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Massive developments of microbial mats following phytoplankton blooms in a naturally eutrophic bay: Implications for nitrogen cycling

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Abstract

Benthic nitrogen processes have received substantial attention because the release of nutrients from sediments can contribute to the requirements of pelagic primary production; their study can also give an estimation of the importance of the sediment as a source or a sink of nutrients. Concepción Bay is located in central Chile and is the largest (167.4 km^2) and most enclosed embayment on the Chilean coastline. The bay is characterized by a strong hydrographic variability produced by the spring/summer seasonal upwelling of Equatorial subsurface waters (ESSW), rich in nutrients ($\sim$25 μM NO_3^-) and poor in oxygen ($<$44.6 μM). The area was studied in order to understand the consequences of phytodetrital deposition and oxygen deficiency on the environment and benthic communities. The study was carried out by sampling at a single station (28-m depth) in the inner part of the bay during winter (June 1998) and spring/summertime (November 1998 and January and March 1999). It was focused on measurements of benthic nitrogen fluxes, sulfate reduction, and denitrification rates before and after a phytoplankton bloom. Additionally, samples from the flocculent layer and from a semipurified bacterial mat were incubated under controlled oxygen conditions to determine NH_4^+ production. NH_4^+ exchange showed a clear seasonal pattern, with influxes during the winter (-7.6 ± 4.9 mmol m^{-2} d^{-1}) and high effluxes during the summer (36.6 and 20.8 mmol m^{-2} d^{-1}) when the accumulation of fresh organic matter (evidenced as chlorophyll *a*) produced a flocculent layer over the sediments. Besides natural hypoxia of the bottom water associated with ESSW, the large input of organic matter resulted in anoxia within the sediment, as a consequence of respiration processes, and an enhancement in sulfate reduction rates (up to 200 mmol m^{-2} d^{-1}). The flocculent layer then provided a favorable environment for the extensive development of *Beggiatoa* spp. mats. Overall, during the sampling period, NO_3^- was consumed at an average rate of 1.33 mmol m^{-2} d^{-1}. In the summer, denitrification appeared to be partially inhibited by the very negative redox conditions and could explain only 24% of the NO_3^- uptake by the sediment. The balance may be due to NO_3^- incorporation into *Beggiatoa* spp. Short incubations with these bacteria suggest that they are able to produce NH_4^+ by dissimilatory NO_3^- reduction, taking advantage of their ability to store NO_3^-, though its uptake was not observed in these experiments. The NH_4^+ flux obtained using *Beggiatoa* spp. mat cultures was 5 mmol m^{-2} d^{-1}, which accounts for 17% of the total NH_4^+ efflux during the summer period (January and March). The ecological implications of a large input of organic matter, evidenced by the presence of a flocculent benthic layer and *Beggiatoa* spp., are discussed in relation to their contribution, during the upwelling season, toward the long-term eutrophication of Concepción Bay.

High rates of primary production in the world oceans take place in coastal areas. The spatial and temporal variability of physical and chemical properties in the water column determine the timing of photosynthetic activity and the relative contribution of a given coastal system to the global nitrogen budget (Lalli and Parsons 1997). At mid-latitudes, especially in upwelling regions, seasonal fluctuations in wind regimes are the main factors that modulate the explosive increases in phytoplankton populations (Barber and Smith 1981). High

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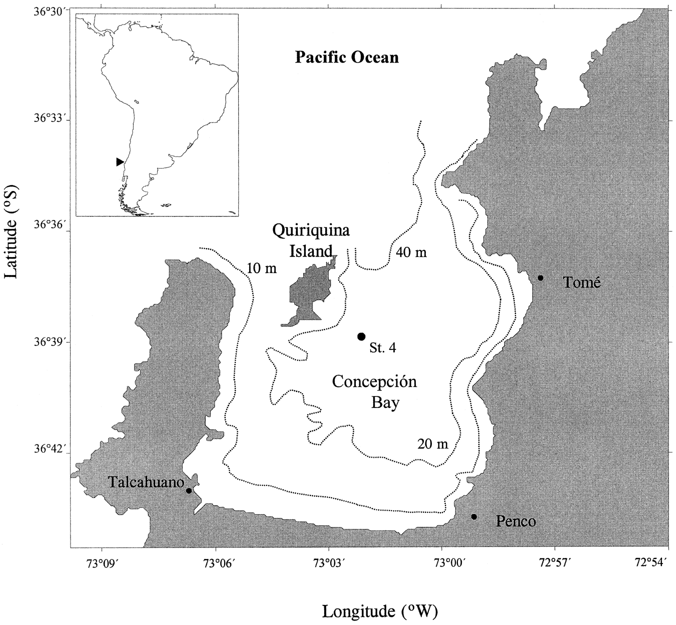

Fig. 1. Map showing the location of Concepción Bay and Sampling Sta. 4.

primary production, and the often delayed responses of heterotrophs, results in much of the pelagic organic matter being exported to the benthos in sinking particles, which become incorporated into the sediments (Suess 1980; Peterson et al. 1988). The responses of benthic microbial communities to the fluctuations of organic matter deposition are mainly related to nitrogen metabolism, and they could be important for nutrient recycling back into the water column (Blackburn 1995). In shallow coastal areas, benthic nutrient fluxes can exert a major control on pelagic productivity by supplying $\geq$50% of the nutrient requirements (Klump and Martens 1983) and influencing the eutrophication of the system.

Here, we report the development of a flocculent layer and *Beggiatoa* spp. bacterial mats over the sediments following a phytoplankton spring bloom and their consequences on nitrogen recycling in a coastal embayment in central Chile. Concepción Bay (Fig. 1) is a large, protected, and relatively shallow (mean depth = 48 m) coastal area located in central Chile (36°40′S, 73°01′W). During spring and summer, the bay is characterized by major phytoplankton blooms as consequence of surface fertilization by upwelling that occurs during as much as 57% of the year (Ahumada et al. 1983). A significant fraction of the carbon production in the bay, 735 g C m^{-2} 0.57 yr^{-1} (Pantoja et al. 1987; Bernal et al. 1989), is not fully incorporated into other trophic levels, 25–40% of the particulate organic matter (POM) produced being transported downwards to the sediments or out to the adjacent continental shelf (Ahumada 1991; Farías et al. 1994). The former leads to highly reduced conditions in the sediments and in the bottom water (Rudolph et al. 1984; Farías and Salamanca 1990), providing a favorable environment for the development of sulfur-oxidizing *Beggiatoa* spp. bacterial mats at the sediment surface (Gallardo 1977, 1979; Schulz et al. 1996). Teske et al. (1999) showed that this large marine bacterium is closely related to *Thioploca araucae* and *Thioploca chileae*. Recent observations also suggest that the dominant morphotype of *Beggiatoa* spp. in this area and *T. araucae* could be the same genera, differing only in the presence or absence of a sheath (Schulz pers. comm.).

