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

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Acknowledgements

Abstract

1   Field experiments were undertaken to measure the influence of hydrodynamics on the

2   removal of phytoplankton by benthic grazers in Suisun Slough, North San Francisco Bay.

3   Chlorophyll *a* concentration boundary layers were found over beds inhabited by the active

4   suspension feeders *Corbula amurensis* and *Corophium alienense* and the passive suspension

5   feeders *Marenzellaria viridis* and *Laonome* sp. Benthic losses of phytoplankton were

6   estimated via both the control volume and the vertical flux approach, in which chlorophyll *a*

7   concentration was used as a proxy for phytoplankton biomass. The rate of phytoplankton loss

8   to the bed was positively correlated to the bed shear stress. The maximum rate of

9   phytoplankton loss to the bed was five times larger than estimated by laboratory derived

10   pumping rates for the active suspension feeders. Reasons for this discrepancy are explored

11   including a physical mechanism whereby phytoplankton is entrained in a near-bed fluff layer

12   where aggregation is mediated by the presence of mucus produced by the infaunal

13   community.

14

1   **Introduction**

2   The shallow water regions of San Francisco Bay are of ecological importance because

3   they support net production of phytoplankton that form the base of the aquatic food web

4   (Cloern 1996). However, benthic grazing by siphonate bivalves can limit the accumulation of

5   phytoplankton biomass in the shallow waters of many systems (Newell 2004; Prins and

6   Escaravage 2005) and is a critical factor in defining ecosystem function in the San Francisco

7   Bay system (Alpine and Cloern 1992; Thompson 2005). It has been hypothesized that the

8   invasion of the clam *Corbula amurensis* in 1986 is largely responsible for the severe

9   reduction in both the magnitude and persistence of the summer to autumn phytoplankton

10   bloom in northern San Francisco Bay (Alpine and Cloern 1992; Jassby et al. 2002). Soon

11   after the *C. amurensis* invasion into San Francisco Bay, several species of fish declined in

12   abundance, partially as a result of severe decreases in phytoplankton availability (Feyrer et al.

13   2003). Furthermore, the extensive shallows of the tidal freshwater portion of the system, the

14   Sacramento-San Joaquin River Delta, have limited and declining primary productivity

15   (Jassby et al. 2002) and large populations of another invasive clam, *Corbicula fluminea*.

16   Recent work by Lucas et al. (2002) shows that grazing by *C. fluminea* is a primary factor in

17   determining if the shallow systems of the Delta are net phytoplankton exporters or net

18   phytoplankton sinks. Thus, the San Francisco Estuary is a system where the control of

19   phytoplankton abundance by non-indigenous, non-farmed bivalve grazers is sufficient to

20   endanger the continued success of native fish as well as key pelagic invertebrate species. Our

21   understanding and ability to estimate the grazing rates of benthic suspension feeders and the

22   physical limits on grazing rates is particularly critical in systems such as this one.

23   The mass balance of phytoplankton can be described as

24
$$\underbrace{\frac{\partial C}{\partial t}}_{\textbf{change in biomass}} = \underbrace{-U\frac{\partial C}{\partial x} - V\frac{\partial C}{\partial y}}_{\textbf{advection}} + \underbrace{w_s\frac{\partial C}{\partial z}}_{\textbf{settling}} - \underbrace{\frac{\partial}{\partial z}\left(-K_z\frac{\partial C}{\partial z}\right)}_{\textbf{turbulent diffusion}} - \underbrace{\psi}_{\textbf{sinks}} + \underbrace{\varphi}_{\textbf{sources}} \qquad (1)$$

1   where U and V are the mean velocities in the x and y directions, C is the concentration of

2   phytoplankton, w_s is the phytoplankton settling rate, K_z is the turbulent eddy diffusivity for

3   phytoplankton, ψ represents the depletion of phytoplankton due to benthic suspension

4   feeding, respiration and zooplankton grazing, and φ represents the sources of phytoplankton

5   such as production and resuspension (Koseff et al. 1993). Eq. 1 indicates that hydrodynamics

6   can directly affect the strength of benthic-pelagic coupling. Indeed, concentration boundary

7   layers (CBL) form when phytoplankton cells removed by beds of bivalves are not replaced by

8   vertical mixing. When CBLs form, the flux of particles to the incurrent siphons of bivalves is

9   reduced. Therefore, the benthic grazing rate (the rate of removal of particles, such as

10   phytoplankton, from the water [m^3 m^{-2} s^{-1}]) is a function of both the pumping rate (the

11   volume of water passing through the siphon per unit time [m^3 s^{-1} ind.$^{-1}$]) and the overlying

12   hydrodynamics. The relative strength of the benthic grazing rate, turbulent diffusion and the

13   phytoplankton settling rate will determine the formation of a CBL.

14   The existence of a CBL above suspension filter feeders has been identified in both

15   laboratory flume experiments (Wildish and Kristmanson 1984; O'Riordan et al. 1993;

16   Butman et al. 1994) and in the field (Frechette and Bourget 1985; Dolmer 2000; Nielsen and

17   Maar 2007), although many of these studies failed to identify quantitative relationships

18   between grazing and hydrodynamics. Ackerman et al. (2001) measured the presence of a

19   CBL above a bed of zebra mussels in Lake Erie during a period of stratification and found

20   that the CBL was dependent on the extent of stratification of the water column. Thompson

21   (1999) found that the CBL above infaunal bivalves in South San Francisco Bay varied in time

22   and space as a function of phytoplankton patchiness, vertical mixing time, and bivalve

23   density and size. Other investigations of benthic grazing have measured fluxes of

24   phytoplankton upstream and downstream of an area of interest with limited vertical sampling

25   (Roegner 1998; Tweddle et al. 2005).

1   Despite great improvements in our knowledge of the effects of benthic grazers on

2   water column seston concentrations, the effect of different hydrodynamic conditions on

3   grazing rates has not been thoroughly quantified. This makes it difficult to assess the system-

4   wide effect of the benthic community on phytoplankton concentrations. Furthermore, it

5   affects our ability to predict the potential effect of exotic benthic species such as the invasive

6   clams *Corbicula fluminea* and *Corbula amurensis*. The objectives of this study were to:

7   measure the rate of phytoplankton removal by the benthos and to determine the relationship

8   between the rate of phytoplankton removal by the benthos and the extent of turbulent mixing

9   in situ. To achieve these objectives, field experiments were carried out at Suisun Slough,

10   North San Francisco Bay whereby the rate of phytoplankton removal by the benthos was

11   estimated via both control volume and vertical flux approaches, with chlorophyll *a* (Chl *a*)

12   concentration used as a proxy for phytoplankton biomass.

13   **Methods**

14   *Study site*

15   The field study was carried out in Suisun Slough in North San Francisco Bay from 30

16   August to 15 September 2005 (Fig. 1). Suisun Slough flows through Suisun Marsh, a large

17   brackish-water marsh. The site was chosen for its relatively uncomplicated tidal flow. The

18   sample site was located approximately halfway along the reach, maximizing its distance from

19   upstream and downstream bends to minimize secondary flows. This section of Suisun Slough

20   is relatively shallow; the depth at the control volume (CV) site ranged from 2.0-3.5 m. All

21   water samples were taken at the center of the channel (Fig. 2). Measurements of the grain size

22   distribution of the sediment in lower Suisun Slough revealed <5% sand (diameter 0.062-2

23   mm), 30-65% silt (0.004-0.062 mm) and 35-45% clay (<0.004 mm) (Hampton et al. 2003).

24   The sediment contained approximately 4% organic matter by dry weight (Department of

25   Water Resources unpubl. data).

1   *Estimating benthic losses*

2   Two methods were employed to estimate the rate of phytoplankton removal by the

3   benthos: the control volume (CV) method and the vertical flux method.

4   *The CV method.* This method uses an imaginary box (the control volume) that

5   encloses the region of interest (Fig. 3). Mass balances for each scalar are then written,

6   including fluxes through the faces of the CV (the control surface= CS), unsteady changes in

7   quantities inside the CV and any non-conservative processes that add or remove material

8   from the CV such as benthic grazing. Mathematically this is expressed by the integral form of

9   the mass conservation relation

10
$$\frac{d}{dt} \int_{CV} C \, dV \;\; + \;\; \int_{CS} C\vec{u} \cdot d\vec{A} \;\; = \;\; J \cdot A_b, \tag{2}$$

11   where C is the concentration of the scalar, $\vec{u}$ is the local transport velocity, $d\vec{A}$ is the local

12   directed surface area element (the direction normal to the surface), J is the mass flux per area

13   of the benthos and A_b is the area of the rectangle A-B-C-D (Fig. 3). Assuming that all losses

14   are due to benthic grazing, the mass flux is related to the benthic grazing rate ($m^3 \, m^{-2} \, s^{-1}$) as

15
$$J = \alpha C_B, \tag{3}$$

16   where C_B is the phytoplankton concentration close to the bed.

