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Clams on stilts: a phytoplankton bioassay investigating effects of wastewater effluent amendments and *Corbicula fluminea* grazing

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ABSTRACT: Shallow-water habitats are being restored in the Sacramento–San Joaquin River Delta with the goal of enhancing phytoplankton production and food availability for higher trophic levels. However, elevated grazing pressure from the non-native freshwater clam *Corbicula fluminea* and localized depletions of dissolved inorganic nitrogen may limit phytoplankton biomass accumulation in restored habitats. To evaluate interactions between nutrients and grazing on phytoplankton productivity and biomass accumulation, Sacramento River water high or low in phytoplankton biomass was amended with wastewater effluent, presence of *C. fluminea*, or both, in 48 h *in situ* incubations. We measured changes in chl *a* concentration, phytoplankton community composition, and photosynthetic efficiency as well as carbon and nitrogen uptake rates as indicators of phytoplankton responses. Diatoms dominated phytoplankton communities before and after incubation. Chl *a* concentrations increased 0.7 and 7.4 times in the high and low phytoplankton biomass controls, respectively, and 4.5 and 14 times in the high and low phytoplankton biomass effluent-added treatments, respectively. In the clam treatments, chl *a* accumulation was suppressed to near zero regardless of effluent additions or initial phytoplankton biomass. In treatments with clams and effluent combined, phytoplankton photosynthetic efficiency was nearly 50% lower than in the effluent-only treatments, suggesting phytoplankton were stressed in the presence of clams. This experiment demonstrated that the presence of clams can prevent the accumulation of phytoplankton biomass, both directly by clam filtering and indirectly by depressing phytoplankton photosynthetic efficiency and rate of growth. We recommend that future wetland restoration projects promoting increased phytoplankton biomass assess clam settlement likelihood as well as nutrient availability.

KEY WORDS: Bioassay · Ammonium addition · Clam addition · Ambient irradiance · Carbon uptake · F_v/F_m · Phytoplankton growth · Clam grazing

1. INTRODUCTION

Situated between the Sacramento and San Joaquin rivers at the head of San Francisco Bay, the Sacramento–San Joaquin Delta (Delta) is comprised of a network of approximately 700 miles (1126 km) of waterways and sloughs across an area that is approximately 890 square miles (2300 km^2) in size (Cloern et al. 2021). This region provides critical habitat for fish, birds, and wildlife. In particular, Delta waterways are

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widely recognized as providing important nursery areas for several threatened or endangered endemic and migratory fish species including Delta smelt *Hypomesus transpacificus*, splittail *Pogonichthys macrolepidotus*, and Chinook salmon *Oncorhynchus tshawytscha* (Brown 2003, Herbold et al. 2014, Colombano et al. 2020).

Agriculture constitutes the principal land use in the Delta (Whipple et al. 2012). As a result, there is substantial drainage of nutrient-rich agricultural tailwater into Delta waterways (Jassby & Cloern 2000, Senn & Novick 2014). In addition, there have historically been high loads of nutrients from discharges of wastewater effluent from urban areas in the region, including Sacramento (Senn & Novick 2014). Whereas many estuarine regions demonstrate positive relationships between nutrient loading and excessive accumulation of phytoplankton, referred to as eutrophication (i.e. Boynton et al. 1982, Gowen et al. 1992, Nixon 1995, 2009, Borum 1996, Kemp et al. 2005, Bricker et al. 2008), some estuarine regions like the Delta have not experienced increased phytoplankton biomass or the impacts of eutrophication in response to increased nutrient loading (Cloern 1999, Jassby 2008). A feature of such nutrient-enriched, low phytoplankton biomass systems is the occurrence of high-energy tidal (and/or riverine) forcing leading to high suspended sediment concentrations and turbidity (Cloern 1987, Cole et al. 1992, Kromkamp & Peene 1995, May et al. 2003, Desmit et al. 2005). In turn, high turbidity results in light limitation of the phytoplankton community and low productivity (Cloern 1999, Jassby et al. 2002, Cloern et al. 2014). Because resuspended sediments rapidly attenuate light with depth, photosynthesis is restricted to the top layer of the water column (i.e. the euphotic zone), and productivity decreases the more time phytoplankton spend below the euphotic zone (Cloern 1987, Alpine & Cloern 1988, Lopez et al. 2006). Growth rates tend to vary inversely with mixed layer depth, and comparisons of shallow shoal versus deep channel habitats demonstrate that productivity and phytoplankton biomass are greater in the shoals compared with the channels (Cloern 1987).

In light-limited, low-productivity systems, additional phytoplankton loss factors such as grazing by clams can have large negative impacts on phytoplankton biomass accumulation (Alpine & Cloern 1992, Caraco et al. 1997, Lucas & Thompson 2012, Kimmerer & Thompson 2014). Understanding the magnitude of the different loss factors acting on phytoplankton biomass (i.e. Mussen et al. 2023) can aid in the management and restoration of carbon (C) flow to higher trophic levels in such systems (Cloern et al. 2021). To support the recovery of threatened and endemic and migratory fish species in the Delta, a major goal is to restore and expand tidal marshes, wetlands, and floodplains based on the premise that these habitats support higher phytoplankton productivity and biomass than the deeper channel habitats (Sommer et al. 2001, Schemel et al. 2004, Jeffres et al. 2008, Lehman et al. 2008).

However, higher productivity in shoal versus channel habitats does not always translate to greater phytoplankton biomass (Cloern 1987). Two invasive clam species that inhabit the Delta, the freshwater *Corbicula fluminea* and the brackish water *Potamocorbula amurensis*, separated in their geographical range by larval salinity tolerances (Crauder et al. 2016), play important roles in limiting phytoplankton biomass accumulation in respective regions of the Delta inhabited by these clams (Alpine & Cloern 1992, Kimmerer & Thompson 2014, Smith et al. 2023). This is a universal trend in light-limited systems where phytoplankton growth rates are commonly matched by clam filtration rates (Cohen et al. 1984, Caraco et al. 1997, Lopez et al. 2006, Lucas & Thompson 2012, Mussen et al. 2023) and clams can filter (turn over) the water column repeatedly (McDowell & Byers 2019). *C. fluminea* is one of the most widespread invasive aquatic clams in the world, due in part to its rapid growth and reproduction rates (Sousa et al. 2008). Over the last century, *C. fluminea*'s distribution has expanded from its native range in Asia, Australia, and Africa to include much of Europe, South America, and North America (Sousa et al. 2008), and its range is predicted to continue expanding due to future climate changes (McDowell et al. 2014). In highly eutrophic systems, *C. fluminea*'s rapid filtering and high assimilation rates (Modesto et al. 2021, 2023) can reduce phytoplankton concentrations and increase water transparency while enriching sediments with nutrients and organic C (Hwang et al. 2010, Patrick et al. 2017, Rong et al. 2021). Due to low phytoplankton productivity in the Delta, the presence of freshwater clams, such as *C. fluminea*, might be a key determinant of the success of shallow habitat creation in amplifying lower trophic level production (Lucas et al. 2002, Lopez et al. 2006).

While clams provide a top-down constraint on the accumulation of phytoplankton biomass, the size of the nutrient pool provides a bottom-up constraint on the absolute amount of phytoplankton biomass that may accumulate in any particular location. Due to light limitation, phytoplankton biomass and chl *a* concentrations typically vary between 2 and 4 $\mu g\ l^{-1}$

year round in the Delta (Jassby et al. 2002). Compared with chl *a*, concentrations of nutrients in the water column are relatively high and could support greater phytoplankton biomass (e.g. Cloern & Jassby 2012). If tidal wetlands and marshes are restored in some of these low-chlorophyll, high-nutrient regions of the Delta, it is not clear whether phytoplankton would be able to increase their productivity sufficiently to outpace filtration by *C. fluminea*, should the clam become established in the newly restored areas (e.g. Lopez et al. 2006, Lucas & Thompson 2012).

To evaluate interactions between elevated nutrient concentrations (bottom-up factor) and grazing by *C. fluminea* (top-down factor) on phytoplankton productivity and biomass accumulation, we designed a bioassay experiment to isolate clam and nutrient treatment effects while controlling for environmental factors such as light levels and water temperature, which also influence phytoplankton growth. The treatments included the presence and absence of clams and the presence and absence of supplemental nutrients in the form of wastewater effluent additions, at 2 different initial phytoplankton biomass levels.

