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# Spatial and Seasonal Patterns in Sediment Nitrogen Remineralization and Ammonium Concentrations in San Francisco Bay, California

JANE M. CAFFREY
*United States Geological Survey*
*345 Middlefield Rd, MS 496*
*Menlo Park, California 94025*

**ABSTRACT: Nitrogen remineralization and extractable ammonium concentrations were measured in sediments from several locations in North and South San Francisco bays. In South Bay, remineralization rates decreased with depth in sediment and were highest in the spring following the seasonal phytoplankton bloom. At the channel stations, peak remineralization lagged peak water-column phytoplankton biomass (as measured by chlorophyll *a*) by a month. Remineralization rates were generally higher in South Bay than North Bay. The lower remineralization rates in North Bay may be a result of anomalously low phytoplankton production and thus reduced deposition to the sediments, as well as low riverine organic inputs to the upper estuary in recent years. Remineralization rates were positively correlated to carbon and nitrogen content of the sediments. In general, ammonium profiles in South Bay sediments showed no increase in deeper (4–8 cm) sediments. In North Bay, ammonium concentrations were greatest at stations with highest remineralization rates, and, in contrast to South Bay, extractable ammonium increased in deeper sediment. Differences in ammonium pools between North Bay and South Bay may be a result of increased irrigation by deep-dwelling macrofauna, which are more abundant in South Bay.**

## Introduction

Ammonium regeneration in sediments is an important link between water column and benthic processes in shallow-water environments. Sedimentation of phytoplankton blooms can be a significant source of organic material to sediments (Jensen et al. 1990; Graf 1992; Kamp-Nielsen 1992; Kemp and Boynton 1992). Following sedimentation, this organic material is decomposed and $NH_4^+$ is released (Klump and Martens 1983). Remineralized $NH_4^+$ may be used directly by benthic algae (Sundbäck and Granéli 1988; Sundbäck et al. 1991) or diffuse out of sediments and become available for phytoplankton production, providing 30–80% of the N requirements for phytoplankton in many temperate estuaries (Blackburn and Henriksen 1983; Kemp and Boynton 1992). Alternatively, $NH_4^+$ produced in the sediments may be oxidized to $NO_3^-$ (nitrification) with some fraction of the $NO_3^-$ subsequently reduced to $N_2$ (denitrification).

San Francisco Bay is a highly urbanized estuary, with a population of approximately 6 million people surrounding the bay. The bay comprises two estuarine systems, each having a different hydrodynamic and freshwater inflow regime (Fig. 1). South Bay is a lagoonal system (salinity 26–30 PSU) whose major inputs of fresh water and nutrients are from sewage treatment plants located at the south end (Nichols et al. 1986). In North Bay, salinity ranges from 0 PSU to 30 PSU. Although there are some nutrient inputs from sewage treatment plants, the major sources of nutrients and fresh water to North Bay are the Sacramento and San Joaquin rivers, which converge in the delta. Riverine inputs were greatly reduced by the 6 yr of drought from 1986 to 1992.

The organic inputs to the sediments of these two systems are very different. River flow is an important factor controlling the inputs of allochthonous material to the bay and regulating stratification, which controls primary production (Cloern 1991). Organic material from the Sacramento and San Joaquin rivers and delta can contribute 75% of the organic inputs to North Bay (Jassby et al. 1993). In addition to river flow, benthic grazing also controls phytoplankton production. Increased grazing due to colonization by the asian clam, *Potamocobula amurensis,* reduced phytoplankton biomass in Suisun Bay between 1986 and 1992 (Alpine and Cloern 1992). Historically, maximum phytoplankton biomass and production occur in the summer in North Bay (Cloern et al. 1983). In contrast, peak phytoplankton biomass and production occur dur-

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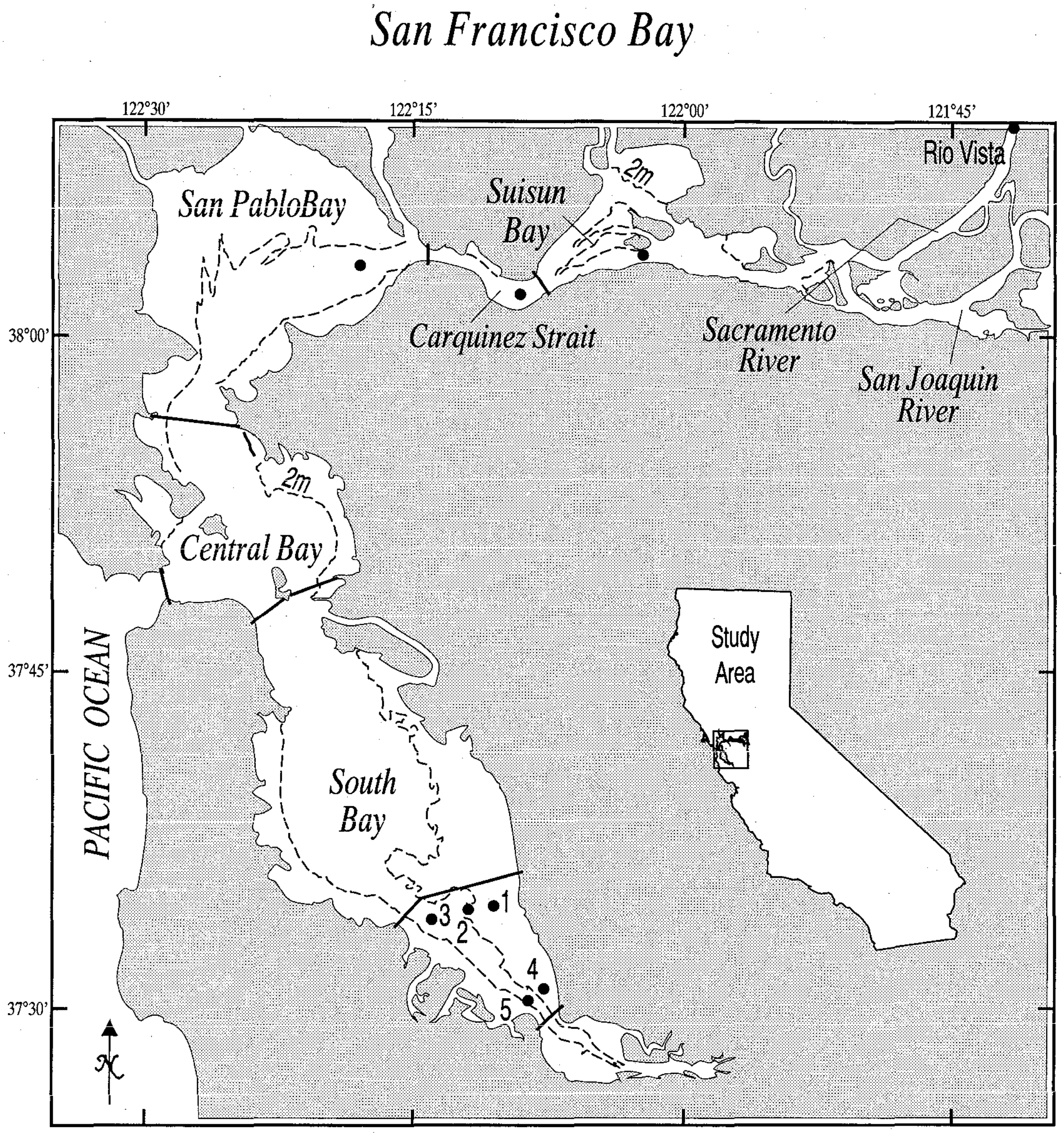

Fig. 1. San Francisco Bay, location of sampling stations.

ing spring in South Bay (Cloern 1991). Phytoplankton and benthic algae represent about 90% of the organic inputs to South Bay (Jassby et al. 1993).