Like *Thioploca* spp., *Beggiatoa* spp. accumulate NO_3^- intracellularly by a factor of several thousand compared to the surrounding seawater (McHatton et al. 1996). It has recently been suggested that marine mats of these bacteria might produce NH_4^+ through dissimilatory NO_3^- reduction to ammonium (DNRA) like *Thioploca* (Farías 1998; Otte et al. 1999). Sweerts et al. (1990) gave evidence that freshwater *Beggiatoa* spp. were able to reduce NO_3^- to nitrogen gas at up to 2.5 mmol m^{-2} d^{-1}. McHatton et al. (1996) suggested that epibionts could be responsible for this production. Measurements of NO_3^- reduction in undisturbed mats of marine *Beggiatoa* spp. from a eutrophic inlet of Denmark accounted for a minimum of 60% DNRA and only 15% of denitrification (Risgaard-Petersen 1995). Indeed, these two potential nitrogen pathways, denitrification and DNRA, have opposing directions and consequences for the ecosystem, because the former represents a loss of nitrogen, whereas DNRA is a conservative process that contributes to NH_4^+ production in the sediments, thus increasing the possibility of eutrophication of coastal areas. Knowledge of the factors and processes that control nutrient recycling is essential to understanding the environmental impact in these coastal systems. We therefore tested the hypothesis that the massive *Beggiatoa* spp. mats in the sediments of Concepción Bay might contribute significantly to benthic NH_4^+ production and to the eutrophic conditions of the area.

Materials and methods

Study site—Concepción Bay is a semienclosed coastal embayment (167.4 km^2), characterized by an orientation and topography that enhance the influence of winds. As a result, the bay has complex hydrographic circulation patterns and experiences strong seasonal upwelling (Sobarzo et al. 1997). During fall/wintertime (~43% of the year), northerly winds predominate, so that sub-Antarctic surface water (SAAW) moves toward the coast, creating conditions for downwelling. This period is characterized by the presence, in the bay, of well-mixed waters with low nutrient concentration and salinity (<34.4%) and high oxygen levels, mainly associated with SAAW diluted by freshwater from high rainfall and river runoff. In late spring and summer, favorable southerly winds cause upwelling events with alternating relaxed and active phases, each of about 1 week's duration (Arcos and Navarro 1986). During upwelling periods, the intrusion of Equatorial subsurface water (ESSW), characterized by high salinity (>34.4%), rich in nutrients (25 μM NO_3^-) and low in oxygen (<45 μM), fertilizes the bay and produces an increase in phytoplankton biomass of ~500 mg Chl *a* m^{-2} and high levels of primary productivity of 3.5–5.75 g C m^{-2} d^{-1} (Ahumada et al. 1983; Pantoja et al. 1987; Ahumada 1991).

The sediments of Concepción Bay are soft, black, reduced muds, rich in organic matter (15–18%; Rudolph et al. 1984). The reduced conditions result from both the low oxygen content of the ESSW and the high carbon oxidation rates at the sediment surface (up to 3 μmol cm^{-3} d^{-1}; Thamdrup and Canfield 1996). The carbon oxidation is mainly coupled to sulfate reduction (Thamdrup and Canfield 1996; Ferdelman et al. 1997), as evidenced by steep dissolved NH_4^+ and sulfide concentration gradients in the pore water of the upper 20 cm of the sediment and by high NH_4^+ fluxes to the overlying waters of ~10 mmol m^{-2} d^{-1} (Farías et al. 1995, 1996).

Sample collection—Sediment cores and water samples were taken at Sta. 4 (36°38′S, 73°02′W; 28-m depth) in winter (June) and spring (November) 1998 and in summer (January and March) 1999. Sediment cores (50–60-cm length) were collected by a model MC 600 multicorer and subcored for analyses. Niskin bottles were used to obtain water samples from various depths and near the bottom to determine dissolved oxygen (DO) and nutrients (NO_3^-, NO_2^-, and NH_4^+).

Biological and chemical features of the sediment—Cores were cut into 1-cm sections, and their porosity, bulk density, organic carbon, total nitrogen, and chlorophyll *a* [Chl *a*] contents were measured. Intact sediment cores were used to measure redox potential. Vertical pore water was recovered under an atmosphere of N_2 by squeezing the sediment core and was later analyzed for NO_3^-, NO_2^-, NH_4^+, and sulfides (H_2S, HS^{-1}, and S^{-2}). The squeezing technique could have caused an overestimation of pore-water NO_3^-, because it releases both the free pore-water NO_3^- and the NO_3^- from the intracellular pool of *Beggiatoa* spp. The relative contribution of each pool was not determined. Small pieces of the bacterial mats and flocculent sediment were fixed in 5% glutaraldehyde with 1% OsO_4 for 1–2 h and in 0.1 M phosphate buffer (pH 7.2–7.4) for 16–24 h. They were then washed in phosphate buffer and distilled H_2O and critically point dried and sputtercoated with Au for scanning microscopy. Abundance and biovolume of *Beggiatoa* spp. were measured in three sediment cores (3.6-cm diameter) in each sampling period. One centimeter of sediment was washed carefully with seawater, and the filaments of *Beggiatoa* spp. were examined using a binocular microscope at ×16 magnification. Filament biomass was determined in the same way as that used for the trichome biomass of *Thioploca* (Schulz et al. 1996). The biomass was calculated from the number of trichomes per square centimeter multiplied by their mean diameter and mean length in each 1-cm section, assuming a trichome density of 1 g cm^{-3}. This method may have underestimated the biomass of *Beggiatoa* spp., because of the absence of sheaths around the filaments, which made their collection, enumeration, and sizing difficult. Macrofaunal abundance was determined by sieving (0.5-mm mesh) all of the material contained in the cores that had previously been used for flux measurements (explained below).

Benthic flux experiments—Three sediment subcores (7.2-cm diameter; 12–16-cm water height, and 6–8-cm sediment height) were transported to the laboratory within 3 h of sampling. In the laboratory, they were wrapped in aluminum foil to exclude light and were preincubated for 6–12 h in a thermoregulated bath containing bottom water at 11 ± 1°C bubbled with N_2 to replicate in situ temperature and oxygen conditions. After preincubation. the subcores were capped and incubated for 3–6 h in the dark and at in situ temperature. The overlying water was kept well mixed using a magnetic stirring bar hanging from the top and fixed in a rubber stopper tap to prevent the resuspension of the sediments. Initial nutrient samples were taken from the bath, while the later nutrient samples were taken from the overlying water of each core. Initial and final oxygen concentrations inside the cores were also measured.

Flocculent layer and bacterial mat experiments—Flocculent layer and *Beggiatoa* spp. mats from cores sampled in March 1999 were used for nutrient flux experiments under controlled oxic and anoxic conditions. For measurements under oxygenated conditions, flocculent sediments were carefully introduced, using a rubber tube connected to a syringe, into 250-cc glass flasks, which were subsequently filled with filter-sterilized seawater by a peristaltic pump. Well-mixed conditions in the overlying water were provided by rotating magnetic bars, as in the benthic flux experiments. For measurements under anoxic conditions, flocculent sediments were introduced, using the same procedure but taking care to avoid oxygen diffusion, into glass flasks (350 cc) with taps previously flushed with N_2 gas; this time, the flasks were then filled with filtered, sterilized oxygen-free seawater. All incubations were performed in darkness at in situ temperature and under controlled pH. Water samples for nutrients (NO_3^-, NO_2^-, and NH_4^+) were taken at 0, 2, 5, 11, 24, 36, and 69 h.