With this bioassay experiment, a shallow-water habitat condition was approximated by incubating the bioassay container *in situ* at the water surface of the Sacramento River. In other words, the community inside the container experienced a constant light field during the day, which would be the case in a shallow-water habitat, rather than being cycled from top to bottom of the water column as they typically would in the Sacramento River and other deeper channels throughout the Delta (i.e. Alpine & Cloern 1988). We tested several hypotheses including that, relative to the initial phytoplankton biomass in each source water, (1) the final phytoplankton biomass would be lower in treatments with clams than in treatments without clams, (2) the final phytoplankton biomass would be higher in the treatments where effluent was added than in treatments without effluent and that differences in initial phytoplankton biomass would magnify this effect, (3) phytoplankton biomass would be greater in treatments with clams and effluent compared with clam-only treatments, and (4) the presence of clams would not impact the specific productivity of phytoplankton.

2. MATERIALS AND METHODS

2.1. Treatments, source water, and initial phytoplankton biomass

Four treatments were tested in the presence of 2 different initial phytoplankton biomass concentrations, for a total of 8 treatments, each in triplicate. The treatments included a control with no additions, additions of clams, additions of treated wastewater effluent (effluent) collected from the Sacramento Regional Wastewater Treatment Plant (SRWTP), and additions of both effluent and clams (Table 1). The lower Sacramento River receives a regular load of effluent from the SRWTP. In 2016, the SRWTP contributed approximately 90% of the river's dissolved inorganic nitrogen (DIN) load during the summer months (Fig. 1). However, in 2021, the SRWTP enacted a new biological nutrient removal process which changed the primary form of DIN in the effluent from ammonium to nitrate and reduced DIN loads in the effluent by roughly 85%. Therefore, the effluent concentrations tested in this study represent historical (i.e. prior to 2021) river conditions with high ammonium concentrations.

The water and initial phytoplankton communities used for these experiments were collected from 2 locations upstream of the SRWTP discharge location

Table 1. Treatments, source water locations (latitude, longitude), and initial nutrient (µmol l^{-1}) and chl *a* (µg l^{-1}) concentrations (±SE of mean of triplicate containers). DSi: dissolved silica

		Control	Effluent	Clam	Effluent+clam
Freeport source water	Chl *a*	1.9 ± 0.09	1.9 ± 0.09	1.9 ± 0. 09	1.9 ± 0.09
Lat.: 38.461796° N	NH_4^+	4.0 ± 0.64	46.4 ± 0.63	4.0 ± 0.64	46.4 ± 0.63
Long.: 121.503731° W	NO_3^-	5.3 ± 0.44	5.8 ± 0.43	5.3 ± 0.44	5.8 ± 0.43
	PO_4^{3-}	1.2 ± 0.04	2.9 ± 0.04	1.2 ± 0.04	2.9 ± 0.04
	DSi	253 ± 2.8	256 ± 2.7	253 ± 2.8	256 ± 2.7
I-5 source water	Chl *a*	8.1 ± 0.09	8.1 ± 0.09	8.1 ± 0.09	8.1 ± 0.09
Lat.: 38.665319° N	NH_4^+	1.8 ± 0.32	44.3 ± 0.32	1.8 ± 0.32	44.3 ± 0.32
Long.: 121.614963° W	NO_3^-	2.6 ± 0.48	3.2 ± 0.47	2.6 ± 0.48	3.2 ± 0.47
	PO_4^{3-}	1.3 ± 0.05	2.9 ± 0.05	1.3 ± 0.05	2.9 ± 0.05
	DSi	294 ± 5.6	297 ± 5.5	294 ± 5.6	297 ± 5.5

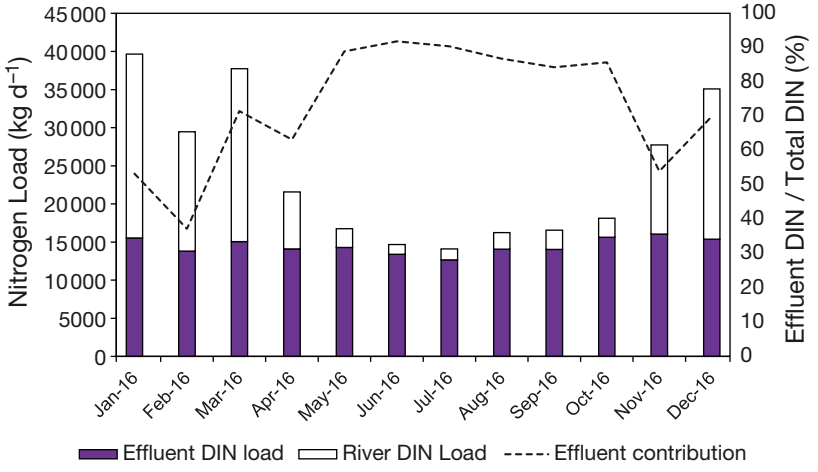

Fig. 1. Dissolved inorganic nitrogen (DIN) loads and percent contribution from the Sacramento Regional Wastewater Treatment Plant to the total Sacramento River DIN load in 2016. Effluent DIN loads calculated from NH_4^+ concentrations and effluent flow. Sacramento River DIN loads calculated from NO_3^- + NO_2^- samples and flow measurements at Freeport Bridge

where background nutrient concentrations were relatively low (Table 1). These locations were the Freeport Bridge (38.461796° N, 121.503731° W) at river mile (RM) 47, about 900 m upstream from the SRWTP discharge location, and the I-5 Bridge (38.665319° N, 121.614963° W), located further upstream at RM 70. The Freeport water source represented a relatively low phytoplankton biomass, deeper channel condition that would receive effluent discharge from the SRWTP. The I-5 water source represented a shallower region of the river with relatively high phytoplankton biomass and low nutrient concentrations and was located upstream in a region that would not receive effluent discharge from the SRWTP. The I-5 location typically has higher clam densities than the Freeport location (Mussen et al. 2023). Water depth, and therefore mixed water depth, at the Freeport location was 7.0 m and the initial chl *a* concentration was 1.9 µg l^{-1}, representing the lower phytoplankton biomass treatment. Water depth at the I-5 location was 2.3 m and the initial chl *a* concentration was 8.1 µg l^{-1}, representing the higher phytoplankton biomass treatment (Table 1). In 2016, *Corbicula fluminea* in the Sacramento River at Freeport averaged 40 clams m^{-2} and 4.7 g m^{-2} ash-free dry weight (AFDW, dry weight − ash weight) and filtered an estimated 0.49 m^3 m^{-2} d^{-1} (roughly 7% of the water column per day), whereas at I-5, *C. fluminea* averaged 123 clams m^{-2} and 10 g m^{-2} AFDW and filtered an estimated 1.2 m^3 m^{-2} d^{-1} (roughly 50% of the water column per day, Mussen et al. 2023).

2.2. Incubations

Whole surface water (i.e. unfiltered water) was collected into 208 l barrels by boat in the early morning on June 9, 2016, at the Freeport and I-5 locations in the Sacramento River. The barrels were transferred to the experimental site at Stan's Yolo Marina (38.487297° N, 121.553228° W), gently mixed with paddles, and subsampled for determinations of initial chl *a* and nutrient concentrations. Water aliquots (8 l) were transferred from the barrels by siphoning into 10 l translucent low-density polyethylene Cubitainers® for incubation.

After the Cubitainers were filled with whole water from the barrels, treatments were added as follows: Control treatments tested river water collected from each location with no additions. See Table 1 for ambient (i.e. background) nutrient concentrations of ammonium (NH_4^+), nitrate plus nitrite (NO_3^- + NO_2^-, hereafter abbreviated as NO_3^-), total dissolved phosphate (PO_4^{3-}), and dissolved silica (DSi). In the effluent treatments, river water was blended with final effluent from the SRWTP in a 58:1 (river water:effluent) ratio. The 58:1 ratio matched the SRWTP's average dilution ratio in the Sacramento River between the years 2000 and 2015. The principal source of DIN in the effluent was ammonium, with 99.4% of the total pool in the form of NH_4^+ and 0.6% in the form of ammonia (NH_3), calculated according to Thurston et al. (1979). The 58:1 dilution resulted in an approximate final NH_4^+ concentration of 50 µmol l^{-1} in the Cubitainers (Table 1).