Benthic macrofauna can also enhance $NH_4^+$ regeneration and alter $NH_4^+$ concentrations in sediments by excretion, bioturbation, and production of fecal pellets (Rhoads 1974; McCaffrey et al. 1980; Kristensen and Blackburn 1987; Yamada and Kayama 1987; Jönsson et al. 1993). Historically, North and South bays have had very different benthic communities (Nichols 1979). Macrofauna biomass in North Bay is low, between 60 g wet wt $m^{-2}$ and 630 g wet wt $m^{-2}$ (Nichols and Pamatmat 1988), and surface-dwelling bivalves predominate in the channel, primarily *Potamocorbula amurensis* (200 g wet wt $m^{-2}$, Nichols et al. 1990). Biomass and abundance of macrofauna, particularly deposit feeders, are greater in South Bay (Nichols and Pamatmat 1988). *Asychis elongata,* a tube-dwelling polychaete, is common in shallow and deep water, with burrows reaching 50 cm deep in sediments, and can occur in very dense patches in South Bay (Nichols 1979). Ventilation of burrows by macrofauna can increase $NH_4^+$ efflux and nitrification rates, thus reducing sediment $NH_4^+$ concentrations (Hammond et al. 1985; Kristensen and Blackburn 1987).

One goal of this research was to compare rates of nitrogen remineralization, as measured by net

TABLE 1. Characteristics of North and South Bay stations, water depth at mean tide, ranges of salinity, temperature, and phytoplankton biomass over an annual cycle in the water column.

| Station | Water Depth m | Salinity Range PSU | Temperature Range °C | Water Column Chlorophyll $a$[a] $\mu g\ l^{-1}$ |
|---|---|---|---|---|
| North Bay | | | | |
| Rio Vista | 11 | 0–0.4 | 8.9–22.5 | 0.7–5.1 |
| Suisun Bay | 8 | 8–12 | 9.6–20.2 | 0.7–2.7 |
| Carquinez Strait | 12 | 13–23 | 9.2–20 | 0.6–3.0 |
| San Pablo Bay | 11 | 20–26 | 9.8–20 | 0.9–3.7 |
| South Bay | | | | |
| 1 | 2 | 27–30 | 10–18 | 1.7–26 |
| 2 | 3 | 27–30 | 10–19 | n.d.[b] |
| 3 | 11 | 28–30 | 9.6–21 | 1.9–27 |
| 4 | 2 | 27–30 | 10.5–21 | n.d. |
| 5 | 12 | 26–30 | 9.4–21 | 1.4–12.8 |

[a] Water column chlorophyll $a$ numbers from Wienke et al. (1992, 1993).

[b] n.d. = no data.

TABLE 2. Depth distributions of nitrogen (N) and carbon (C) content and porosity in sediments at North and South Bay stations.

| Station | Depth (cm) | N[a] (% dry weight) | C[a] (% dry weight) | Porosity[b] |
|---|---|---|---|---|
| North Bay | | | | |
| Rio Vista | 0–1 | 0.05 | 0.5 | 0.56 |
| | 1–2 | 0.05 | 0.6 | 0.52 |
| | 2–4 | 0.05 | 0.4 | 0.51 |
| | 4–6 | 0.02 | 0.2 | 0.48 |
| | 6–8 | n.d.[c] | n.d. | 0.31 |
| Suisun Bay | 0–1 | 0.04 | 0.5 | 0.51 |
| | 1–2 | 0.04 | 0.6 | 0.51 |
| | 2–4 | 0.05 | 0.7 | 0.51 |
| | 4–6 | 0.07 | 1.1 | 0.52 |
| | 6–8 | n.d. | n.d. | 0.48 |
| Carquinez Strait | 0–1 | 0.11 | 1.4 | 0.66 |
| | 1–2 | 0.09 | 1.4 | 0.66 |
| | 2–4 | 0.08 | 1.1 | 0.67 |
| | 4–6 | 0.10 | 1.5 | 0.66 |
| | 6–8 | n.d. | n.d. | 0.67 |
| San Pablo | 0–1 | 0.01 | 0.1 | 0.49 |
| | 1–2 | 0.01 | 0.1 | 0.48 |
| | 2–4 | 0.04 | 0.5 | 0.53 |
| | 4–6 | 0.06 | 0.8 | 0.56 |
| | 6–8 | 0.06 | 0.8 | 0.57 |
| South Bay | | | | |
| 1 | 0–1 | 0.12 | 1.1 | 0.74 |
| | 1–2 | 0.08 | 1.2 | 0.67 |
| | 2–4 | 0.07 | 1.0 | 0.60 |
| | 4–6 | 0.05 | 0.7 | 0.54 |
| | 6–8 | 0.06 | 0.8 | 0.56 |
| 2 | 0–1 | 0.12 | 1.2 | 0.82 |
| | 1–2 | 0.15 | 1.3 | 0.77 |
| | 2–4 | 0.11 | 1.2 | 0.75 |
| | 4–6 | 0.11 | 1.3 | 0.73 |
| | 6–8 | 0.11 | 1.3 | 0.72 |
| 3 | 0–1 | 0.14 | 1.4 | 0.80 |
| | 1–2 | 0.14 | 1.7 | 0.81 |
| | 2–4 | 0.16 | 1.4 | 0.78 |
| | 4–6 | 0.14 | 1.5 | 0.77 |
| | 6–8 | 0.14 | 1.5 | 0.77 |
| 4 | 0–1 | 0.13 | 1.1 | 0.82 |
| | 1–2 | 0.11 | 1.2 | 0.80 |
| | 2–4 | 0.12 | 1.3 | 0.77 |
| | 4–6 | 0.12 | 1.2 | 0.74 |
| | 6–8 | 0.11 | 1.2 | 0.72 |
| 5 | 0–1 | 0.14 | 1.4 | 0.82 |
| | 1–2 | 0.14 | 1.4 | 0.79 |
| | 2–4 | 0.13 | 1.4 | 0.77 |
| | 4–6 | 0.12 | 1.4 | 0.77 |
| | 6–8 | 0.12 | 1.6 | 0.76 |

[a] %C = mg C (mg dry wt)$^{-1}$ × 100, %N = mgN (mg dry wt)$^{-1}$ × 100.

[b] Porosity for each layer calculated from percent water in sediment (cm$^3$ water/cm$^3$ whole sediment), assuming sediment density of 2.6 g cm$^{-3}$.

[c] n.d. = no data.

$NH_4^+$ production, and $NH_4^+$ concentrations in North Bay and South Bay sediments. This included investigating the depth distribution of net $NH_4^+$ production and seasonal changes in these rates. Because net $NH_4^+$ production is controlled by concentrations of reactive organic matter (Klump and Martens 1983, 1989), remineralization rates in San Francisco Bay may respond to the timing and source of organic matter, which differ between North and South Francisco bays. A second objective was to examine the relationship between remineralization rates and sediment $NH_4^+$ concentrations, and determine the turnover time of $NH_4^+$ in the sediments. An increase in sediment $NH_4^+$ concentration indicates greater production by remineralization than loss by processes such as nitrification or $NH_4^+$ flux out of sediments.

## Materials and Methods

Sampling locations were selected from sites of ongoing long-term monitoring of benthic communities by the United States Geological Survey. In addition, stations in the channel coincided with hydrographic stations, which were sampled monthly by the United States Geological Survey. Sediment samples were collected at four stations in North San Francisco Bay: Rio Vista (hydrographic station 657), Suisun Bay (station 6), Carquinez Strait (station 8), and San Pablo Bay (station 12.5); and five stations in South San Francisco Bay (Fig. 1). The North Bay stations occur along a salinity gradient from fresh water (Rio Vista) to 20–26 PSU (San Pablo Bay). The South Bay stations, which are split into two transects, are located along a longitudinal gradient. Water depths at these stations ranged from 2 m to 12 m (Table 1). Stations 3 and

5 are located in the channel, while the others are located on the shoals.