In parallel with the flocculent layer experiments, measurements were made by using partially purified field samples of *Beggiatoa* spp. Tufts of *Beggiatoa* spp. were carefully extracted from cores using a rubber tube extension to a syringe and were gently washed with sterilized seawater to eliminate the visible sediment particles. After washing, the samples of *Beggiatoa* spp. were introduced into Erlenmeyer flasks (60 cc) filled with oxygen-free filtered and sterilized seawater. A flask containing only sterilized seawater was used as a control. All flasks were fitted with taps, and needles were used for N_2 gas bubbling and water sample extraction. The mat was incubated for 69 h, and the water was sampled at various intervals for nutrient analysis (NO_3^-, NO_2^-, and NH_4^+). Qualitative observations, such as the motility and vertical position of the *Beggiatoa* spp. filaments during the incubation, indicated that the culture conditions were satisfactory. Previous studies had shown the sensitivity of *Beggiatoa* spp. to oxygen increase, the filaments withdrawing and curling up tightly (Møller et al. 1985).

Denitrification, sulfate reduction, and NH_4^+ production rates—During November 1998 and January and March 1999, four sediment cores were collected in Plexiglas tubes (3.6-cm diameter, 10-cm water height, and 5-cm sediment height) to determine denitrification rates. These were measured using the Isotope Pairing Method (IPM) (Nielsen 1992). For each core, $^{15}NO_3^-$ was added (10 mM stock solution 99.6% $^{15}NO_3^-$) to the overlying water to obtain a final concentration of 30–50 μM. The cores were closed with rubber stoppers, mixed with a magnetic stirrer, and incubated for 3–4 h in darkness at in situ temperature. After incubation, the microbial activity was stopped at 1.5–2-h intervals by the addition of 3 ml $ZnCl_2$ solution (50% w/w), and the whole core was mixed with a rod. Duplicate slurry samples were then gently transferred by syringe to 6-ml glass vials (Exatainer, Labco) containing 250 μl of $ZnCl_2$ solution. The samples were analyzed by mass spectrometry at The National Environmental Research Center (NERI) in Silkeborg (Denmark). Denitrification rates were calculated according to Nielsen (1992). This method permitted the measurement of denitrification both from NO_3^- diffusing from the overlying water and from NO_3^- within the sediments. The denitrification rate of $^{15}NO_3^-$ added to the overlying water (D_{15}) was obtained from the production rates of the labeled N_2 species ($D_{15} = {}^{14}N^{15}N + 2({}^{15}N^{15}N)$).The rate of denitrification or denitrification coupled to nitrification (D_{14}) in the sediment was calculated indirectly from D_{15} ($D_{14} = D_{15} \times ({}^{14}N^{15}N/2({}^{15}N^{15}N))$). Finally, total denitrification was calculated according to Nielsen (1992).

Sulfate reduction rate measurements were performed with two subcores (3-cm diameter) from independent multicore drops using the whole-core injection method (Jørgensen 1978). The 400 Kbecq of ‘‘carrier free’’ $^{35}SO_4^-$ was injected at 1-cm intervals in the top 15 cm of the sediment. Incubations were performed in the dark for 6 h at in situ temperatures within 24 h of obtaining the core. After incubation, the subcores were sliced at 1-cm intervals; the slices were fixed with 20% Zn acetate, then frozen at -20°C until analysis within the following 30 d. For this, the fixed slices were unfrozen and centrifuged to recover the nonreduced $^{35}SO_4^-$ in the interstitial water. The solids remaining were digested at high temperature under anoxic conditions with concentrated HCl and $CrCl_2$ to convert the elemental sulphur, volatile-acid sulfides, and pyrite to H_2S (Canfield et al. 1986), the H_2S released being trapped with 5% Zn acetate. The $^{35}S^-$ was counted in a Packard 1600 TR scintillation counter. Parallel measurements of porosity and the pore-water sulfate concentration were used in the calculations of the integrated sulfate reduction rates (SRRs) per unit area.

Sample analysis—Oxygen concentrations from the water overlying the cores and at the bottom of the water column were determined by a semiautomatic version of Winkler microtitration (Williams and Jenkinson 1982), using a method modified from Strickland and Parsons (1972). The microtitration was performed with a Dosimat (665, Metrohom), and the endpoint was determined with a photoelectric cell connected to a chart recorder (C.V. = 0.03–1%). Samples for NO_3^- and NO_2^- were filtered and frozen and were later analyzed by standard colorimetric methods modified for small volumes (Strickland and Parsons 1972). NH_4^+ was determined following the technique of Solorzano (1969) modified for a 1-ml sample.

The redox potentials in the sediments were measured with platinum electrodes inserted into intact sediment at 1-cm intervals along a core liner, and sediment porosity was determined by water loss after drying to constant temperature. Organic C and total N were determined in acidified and freeze-dried samples using a carbon/nitrogen/sulfide (CNS) elemental analyzer (Carlo Erba NA-1500), and sediment Chl *a* concentration was obtained by fluorometry of the thawed samples (Gutiérrez et al. 2000).

Table 1. General features of Concepción Bay bottom-water (Sta. 4). nm, not measured.

Period	Temperature (°C)	Salinity (psu)	Dissolved oxygen (μM)	Nutrient concentrations (μM)		
				NH_4^+	NO_3^-	NO_2^-
Jun 98	14.4	33.77	192.9	nm	8.1	0.0
Nov 98	10.4	34.41	15.2	5.5	13.4	0.9
Jan 99	10.4	34.60	3.1	12.9	0.4	0.14
Mar 99	11.8	34.31	3.1	28.3	1.0	0.5

Data analysis—Nutrient fluxes measured by the sediment incubations and *Beggiatoa* spp. and flocculent layer experiments were calculated from the slope of the best-fit linear regression of nutrient concentrations in the overlying water against time. Positive values indicate net release of nutrients from the sediment (effluxes), and negative values indicate fluxes from the overlying water into the sediments (influxes). In the case of the flocculent layers and *Beggiatoa* spp. mats, the fluxes were expressed in micromoles of nitrogen per gram (wet sediments or wet biomass, respectively) per day. To obtain the mean flux for a given period, the different values obtained for individual cores were averaged. The uncertainty was calculated as the combined error of each flux rate variance. The correlations between abiotic factors (T°, O_2), biotic variables (*Beggiatoa* biomass, sulfate reduction rate, and Chl *a*) and NH_4^+ fluxes were also examined. The variations in macrofauna abundance in different periods were assessed by analysis of variance (ANOVA) on log-transformed data.

