Effects of nitrogen source, concentration, and irradiance on growth rates of two diatoms endemic to northern San Francisco Bay

Gry Mine Berg¹,* , Sara Driscoll¹, Kendra Hayashi², Raphael Kudela²

¹Applied Marine Sciences, 911 Center Street, Santa Cruz, California 95060, USA
²Ocean Sciences Department, 1156 High Street, University of California Santa Cruz, Santa Cruz, California 95064, USA

ABSTRACT: Impacts on growth rates from exposure to ammonium (NH₄⁺) and nitrate (NO₃⁻), at non-limiting concentrations, in combination with irradiances varying from 25 to 600 µmol photons m⁻² s⁻¹ were investigated in the pelagic diatom Thalassiosira weisflogii and the benthic diatom Entomoneis paludosa recently isolated from Suisun Bay in northern San Francisco Bay. Growth rates were higher in T. weisflogii (0.76 ± 0.3 d⁻¹) compared with E. paludosa (0.58 ± 0.2 d⁻¹) across all irradiances and nitrogen (N) treatments. Differences in growth rates with N source were regulated by irradiance in both diatoms and were greatest at the intermediate irradiance due to saturation of rates at 85 µmol photons m⁻² s⁻¹ when growing on NH₄⁺ and at 200 µmol photons m⁻² s⁻¹ when growing on NO₃⁻. Notable physiological differences between these 2 diatoms included a larger range in the quantum yield of photosystem II (Fv/Fm) and in chlorophyll a per cell as a function of irradiance in T. weissflogii compared with E. paludosa. In addition, a negative interaction of high NH₄⁺ concentration (1000 µmol l⁻¹) and irradiance (≥200 µmol photons m⁻² s⁻¹) was observed on growth rates in E. paludosa that was not evident in T. weissflogii. Differences in physiological parameters of these diatoms are discussed in relation to their distributions and frequency of occurrence in Suisun Bay.

KEY WORDS: Ammonium · Irradiance · Diatoms · Entomoneis · Thalassiosira · Suisun Bay · San Francisco Bay

1. INTRODUCTION

Suisun Bay, situated in the northern part of San Francisco Bay, USA, has experienced numerous environmental changes in the last 2 to 3 decades, some of which have contributed to a general decline in phytoplankton biomass (Alpine & Cloern 1992, Lehman 1996, 2000, Jassby 2008). These changes include increased grazing pressure following an invasion by the Asian clam Potamocorbula amurensis (Carlton et al. 1990, Alpine & Cloern 1992), increases in nitrogen (N) inputs from wastewater discharge (Jassby 2008), exposure to a broad suite of herbicides (Orlando et al. 2014), changes in water residence times, and increases in water temperature (Jassby 2008), to mention a few. These changes were added on top of a system that already experienced acute light limitation (Cole & Cloern 1984, 1987, Jassby et al. 2002) resulting from relatively high levels of sediments carried with the Sacramento River and localized wind-wave sediment resuspension (Goodwin & Denton 1991, Ruhl & Schoellhamer 2004, Moskalski & Torres 2012, Schoellhamer et al. 2012). In turn, the decrease in phytoplankton biomass has been hypothesized to be partially responsible for decreases in biomass of higher trophic levels, including zooplankton and...

Of the bottom-up factors that could negatively impact phytoplankton growth, the two that have received the most attention are excessive ammonium (NH$_4^+$) build-up from wastewater effluent (Dugdale et al. 2007, Parker et al. 2012, Esparza et al. 2014, Kraus et al. 2017) and light limitation due to high turbidity (Cole & Cloern 1984, 1987, Alpine & Cloern 1988, Jassby et al. 2002). These factors are linked in that light limitation, resulting in low levels of primary productivity and biomass, allows dissolved nutrients to accumulate in the water column. As a result, the median chlorophyll a concentration in Suisun Bay (2.0 µg l$^{-1}$) is ~12-fold lower than what could be expected if the ambient nitrogen available in the water column was converted into phytoplankton biomass (Cloern & Jassby 2012).