Sediment cores (2.5 or 4.5 cm i.d.) were taken out of Van Veen grabs. Only grabs with intact surficial sediments were used for coring. Samples were analyzed for percent water, extractable $NH_4^+$ concentrations, net $NH_4^+$ production, carbon (C) content, and nitrogen (N) content. Surface water temperature and salinity were measured at each station. In North Bay, sediments were collected in August and November 1991, and January, March, and June 1992, during a period of low river flow. Samples were also collected at Rio Vista and Suisun Bay in January and May 1993 when river flows were considerably higher than in 1992. South Bay station 3 was sampled intensively to examine seasonal patterns in $NH_4^+$ production, particularly before and after the spring phytoplankton bloom. Sediments were collected at station 3 in July and September 1991, and January, April, May, June, and September 1992. Spatial variability in South Bay was examined by sampling stations 1, 2, 4, and 5 in September 1991, and January and September 1992. Additional cores were collected at stations 1 and 2 in April 1992 and at stations 4 and 5 in May 1992.

### EXTRACTABLE $NH_4^+$

Triplicate sediment cores were sliced at five depth intervals (0–1 cm, 1–2 cm, 2–4 cm, 4–6 cm, and 6–8 cm) and $NH_4^+$ was extracted with 2 M NaCl (10 g sediment per 10 ml NaCl). NaCl is as effective an extractant as KCl (Blackburn 1986) but prevents damage to benthic organisms (Lomstein et al. 1989). Sediment extracts were centrifuged, filtered, and frozen. $NH_4^+$ concentrations in sediment extracts were measured by the salicylate-hypochlorite method (Bower and Holm-Hansen 1980) as modified for automated analysis (Hager 1993).

### NET $NH_4^+$ PRODUCTION

Net $NH_4^+$ production was measured according to Aller and Yingst (1980). Triplicate sediment cores were sliced at four depth intervals (0–1 cm, 1–2 cm, 2–4 cm, and 4–8 cm), except in August and September 1991 when cores were sliced into five depth intervals (0–1 cm, 1–2 cm, 2–4 cm, 4–6 cm, and 6–8 cm). The triplicate sediment sections were thoroughly mixed together and packed into six 7-ml plastic scintillation vials, which were incubated in the laboratory at in situ temperatures for 8 d. Any visible macrofauna were picked out of the sediments, although small macrofauna and meiofauna were probably present. Initial $NH_4^+$ concentrations were determined on samples from the homogenized sediment at time zero ($t_0$). Duplicate vials were sampled for $NH_4^+$ at 2-d, 4-d and 8-d intervals. Sediment $NH_4^+$ was extracted with 2 M NaCl and analyzed as described above. Net $NH_4^+$ production was calculated for each sediment interval as the slope of $NH_4^+$ concentration versus time for the linear portion of the curve. Standard errors of the slope were also calculated.

### SEDIMENT CHARACTERISTICS

Subsamples of wet sediment, approximately 8 g, from the five depth intervals (0–1 cm, 1–2 cm, 2–4 cm, 4–6 cm, and 6–8 cm) were weighed, dried at 60°C for a minimum of 48 h, and reweighed for calculation of percent water content. The dried sediment samples were ground with mortar and pestle and analyzed without acidification for C content and N content on a Perkin Elmer elemental analyzer (Wienke and Cloern 1987). Depth profiles of both C and N content were made at all stations in either August or September 1991; only surficial (0–1 cm) sediments were analyzed on the subsequent sampling dates. Benthic chlorophyll *a* and phaeopigments were measured in cores collected at stations 1 and 3 from February to September 1992 and analyzed as described in Thompson et al. (1981).

### STATISTICS

Analysis of variance and correlation analysis were made using SYSTAT (Wilkinson 1990). For the analysis of variance, the data were divided into three sampling periods: November to February, March to May, and June to October. These periods reflect the typical climatic regime of San Francisco Bay: a rainy season with low water temperatures and periods of high river discharge; a transitional period when temperatures are increasing while precipitation and discharge are intermittent; and a dry season with higher water temperatures (Conomos et al. 1979). In addition to season, the effect of station and depth on net $NH_4^+$ production were compared in the analysis of variance.

## Results

Temperatures were similar in North and South bays, while the range of salinity and phytoplankton biomass were very different (Table 1). On average, chlorophyll *a* concentrations in North Bay were about half the values measured in South Bay, except during the spring bloom in South Bay when chlorophyll *a* concentrations were an order of magnitude greater than North Bay concentrations (Table 1). The average sediment C and N values were lower at North Bay stations than at South Bay stations (Table 2). Sediment porosity was also lower in North Bay, particularly in Suisun and San Pablo Bay sediments, which were coarse sands,

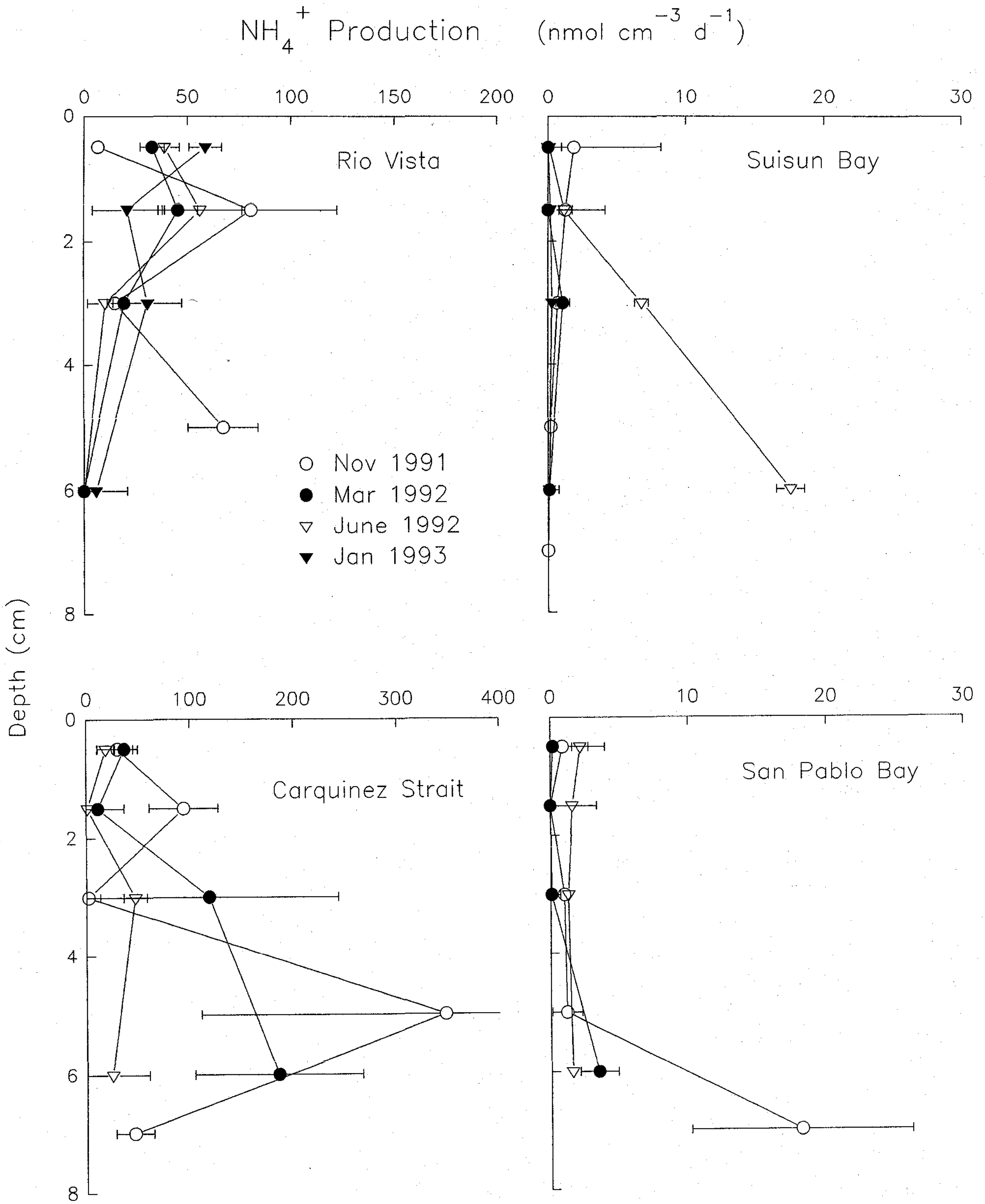

Fig. 2. Production of $NH_4^+$ (nmol $cm^{-3}$ $d^{-1}$) with depth (cm) at North Bay stations in November 1991, March 1992, June 1992, and January 1993. Note change in scales of rates among individual stations.

while South Bay stations 2–5 had a finer silty-clay texture (Table 2).

