

Hydrodynamic control of phytoplankton loss to the benthos in an estuarine environment

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Abstract

Field experiments were undertaken to measure the influence of hydrodynamics on the removal of phytoplankton by benthic grazers in Suisun Slough, North San Francisco Bay. Chlorophyll *a* concentration boundary layers were found over beds inhabited by the active suspension feeders *Corbula amurensis* and *Corophium alienense* and the passive suspension feeders *Marenzelleria viridis* and *Laonome* sp. Benthic losses of phytoplankton were estimated via both the control volume and the vertical flux approach, in which chlorophyll *a* concentration was used as a proxy for phytoplankton biomass. The rate of phytoplankton loss to the bed was positively correlated to the bed shear stress. The maximum rate of phytoplankton loss to the bed was five times larger than estimated by laboratory-derived pumping rates for the active suspension feeders. Reasons for this discrepancy are explored including a physical mechanism whereby phytoplankton is entrained in a near-bed fluff layer where aggregation is mediated by the presence of mucus produced by the infaunal community.

The shallow water regions of San Francisco Bay are of ecological importance because they support net production of phytoplankton that form the base of the aquatic food web (Cloern 1996). However, benthic grazing by siphonate bivalves can limit the accumulation of phytoplankton biomass in the shallow waters of many systems (Newell 2004; Prins and Escaravage 2005) and is a critical factor in defining ecosystem function in the San Francisco Bay system (Alpine and Cloern 1992; Thompson 2005). It has been hypothesized that the invasion of the clam *Corbula amurensis* in 1986 is largely responsible for the severe reduction in both the magnitude and persistence of the summer to autumn phytoplankton bloom in northern San Francisco Bay (Alpine and Cloern 1992; Jassby et al. 2002). Soon after the *C. amurensis* invasion into San Francisco Bay, several species of fish declined in abundance, partially as a result of severe decreases in phytoplankton availability (Feyrer et al. 2003). Furthermore, the extensive shallows of the tidal freshwater portion of the system, the Sacramento–San Joaquin River Delta, have limited and declining primary productivity (Jassby et al. 2002) and large populations of another invasive clam, *Corbicula fluminea*. Recent work by Lucas et al. (2002) shows that grazing by *C. fluminea* is a primary factor in determining whether the shallow systems of the Delta are net phytoplankton exporters or net phytoplankton sinks. Thus, the San Francisco estuary is a system where the control of phytoplankton abundance by nonindigenous, nonfarmed bivalve grazers is sufficient to endanger the continued success of native fish as well as key pelagic invertebrate species. Our understanding and ability to estimate the grazing rates of benthic suspension feeders and the physical limits on grazing rates is particularly critical in systems such as this one.

The mass balance of phytoplankton can be described as

$$\underbrace{\frac{\partial C}{\partial t}}_{\text{change in biomass}} = \underbrace{-U \frac{\partial C}{\partial x} - V \frac{\partial C}{\partial y}}_{\text{advection}} + \underbrace{w_s \frac{\partial C}{\partial z}}_{\text{settling}} - \underbrace{\frac{\partial}{\partial z} \left(-K_z \frac{\partial C}{\partial z} \right)}_{\text{turbulent diffusion}} - \underbrace{\psi}_{\text{sinks}} + \underbrace{\phi}_{\text{sources}} \quad (1)$$

where U and V are the mean velocities in the x and y directions; C is the concentration of phytoplankton; w_s is the phytoplankton settling rate; K_z is the turbulent eddy diffusivity for phytoplankton; ψ represents the depletion of phytoplankton due to benthic suspension-feeding, respiration, and zooplankton grazing; and ϕ represents the sources of phytoplankton such as production and resuspension (Koseff et al. 1993). Equation 1 indicates that hydrodynamics can directly affect the strength of benthic–pelagic coupling. Indeed, concentration boundary layers (CBL) form when phytoplankton cells removed by beds of bivalves are not replaced by vertical mixing. When CBLs form, the flux of particles to the incumbent siphons of bivalves is reduced. Therefore, the benthic grazing rate (the rate of removal of particles, such as phytoplankton, from the water [$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$]) is a function of both the pumping rate (the volume of water passing through the siphon per unit time [$\text{m}^3 \text{s}^{-1} \text{ind}^{-1}$]) and the overlying hydrodynamics. The relative strength of the benthic grazing rate, turbulent diffusion, and the phytoplankton settling rate will determine the formation of a CBL.

The existence of a CBL above suspension filter feeders has been identified in both laboratory flume experiments (Wildish and Kristmanson 1984; O’Riordan et al. 1993; Butman et al. 1994) and in the field (Frechette and Bourget 1985; Dolmer 2000; Nielsen and Maar 2007), although many of these studies failed to identify quantitative

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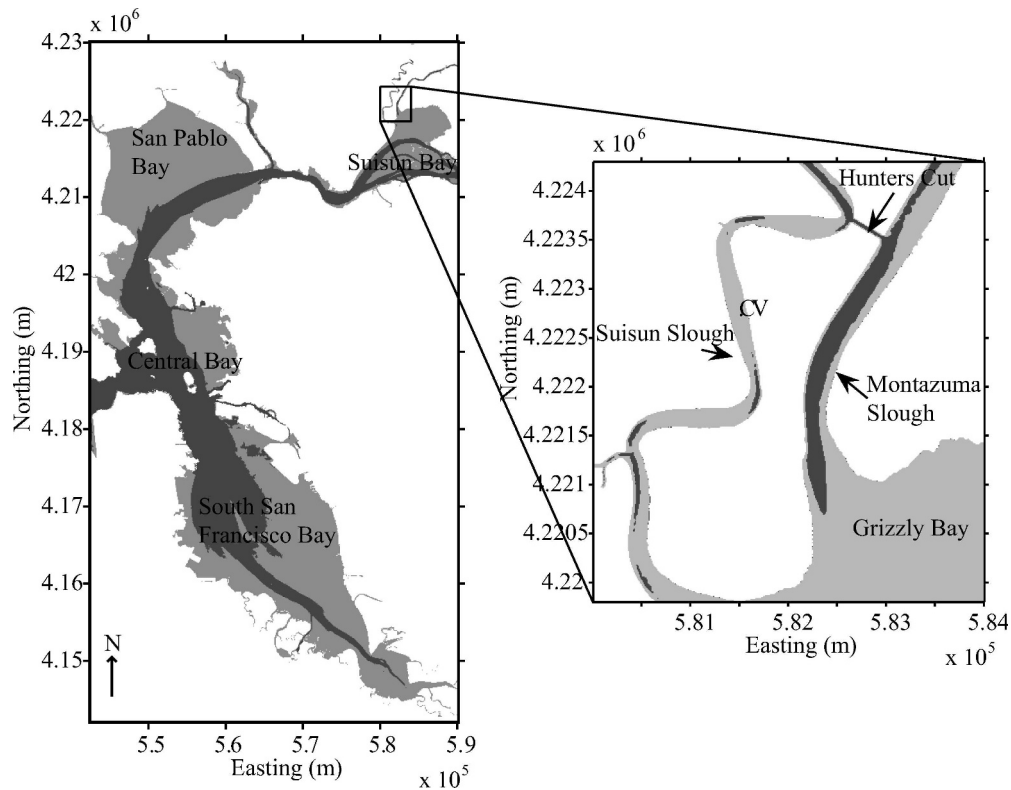


Fig. 1. Bathymetric contours and site map of the lower reaches of Suisun Slough showing the location of the control volume site (CV). The darker gray areas indicate depths greater than 6 m.

relationships between grazing and hydrodynamics. Ackerman et al. (2001) measured the presence of a CBL above a bed of zebra mussels in Lake Erie during a period of stratification and found that the CBL was dependent on the extent of stratification of the water column. Thompson (1999) found that the CBL above infaunal bivalves in South San Francisco Bay varied in time and space as a function of phytoplankton patchiness, vertical mixing time, and bivalve density and size. Other investigations of benthic grazing have measured fluxes of phytoplankton upstream and downstream of an area of interest with limited vertical sampling (Roegner 1998; Tweddle et al. 2005).

Despite great improvements in our knowledge of the effects of benthic grazers on water column seston concentrations, the effect of different hydrodynamic conditions on grazing rates has not been thoroughly quantified. This makes it difficult to assess the system-wide effect of the benthic community on phytoplankton concentrations. Furthermore, it affects our ability to predict the potential effect of exotic benthic species such as the invasive clams *C. fluminea* and *C. amurensis*. The objectives of this study were to measure the rate of phytoplankton removal by the benthos and to determine the relationship between the rate of phytoplankton removal by the benthos and the extent of turbulent mixing in situ. To achieve these objectives, field experiments were carried out at Suisun Slough, North San Francisco Bay, whereby the rate of phytoplankton removal by the benthos was estimated via both control volume and vertical flux approaches, with chlorophyll *a* (Chl *a*) concentration used as a proxy for phytoplankton biomass.

Methods

Study site—The field study was carried out in Suisun Slough in North San Francisco Bay from 30 August to 15 September 2005 (Fig. 1). Suisun Slough flows through Suisun Marsh, a large brackish-water marsh. The site was chosen for its relatively uncomplicated tidal flow. The sample site was located approximately halfway along the reach, maximizing its distance from upstream and downstream bends to minimize secondary flows. This section of Suisun Slough is relatively shallow; the depth at the control volume (CV) site ranged from 2.0 to 3.5 m. All water samples were taken at the center of the channel (Fig. 2). Measurements of the grain size distribution of the sediment in lower Suisun Slough revealed <5% sand (diameter 0.062–2 mm), 30–65% silt (0.004–0.062 mm), and 35–45% clay (<0.004 mm) (Hampton et al. 2003). The sediment contained approximately 4% organic matter by dry weight (Department of Water Resources unpubl.).

Estimating benthic losses—Two methods were employed to estimate the rate of phytoplankton removal by the benthos: the control volume (CV) method and the vertical flux method.