While the impacts of elevated NH$_4^+$ concentrations and low light have been studied separately in Suisun Bay, they have not been studied simultaneously under controlled conditions. The interaction between light and nutrients is particularly pertinent to Suisun Bay as it is a mosaic of different light−nutrient environments varying from deep, dark channels to shallow, well-lit banks (Alpine & Cloern 1988) superimposed by steep concentration gradients in inorganic nutrients (Dugdale et al. 2007, Jassby 2008). To investigate the impact of changes in light and nutrients simultaneously on phytoplankton growth in Suisun Bay, several species of phytoplankton were isolated into pure cultures (Berg et al. 2017). By using recent isolates from upper San Francisco Bay, we avoided issues related to extrapolation of results using strains from other geographic regions to our locale as well as issues related to genetic adaptations resulting from growth at unnaturally high N (in most cases, nitrate only) concentrations for many decades (Lakeman et al. 2009). In addition, by using pure cultures rather than field populations, we were able to ascribe physiology associated with growth on different N sources to a particular phytoplankton taxon.

Two of the isolated species, Thalassiosira weissflogii and Entomoneis paludosa, were endemic to Suisun Bay and belong to genera that dominate phytoplankton community composition depending on season and location (Lehman 1996, Cloern & Dufford 2005, Glibert et al. 2014). These 2 species are ecologically distinct in that T. weissflogii is a centric diatom residing in the pelagic zone, whereas E. paludosa is a pennate diatom comprising part of the microphytobenthos that typically resides on the sediment surface (Ribeiro et al. 2003, Forster & Martin-Jézéquel 2005). Both pelagic and microphytobenthic communities may be exposed to gradients in irradiance and nutrients, but these gradients may differ in steepness. For example, gradients in irradiance may be less steep at the sediment surface compared with what is experienced by a phytoplankter that is mixed from the bottom to the surface of the water column. Because of lower mean irradiances, benthic productivity may be less than pelagic water column productivity (Kromkamp et al. 1995, Cullen & MacIntyre 1998, Underwood & Kromkamp 1999). In contrast, gradients in nutrients may be steeper in the sediments where organic matter deposition and nutrient remineralization are more concentrated compared with the water column (Admiraal 1977b, Krom 1991). In a previous report, both T. weissflogii and E. paludosa isolated from Suisun Bay were found to tolerate ammonium concentrations in excess of 1000 µmol l$^{-1}$ (Berg et al. 2017). Environmental parameters such as salinity and temperature are also important with respect to the distributions of both pelagic and benthic phytoplankton (Admiraal 1977a, MacIntyre et al. 1996, Underwood & Provot 2000, Boyd et al. 2013).

In addition to gradients at the sediment-water interface, microphytobenthic communities are frequently exposed to wind-induced waves and tides that scour the surface of the sediments and suspend them into the water column (de Jonge & van Beusekom 1995). In San Francisco Bay, currents, tides, river flow, and wind combine to provide a high level of turbulence and water column churn (Cloern 1991, 1996, Moskalski & Torres 2012). Benthic diatoms in this system become suspended together with sediments into the water column and increasingly dominate pelagic phytoplankton community composition (Gilbert et al. 2014, Kraus et al. 2017). Given recent increases in contribution of benthic diatoms to pelagic phytoplankton community composition in Suisun Bay, high tolerance of benthic diatoms to ammonium (NH$_4^+$), and elevated concentrations of NH$_4^+$ in this system, we wanted to investigate whether tolerance to varying combinations of light and nutrients could help characterize the ecological niches of T. weissflogii and E. paludosa.

To characterize the extent to which growth rates of these diatoms would be modulated by exposure to varying NH$_4^+$ concentrations in combination with varying irradiances, the impacts to growth rates of 3 different nitrogen (N) concentrations (under non-limiting conditions), using nitrate (NO$_3^-$) or NH$_4^+$ as the sole source of N for growth, under 4 different irradiances, were investigated in T. weissflogii and E. paludosa. When T. weissflogii and E. paludosa were...
isolated from Suisun Bay for the present study, both were key members of the pelagic phytoplankton community. We also wanted to investigate whether any of the 3 factors tested (N source, N concentration, or irradiance) influenced growth rates to the extent that the factor could affect the outcome of competition between these 2 species.