### NORTH BAY

$NH_4^+$ production was variable among the four North Bay stations (Fig. 2). Rates were very low in Suisun Bay and San Pablo Bay, usually less than 20 nmol $cm^{-3}$ $d^{-1}$ (Fig. 2). In contrast, net $NH_4^+$ production at Rio Vista was usually higher, from 10 nmol $cm^{-3}$ $d^{-1}$ to 80 nmol $cm^{-3}$ $d^{-1}$, while rates at the Carquinez Strait station were much higher, particularly in November and March when rates in the deeper layers reached 350 nmol $cm^{-3}$ $d^{-1}$ (Fig. 2). An ANOVA indicated that net $NH_4^+$ production rates at the North Bay stations were significantly different ($p < 0.001$) from one another; however, neither depth ($p < 0.09$), nor season ($p < 0.72$) were significant. Net $NH_4^+$ production was probably not significantly different among the four different depth intervals because at one station (Rio Vista) $NH_4^+$ production was higher in the surface layers while the pattern was the opposite at the Carquinez Strait station, where $NH_4^+$ production was usually higher below 2 cm than above (Fig. 2). At the Suisun Bay and San Pablo Bay stations, there were no consistent differences in $NH_4^+$ production with depth. North Bay stations did not have consistent seasonal patterns in integrated (0–8 cm) $NH_4^+$ production (Fig. 3). Rates were highest at Rio Vista and San Pablo Bay in November 1991, and in June 1992 in Suisun Bay. $NH_4^+$ production measured at Suisun Bay in January and May 1993 was low, about 0.01 mmol $m^{-2}$ $d^{-1}$, as was $NH_4^+$ production in Rio Vista in May 1993 (Fig. 3). In January 1993 at Rio Vista, $NH_4^+$ production was an order of magnitude higher than in January 1992.

Extractable $NH_4^+$ concentrations usually increased with depth in the North Bay, although concentrations varied among stations (Fig. 4). $NH_4^+$ concentrations were lowest in Suisun Bay, less than 20 nmol $cm^{-3}$ in November and March. Concentrations at Rio Vista and San Pablo Bay ranged from 100 nmol $cm^{-3}$ in the 0–1 cm layer to 400 nmol $cm^{-3}$ in deeper layers, except at Rio Vista in March when concentrations were higher, and San Pablo Bay in June when concentrations were very low (Fig. 4). The Carquinez Strait station had the highest concentrations, up to 3,500 nmol $cm^{-3}$ in the 6–8 cm depth, and little seasonal change in concentrations (Fig. 4). The extractable $NH_4^+$ concentrations should be interpreted with caution because of possible disturbance or loss of porewater from the Van Veen grab during collection. This would have been more of a problem in the sandy sediments from Suisun and San Pablo bays.

$NH_4^+$ concentrations seemed to follow $NH_4^+$ production, with higher rates and concentrations at Carquinez Strait, intermediate rates and concentrations at Rio Vista, and low rates and concentrations in Suisun and San Pablo bays. $NH_4^+$ production and extractabled $NH_4^+$ concentrations were positively correlated in the North Bay ($r = 0.45$, $p < 0.001$).

### SOUTH BAY

Rates of $NH_4^+$ production decreased with depth at South Bay stations during most months, except at station 2 in April and station 3 in September (Fig. 5). The highest rates at station 3 were in the 0–1 cm layers in July 1991 and May 1992 (Fig. 5). An ANOVA of the South Bay data showed that $NH_4^+$ production was significantly different between depths ($p = 0.002$), but station ($p = 0.76$) and season ($p = 0.07$) were not significant.

$NH_4^+$ production integrated over the top 8 cm in South Bay ranged from 0.4 mmol $m^{-2}$ $d^{-1}$ in January to 12.3 mmol $m^{-2}$ $d^{-1}$ in May (Fig. 3). Stations 2, 3, 4, and 5 had peak $NH_4^+$ production rates in the spring (Fig. 3). $NH_4^+$ production at station 1 was high in September in 1991 and 1992, while rates at station 4 were high in September 1991 and May 1992 (Fig. 3). Spatial variability in South Bay was greatest during the spring and fall of 1992.

Extractable $NH_4^+$ concentrations varied between 100 nmol $cm^{-3}$ and 300 nmol $cm^{-3}$ and usually showed little change with depth (Fig. 6). On several occasions, $NH_4^+$ concentrations did increase with depth: at station 1 in April, at station 3 in April, May, and September 1992, and at station 5 in September (Fig. 6).

## Discussion

Net $NH_4^+$ production rates in San Francisco Bay sediments are comparable to rates measured in other sediments (Table 3). Profiles showing an exponential decrease in $NH_4^+$ production with depth in the South Bay are very similar to those from Danish coastal waters (Blackburn and Henriksen 1983), Long Island Sound (Aller and Yingst 1980; Mackin and Swider 1989), Cape Lookout Bight (Klump and Martens 1989), and Georgia Bight (Hopkinson 1987). In contrast, the seasonal pattern was quite different between San Francisco Bay and most of these locations, which had peak sum-

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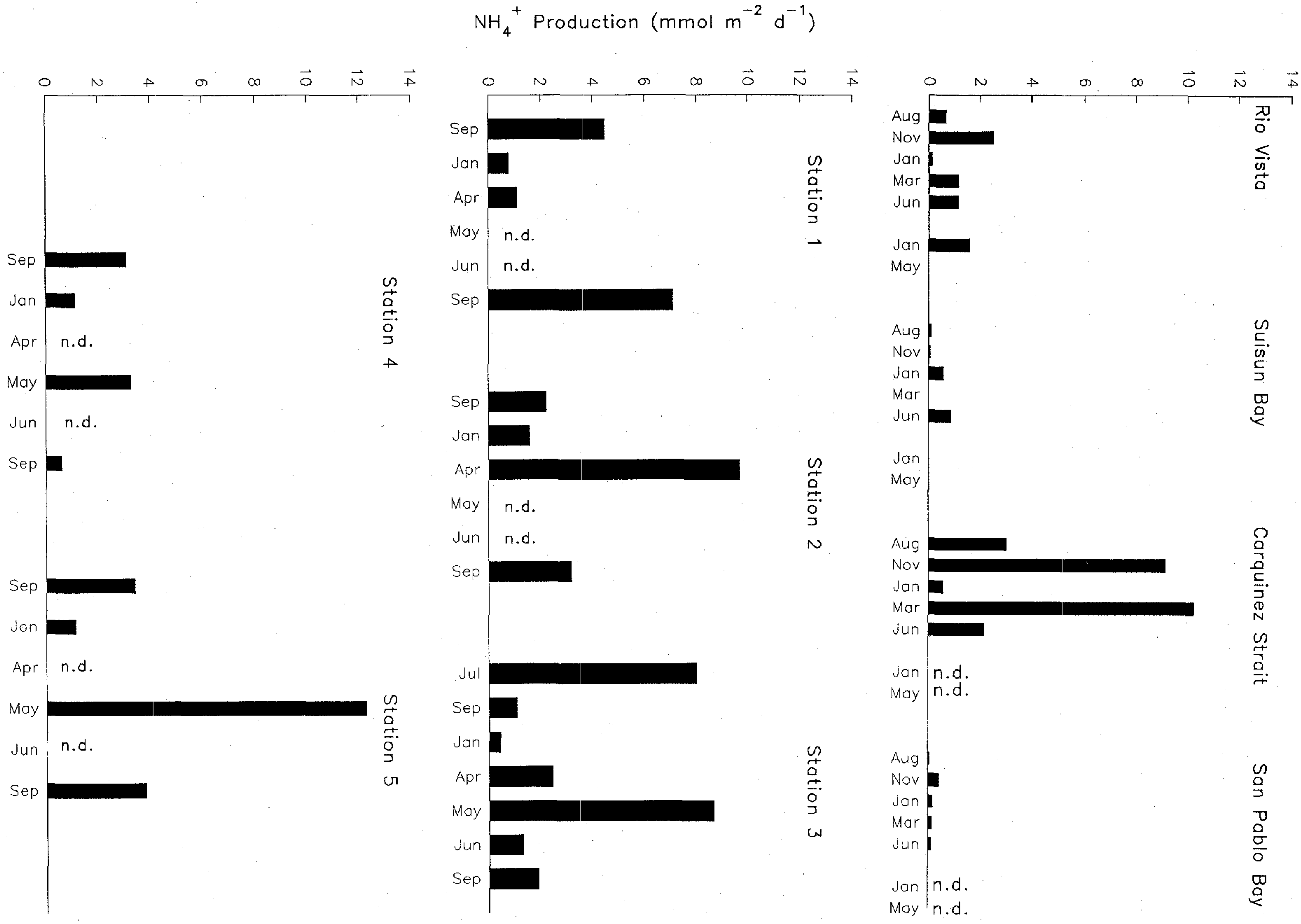
Fig. 3. Integrated (0–8 cm) $NH_4^+$ production from August 1991 to May 1993 in North Bay and July 1991 to September 1992 in South Bay.