The CV method: This method uses an imaginary box (the control volume) that encloses the region of interest (Fig. 3). Mass balances for each scalar are then written, including fluxes through the faces of the CV (the control surface [CS]), unsteady changes in quantities inside the CV, and any nonconservative processes that add or remove

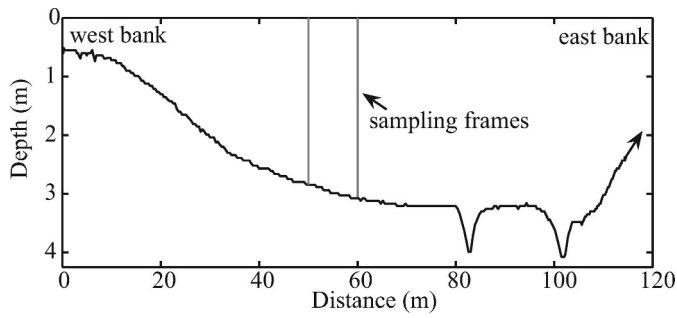


Fig. 2. Cross section of channel where control volume was situated. From the west bank a subtidal mud flat leads to a gentle slope to the flat bottom. The east bank is steep sided.

material from the CV such as benthic grazing. Mathematically this is expressed by the integral form of the mass conservation relation

$$\frac{d}{dt} \int_{CV} C dV + \int_{CS} C \vec{u} \cdot d\vec{A} = J A_b \quad (2)$$

where C is the concentration of the scalar, \vec{u} is the local transport velocity, $d\vec{A}$ is the local directed surface area element (the direction normal to the surface), J is the mass flux per area of the benthos and A_b is the area of the rectangle A-B-C-D (Fig. 3). Assuming that all losses are due to benthic grazing, the mass flux is related to the benthic grazing rate ($\text{m}^3 \text{m}^{-2} \text{s}^{-1}$) as

$$J = \alpha C_B \quad (3)$$

where C_B is the phytoplankton concentration close to the bed.

As an exact expression, Eq. 2 requires that C and \vec{u} be known everywhere inside the control volume. However, in practice, each of the required integrals were estimated from limited pointwise velocity and concentration measurements. In the experiments, phytoplankton were sampled along each vertical corner of a $10 \times 20 \text{ m}$ control volume (Fig. 3). To capture vertical variations in phytoplankton concentration, Chl a samples were collected at eight heights spaced approximately logarithmically from the sediment-water interface to the water surface. In terms of this sampling arrangement and substituting in Eq. 3 we can then approximate Eq. 2 as

$$\begin{aligned} & WHL \frac{\Delta \bar{C}}{\Delta t} + W \left[- \int_0^H C_{AB}(z) u(z) dz + \int_0^H C_{CD}(z) u(z) dz \right] \\ & + L \left[- \int_0^H C_{BD}(z) v(z) dz + \int_0^H C_{AC}(z) v(z) dz \right] = \alpha C_B WL \end{aligned} \quad (4)$$

where W is the width, L is the length, and H is the height of the control volume; u is the lengthwise oriented velocity; v is the widthwise oriented velocity; C_{AB} , C_{CD} , C_{BD} , and C_{AC} are the representative vertical distributions of Chl a concentration for each face, averaged from the measurements at each corner; and \bar{C} is the volume-averaged Chl a concentration.

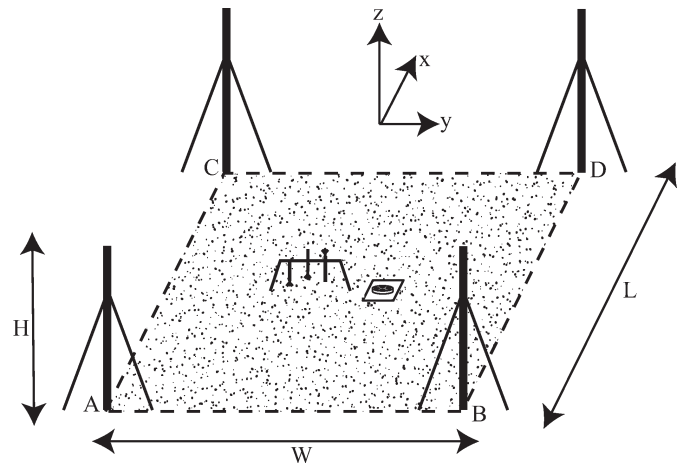


Fig. 3. A schematic drawing of the control volume. The four water sampling frames are shown at the corners of the control volume. The instruments shown in the center of the CV are measuring the hydrodynamics. The dominant flow is in the x direction.

The vertical flux method: This method uses the near-bed Chl a concentration gradient and the vertical turbulent diffusivity to estimate the benthic grazing rate. The vertical turbulent diffusivity K_z in channel flow can be modeled as a parabolic distribution

$$K_z = \kappa u_* b z \left(1 - \frac{z}{h} \right) \quad (5)$$

where $\kappa = 0.41$ is the von Karman constant (Fischer et al. 1979). Close to the bed where $z/h \sim 0$ Eq. 5 can be approximated as

$$K_z = \kappa u_* b z \quad (6)$$

If Eq. 1 is integrated from some height z to the water surface at $z = h$, using the condition that the flux through the water surface is 0, we find that

$$\begin{aligned} & \int_z^h \left(\frac{\partial C}{\partial t} + U \frac{\partial C}{\partial x} + V \frac{\partial C}{\partial y} + \psi - \phi \right) dz \\ & = -w_s C(z) - K_z \frac{\partial C}{\partial z} \Big|_z = F(z) \end{aligned} \quad (7)$$

Here F represents the total flux toward (or away from the bed) at any height. If phytoplankton biomass is removed near the bed, F will decrease with height above the bed (assuming uniform vertical velocity with depth and that the growth of phytoplankton occurs on timescales much larger than the time for the water column to be mixed). If we consider a region near the bed, F will be approximately constant, say F_B , and K_z will be linear with height; thus, neglecting settling, Eq. 7 can be written as

$$-K_z \frac{\partial C}{\partial z} = -\kappa u_* b z \frac{\partial C}{\partial z} = F_B \quad (8)$$

Integration of Eq. 8 shows that near the bed, the concentration is expected to vary logarithmically with height

$$C(z) = d \ln \frac{z}{z_c} + C_B \quad (9)$$

where $d = F_B/\kappa u_{*b}$, z_c is the height at which the benthic grazers are removing the Chl *a* and C_B is the concentration of Chl *a* at z_c . The vertical flux of Chl *a* at the height of benthic feeding z_c can be expressed as the product of the grazing rate α and C_B

$$F_B(z_c) = \alpha C_B \quad (10)$$

Therefore, the benthic grazing rate can be estimated as

$$\alpha = \frac{\kappa u_{*b} d}{C_B} \quad (11)$$

where u_{*b} can be estimated from the near-bed acoustic Doppler velocimeter (ADV) measurements. Note that since we have neglected settling, which has the same sign as the diffusive flux, Eq. 11 is an underestimate of α .

Least-squares regression was used to find d and C_B for each vertical profile of Chl *a*, with $z_c = 5 \times 10^{-3}$ m. The fits were performed using at least four samples adjacent to the bed for all combinations of the possible eight vertical samples and allowing for the possibility of one outlier in the CBL. The set of samples that resulted in the highest r^2 value was selected for further analysis if the fit was significant at the 95% confidence level and $r^2 > 0.6$. Replicate sampling of the vertical profiles was not possible, therefore the error in d and C_B was estimated using the bootstrap method, whereby subsets of data are generated based on a random sampling of the data (Bendat and Piersol 2000). Bootstrap samples were created by resampling each Chl *a* profile 1000 times, independently and with replacement. Least-squares regression of the bootstrap generated data resulted in 1000 estimates of d and C_B , the mean of the estimates of d and C_B is the “best fit,” and the standard deviation of the estimates of d and C_B is used to estimate the uncertainty. The friction velocity u_{*b} was estimated from the covariance of the streamwise u and vertical w velocity ADV time series (Voulgaris and Trowbridge 1998). The error in the u_{*b} estimate was negligible (2% at the 95% confidence level).

Measurement techniques—The water sampling was undertaken during two 30-h experiments conducted 12 d apart. To enable the collection and processing of water samples, the experiments were staged from a houseboat. The water sampling frames were constructed to collect samples at eight discrete heights (0.1, 0.15, 0.2, 0.25, 0.35, 0.5, 1, and 2.5 m) above the bed. The intake tubes were extended away from the central support to prevent potential mixing of the water by the presence of the frame. The water sampling frames were manually reoriented into the direction of the mean flow at each slack tide for the same reason. Ten-minute integrated water samples were collected every hour for each 30-h experiment via 30-m lengths of tube and peristaltic pumps operating at 90 mL min⁻¹. The 10-min sampling time was chosen to ensure the water column was turning over a few times during the sampling period and to ensure the intake velocity was not excessive. Phytoplankton biomass was estimated from fluorometrically determined Chl *a* concen-

tration (Parsons et al. 1984). This technique involved immediately filtering the collected water sample through Whatman GF/F filters, which were then stored at -80°C . The filters were later extracted in 90% acetone overnight and centrifuged, and Chl *a* concentration of the extract was measured with a fluorometer (Model 10, Turner Designs).

In addition to the discrete water sample measurements, continuous time series of Chl *a* fluorescence was obtained in situ (self-contained underwater fluorescence apparatus (SCUFA), Turner Designs). A fluorometer with a sampling interval of 30 s was placed close to the inlet 1 m above the bed on the southwest water sampling frame. The fluorometer was calibrated via multiple regression using the extracted Chl *a* concentration from the pumped samples and turbidity measured by the SCUFA. Phytoplankton samples for species composition were collected every 6 h during the 30-h experiments. The samples were preserved in acid-Lugols solution and examined in a phase contrast inverted microscope to identify the most common taxa and estimate their biovolume from measured cell dimensions (Cloern and Dufford 2005).

Throughout the two 30-h experiments, zooplankton tows were performed every 6 h. The zooplankton samples were collected with a 50- μm mesh, 0.5-m diameter net towed a distance of 100 m obliquely across the downstream face of the sample area. Zooplankton were preserved in 5% buffered formalin with Rose Bengal dye. One microliter subsamples were examined in a Sedgewick-Rafter cell, and all zooplankton (primarily rotifers, copepods, and cladocerans) were counted and identified to species or genus; lengths of 20 individuals in each category were measured.

Individual dry weights of zooplankton were estimated from published length-weight relationships or from published dry-weight data for specific taxa. Dry weight was converted to carbon using a carbon:dry weight ratio of 0.48 (Lopez et al. 2006). Zooplankton community grazing was estimated from an Ivlev function describing ingestion rate as a hyperbolic function of phytoplankton biomass, where ingestion rate approaches a maximum at a phytoplankton biomass of 300 mg C m⁻³. The estimated ingestion rate I was calculated for each taxon via (Lopez et al. 2006)

$$I_i = 0.95 m_i^{0.8} e^{0.069(T-10)} (1 - e^{-0.01PB}) \quad (12)$$

where m_i is the body size, T is the water temperature ($^\circ\text{C}$), and PB is the phytoplankton biomass.

The currents were measured at the center of the control volume using an upward looking 1200 kHz acoustic Doppler current profiler (ADCP, RD Instruments) operating in mode 12 sampling at 1 Hz, with 7-cm bins and the first bin approximately 0.5 m above the sediment–water interface. The currents close to the bed were measured at 16 Hz using an array of three acoustic Doppler velocimeters (ADVs, Nortek AS) sampling at heights of 0.15, 0.3, and 0.45 m above the bed.

