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CHAPTER 7

NITRIFICATION, DENITRIFICATION AND NITROGEN FIXATION IN BOTTOM SEDIMENTS OF LAGOONS OF THE SEYCHELLES ISLANDS

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ABSTRACT

Major processes of the nitrogen cycle (i.e., nitrogen fixation, denitrification, ammonia mineralization and nitrification) were investigated in coastal sediments of several Seychelles Islands. Sediments were represented by carbonate sands, except in Victoria Harbor where they were carbonate silt. Nitrogen fixation was measured by acetylene reduction assay, other processes were studied by an experimental flow-through system with regulated nitrogen and oxygen concentrations. In anoxic conditions, nitrate reduction to nitrite and denitrification were determined in all sediment samples. The rates of these processes are rather low, the constants of Michaelis-Menten's equation are adduced; V_{max} shows values ranging from 0.2-1 $\mu M \cdot cm^{-3} \cdot h^{-1}$, $K_m \approx$ 15-30 μM.

Nitrification did not occur in sandy sediments, and showed low rates ($V_{max} \approx 0.1\ \mu M \cdot cm^{-3} \cdot h^{-1}$, $K_m \approx$ 12-15 μM) in silty sediments. Denitrification and nitrification rates were dependent on oxygen tension in silty sediments. Overall, the rates of nitrogen transformation in benthic coastal sediments of the Seychelles Islands are considerably lower than in temperate regions. It is probable that the nitrogen cycle in these coastal waters is mainly controlled by processes in very deep vs. shallow waters.

INTRODUCTION

Nitrogen and phosphorus are the most important limiting nutrients and their chemical and biological cycles significantly determine the productivity of marine ecosystems. Dinitrogen is the main component of the atmosphere and a great amount is dissolved in seawater, whereas the concentration of dissolved inorganic nitrogen compounds is usually very low. Dinitrogen is rather inert chemically and only a few bacteria and Cyanophyta can bind it in the form of ammonia during nitrogen fixation. Another process of nitrogen binding, which is less significant at an oceanographic scale, is nitrogen oxidation by atmospheric oxygen during thunderstorm electrical discharges, with products falling into the ocean via rain.

The formation of dinitrogen (to a lesser degree - nitrous oxide) from nitrogen combinations is called denitrification, with both gases being ultimately released into the atmosphere. Denitrification is a microbiological process, chiefly the result of nitrate and nitrite reduction in anoxic conditions. During nitrification, i.e., microbial oxidation of ammonia to nitrite, small amounts of nitrous oxide

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are released, especially at low oxygen concentrations. In the end, low concentrations of nitrogen compounds in seawater are the result of equilibrium between nitrogen fixation, nitrogen input from land and the atmosphere and denitrification. The natural cycle of nitrogen transformation is complex, including numerous nitrogen compounds with different valency, which can act either as oxidizers or reducers (Fig. 1).

It is generally accepted that in oxic (aerobic, oxidative) conditions nitrification mainly occurs, whereas in anoxic (reductive) conditions oxidized nitrogen forms are reduced to dinitrogen and nitrous oxide and also to ammonia (Prosser 1986, Seitzinger 1986). According to established concepts, denitrification is limited to anoxic oceanic and isolated seawaters as well as to the reductive zone of marine sediments. However, microbial strains have been isolated that can denitrify in the presence of oxygen and in oxidative environments (Robertson and Kuenen 1984). The importance and occurrence of this process in nature has not been studied.

There are different versions of the nitrogen cycle in various marine sediments: the pattern for two-layer sediments with aerobic and anaerobic zones (Vanderborght et al. 1977) and the pattern of anaerobic niche in aerobic sediments (Jørgensen 1977, Jahnke 1985) with different modifications. The experimental verification of these patterns is very difficult because of the diversity of marine sediments and the necessity to understand several intrinsic parameters of a pattern which are difficult or impossible to determine in vitro. Certain methodical difficulties arise while studying separate processes of the nitrogen cycle and their interactions in marine sediments. In sediment pore waters all nitrogen combinations are present in low concentrations and depending on redox potential they can be readily metabolized in opposite directions. Nitrogen has no long lived radioisotopes which makes it difficult to use radioactive indicators. In vivo, both of the stable isotopes N^{14} and N^{15} are found in comparable concentrations, which decreases the sensitivity of N^{14}/N^{15} methods and requires long incubations. Consequently, new technical methods for investigation of nitrogen transformations in marine sediments are needed.