2. MATERIALS AND METHODS

2.1. Sampling

Samples of phytoplankton were surveyed and collected along a cruise track that traversed Suisun Bay and its principal freshwater source, the Sacramento River, on 28 to 29 January 2014. During the survey, 33 discrete stations were sampled from the R/V ‘Questuary’ from the northernmost Stn 32 at the I-80 bridge in the Sacramento River to the southernmost Stn 1 in Suisun Bay. Samples for enumeration of phytoplankton abundance and isolation of phytoplankton into pure cultures were collected at 1 m depth from a smaller subset of stations (12 stations) along this survey track using a rosette sampler. Temperature and salinity data were obtained from a CTD attached to the rosette sampler. In addition, data on turbidity at each station was obtained using a YSI 6600v2 sonde.

2.2. Experimental conditions

Whole water was brought back to the laboratory where clonal, non-axenic cultures of the estuarine diatoms *Thalassiosira weissflogii* and *Entomoneis paludosa* were established by micropipette isolations of single cells from Suisun Bay according to Berg et al. (2017). Sterile techniques were used during all aspects of culturing. Stock cultures were maintained at 85 µmol photons m$^{-2}$ s$^{-1}$ at 15.5°C and a salinity of 10 using NO$_3^-$ as the N source. Before the start of an experiment, cultures were spun down, rinsed with N-free medium, and re-suspended in triplicate into dilute batch cultures containing 200 ml of medium with f/2 nutrient + silica solution lacking N (Goldman & McCarthy 1978). The nutrient solution was modified by the addition of N to give final concentrations of 20, 100, and 1000 µmol l$^{-1}$, either in the form of NH$_4^+$ or NO$_3^-$. In the case of the cultures with NH$_4^+$ added, the fraction of total ammonia (NH$_4^+$ + NH$_3$) that was composed of unionized NH$_3$ at a salinity of 10, temperature of 15.5°C, and pH of 8.3 (i.e. 3–6%; Khoo et al. 1977) was calculated to range from 0.6 to 1.2 µmol l$^{-1}$ in the 20 µmol NH$_4^+$ l$^{-1}$ cultures, 3 to 6 µmol l$^{-1}$ in the 100 µmol NH$_4^+$ l$^{-1}$ cultures, and 30 to 60 µmol l$^{-1}$ in the 1000 µmol NH$_4^+$ l$^{-1}$ cultures. Nitrogen concentrations were checked periodically throughout the growth phase of the cultures. Strains were cultured at 4 incident irradiances representing low (25 µmol photons m$^{-2}$ s$^{-1}$), intermediate (85 µmol photons m$^{-2}$ s$^{-1}$), high (200 µmol photons m$^{-2}$ s$^{-1}$), and inhibiting (600 µmol photons m$^{-2}$ s$^{-1}$) light. The cultures were maintained on a 12 h light:12 h dark (L:D) cycle under cool-white fluorescent lights at a temperature of 15.5 ± 1°C. Each culture was sampled daily, at noon, for physiological evaluations as described below.

2.3. Sample analyses

The physiology of each species was evaluated through daily measurements of the quantum yield of photosystem II (PSII), cell abundance, and chlorophyll a (chl a) concentration. Nitrogen concentrations (NH$_4^+$ and NO$_3^-$) were assayed periodically. The quantum yield of PSII ($F_v/F_m$) was measured by pulse-amplitude-modulated (PAM) fluorometry (Heinz-Walz WATER-PAM). The PAM was blanked with 0.2 µm filtered culture media. For assessment with PAM, aliquots were removed from the primary culture and dark-adapted for at least 10 min. After dark adaptation, background chl a fluorescence ($F_0$) and maximal chl a fluorescence following a saturating pulse ($F_m$) were measured to derive the variable ($F_v$) over maximum chl a fluorescence according to:

$$
\frac{F_v}{F_m} = \left(\frac{F_m - F_0}{F_m}\right)
$$

(1)