Vertical temperature structure at the center of the control volume was measured by an array of thermistors (SBE39, Seabird Electronics) positioned every 0.5 m and sampling at 2-min intervals. Conductivity was measured at

Table 1. Relationships used to estimate pumping rates (PR) for active filter-feeding species present at the Suisun Slough site. Here W is the tissue ash-free dry weight (g), T is the water temperature ($^{\circ}\text{C}$), and L is the length (mm).

Clam species	PR (L d^{-1})	L to W relationship	Source
<i>M. petalum</i>	0.1–0.4 ind^{-1}		Hummel (1985)
<i>C. amurensis</i>	180 W ($5 < T < 10$) 270 W ($10 < T < 15$) 400 W ($T > 15$)	$\ln W =$ 2.81 $\ln L +$ 4.81	Cole et al. (1992)
<i>C. alienense</i> *	1.9–2.2 ind^{-1}		Riisgard (2007)
<i>Laonome</i> sp.†	1.7 ind^{-1}		Dales (1957)

* Based on PR relationship for *C. volutator*.

† Based on PR relationship for *S. pavinina*.

two heights (0.3 and 0.9 m above the bed) (SBE16+, Seabird Electronics). A wind station (Model 05103, RM Young) was mounted above the houseboat, 4.7 m above the water, to provide 10-min-averaged wind speed and direction data.

At the conclusion of the experiment, the benthos in the control volume (33 samples) and the areas surrounding (eight samples) were systematically sampled using a 0.05 m^2 van Veen grab to gauge spatial variability in community composition. The grab was fabricated by the U.S. Geological Survey, is weighted, and has a measured penetration depth of approximately 10 cm. Samples were sieved through a 0.5-mm screen, preserved in 10% buffered formalin for no more than a week, transferred to 70% ethyl alcohol for storage, and stained with Rose Bengal before sorting. All organisms were removed, identified, and counted. Benthic grazing was estimated from published pumping rates for the various suspension-feeding organisms according to the equations presented in Table 1.

Results

Physical conditions—Grazing experiment 1 experienced maximum flood and ebb velocities of 0.5 m s^{-1} (Fig. 4). During experiment 2, 12 d later, the maximum currents were slightly smaller (Fig. 5). A weak secondary circulation was present, presumably due to slight channel curvature (Figs. 4B and 5B). During both flood and ebb tides, the surface water tended to flow toward the west bank while the bottom water flowed toward the east. During the long ebb tides, the entire water column had a positive cross-stream velocity, accompanied by maximum streamwise Reynolds stresses. The drag coefficient was estimated to be $C_d = 1.1 \times 10^{-3}$.

Wind speeds ranged from 0 to 6 m s^{-1} during both of the grazing experiments and followed a diurnal pattern, with maximum wind speeds in the afternoon and minimum wind speeds around 05:00 h. Winds emanated from directions ranging from west-southwest to west.

Over the duration of grazing experiment 1, the salinity ranged from 6.9 to 7.6 and the water temperature ranged from 21 $^{\circ}\text{C}$ to 22.5 $^{\circ}\text{C}$. Salinity was on average slightly higher in experiment 2, ranging from 7.4 to 8.3, and water temperatures were on average slightly cooler, ranging from 18 $^{\circ}\text{C}$ to 19.5 $^{\circ}\text{C}$. Short-lived periods (typically less than 1 h) of stratification occurred around slack tide, when current speeds were slow. Salinity stratification occurred after low–low water and temperature stratification occurred at the end of the daytime ebb tide. Stratification was accompanied by increases in vertical shear, particularly in the cross-channel direction (not shown).

Biological conditions—The midwater column concentration of Chl *a* ranged from 4 to 10 $\mu\text{g L}^{-1}$ at the CV site during experiment 1. During the second experiment, 12 d later, the Chl *a* concentrations had decreased significantly and ranged from 2 to 5 $\mu\text{g L}^{-1}$. Large and rapid changes in Chl *a* concentration were observed at the CV site during both experiments, likely due to the advection of higher concentration water masses past the CV site. During the first experiment, 70% of the phytoplankton biomass was distributed roughly equally among seven different species (Table 2). Diatoms were the dominant taxa, comprising 60% of the biomass, followed by cryptophytes (21%). During experiment 2, diatoms accounted for 82% of the phytoplankton biomass, dominated by *Guinardia delicatula* (40% of total biomass).

The zooplankton community was similar during both experiments and was dominated by the introduced copepod, *Oithona davisae* (Ferrari and Orsi 1984) (Table 3). *O. davisae* consumes flagellates (both autotrophic and heterotrophic) but does not consume diatoms (Uchima 1988). *Acartiella sinensi*, an introduced grazing calanoid copepod, contributed over 70% of the zooplankton herbivorous grazing. Benthic herbivorous Harpacticoid copepods were the only other significant contributors to phytoplankton grazing. The average estimated grazing rate for the herbivorous zooplankton community was 540 $\mu\text{g C m}^{-3} \text{d}^{-1}$ or $1.7 \times 10^{-2} \mu\text{g Chl } a \text{ L}^{-1} \text{d}^{-1}$ for experiment 1 and 210 $\mu\text{g C m}^{-3} \text{d}^{-1}$ or $6.3 \times 10^{-3} \mu\text{g Chl } a \text{ L}^{-1} \text{d}^{-1}$ for experiment 2, assuming a phytoplankton C:Chl *a* ratio of 32 (Cloern et al. 1995).

The dominant filter feeders at the Suisun Slough site were the two species of clams (*C. amurensis* and *Macoma petalum*), a tube-forming amphipod (*Corophium alienense*), and, to a lesser extent, a tube dwelling Sabellid polychaete (*Laonome* sp.) (Table 4). The pumping rates of the *C. amurensis* and *M. petalum* populations were calculated to be $< 1 \text{ m}^3 \text{ m}^{-2} \text{d}^{-1}$ using published pumping rates obtained from laboratory experiments (Table 1). *C. alienense* is an introduced benthic amphipod that creates a current in its U-shaped tube by metachronal beating of the pleopods. Although there is no available literature for *C. alienense* feeding rates, the feeding behavior and rate of the congener *Corophium volutator* has been estimated to be 78–93 mL h^{-1} for individuals of comparable size to the *C. alienense* seen in this study (≈ 6 mm in rostrum to telson length) (Riisgard 2007). Given that the average abundance

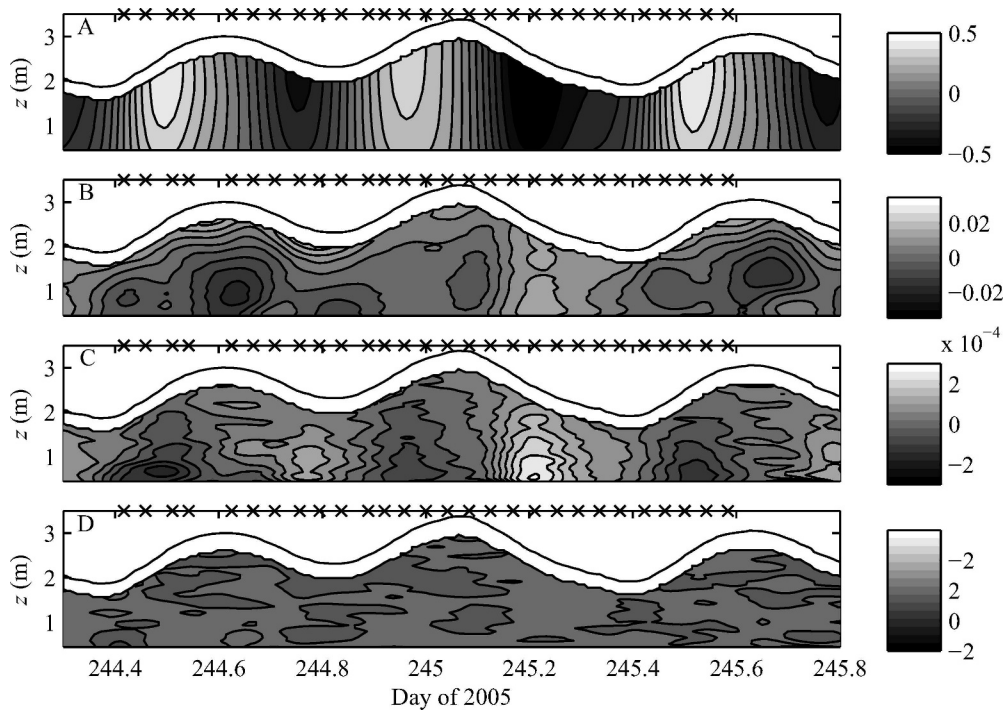


Fig. 4. Time series of (A) streamwise currents (m s^{-1}), (B) cross-stream currents (m s^{-1}), (C) $u'w'$ ($\text{m}^2 \text{s}^{-2}$), and (D) $v'w'$ ($\text{m}^2 \text{s}^{-2}$), for the duration of the first grazing experiment. The crosses mark the times when vertical profiles of chlorophyll *a* were measured.

of *C. alienense* at the site was $3800 \pm 800 \text{ ind m}^{-2}$ (95% confidence interval) and assuming that *C. alienense* and *C. volutator* have similar pumping rates, the maximum pumping rate for *C. alienense* would be $9 \pm 2 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$

(95% confidence interval). The *Laonome* sp. was not identified to the species level; however, it is assumed to process particles with a ciliary pump on the crown as described for other Sabellids (Fauchald and Jumars 1979).