NH$_4^+$ Production (mmol m$^{-2}$ d$^{-1}$)
0
2
4
6
8
10
12
14
Rio Vista
Aug
Nov
Jan
Mar
Jun
Jan
May
Suisun Bay
Aug
Nov
Jan
Mar
Jun
Jan
May
Carquinez Strait
Aug
Nov
Jan
Mar
Jun
Jan n.d.
May n.d.
San Pablo Bay
Aug
Nov
Jan
Mar
Jun
Jan n.d.
May n.d.
Station 1
Sep
Jan
Apr
May n.d.
Jun n.d.
Sep
Station 2
Sep
Jan
Apr
May n.d.
Jun n.d.
Sep
Station 3
Jul
Sep
Jan
Apr
May
Jun
Sep
Station 4
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Station 5
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Apr n.d.
May
Jun n.d.
Sep

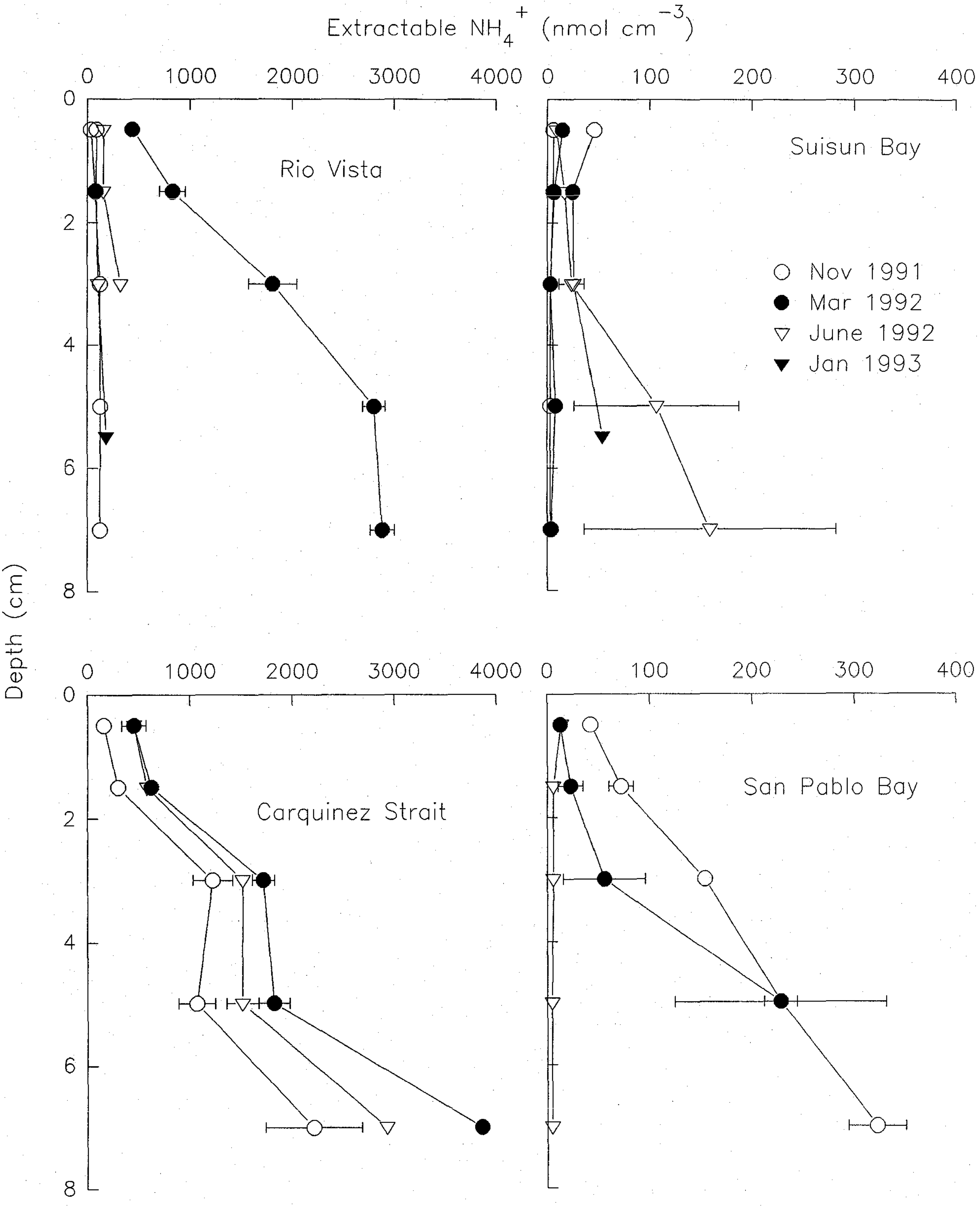

Fig. 4. Extractable $NH_4^+$ concentrations (nmol $cm^{-3}$) with depth (cm) at North Bay stations in November 1991, March 1992, June 1992, and January 1993. Note change in scale for concentrations among individual stations.