Integrated SRRs were calculated for 15-cm sediment columns and expressed in micromoles per square meter per day. Indirect rates of NH_4^+ production were calculated assuming (1) that the organic matter degraded by sulfate reduction conformed to the Redfield stoichiometry of 106 C : 16 N : 1 P, so that

$$(CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 53SO_4^{2-}$$
$$= 106HCO_3^- + 16NH_3 + H_3PO_4 + 53H_2S$$

(Bailey 1987),

and (2) a coefficient of adsorption K = 1.3 (Mackin and Aller 1984).

$$NH_4^+ \text{ production} = \text{sulfate reduction rate} \times (16N/53S)/(K + 1)$$

Results

Hydrographic data of the water column—Temperature, salinity, DO, and nutrient concentrations in the bottom water at Sta. 4 are given in Table 1. The near-bottom temperature had maximum values in winter, the season associated with strong vertical mixing in the water column (Ahumada and Chuecas 1979). The salinity was characteristic of hydro-

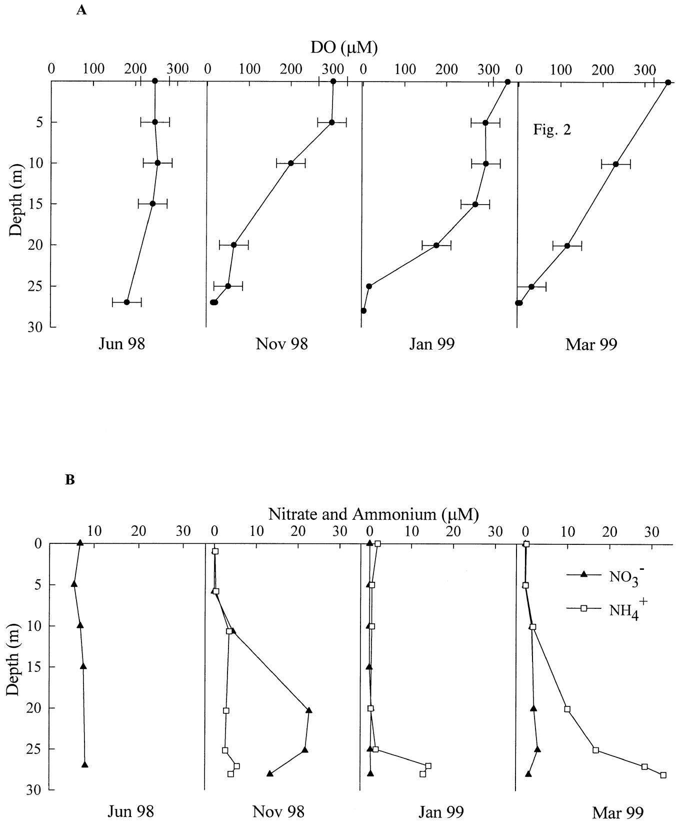

Fig. 2. (A) DO, and (B) vertical profiles of nutrient concentration at Sta. 4, Concepción Bay.

graphic regimes reported for the area (Ahumada et al. 1983), ranging between 33.77 and 34.60 psu. Bottom DO presented maximum concentrations in the wintertime and minimum concentrations in the summertime (192 and 3 μM, respectively); the lower value represents the limit of detection of the analytical method, so that DO in the summertime could be even lower, perhaps zero. Vertical profiles of DO and nutrient concentrations in the water column are shown in Fig. 2A,B. The vertical DO distribution showed a clear oxycline during the spring and summertime associated with the water mass distribution during the upwelling regime, i.e., sub-Antarctic surface water (ASSW) in the upper layer and ESSW in the bottom layer. During the winter, DO did not vary with depth because of the complete mixing of the water column. During the summer, NO_2^- and NO_3^- concentrations in the bottom water were different from those expected for ESSW (e.g., for NO_3^-, 15–25 μM; Ahumada et al. 1983) (Table 1; Fig. 2B). Those features and the high concentration of NH_4^+ in the bottom water (~13–28 μM) during the summer season suggest that significant nitrogen transformations, such as DNRA processes, were taking place, in the bottom water and/or sediment surface (Table 1).

General sediment features—Sediments from Concepción Bay (Sta. 4) consisted of a black mud associated with high percentages of organic matter (15–18%) and high porosity (average of 90% v/v) during almost all the year. The vertical distribution of redox potential (E_h) revealed reducing conditions even at the top of the sediments and in the bottom water during the summer (around −150 mv); however, in winter (e.g., June), the redox conditions were positive (>100 mv). Sediment surface concentrations of Chl *a* showed a large fluctuation during the year, from 0.05 to 2.1 mg g^{-1} (Table 2). The marked differences between Chl *a* values in the winter/spring period (0.05 mg g^{-1}) and summer period (2.1 mg g^{-1}) indicated significant input of organic matter, principally phytodetritus following upwelling events. Vertical pore-water profiles of nitrogen compounds (NO_3^-, NO_2^-, and NH_4^+) and sulfide are presented in Fig. 3. NH_4^+ profiles in the sediment showed a trend from lower, and almost constant, concentrations in the wintertime to much higher values during the summertime (from 65 to 996 μM at the surface and from 65 to 820 μM at 14-cm depth). During June 1998, NO_3^- concentrations decreased with depth. Summer NO_2^- and NO_3^- profiles exhibited peaks at different depths, with concentrations similar to or higher than in the overlying water (e.g., January 1999). These were probably artifacts produced by the core-squeezing technique (explained above). The distribution of sulfide was similar to that of NH_4^+, with constant, low concentrations during the winter and spring and extremely high concentrations, up to 2,000 μM, during the summer. NH_4^+ and sulfide pool sizes (0–15-cm depth) are listed in Table 2. High NH_4^+ and sulfide pools, indicators of highly reduced conditions in the surface sediments, were present during the period of strong upwelling. This was also the case for the *Beggiatoa* spp. biomass (Table 2). The benthic macrofauna were dominated by small polychaetes, which contributed 81–93% of the total abundance. The differences in both *Beggiatoa* spp. and macrofauna biomass between wintertime and summertime were statistically significant ($P < 0.01$).

Table 2. General features of Concepción Bay sediments (Sta. 4).

Period	Chl *a* (0–1 cm) (mg g^{-1})	Pore-water pool size (0–15 cm) (mmol m^{-2})				*Beggiatoa* spp. biomass (g m^{-2})	Macrofauna abundance	
		NH_4^+	NO_3^-	NO_2^-	S*		(Ind m^{-2})	(% of polychaetes)
Jun 98	0.05 ± 0.01	20	2.00	0.10	16	0.5 ± 0.2	44, 19 ± 6, 96	89
Nov 98	0.19 ± 0.18	16	1.30	0.10	0.40	2.4 ± 1.6	34, 42 ± 5, 40	94
Jan 99	2.08 ± 1.14	70	3.20	1.00	237	35.5 ± 0.0	18, 48 ± 15, 33	83
Mar 99	1.19 ± 0.03	142	0.04	0.40	178	29.9 ± 17.4	1, 62 ± 539	81

* All forms of sulfide (H_2S, HS^{-1}, S^{-2}).