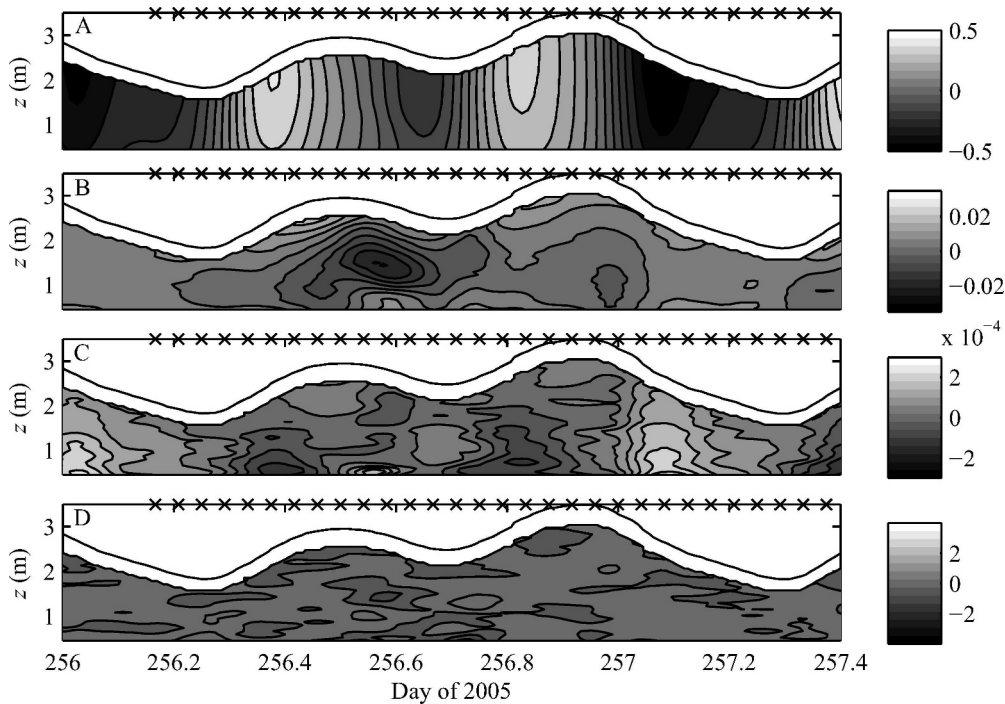


Fig. 5. Time series of (A) streamwise currents (m s^{-1}), (B) cross-stream currents (m s^{-1}), (C) $u'w'$ ($\text{m}^2 \text{s}^{-2}$), and (D) $v'w'$ ($\text{m}^2 \text{s}^{-2}$), for the duration of the second grazing experiment. The crosses mark the times when vertical profiles of chlorophyll *a* were measured.

Table 2. Mean phytoplankton community composition and percentage biovolume by species and by taxonomic division for experiments 1 and 2 in Suisun Slough.

%	Division	Genus species	%	Division
Experiment 1 by species			Experiment 1 by taxonomic division	
11	Bacillariophyta	<i>Cyclotella striata</i>	60	Bacillariophyta
10	Bacillariophyta	<i>Entomoneis paludosa</i>	21	Cryptophyta
10	Bacillariophyta	<i>Guinardia delicatula</i>	10	Eustigmatophyta
10	Eustigmatophyta	<i>Nannochloropsis</i> sp.	8	Euglenophyta
9	Cryptophyta	<i>Rhodomonas marina</i>	1	Cyanophyta
9	Bacillariophyta	<i>Cerataulina pelagica</i>		
8	Bacillariophyta	<i>Thalassiosira hendeyi</i>		
7	Cryptophyta	<i>Hemiselmis virescens</i>		
5	Bacillariophyta	<i>Gyrosigma macrum</i>		
4	Cryptophyta	<i>Teleaulax amphioxeia</i>		
4	Euglenophyta	<i>Eutreptiella braarudii</i>		
3	Euglenophyta	<i>Eutreptiella gymnastica</i>		
3	Bacillariophyta	<i>Gyrosigma fasciola</i>		
2	Bacillariophyta	<i>Cyclotella</i> sp.		
1	Euglenophyta	<i>Eutreptiella eupharyngea</i>		
1	Bacillariophyta	<i>Thalassiosira</i> sp.		
1	Cyanophyta	<i>Aphanothece</i> sp.		
Experiment 2 by species			Experiment 2 by taxonomic division	
40	Bacillariophyta	<i>Guinardia delicatula</i>	82	Bacillariophyta
13	Bacillariophyta	<i>Leptocylindrus minimus</i>	8	Eustigmatophyta
11	Bacillariophyta	<i>Thalassiosira hendeyi</i>	7	Cryptophyta
10	Bacillariophyta	<i>Gyrosigma macrum</i>	1	Euglenophyta
8	Eustigmatophyta	<i>Nannochloropsis</i> sp.	1	Cyanophyta
4	Bacillariophyta	<i>Cyclotella striata</i>		
4	Cryptophyta	<i>Hemiselmis virescens</i>		
2	Cryptophyta	<i>Rhodomonas marina</i>		
2	Bacillariophyta	<i>Entomoneis paludosa</i>		
2	Bacillariophyta	<i>Chaetoceros subtilis</i>		
1	Cyanophyta	<i>Aphanothece</i> sp.		
1	Dinophyta	<i>Protopteridinium brevipes</i>		

Only species that make up more than 1% of total biovolume are listed.

The *Laonome* sp. in the San Francisco estuary was of similar size and morphology as *Sabella pavonina*, a species reported to have a filtering rate of $1.7 \text{ L d}^{-1} \text{ ind}^{-1}$ (Dales 1957). The mean abundance of *Laonome* sp. at the site was $400 \pm 100 \text{ ind m}^{-2}$; thus the pumping rate for the

population was $0.7 \pm 0.2 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$. The total pumping rate for all active suspension feeders was approximately $10 \pm 3 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$.

The other abundant species at the sampling location was the polychaete *Marenzelleria viridis* ($200 \pm 70 \text{ ind m}^{-2}$), a

Table 3. Zooplankton community composition shown as abundance and as percentage contribution of herbivorous grazing for Suisun Slough experiments 1 and 2.

Division	Experiment 1		Experiment 2	
	Abundance (ind m^{-3})	% contribution herbivorous grazing	Abundance (ind m^{-3})	% contribution herbivorous grazing
Copepods				
Nauplii N1–2	7741		8006	
Nauplii N3–6	2520	<1	4072	2.5
<i>Oithona davisae</i>	12,561	3	8649	17
<i>Acartiella sinensis</i>	261	78	109	72
<i>Tortanus dextrilobatus</i>	48		20	
<i>Harpacticoids</i> sp.	69	18.5	12	6.5
Rotifers				
<i>Brachionus</i> sp.	0		10	1.5
Unidentified	6	<1	3	<1
<i>Notholca</i> sp.	0		5	<1
Other				
<i>Barnacle nauplii</i>	39		54	

Table 4. Abundance of persistent benthic invertebrates species (≥ 1 ind grab⁻¹) based on the average of 41 grab samples in and around the CV site, 95% confidence intervals are shown. Feeding group for each species shown with literature reference for trophic assignments. Estimated pumping rates are shown for active suspension feeders with 95% confidence intervals.

Taxa	Ind m ⁻²	Feeding group	Sediment habitat	Pumping rate (m ³ m ⁻² d ⁻¹)
Annelida				
Oligochaeta				
Tubificidae	3100±200	Deep deposit feeder*	Deep errant burrows*	
Polychaeta				
Neriedae				
<i>Neanthes limnicola</i>	30±10	Deposit feeder†	Mucus tubes‡	
Spionidae				
<i>M. viridis</i>	200±70	Passive suspension and deposit feeder§	Mucus and sediment tubes‡	
Sabellidae				
<i>Laonome</i> sp.	400±100	Active suspension feeder†	Mucus tubes‡	0.7±0.2
Arthropoda				
Crustacea				
Cumacea				
<i>Nippoleucon hinumensis</i>	20±5	Deposit feeder	Free living at surface	
Amphipoda				
<i>C. alienense</i>	3800±800	Active suspension and deposit feeder¶	Mucus tubes#	9±2
<i>G. daiberi</i>	50±10	Scraper, partly pelagic**	Free living at surface††	
Mollusca				
Bivalvia				
<i>C. amurensis</i>	440±150	Active suspension feeder‡‡	Shallow burrows§§	0.6±0.1
<i>M. petalum</i>	23±7	Active suspension and deposit feeder	Deep burrows	0.009±0.003

* Brinkhurst and Gelder (2001).

† Fauchald and Jumars (1979).

‡ Rouse and Pleijel (2001).

§ Daunys et al. (1999).

|| Barnes (1980).

¶ Moller and Riisgard (2006).

Meadows et al. (1990).

** A. R. Stewart (U.S. Geological Survey, pers. comm. based on stable isotopes).

†† Bousfield (1969).

‡‡ Penry (2000).

§§ Carlton et al. (1990).

||| Hummel (1985).

tube dwelling Spionid that either passively filter feeds or surface deposit feeds, depending on food availability (Daunys et al. 1999). Other members of the benthic community were either too sparse (≤ 1 ind sample⁻¹) or were deposit feeders unlikely to feed on either suspended or recently settled phytoplankton (e.g., oligochaetes, *Gammarus daiberi*) (Table 4).

The formation of concentration boundary layers—The time series of vertical profiles of Chl *a* concentration for experiments 1 and 2 exhibit a depletion of Chl *a* adjacent to the bed for a range of different surface Chl *a* concentrations (Fig. 6). Individual profiles were normalized by the depth-averaged concentration and averaged over the four sampling locations and all sampling times for each experiment to produce nondimensionalized Chl *a* concentration profiles (Fig. 7). Error bars indicate two standard deviations from the average normalized concentration. The ensemble-averaged normalized profile for experiment 1 indicates that on average there was a considerable depletion of Chl *a* toward the bed. The sample closest to the bed was on average 13% lower than the depth-averaged concentra-

tion and 22% lower than the near surface concentration. The ensemble-averaged profile from experiment 1 was well described by the theoretical logarithmic CBL profile (Eq. 9). The ensemble-averaged vertical profile for experiment 2 also showed depletion of Chl *a* toward the bed; however, the profile did not decrease monotonically toward the bed. On average the sample closest to the bed was 5% lower than the depth-averaged concentration and 12% lower than the near surface concentration.

Concentration boundary layers persisted under a variety of physical conditions including ebb (e.g., Fig. 8A) and flood (e.g., Fig. 8B) tides and periods of stratification (e.g., Fig. 8C). During some sampling periods, the vertical Chl *a* distribution was very similar at all four sampling locations (Fig. 8A). However, at other times, the concentration profile was different at each location (Fig. 8B). This difference was most likely due to cross-channel variability in Chl *a* concentrations. During many sampling periods in both experiments, the resultant profiles displayed a strong cross-channel gradient, with higher concentrations at the eastward sampling locations that were closer to the deepest part of the channel.

