdly, conditions in Pacheco Slough were more favorable than in Suisun Bay, resulting in a several-fold increase in the diatom population. And lastly, conditions upstream in Pacheco Slough were not favorable for the growth of any phytoplankton despite high nutrient (particularly high NO_3^-) concentrations. We will discuss each of these observations in turn.

In Suisun Bay, as well as other high-nutrient coastal areas around the world, centric diatoms such as *Cyclotella* sp., *Thalassiosira* sp., *Coscinodiscus* sp., and *Aulacoseira* sp. are the most commonly observed bloom formers (Arthur & Ball 1979, Ball & Arthur 1979, Prasad et al. 1990, Lehman 1996, 2000, Collos et al. 2005). The genus *Cyclotella* has also been reported to dominate algal blooms in high-nutrient freshwater systems (Muylaert & Sabbe 1996, Wehr & Descy 1998, Mitrovic et al. 2008, Beaver et al. 2013). While these species have been reported to grow uninhibited in eutrophic estuaries at NH_4^+ and NO_3^- concentrations approaching several hundred $\mu\text{mol l}^{-1}$ (Collos et al. 2005, Collos & Harrison 2014), other investigators have questioned whether concentrations of NH_4^+ as low as 30 $\mu\text{mol l}^{-1}$ near wastewater discharges negatively impact phytoplankton production (Thomas et al. 1974, MacIsaac et al. 1979, Glibert et al. 2011, Parker et al. 2012). Whereas 30 $\mu\text{mol l}^{-1}$ is high for a marine system, culture investigations demonstrate that negative impacts on phytoplankton growth and production by nutrients typically occur at much greater concentrations. For example, in a screen of freshly isolated phyto-

plankton from California coastal water, Thomas et al. (1980) found no inhibition of photosynthesis or growth at concentrations varying from 5 to 200 $\mu\text{mol l}^{-1}$ NH_4^+ in several diatoms.

In a recent review of phytoplankton NH_4^+ tolerance thresholds, Collos & Harrison (2014) reported that the optimal NH_4^+ concentration for growth of diatoms in culture was on average 340 $\mu\text{mol l}^{-1}$, and that growth inhibition (as defined by a reduction in growth

Table 3. Diatom species composition on 17 September 2012 at Stns DWR-D7, USGS6, USGS7, and USGS8 in Suisun Bay, compared with downstream in Pacheco Slough on 14, 18, 21, and 27 September (D914, D918, D921, D927, respectively), upstream in Pacheco Slough on 14, 18, 21, and 27 September (U914, U918, U921, U927), and in the basin on 14, 18, and 27 September (B914, B918, B927)