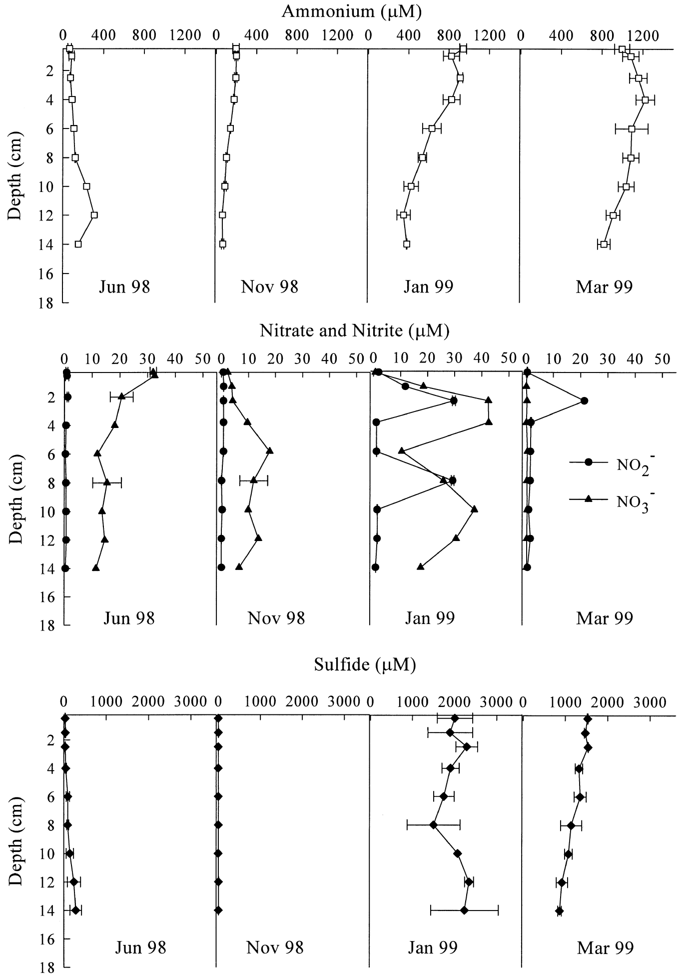

Fig. 3. Nitrogen species and sulfide pore-water concentration profiles of Concepción Bay sediments (Sta. 4).

Flocculent layer—In the summer, a black flocculent layer (5–10 cm thick) developed over the water–sediment interface, with bacterial mats clearly visible on its surface. Scanning electron microscopy showed that this layer contained principally diatom detritus, *Beggiatoa* spp., some fecal pellets, and clay minerals (Fig. 4A). It can be seen that chains of *Beggiatoa* spp. bound together various sedimentary particles such as fragments of diatoms and clay minerals to produce the texture of the surface bottom sediment in this area (Fig. 4B).

Benthic flux across the sediment–water interface—The means of the measured NH_4^+ and NO_3^- fluxes for each sampling period are given in Table 3. Influxes of NH_4^+ were observed only in June, while effluxes of NH_4^+ were observed during the spring/summer period. The temporal pattern of NH_4^+ flux across the sediment–water interface is shown in Fig. 5A. The NH_4^+ fluxes showed significant correlations with DO ($r^2 = 0.74$, $P < 0.01$) (Fig. 5B), SRRs, Chl *a* concentrations, and *Beggiatoa* spp. biomass ($r^2 > 0.90$, $P < 0.01$; Fig. 5C,D). The NO_3^- fluxes, by contrast, were always into the sediment but varied regardless of the season by an order of magnitude (Table 3). Denitrification or NO_3^- consumption by *Beggiatoa* spp. mats could explain part of these influxes.

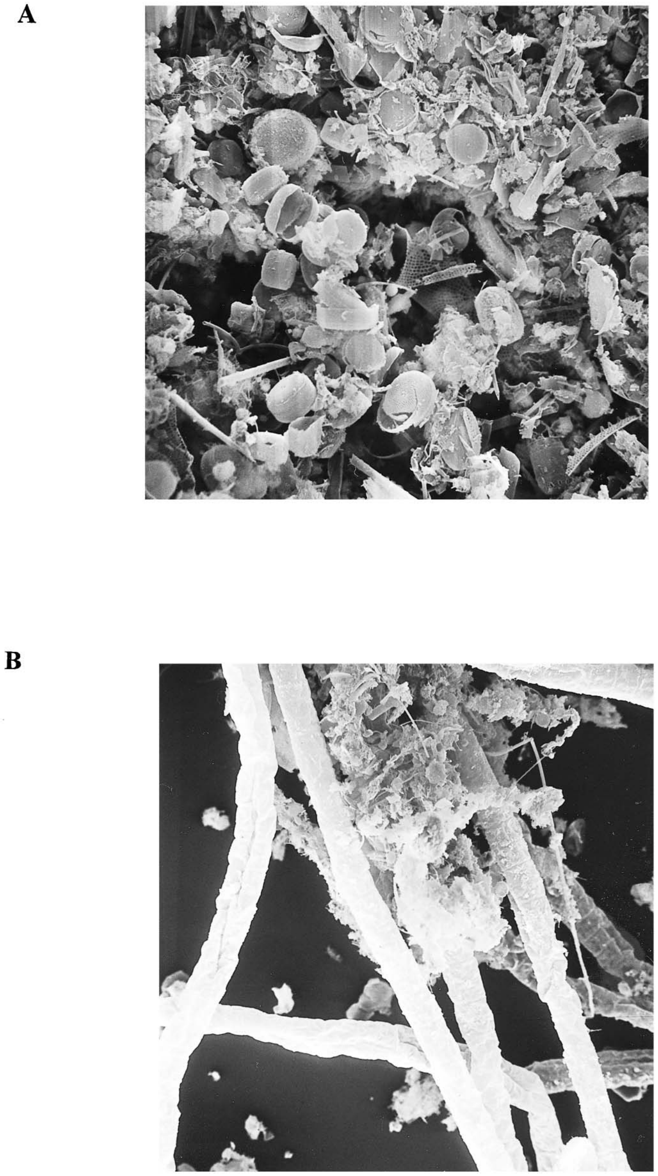

Fig. 4. Scanning electron microscopy photographs showing (A) sediment with diatom detritus, and (B) *Beggiatoa* spp. cell chains with detritus aggregates.

NH_4^+ fluxes in the flocculent layer and in the Beggiatoa *spp. mats*—Nutrient fluxes and their statistical parameters for the incubated flocculent layer, in the presence and absence of oxygen, and for *Beggiatoa* spp. bacterial mats are listed in Table 4. Under anoxic conditions, NH_4^+ fluxes were higher in the flocculent layer experiments than under oxic conditions. For both conditions, NO_3^- fluxes were negative or not significantly different from zero (Table 4). During all of the *Beggiatoa* spp. mat experiments, the NH_4^+ concentrations increased with time, but there was no uptake of NO_3^- from the culture medium. Considering that bacterial mats were incubated in the bottom water with a low NO_3^- con-

Table 3. Nutrient flux rates and nitrogen processes across the sediment–water interface in Concepción Bay (Sta. 4).