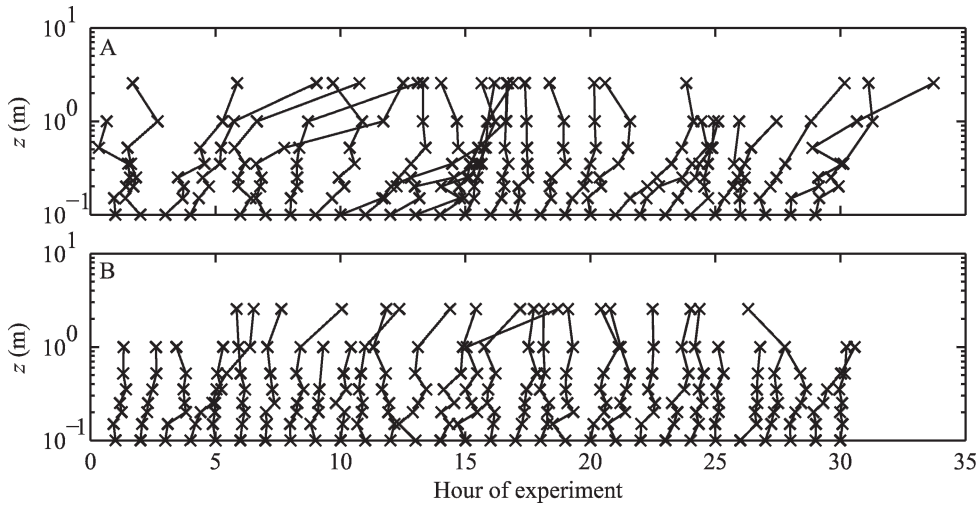


Fig. 6. Time series of four averaged vertical profiles of chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) (“waterfall plot”) for (A) experiment 1 (B) experiment 2. Concentrations are relative to the near-bed concentration.

When the water column stratified, the surface and near-bed Chl *a* concentrations became distinctly different (Fig. 8C), with subsurface concentrations being much lower than at the surface (a difference of roughly $2.5 \mu\text{g L}^{-1}$). The temperature profile indicates that the higher concentrations persisted in the surface water due to incomplete mixing of the surface water.

Equation 9 was an appropriate model for the CBLs formed during these experiments (e.g., Fig. 9). Least-squares fitting of Eq. 9 with the measured Chl *a* concentration profiles revealed that C_B ranged from 2.6 to $7.2 \mu\text{g L}^{-1}$ with a mean value of $4.4 \mu\text{g L}^{-1}$ during experiment 1 (mean error $0.1 \mu\text{g L}^{-1}$). C_B was considerably lower during experiment 2, ranging from 0.77 to $3.2 \mu\text{g L}^{-1}$ with a mean value of $2.1 \mu\text{g L}^{-1}$ (mean error $0.3 \mu\text{g L}^{-1}$). The time series of the gradient of the CBL d (Eq. 9); the estimated grazing rate α ; and the corresponding bed shear velocity, surface Chl *a* concentration, and the normalized Richardson number are shown in Fig. 10 (experiment 1)

and Fig. 11 (experiment 2). The Richardson number, an index of stratification, is defined as $\text{Ri} = (g\Delta\rho\Delta z) / [\rho_m(\Delta u)^2]$, where g is gravity, ρ_m is the reference density, Δu is the velocity shear, and $\Delta\rho$ the change in density over a layer of thickness Δz . We defined the critical Richardson number $\text{Ri}_c = 0.25$ such that $\log_{10} (\text{Ri}/\text{Ri}_c) > 0$ indicates stable stratification (Lewis 1997). During both of the experiments, d exhibited little spatial variability within the sampling region. However, on many occasions only one of the four profiles was identified as a CBL. In experiment 1, a CBL was identified for at least one of the four sampling locations during 26 out of the 28 sampling periods. In experiment 2, a CBL was identified for 23 of the 30 sampling periods. During experiment 1, CBLs were absent during periods corresponding to low bed shear velocity (Fig. 10). This pattern was less consistent in experiment 2, where no CBLs were measured for a 4-h period (Fig. 11). However, three of these seven samples corresponded with extremely low Chl *a* concentrations.

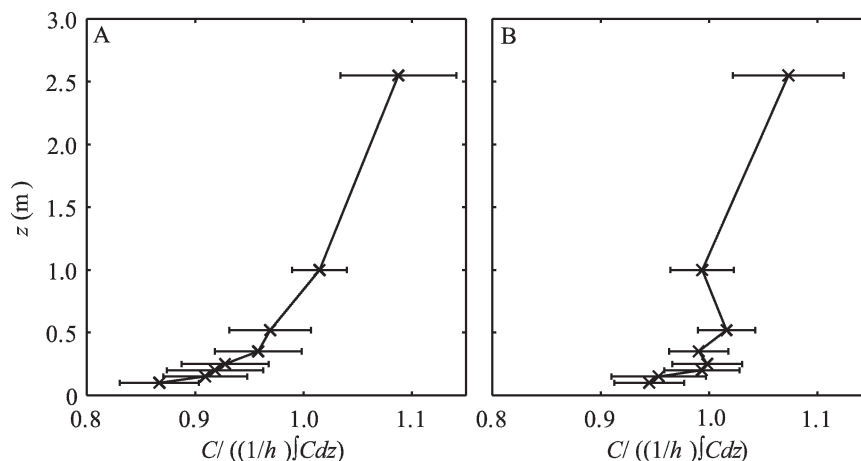


Fig. 7. Ensemble-averaged dimensionless profiles for (A) experiment 1 and (B) experiment 2. The nondimensionalization involves dividing the local value of the concentration by the depth-averaged concentration for that profile.

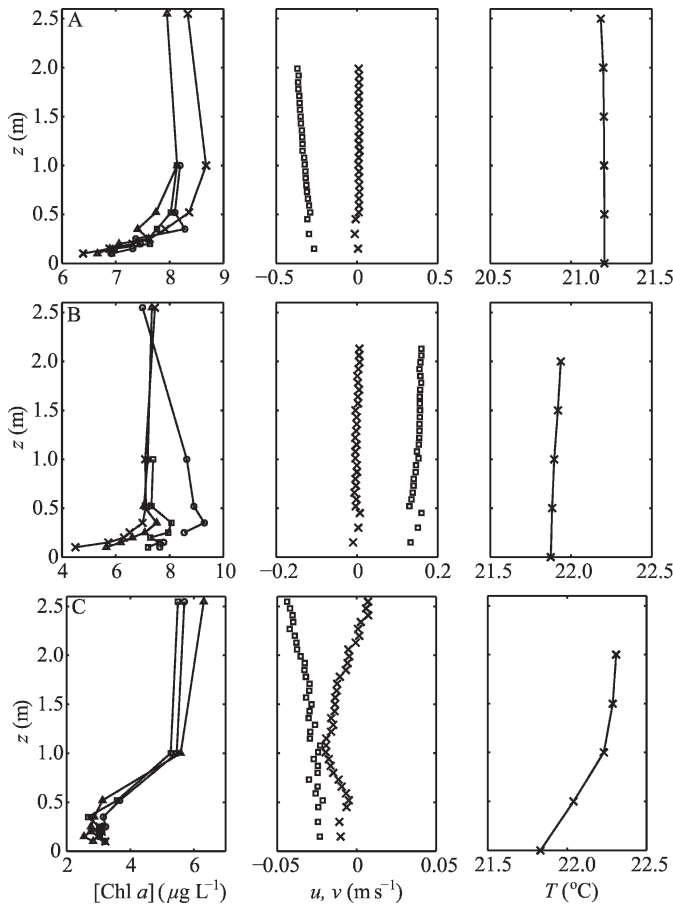


Fig. 8. Examples of corresponding chlorophyll *a*, velocity, and temperature profiles for Suisun Slough (A) experiment 1, sample 20, (B) experiment 1, sample 11, and (C) experiment 1, sample 6. Chlorophyll *a* concentration is shown for the four sample sites: northeast (cross), northwest (square), southeast (triangle), and southwest (circle), and *u* and *v* are the streamwise (square) and cross-stream (cross) velocities, respectively.

Rate of phytoplankton removal by the benthos—The benthic grazing rate α calculated using Eq. 11 (Figs. 10B and 11B) exhibited significant variation both in time and between the four sampling frames. We can see from Eq. 11 that in order for the grazing rate to be positively correlated with u_{*b} , C_B/d has to be constant over the measured range of u_{*b} . C_B/d showed no clear trend over the range of u_{*b} measured (Fig. 12), indicating that the grazing rate of the benthic organisms was approximately a linear function of the bed shear velocity. Although the error in C_B/d was often large, no systematic difference was seen between the four water sampling frames or between the two experiments. The grazing rate can therefore be modeled by

$$\alpha = Gu_{*b} \quad (13)$$

where $G = \kappa d/C_B$ was assumed to be a constant for this site. G was determined from a weighted mean of d/C_B , where the weight was determined by the magnitude of the confidence interval for each estimate of d/C_B .

Although efforts were made to distribute the weight of the water sampling frames to prevent the frames from

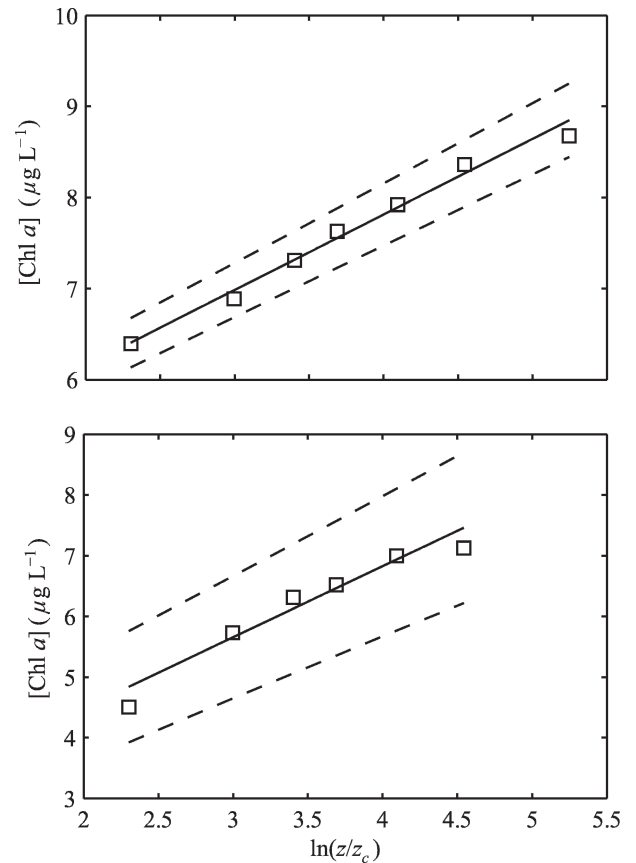


Fig. 9. Examples of least-squares fit of Eq. 9 (solid line) to measured CBLs (squares). (A) experiment 1, sample 10, northeast site ($r^2 = 0.98$); and (B) experiment 2, sample 11 ($r^2 = 0.95$). One standard deviation confidence intervals of the individual prediction are indicated by the dashed lines.

sinking into the fine sediment, it is likely that the actual heights of the water intake were offset by 0–10 cm (the height of the lowest intake). Because the ratio of C_B/d is sensitive to this offset, a range of values of G and α for different assumed vertical offsets are shown in Table 5. The difference between the average value of G for each of the experiments was small, despite the large changes in phytoplankton concentration between the two experiments.