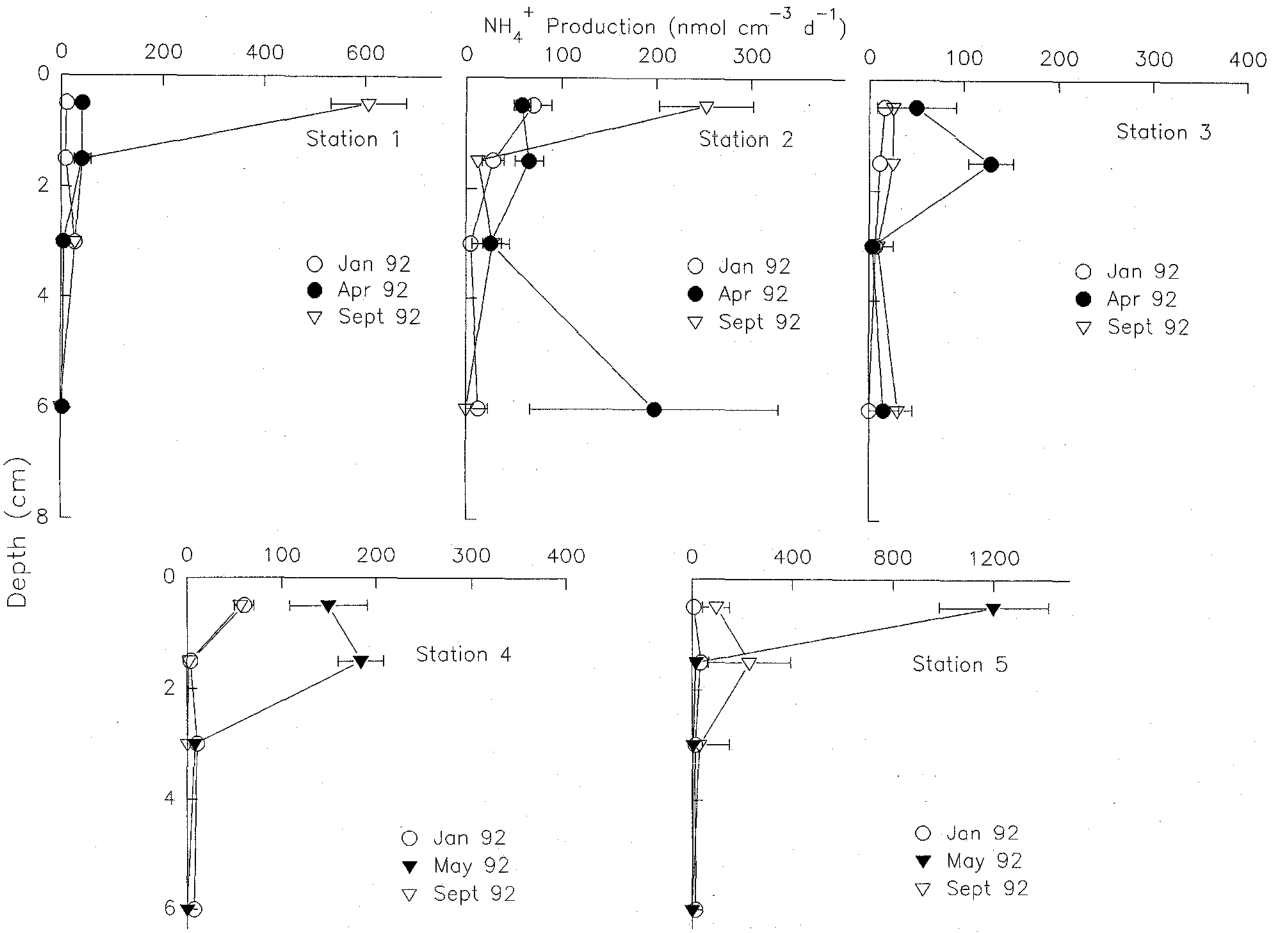

Fig. 5. Production of $NH_4^+$ (nmol $cm^{-3}$ $d^{-1}$) with depth (cm) at South Bay stations 1, 2, and 3 in January, April, and September 1992 and at stations 4 and 5 in January, May, and September 1992. Note change in scales of rates among individual stations.

mer rates. Rates in San Francisco Bay were not driven by temperature, which ranges from 8°C to 22°C. Because San Francisco Bay has a Mediterranean-type climate, factors other than temperature seem to control $NH_4^+$ production, principally the timing of organic inputs in South Bay and the sediment type in North Bay. Highest rates usually occurred in the spring in South Bay and were variable at North Bay stations.

### SPATIAL VARIABILITY

Jassby et al. (1993) have attributed interannual variability in organic inputs to North Bay to the annual changes in river discharge, with higher POC inputs during periods of high river flow. During the period of this study, organic inputs to North Bay were probably reduced because of the drought conditions, as well as lower in situ production from benthic grazing. Daily river flow during the period of August 1991–June 1992 averaged 113 $m^3$ $s^{-1}$, with peak daily flows of about 300 $m^3$ $s^{-1}$ during January, March, and April 1992 (S. Greene personal communication). Average river flow was much higher in 1993 (about 1,100 $m^3$ $s^{-1}$ from Dec 1992–May 1993) with peaks of 2,300 $m^3$ $s^{-1}$ (S. Greene personal communication). Winter river flow in nondrought years usually exceeds 1,000 $m^3$ $s^{-1}$ (Nichols et al. 1986). Low $NH_4^+$ production and lack of a seasonal pattern may result from low and intermittent inputs of organic matter from riverine sources. However, despite higher river flows in 1993, $NH_4^+$ production at the Suisun Bay station was low, while at the Rio Vista station, production was high in January but zero in May. This suggests that riverine inputs of organic matter were not the sole factor controlling $NH_4^+$ production in North Bay.

The low rates of $NH_4^+$ production in Suisun Bay and San Pablo Bay also may be related to sediment texture. Sediment organic content is normally lower in sands than in silts and clays. Sediments at these two stations were coarse sand that had very low C (0.3%) and N (0.03%) contents. In contrast the finer, more clayey sediments at the

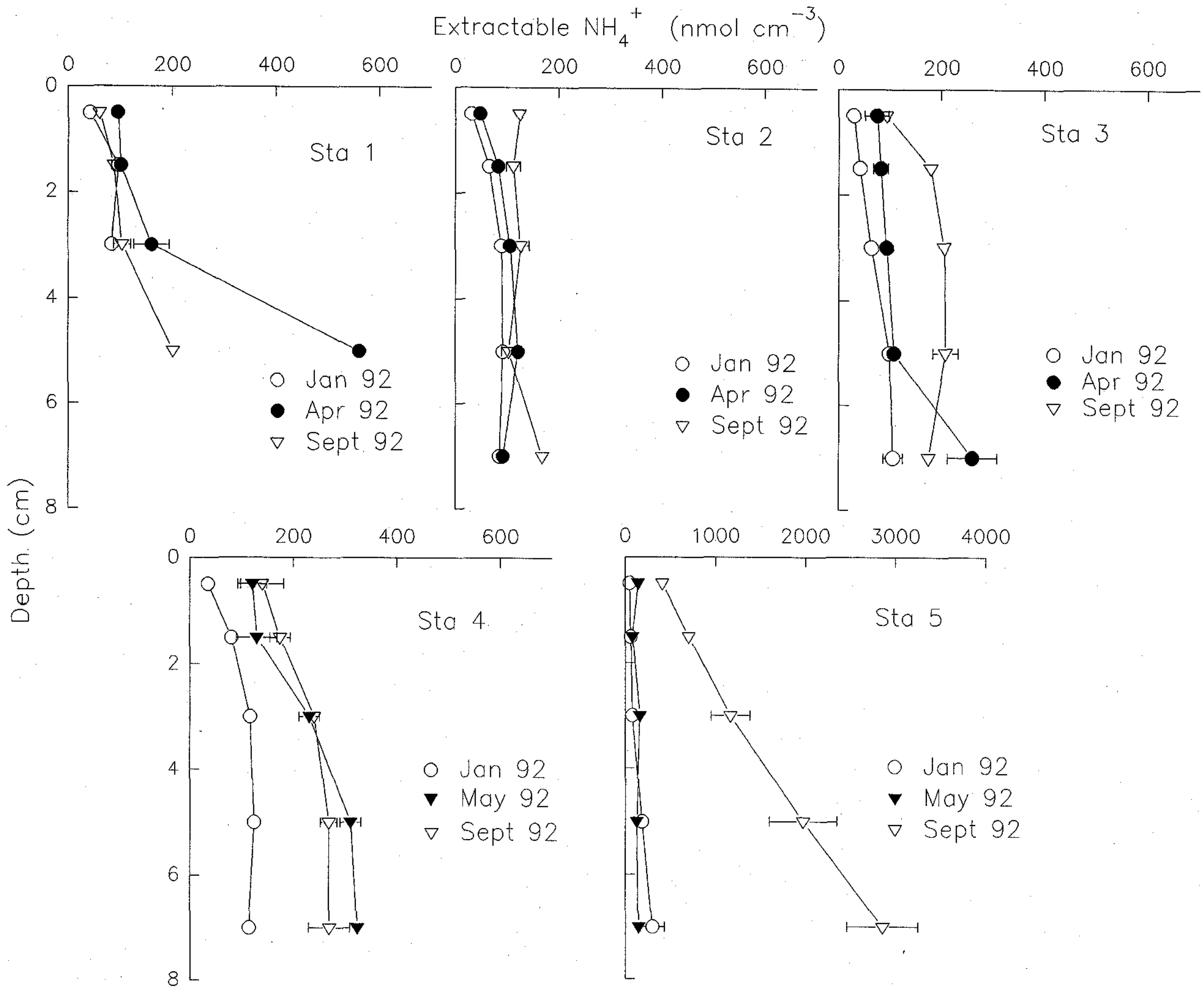

Fig. 6. Extractable $NH_4^+$ concentrations (nmol $cm^{-3}$) with depth (cm) at South Bay stations 1, 2, and 3 in January, April, and September 1992 and at stations 4 and 5 in January, May, and September 1992. Note change in scale for concentrations among individual stations.