Clam treatments included the addition of 1 *C. fluminea* individual per Cubitainer. Our study focused on *C. fluminea*, as they are the only clam species occurring in the Sacramento River near the SRWTP discharge location (Peterson & Vayssieres 2010). Clams were collected by boat from the Sacramento River at the I-5 location 1 d before the experiment, using a 35 cm wide trawling dredge and maintained in a chilled cooler overnight. We selected clams with shell lengths of 13 ± 0.1 mm (average ± SE) and estimated AFDW of 27 ± 1 mg for the experiment, so that the tested clam biomass per water volume in the Cubitainers (27 mg/8 l = 3.4 mg l^{-1}) was similar to that previously documented for the I-5 clam collection site (3.8 mg l^{-1}, Mussen et al. 2023). *C. fluminea* filtering rates were estimated from a temperature-corrected

correlation to AFDW, empirically derived for the Delta population by Foe & Knight (1986). The AFDW of *C. fluminea* was estimated from a correlation to shell length (Lopez et al. 2006). *C. fluminea* with similar shell lengths collected at the same time from the same location were expected to graze on phytoplankton at similar rates (Lauritsen 1986), although *C. fluminea* filtering rates can increase when food concentrations are low.

Each clam was placed in a 2 × 2 × 3.5 cm steel mesh cage with square 6.4 × 6.4 mm hole spacing. The clam cage was affixed to the middle of a 6 mm diameter, 30 cm long clear acrylic rod suspended from the lid of the bioassay container using small sections of plastic tubing added to the rod at the top and base of the clam cage (Fig. 2). This configuration ensured that the clam remained near the center of the floating container, regardless of the container's orientation in the water column. The central positioning of the clam and the absence of river sediment prevented *C. fluminea* from pedal feeding on settled organic matter (Hakenkamp & Palmer 1999). Cubitainers were placed in floating mesh-walled enclosures tied off to a dock, allowing them to remain at ambient river temperatures (22.5 ± 1.5°C) and receive mild agitation from surface waves. Neutral-density screening was attached across the top and sides of the Cubitainers to provide shading. The level of reduction in photosynthetically active radiation by the shading was determined by averaging multiple measurements at the water's surface and in the water inside a Cubitainer using a LI-COR Underwater Planar Quantum Sensor (LI-192). The light level inside the Cubitainers was approximately 120 µmol photons m^{-2} s^{-1}, which equaled 6% of surface irradiance (i.e. a reduction of 94% of incident irradiance).

Fig. 2. Floating 10 l Cubitainer used in the bioassays, with a section of 1 side wall removed to display the position of the suspended wire mesh cage and clam

Samples were collected from each Cubitainer after 48 h by filling acid-cleaned 2 l polycarbonate bottles that were used as transfer containers. Following sample collection, transfer containers were transported in coolers roughly 100 m to a filtration station for further processing and analysis of concentrations of turbidity, nutrients, chl *a*, and phytoplankton community composition. In addition, incubations for determinations of phytoplankton productivity were performed.

2.3. Sample processing and rate measurements

Measurements of dissolved oxygen (DO) and temperature were performed in the Cubitainers immediately prior to sample collection using hand-held Extech DO600 and Extech PH100 meters, respectively. Turbidity was measured using a Hach 2100P turbidimeter (US Environmental Protection Agency [USEPA] method 180.1). Water samples for nutrient analyses, including NH_4^+, NO_3^-, PO_4^{3-}, and DSi, were filtered through a 0.45 µm filter, preserved with acidification, and stored refrigerated for later analysis at the Regional San Environmental Laboratory using USEPA methods 350.1, 353.2, 365.4, and 200.8, respectively. For chl *a* analysis, a 250 ml water sample was filtered onto glass fiber filters (Whatman GF/F, 0.7 µm nominal pore size), and the filter was stored frozen until analysis using acetone extraction according to standard method 10200 H. Water samples for phytoplankton enumeration were collected into 250 ml amber bottles and preserved with Lugol's solution (5 ml addition per 250 ml water sample). Samples for phytoplankton were enumerated by BSA Environmental as described in Beaver et al. (2013). The biovolumes of phytoplankton cells were estimated by matching the cell's shape to a geometric shape with a known volume (Hillebrand et al. 1999). When possible, biovolume estimates in each sample were calculated from 10 cells per taxon. Picoplankton cells (≤2 µm) were collected in 50 ml centrifuge tubes and preserved with 50% glutaraldehyde solution (1 ml addition per 25 ml water sample), stored refrigerated,

and enumerated by BSA Environmental following the methods of Hall (1991) and MacIsaac & Stockner (1993). The biovolumes of cyanobacteria ⩽2 µm were subtracted from the picoplankton biomass estimates in each treatment prior to statistical analysis.

Phytoplankton productivity was assessed in 2 different ways, by determining the photochemical efficiency of photosystem II (PSII) and by determining the C uptake rate, measured by the addition of ^{13}C-bicarbonate. In addition to C uptake, rates of nitrogen (N) uptake were determined using additions of the stable isotopes ^{15}N-NH_4^+ and ^{15}N-NO_3^-.

PSII photochemical efficiency, commonly measured as variable fluorescence (F_v) over maximal fluorescence (F_m) (F_v/F_m), has been widely used to characterize the *in situ* physiological state of natural phytoplankton communities over large spatial scales (i.e. Coale et al. 1996, Boyd & Abraham 2001, Kromkamp & Forster 2003, Dijkman & Kromkamp 2006, Berg et al. 2011, Kudela et al. 2017, Sezginer et al. 2021). In eukaryotic phytoplankton, F_v/F_m typically varies between 0.1 (more stressed and slower growing) and 0.75 (healthy and fast growing), depending on the physiological status of the cells (Greene et al. 1991, Geider et al. 1993). Over smaller spatial scales, measurements of F_v/F_m have been used to demonstrate physiological changes in field bioassays with natural phytoplankton populations (e.g. Moore et al. 2005, Kudela et al. 2017, Strong et al. 2021). In the Delta, changes in F_v/F_m have been used to characterize alleviation of light limitation (Strong et al. 2021) and onset of toxicity in newly isolated phytoplankton cells (Berg et al. 2017). The advantage of using F_v/F_m is that the response time is on the order of minutes to hours following the onset of the stress, resulting in significant time savings compared with waiting for a response in growth rates (Kromkamp et al. 2005).

In the Cubitainers, F_v/F_m was measured using a PhytoFlash Active Fluorometer (Turner Designs) following dark acclimation of duplicate 5 ml subsamples. Prior to measurements, the optimal dark acclimation time required to relax non-photochemical quenching processes and maximize fluorescence was assessed by following changes in the baseline fluorescence, F_0, in the dark (e.g. Sezginer et al. 2021). F_0 relaxation was observed after 5 min, and no changes in F_v/F_m values were observed in trials with dark adaptations of 5, 10, and 20 min. Shorter acclimation requirements typically reflect low light-adapted and nutrient-sufficient cells (i.e. McLaughlin et al. 2020, Sezginer et al. 2021). F_v/F_m was calculated as:

$$F_v/F_m = \frac{(F_m - F_0)}{F_m} \quad (1)$$

where F_0 was measured following dark adaptation, and F_m was measured following a saturating pulse of light.

Uptake determinations of N and C were made using the stable isotope tracers ^{15}N-NO_3^- and ^{15}N-NH_4^+ (for N uptake) and ^{13}C-bicarbonate (for C uptake). Subsamples from each Cubitainer were partitioned into 2 acid-cleaned 250 ml polycarbonate square bottles and spiked with both N and C isotopes. The first bottle received ^{15}N-NO_3^- and ^{13}C-bicarbonate, while the second bottle received ^{15}N-NH_4^+ and ^{13}C-bicarbonate. These incubations produced 2 replicate measurements of bicarbonate uptake and single measurements of NO_3^- and NH_4^+ uptake for each Cubitainer, yielding 3 and 6 replicates for each N source and C source, respectively, per treatment. N isotopes were added to produce final concentrations of 0.05 or 4 µmol ^{15}N-NH_4^+ l^{-1} and 0.05 or 0.8 µmol ^{15}N-NO_3^- l^{-1}, depending on whether the treatment had no effluent or effluent added, respectively. Additions of ^{13}C-bicarbonate were made to a final concentration of 100 µmol ^{13}C l^{-1}. Both N and C isotope additions served to approximate 10% of the ambient concentrations of NH_4^+, NO_3^-, and bicarbonate. After the bottles were spiked with tracers, they were placed back into the floating enclosures used to house the Cubitainers and incubated for 4 h. Uptake incubations were terminated via vacuum filtration of 125 to 250 ml onto combusted 25 mm Whatman glass fiber filters (GF/F). Following filtration, samples were placed in sterile 2 ml Eppendorf microcentrifuge tubes, oven dried at 50°C overnight, and stored in a desiccator until processed for mass spectrometric analysis at the University of California, Davis, Stable Isotope Facility. Specific (h^{-1}) and absolute (µmol N l^{-1} h^{-1} or mg C l^{-1} h^{-1}) rates of C and N uptake were calculated according to Slawyk et al. (1977, 1979).