Equation 11 assumes phytoplankton settling is negligible; significant settling would result in underestimation of the grazing rate. We estimate that phytoplankton settling velocities were on the order of 0.1 to 1 m d⁻¹ (Lannergren 1979; Bienfang 1981; Koseff et al. 1993) and were therefore negligible compared with the estimated magnitude of the vertical turbulent flux term and are thus not considered to be an important component in our estimates.

The benthic grazing rate was also estimated via the control volume method. We estimate that individual estimates of α have an error of approximately 20%. Robust linear least-squares regression of the estimated benthic grazing rate via the control volume method vs. the bed shear velocity reveals

$$\alpha_{CV} = (3.1 \times 10^{-2} \pm 1.2 \times 10^{-2})u_{*b} \quad (14)$$

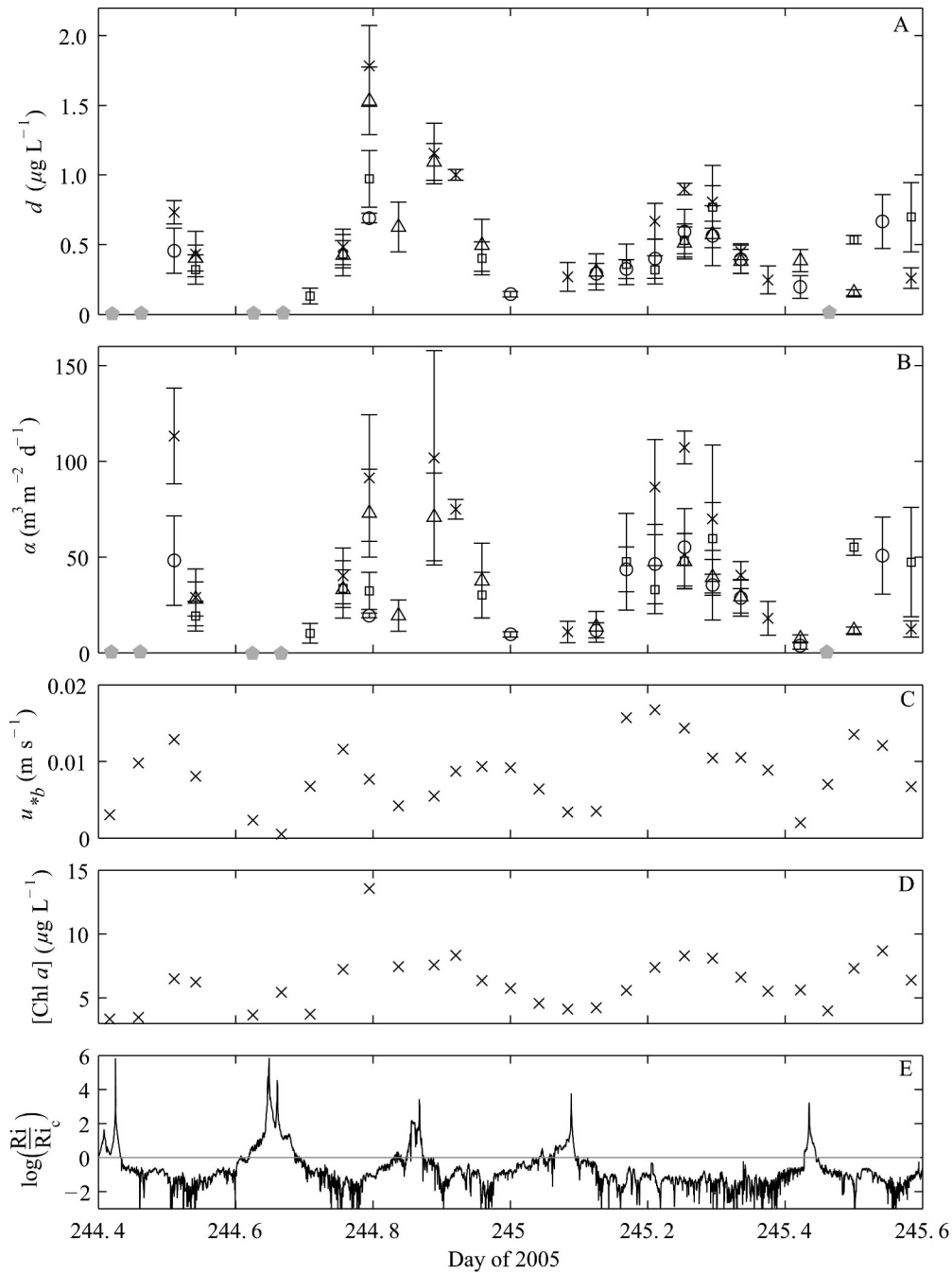


Fig. 10. Time series of (A) gradient of CBL d (average confidence interval $0.13 \mu\text{g L}^{-1}$), (B) grazing rate α (average confidence interval $15 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$), (C) bed shear velocity u_{*b} , (D) surface chlorophyll a concentration, and (E) $\log(\text{Ri}/0.25)$ at $z = 0.6 \text{ m}$, for experiment 1. northeast (cross), northwest (square), southeast (triangle), and southwest (circle) ($z_c = 0.5 \text{ cm}$ and frame offset = 5 cm). Assuming $\text{Ri} = 0.25$ is the critical Ri number, $\log(\text{Ri}/0.25) > 0$ indicates stable stratification. One standard deviation confidence intervals are shown for d and α .

where the uncertainty is at the 95% confidence level and $r^2 = 0.81$ (Fig. 13A). The coefficient compares well with G calculated via the vertical flux method (Table 5).

Zooplankton grazing estimated via Eq. 12 was negligible compared with the average measured net loss of Chl a in the control volume. For example, during experiment 1 the loss due to zooplankton grazing was $0.1 \mu\text{g Chl } a \text{ s}^{-1}$, whereas the average loss of Chl a in the control volume

throughout experiment 1 was $500 \mu\text{g Chl } a \text{ s}^{-1}$. It is therefore reasonable to assume that losses of Chl a cannot be attributed solely to zooplankton grazing.

Discussion

Mass-transfer limited flux of phytoplankton to the bed—
Two independent analysis methods for estimating the flux

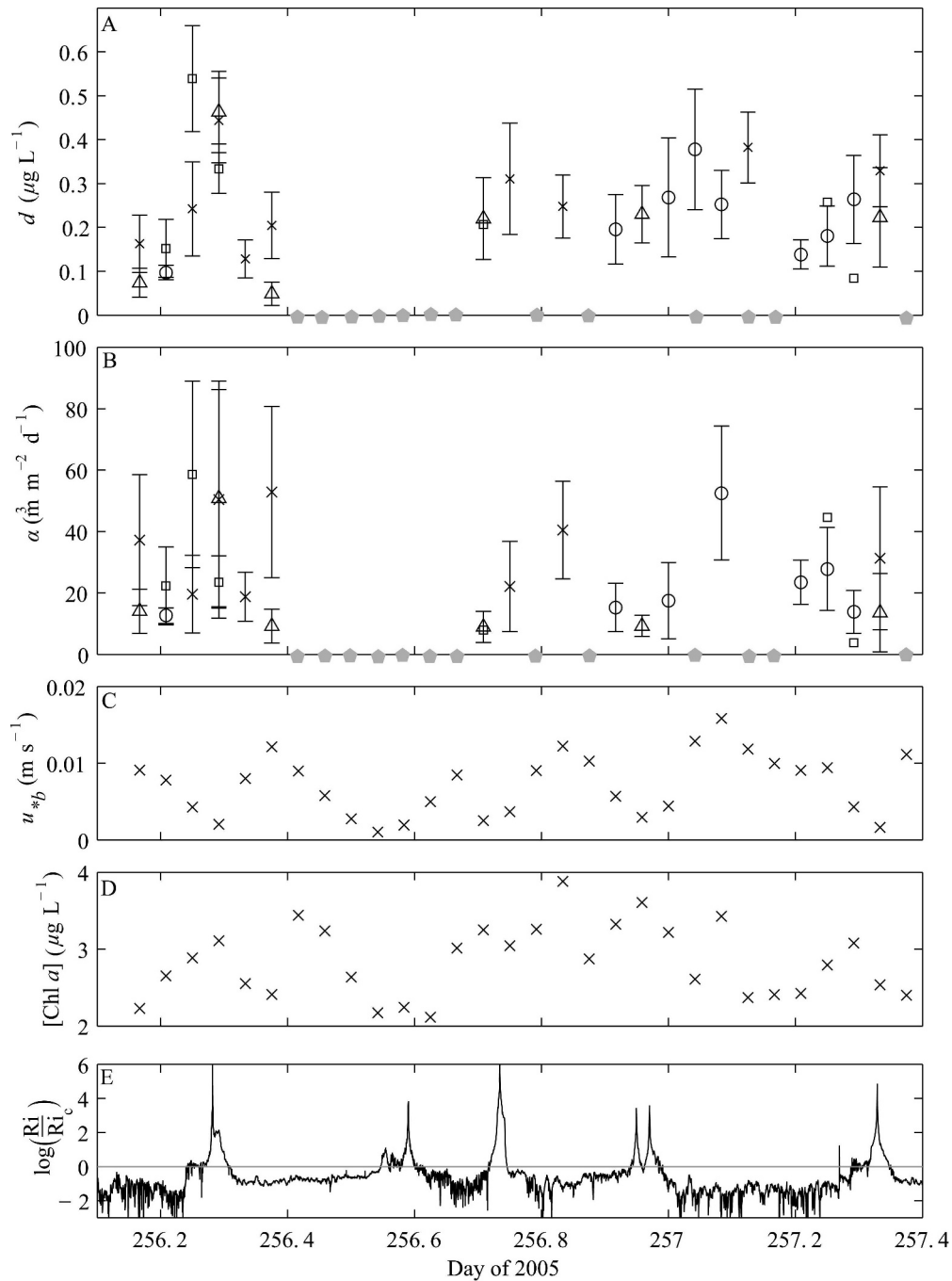


Fig. 11. Time series of (A) gradient of CBL d (average confidence interval $0.28 \mu\text{g L}^{-1}$), (B) grazing rate α (average confidence interval $18 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$), (C) bed shear velocity u_{*b} , (D) surface chlorophyll a concentration, and (E) $\log(\text{Ri}/0.25)$ at $z = 0.6 \text{ m}$, for experiment 2. northeast (cross), northwest (square), southeast (triangle), and southwest (circle) ($z_c = 0.5 \text{ cm}$ and frame offset = 5 cm). Assuming $\text{Ri} = 0.25$ is the critical Ri number, $\log(\text{Ri}/0.25) > 0$ indicates stable stratification. One standard deviation confidence intervals are shown for d and α .

of phytoplankton to the bed, the control volume method and the vertical flux method, were generally in good agreement and revealed significant losses of Chl a to the benthos. The benthic grazing rate was positively correlated with the bed shear velocity, which ranged from 2×10^{-3} to $1.8 \times 10^{-2} \text{ m s}^{-1}$, indicating that the loss of Chl a to the bed was mass-transfer limited. Benthic grazing rates, estimated by both the control volume method and the

vertical mass flux method, are shown in Fig. 13B as a function of the bed shear velocity. The lines of best fit approximate the data reasonably well, and the two methods resulted in a significantly similar slope.