Rio Vista and Carquinez Strait stations had higher C (0.7% and 1.2%) and N (0.06% and 0.09%) contents (Table 2, Nichols and Thompson 1985). In addition, sand is sometimes dredged from the channel at the Suisun Bay station (B. Richards personal communication) and this disruption would have had a significant impact on benthic processes. In other systems, the relationship between remineralization rates and sediment texture or organic content does not follow a consistent pattern. Remineralization rates were higher in organic-rich sediments in Flax Pond than from Long Island Sound (Mackin and Swider 1989). In contrast, Boon and Cain (1988) found no relationships between $NH_4^+$ production and clay content, organic matter, total N content, C:N ratio, or extractable $NH_4^+$ concentrations in a variety of salt marsh and mangrove sediments.

Net $NH_4^+$ production was significantly higher ($p < 0.005$) and less variable at South Bay stations than at North Bay stations. Only at the Carquinez Strait station were rates as great as those in the South Bay. In contrast to the pattern of South Bay, rates of $NH_4^+$ production at Carquinez Strait were greater at deeper depths in the sediment. Carquinez Strait sediments have a high clay content so the high $NH_4^+$ production rates may be a result of high organic matter concentrations associated with these fine-grained sediments. $NH_4^+$ production in South Bay usually decreased at depths > 2 cm. Sediment types at South Bay stations were very similar: fine grained at stations 2, 3, 4, and 5, and muddy-

TABLE 3. Production of $NH_4^+$ measured in coastal sediments.

| Location | Rate (mmol $m^{-2}$ $d^{-1}$) | Reference |
|---|---|---|
| Bering Shelf | 2.9 | Lomstein et al. 1989 |
| Tague Reef, St. Croix | 3.5 ± 1.6 | Williams et al. 1985 |
| Long Island Sound, USA | 3.2–7.6 | Aller and Yingst 1980, Mackin and Swider 1989 |
| Danish coastal waters | 3.6–10.6 | Blackburn and Henriksen 1983 |
| Limfjorden, Denmark | 13.0 | Blackburn 1979 |
| Georgia Bight, USA | 8.8–19.1 | Hopkinson 1987 |
| Cape Lookout Bight, USA | 26.4 | Klump and Martens 1989 |
| Flax Pond, USA | 5–48 | Mackin and Swider 1989 |
| Japanese coastal waters | 2.1–63 | Sumi and Koike 1990 |
| North San Francisco Bay, USA | 0.0–10.3 | This study |
| South San Francisco Bay, USA | 0.4–12.3 | This study |

sand at station 1 (Nichols and Thompson 1985). The N or C content in the sediments was positively correlated ($p < 0.01$) with average $NH_4^+$ production (Fig. 7).

Turnover of $NH_4^+$ in sediments was also very different between North and South bays, with very slow rates of turnover in North Bay compared to South Bay (Table 4). $NH_4^+$ concentrations in the sediments (0–8 cm) were estimated to take between 3 d and 1,000 d to turn over in North Bay, while $NH_4^+$ in South Bay frequently turned over in less than 5 d. This is consistent with the depth distribution of $NH_4^+$ production, which suggests that remineralization in North Bay is dependent on previously accumulated organic matter instead of fresh organic matter. These turnover times also illustrate the dynamic nature of nitrogen in South Bay sediments, where turnover times for most of the surficial South Bay sediments in May are less than 1 d. Turnover rates were somewhat lower in the winter, although that was not a consistent feature.

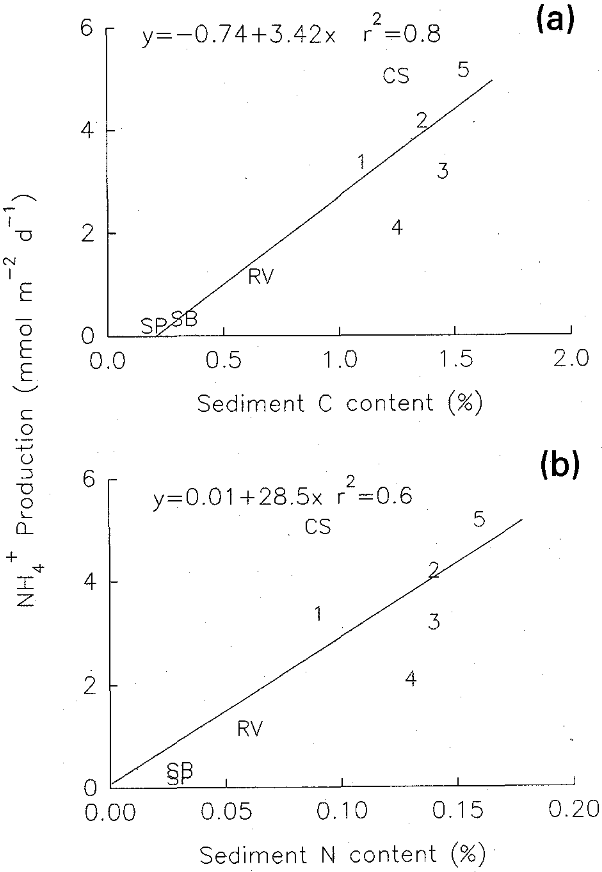

Fig. 7. Average $NH_4^+$ production (mmol $m^{-2}$ $d^{-1}$) versus average N (a) or average C (b) content (% dry weight) in sediments from North and South San Francisco Bay stations.

Despite higher sediment $NH_4^+$ production rates, $NH_4^+$ concentrations did not build-up in South Bay sediments as they did in North Bay. Sediment $NH_4^+$ pools are controlled by a variety of physical (diffusion, advection), chemical (sorption/desorption reactions), and biological factors. Biological factors include $NH_4^+$ production, loss of $NH_4^+$ through nitrification, uptake by benthic algae and the effect of macrofauna. Because of the highly turbid water in San Francisco Bay, benthic algae would have the greatest impact in the shoals. Although benthic algal production or nutrient uptake has not been measured in the bay, studies in other estuaries (Sundbäck and Granéli 1988; Sundbäck et al. 1991; Rizzo et al. 1992) have shown that benthic algae can take up nitrogen mineralized in sediments and have a significant effect on nitrogen fluxes across the sediment-water interface.

Macrofaunal irrigation, particularly by species such as *Asychis elongata*, can increase transport of $NH_4^+$ out of sediments and may be responsible for the uniform $NH_4^+$ concentration with depth in South Bay. In the channel at station 3, biomass of *Asychis elongata* can reach 45 g wet weight $m^{-2}$ and is about 50% of the total macrofaunal biomass, while in the shoals at station 1, mollusks dominate macrofaunal biomass, which can reach 800 g wet weight $m^{-2}$ (J. Caffrey and J. Thompson unpubli-

TABLE 4. Turnover rate of $NH_4^+$ in San Francisco Bay sediments integrated over depth of 0–8 cm.

| Station | Turnover Rate $d^{-1}$ | | | | | | |
|---|---|---|---|---|---|---|---|
| | South Bay | | | | | | |
| | July 1991 | September 1991 | January 1992 | April 1992 | May 1992 | June 1992 | September 1992 |
| 1 | n.d.[a] | 0.6 | 0.3 | 0.2 | n.d. | n.d. | 2.0 |
| 2 | n.d. | 0.3 | 0.3 | 1.7 | n.d. | n.d. | 0.4 |
| 3 | 0.9 | 0.2 | 0.1 | 0.2 | 0.5 | 0.2 | 0.1 |
| 4 | n.d. | 0.4 | 0.1 | n.d. | 0.2 | n.d. | 0.03 |
| 5 | n.d. | 0.7 | 0.1 | n.d. | 1.7 | n.d. | 0.1 |
| | North Bay | | | | | | |
| | August 1991 | November 1991 | January 1992 | March 1992 | June 1992 | January 1993 | May 1993 |
| Rio Vista | 0.1 | 0.4 | 0.03 | 0.02 | 0.1 | 0.4 | 0.0 |
| Suisun Bay | 0.001 | 0.2 | 0.3 | 0.002 | 0.25 | 0.004 | 0.01 |
| Carquinez Strait | 0.02 | 0.1 | 0.004 | 0.1 | 0.03 | n.d. | n.d. |
| San Pablo Bay | 0.01 | 0.03 | 0.03 | 0.04 | 0.4 | n.d. | n.d. |

[a] n.d. = no data.