17   As an exact expression, Eq. 2 requires that C and $\vec{u}$ be known everywhere inside the

18   control volume. However, in practice, each of the required integrals were estimated from

19   limited pointwise velocity and concentration measurements. In the experiments,

20   phytoplankton were sampled along each vertical corner of a 10 x 20 m control volume (Fig.

21   3). To capture vertical variations in phytoplankton concentration, Chl *a* samples were

22   collected at eight heights spaced approximately logarithmically from the sediment-water

23   interface to the water surface. In terms of this sampling arrangement and substituting in Eq. 3

24   we can then approximate Eq. 2 as

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

where W is the width, L is the length and H is the height of the control volume; u is the

length-wise oriented velocity and v is the width-wise oriented velocity; C_{AB}, C_{CD}, C_{BC}, and

C_{AD} are the representative vertical distributions of Chl a concentration for each face, averaged

from the measurements at each corner; and $\overline{C}$ is the volume averaged Chl a concentration.

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

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

where $\kappa=0.41$ is the von Karman constant (Fischer et al. 1979). Close to the bed where $z_c/h\sim 0$

Eq. 5 can be approximated as

$$
K_z=\kappa u_{*b}z.
\tag{6}
$$

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

$$
\int_z^h\left(\frac{\partial C}{\partial t}+U\frac{\partial C}{\partial x}+V\frac{\partial C}{\partial y}+\psi-\varphi\right)dz=-w_s C(z)-K_z\left.\frac{\partial C}{\partial z}\right|_z=F(z).
\tag{7}
$$

Here F represents the total flux towards (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

1
$$-K_z \frac{\partial C}{\partial z} = -\kappa u_{*b} z \frac{\partial C}{\partial z} = F_B \,. \tag{8}$$

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

3 logarithmically with height

4
$$C(z) = d \ln \frac{z}{z_c} + C_B \,, \tag{9}$$

5 where $d = F_B / \kappa u_{*b}$, z_c is the height at which the benthic grazers are removing the Chl a and

6 C_B is the concentration of Chl a at z_c. The vertical flux of Chl a at the height of benthic

7 feeding z_c can be expressed as the product of the grazing rate α and C_B

8
$$F_B(z_c) = \alpha C_B \,. \tag{10}$$

9 Therefore, the benthic grazing rate can be estimated as

10
$$\alpha = \frac{\kappa u_{*b} d}{C_B} \,, \tag{11}$$

11 where u_{*b} can be estimated from the near-bed acoustic Doppler velocimeter (ADV)

12 measurements. Note that since we have neglected settling, which has the same sign as the

13 diffusive flux, Eq. 11 is an underestimate of α .

14   Least squares regression was used to find d and C_B for each vertical profile of Chl a,

15 with $z_c = 5 \times 10^{-3}$ m. The fits were performed using at least four samples adjacent to the bed

16 for all combinations of the possible eight vertical samples and allowing for the possibility of

17 one outlier in the CBL. The set of samples that resulted in the highest r^2 value was selected

18 for further analysis if the fit was significant at the 95% confidence level and $r^2 > 0.6$. Replicate

19 sampling of the vertical profiles was not possible, therefore the error in d and C_B was

20 estimated using the bootstrap method, whereby subsets of data are generated based on a

21 random sampling of the data (Bendat and Piersol 2000). Bootstrap samples were created by

22 re-sampling each Chl a profile 1000 times, independently and with replacement. Least-

23 squares regression of the bootstrap generated data resulted in 1000 estimates of d and C_B, the

1   mean of the estimates of d and C_B is the "best fit" and the standard deviation of the estimates

2   of d and C_B is used to estimate the uncertainty. The friction velocity u_{*b} was estimated from

3   the covariance of the streamwise u and vertical w velocity ADV time series (Voulgaris and

4   Trowbridge 1998). The error in the u_* estimate was negligible (2% at the 95% confidence

5   level).

6   ***Measurement techniques***

7   The water sampling was undertaken during two 30-h experiments conducted 12 d

8   apart. To enable the collection and processing of water samples, the experiments were staged

9   from a houseboat. The water sampling frames were constructed to collect samples at eight

10   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

11   were extended away from the central support to prevent potential mixing of the water by the

12   presence of the frame. The water sampling frames were manually reoriented into the direction

13   of the mean flow at each slack tide for the same reason. Ten minute integrated water samples

14   were collected every hour for each 30-h experiment via 30 m lengths of tube and peristaltic

15   pumps operating at 90 mL min^{-1}. The 10 min sampling time was chosen to ensure the water

16   column was turning over a few times during the sampling period and to ensure the intake

17   velocity was not excessive. Phytoplankton biomass was estimated from fluorometrically-

18   determined Chl a concentration (Parsons et al. 1984). This technique involved immediately

19   filtering the collected water sample through Whatman GF/F filters which were then stored at

20   -80°C. The filters were later extracted in 90% acetone overnight, centrifuged and Chl a

21   concentration of the extract was measured with a fluorometer (Model 10, Turner Designs).

22   In addition to the discrete water sample measurements, continuous time series of Chl

23   a fluorescence was obtained in situ (self-contained underwater fluorescence apparatus

24   (SCUFA), Turner Designs). A fluorometer with a sampling interval of 30 s was placed close

25   to the inlet 1 m above the bed on the SW water sampling frame. The fluorometer was

1   calibrated via multiple regression using the extracted Chl *a* concentration from the pumped

2   samples and turbidity measured by the SCUFA. Phytoplankton samples for species

3   composition were collected every six hours during the 30-h experiments. The samples were

4   preserved in acid-Lugols solution and examined in a phase contrast inverted microscope to

5   identify the most common taxa and estimate their biovolume from measured cell dimensions

6   (Cloern and Dufford 2005).

7   Throughout the two 30-h experiments, zooplankton tows were performed every six

8   hours. The zooplankton samples were collected with a 50 μm mesh, 0.5 m diameter net

9   towed a distance of 100 m, obliquely across the downstream face of the sample area.

10   Zooplankton were preserved in 5% buffered formalin with Rose Bengal dye. 1 mL

11   subsamples were examined in a Sedgewick-Rafter cell and all zooplankton (primarily

12   rotifers, copepods, and cladocerans) were counted and identified to species or genus; lengths

13   of 20 individuals in each category were measured.

14   Individual dry weights of zooplankton were estimated from published length-weight

15   relationships or from published dry-weight data for specific taxa. Dry weight was converted

16   to carbon using a carbon:dry weight ratio of 0.48 (Lopez et al. 2006). Zooplankton

17   community grazing was estimated from an Ivlev function describing ingestion rate as a

18   hyperbolic function of phytoplankton biomass, where ingestion rate approaches a maximum

19   at a phytoplankton biomass of 300 mg C m^{-3}. The estimated ingestion rate *I* was calculated

20   for each taxon via (Lopez et al. 2006)

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

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

23   biomass.

24   The currents were measured at the center of the control volume using an upward

25   looking 1200 kHz acoustic Doppler current Profiler (ADCP, RD Instruments) operating in

1 mode 12 sampling at 1Hz, with 7 cm bins and the first bin approximately 0.5 m above the

2 sediment-water interface. The currents close to the bed were measured at 16 Hz using an

3 array of three acoustic Doppler velocimeters (ADVs, Nortek AS) sampling at heights of 0.15,

4 0.3, 0.45, and 1.45 m above the bed.

5   Vertical temperature structure at the center of the control volume was measured by an

6 array of thermistors (SBE39, Seabird Electronics) positioned every 0.5 m and sampling at 2

7 min intervals. Conductivity was measured at two heights (0.3 and 0.9 m above the bed)

8 (SBE16+, Seabird Electronics). A wind station (Model 05103, RM Young) was mounted

9 above the houseboat, 4.7 m above the water, to provide 10 min-averaged wind speed and

10 direction data.

11   At the conclusion of the experiment, the benthos in the control volume (33 samples)

12 and the areas surrounding (eight samples) were systematically sampled using a 0.05 m^2 van

13 Veen grab to gauge spatial variability in community composition. The grab was fabricated by

14 the United States Geological Survey, is weighted, and has a measured penetration depth of

15 approximately 10 cm. Samples were sieved through a 0.5 mm screen, preserved in 10%

16 buffered formalin for no more than a week, transferred to 70% ethyl alcohol for storage, and

17 stained with Rose Bengal before sorting. All organisms were removed, identified and

18 counted. Benthic grazing was estimated from published pumping rates for the various

19 suspension feeding organisms according to the equations presented in Table 1.