We used the method of flow-through percolation of a thin layer of sediments by seawater with regulated concentrations of oxygen and various nitrogen forms (Nedwell 1982, Esteves et al. 1986). In such experiments, percolation of the solution through a given sediment substitutes for natural diffusion in sediment pore waters and eliminates methodological limitations caused by diffusion. The time of microbiological and chemical reactions between solution and sediment depends on the rate of water flow-through and is not long, in our experiments it is only several minutes. The input of oxygen and certain nitrogen combinations in the system may be either maintained constant or changed according as conditions required . The data obtained under such controlled conditions can be extrapolated to natural conditions with only great care.

METHODS AND MATERIALS

Sediments. Sediments were sampled during January-March 1989. They were collected by SCUBA diving using glass and titanium tubes (diameter - 5 cm) with rubber stoppers, and immediately delivered to the laboratory for treatment. Sediments were pushed out of the tubes by piston and pH, Es and Eh values were measured directly in the tube using glass, silversulfide and platinum electrodes, with silverchloride reference electrodes. Total hydrogen sulfide content was determined by electrode potentials and pH, using dissociation constants for hydrogen sulfide in seawater: $PK_1 = 7.01$ and $PK_2 = 13.58$. However, the values obtained should be regarded as relative ones, because K_2 values may vary considerably according to different authors' data (Morse et al. 1987). Sedimentary samples were cut into 3 cm layers and the pore waters were separated from the silt by centrifugation. Pore waters could not be separated from sand sediments either by centrifugation or by pressing, and the almost complete lack of a liquid phase made it impossible to

use electrodes, except in the surface layers. Samples of 1 cm thick surface layers were extracted by 90% acetone and concentrations of chlorophyll and pheophytin in the extracts were measured by spectrophotometer. In all the experiments, sediment samples from a 2-5 cm layer were used, which contain almost no native chlorophyll. Sediment samples from 6-12 tubes were mixed to obtain greater homogeneity.

Sediment porosity was determined by drying the samples to a constant weight at 105°C. The organic matter content was estimated by dichromate combustion at 140°C with silver sulphate. The nitrogen and phosphorus content was measured by photometer after digestion of samples by sulphur and perchloric acids (Anon. 1979). Total iron content was determined by the method of atomic absorption in the analytical laboratory of the Institute of Geology after solvation of samples in a mixture of nitric and hydrofluoric acids.

Experimental apparatus. Sediment samples consisting of 1.2-1.5 cm layers were placed in 50 cm flow-through cells (Fig. 2). Intermediate filters in the sediment (glassfiber paper Whatman GFC or special analytical dense paper Filtrack 388, DDR) prevented erosion of the sediments by uneven water flow. The cell output filtrate was optically clear and was used in spectrophotometric measurements. The flow-through system (Fig. 3) consisted of nine parallel cells with sediments and three direct control channels without cells. The flow-through system was provided by a multi-channel peristaltic pump; 12 lines of the system were divided into 3 groups, each of them had 2 cells with native sediments, a cell with sterilized sediments and a direct channel without cells to control the content of input water. Each group was used for measurements after addition of known concentrations of ammonia, nitrites and nitrates.

Because the silicone tubes of the pump and the chlorvinyl connections are permeable to oxygen, special means were used to obtain anoxic conditions. The peristaltic pump and all plastic connections were placed into a hermetic chamber filled with helium, oxygen or a mixture and the main vessel with its seawater reserve and intermediate mixing vessels were flushed with the same gas mixture. All outer connections of the apparatus were made of glass. The oxygen concentration at the output could be maintained both constant or changed together with the gas content during the experiments.