2.4. Calculations and statistical analyses

The yield of chl *a* from depletion of DIN in the cultures was estimated from a regression of chl *a* (µg) increases and DIN (µmol) losses in the control and effluent treatments (e.g. Gowen et al. 1992, Cloern & Jassby 2012). The slope of this relationship (1.35), representing the yield of chl *a* from N, was used to estimate the amount of chl *a* grazed by clams (chl a_g) in clam and effluent+clam treatments as follows:

$$\text{Chl } a_g = 1.35\,(\text{DIN}_i - \text{DIN}_f) \quad (2)$$

where the subscripts i and f indicate initial and final concentrations, respectively, of DIN.

Generation time (G), or doublings per day, of phytoplankton was estimated from the growth rate (μ_{chl}) based on changes in chl *a* and chl a_g as:

$$G(\mathrm{d}^{-1}) = \frac{\mu_{chl}}{\ln(2)} \quad (3)$$

where

$$\mu_{chl}(\mathrm{d}^{-1}) = \frac{\ln\left(\frac{Chl_f}{Chl_i}\right)}{t} \quad (4)$$

where the subscripts i and f indicate initial and final concentrations, respectively, of chl *a* or chl a_g, and t is the duration, in days, of the incubation.

Chl *a* consumed by clams in each treatment was calculated by subtracting the final measured chl *a* concentration from the initial concentration plus the estimated chl *a* production based on the change in DIN multiplied by the Cubitainer volume (8 l).

Comparisons among individual treatment means were analyzed using ANOVA tests with significant differences among means identified by Tukey-Kramer analysis ($\alpha = 0.05$) using Statistics Kingdom (2017). Following a square root transformation of the C uptake rates at I-5, all residuals met the assumptions of normal distributions (Shapiro-Wilk test) and equal standard deviations (Levene's test). Bray-Curtis dissimilarity (Bray & Curtis 1957) was calculated between the Freeport and I-5 water sources in the initial conditions and, control, effluent, clam, and effluent+clam treatments based on differences in the biovolume of phytoplankton divisions. We reasoned that biovolume (an indicator of biomass) provided a more meaningful measure of nutrient drawdown potential as well as food availability in the river than phytoplankton species counts.

3. RESULTS

In water samples from I-5, the initial average chl *a* concentration (8.1 µg l^{-1}) was not significantly different from the final average chl *a* concentration in the control treatment (5.3 µg l^{-1}, Fig. 3A), indicating a lack of phytoplankton growth. However, in water samples collected from Freeport, the initial average chl *a* (1.9 µg l^{-1}) was significantly lower than the final average chl *a* in the control treatment (14 µg l^{-1}, $F_{4,13}$ = 22.6, $p < 0.001$, Fig. 3B), indicating positive phytoplankton growth. Final chl *a* concentrations, reaching 25 to 30 µg l^{-1}, were significantly higher in treatments with added effluent, compared to control treatments for both the I-5 ($F_{4,13}$ = 22.6, $p < 0.001$) and Freeport ($F_{4,13}$ = 50.0, $p = 0.001$) water sources. Final chl *a* concentrations in I-5 water were similar between the control and clam treatments, but chl *a* concentrations in Freeport water were 7-fold higher in the control than clam treatments ($F_{4,13}$ = 50.0, $p = 0.001$). For both water sources, chl *a* concentrations were similar between the effluent+clam treatment and the clam treatment.

Phytoplankton biovolume was dominated by Bacillariophyta (diatoms) in both the initial samples (>80%) and samples following incubation (63–79%, Fig. 3C,D). Diatoms in the genus *Thalassiosira* were common in the initial populations from both locations and provided the greatest contribution to phytoplankton biovolume in most treatments following the 48 h incubation, ranging from 14 to 43% (Table 2). Other common diatoms included *Melosira* sp. and *Synedra* sp., which provided <1 to 41% of the biovolume among treatments.

Cyanobacteria remained below 1% of the total community biovolume in the controls and treatments. In the Freeport water source, picoplankton varied from 13 to 21% of total community biovolume in controls as well as treatments. In the I-5 water source, picoplankton varied to a greater extent as a percentage of total community biovolume, comprising 8% in the control, 5% in the effluent treatment, 16% in the clam treatment, and 21% in the effluent+clam treatment. Picoplankton composed an increased proportion of the biovolume in all treatments following incubation but remained ⩽21% of the total biovolume. Bray-Curtis dissimilarity was greatest in the initial conditions (0.49) and effluent (0.49) treatment, indicating higher phytoplankton community differences between the I-5 and Freeport locations compared to the dissimilarity occurring in the control (0.21), clam (0.21), and effluent+clam (0.38) treatments.

Effluent treatments had substantially higher initial NH_4^+ concentrations compared to treatments without effluent amendment (Table 3). NH_4^+ concentrations decreased in all treatments, with the greatest percent reduction occurring in the Freeport control and the least occurring in the effluent+clam treatments. NO_3^- concentrations also declined in all treatments, with the greatest percentage reduction occurring in the controls. Phosphate concentrations remained >0.047 mg l^{-1} (1.5 µmol l^{-1}) in all treatments following incubation.

In the effluent treatments, total N uptake (µmol l^{-1} h^{-1}) was dominated by NH_4^+ uptake, whereas in the treatments without effluent addition, total N uptake comprised a mix of both NH_4^+ and NO_3^- uptake (Fig. 3E,F). Phytoplankton in the I-5 effluent