	Nutrient fluxes					
Period	NH_4^+ (mmol m^{-2} d^{-1})	NO_3^- (mmol m^{-2} d^{-1})	Net N exchange (mmol m^{-2} d^{-1})	Denitrification (mmol m^{-2} d^{-1})	Sulfate reduction (mmol m^{-2} d^{-1})	Ammonification* (mmol m^{-2} d^{-1})
Jun 98	−7.64 ± 4.96	−0.23 ± 0.44	−7.87	nm	57.36 ± 2.72	7.5 ± 0.4
Nov 98	2.00 ± 0.89	−2.17 ± 1.88	−0.17	1.30 ± 0.22 (67%)†	53.26 ± 8.09	6.9 ± 1.1
Jan 99	36.56 ± 6.41	−0.08 ± 0.03	36.48	0.25 ± 0.03 (78%)†	107.46 ± 6.36	14.09 ± 0.8
Mar 99	20.77 ± 6.03	−2.83 ± 0.75	17.94	0.18 ± 0.03 (94%)†	266.36 ± 26.10	34.94 ± 3.4

* Ammonification was estimated from sulfate reduction rate.

† Percentage of Dn (nitrification–denitrification coupled) with respect to total denitrification. nm, not measured. Negative values indicate influxes.

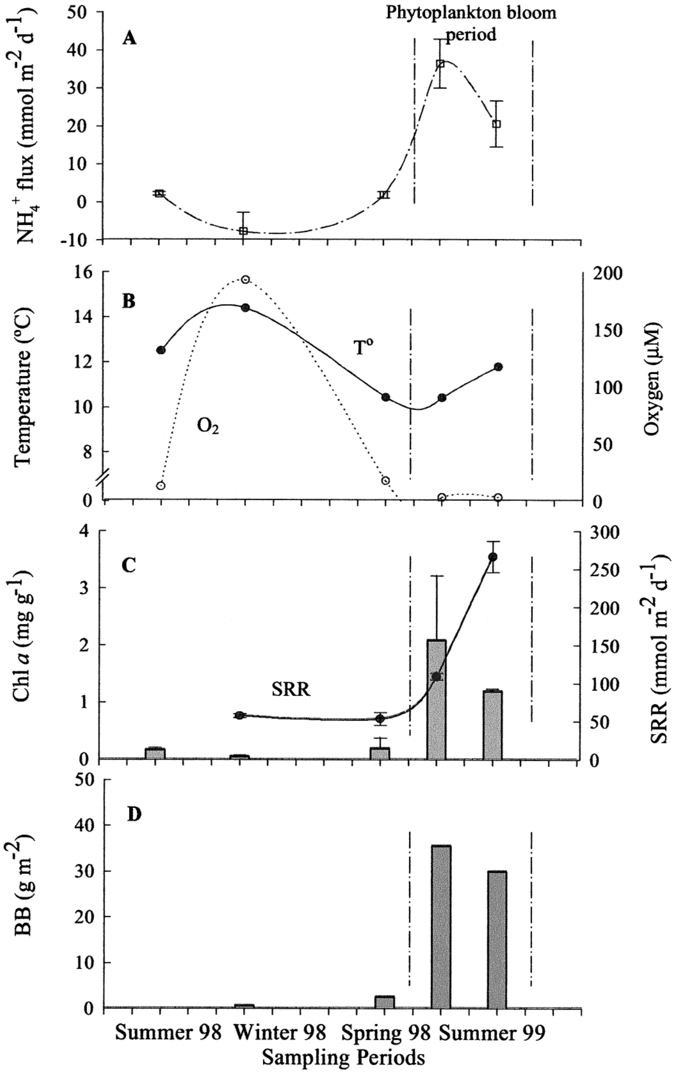

Fig. 5. Temporal variation of (A) ammonium exchange, (B) temperature and oxygen, (C) Chl *a* in the sediment surface and SRRs, and (D) biomass of *Beggiatoa* spp. (BB) during the study period. The dashed lines indicate the period of phytoplankton blooms (spring 1998/summer 1999). Ammonium fluxes from summer 1998 were provided by Salamanca and Muñoz (unpubl. data).

centration (*see Table 1*), the bacteria might have used their NO_3^- internal pool to produce NH_4^+. The absence of high concentrations of NO_2^- during the incubations implied that *Beggiatoa* spp. were not stressed or damaged during the experiments, as observed for *Thioploca* spp. by Otte et al. (1999).

Denitrification, SRRs, and NH_4^+ production—The highest denitrification activity (1.30 mmol m^{-2} d^{-1}) was found only during November 1998 (Table 3). Afterwards, it decreased to a level as low as 0.18 mmol m^{-2} d^{-1} during the summer periods (*see* January and March 1999). More than 67% of the total denitrification was based on NO_3^- produced in the sediment by nitrification (i.e., Dn : coupled nitrification–denitrification). The SRRs integrated over a 0–15-cm depth (Table 3) tracked the expected seasonal pattern, with maximum values during upwelling periods. NH_4^+ production values were calculated indirectly, assuming that all the organic matter was degraded by sulfate reduction, a reasonable approximation during the summer when oxygen concentrations at the bottom are practically zero (Jørgensen 1983). SRR values were higher in the summer months, particularly in January as expected, but different for the NH_4^+ fluxes, where the maximum values were in March instead of January (Table 3).

Discussion

Phytoplankton bloom consequences—The results of this study reflect the occurrence of phytoplankton blooms from November to March. Following the blooms, a dark flocculent layer (5–6 cm thick), described as "soupy," developed on the sediment surface in Concepción Bay (Thamdrup and Canfield 1996; Ferdelman et al. 1997). It is present only during the summer and has some of the characteristics of a "nepheloid benthic or bottom layer," i.e., high porosity (>97% of water) and large quantities of unconsolidated organic matter and phytoplankton. Ransom et al. (1998) reported the presence of a "nepheloid layer" with the prevalence of clay organic-rich aggregates, which are suggested to be formed by the deposition of pelagic marine snow. In fact, the flocculent layer on the sediments of Concepción Bay could be the result of the aggregation and coagulation of large quantities of both living and dead phytoplankton that sink to the bottom. This rapid and continuous supply of

Table 4. Nutrient flux rates obtained from incubations of the flocculent layer and *Beggiatoa* spp. mats from Sta. 4 in Concepción Bay. Experiment date, March 1999. 1A, anaerobic flocculent layer; 1B, aerobic flocculent layer; BBM, *Beggiatoa* spp. bacterial mats. Negative values indicate influxes. Controls did not show changes in ammonium or nitrate concentration.

	NH_4^+ flux (μmol g^{-1} [wet weight] d^{-1})			NO_3^- flux (μmol g^{-1} [wet weight] d^{-1})		
Experiments		*t*	*P-v*		*t*	*P-v*
1A	1.68 ± 0.24	5.92	0.00	−0.06 ± 0.06	−2.30	0.11*
1B	0.28 ± 0.09	3.33	0.01	−0.10 ± 0.06	−2.80	0.11*
BBM	126.00 ± 1.00	8.99	0.00	0.00 ± 0.00	0.53	0.05

* Not significant ($P > 0.05$).

fresh material and a low shear stress over the sediment are favorable for the persistence of the layer during the summer. The implications of the flocculent layer for carbon and nutrient cycling could be very important. Some of the layer could be exported offshore, as a source of carbon for deeper areas, while locally, the high levels of fresh organic matter and the low oxygen concentration provide a geochemical environment favorable for sulfate reduction and the preferential release of NH_4^+. These summer conditions are also ideal for the development of mats of *Beggiatoa* spp. on the sediment, because the H_2S produced reaches the surface, and NO_3^- is present in the ESSW bottom-water layer. The flocculent layer is effectively a completely different phase from the sediments per se and from the water column, and it can be thought of as a vertical laminated organo-sedimentary structure developing on the solid surface, dominated only by few functional groups of microbes (Gemerden 1993). Therefore, the processes and factors controlling the temporal and spatial variability of this layer in Concepción Bay were carefully studied in order to discover their implications in the degradation of organic matter.