Samples for cell enumeration were preserved with acid Lugol’s solution (20 µl Lugol’s per ml culture volume) and stored cool (4°C) in the dark until enumeration with a Zeiss Axiovert 200 inverted microscope using a Parsons counting chamber. Geometric shapes of the cells were based on measurements of 10 organisms per taxon. Cell volumes were estimated by applying the geometric shapes that most closely matched the cell shape (Hillebrand et al. 1999). Abundances were estimated by random field counts totaling 400 unicells. Cell-specific growth rates (d$^{-1}$) were computed by fitting the exponential function:

$$
C = C_0 e^{\mu t}
$$

(2)

to the data from the exponential growth phase, where $C$ is the cell abundance, $C_0$ is the starting cell abun-
dance, μ is the growth constant (d⁻¹), and t is time (d). All calculations and statistical tests were carried out using R software (R Core Team 2016).

Samples for chl a determination were collected onto glass-fiber filters (Whatman GF/F) and processed immediately using the non-acidification method (Welschmeyer 1994). Samples for nutrient (NO₃⁻ and NH₄⁺) analysis were filtered (Whatman GF/F) and stored frozen until processing. Ammonium was analyzed using the orthophthalaldehyde (OPA) method, and relative fluorescence units were obtained via fluorometry (TD-700, Turner Designs) according to Holmes et al. (1999). Nitrate was analyzed using a Lachat QuikChem 8500 Flow Injection Analyst System and Omnion 3.0 software (Lachat Instruments, Hach).

3. RESULTS

At the time of sampling, phytoplankton belonging to the *Thalassiosira* genus dominated phytoplankton community biomass throughout Suisun Bay, whereas *Entomoneis paludosa* dominated phytoplankton community biomass at stations in the X2 region where the salinity changes from freshwater to brackish water (Fig. 1). For the current study, *T. weissflogii* was isolated from Stn 6, while *E. paludosa* was isolated from Stn 19. Salinities were 11.5 and 1.4, and turbidities were 5 and 15 NTU, at Stns 6 and 19, respectively (Fig. 1A,B). The temperature was 11°C at both stations. These newly isolated diatom species were relatively large (Fig. 2). The dimensions for *E. paludosa* were approximately 50 µm length by 20 µm width,
yielding a mean cell volume of 15 580 ± 2 500 µm³. The mean diameter of T. weissflogii was 32 µm, yielding a mean cell volume of 6447 ± 804 µm³ (Fig. 2).

Fv/Fm was slightly greater in E. paludosa (ranging from 0.49 to 0.76) than T. weissflogii (ranging from 0.39 to 0.74) particularly at the intermediate irradiance (Fig. 3A–D). However the difference in Fv/Fm as a function of species was not statistically significant (F1,142 = 3.4, p = 0.07). Nor was the difference in Fv/Fm as a function of N source statistically different in either E. paludosa (F1,70 = 0.02, p = 0.89) or T. weissflogii (F1,70 = 1.2, p = 0.27). Similarly, there was no significant effect of N source on growth rate at the lowest irradiance (Fig. 3I–L). However, there was a significant negative effect of irradiance on the chl a quota in T. weissflogii (0.76 ± 0.3 d⁻¹) compared with E. paludosa (0.58 ± 0.2 d⁻¹) across all treatments (Fig. 3I–L). Growth rates in both E. paludosa (r² = 0.17, slope = 0.0038, F1,70 = 14, p = 0.0038) and T. weissflogii (r² = 0.41, slope = 0.0008, F1,70 = 48, p = 1.6 × 10⁻⁹) were significantly impacted by irradiance. In both diatoms, the largest increase in growth rate occurred between the low and intermediate irradiances when grown on NH₄⁺ (Fig. 3I,K). When grown on NO₃⁻, there was an additional increase between the intermediate and high irradiance (Fig. 3J,L).

In contrast with irradiance, there was no significant impact on growth rate in E. paludosa (F1,70 = 0.3, p = 0.6) or T. weissflogii (F1,70 = 3.5, p = 0.07) by either N source or N concentration (F1,70 = 4, p = 0.06 and F1,70 = 0.02, p = 0.88, respectively) across all irradiances (Fig. 3I–L). However, there was a negative interaction between growth on the highest NH₄⁺ concentration and the 2 highest irradiances in E. paludosa (Fig. 3I). As a result, growth rates in E. paludosa decreased 40% from the intermediate to high irradiance when grown at 1000 µmol NH₄⁺ l⁻¹ (Fig. 3I). No such decrease was observed when grown on NO₃⁻ (Fig. 3J).