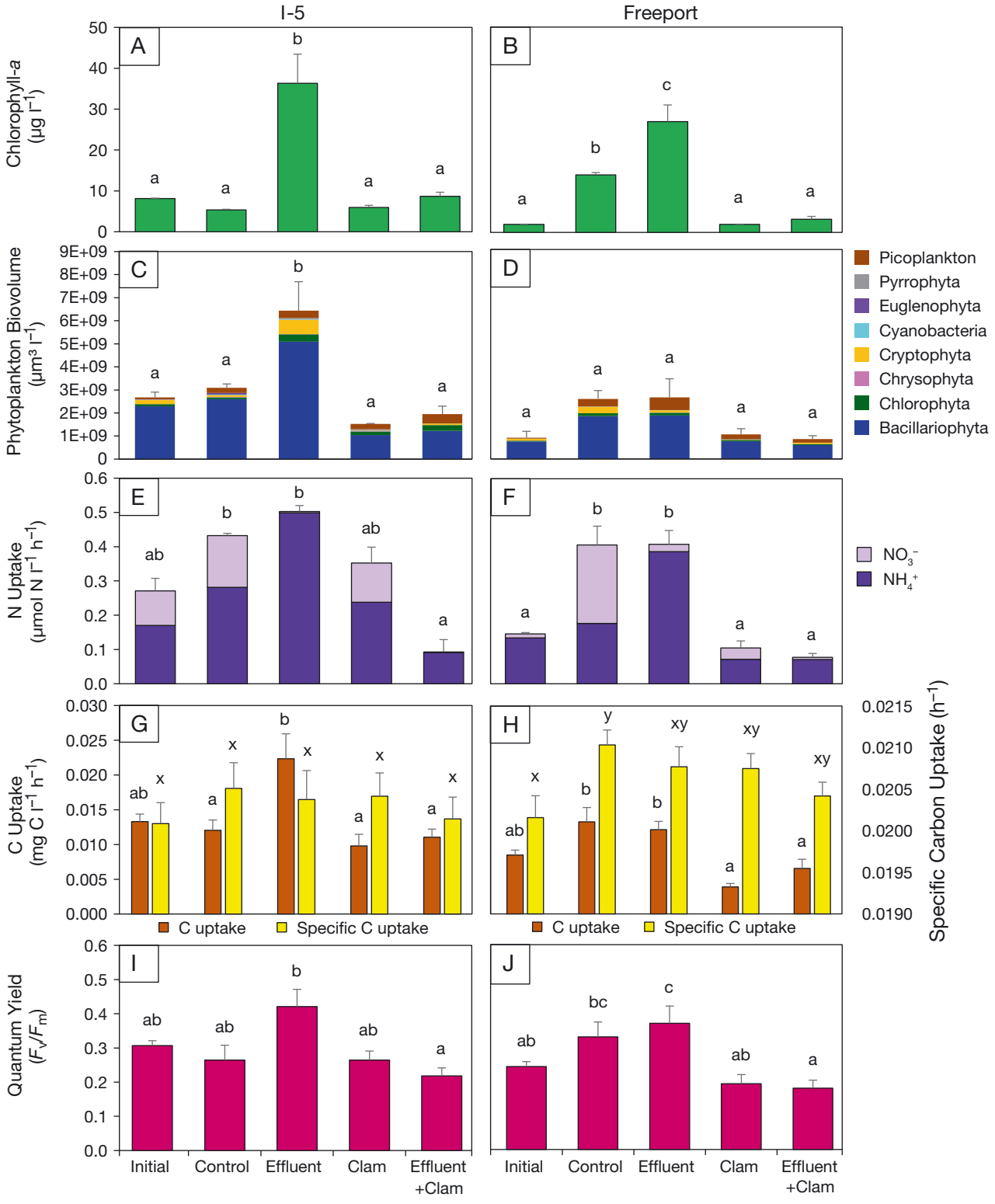

Fig. 3. Mean (+SE) of (A,B) chl *a* concentrations (µg l^{-1}), (C,D) phytoplankton biovolume (µm^3 l^{-1}) by taxonomic division, (E,F) NH_4^+ and NO_3^- uptake rates (mg C l^{-1} d^{-1}), (G,H) C uptake (mg C l^{-1} h^{-1}) and specific C uptake (h^{-1}), and (I,J) PSII photosynthetic efficiency (i.e. quantum yield, F_v/F_m). Initial measurements and final measurements following triplicate 48 h Cubitainer incubations for control, effluent, clam, and effluent+clam treatments from Sacramento River water collected near I-5 Bridge (A,C,E,G,I) and Freeport Bridge (B,D,F,H,J). Significant differences (α = 0.05) from individual ANOVA analyses are indicated by separate letters, with C uptake and specific C uptake analyzed separately

Table 2. Percentage of total biovolume (BV) provided by the top 5 dominant phytoplankton genera identified by enumeration. Water was sourced from near the I-5 Bridge and Freeport Bridge in the Sacramento River, with n = 6 initial samples and n = 3 for incubation treatments per location

I-5 Treatment	Genus	BV (%)	**Freeport** Treatment	Genus	BV (%)
Initial	*Melosira* spp.	17	Initial	*Fragilaria* spp.	26
	Thalassiosira sp.	16		*Thalassiosira* sp.	20
	Synedra spp.	14		*Synedra* spp.	9
	Cyclotella spp.	9		*Rhodomonas* sp.	8
	Rhodomonas spp.	6		*Navicula* spp.	5
Control	*Synedra* spp,	24	Control	*Thalassiosira* sp.	38
	Thalassiosira sp.	22		*Cyclotella* spp,	18
	Melosira spp.	15		*Rhodomonas* sp.	9
	Cyclotella spp.	12		*Aulacoseira* spp.	8
	Nitzschia spp.	4		*Fragilaria* sp.	5
Effluent	*Thalassiosira* sp.	30	Effluent	*Thalassiosira* sp.	43
	Melosira sp.	17		*Skeletonema* sp.	34
	Rhodomonas spp.	9		*Rhodomonas* sp.	3
	Cyclotella spp.	8		*Cyclotella* spp.	3
	Synedra sp.	5		*Monoraphidium* spp.	3
Clam	*Thalassiosira* sp.	18	Clam	*Melosira* sp.	41
	Synedra spp.	18		*Thalassiosira* sp.	14
	Melosira sp.	15		*Fragilaria* sp.	12
	Nitzschia spp.	8		*Cyclotella* spp.	9
	Monoraphidium spp.	7		*Aulacoseira* spp.	7
Effluent+ clam	*Thalassiosira* sp.	23	Effluent+ clam	*Thalassiosira* sp.	40
	Melosira sp.	9		*Aulacoseira* spp.	16
	Nitzschia spp.	8		*Synedra* spp.	8
	Asterionella sp.	7		*Cyclotella* spp.	7
	Cyclotella spp.	6		*Rhodomonas* sp.	6

Table 3. Mean initial parameter values (n = 6) and the average fold change in each treatment (control, effluent, clam, and effluent+clam) after 48 h incubations (n = 3). Water was sourced downstream of the I-5 Bridge and upstream of the Freeport Bridge in the Sacramento River, CA, USA. Initial dissolved N concentrations in treatments with effluent additions are shown in parentheses. DO: dissolved oxygen, NTU: nephelometer turbidity units

I-5 Sample time: Value:		Initial 0.0 h absolute	Control 48 h fold change	Effluent 48 h fold change	Clam 48 h fold change	Effluent+clam 48 h fold change
Chl *a*	$\mu g\ l^{-1}$	8.1	0.7	4.5	0.7	1.1
Phytoplankton biovolume	$\mu m^3\ l^{-1}$	2.68×10^9	1.1	2.3	0.5	0.6
Ammonium (with effluent)	$\mu mol\ l^{-1}$	1.8 (44)	0.7	0.5	0.6	0.8
Nitrate+nitrite (with effluent)	$\mu mol\ l^{-1}$	2.6 (3.1)	0.4	0.8	0.8	0.7
C uptake	$mg\ C\ l^{-1}\ h^{-1}$	0.013	0.9	1.7	0.7	0.8
N uptake	$\mu mol\ N\ l^{-1}\ h^{-1}$	0.3	1.6	1.9	1.3	0.3
F_v/F_m		0.3	0.9	1.4	0.9	0.7
DO	$mg\ l^{-1}$	8.1	1.1	1.3	1.1	1.1
Turbidity	NTU	10.8	0.4	0.5	0.4	0.4

Freeport Sample time: Value:		Initial 0.0 h absolute	Control 48 h fold change	Effluent 48 h fold change	Clam 48 h fold change	Effluent+clam 48 h fold change
Chl *a*	$\mu g\ l^{-1}$	1.9	7.4	14.2	1.0	1.7
Phytoplankton biovolume	$\mu m^3\ l^{-1}$	9.13×10^8	2.6	2.5	1.0	0.8
Ammonium (with effluent)	$\mu mol\ l^{-1}$	4.0 (46)	0.3	0.6	0.4	0.8
Nitrate+nitrite (with effluent)	$\mu mol\ l^{-1}$	5.3 (5.8)	0.2	0.9	0.8	0.8
C uptake	$mg\ C\ l^{-1}\ h^{-1}$	0.008	1.6	1.4	0.5	0.8
N uptake	$\mu mol\ N\ l^{-1}\ h^{-1}$	0.1	2.8	2.8	0.7	0.5
F_v/F_m		0.2	1.4	1.5	0.8	0.7
DO	$mg\ l^{-1}$	7.9	1.2	1.3	1.1	1.1
Turbidity	NTU	3.6	0.8	0.8	0.6	0.6

treatments had significantly higher rates of N uptake compared to those in the effluent+clam treatments ($F_{4,10}$ = 6.86, p = 0.005). N uptake in phytoplankton from Freeport was also significantly reduced in the presence of clams ($F_{4,10}$ = 26.0, p < 0.001).

Phytoplankton primary production, or C uptake (mg C l^{-1} h^{-1}), was greatest ($F_{4,25}$ = 5.54, p = 0.002) in the effluent treatment from I-5 (Fig. 3G). In the Freeport samples, primary production in the effluent treatment was similar to that of the control but was significantly greater ($F_{4,25}$ = 9.15, p = 0.037) than that of the effluent+clam treatment (Fig. 3H). Specific C uptake (h^{-1}) was substantially greater in the control compared with initial conditions, significantly so for the Freeport location ($F_{4,10}$ = 6.86, p = 0.05), suggesting that the incubation conditions promoted productivity relative to conditions *in situ* (Fig. 3G,H). Phytoplankton also showed a non-significant trend of greater specific C uptake rates in controls than those in the effluent+clam treatments for both locations.

In general, F_v/F_m followed a similar trend to the phytoplankton biomass and was higher in the effluent treatments compared to control and clam treatments for both water sources (Fig. 3I,J). In the I-5 water source, F_v/F_m in the effluent treatment was significantly higher ($F_{4,13}$ = 3.71, p = 0.023) than that in the effluent+clam treatment (Fig. 3I). In the Freeport water source, F_v/F_m significantly increased ($F_{4,13}$ = 6.86, p = 0.045) in the effluent treatment compared to the initial values (Fig. 3J) and was significantly higher ($F_{4,13}$ = 6.86, p ⩽ 0.014) than those in the effluent+clam treatment. During incubation, average DSi concentrations decreased from 294 to 278 µmol l^{-1} in the I-5 treatments and remained at 253 µmol l^{-1} in the Freeport treatments. DO concentrations increased and turbidity decreased in all treatments following incubation (Table 3). All clams were alive at the conclusion of the 48 h incubations, indicated by the closure of their shells in response to a gentle physical agitation.