Another important consequence of the large input of organic matter to the sediments is the oxygen consumption during its degradation, because oxygen regulates and influences the chemistry of sediments and benthic nutrient fluxes. Decreases in oxygen concentrations may have fatal consequences for fishes and higher benthic life and may have caused the mortalities observed in Concepción Bay (Falke 1950; Gallardo et al. 1972; Carrasco 1996). In accordance with this, our data showed a significant decrease ($P < 0.01$) in the abundance of benthic macrofauna during the upwelling season in comparison with the rest of the year. Moreover, when the oxygen supply falls or the demand for it increases, major changes occur in the sediment and pore-water chemistry, with consequences in the dominant metabolic microbial pathways and the products released to the environment (Klump and Martens 1983). In the case of nitrogen, the principal form exported from the sediments to the water column (e.g., NO_3^-, N_2, or NH_4^+) basically depends on a delicate balance between organic nitrogen remineralization, nitrification, and denitrification (Risgaard-Petersen et al. 1994; Rysgaard et al. 1994). All of these processes are regulated by the presence or absence of oxygen, the organic detritus sedimentation, and respiratory activity (Klump and Martens 1983). In Concepción Bay, the balance determined that NH_4^+ was the predominant nitrogenous species released from the sediment during the summertime. In contrast, during the wintertime and before the phytoplankton bloom, NH_4^+ fluxes were negative (−7.64 mmol m^{-2} d^{-1}), and pore-water concentrations were relatively low (Tables 2, 3).

Effect of phytoplankton blooms on benthic NH_4^+ production and release to the water column—Previous studies found annual average NH_4^+ fluxes of 3.4 mmol m^{-2} d^{-1} from the sediments of Concepción Bay (Farías et al. 1995, 1996), much higher than from estuarine, coastal lagoon, and shelf sediments, which ranged from 0.06 to 2.2 mmol m^{-2} d^{-1} (Valiela 1995). In the present study, the mean NH_4^+ flux was 12 mmol m^{-2} d^{-1} (Table 3)—more than three times higher than previously reported. This could indicate a possible natural long-term eutrophication of the area. The NH_4^+ fluxes clearly followed a seasonal pattern associated with coastal upwelling. After the sedimentation of the phytoplankton bloom, NH_4^+ fluxes increased, reaching maximum values of 36 mmol m^{-2} d^{-1} (Table 3). The seasonal variability is explicable in terms of the increase in the availability of labile organic nitrogen in the detritus, the minimum oxygen values, and the subsequent inhibition of nitrification by sulfide compounds, as recently reported by Joye and Hollibaugh (1995). It is evident that the benthic system of Concepción Bay responds rapidly to the arrival of detritus from the water column.

During the summer conditions, bottom-water natural hypoxia (<1 ml dissolved oxygen L^{-1}) occurs associated with ESSW and oxygen consumption due to the remineralization of the large input of organic matter, together with chemical and biologically mediated processes such as sulfide reoxidation to sulfate (Jørgensen 1982), resulting in benthic anoxic events. Under these conditions, the degradation of fresh organic matter was expected to occur almost totally through sulfate reduction. This seemed to be the situation in March, when the highest sulfate reduction rate (265 mmol m^{-2} d^{-1}) was observed (Table 3). In January, the sulfate reduction rate was only 108 mmol m^{-2} d^{-1} (Table 3), suggesting that fresh organic matter was available for hydrolytic and fermenting bacteria but not for sulfate-reducing bacteria (Jørgensen 1983).

The organic detritus in the sediment following sedimentation consists of a complex mixture of organic matter and bacterial residues that may not be directly degraded by sulfate-reducing bacteria. Hydrolytic and fermenting bacteria perform the role of making POM available (e.g., as fatty acids and amino acids) to other bacteria such as the sulfate-reducing types (Jørgensen 1983). This might explain the relationship between the rate of sulfate reduction and the quality of sediment organic matter. In January, the surface Chl *a* concentration was 2.08 mg g^{-1}, and pheopigment : Chl *a* was 0.59, while in March, they were 1.12 mg g^{-1} and 2.61, respectively. These values indicated that the surface organic matter in January was ''less degraded'' and consequently more complex than in March, when it could have been more readily used by sulfate-reducing bacteria, as reflected in the highest SRRs.

The question is whether the degradation of organic matter by sulfate reduction can entirely explain the observed NH_4^+ sediment fluxes. If so, maximum values of NH_4^+ fluxes would also be expected during March. But the present data show that the maximum occurs in January (36.6 mmol m^{-2} d^{-1}) (Table 3), when sulfate reduction was 108 mmol m^{-2} d^{-1}, and NH_4^+ production associated with this process was calculated to be 13.4 mmol m^{-2} d^{-1}. Other processes must therefore be involved to explain the relationship between NH_4^+ flux and NH_4^+ production. First, it may be that, during hydrolytic and fermentative processes, NH_4^+ is also produced from organic matter. However, the magnitude of this potential source is not known, as it has been poorly studied; calculating only NH_4^+ production due to respiration related to sulfate reduction could have resulted in an important underestimation of NH_4^+ during the first stage of organic matter degradation. A second important point is NH_4^+ assimilation by microorganisms, which has not yet been explored in the area. Finally, another source of NH_4^+ could be the DNRA process in the *Beggiatoa* spp. mats, which increase their biomass during the summer (~40 g m^{-2}). DNRA could also take place in other, still unknown bacteria associated with reduced sediments of Concepción Bay. In addition, Fig. 5 indicates similar temporal patterns between *Beggiatoa* spp. biomass (BBM), Chl *a*, SRRs, and NH_4^+ release. BBM was directly related to the input of organic matter to the sediments and the sulfide concentration.

Effect of Beggiatoa *spp. mats and flocculent layer in NH_4^+ fluxes*—The development of a flocculent layer during the summer months provides a favorable environment for the growth of *Beggiatoa* spp. life. The prevailing physicochemical conditions—i.e., the high input of organic matter, oxygen consumption, and high levels of sulfide at the surface sediments—are essential for the metabolism of this bacteria. *Beggiatoa* is a Beggiatoaceae closely related to *T. araucae* and *T. chileae* (Teske et al. 1995). Recent studies of ribosomal ribonucleic acid (rRNA) sequences in the two genera have shown that they have important genotypic, in addition to phenotypic, similarities (Teske et al. 1999). Both bacteria can accumulate high intracellular concentrations of NO_3^- (300–500 mM) and elemental sulfur (Fossing et al. 1995; McHatton et al. 1996; Jørgensen and Gallardo 1999). It is known that NO_3^-, in the absence of oxygen, might be used as a terminal electron acceptor and might be reduced in two ways: (1) to gaseous products by denitrification, or (2) by a poorly understood DNRA (Sørensen 1978).