There was an effect of N source on growth rate at the intermediate irradiance in T. weissflogii (Fig. 3K–L, F1,16 = 187, p = 3.05 × 10⁻¹⁰). At this irradiance, growth on NH₄⁺ was 69% faster than growth on NO₃⁻ (Fig. 4). Although not statistically significant, growth rates were also faster (28%) on NH₄⁺ than on NO₃⁻ in E. paludosa at the intermediate irradiance (Fig. 4). This difference in growth rates with N source at the intermediate irradiance can be attributed to the difference in irradiance at which maximum growth rates were reached when growing on NH₄⁺ vs NO₃⁻. In both species, near-maximum growth rates were reached at the intermediate irradiance when grow-

Fig. 2. Light microscopy image of a culture of (A) E. paludosa and (B) T. weissflogii. Scale bar = 25 µm.
ing on NH$_4^+$, while the maximum was not reached until the high irradiance when growing on NO$_3^-$ (Fig. 3J, L). As a result, the difference in growth rates between the 2 N sources was greatest at the intermediate irradiance. At the highest irradiances, growth rates on NO$_3^-$ had caught up to rates on NH$_4^+$, and there was no substantial difference. At the lowest irradiance, growth rates were similarly low on both N sources in both species (Fig. 4).

4. DISCUSSION

In recent years, blooms of benthic diatoms have become more common in Suisun Bay in the northern portion of San Francisco Bay. In particular, occasional blooms of the benthic chain-forming diatom *Entomoneis paludosa* have been observed throughout Suisun Bay (e.g. Glibert et al. 2014). Because *E. paludosa* is a benthic species and therefore acclimated to
high NH₄⁺ concentrations fluxing out of the sediments (i.e. Admiraal 1977b, Jauffrais et al. 2016), and water column NH₄⁺ concentrations in Suisun Bay are relatively high (Jassby 2008), it is possible that pelagic blooms of this species are related to shifts in N concentration and species. It has been hypothesized that growth of pelagic diatoms is inhibited by NH₄⁺ at concentrations above 4 µmol l⁻¹ (Dugdale et al. 2007) although this has not been demonstrated on a physiological level (Collos & Harrison 2014, Berg et al. 2017). We wanted to investigate how growth rates of the pelagic diatom *Thalassiosira weissflogii*, potentially more sensitive to NH₄⁺ and less sensitive to irradiance, and the benthic diatom *E. paludosa*, potentially less sensitive to NH₄⁺ and more sensitive to irradiance, would compare under varying conditions of irradiance and N sources and concentration at non-limiting levels of nutrients. We specifically tested non-limiting levels as earlier analyses had hypothesized that changes in N speciation at non-limiting levels could affect phytoplankton growth rates and competitive interactions (Dugdale et al. 2007, Glibert et al. 2011). In contrast with earlier reports, no significant impact of N source on growth rates were demonstrated in the 2 diatom species tested here. Of the 3 environmental variables tested, irradiance had the largest and most significant influence on growth rates.

At the temperatures used in the current experiments (15.5°C), *T. weissflogii* outgrew *E. paludosa* across all treatments with an average growth rate difference of 0.18 d⁻¹. This growth rate difference was greater at high light (0.3 d⁻¹) compared with low light (0.07 d⁻¹). We noted physiological differences between these 2 diatoms that could underpin the pattern of a larger growth rate difference at high light compared with low light. One was a smaller range in *Fv/Fm* in *E. paludosa* compared with *T. weissflogii*, 0.27 vs. 0.35, respectively. Another was less plasticity in chl a quota, varying 5-fold in *E. paludosa* and 11-fold in *T. weissflogii*.