20 **Results**

21 ***Physical conditions***

22   Grazing expt. 1 experienced maximum flood and ebb velocities of 0.5 m s^{-1} (Fig. 4).

23 During expt. 2, 12 d later, the maximum currents were slightly smaller (Fig. 5). A weak

24 secondary circulation was present, presumably due to slight channel curvature (Figs. 4B and

25 5B). During both flood and ebb tides, the surface water tended to flow towards the west bank

1   while the bottom water flowed towards the east. During the long ebb tides, the entire water

2   column had a positive cross-stream velocity, accompanied by maximum streamwise

3   Reynolds stresses. The drag coefficient was estimated to be C_d=1.1x10^{-3}.

4   Wind speeds ranged from 0-6 m s^{-1} during both of the grazing experiments, and

5   followed a diurnal pattern, with maximum wind speeds in the afternoon and minimum wind

6   speeds around 05:00 h. Winds emanated from directions ranging from WSW to W.

7   Over the duration of grazing expt. 1, the salinity ranged from 6.9 to 7.6 and the water

8   temperature ranged from 21-22.5^{o}C. Salinity was on average slightly higher in expt. 2,

9   ranging from 7.4-8.3 and water temperatures were on average slightly cooler, ranging from

10   18-19.5^{o}C. Short-lived periods (typically less than 1 h) of stratification occurred around slack

11   tide, when current speeds were slow. Salinity stratification occurred after low-low water and

12   temperature stratification occurred at the end of the day-time ebb tide. Stratification was

13   accompanied by increases in vertical shear, particularly in the cross-channel direction (not

14   shown).

15   ***Biological conditions***

16   The mid-water column concentration of Chl *a* ranged from 4-10 μg L^{-1} at the CV site

17   during expt. 1. During expt. 2, 12 d later, the Chl *a* concentrations had decreased significantly

18   and ranged from 2 to 5 μg L^{-1}. Large and rapid changes in Chl *a* concentration were observed

19   at the CV site during both experiments, likely due to the advection of higher concentration

20   water masses past the CV site. During expt. 1, 70% of the phytoplankton biomass was

21   distributed roughly equally among seven different species (Table 2). Diatoms were the

22   dominant taxa, comprising 60% of the biomass, followed by cryptophytes (21%). During

23   expt. 2, diatoms accounted for 82% of the phytoplankton biomass, dominated by *Guinardia*

24   *delicatula* (40% of total biomass).

1   The zooplankton community was similar during both experiments and was dominated

2   by the introduced copepod, *Oithona davisae* (Ferrari and Orsi 1984) (Table 3). *O. davisae*

3   consumes flagellates (both autotrophic and heterotrophic) but does not consume diatoms

4   (Uchima 1988). *Acartiella sinensi,* an introduced grazing calanoid copepod, contributed over

5   70% of the zooplankton herbivorous grazing. Benthic herbivorous Harpacticoid copepods

6   were the only other significant contributors to phytoplankton grazing. The average estimated

7   grazing rate for the herbivorous zooplankton community was 540 μg C m^{-3} d^{-1} or 1.7 x 10^{-2}

8   μg Chl *a* L^{-1} d^{-1} for expt. 1 and 210 μg C m^{-3} d^{-1} or 6.3 x 10^{-3} μg Chl *a* L^{-1} d^{-1} for expt. 2,

9   assuming a phytoplankton C:Chl *a* ratio of 32 (Cloern et al. 1995).

10   The dominant filter feeders at the Suisun Slough site were the two species of clams

11   (*Corbula amurensis* and *Macoma petalum),* a tube-forming amphipod (*Corophium*

12   *alienense*), and to a lesser extent, a tube dwelling Sabellid polychaete (*Laonome* sp) (Table

13   4). The pumping rates of the *C. amurensis* and *M. petalum* populations were calculated to be

14   <1 m^3 m^{-2} d^{-1} using published pumping rates obtained from laboratory experiments (Table 1).

15   *C. alienense* is an introduced benthic amphipod that creates a current in its U-shaped tube by

16   metachronal beating of the pleopods. Although there is no available literature for *C. alienense*

17   feeding rates, the feeding behavior and rate of the congener *C. volutator* has been estimated

18   to be 78-93 mL h^{-1} for individuals of comparable size to the *C. alienense* seen in this study ($\approx$

19   6 mm in rostrum to telson length) (Riisgard 2007). Given that the average abundance of *C.*

20   *alienense* at the site was 3800 ± 800 ind. m^{-2} (95% confidence interval) and assuming that *C.*

21   *alienense* and *C. volutator* have similar pumping rates, the maximum pumping rate for *C.*

22   *alienense* would be 9 ± 2 m^3 m^{-2} d^{-1} (95% confidence interval). The *Laonome* sp. was not

23   identified to the species level, however, it is assumed to process particles with a ciliary pump

24   on the crown as described for other Sabellids (Fauchald and Jumars 1979). The *Laonome* sp.

25   in the San Francisco Estuary was of similar size and morphology as *Sabella pavonina*, a

1   species reported to have a filtering rate of 1.7 L day^{-1} ind.$^{-1}$ (Dales 1957). The mean

2   abundance of *Laonome* sp. at the site was 400 ± 100 ind. m^{-2}, thus the pumping rate for the

3   population was 0.7 ± 0.2 m^3 m^{-2} d^{-1}. The total pumping rate for all active suspension feeders

4   was approximately 10 ± 3 m^3 m^{-2} d^{-1}.

5   The other abundant species at the sampling location was the polychaete *Marenzellaria*

6   *viridis* (200 ± 70 ind. m^{-2}), a tube dwelling Spionid that either passively filter feeds or

7   surface deposit feeds, depending on food availability (Daunys et al. 1999). Other members of

8   the benthic community were either too sparse (≤ 1 ind. sample^{-1}) or were deposit feeders

9   unlikely to feed on either suspended or recently settled phytoplankton (e.g., oligochaetes,

10 *Gammarus daiberi*) (Table 4).

11 ***The formation of concentration boundary layers***

12   The time series of vertical profiles of Chl *a* concentration for expts. 1 and 2 exhibit a

13 depletion of Chl *a* adjacent to the bed for a range of different surface Chl *a* concentrations

14 (Fig. 6). Individual profiles were normalized by the depth-averaged concentration and

15 averaged over the four sampling locations and all sampling times for each experiment to

16 produce non-dimensionalized Chl *a* concentration profiles (Fig. 7). Error bars indicate two

17 standard deviations from the average normalized concentration. The ensemble-averaged

18 normalized profile for expt. 1 indicates that on average there was a considerable depletion of

19 Chl *a* towards the bed. The sample closest to the bed was on average 13% lower than the

20 depth-averaged concentration and 22% lower than the near surface concentration. The

21 ensemble-averaged profile from expt. 1 was well described by the theoretical logarithmic

22 CBL profile (Eq. 9). The ensemble-averaged vertical profile for expt. 2 also showed depletion

23 of Chl *a* towards the bed, however, the profile did not decrease monotonically towards the

24 bed. On average the sample closest to the bed was 5% lower than the depth-averaged

25 concentration and 12% lower than the near surface concentration.

1   Concentration boundary layers persisted under a variety of physical conditions

2   including ebb (e.g., Fig. 8A) and flood (e.g., Fig. 8B) tides and periods of stratification (e.g.,

3   Fig. 8C). During some sampling periods, the vertical Chl *a* distribution was very similar at all

4   four sampling locations (Fig. 8A). However, at other times, the concentration profile was

5   different at each location (Fig. 8B). This difference was most likely due to cross-channel

6   variability in Chl *a* concentrations. During many sampling periods in both experiments, the

7   resultant profiles displayed a strong cross channel gradient, with higher concentrations at the

8   eastward sampling locations that were closer to the deepest part of the channel.

9   When the water column stratified, the surface and near-bed Chl *a* concentrations

10   became distinctly different (Fig. 8C), with subsurface concentrations being much lower than

11   at the surface (a difference of roughly 2.5 μg L^{-1}). The temperature profile indicates that the

12   higher concentrations persisted in the surface water due to incomplete mixing of the surface

13   water.