Concentrations of nitrogen combinations at the input were varied from 0-50 or 100 μM, according to a given protocol, by reserve solutions of ammonia, nitrites and nitrates supplied by an auxiliary peristaltic pump into mixing vessels with seawater. The resultant solutions with increasing concentrations (to a ratio of 1:15 with seawater) were pumped through other channels of this pump to the cell inputs of the main pump. In the experiments, seawater filtered through Millepore 0.45 μm pore size filters was used.

Processes taking place in the input part of the apparatus were simulated by a form of differential equations and solved by computer. During the preliminary computer experiments, reserve solution concentrations and mixing vessel volumes were chosen in such a way that input concentrations increased throughout the experiment according to the given task.

Measurements and stability of results. All measurements were made at 23-24°C and the flow rate in each cell was 0.14 $l \cdot h^{-1}$. Experiments were begun by washing the cells in pure seawater for 6-8 h in order to remove previous pore waters and facilitate ammonia desorption; then biogenes were added and 7-8 series of measurements were made during 12-14 h.

At a constant concentration of oxygen input, after the initial washing of ammonia, the change of ammonia, nitrate and nitrite input concentrations resulted in a new equilibrium at the output within 1-1.5 h. At a constant concentration of oxygen input, the effects remained rather constant

throughout the entire period of measurements, usually increasing after 10-12 h. However, in hyperoxic conditions using pure oxygen, the nitrification rate usually began to decrease within 6-8 h.

Sterilization. In addition to biological processes, physico-chemical effects of absorption also develop in a flow-through system. Therefore, adequate control measurements are very important. We had found beforehand that heat sterilization of sediments, sterilization by formaldehyde or other chemical methods, e.g., mercuric chloride, cause substantial changes in the organic content of sediments, which are incompatible with the chemical analyses. We used sterilization by chloroform, 5 ml of which was added into the upper part of the cell and remained in the cell during the entire experiment gradually dissolving in the flow. Under the presence of chloroform, all oxidation and reduction processes of the nitrogen cycle were inhibited, excluding reduction which was not fully inhibited. Within 6-10 h during the experiments, nitrate reduction began to develop in chloroform-sterilized cells and at the end of the experiment nitrate reduction in cells with native sediments reached 5-10%.

Blank corrections were calculated on the basis of concentration changes in sterilized cells. These corrections are small, usually in the range of 0.1-0.5 μM, but they limit the accuracy of the method while using low concentrations of organisms.

Oxidized and reduced sediment forms. Silt collected in the samples from Victoria Harbor exists in two forms. An oxidized form of nearly white color is found at the surface of sediments which remain in contact with water and air and also may be found in deeper sediment strata exposed to percolating water saturated with oxygen. A reduced form of gray color is observed in lower sediment strata under conditions of percolating anaerobic solutions. The existence of these two forms is probably related to the condition of active sediment iron which changes its valency. In a flow-through system, these two forms convert from one to another depending on the oxygen concentration in the flow, but such transformation requires at least several hours. The reduced sediments form takes up oxygen from the water and this uptake is retarded by chloroform. This may explain why anaerobic processes are supported for some time in flow-through cells during percolation of reduced sediments, even by water undersaturated in oxygen, and nitrification can be observed as well. Inertiality of sediments shows a much stronger response to changes of oxygen concentration at the input than to changes of ammonia, nitrite and nitrate concentrations that is independent of the flushing of a cell up to equilibrium with solution (Table 1). In sterilized cells, the oxidized sediment form becomes reduced very slowly in the absence of oxygen, but the reduced form becomes oxidized relatively quicker than in cells with native unsterilized sediments. Under percolation by water in equilibrium with the air, an almost complete absence of oxygen at the cell output can be observed due to the high oxygen uptake by reduced sediments. At present, it is impossible to separate the possible presence of anaerobic microzones in sediments from the possibility of reduction processes with Fe^{++} in the aerobic zone.