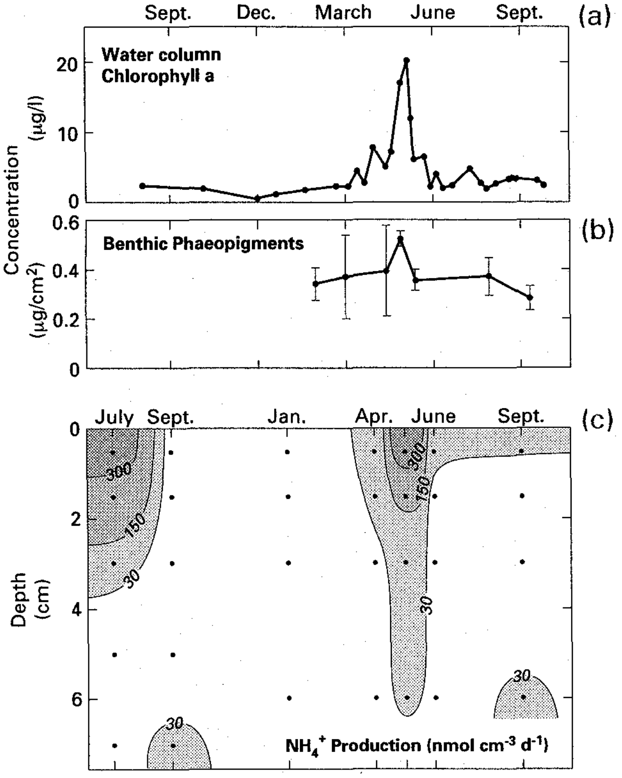

Fig. 8. Water column chlorophyll *a* (µg $l^{-1}$) versus month plotted from Wienke et al. (1992, 1993) (a), benthic phaeopigments (µg $cm^{-2}$) versus month (b), and $NH_4^+$ production (nmol $cm^{-3}$ $d^{-1}$) with depth (cm) and month (c) at South Bay station 3.

shed data). In North Bay, bioturbation from surface-dwelling bivalves seems to have little effect on sediment $NH_4^+$ concentrations. *Potamocorbula amurensis,* which is the dominant species in North Bay, reached about 200 g wet weight $m^{-2}$ in the late 1980s (Nichols et al. 1990) and currently remains at that level (J. Thompson personal communication). South Bay $NH_4^+$ profiles are very similar to those measured by Hammond et al. (1985) at a shallow site in the South Bay and to profiles from other heavily bioturbated estuarine and marine sediments (Aller and Yingst 1980; McCaffrey et al. 1980; Kristensen and Blackburn 1987).

### SEASONAL VARIABILITY

The seasonal pattern of $NH_4^+$ production was very different between North and South bays (Fig. 3). Rates from North Bay stations did not have a strong seasonal pattern. In contrast, at four of five South Bay stations, $NH_4^+$ production was highest in the spring. This may be related to the timing of organic inputs to the two systems. In South Bay where autochthonous inputs are more important, primary production and subsequent organic deposition are greatest in the spring. The peak phytoplankton biomass in the water column near station 3 was in early April (Fig. 8a; Wienke et al. 1992, 1993), followed by a peak in benthic phaeopigments in late April (Fig. 8b) and high $NH_4^+$ production in May (Fig. 8c). $NH_4^+$ production in the channel, stations 3 and 5, was particularly intense in the spring. This may be the result of increased trapping of organic material in the chan-

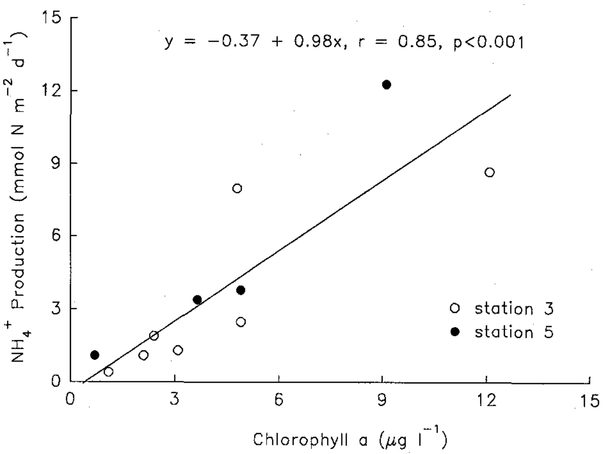

Fig. 9. Integrated (0–8 cm) $NH_4^+$ production (mmol $m^{-2}$ $d^{-1}$) versus water column chlorophyll *a* ($\mu g\ l^{-1}$) from the month prior to $NH_4^+$ production measurements at South Bay channel stations 3 and 5.

nel. Organic matter swept off the shoals during ebb tides may accumulate and decompose in the channel (Huzzey et al. 1990). By June, $NH_4^+$ production at station 3 declined to pre-bloom values (Fig. 8). In the South Bay channel stations, $NH_4^+$ production in the sediments was positively correlated with water-column chlorophyll *a* concentrations from the preceding month ($p < 0.001$, $r = 0.9$, Fig. 9). This suggests that there is a link between organic production in the water column and $NH_4^+$ production in the sediments. This link may be direct, deposition of the phytoplankton bloom and subsequent remineralization, or it may be indirect, grazing by benthic fauna on the phytoplankton and mineralization of fecal pellets. The importance of this indirect link between water-column chlorophyll *a* and remineralization is supported by peaks in secondary production of mollusks in South Bay 1 mo to 2 mo following peak water-column chlorophyll *a* concentrations (J. Thompson personal communication).

This pattern of enhanced $NH_4^+$ production and benthic flux following deposition of phytoplankton blooms has been observed in a variety of systems (e.g., Kiel Bight [Graf 1992]; Aarhus Bay [Jensen et al. 1990]). In North Bay, phytoplankton production is typically greatest in the summer, but primary production was never as high as in South Bay. Chlorophyll *a* in the water column during this study period averaged about 2 $\mu g\ l^{-1}$ (Wienke et al. 1992, 1993). Riverine organic inputs have also decreased since the drought (Jassby et al. 1993). Thus, the lack of a strong seasonal pattern in North Bay may be related to the declines in both autochthonous plankton production and in organic inputs from the river. Reduced organic inputs to the sediments may explain the low $NH_4^+$ production observed at most North Bay stations compared with South Bay. Intermittent high organic inputs to the estuary associated with high river discharge is a pattern commonly found in many estuaries (Burton 1988; Burney 1990). $NH_4^+$ production in North Bay may be more dependent on organic inputs from previous months or years, while $NH_4^+$ production in South Bay is controlled by recent organic inputs (days to weeks).

The temporal patterns of $NH_4^+$ production and turnover were very different between North and South bays. These results suggested $NH_4^+$ production in South Bay was closely linked to the phytoplankton production, particularly the spring bloom, although there seemed to be a 1-mo lag between accumulation of biomass in the water column and $NH_4^+$ production in the sediment. This relationship was clearly observed in South Bay channel stations (3 and 5), where $NH_4^+$ production was correlated with water-column chlorophyll *a* concentrations from the prior month (Figs. 5 and 9). The source of organic matter being remineralized in North Bay was less clear. $NH_4^+$ concentrations in South Bay seemed to be strongly influenced by macrofaunal bioturbation. This was not the case in North Bay, which had a very different benthic community than South Bay.

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