14   Eq. 9 was an appropriate model for the CBLs formed during these experiments (e.g.,

15   Fig. 9). Least squares fitting of Eq. 9 with the measured Chl *a* concentration profiles revealed

16   that C_B ranged from 2.6 to 7.2 μg L^{-1} with a mean value of 4.4 μg L^{-1} during expt. 1 (mean

17   error 0.1 μg L^{-1}). C_B was considerably lower during expt. 2 ranging from 0.77 to 3.2 μg L^{-1}

18   with a mean value of 2.1 μg L^{-1} (mean error 0.3 μg L^{-1}). The time series of the gradient of the

19   CBL *d* (Eq. 9), the estimated grazing rate α, and the corresponding bed shear velocity,

20   surface Chl *a* concentration, and the normalized Richardson number are shown in Fig. 10

21   (expt. 1) and Fig. 11 (expt. 2). The Richardson number, an index of stratification, is defined

22   as $\mathrm{Ri} = \dfrac{g \Delta \rho \Delta z}{\rho_m (\Delta u)^2}$, where *g* is gravity, ρ_m is the reference density, and Δu is the velocity shear

23   and $\Delta \rho$ the change in density over a layer of thickness Δz. We defined the critical Richardson

24   number $\mathrm{Ri_c} = 0.25$ such that $\log_{10}(\mathrm{Ri}/\mathrm{Ri_c}) > 0$ indicates stable stratification (Lewis 1997).

1   During both of the experiments, d exhibited little spatial variability within the sampling

2   region. However, on many occasions only one of the four profiles was identified as a CBL. In

3   expt. 1, a CBL was identified for at least one of the four sampling locations during 26 out of

4   the 28 sampling periods. In expt. 2, a CBL was identified for 23 of the 30 sampling periods.

5   During expt. 1, CBLs were absent during periods corresponding to low bed shear velocity

6   (Fig. 10). This pattern was less consistent in expt. 2, where no CBLs were measured for a

7   four-hour period (Fig. 11). However, three of these seven samples corresponded with

8   extremely low Chl a concentrations.

9   ***Rate of phytoplankton removal by the benthos***

10   The benthic grazing rate α calculated using Eq. 11 (Figs. 10B and 11B), exhibited

11   significant variation both in time and between the four sampling frames. We can see from Eq.

12   11 that in order for the grazing rate to be positively correlated with u_{*b}, C_B/d has to be

13   constant over the measured range of u_{*b}. C_B/d showed no clear trend over the range of u_{*b}

14   measured (Fig. 12), indicating that the grazing rate of the benthic organisms was

15   approximately a linear function of the bed shear velocity. Although the error in C_B/d was

16   often large, no systematic difference was seen between the four water sampling frames or

17   between the two experiments. The grazing rate can therefore be modeled by

18   $$\alpha = Gu_{*b},\tag{13}$$

19   where $G=\kappa d/C_B$ was assumed to be a constant for this site. G was determined from a

20   weighted mean of d/C_B, where the weight was determined by the magnitude of the confidence

21   interval for each estimate of d/C_B.

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

23   prevent the frames from sinking into the fine sediment, it is likely that the actual heights of

24   the water intake were offset by 0-10 cm (the height of the lowest intake). Because the ratio

25   of C_B/d is sensitive to this offset, a range of values of G and α for different assumed vertical

1   offsets are shown in Table 5. The difference between the average value of G for each of the

2   experiments was small, despite the large changes in phytoplankton concentration between the

3   two experiments.

4   Eq. 11 assumes phytoplankton settling is negligible; significant settling would result

5   in underestimation of the grazing rate. We estimate that phytoplankton settling velocities

6   were on the order of 0.1 to 1 m d^{-1} (Lannergren 1979; Bienfang 1981; Koseff et al. 1993) and

7   were therefore negligible compared with the estimated magnitude of the vertical turbulent

8   flux term and are thus not considered to be an important component in our estimates.

9   The benthic grazing rate was also estimated via the control volume method. We

10   estimate that individual estimates of α have an error of approximately 20%. Robust linear

11   least squares regression of the estimated benthic grazing rate via the control volume method

12   versus the bed shear velocity reveals

13
$$\alpha_{CV} = (3.1 \text{x} 10^{-2} \pm 1.2 \text{x} 10^{-2}) u_{*b} . \tag{14}$$

14   where the uncertainty is at the 95% confidence level and r^2=0.81 (Fig. 13A). The coefficient

15   compares well with G calculated via the vertical flux method (Table 5).

16   Zooplankton grazing estimated via Eq. 12 was negligible compared with the average

17   measured net loss of Chl a in the control volume. For example, during expt. 1 the loss due to

18   zooplankton grazing was 0.1 μg Chl a s^{-1}, whereas the average loss of Chl a in the control

19   volume throughout expt. 1 was 500 μg Chl a s^{-1}. It is therefore reasonable to assume that

20   losses of Chl a cannot be attributed solely to zooplankton grazing.

21   **Discussion**

22   ***Mass-transfer limited flux of phytoplankton to the bed***

23   Two independent analysis methods for estimating the flux of phytoplankton to the

24   bed, the control volume method and the vertical flux method, were generally in good

25   agreement and revealed significant losses of Chl a to the benthos. The benthic grazing rate

1   was positively correlated with the bed shear velocity, which ranged from 2×10^{-3} to 1.8×10^{-2}

2     $m\ s^{-1}$, indicating that the loss of Chl a to the bed was mass-transfer limited. Benthic grazing

3   rates, estimated by both the control volume method and the vertical mass flux method, are

4   shown in Fig. 13B as a function of the bed shear velocity. The lines of best fit approximate

5   the data reasonably well and the two methods resulted in a significantly similar slope.

6   Our third method of estimating benthic grazing rates, using measured abundance and

7   biomass of the benthic community and laboratory derived pumping rates, was five times

8   smaller ($10\ m\ d^{-1}$) than the maximum benthic grazing estimates from the field experiments

9   ($\sim 50\ m\ d^{-1}$). Filtration (and phytoplankton ingestion) rates for benthic organisms are

10   generally smaller than calculated pumping rates due to the formation of CBLs, the refiltration

11   of water (O'Riordan et al. 1995) and the intermittency of pumping (Ortmann and Grieshaber

12   2003) so this finding was troubling. A similar discrepancy in the maximum estimated benthic

13   grazing rates of Chl a measured via the vertical flux method ($\approx 60\ m\ d^{-1}$) and the pumping

14   rates based on clam biomass ($6\ g\ m^{-2}$) was observed by Thompson (1999) in South San

15   Francisco Bay.

16   It is possible that the benthic community biomass was underestimated. However,

17   according to the laboratory derived pumping rates, the biomass of $C.\ amurensis$ required to

18   produce α=6-50 m d^{-1}, is 15-125 g dry tissue weight m^{-2}. We estimated the dry tissue weight

19   of $C.\ amurensis$ at the site to be approximately $2\ g\ m^{-2}$ and, due to the extensive sampling of

20   the benthic community, it is unlikely that we under-sampled $C.\ amurensi$ by this much. Our

21   van Veen grab is unlikely to under-sample tube dwelling $C.\ alienense$ as their burrows are <

22   10 cm deep. Surface dwelling $C.\ alienense$ will avoid capture in the grab, however, if we

23   assume that the proportion of surface dwelling (deposit feeding) $C.\ alienense$ was the same

24   during the grab sampling as during the two experiments then the calculated pumping rate will

25   reflect the tube dwelling (filter feeding) population. Furthermore, comparison with long-term

1 records of benthic composition at a nearby site indicated our measured density was within the

2 typical range measured in autumn (BDAT 2008).

3   Laboratory derived pumping rates have a number of shortcomings which may account

4 for the difference between the maximum benthic loss rate and community pumping rate (for a

5 review see Riisgard 2001). Furthermore, measurements of pumping rates have not been made

6 for the species of *Corophium* and *Laonome* sampled here. Therefore pumping rates had to be

7 estimated using pumping rate relationships for similar organisms. Macrobenthos have also

8 been found to display a large range of pumping rates, for example, Riisgard (2007) found

9 pumping rates for *C. volutator* ranged from 18.3 to 93 mL h^{-1} ind.$^{-1}$. Some of this variability

10 has been attributed to the organisms' size, the temperature and the food concentration,

11 however, variability in pumping rate is not well understood. The population pumping rates

12 shown in Table 4 are estimates of their maximum pumping rates based on the available

13 literature. Further measurements and understanding of pumping rates are required to quantify

14 the contribution of benthic grazing to the measured benthic loss. We consider two alternate

15 mechanisms that could result in the measured mass-transfer limited flux of phytoplankton to

16 the bed: turbulent deposition and near-bed aggregation, below.

17 *Alternatives to benthic grazing*

18   An alternative mechanism that may account for the measured loss of Chl *a* at the bed

19 involves the turbulent deposition of the phytoplankton cells to the sediment. Turbulent

20 deposition describes the transport of particles by vertical mixing to a solid boundary as

21 opposed to settling which occurs by gravity. Studies of sediment transport (Kaftori et al.