Nitrogen fixation rate measurements. Nitrogen fixation rate was measured by the acetylene reduction method (Stewart et al. 1967). Sediment samples were put in 125 ml vessels filled with seawater, saturated with acetylene and incubated at 23-25°C (which corresponds to the ambient temperature). To measure ethylene produced by the reduction of acetylene using gas chromatography, water was sampled by vacuumed bottles (Odintsov 1981). The theoretical ratio

$$\frac{C_2H_4}{N_2} = 3$$

was used for the calculations.

Analytical methods. The oxygen concentration in water was determined by syringe modification of the Winkler method. Glass syringes (10 ml) were connected with cell outputs. Special measurements were made to determine corrections for oxygen solubility in reagents, which may be significant at low oxygen concentrations in water. The average accuracy of the oxygen determination was ± 0.1 ml·l^{-1}. Oxygen concentrations at cell inputs were on the average 0.1 ml·l^{-1} when the system was flushed with helium, 4.8 ml·l^{-1} when water in equilibrium with air was used and 14.5-16 ml·l^{-1} when oxygen was bubbled.

Ammonia and nitrite concentrations were determined by spectrophotometer (Anon. 1979). Nitrates were preliminarily reduced to nitrites in a capillary column with cadmium-covered copper wire. The presence of nitrites during ammonia determinations causes a decrease of the optical density of the solution. On the basis of double standard solutions of ammonia and nitrites, a corrective program was developed by computer, which permits the determination of actual ammonia concentrations as a function of apparent concentrations in the presence of nitrite. However, the accuracy of the method sharply decreases if the ammonia concentration is an order of magnitude less than the nitrite concentration. This problem hampers measurements of nitrate and nitrite reduction rates in anoxic conditions (since nitrate reduction occurs in samples).

Treatment and presentation of results. The rates of the separate processes of nitrogen compound uptake, reduction and oxidation in a flow-through system depend on the concentration and activity of certain enzymes, substrata and the resultant products, such as temperature changes and oxygen concentration. As a first approximation, we assume that the rate of the process can be calculated using the Michaelis-Menten (MM) equation:

$$V = \frac{V_{max} \cdot S}{(K_m + S)}$$

where V_{max} and K_m are constants of the equation, S is the substrate concentration and V is the reaction rate. Equation parameters were calculated by the least squares deviation method using an algorithm for constant deviation (Cornish-Bowden 1977). The MM equation is suitable only for reactions in homogeneous liquid media and its application for flow-through systems is an approximation. For example, if the input concentration is treated as an independent variable and it decreases in a cell, methodological deviations arise that lead to an apparent increase.

If we assume that the flow of solution through sediments in a cell is homogeneous, then the enzyme reaction can be treated as a time-dependent process in homogeneous sediments and can be described using the integral form of the MM equation:

$$T = R^2 \cdot HP/V \qquad V_{max} \cdot T = S_o - S + K_m \cdot 1_n(S_o/S)$$

where R is the cell radius, H is the thickness of the sediment layer, P is the porosity, V is the flow rate; S_o is the input substrate (or product) concentration and S is the output substrate (or product) concentration. Linear anamorphosis of this equation (Cornish-Bowden 1979) was used in the calculation of equation parameters using measurements in the flow-through system. The V_{max} values obtained did not differ statistically from those calculated using the usual form of the MM equation, but K values were significantly lower (2-3 times). Unfortunately, the integral form can be used without significant complications only for a single product release or substrate uptake. If the substrate converts into several products, the usual form of the MM equation is employed, which should be regarded as method of experimental data presentation without reference to the process mechanisms. Tables 1-7 present values obtained with the usual form of the MM equation.

RESULTS AND DISCUSSION

Sediments. Sediments collected around low calcareous atolls are rather similar (Tables 2 and 3). They are mostly light carbonate sands without macrofauna or indications of bioturbation. Natural chlorophyll concentrations are very low (sediments from Cöetivy Atoll not included). Except in samples from Desroches Island, the hydrogen sulfide is present as detected by odor and sulfide electrode measurements. Oxic or suboxic conditions are characteristic of surface layers; lower sediment strata are slightly reduced. It should be noted that redox measurements in the presence of hydrogen sulfide are unreliable, because the platinum electrode is very sensitive to minute traces of H_2S.

