

## COMMENT

## Potential role of bacterial mats in the nitrogen budget of marine sediments: the case of *Thioploca* spp.

Laura Farías\*

Programa Regional de Oceanografía Física y Clima (PROFC), Universidad de Concepción, Casilla 160-C, Concepción 3, Chile

The main source of organic matter to estuarine and shelf sediments is the deposition of detrital material from plankton in the water column (Suess 1980). The release of nutrients from the sediments is considered to be regulated (feedback mechanism) by the rate at which organic detritus reaches the bottom, the rate at which this detritus is decomposed (mainly by heterotrophic bacteria), and the rate at which nutrients released to pore waters are transported to overlying waters by diffusion and bioturbation. Furthermore, the regeneration of nutrients from the sediments of shallow, near-shore marine environments could be supplying more than half of the required nitrogen for primary production (Rowe et al. 1975).

However, recent observations (Fossing et al. 1995) suggest that prokaryotic metabolic processes associated with benthic microbial mats of the genus *Thioploca* could be responsible for converting the most abundant form of new nitrogen ( $\text{NO}_3^-$ ) into biologically (intracellular) available substrate. This would be an important mechanism for introducing dissolved N into the seabed of the eastern Pacific shelf, representing about a third of the total N input into the sediments, when compared to the input via the rain of detritus and assuming that 10% of the primary production of  $9.6 \text{ g C m}^{-2} \text{ d}^{-1}$  reaches the bottom. These and other observations (e.g. hydrothermal vents) demand a reassessment of the classic view of the benthic-pelagic coupling in marine systems.

Mats of giant filamentous bacteria were first observed off northern Chile under the Peru-Chile Undercurrent (Gallardo 1963). They were later identified from central Chile as being made up of dense populations of *Thioploca* spp. (Beggiatoaceae) with biomasses of between 10 and  $1000 \text{ g m}^{-2}$ , potentially covering more than  $40\,000 \text{ km}^2$  of the sea bottom off southern

Peru to central Chile (Gallardo 1977). The undercurrent is associated with the Equatorial Subsurface Water (ESSW) and is characterised by high salinity, low oxygen and nutrient-rich waters, which are source waters for wind-driven coastal upwelling that fertilises the Chilean and Peruvian coasts (Wooster & Gilmartin 1961). The ESSW impinges on the seabed between depths of 50 and 280 m, creating a benthic environment with extended periods of suboxic and anoxic conditions that fluctuate intra-annually and interannually (e.g. with El Niño) and have a strong influence on the mats' distribution and biomass.

The metabolism of these marine bacteria has remained a mystery long after their discovery. An intensive field study of biogeochemical processes in sediments of the continental shelf in central Chile ( $36^\circ \text{ S}$ ) was carried out in 1994 through a joint effort between German (Max Planck Institute for Marine Microbiology) and Chilean (University of Concepción) researchers with the goal of understanding the metabolic pathways of *Thioploca* spp. Fossing et al. (1995) reported that *Thioploca* cells are able to concentrate nitrate up to 500 mM in a liquid vacuole that occupies >80% of the cell volume. This vacuole is surrounded by numerous sulphur globules embedded in the cytoplasm. They observed  $\text{NO}_3^-$  uptake rates by *Thioploca* of ca  $2.1 \text{ mmol m}^{-2} \text{ d}^{-1}$ , suggesting that they oxidise hydrogen sulphide using nitrate and behave as sulphide-oxidising denitrifiers. These observations were accompanied by flume studies that show chemotactic response towards nitrate-rich overlying waters with low oxygen conditions (Huettel et al. 1996).

The fate of the large  $\text{NO}_3^-$  pool inside the vacuoles of *Thioploca* spp. in this area has remained unclear. Thamdrup & Canfield (1996) found that sediment  $\text{NO}_3^-$  consumption during incubations was not directly coupled to carbon oxidation (i.e. dissimilatory nitrate reduction), suggesting that the  $\text{NO}_3^-$  consumed may be reduced to  $\text{NH}_4^+$  rather than to  $\text{N}_2$ , which would

\*E-mail: lfarias@profc.udec.cl

increase the oxidative capacity of the  $\text{NO}_3^-$  pool by 60% (i.e. not  $\text{NO}_3^- + 5e^- \rightarrow 1/2 \text{N}_2$  but  $\text{NO}_3^- + 8e^- \rightarrow \text{NH}_4^+$ ). Furthermore, Ferdelman et al. (1997) estimated that *Thioploca* were only responsible for 16 to 34% of the total sulphide removal in the shelf sediments.

Independently, a field study in Concepción Bay ( $36^\circ 40' \text{ S}$ ,  $73^\circ 02' \text{ W}$ ) and adjacent continental shelf sediments was carried out to determine the fate of organic nitrogen using a mass balance approach between nitrogen input (detritus input obtained with sediment trap) and output (i.e. ammonium and nitrate fluxes across the sediment-water interface and nitrogen burial in deeper layers of the sediment column) for a period that included seasonal variations in the hydrographic process (Fariás et al. 1996, Fariás 1998). Within the bay, an estimate of 85 to 93% nitrogen regeneration was obtained. However, at the offshore location where *Thioploca* is present, the input was estimated to be lower than the output, even without considering other possible outputs such as  $\text{N}_2\text{O}$ ,  $\text{N}_2$  and DON. In addition, an important and unexpected source of ammonium from the sediments to the water column was recorded, being on average  $10 \text{ mmol m}^{-2} \text{ d}^{-1}$ , although fluxes of up to  $25 \text{ mmol m}^{-2} \text{ d}^{-1}$  were measured during summer, when *Thioploca* reaches a maximum biomass.