DWR-D7 <i>Cyclotella scaldensis</i> <i>Thalassiosira</i> spp. <i>Cyclotella</i> sp. <i>Stephanodiscus</i> sp. <i>Cocconeis placentula</i> <i>Navicula minuscula</i> <i>Tryblionella debilis</i> <i>Pleurosigma</i> sp. <i>Aulacoseira</i> sp. <i>Actinopterychus senarius</i>	USGS6 <i>Thalassiosira eccentrica</i> <i>Aulacoseira ambigua</i> <i>Achnantheidium minutissimum</i> <i>Cocconeis placentula</i> <i>Nitzschia</i> sp. <i>Tryblionella</i> sp. <i>Asterionella formosa</i> <i>Epithemia</i> sp. <i>Synedra ulna</i> <i>Cyclotella scaldensis</i>	USGS7 <i>Aulacoseira subarctica</i> <i>Epithemia adnata</i> <i>Cyclotella scaldensis</i> <i>Cyclotella</i> sp. <i>Hantzschia</i> sp. <i>Actinocyclus</i> sp. <i>Cocconeis placentula</i> var. <i>lineata</i> <i>Tryblionella navicularis</i> <i>Cymbella</i> sp. <i>Gyrosigma</i> sp.	USGS8 <i>Cyclotella scaldensis</i> <i>Thalassiosira</i> spp. <i>Cyclotella</i> sp. <i>Stephanodiscus</i> sp. <i>Cocconeis placentula</i> <i>Navicula minuscula</i> <i>Tryblionella debilis</i> <i>Pleurosigma</i> sp. <i>Aulacoseira</i> sp. <i>Actinopterychus senarius</i>
D914 <i>Cyclotella scaldensis</i> <i>Nitzschia</i> spp. <i>Cyclotella</i> spp. <i>Gomphonema parvulum</i> <i>Actinocyclus normanii</i> <i>Cocconeis placentula</i> <i>Nitzschia palea</i> <i>Planothidium</i> sp. <i>Diploneis</i> sp. <i>Bacillaria paxillifer</i>	D918 <i>Cyclotella scaldensis</i> <i>Nitzschia</i> spp. <i>Cyclotella</i> spp. <i>Melosira varians</i> <i>Craticula buderi</i> <i>Gyrosigma wansbeckii</i> <i>Actinocyclus</i> sp. <i>Gomphonema parvulum</i> <i>Geissleria decussis</i> <i>Psammothidium</i> sp.	D921 <i>Cyclotella scaldensis</i> <i>Nitzschia</i> spp. <i>Cyclotella</i> spp. <i>Craticula halophila</i> <i>Thalassiosira</i> cf. <i>eccentrica</i> <i>Nitzschia clausii</i> <i>Rhoicosphenia abbreviata</i> <i>Navicula tripunctata</i> <i>Aulacoseira</i> sp. <i>Cocconeis placentula</i>	D927 <i>Nitzschia archibaldii</i> <i>Cyclotella scaldensis</i> <i>Thalassiosira</i> sp. <i>Cyclotella</i> sp. <i>Thalassiosira</i> cf. <i>eccentrica</i> <i>Bacillaria paxillifer</i> <i>Nitzschia inconspicua</i> <i>Rhopalodia gibba</i> <i>Craticula molesta</i> <i>Tryblionella granulata</i>
U914 <i>Nitzschia</i> spp. <i>Fragilaria crotonensis</i> <i>Cocconeis placentula</i> <i>Synedra ulna</i> <i>Cyclotella</i> spp. <i>Fragilaria capucina</i> <i>Nitzschia palea</i> <i>Bacillaria paxillifer</i> <i>Pleurosira laevis</i> <i>Nitzschia subacicularis</i>	U918 <i>Nitzschia</i> spp. <i>Amphora minutissima</i> <i>Fragilaria capucina</i> <i>Cocconeis pediculus</i> <i>Gomphonema parvulum</i> <i>Cyclotella</i> spp. <i>Craticula halophila</i> <i>Geissleria decussis</i> <i>Rhoicosphenia abbreviata</i> <i>Navicula vanhoeffenii</i>	U921 <i>Cocconeis placentula</i> <i>Amphora minutissima</i> <i>Fragilaria capucina</i> <i>Cyclotella</i> sp. <i>Nitzschia acicularis</i> <i>Nitzschia perminuta</i> <i>Nitzschia reversa</i> <i>Nitzschia</i> sp. <i>Sellaphora pupula</i> <i>Surirella minuta</i>	U927 <i>Nitzschia</i> cf. <i>archibaldii</i> <i>Cocconeis placentula</i> <i>Nitzschia</i> spp. <i>Synedra acus</i> <i>Melosira varians</i> <i>Stephanocyclus meneghiniana</i> <i>Sellaphora pupula</i> <i>Nitzschia draveillensis</i> <i>Nitzschia palea</i> <i>Fragilaria capucina</i>
B914 <i>Cyclotella</i> sp. <i>Gomphonema parvulum</i> <i>Nitzschia palea</i>	B918 <i>Nitzschia palea</i> <i>Gomphonema parvulum</i> <i>Gomphonema</i> sp.	B927 <i>Sellaphora pupula</i> <i>Gomphonema parvulum</i> <i>Navicula cryptotenella</i>	

rate of 50 %) occurred on average at $750 \mu\text{mol l}^{-1}$. As noted by these authors, chlorophytes and cyanobacteria generally have greater NH_4^+ tolerance thresholds than diatoms, and diatoms typically have greater tolerance thresholds than dinoflagellates (Collos & Harrison 2014). There are notable exceptions to these thresholds for NH_4^+ tolerance, as illustrated by the centric diatom *Cyclotella* sp. which can grow at a concentration of $3000 \mu\text{mol NH}_4^+ \text{l}^{-1}$ in culture without experiencing growth inhibition (Pahl et al. 2012). Most importantly, these thresholds are far above the concentrations of NH_4^+ occurring in Suisun Bay that have been suggested to place diatoms at a disadvantage relative to dinoflagellates and cyanobacteria