22 1995) and atmospheric aerosol deposition (Brooke et al. 1992) have shown that particle

23 deposition is enhanced in turbulent flow. The transfer coefficient or deposition velocity V is a

24 loss term like the benthic grazing rate α in the mass balance equation, but is defined as the

25 particle mass transfer rate divided by the bulk concentration of the particles.

1   The deposition of particles from a turbulent fluid to a solid boundary can follow one

2 of three regimes depending on the particles size and density, as well as the fluids density and

3 viscosity (Wood 1981). The theory estimates that for an average diatom cell of 40 μm the

4 deposition velocity is $V = 3 \times 10^{-7} u_{*b}$. the coefficient is five orders of magnitude smaller than

5 the measured constant of proportionality G (Eq.14 and Table 5). Clay particles and diatoms

6 cells may aggregate to form flocs of diameter 100-500 μm (Kranck and Milligan 1992).

7 Assuming a floc size of 250 μm results in $V = 1 \times 10^{-6} u_{*b}$; the coefficient is four orders of

8 magnitude smaller than the measured constant of proportionality G (Eq.14 and Table 5).

9 Therefore, we conclude that turbulent deposition of either individual diatoms cells or

10 aggregates containing diatoms contributed minimally to losses of phytoplankton at the bed.

11   Alternatively, the larger than anticipated estimates of phytoplankton loss at the bed

12 may be explained by the aggregation of phytoplankton in a near-bed "fluff" layer

13 (Stolzenbach et al. 1992). A fluff layer is characterized by loosely aggregated material of

14 high porosity (Fig. 14). The fluff layer is hydrodynamically active, and therefore particle

15 transport into this layer is not limited by transport across a laminar sublayer. A fluff layer is

16 likely to exist at the Suisun Slough site due to the high clay content of the sediment and

17 proximity of the slough to multiple particles sources of biological origin (marsh sediment and

18 plants, bay sediment, freshwater, and estuarine water sources). Particle aggregation would be

19 enhanced in the fluff layer due to both the large number of particles and the large shear

20 stresses, resulting in an increased collision frequency of particles (Jahmlich et al. 2002;

21 Colomer et al. 2005). For this reason, the positive correlation found between the estimated

22 rate of phytoplankton removal by the benthos α and the bed shear velocity supports the near-

23 bed aggregation mechanism. Furthermore, aggregation has been shown to be enhanced by the

24 presence of biological material such as transparent exopolymer particles (Sanford et al. 2001;

25 Jahmlich et al. 2002). Suspension-feeding benthic animals produce feces and pseudofeces as

1   well as an extracellular mucus-like material (Davies and Hawkins 1998; Murray et al. 2002).

2   Tube dwelling polychaetes and amphipods also produce extracellular polymeric material for

3   structural support (Meadows et al. 1990; Murray et al. 2002). The pseudofeces and mucus

4   produced by the benthic community can rapidly bind particles such as sediment and

5   phytoplankton (Meadows et al. 1990).

6   If aggregation of phytoplankton was occurring in a near-bed fluff layer, it is likely

7   that phytoplankton would then be incorporated into the consolidated sediment. In this

8   experiment the lowest water sample was taken at approximately 10 cm above the bed, higher

9   than the extent of a typical fluff layer, however, Thompson 's (1999) near-bed measurements

10 showed a local increase in Chl a concentration a few centimeters above the bed, lending

11 support to this hypothesis.

12   Comparing the carbon needed to support the benthic community with the carbon

13 produced by the phytoplankton in this system identified the near-bed aggregation mechanism

14 as a plausible explanation for the high flux of phytoplankton to the bed. Several studies have

15 concluded that a high percentage of the carbon that is used by the metazoans in this estuary is

16 derived from bay or river produced phytoplankton (Jassby et al. 2002; Sobczak et al. 2002).

17 Over 90% of the bioavailable particulate organic matter has been shown to be phytoplankton

18 based in Suisun Slough (Sobczak et al. 2005) and so it is phytoplankton primary production

19 in the marsh that is likely to be most critical to the benthic feeders in our experimental area.

20 As seen in Suisun Bay, the phytoplankton biomass greatly declined following the

21 introduction of *Corbula amurensis* in 1986 (Alpine and Cloern 1992). The phytoplankton

22 biomass seasonal cycle (peak in spring), maximum biomass (<10 μg L^{-1} Chl a), and average

23 biomass for the rest of the year (2-3 μg L^{-1} Chl a) are now similar in the marsh, sloughs and

24 channels of Suisun Marsh and Suisun Bay (R.L. Brown unpubl.). We therefore feel

25 comfortable using estimates of gross primary production made for Suisun Bay $\leq$50 g C m^{-2}

1   yr^{-1} (Alpine and Cloern 1992; Jassby 2006) in this comparison. We have estimated secondary

2   production in this benthic community using published production:biomass (P:B) values for

3   other temperate estuaries where these values are available. If there were no appropriate

4   estimates in similar systems we used "universal" P:B values calculated by Schwinghamer et

5   al. (1986). Trophic efficiency of the benthic invertebrates in the Suisun Slough community

6   (Table 7) was assumed to be 10% except for *C. amurensis*, which, due to recent estimates of

7   25% trophic efficiency for a similarly opportunistic bivalve *Corbula fluminea* (McMahon

8   1999), was estimated for both 10% and 25% efficiency. A comparison of carbon produced by

9   phytoplankton in this system (~50 g C m^{-2} yr^{-1}) and that consumed by a combination of the

10   surface deposit and suspension feeding members of the benthic community (~50-60 g C m^{-2}

11   yr^{-1}) shows them to be remarkably similar (Table 6). This comparison can be used as support

12   for the hypothesis that the phytoplankton are an important food source for the passive

13   suspension feeders and surface deposit feeders but it does not exclude the importance of other

14   sources of food to these infauna. One other possible source of food, benthic microalgae, are

15   unlikely to be a large source of carbon for the infauna as the light attenuation is rapid in this

16   turbid estuary, so benthic microalgae are likely limited to the intertidal and shallow subtidal

17   reaches of the system. Jassby et al. (1993) estimated that benthic microalgae represented

18   <10% of the biologically available carbon in the northern estuary.

19   Further measurements in the near-bed region are required to investigate the

20   importance of the near-bed aggregation mechanism as a means of accelerating the transfer of

21   pelagic carbon sources to the passive suspension and deposit feeders in the benthic

22   community. Such a transport and near-bed retention mechanism may reduce the delivery time

23   for the pelagic carbon to the deposit feeders in shallow, turbulent systems such as San

24   Francisco Estuary. These near-bed bio-physical processes may be capable of limiting pelagic

1   phytoplankton biomass and primary production in a manner similar to that seen with filter-

2   feeding organisms.

3   ***Evaluation of methodology***

4   Although the two methods of analysis that were applied to estimate the flux of

5   phytoplankton to the benthos generally showed good agreement, some difference in

6   reliability were noted. The vertical flux method often failed close to slack tide when the

7   vertical mixing was minimal while the control volume method was adversely affected by

8   spatial patchiness in Chl a concentration.

9   CBLs were not always found at each of the four sampling locations and a CBL was not

10   identified at any of the four sampling locations for nine of the 58 sampling periods. Local,

11   short-lived turbulent mixing events as well as small-scale patchiness of Chl a will lead to

12   instantaneous variations in the local Chl a concentration. The 10 min sampling period was

13   chosen as a compromise between allowing sufficient time for the turbulence to "see" the

14   entire water column while ensuring the physical parameters did not change significantly. To

15   guarantee that vertical profiles of Chl a concentration were not influenced by short period

16   mixing events, the sampling period should be greater than $h/0.3u_{*b}$ (Fischer et al. 1979). This

17   was not achieved close to slack tides when the bed shear velocity was small and may account

18   for the absence of measured CBLs coinciding with low bed shear velocities. The absence of a

19   CBL has previously been attributed to behavioral adaptations of the benthic organisms in

20   response to increased suspended sediment load or the presence of predators. However, the

21   variability in the identification of a CBL at the four sampling sites indicates that

22   phytoplankton patchiness and sampling error may, without invoking the possible variability

23   in animal behavior, account for the absence of identified CBLs at all four sampling site on

24   occasion.

1   Positive fluxes of Chl a were calculated via the control volume method for 18 of the

2   sampling periods for which CBLs were identified, indicating failure of the control volume

3   method at these times. The control volume method is susceptible to error under spatially

4   patchy conditions. For example, gradients in Chl a in the cross-stream direction may lead to

5   false estimates of net positive fluxes of phytoplankton from the control volume. Arranging

6   the water sampling frames and physical instrument array in a formation that allows both

7   methods to be applied introduces redundancy, improving confidence in a difficult

8   measurement, therefore we recommend future studies adopt a similar sampling configuration.