Our third method of estimating benthic grazing rates, using measured abundance and biomass of the benthic community and laboratory-derived pumping rates, was five times smaller (10 m d^{-1}) than the maximum benthic

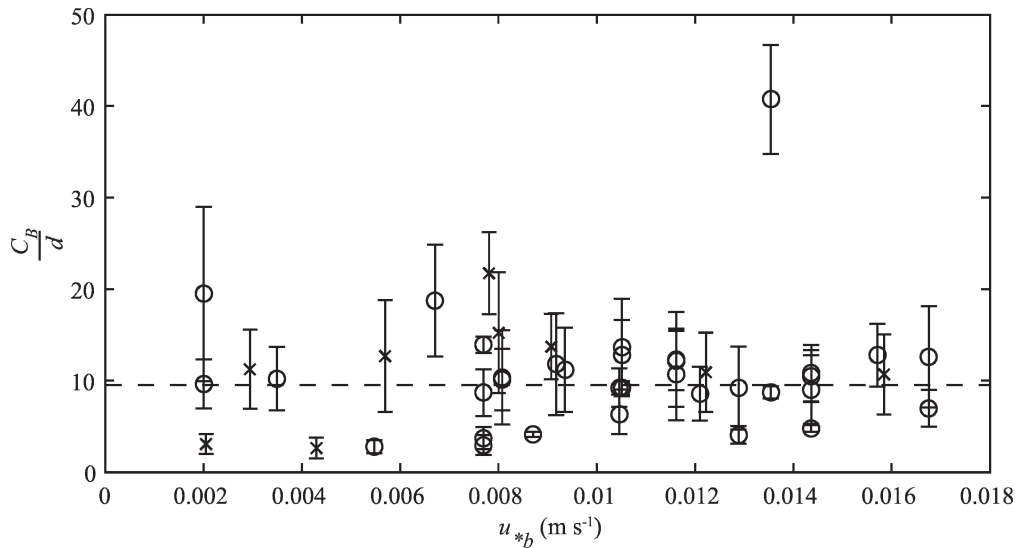


Fig. 12. Concentration at the bed normalized by the gradient of the CBL (C_B/d) vs. the bed shear velocity u_{*b} . Estimates of C_B and d were made assuming the frame had sunk 5 cm into the sediment and that $z_c = 0.5$ cm. Results from experiment 1 (circle), experiment 2 (crosses). The dashed lines indicates the mean value of $C_B/d = 9.5$.

grazing estimates from the field experiments ($\sim 50 \text{ m d}^{-1}$). Filtration (and phytoplankton ingestion) rates for benthic organisms are generally smaller than calculated pumping rates due to the formation of CBLs, the refiltration of water (O’Riordan et al. 1995), and the intermittency of pumping (Ortmann and Grieshaber 2003), so this finding was troubling. A similar discrepancy in the maximum estimated benthic grazing rates of Chl *a* measured via the vertical flux method ($\approx 60 \text{ m d}^{-1}$) and the pumping rates based on clam biomass (6 g m^{-2}) was observed by Thompson (1999) in South San Francisco Bay.

It is possible that the benthic community biomass was underestimated. However, according to the laboratory-derived pumping rates, the biomass of *C. amurensis* required to produce $\alpha = 6\text{--}50 \text{ m d}^{-1}$ is $15\text{--}125 \text{ g dry tissue weight m}^{-2}$. We estimated the dry tissue weight of *C. amurensis* at the site to be approximately 2 g m^{-2} and, due to the extensive sampling of the benthic community, it is unlikely that we undersampled *C. amurensis* by this much. Our van Veen grab is unlikely to undersample tube dwelling *C. alienense*, since their burrows are <10 cm deep. Surface dwelling *C. alienense* will avoid capture in the grab; however, if we assume that the proportion of surface dwelling (deposit feeding) *C. alienense* was the same during

the grab sampling as during the two experiments then the calculated pumping rate will reflect the tube dwelling (filter feeding) population. Furthermore, comparison with long-term records of benthic composition at a nearby site indicated our measured density was within the typical range measured in autumn (BDAT 2008).

Laboratory-derived pumping rates have a number of shortcomings that may account for the difference between the maximum benthic loss rate and community pumping rate (for a review see Riisgard 2001). Furthermore, measurements of pumping rates have not been made for the species of *Corophium* and *Laonome* sampled here. Therefore pumping rates had to be estimated using pumping rate relationships for similar organisms. Macrobenthos have also been found to display a large range of pumping rates, for example, Riisgard (2007) found pumping rates for *C. volutator* ranged from 18.3 to $93 \text{ mL h}^{-1} \text{ ind}^{-1}$. Some of this variability has been attributed to the organisms’ size, the temperature, and the food concentration; however, variability in pumping rate is not well understood. The population pumping rates shown in Table 4 are estimates of their maximum pumping rates based on the available literature. Further measurements and understanding of pumping rates are required to

Table 5. Mean values of the ratio $G = 0.41d/C_B$ for each of the experiments and the collective average. The corresponding range of α values (calculated from average G for both experiments) for the range of bed shear stress $u_{*b} = 0.002\text{--}0.018 \text{ m s}^{-1}$. We have presented 95% confidence intervals for estimates.

Assumptions	Average $G=0.41d/C_B$			$\alpha \text{ (m d}^{-1}\text{)}$
	Experiment 1	Experiment 2	Both	
Frame sunk 0 cm, $z_c=0.5$ cm	$5.7 \times 10^{-2} \pm 1.8 \times 10^{-2}$	$4.1 \times 10^{-2} \pm 1.5 \times 10^{-2}$	$5.0 \times 10^{-2} \pm 1.7 \times 10^{-2}$	8.6–78
Frame sunk 5 cm, $z_c=0.5$ cm	$3.8 \times 10^{-2} \pm 1.2 \times 10^{-2}$	$3.1 \times 10^{-2} \pm 1.0 \times 10^{-2}$	$3.5 \times 10^{-2} \pm 1.1 \times 10^{-2}$	6.0–54
Frame sunk 9 cm, $z_c=0.5$ cm	$2.1 \times 10^{-2} \pm 0.6 \times 10^{-2}$	$2.0 \times 10^{-2} \pm 0.7 \times 10^{-2}$	$2.0 \times 10^{-2} \pm 0.6 \times 10^{-2}$	3.4–31

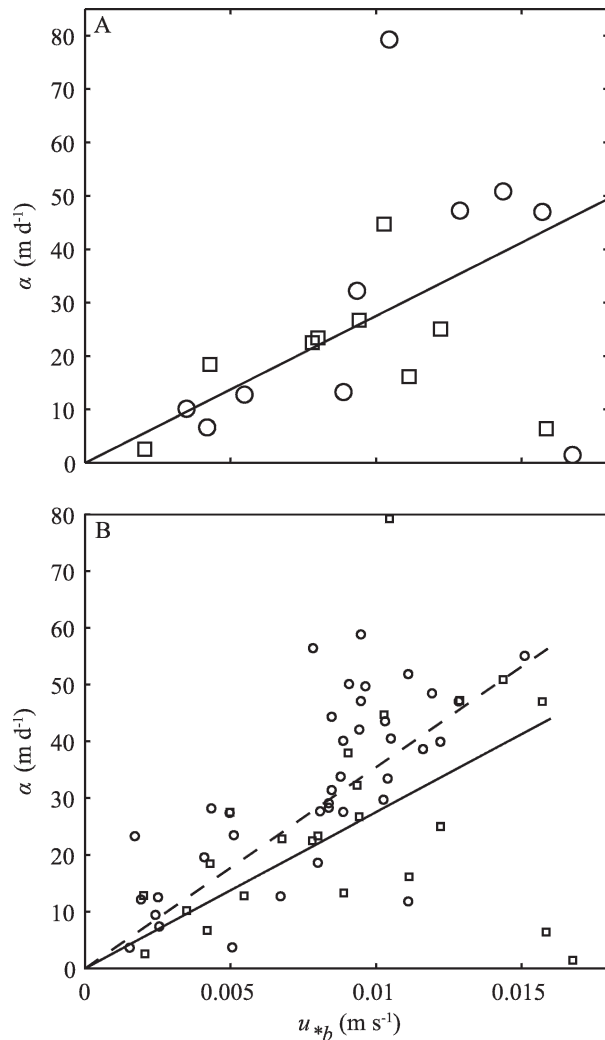


Fig. 13. (A) Benthic grazing rate α calculated via the control volume method vs. the bed shear velocity u_{*b} . The best fit robust linear regression is shown. Results from experiment 1 (circles), experiment 2 (squares). (B) Benthic grazing rate α calculated via the control volume method (squares) and vertical flux method (circles) vs. the bed shear velocity u_{*b} . The best fit robust linear regression is shown for each method; control volume method (solid line) and vertical flux method (dashed line).

quantify the contribution of benthic grazing to the measured benthic loss. We consider two alternate mechanisms that could result in the measured mass-transfer limited flux of phytoplankton to the bed: turbulent deposition and near-bed aggregation, below.

Alternatives to benthic grazing—An alternative mechanism that may account for the measured loss of Chl *a* at the bed involves the turbulent deposition of the phytoplankton cells to the sediment. Turbulent deposition describes the transport of particles by vertical mixing to a solid boundary as opposed to settling, which occurs by gravity. Studies of sediment transport (Kaftori et al. 1995) and atmospheric aerosol deposition (Brooke et al. 1992) have shown that particle deposition is enhanced in turbulent flow. The

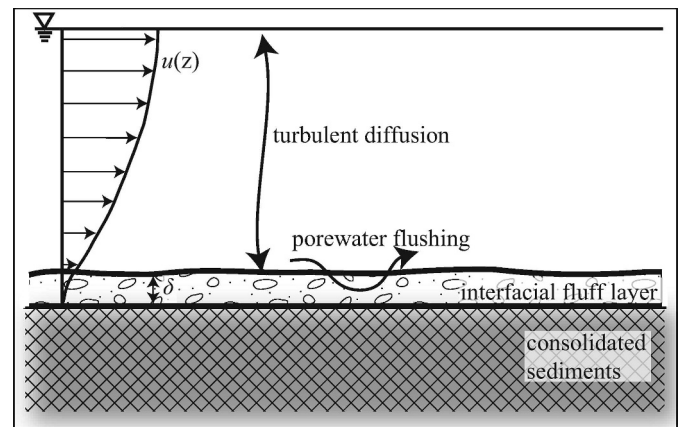


Fig. 14. Schematic of aggregation of pelagic phytoplankton in a near-bed fluff layer (adapted from Stolzenbach et al. 1992).

transfer coefficient or deposition velocity V is a loss term like the benthic grazing rate α in the mass balance equation, but it is defined as the particle mass-transfer rate divided by the bulk concentration of the particles.