More recently, experiments using mixed cultures of *Thioploca* spp. provided evidence of NO_3^- reduction to NH_4^+ by this genus (Otte et al. 1999). Studies of freshwater and brackish-water *Beggiatoa* spp. showed that, by contrast, these bacteria could be denitrifiers, reducing NO_3^- to elemental N_2 (Sweerts et al. 1990). Measurements on undisturbed mats of *Beggiatoa* spp. in reduced marine sediments from Denmark showed high DNRA : denitrification (Risgaard-Petersen 1995). The present study, using mixed cultures of semipurified *Beggiatoa* spp., provides some indications that this marine bacteria can reduce NO_3^- to NH_4^+ as the predominant product by a dissimilatory pathway. This metabolic pathway could have a profound impact on the nitrogen budget of the system. Unlike denitrification, which produces a net loss of nitrogen, this mechanism conserves dissolved fixed nitrogen, making it available for other microorganisms in Concepción Bay and, potentially, in other coastal zones.

The experiments with *Beggiatoa* spp. mats and flocculent layer associated with the bacteria reported here demonstrate that, although there were NH_4^+ fluxes to the overlying water, there were no changes in the NO_3^- concentration during the short period of incubation. This could be related to the fact that *Beggiatoa* spp. are able to store large concentrations of NO_3^- that can be used when unfavorable external conditions are present (McHatton et al. 1996).

Assuming a biomass of ~40 g m^{-2}, as observed during the summer, and an NH_4^+ production of 126 μmol g^{-1} (wet weight of bacteria) d^{-1}, the NH_4^+ production would be approximately 5 mmol m^{-2} d^{-1}, and the DNRA could contribute almost 17% of the average NH_4^+ efflux during the summer (~29 mmol m^{-2} d^{-1}) from the sediments of Concepción Bay.

Another estimate of DNRA can be made by subtracting the denitrification rate from the NO_3^- uptake rate. For March, this gives an average rate of ~2.7 mmol m^{-2} d^{-1}, but for January, the DNRA would be zero. This estimation may not be valid, however, because the uptake of NO_3^- and release of NH_4^+ could occur on different timescales, the latter because of *Beggiatoa*'s ability to store nitrogen, independent of the environmental conditions. The presence of an organism like *Beggiatoa* makes it more difficult to interpret field data, so time-based budgets must be approached with care.

In addition, the physiological state of this bacterium is important since with plenty of NO_3^- or during the first phase of NO_3^- storage, a minimum NH_4^+ production rate would result. A different physiological state could be a possible explanation for the higher NO_3^- uptake in March than in January in spite of the lower NH_4^+ efflux and denitrification rates. Further experiments with *Beggiatoa* spp. cultures are needed to evaluate directly the DNRA nitrogen pathway that may operate under various environmental conditions.

Effect of phytoplankton blooms on sediment denitrification—Denitrification, the transformation of NO_3^- to gaseous N_2, represents a natural nutrient sink and may mitigate the increasing nitrogen input to coastal environments (Jørgensen and Sørensen 1988). But the quantitative significance of the process in attenuating the flux of nitrogen through coastal embayments, estuaries, and coastal lagoons is not well established. Blackburn (1990), Blackburn and Blackburn (1993), and Sloth et al. (1995) showed that when organic loading increases significantly in coastal areas, nitrogen removal through denitrification decreases. In Concepción Bay, denitrification decreased from 1.5 mmol m^{-2} d^{-1} (November 1998) to near zero values in January and March 1999 (Table 3), when organic sedimentation onto the sediments increased. These values were much lower than those measured by IPM in adjacent shelf sediments at the same time of 2.4–3.8 mmol m^{-2} d^{-1} (Farías unpubl. data). During the summer, denitrification appeared to be partially inhibited by negative redox conditions and high sulfide concentrations in the sediments and overlying bottom water produced by high SRRs (~100–270 mmol m^{-2} d^{-1}). The inhibition of denitrification by the presence of sulfide has been previously reported by Sørensen et al. (1987). Nevertheless, NO_3^- was taken up by the sediment at an average rate of 2.17 mmol m^{-2} d^{-1}. Because this uptake was not explained completely by denitrification, it could be associated with the metabolism of *Beggiatoa* spp. Unfortunately, this process would not easily be detected by the IPM, because it takes a long time for the labeled NO_3^- to enter the cellular pool (Risgaard-Petersen 1995).

The potential role of benthic fluxes in the supply of NH_4^+ *to the productivity of the water column*—NH_4^+, being already more reduced than NO_3^- or NO_2^-, is preferentially consumed by phytoplankton (Harrison 1980). Considering that the average primary production of Concepción Bay during upwelling is 292 mmol C m^{-2} d^{-1} (Pantoja et al. 1987), the requirements for nitrogen uptake, assuming a C : N of 6.6, are 44 mmol m^{-2} d^{-1}. Based on a summer average of benthic NH_4^+ effluxes of 29 mmol m^{-2} d^{-1}, benthic processes can supply up to 66% of the total nitrogen required to sustain photosynthetic carbon fixation. Nitrogen is required not only for primary producers but also for bacterioplankton, which, in the bay, may have a production rate of 52.5 mmol C m^{-2} d^{-1} (Bernal et al. 1989; Pantoja et al. 1989), so that an additional nitrogen supply of 8 mmol m^{-2} d^{-1} would be needed and could also be supplied by benthic fluxes.

Conclusions

In Concepción Bay, preformed nutrients associated with coastal upwelling trigger an increase in primary productivity and organic matter exported to the sediment that consequently change oxygen concentrations and redox potentials in the sediments. This causes a shift from oxidizing toward anaerobic remineralization of organic matter, with sulfate reduction being stimulated. The pore water accumulates high concentrations of sulfide and induces a subsequent inhibition of nitrification and denitrification. These conditions favor the development of large filamentous sulfur bacterial mats of *Beggiatoa* spp. and a major release of NH_4^+ from the sediments to the water column, resulting mainly from organic matter remineralization and, secondarily, from the NH_4^+ production of *Beggiatoa* spp.

In the water column, this NH_4^+ could arrive in the euphotic zone and contribute to regenerated primary production or be oxidized to NO_3^-. Therefore, in shallow areas like Concepción Bay where upwelling events take place and a close pelagic–benthic coupling exists (Graf 1992), primary production may result from both newly upwelled nutrients and recycled nutrients from the sediments. After the sedimentation of a phytoplankton bloom, the conditions in the sediments favor the release of NH_4^+ to the water column, this being a potential nitrogen source for pelagic production.

The seawater in Concepción Bay contains high nutrient concentrations and is consequently highly productive in terms of the amount of organic matter produced by the phytoplankton. This can be used to classify it as an eutrophic or a hypertrophic bay, because the increase in the rate of primary production is actually used to define an eutrophicated system (Nixon 1995). An important cause of eutrophication is the increase in nutrient supply. The consequences of eutrophication for sediments are diverse: hypoxia, reduced conditions, and development of important bacterial mats. This work suggests that these factors in Concepción Bay contribute to maintain the nitrogen in the system and could contribute to a long-term eutrophication.

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