Based on the change in DIN that occurred during the bioassay, and the correlation between chl *a* and DIN (Fig. 4A), the magnitude of phytoplankton biomass that was produced and grazed in clam treatments between the low initial phytoplankton biomass (Freeport) and high initial phytoplankton biomass (I-5) water sources was estimated (Fig. 4B). Based on our estimations, a similar amount of chl *a* was produced and grazed in equivalent treatments between the 2 water sources (Fig. 4). On a per clam basis, slightly more than double the average phytoplankton biomass was consumed (µg chl *a* $clam^{-1}$ d^{-1}, SE) in the effluent+clam treatments, I-5 (44, 5.1) and Freeport (49, 2.8), compared to the clam-only treatment, I-5 (18, 4.9) and Freeport (20, 3.0). Because initial chl *a* concentrations differed substantially in the 2 water sources, the production of similar amounts of chl *a* over the course of the 2 d incubation period meant that the phytoplankton in the Freeport water source grew and doubled more quickly compared with the I-5 water source. Within each water source, phytoplankton were expected to grow at a similar rate between the control and the clam treatment and between the effluent and effluent+clam treatment. We examined this assumption by calculating the theoretical increase in phytoplankton biomass, given the starting DIN and chl *a* concentrations, with the actual increase in phytoplankton biomass (including the biomass grazed by the clams). In the Freeport water source, up to 2.9 biomass doublings could have theoretically occurred, while in the I-5 source, <1 doubling could have occurred (Table 4). Based on the actual DIN drawdown, 1.9 doublings occurred in the Freeport clam treatment, and 2.6 doublings, close to the theoretical maximum, occurred in the Freeport control treatment, where the final chl *a* concentration reached 14 µg l^{-1}. In other words, phytoplankton biomass accumulation was reduced in the clam treatment compared with the control treatment in the Freeport water source. In contrast, chl *a* concentrations did not change over the course of the incubation in the I-5 control, where the initial nutrient concentration relative to initial chl *a* concentration was too low to support an increase in phytoplankton biomass. Accordingly, final chl *a* concentrations in the control and clam treatments were similar, and similar to the theoretical prediction of increase, for the I-5 water source.

The effluent+clam treatments had greater initial N concentrations relative to phytoplankton biomass, allowing a higher potential for phytoplankton biomass production in both water sources (Table 4). Accordingly, there was a higher potential for chl *a* doublings in the treatments with effluent added. Actual chl *a* doublings in the effluent treatment were higher for the Freeport water source compared with the I-5 source, suggesting again that the Freeport phytoplankton grew faster than the I-5 phytoplankton (Table 4). Chl *a* doublings in the effluent+clam treatment were reduced by 21% relative to the effluent-only treatment in the Freeport water source and by 41% in the effluent+clam relative to the effluent-only treatment for the I-5 water source (Table 4).

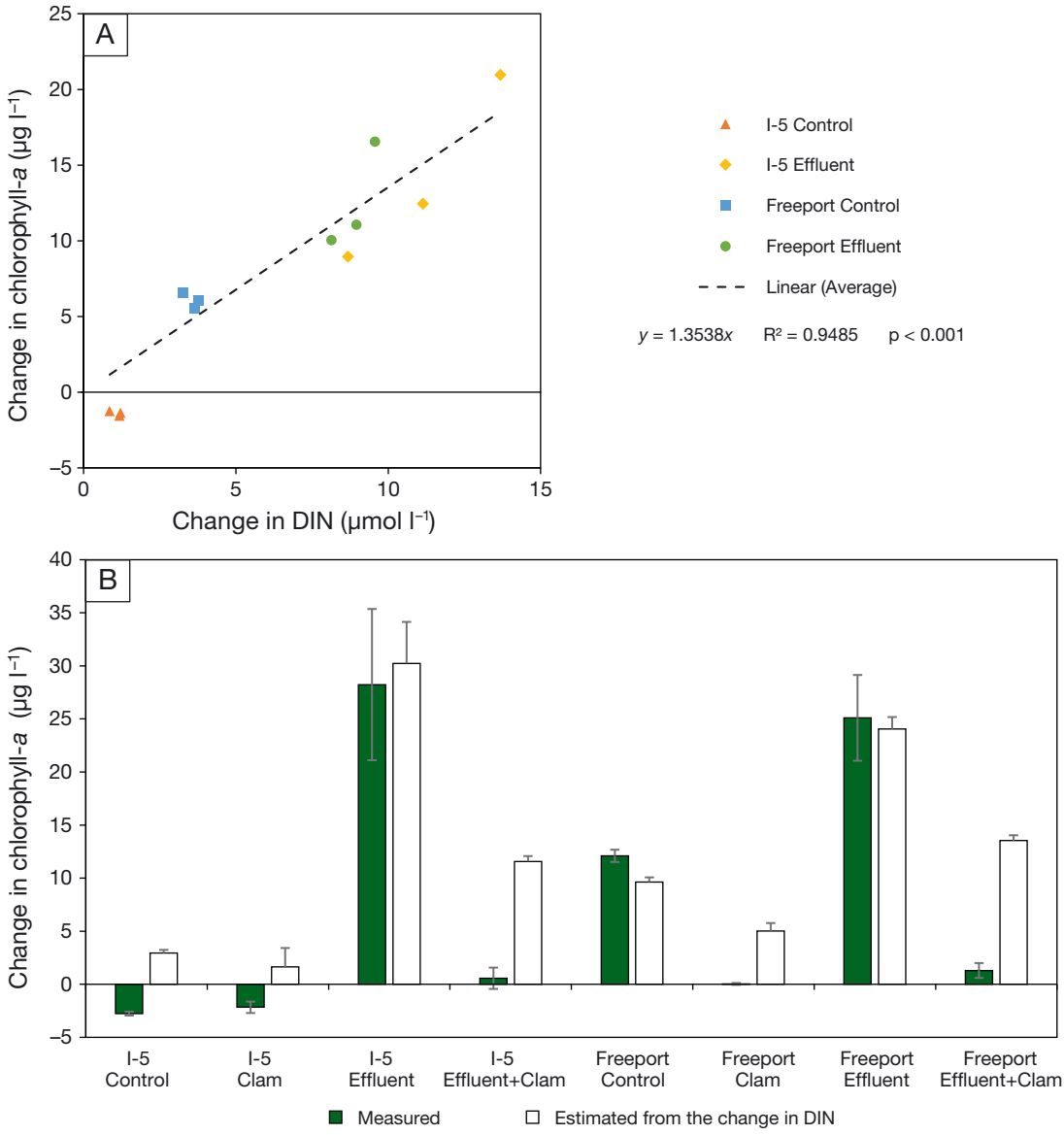

Fig. 4. (A) Correlation between change in chl *a* (µg l^{-1}) and change in DIN (µmol l^{-1}) in Cubitainers without clams (n = 12) following 48 h incubations (negative chl *a* values indicate losses). (B) Mean (+SE) change in chl *a* (µg l^{-1}) following 48 h incubations for each treatment, based on measured chl *a* concentrations (n = 3), and estimated production of chl *a* based on the reduction in DIN concentrations (n = 3)

Table 4. Maximum achievable (i.e. potential) phytoplankton biomass doublings (based on the size of the initial N pool compared with initial chl *a* concentration), observed chl *a* doublings (based on the difference in final and initial chl *a* measurements), and estimated chl *a* doublings (based on the reduction of DIN over the course of the 2 d incubation period)

Chl *a* doublings	Potential doubling based on initial DIN		Measured doubling based on Δ in chl *a*		Estimated doubling based on Δ in DIN	
	Freeport	I-5	Freeport	I-5	Freeport	I-5
Control	2.9	0.8	2.9	−0.6	2.6	0.4
Clam	2.9	0.8	0.0	−0.5	1.9	0.2
Effluent	5.2	3.2	3.8	2.1	3.8	2.2
Effluent+clam	5.2	3.2	0.7	0.1	3.0	1.3

4. DISCUSSION

This study demonstrated that *Corbicula fluminea* can be a highly efficient grazer of phytoplankton in small-volume experimental systems. Over the course of a 2 d incubation, phytoplankton biomass in clam treatments was either the same or reduced relative to the initial biomass at the start of the experiment. This confirmed our hypothesis that the final phytoplankton biomass would be lower in treatments with clams compared with treatments without clams. Given that we wanted to be able to tell whether phytoplankton were just as productive in the presence of clams as in their absence, we needed an additional method to estimate the biomass of phytoplankton that the clams were able to consume. The reduction of water column nutrient concentrations in the treatments was measurable and could be related to production or yield of unmeasured (i.e. ingested) chlorophyll via simple stoichiometry (e.g. Gowen et al. 1992). Accordingly, we estimated the total amount of phytoplankton biomass produced in the Cubitainers with clams, whether suspended, attached to walls, or grazed, by calculating the expected chl *a* yield from reductions in DIN. This allowed us to compare the extent of chl *a* produced and grazed in the various clam treatments with that in the non-clam treatments.