(Glibert 2010, Glibert et al. 2011), and to reduce their growth (Dugdale et al. 2007, Parker et al. 2012), suggesting that the changes in phytoplankton composition and growth observed in those investigations were due to factors other than NH_4^+ concentration.

The present data also demonstrate that at non-limiting concentrations, nutrient ratios are not good predictors of phytoplankton community composition. For example, Suisun Bay and the downstream location had similar salinities (11 ± 3 and 4 ± 3.6 , respectively) and turbidities (26 ± 7 and 27 ± 11 , respectively), but the downstream location had greater NH_4^+ concentrations, N:P ratios, and $\text{NH}_4^+:\text{NO}_3^-$ ratios than Suisun Bay. Phytoplankton biomass down-

Fig. 7. Changes in salinity at slack tide at the 3 different sampling sites

Fig. 8. Mean concentrations of (A) nutrients and ratios of N:P and $\text{NH}_4^+:\text{NO}_3^-$, and (B) chl a, phytoplankton taxa, and ratios of diatoms to other phytoplankton taxa upstream, in the basin, downstream, and in Suisun Bay

stream was 30-fold greater than in Suisun Bay, but, despite dissimilar nutrient ratios, the taxonomic composition overlapped in terms of the ratio of diatoms:others (9.5 ± 1 and 48 ± 87 , respectively) as well as in the dominant phytoplankton species (i.e. *C. scaldensis*). Likewise, the upstream location and

the basin had similar salinities (0.6 ± 0.05 and 0.5 ± 0.03 , respectively) and turbidities (2 ± 0.5 and 5 ± 1.7 NTU, respectively), but NH_4^+ concentrations, N:P ratios, and $\text{NH}_4^+:\text{NO}_3^-$ ratios were greater in the basin than upstream. Phytoplankton biomass in the basin was 80-fold greater than upstream, but, contrary to the comparison between downstream and Suisun Bay, the taxonomic composition between upstream and the basin differed substantially as defined by the ratio of diatoms:others (9.5 ± 8 vs. 0.02 ± 0.02 , respectively) and the dominant phytoplankton species (*Nitzschia* and *Fragilaria* diatoms versus *Lepocinclis* and *Phacus* euglenophytes).

These observations can be reconciled if we consider that in the first example (Suisun Bay and downstream), the seeding populations between the 2 sites were similar, whereas in the second example (upstream and the basin), the seeding populations were very different; the basin was a semi-enclosed system most likely seeded by dormant algal spores from the sediments, whereas the upstream location was seeded by exchange with Walnut and Grayson Creeks.

Differences in seeding populations can also be used to argue for the divergence in population trajectories between downstream and the basin, despite similarly high N:P (58 ± 14 and 65 ± 60 , respectively) and $\text{NH}_4^+:\text{NO}_3^-$ (122 ± 115 and 26 ± 32 , respectively) ratios in both locations. However, a number of factors besides the seeding population disparity could have acted to maintain divergent phytoplankton populations, including salinity, turbidity, turbulence (from tidal action), and temperature. The ability of diatoms to dominate environments that have high rates of flow, mixing, turbulence, and nutrient concentrations is well documented (Margalef 1978, Margalef et al. 1979, Smayda 1997, Smayda & Reynolds 2001, Collos et al. 2005, Sarthou et al. 2005). But why did diatoms imported from Suisun Bay grow so much better when they entered Pacheco Slough given that Suisun Bay is also a high-nutrient, high-turbulence environment?