Being able to vary photosynthetic efficiency (short-term acclimation response to excess irradiance) and chl a quota (longer-term acclimation response to excess irradiance) can enable a species to acclimate more readily in response to change and thereby avoid damage to the cell under high light. Effective dissipation of excess energy at the point where light energy is harvested, as heat or fluorescence, called non-photochemical quenching, can prevent the build-up electrons that combine with oxygen to form oxygen radicals that damage the D1 protein of PSII (Vass et al. 1992, Aro et al. 1993, Clarke et al. 1993, Wu et al. 2012). This damage results in inhibition of photosynthesis (photoinhibition) which may or may not be reversible depending on how efficient the cell’s repair mechanisms are (Vass et al. 1992, Clarke et al. 1993, Nixon et al. 2010, Campbell & Tyystjärvi 2012, Wu et al. 2012). Temporary diversion of excess energy reduces the photosynthetic efficiency of the cell but prevents long-term damage and mortality of the cells. Cells that do not have the ability to dissipate excess energy do not experience short-term decreases in photosynthetic efficiency but may not be able to adapt and as a consequence may not survive (Cullen & MacIntyre 1998). It is possible that the ability of *T. weissflogii* to decrease its photosynthetic efficiency and its chl a quota to a greater degree than *E. paludosa* enables it to maintain a better level of photoprotection and to attain a higher growth rate at high irradiances.

In addition to having less plasticity in photophysiological parameters, there was a negative interaction of high irradiance and high NH₄⁺ concentration in *E. paludosa*, resulting in a 40% decrease in the growth rate, which was not evident in *T. weissflogii*. Such an interaction has been observed previously for *E. paludosa* (Admiraal 1977b), and it can be explained physiologically by direct damage to PSII from competitive binding of NH₄ with the oxygen evolution complex (Kallqvist & Svenson 2003, Drath et al. 2008, Collos & Harrison 2014). In other words, addition of high concentrations of NH₄⁺, a fraction of which will be com-
posed of NH$_3$ depending on temperature and pH (e.g. Khoo et al. 1977), will allow NH$_3$ to diffuse freely into the cell, resulting in photodamage. The impact of this damage will depend on the photorepair mechanisms present in the cell (Drath et al. 2008). A negative impact on growth of high NH$_4^+$ at high irradiances suggests that *E. paludosa* has an inferior photodamage repair mechanism compared with *T. weissflogii*. At the lower irradiances (25 to 85 µmol photons m$^{-2}$ s$^{-1}$), growth in *E. paludosa* was not inhibited by the highest NH$_4^+$ concentration tested here.

The combination of the high NH$_4^+$ concentration with constant high irradiance used here would not be expected to occur in Suisun Bay where water column NH$_4^+$ concentrations typically range from 2 to 11 µmol l$^{-1}$, fluxes of NH$_4^+$ out of the sediments to the water column are below 100 µmol NH$_4^+$ m$^{-2}$ h$^{-1}$ (Cornwell et al. 2014), and depth-averaged integrated irradiances are typically below 100 µmol photons m$^{-2}$ s$^{-1}$ (Table 1). The intermediate irradiance used in the current experiments would probably be more applicable to depth-averaged irradiance conditions encountered in Suisun Bay (Table 1). Interestingly, the difference in growth rates between NH$_4^+$ and NO$_3^-$ was the greatest in both species at the intermediate irradiance.

A large growth rate difference between NH$_4^+$ and NO$_3^-$ at intermediate irradiances, but not at low or high irradiances, has been observed in several other phytoplankton species (Paasche 1971, Thompson et al. 1989; Wood & Flynn 1995, Tong et al. 2016). This difference can be explained by the maximum growth rate being reached at a lower irradiance when growing on NH$_4^+$ than when growing on NO$_3^-$ (i.e. Wood & Flynn 1995), resulting from the requirement of additional energy (i.e. 25–40%) and enzymatic steps associated with the reduction of NO$_3^-$ (Thompson et al. 1989, Turpin 1991, Raven et al. 1992, Levasseur et al. 1993, Herrero et al. 2001, Brown et al. 2009). The difference in growth rates with N source may not be easy to detect unless a range of irradiances are tested as the difference disappears at higher (and lower) irradiances. Many studies have demonstrated no difference in growth regardless of N source, and some have greater growth rates on NO$_3^-$ compared with NH$_4^+$ (Thompson et al. 1989, Levasseur et al. 1993, Clark & Flynn 2000, Herndon & Cochlan 2007, Strom & Bright 2009, Thessen et al. 2009, Berg et al. 2017). Whether a lack of growth rate difference with N source is due to testing at irradiances that are too high, and/or because the extra energy cost to the cell when using NO$_3^-$ is compensated for by changes in metabolic parameters, is not clear. Previous studies have demonstrated variations in chl a quota, N quota, cellular C:N ratio, and photosynthetic efficiency with growth on NO$_3^-$ versus NH$_4^+$ (Levasseur et al. 1993, Wood & Flynn 1995, Flynn 2001).