I proposed that *Thioploca* could be catalysing reactions like nitrite ammonification, a metabolic pathway that has not been considered for *Thioploca* yet, but which has been reported for other organisms (Schlengel 1981). The proposed mechanism for *Thioploca* spp. could explain the high fluxes of ammonium observed across the sediment-water interface off Concepción, Chile (Fariás et al. 1996, Fariás 1998) and would contribute to the low  $\text{CO}_2:\text{NH}_4^+$  accumulation ratios found near the surface in the bay and on shelf sediments (Thamdrup & Canfield 1996).

Many facultative anaerobic or fermenting bacteria are able to produce nitrate reductase and to couple nitrite formation to electron transport phosphorylation but, unlike the denitrifiers, they are not able to reduce nitrite to dinitrogen. They either excrete nitrite or reduce ammonium via the assimilatory nitrite reductase systems. The reduction of nitrate to ammonium was hypothesised early by Fewson & Nicholas (1961) and afterwards measured in marine sediment by Sørensen (1978). This process was clearly dissimilative and may have an energetic rather than a nutritional value; however, the ecological and physiological significance of this process is still unknown.

The results discussed above suggest that inputs ( $\text{NO}_3^-$  uptake) and outputs ( $\text{NH}_4^+$  release) associated with *Thioploca* spp. have quantitative importance and indicate that there are other significant inputs and outputs of nitrogen compounds to and from the benthic

system, i.e. an active uptake of  $\text{NO}_3^-$  and release of  $\text{NO}_2^-/\text{NH}_4^+$  or  $\text{N}_2$ . This alternative nitrogen pathway should be evaluated against the conventional view of nutrient elements coming mainly from the remineralisation and recycling of planktonic detrital particles. Also, marine sediments represent a nitrogen sink for marine ecosystems via denitrification and permanent burial of organic matter. Bacterial mats could also contribute significantly to the nitrogen loss, not only through their metabolic activities but also through their biomass preservation and burial in the sediments.

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#### LITERATURE CITED

- Fariás L, Chuecas LA, Salamanca MA (1996) Effect of coastal upwelling on nitrogen regeneration from sediments and ammonium supply to the water column in Concepcion Bay. *Estuar Coast Shelf Sci* 43:137–155
- Fariás L (1998) Destino del nitrógeno orgánico en sedimentos de una bahía eutrofizada: reciclaje vs acumulación. PhD dissertation, Universidad de Concepción
- Ferdelman TG, Lee C, Pantoja S, Harder J, Bebout BM, Fossing H (1997) Sulfate reduction and methanogenesis in a *Thioploca*-dominated sediment off the coast of Chile. *Geochim Cosmochim Acta* 61:3065–3079
- Fewson CA, Nicholas DJD (1961) Utilisation of nitrate by microorganisms. *Nature* 190:2–7
- Fossing H, Gallardo VA, Jørgensen BB, Hüttel M, Nielsen LP, Schulz H, Canfield DE, Foster S, Glud RN, Gundersen JK, Küver J, Ramsing NB, Teske A, Thamdrup B, Ulloa O (1995) Concentration and transport of nitrate by the mat-forming sulphur bacterium *Thioploca*. *Nature* 374:713–715
- Gallardo VA (1963) Notas sobre la densidad de la fauna bentónica en el sublitoral del norte de Chile. *Gayana Zool* 10: 3–15
- Gallardo VA (1977) Large benthic microbial community in sulphide biota under Peru-Chile subsurface countercurrent. *Nature* 268:331–332
- Hüttel M, Forster S, Kloser S, Fossing H (1996) Vertical migration in the sediment-dwelling sulfur bacteria *Thioploca* spp.: overcoming diffusive limitations. *Appl Environ Microbiol* 62: 1863–1872
- Schlengel HG (1981) Microorganisms involved in the nitrogen and sulfur cycles. In: Bothe H, Trebst A (eds) *biology of inorganic nitrogen and sulfur*. Springer-Verlag, Berlin, p 3–11
- Thamdrup B, Canfield DE (1996) Pathway of carbon oxidation in the continental margin off central Chile. *Limnol Oceanogr* 41:1629–1650
- Rowe G, Clifford CH, Smith KL, Hamilton L (1975) Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. *Nature* 255:215–217
- Sørensen J (1978) Capacity for denitrification and reduction of nitrate to ammonia in a coastal marine sediment. *Appl Environ Microbiol* 35:301–305
- Suess E (1980) Particulate organic flux in the ocean: surface productivity and oxygen utilization. *Nature* 288:260–263
- Wooster WS, Gilmartin M (1961) The Peru-Chile undercurrent. *J Mar Res* 19:97–122