9   ***Implications for models***

10   The linear relationship between α and u_{*b} has the potential to be used to incorporate

11   the effect of the formation of CBLs on the rate of loss of phytoplankton to the bed into

12   system-level phytoplankton models that do not resolve the fine vertical structure close to the

13   bed, and hence, the formation of CBLs. However, the constant G is likely to be spatially and

14   temporally variable, due to both biological and physical factors, and needs to be further

15   explored. Biological factors include: variability in the benthic community, including

16   variability in the species composition, abundance and size, pumping rates of the organisms,

17   mucus production and, possible behavioral adaptations; and variability in the phytoplankton

18   community, including concentration and viability. Physical factors that are likely to be

19   important include the sediment type, which will influence aggregate formation and the

20   existence of a near-bed fluff layer, and proximity to intermittently flooded, but biologically

21   active substrates, such as those in marshes, that are known to produce dissolved and

22   particulate organic matter.

23

1

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5

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 (^{o}C) and L is the length (mm).

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

Here; * based on PR relationship for *Corophium volutator*; ** based on PR relationship for *Sabella pavonina*

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

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

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

Table 3 Zooplankton community composition shown as abundance and as percentage contribution of herbivorous grazing for Suisun Slough expts. 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
Oithona davisae	12561	3	8649	17
Acartiella sinensis	261	78	109	72
Tortanus dextrilobatus	48		20	
Harpacticoids sp.	69	18.5	12	6.5
Rotifers				
Brachionus sp.	0		10	1.5
Unidentified	6	<1	3	<1
Notholca sp.	0		5	<1
Other				
Barnacle nauplii	39		54	

Table 4. Abundance of persistent benthic invertebrates species ($\geq$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[1]	Deep errant burrows[1]	
Polychaeta				
Neriedae				
Neanthes limnicola	30 ± 10	Deposit feeder[2]	Mucus tubes[9]	
Spionidae				
Marenzellaria viridis	200 ±70	Passive suspension and deposit feeder[3]	Mucus and sediment tubes[9]	
Sabellidae				
Laonome sp.	400 ±100	Active suspension feeder[2]	Mucus tubes[9]	0.7 ± 0.2
Arthropoda				
Crustacea				
Cumacea				
Nippoleucon hinumensis	20 ±5	Deposit feeder[4]	Free living at surface[4]	
Amphipoda				
Corophium alienense	3800 ± 800	Active suspension and deposit feeder[5]	Mucus tubes[10]	9 ± 2
Gammarus daiberi	50 ± 10	Scraper, partly-pelagic[6]	Free living at surface[11]	
Mollusca				
Bivalvia				
Corbula amurensis	440 ± 150	Active suspension feeder[7]	Shallow burrows[12]	0.6 ± 0.1
Macoma petalum	23 ± 7	Active suspension and deposit feeder[8]	Deep burrows[8]	0.009 ± 0.003

(1) Brinkhurst and Gelder (2001); (2) Fauchald and Jumars (1979); (3) Daunys et al. (1999); (4) Barnes (1980); (5) Moller and Riisgard (2006); (6) A. R. Stewart (U.S. Geological Survey, personal communication based on stable isotopes); (7) Penry (2000); (8) Hummel (1985); (9) Rouse and Pleijel (2001); (10) Meadows et al. (1990); (11) Bousfield (1969); (12) Carlton et al. (1990).

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 $u_{*b}=0.002$-0.018 m s^{-1}. We have presented 95% confidence intervals for estimates.

Assumptions	Average $G=0.41d/C_B$			α (m d^{-1})
	expt 1	expt 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

Table 6 Estimated biomass P:B (g m^{-2}), secondary production P (g C m^{-2} yr^{-1}), and carbon (C)

consumed (g C m^{-2} 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 wt.	C wt.	P:B	P	C consumed
Corbula amurensis	-	1.8	0.7 (1)	2 (2)	1.4	6-14
Macoma petalum	-	1.4	0.6 (1)	1.5 (3)	0.8	8
Corophium alienense	6	0.9 (4)	0.3 (4)	10 (5)	3	30
Polychaeta + Oligochaeta (8)	6	0.8 (4)	0.3 (6)	2 (7)	0.6	6
Community Total		5	2		6	50-60

(1) Cloern et al. 1993; (2) Thompson unpubl. ; (3) Robertson 1979; (4) Lie 1968; (5) Cunha et al. 2000; (6)
Rowe 1983 (conversion factor of 0.375); (7) Schwinghamer et al. 1986; (8) Oligochaeta < 10% of weight

FIGURE CAPTIONS

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 grey areas indicate depths greater than 6 m.

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.

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

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

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

Fig. 6 Time series of 4-averaged vertical profiles of chlorophyll a concentration (μg L^{-1}) ("waterfall plot") for (A) expt. 1 (B) expt. 2. Concentrations are relative to the near-bed concentration.

Fig. 7 Ensemble-averaged dimensionless profiles for (A) expt. 1 and (B) expt. 2. The non-dimensionalization 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) expt. 1, sample 20, (B) expt. 1, sample 11, and (C) expt. 1, sample 6. Chlorophyll *a* concentration is shown for the 4 sample sites: NE (cross), NW (square), SE (triangle), and SW (circle), and *u* and *v* are the streamwise (square) and cross-stream (cross) velocities, respectively.

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

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

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

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 expt. 1 (circle),

expt. 2 (crosses). The dashed lines indicates the mean value of C_B/d=9.5.

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

expt. 1 (circles), expt. 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).

Fig. 14 Schematic of aggregation of pelagic phytoplankton in a near-bed fluff layer