While there was a difference in growth rates with N source at the intermediate irradiance in the current experiment, averaged across all the irradiances, this difference was no longer significant in either diatom. Because phytoplankton in Suisun Bay are mixed from the top to the bottom of the water column (i.e. mixed layer depth is the same as the total water column depth; Cloern 1991) and therefore experience a range of irradiances in each mixing cycle, N source effects should be averaged across a range of irradiances. Another important note with respect to the use of different N sources is that, as demonstrated here and in other studies (Paasche 1971, Thompson et al. 1989, Wood & Flynn 1995, Tong et al. 2016), irradiance is the principal driver. At any given irradiance, phytoplankton are likely to use the same N source or N mix. Consequently, all phytoplankton are more likely to use NH$_4^+$ under the low-intermediate irradiances and non-limiting NH$_4^+$ conditions that prevail in Suisun Bay, and competition among species will be driven by intrinsic growth rate differences rather than use of different N sources.

The reason that *E. paludosa* is able to bloom in parts of Suisun Bay, despite growing at a slower rate than species of the *Thalassiosira* genus, may not be linked to either irradiance or NH$_4^+$ concen-

<table>
<thead>
<tr>
<th>Station</th>
<th>Depth (m)</th>
<th>NH$_4^+$ (µmol l$^{-1}$)</th>
<th>Irradiance (µmol photons m$^{-2}$ s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17 (USGS3)</td>
<td>11.4</td>
<td>2.4</td>
<td>20.7</td>
</tr>
<tr>
<td>12 (Grizzly Bay)</td>
<td>6.4</td>
<td>4.5</td>
<td>62.0</td>
</tr>
<tr>
<td>8 (Middle Suisun)</td>
<td>5.9</td>
<td>4.7</td>
<td>62.7</td>
</tr>
<tr>
<td>6 (USGS5)</td>
<td>11</td>
<td>3.8</td>
<td>46.1</td>
</tr>
<tr>
<td>4 (USGS6)</td>
<td>12.5</td>
<td>5.9</td>
<td>41.3</td>
</tr>
<tr>
<td>2 (USGS7)</td>
<td>18</td>
<td>10.9</td>
<td>31.4</td>
</tr>
<tr>
<td>Winter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17 (USGS3)</td>
<td>11.4</td>
<td>13.2</td>
<td>30.4</td>
</tr>
<tr>
<td>12 (Grizzly Bay)</td>
<td>6.4</td>
<td>10.2</td>
<td>78.6</td>
</tr>
<tr>
<td>8 (Middle Suisun)</td>
<td>5.9</td>
<td>10.2</td>
<td>15.4</td>
</tr>
<tr>
<td>6 (USGS5)</td>
<td>11</td>
<td>10.4</td>
<td>17.7</td>
</tr>
<tr>
<td>4 (USGS6)</td>
<td>12.5</td>
<td>10.9</td>
<td>26.1</td>
</tr>
<tr>
<td>2 (USGS7)</td>
<td>18</td>
<td>10.9</td>
<td>61.5</td>
</tr>
</tbody>
</table>
trations. As illustrated in Fig. 1 the distribution of these 2 genera, when they co-occur, is at opposing ends of the salinity spectrum in Suisun Bay. Diatoms of the *Thalassiosira* genus tend to dominate at salinities >1.5, whereas *E. paludosa* dominates at salinities around 1.5 and less. A number of studies have indicated that salinity is an important factor with respect to distributions of phytoplankton and microphytobenthos and competitive interactions (McIntire 1978, Admiraal et al. 1984, Underwood et al. 1998, Underwood & Provit 2000). Temperature is another potentially important factor in regulating growth rates and competitive interactions (Epplley 1972, Admiraal 1977a, Anderson 2000, Butterwick et al. 2005, Boyd et al. 2013). Studies to date suggest that the temperature optimum for growth of the *Thalassiosira* genus, between 15 and 20°C (Boyd et al. 2013), is lower than the temperature optimum of *E. paludosa*, which is 25°C (Admiraal 1977a). Because water temperatures have been increasing by up to 0.21°C per year in upper Suisun Bay and in the Delta (Jassby 2008), it may be that the warming of the water has provided an opportunity for *E. paludosa* to out-grow pelagic diatom species such as *Thalassiosira* spp. within a specific salinity range.