One concern in these experiments with relatively high additions of effluent-derived ammonium is that the concentration of un-ionized ammonia (NH_3), which is toxic to aquatic life, would impact the physiology of the clams. At the concentrations tested here, both the total ammonia (0.65 mg l^{-1}) and the NH_3 fraction (0.004 mg l^{-1}) were well below concentrations determined to cause 50% mortality (LC_{50}) for adult *C. fluminea*, 13.96 mg l^{-1} total ammonia and 0.88 mg l^{-1} un-ionized ammonia (NH_3) (Cherry et al. 2005), and therefore were unlikely to directly affect *C. fluminea* feeding behaviors in our study. Total ammonia concentration in our treatments was also lower than the USEPA's aquatic life ambient water quality criteria for total ammonia (1.9 mg l^{-1}, USEPA 2013), which includes protection for freshwater bivalves.

4.1. Phytoplankton biomass produced and grazed across treatments

The similarity in phytoplankton produced, and subsequently grazed, between the I-5 and Freeport water sources was surprising given that the starting chl *a* concentration was 4-fold higher in the I-5 compared to Freeport water source. However, this could be explained by a higher initial DIN concentration relative to phytoplankton biomass in the Freeport (DIN:chl *a* [µmol:µg] ratio of 5) compared with the I-5 (DIN:chl *a* of 0.5) water source, allowing the Freeport phytoplankton to grow and catch up to the biomass of the I-5 water source. But chl *a* reductions due to the presence of clams in the effluent+clam treatment kept pace with the additional phytoplankton production in the presence of effluent and cropped chl *a* accumulation to similar levels in both clam treatments. The clams also grazed down the initial difference in biomass between the 2 water sources. As a result, we reject our hypothesis that phytoplankton biomass would be greater in the effluent+clam treatment compared with the clam-only treatment and that the degree of accumulation in biomass in the effluent+clam treatment would depend on the initial phytoplankton biomass.

Clam grazing can also mask the amount of phytoplankton biomass that is produced in a natural system. For example, 2 shallow-water locations in the Delta, Franks Tract and Mildred Island, had different densities of *C. fluminea*, resulting in a 10-fold higher grazing rate in Franks Tract (4.4 m^3 m^{-2} d^{-1} grazing rate) compared with Mildred Island (0.4 m^3 m^{-2} d^{-1} grazing rate). The difference in grazing rates masked the greater rate of phytoplankton production in Franks Tract, as both locations had similar chlorophyll concentrations and phytoplankton biomass (Lucas et al. 2002). Invasion by *C. fluminea* highlights potential challenges with respect to the ability of restored shallow-water habitats to function as sources of C to higher trophic levels in the Delta. Both our Cubitainer experiments and prior measurements in natural systems (e.g. Lucas et al. 1999, 2002) demonstrate that the presence or absence of clams may determine whether a system will function either as a sink or as a source of phytoplankton biomass.

Compared to the controls, we observed a much greater increase in chl *a* in the effluent-only treatments, underscoring the stimulatory impact that wastewater-derived nutrients can have on phytoplankton growth in the absence of clam grazing (Preisner et al. 2020). The 14-fold increase in chl *a* in the Freeport effluent treatment (Table 3) was consistent with previous effluent addition experiments, demonstrating a 14-fold increase in chl *a* over a 2 d incubation period (Strong et al. 2021). Rapid phytoplankton growth in the effluent treatments was enabled by the large source of DIN and a constant high source of irradiance throughout the day. In the Delta, high-nutrient, high-irradiance conditions are uncommon in river channels, which tend to have high nutrients

and low irradiance, but can occur in terminal sloughs, such as the Sacramento Deep Water Ship Channel. In terminal sloughs, phytoplankton biomass can become elevated when the muted tidal exchange and dispersive flux are high enough to supply nutrients from the downstream waterway but sufficiently low to provide increased water residence time and occasional thermal stratification that promote the growth and accumulation of phytoplankton biomass (Lenoch et al. 2021, Young et al. 2021a, Loken et al. 2022). Under these conditions, DIN concentrations can become depleted upstream of the tidal exchange zone (Downing et al. 2016, Loken et al. 2022).

4.2. Variations in phytoplankton growth rates by water source

Because there were no restrictions on N availability (relative to initial phytoplankton biomass) in the effluent treatments, we hypothesized that final phytoplankton biomass would accumulate in proportion to initial phytoplankton biomass levels. Instead, phytoplankton grew roughly twice as fast in the Freeport versus I-5 water source, both in the absence (3.8 versus 2.2 doublings, respectively) and presence (3.0 versus 1.3 doublings, respectively) of clams.

The final chl *a* concentrations attained in the effluent treatments were representative of bloom conditions (i.e. $\geqslant$25 µg chl *a* l^{-1}) with respect to San Francisco Bay and the Delta (Sutula et al. 2017). At the outset of this experiment, we did not expect N-sufficient rates of phytoplankton growth to exceed 1 doubling per day (i.e. 2 doublings over the course of the incubation period), as this is considered a fast rate of growth for phytoplankton in upper San Francisco Bay and the northern Delta. For example, rates of phytoplankton growth along shoals in northern San Francisco Bay typically vary from 0.2 to 0.4 doubling per day (Alpine & Cloern 1988) and from −0.1 to 0.6 doubling per day in the lower Sacramento River (Kraus et al. 2017). Therefore, a rate of 2 doublings per day in the Freeport effluent treatment was above expectation. Faster growth by phytoplankton from the Freeport location compared with phytoplankton from the I-5 location could indicate that these 2 communities were pre-conditioned differently.

Part of the variation in conditioning could be related to differences in light acclimation, that is, how well the phytoplankton at these 2 locations were adapted to transition from low to high light levels. Low light-acclimated phytoplankton (i.e. phytoplankton that grow well under darker conditions) increase their rate of cell division in response to increased light faster than do phytoplankton that are high light acclimated (Post et al. 1984, Falkowski & LaRoche 1991, Pfannschmidt 2005, Kropuenske et al. 2010). One reason for this is to dilute and reduce the amount of chl *a* per cell to provide photoprotection (Post et al. 1984). Our results suggest that the initial phytoplankton community at Freeport could have been relatively low light acclimated compared with the I-5 community, explaining the difference in growth rates between phytoplankton from these 2 water sources once they were transferred to constant daytime high light conditions. This is consistent with the Freeport community, collected from a location with a water depth of 7.0 m, being acclimated to spending longer periods of time below the euphotic zone compared with the I-5 community, collected from a location with a water depth of 2.3 m.

4.3. Impact of clam presence on phytoplankton physiology

We assumed that the consumption of phytoplankton by clams would not alter the productivity or growth rates of the remaining non-grazed phytoplankton cells. Therefore, it was surprising that the F_v/F_m in the effluent+clam treatments was roughly half, and significantly different from, that in the effluent treatment. This result suggested that grazing by clams lowered photosynthetic efficiency and caused physiological stress to the phytoplankton. In turn, this suggested that our hypothesis that clam grazing would not impact the physiology and specific productivity of phytoplankton ought to be rejected. In contrast with F_v/F_m, the influence of clam grazing was less with respect to specific C uptake rates, which were only slightly reduced in the effluent+clam treatment compared to the effluent treatments. One potential reason that there was a greater negative impact on F_v/F_m than on specific C uptake in the presence of clams could be due to the difference in incubation time of these 2 measurements. Because the C uptake measurement incubation lasted 4 h, it may have given the phytoplankton time to adjust their physiology to the absence of clams. In contrast, F_v/F_m measured after 5 min probably reflected the physiology of the phytoplankton in the Cubitainers more accurately. It is commonly hypothesized that longer incubation times are less reflective of *in situ* photochemistry (e.g. Sezginer et al. 2021).