(adapted from Stolzenbach et al. 1992).
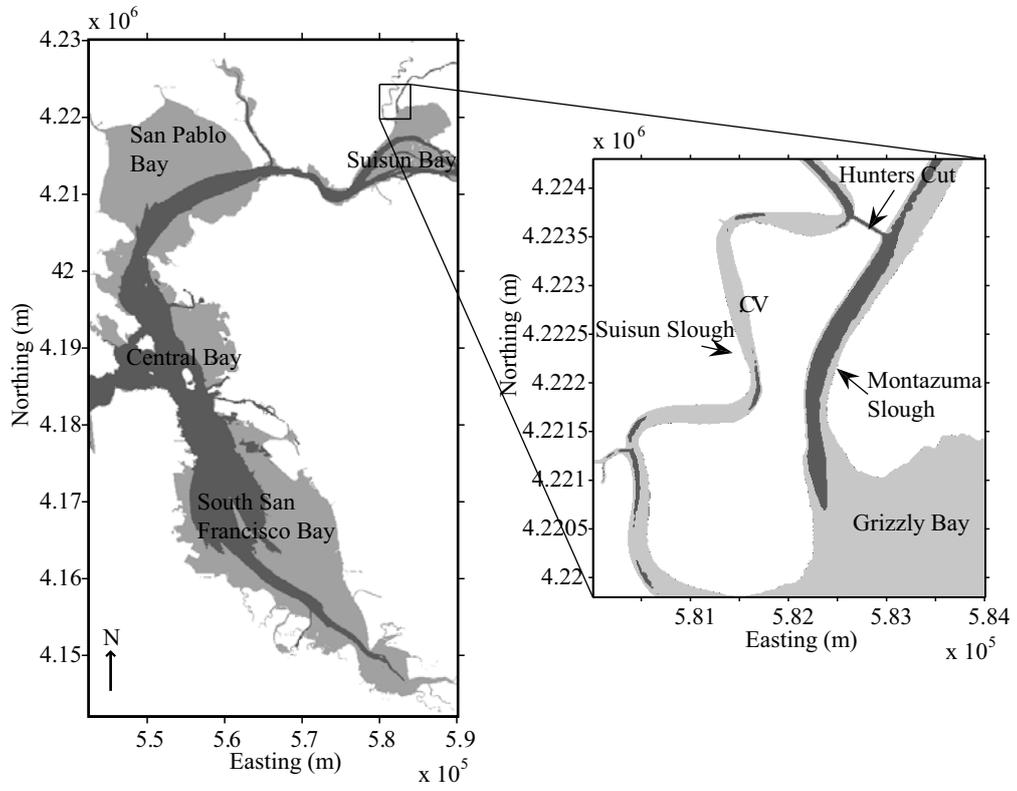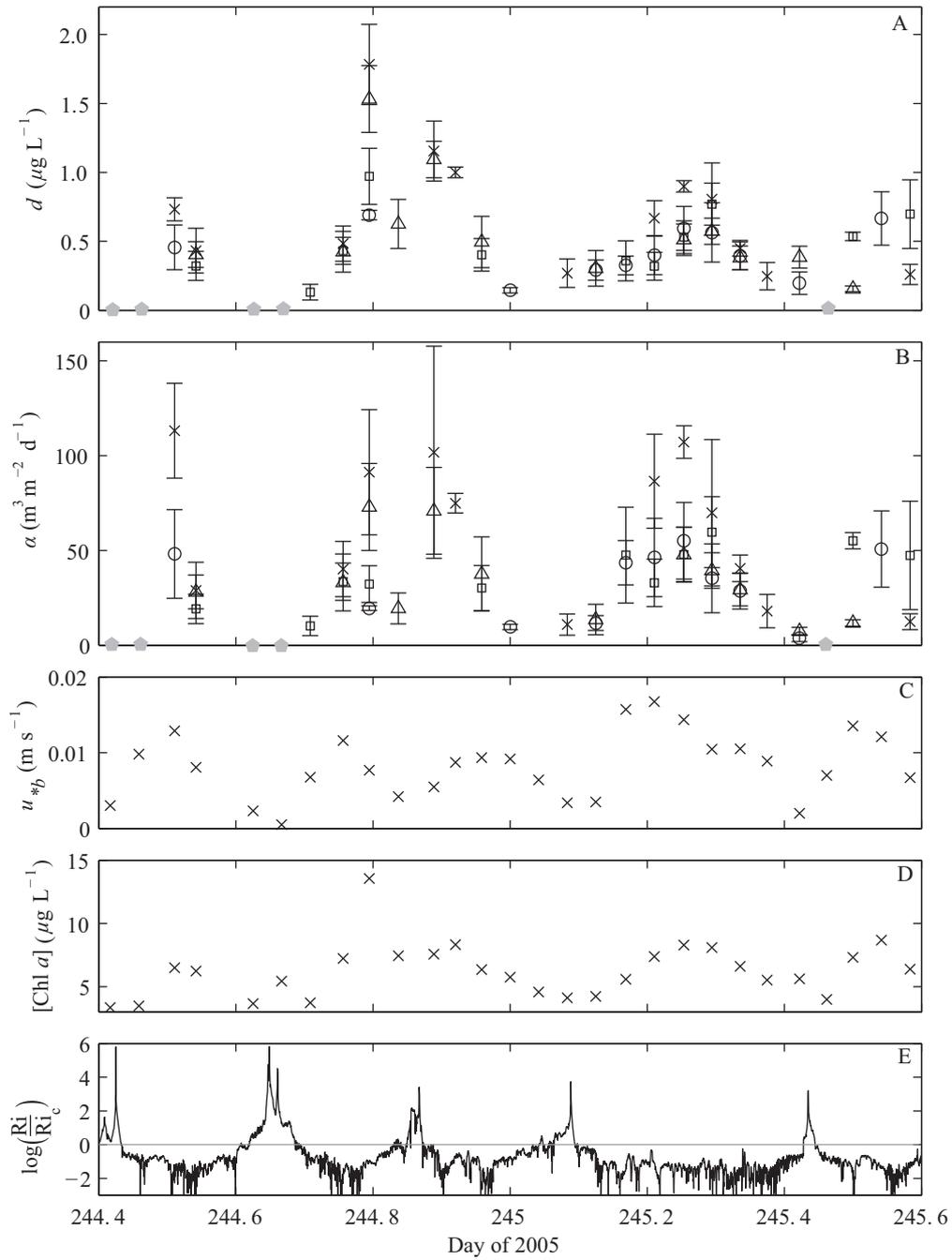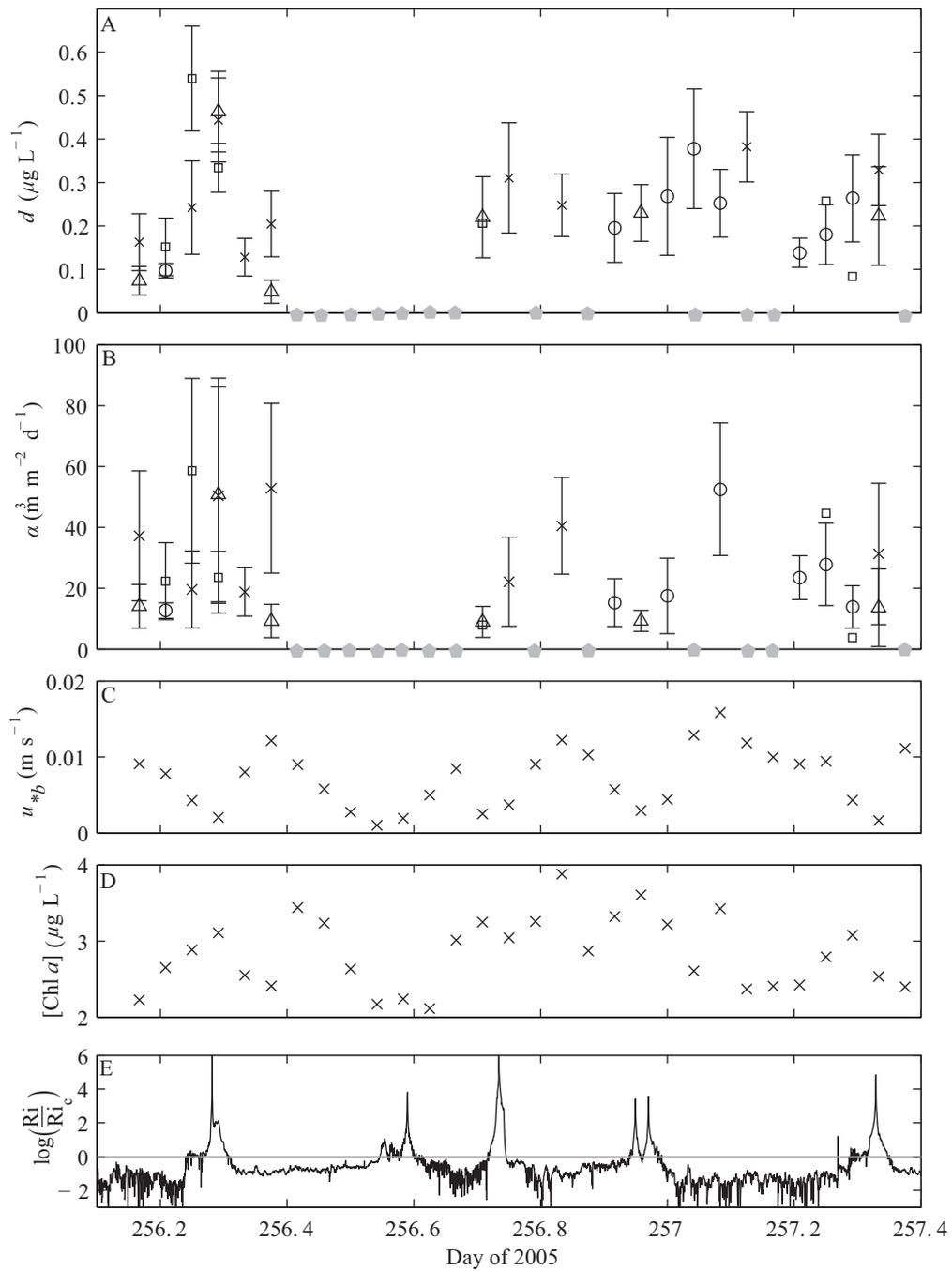
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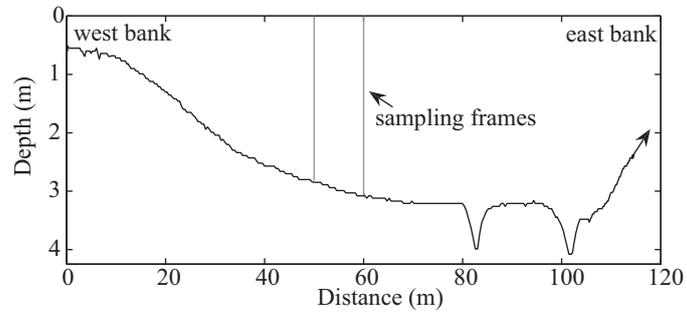
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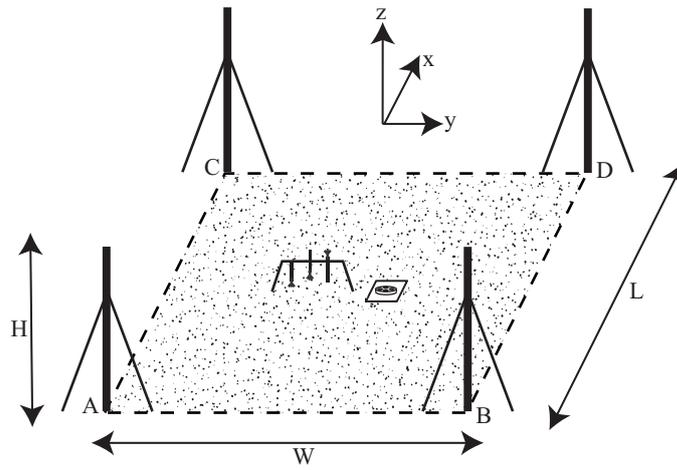
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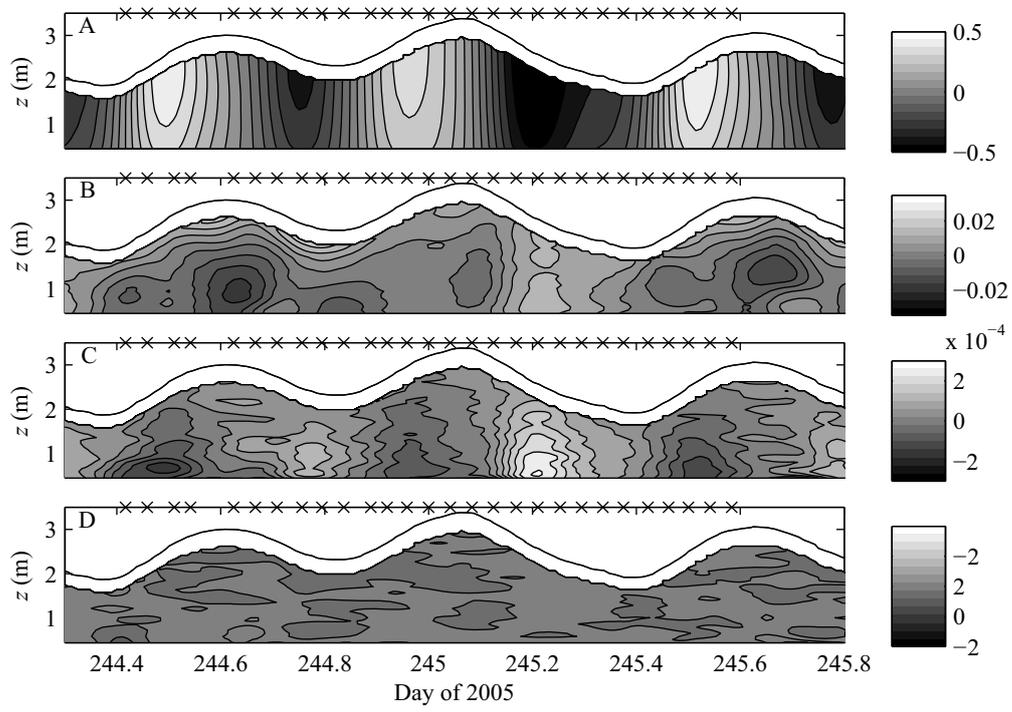