The deposition of particles from a turbulent fluid to a solid boundary can follow one of three regimes depending on the particle size and density, as well as the fluid density and viscosity (Wood 1981). The theory estimates that for an average diatom cell of $40 \mu\text{m}$ the deposition velocity is $V = 3 \times 10^{-7}u_{*b}$, the coefficient is five orders of magnitude smaller than the measured constant of proportionality G (Eq. 14 and Table 5). Clay particles and diatom cells may aggregate to form flocs of diameter $100\text{--}500 \mu\text{m}$ (Kranck and Milligan 1992). Assuming a floc size of $250 \mu\text{m}$ results in $V = 1 \times 10^{-6}u_{*b}$; the coefficient is four orders of magnitude smaller than the measured constant of proportionality G (Eq. 14 and Table 5). Therefore, we conclude that turbulent deposition of either individual diatom cells or aggregates containing diatoms contributed minimally to losses of phytoplankton at the bed.

Alternatively, the larger than anticipated estimates of phytoplankton loss at the bed may be explained by the aggregation of phytoplankton in a near-bed “fluff” layer (Stolzenbach et al. 1992). A fluff layer is characterized by loosely aggregated material of high porosity (Fig. 14). The fluff layer is hydrodynamically active, and therefore particle transport into this layer is not limited by transport across a laminar sublayer. A fluff layer is likely to exist at the Suisun Slough site because of the high clay content of the sediment and proximity of the slough to multiple particle sources of biological origin (marsh sediment and plants, bay sediment, freshwater and estuarine water sources). Particle aggregation would be enhanced in the fluff layer because of both the large number of particles and the large shear stresses, resulting in an increased collision frequency of particles (Jahmlich et al. 2002; Colomer et al. 2005). For this reason, the positive correlation found between the estimated rate of phytoplankton removal by the benthos α and the bed shear velocity supports the near-bed aggregation mechanism. Furthermore, aggregation has been shown to be enhanced by the presence of biological material such as transparent exopolymer particles (Sanford

Table 6. Estimated biomass P:B (g m^{-2}), secondary production P ($\text{g C m}^{-2} \text{yr}^{-1}$), and carbon (C) consumed ($\text{g C m}^{-2} \text{yr}^{-1}$) by each invertebrate group assuming a 10% trophic efficiency for all groups except *C. amurensis* which is shown with a 10% and 25% trophic efficiency. Dry weight was measured for the bivalves and estimated from wet weight for the remaining groups.

Species or species group	Wet wt.	Dry		P:B	P	C consumed
		wt.	C wt.			
<i>C. amurensis</i>	—	1.8	0.7*	2†	1.4	6–14
<i>M. petalum</i>	—	1.4	0.6*	1.5‡	0.8	8
<i>C. alienense</i>	6	0.9§	0.3§	10	3	30
Polychaeta + Oligochaeta**	6	0.8§	0.3¶	2#	0.6	6
Community total		5	2		6	50–60

* Cloern et al. (1993).

† Thompson unpubl.

‡ Robertson (1979).

§ Lie (1968).

|| Cunha et al. (2000).

¶ Rowe (1983) (conversion factor of 0.375).

Schwinghamer et al. (1986).

** Oligochaeta <10% of weight.

et al. 2001; Jahmlich et al. 2002). Suspension-feeding benthic animals produce feces and pseudofeces as well as an extracellular mucus-like material (Davies and Hawkins 1998; Murray et al. 2002). Tube dwelling polychaetes and amphipods also produce extracellular polymeric material for structural support (Meadows et al. 1990; Murray et al. 2002). The pseudofeces and mucus produced by the benthic community can rapidly bind particles such as sediment and phytoplankton (Meadows et al. 1990).

If aggregation of phytoplankton was occurring in a near-bed fluff layer, it is likely that phytoplankton would then be incorporated into the consolidated sediment. In this experiment the lowest water sample was taken at approximately 10 cm above the bed, higher than the extent of a typical fluff layer; however, Thompson's (1999) near-bed measurements showed a local increase in Chl *a* concentration a few centimeters above the bed, lending support to this hypothesis.

Comparing the carbon needed to support the benthic community with the carbon produced by the phytoplankton in this system identified the near-bed aggregation mechanism as a plausible explanation for the high flux of phytoplankton to the bed. Several studies have concluded that a high percentage of the carbon that is used by the metazoans in this estuary is derived from bay- or river-produced phytoplankton (Jassby et al. 2002; Sobczak et al. 2002). Over 90% of the bioavailable particulate organic matter has been shown to be phytoplankton based in Suisun Slough (Sobczak et al. 2005), and so it is phytoplankton primary production in the marsh that is likely to be most critical to the benthic feeders in our experimental area. As seen in Suisun Bay, the phytoplankton biomass greatly declined following the introduction of *C. amurensis* in 1986 (Alpine and Cloern 1992). The phytoplankton biomass seasonal cycle (peak in spring), maximum biomass ($<10 \mu\text{g L}^{-1}$ Chl *a*), and average

biomass for the rest of the year ($2\text{--}3 \mu\text{g L}^{-1}$ Chl *a*) are now similar in the marsh, sloughs, and channels of Suisun Marsh and Suisun Bay (R.L. Brown unpubl.). We therefore feel comfortable using estimates of gross primary production made for Suisun Bay $\leq 50 \text{g C m}^{-2} \text{yr}^{-1}$ (Alpine and Cloern 1992; Jassby 2006) in this comparison. We have estimated secondary production in this benthic community using published production:biomass (P:B) values for other temperate estuaries where these values are available. If there were no appropriate estimates in similar systems we used "universal" P:B values calculated by Schwinghamer et al. (1986). Trophic efficiency of the benthic invertebrates in the Suisun Slough community (Table 6) was assumed to be 10% except for *C. amurensis*, which, due to recent estimates of 25% trophic efficiency for a similarly opportunistic bivalve *Corbicula fluminea* (McMahon 1999), was estimated for both 10% and 25% efficiency. A comparison of carbon produced by phytoplankton in this system ($\sim 50 \text{g C m}^{-2} \text{yr}^{-1}$) and that consumed by a combination of the surface deposit and suspension-feeding members of the benthic community ($\sim 50\text{--}60 \text{g C m}^{-2} \text{yr}^{-1}$) shows them to be remarkably similar (Table 6). This comparison can be used as support for the hypothesis that the phytoplankton are an important food source for the passive suspension feeders and surface deposit feeders, but it does not exclude the importance of other sources of food to these infauna. One other possible source of food, benthic microalgae, are unlikely to be a large source of carbon for the infauna since the light attenuation is rapid in this turbid estuary, so benthic microalgae are likely limited to the intertidal and shallow subtidal reaches of the system. Jassby et al. (1993) estimated that benthic microalgae represented <10% of the biologically available carbon in the northern estuary.

Further measurements in the near-bed region are required to investigate the importance of the near-bed aggregation mechanism as a means of accelerating the transfer of pelagic carbon sources to the passive suspension and deposit feeders in the benthic community. Such a transport and near-bed retention mechanism may reduce the delivery time for the pelagic carbon to the deposit feeders in shallow, turbulent systems such as San Francisco estuary. These near-bed biophysical processes may be capable of limiting pelagic phytoplankton biomass and primary production in a manner similar to that seen with filter-feeding organisms.

Evaluation of methodology—Although the two methods of analysis that were applied to estimate the flux of phytoplankton to the benthos generally showed good agreement, some differences in reliability were noted. The vertical flux method often failed close to slack tide when the vertical mixing was minimal, while the control volume method was adversely affected by spatial patchiness in Chl *a* concentration.

CBLs were not always found at each of the four sampling locations, and a CBL was not identified at any of the four sampling locations for 9 of the 58 sampling periods. Local, short-lived turbulent mixing events as well as small-scale patchiness of Chl *a* will lead to instantaneous

variations in the local Chl *a* concentration. The 10-min sampling period was chosen as a compromise between allowing sufficient time for the turbulence to “see” the entire water column while ensuring the physical parameters did not change significantly. To guarantee that vertical profiles of Chl *a* concentration were not influenced by short period mixing events, the sampling period should be greater than $h/0.3u_{*b}$ (Fischer et al. 1979). This was not achieved close to slack tides when the bed shear velocity was small and may account for the absence of measured CBLs coinciding with low bed shear velocities. The absence of a CBL has previously been attributed to behavioral adaptations of the benthic organisms in response to increased suspended sediment load or the presence of predators. However, the variability in the identification of a CBL at the four sampling sites indicates that phytoplankton patchiness and sampling error may, without invoking the possible variability in animal behavior, account for the absence of identified CBLs at all four sampling sites on occasion.

Positive fluxes of Chl *a* were calculated via the control volume method for 18 of the sampling periods for which CBLs were identified, indicating failure of the control volume method at these times. The control volume method is susceptible to error under spatially patchy conditions. For example, gradients in Chl *a* in the cross-stream direction may lead to false estimates of net positive fluxes of phytoplankton from the control volume. Arranging the water sampling frames and physical instrument array in a formation that allows both methods to be applied introduces redundancy, improving confidence in a difficult measurement; therefore we recommend future studies adopt a similar sampling configuration.

Implications for models—The linear relationship between α and u_{*b} has the potential to be used to incorporate the effect of the formation of CBLs on the rate of loss of phytoplankton to the bed into system-level phytoplankton models that do not resolve the fine vertical structure close to the bed and, hence, the formation of CBLs. However, the constant G is likely to be spatially and temporally variable, as a result of both biological and physical factors, and needs to be further explored. Biological factors include variability in the benthic community, including variability in the species composition, abundance, and size; pumping rates of the organisms; mucus production; possible behavioral adaptations; and variability in the phytoplankton community, including concentration and viability. Physical factors that are likely to be important include the sediment type, which will influence aggregate formation and the existence of a near-bed fluff layer, and proximity to intermittently flooded, but biologically active substrates, such as those in marshes, that are known to produce dissolved and particulate organic matter.

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