In summary, typical NH$_4^+$ concentrations in Suisun Bay do not inhibit growth of either *T. weissflogii* or *E. paludosa*. At irradiances and mixing regimes characteristic of Suisun Bay, the pelagic diatom *T. weissflogii* would likely be at a competitive advantage given its higher growth rates and photophysiological adaptations suitable for exploiting variable irradiance. Our findings are consistent with global findings that pelagic diatoms are adapted for growth in low-light environments with a high degree of turbulence (Margalef 1978, Kudela 2010, Edwards et al. 2015, Richardson et al. 2016) and that pelagic diatoms typically have higher rates of primary productivity than benthic diatoms (Kromkamp et al. 1995, Underwood & Kromkamp 1999). Episodic blooms of pelagic versus microphytobenthic species in Suisun Bay could be controlled by variations in water column stability, temperature, and salinity. Increased residence time, and thereby increased stratification and temperatures, could accelerate growth of *E. paludosa* at the sediment surface, allowing it to build up a large seed community. With an episodic increase in turbulence, this community could become suspended into the water column and outcompete centric pelagic diatoms from the *Thalassiosira* genus, as observed during the spring bloom of *E. paludosa* in 2014 at the height of drought conditions (Glibert et al. 2014).

Acknowledgements. Special thanks to Dane Hardin for help with statistical analyses. This research was funded through the Interagency Ecological Program by the Sacramento Regional County Sanitation District award 90000094 to R.K. and award 80000089 to G.M.B. Further support was provided through the California Water Resources Control Board Award 22-1509-5082 to R.K., and the Central Contra Costa Sanitary District award 40969 to R.K. and award 42218 to G.M.B.

LITERATURE CITED


Admiraal W (1977b) Tolerance of estuarine benthic diatoms to high concentrations of ammonia, nitrite ion, nitrate ion and orthophosphate. Mar Biol 43:307–315


Alpine AE, Cloern JE (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr 37:946–955


Clarke AK, Soitamo A, Gustafsson P, Oquist G (1993) Rapid interchange between two distinct forms of cyanobacterial photosystem II reaction-center protein D1 in response
to photoinhibition. Proc Natl Acad Sci USA 90:9973–9977


Eppl ey RW (1972) Temperature and phytoplankton growth in the sea. Fish Bull 70:1063–1085


Krom M (1991) Importance of benthic productivity in controlling the flux of dissolved inorganic nitrogen through the sediment-water interface in a hypertrophic marine ecosystem. Mar Ecol Prog Ser 78:163–172


Kudela RM (2010) Does horizontal mixing explain phyto-
plankton dynamics? Proc Natl Acad Sci USA 107: 18235−18236


Moskaliski S, Torres R (2012) Influences of tides, weather, and discharge on suspended sediment concentration. Cont Shelf Res 37:36−45


Strom SL, Bright KJ (2009) Inter-strain differences in nitrogen use by the coccolithophore Emiliania huxleyi and consequences for predation by a planktonic ciliate. Harmful Algae 8:811−816


Submitted: October 12, 2018; Accepted: February 21, 2019

Proofs received from author(s): April 8, 2019

Copyright © 2019. Published by Elsevier Inc.