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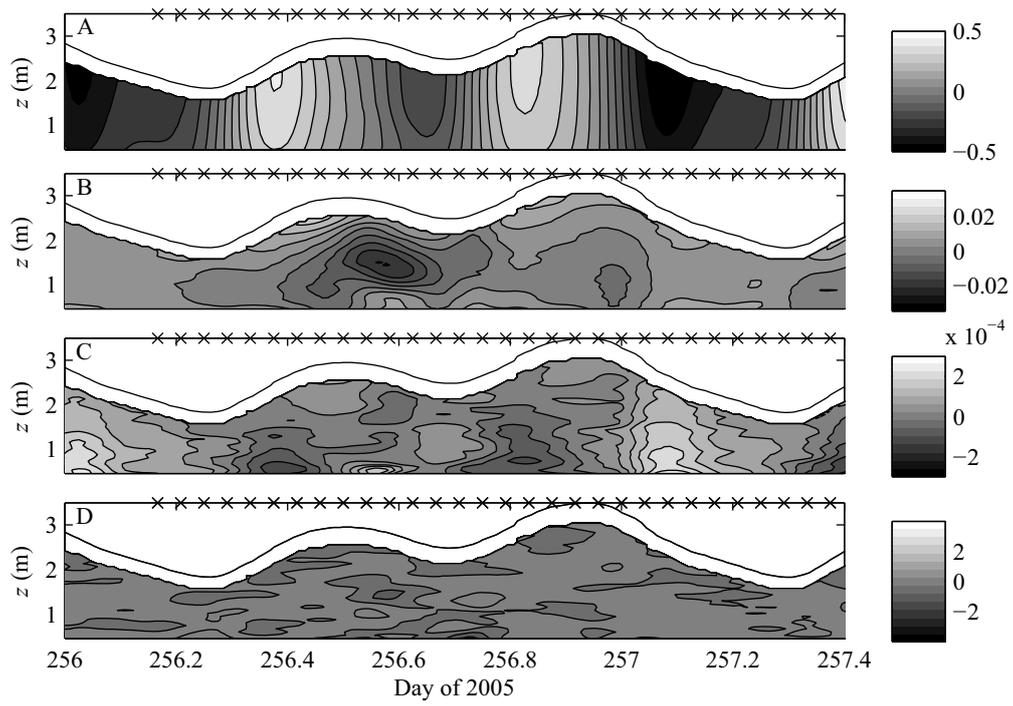
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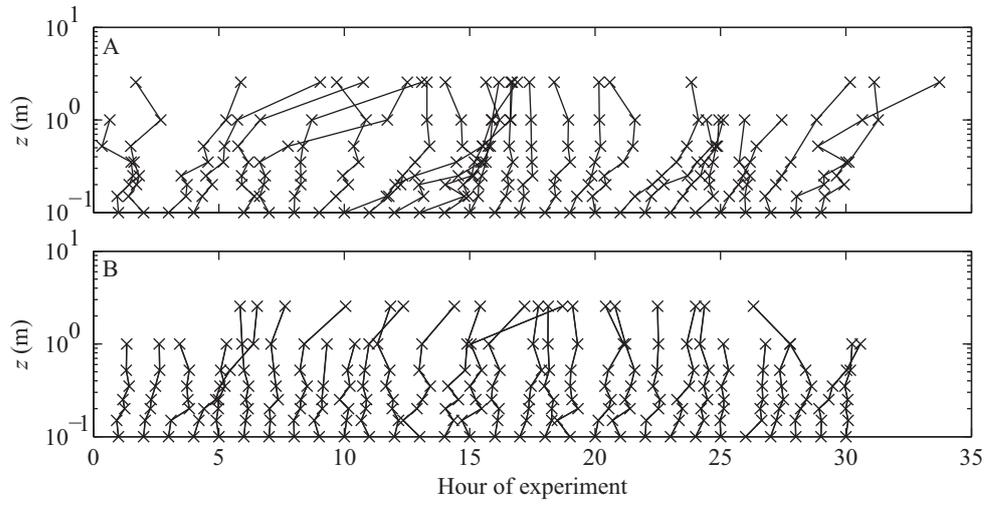
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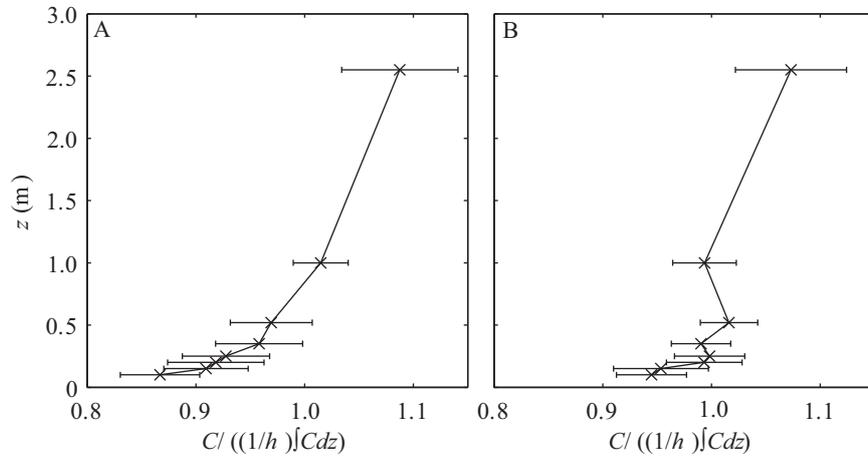
Fig. 7

Fig. 8

Fig. 9

Fig. 10

Fig. 11

11

Fig. 12

Fig. 13

Fig. 14