A significant decrease in water column depth, therefore an increase in the average irradiance, may have contributed to the increase in diatom abundance in Pacheco Slough over Suisun Bay. Average water column irradiance (integrated PAR/water column depth) calculated from PAR profiles at Stns USGS5, USGS6, USGS7 and USGS8 in Suisun in the month of September ranged from 6 to 50 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and light attenuation coefficients ranged from 0.91 to 1.34 m^{-1} (data from USGS water quality monitoring program). Turbidity at these same stations ranged from 20 to 33 NTU, similar to Pacheco

Slough (27 ± 11 NTU). Going from Stn USGS7 in Suisun Bay (outside the entrance to Pacheco Slough) to Pacheco Slough, average irradiance increased from $45 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $519 \mu\text{mol m}^{-2} \text{s}^{-1}$. It is likely that phytoplankton productivity and growth increased commensurately with the increase in irradiance, leading to the abnormally high chl *a* levels observed at the downstream location.

Given the higher mean irradiance levels in Pacheco Slough, it would be expected that the upstream phytoplankton community would attain a biomass level such that nutrients would essentially be depleted. Contrary to expectation, low chl *a* concentrations were coupled with NO_3^- concentrations of $39 \pm 8 \mu\text{mol l}^{-1}$ and P concentrations of $3.8 \pm 0.5 \mu\text{mol l}^{-1}$ (Fig. 8). The fact that neither NO_3^- nor P was drawn-down upstream suggests that there was a micronutrient or trace metal that limited the upstream phytoplankton community. The limiting agent could have been supplied with the wastewater effluent, allowing the phytoplankton at the downstream location to grow. Alternatively, if the limiting agent did not affect NH_4^+ assimilation, the phytoplankton at the downstream location could have been utilizing NH_4^+ exclusively, which was on average 300-fold greater than upstream and is consistent with a general preference for NH_4^+ over NO_3^- by phytoplankton (Cresswell & Syrett 1979, Syrett 1981, 1988, Fernandez & Cardenas 1989, Huppe et al. 1994, Berges et al. 1995, Hildebrand & Dahlin 2000, He et al. 2004, Song & Ward 2007).

In summary, we have demonstrated that diatoms are not particularly susceptible to atypically high NH_4^+ concentrations and that they are not outcompeted by other taxa when NH_4^+ is the main source of N available for growth. Diatom species composition and diversity overlapped in Suisun Bay and the downstream location, suggesting that phytoplankton seed composition was an important parameter with respect to the phytoplankton community that developed. The dominant phytoplankton species in this community was the centric diatom *C. scaldensis*, which also dominated the phytoplankton communities at several stations throughout Suisun Bay. In addition to high NH_4^+ concentrations, relief from constant light limitation owing to a shallower water column (therefore increased irradiance) likely contributed to the relatively high biomass accumulation of *C. scaldensis* in Pacheco Slough compared with Suisun Bay. *C. scaldensis* thrived at NH_4^+ concentrations as high as $1350 \mu\text{mol l}^{-1}$, suggesting that promoting diatom growth does not require decreasing NH_4^+ concentrations as recently suggested (Dugdale

et al. 2007, Glibert 2010, Parker et al. 2012). A more holistic understanding of how light, seed populations, turbidity, mixing, and residence time of water interact with available nutrients and trace metals is needed in order to understand the factors that govern phytoplankton growth in this region.

Acknowledgements. Many thanks to Tara Schraga for sharing PAR data from Suisun Bay. We also thank Tri Nguyen, Anita Setty, Salvador Rosales, Charles Burch, Jackeline Campos, James Wan and Ana Dias for help with laboratory analyses and field work. We gratefully acknowledge Jeff Miller and C. Walker for help with chl *a* analyses, and John R. Beaver for all the help related to phytoplankton enumeration. We thank Velisa Parks for her assistance in preparing this manuscript.

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*Editorial responsibility: Max Tilzer,
Konstanz, Germany*

*Submitted: January 29, 2014; Accepted: June 26, 2014
Proofs received from author(s): August 19, 2014*