Why clam presence triggered a decrease in F_v/F_m and photochemical efficiency is not clear. One pos-

sibility is that the clams reduced F_v/F_m through selective grazing. In river systems, *C. fluminea* are known to consume a wide variety of algal species (Boltovskoy et al. 1995) but may selectively feed on diatoms and avoid ingesting colonial cyanobacteria, potentially causing taxonomic shifts in the phytoplankton community (Bolam et al. 2019). Prey selection in bivalves may be mediated by optical (Yahel et al. 2009) or chemosensory properties (Kohn 1961, Beninger et al. 2008, Rato et al. 2023). Because cyanobacteria typically have lower maximum F_v/F_m than eukaryotic phytoplankton, due to fluorescence emission from phycobilisome pigments that contribute to their F_0 (Campbell et al. 1996, 1998), a shift towards cyanobacterial dominance through prey selection could have influenced measurements of F_v/F_m. Across treatments, cyanobacteria remained below 1% and diatoms above 63% of the total phytoplankton community biovolume, suggesting that selective clam grazing did not substantially increase the proportion of cyanobacteria or skew F_v/F_m measurements in our experiment.

Another potential explanation for the decrease in F_v/F_m in the ungrazed phytoplankton is that they sensed the presence of the clam. Sensing of predators at a distance has been documented for diatoms in the presence of grazers such as zooplankton (Brownlee 2008, Hardardottir et al. 2019). Sensing is typically mediated by signaling mechanisms that perceive external cues such as lipids and amino acids released by the predators (Selander et al. 2015, Wohlrab et al. 2016, Grebner et al. 2019, Hardardottir et al. 2019) or compounds released by the phytoplankton being grazed (Vardi et al. 2006, Brownlee 2008). For example, the release of amino acids by copepods has been shown to trigger toxin production in some diatoms and dinoflagellates (Wohlrab et al. 2010, Tammilehto et al. 2015, Lundholm et al. 2018). The release of aldehydes by phytoplankton cells being grazed has been shown to trigger a chemical signaling cascade in the remaining phytoplankton cells that ends in nitric oxide production in the chloroplasts, leading to a reduction in PSII photosynthetic efficiency and growth (Vardi et al. 2006, 2008).

If the release of compounds from the grazed phytoplankton in the Cubitainers was sensed by the remaining phytoplankton and resulted in a decrease in F_v/F_m, it could be possible that it resulted in a stronger negative response than what would be expected in a natural environment. In the latter, we might expect concentrations of the chemical cues to be diluted compared to the Cubitainer environment. Nevertheless, our experiment indicates that the Cubitainer may be a good format for investigating sensing and signaling in phytoplankton in response to grazing. In addition, our results suggest that the influence of clams on phytoplankton is not only restricted to the cropping of biomass but also could result in a depression in productivity which may have downstream impacts if affected phytoplankton or the inhibitory chemical signals are transported out of the zone of grazing impact. This could be important for marsh restoration projects that seek to promote the accumulation of phytoplankton and transfer of C biomass to higher trophic levels (e.g. Cloern et al. 2021).

Diatoms provided ⩾63% of the phytoplankton biovolume, suggesting that selective clam grazing did not substantially alter the dominant taxonomic divisions during the 48 h incubations. Furthermore, initial differences in diatom biovolumes and the responses of diatoms to the Cubitainer treatments drove the observed differences in the Bray-Curtis dissimilarity between the I-5 and Freeport water sources. Many of the dominant phytoplankton genera in our study (Table 2) matched those common in the Columbia River, Washington, USA, including *Melosira* sp., *Cyclotella* sp., *Fragilaria* sp., and *Aulacoseira* sp. (Bolam et al. 2019).

Picoplankton provided a minor contribution to the total biovolume, but picoplankton biovolume increased following incubation in all treatments. This indicates that the Cubitainer environment might be favorable to picoplankton growth (i.e. no turbulence and constant surface irradiance). Rong et al. (2021) found significantly less accumulation of chl *a* from pico-sized cells in larger mesocosms containing numerous *C. fluminea*, but a reduction of picoplankton biovolume in the presence of clams was not pronounced in our study.

4.4. Limitations of the Cubitainer design

It is important to consider that *C. fluminea*'s filtering likely extended to a greater percentage of the water volume in the Cubitainers than it would in a natural system, where a clam's access to phytoplankton may be more dependent on the water depth and residence time. Using *C. fluminea* pumping rates determined by Foe & Knight (1986), and assuming that grazing and filtration rates remained constant across phytoplankton concentrations (Rollwagen-Bollens et al. 2021), clams were predicted to filter 6.8 of the 8 l water volume in the Cubitainer over 48 h. Therefore, up to 85% of water in the Cubitainers could theoretically be cleared by the clam in each treatment. Handling and acclimation to a new water source may have

stressed *C. fluminea* and impacted its grazing rates. *C. fluminea* in our studies were adapted to water conditions at I-5, so their grazing behaviors in the Freeport water might have changed over a longer exposure duration to match the reduced phytoplankton concentration. A 1 wk acclimation period was required for *Corbicula leana* to reduce their grazing rates after their water source was switched to Korean lake water containing *Microcystis aeruginosa* (Hwang et al. 2010). Future studies should also evaluate potential seasonal differences in *C. fluminea* grazing within the Sacramento River, as *C. fluminea* in the lower river Rhine (Germany and The Netherlands) can experience dramatic reductions in body mass and condition during summer months, likely due to starvation from low phytoplankton availability (Vohmann et al. 2010).

Although decreases in chl *a* in the clam treatments in our experiments suggested the clams were efficient at removing phytoplankton biomass, some phytoplankton may have avoided being grazed. For example, water near the suspended clams may have been filtered repeatedly, potentially establishing a low phytoplankton concentration boundary layer near the center of the Cubitainer (Jones et al. 2009), leaving areas near the edges of the Cubitainers ungrazed. In addition, some diatoms may have avoided clam grazing by settling to the bottom or attaching themselves to the walls of the Cubitainers. The influence of attached algae (i.e. periphyton) may be enhanced in experimental systems with a relatively large wall area:water volume ratio (Berg et al. 1999, Petersen et al. 2003). Enumeration of the phytoplankton community demonstrated that in addition to the pelagic diatom *Thalassiosira* sp., diatoms such as *Synedra* sp., *Fragilaria* sp., and *Melosira* sp., which typically originate as part of periphytic assemblages in the benthos (e.g. Li et al. 2010, Hill et al. 2011, Chen et al. 2016), were common in the phytoplankton community composition of some treatments at the beginning and end of the experiments (Table 2). However, the estimation of total phytoplankton biomass produced based on the change in DIN in the Cubitainers incorporated production from all phytoplankton species. In natural systems, *C. fluminea* also has direct effects on sediment dynamics and nutrient flux. For example, *C. fluminea* bioturbation can release nutrients from river sediments into the water column, and their faeces and pseudofaeces will transfer nutrients from the water column into the river sediments (Vaughn & Hakenkamp 2001, Modesto et al. 2023). These effects were not evaluated in our bioassay experiments.

4.5. Implications for marsh restoration

Translating our findings to marsh restoration projects, we predict that the invasion of restored areas by *C. fluminea* may pose a serious challenge with respect to promoting the accumulation of phytoplankton biomass. Future examinations of phytoplankton growth and clam biomass fluctuations may yield insights into whether conditions identified in our experiments can also increase phytoplankton growth and biomass accumulation in natural settings such as floodplains, setback levees, and dead-end side channels. It is also important to recognize that the growth rates of multiple types of primary producers are enhanced in shallow-water habitats, including those of emergent vegetation, which provide food web support to consumers in addition to phytoplankton (Young et al. 2021b).

Sacramento River floodplain restoration projects may offer a potential solution to the challenge of invasion by clams such as *C. fluminea*, as these regions remain dry throughout much of the year. When the floodplains are inundated during winter and spring storms, or by controlled management actions, phytoplankton and zooplankton grow rapidly in the shallow, high residence time water (Schemel et al. 2004, Ahearn et al. 2006). Newly released juvenile *C. fluminea* may also be transported into the inundated floodplains by the river but would require 3 to 6 mo to mature (McMahon 2002), limiting their colonization rate and grazing impacts. Zooplankton growth is especially high in floodplains, due to grazing of both phytoplankton and detrital C sources (Jeffres et al. 2020). Native California fishes are adapted to enter these floodplains and maximize their growth on the abundant invertebrate food resources (Moyle et al. 2007). However, to benefit from these habitats in years with moderate precipitation (resulting in river flows < 400 m^3 s^{-1}), fish may require improved horizontal connectivity between the floodplains and mainstem rivers to access the resources (Bellido-Leiva et al. 2022).

To support robust phytoplankton growth in future marsh restoration projects, there may be value in research conducted to evaluate the physical and biological factors that reduce non-native clam settlement and grazing pressure in shallow wetlands. We also recommend that wetland restoration programs in the Delta monitor changes in chl *a* and N drawdown occurring during periods of wetland inundation to characterize conditions that limit or constrain phytoplankton growth and to identify the phytoplankton biomass capacity of the system.

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