Sediment samples collected off the high granitic island of Mahé in Victoria Harbor are fine carbonate silts with a small admixture of terrigenous materials. They are similar to sand sediments in terms of their general chemical composition, redox potential and pH values, but they differ by having a greater dispersion and higher iron concentration. At 12-15 cm in depth, silt sediments are followed by a sand layer which is similar to that sampled on atolls. Pore waters were centrifuged from the silt sediments, but they were minimal. These pore waters contain ammonia and orthophosphate, which increase in concentration with depth, as well as low concentrations of nitrites and nitrates (Table 4).

Ammonia mineralization. Ammonia mineralization was noted in anoxic conditions in all sediment samples of the flow-through system, although it was not very intensive (Table 5). The given values refer only to microbial production of ammonia inhibited by chloroform, since ammonia evolution also occurs in sterilized samples for a long time at very low rates, related to desorption from surfaces of sediment fractions. However, the values of biological ammonification were obtained during sediment percolation by seawater without ammonia; e.g., its evolution rate decreases with increased ammonia concentration at the input, and at concentrations of 50-100 μM, its production ceases, or in some samples, a slight uptake occurs. In anoxic conditions, very low ammonia uptake at the lower concentrations was observed only in sediments from Desroches Island (Table 5). Ammonia concentration was not measured in the pore waters of sand sediments, so the ammonification rates obtained by sediment percolation of seawater without ammonia cannot be applied to the natural conditions. In oxic silt samples, ammonia mineralization does not occur and ammonia uptake takes place due to the nitrogen fixation process. In sand, in the presence of oxygen, this process was not observed.

Nitrate reduction and nitrite and nitrate denitrification. In anoxic conditions, all sediment samples show the uptake of nitrites and nitrates and the dependence of such process rates on input concentration can be described by the MM equation (Table 5). In all cases, nitrate reduction occurs, apparently partially induced by the presence of nitrate, which is why K_m values for nitrate reduction in most cases are higher than those for nitrate and nitrite uptake. The ratio of nitrates reduced into nitrites to nitrate uptake increases from trace amounts at nitrite input concentrations as low as 4 μM to one-third at 30 μM. This finding conforms to the assumption that nitrate and nitrite uptake represents denitrification. Application of the integral MM equation shows that the K_m values, given in Tables 1-7, are 2-2.5 times higher than the actual values, i.e., maximum process rates are reached at low concentrations (from one to several tens of micromoles). That is why the maximum rates possible for denitrification processes are low and the sensitivity of methods available for estimation of molecular nitrogen and nitrous oxide are not sufficient for direct measurements of denitrification.

In the silt sediments of Victoria Harbor, the intensity of denitrification is higher than in the sandy sediments, despite similar concentrations of organic matter. This is probably due to greater quantities of bacteria in the more dispersed sediments. When water with oxygen levels in

equilibrium with air is used at a flow-through system input, nitrate reduction only occurs in traces and nitrate and nitrite uptake rates are sharply decreased. Hyperoxic conditions lead to a complete cessation of ammonification and reduction processes of the nitrogen cycle.

Nitrification. The sand sediments from low coral atolls do not take up ammonia and do not oxidize it into nitrite (or nitrite into nitrate) irrespective of the oxygen concentrations of the input water, i.e., no nitrification processes can be found. Such sandy sediments are different from those of temperate regions, where nitrification processes are common and may be found during all seasons (Wollast 1981, Kaplan 1983). Sandy sediments off the Vietnamese coasts also are characterized by significant rates of nitrification (Propp et al. 1988). Similarly, the silt sediments of Victoria Harbor are characterized by appreciable (though low) rates of nitrification processes (Table 6), which are suppressed in hyperoxic environments. At present there is no simple explanation of these differences. Several factors may be involved: e.g., bacterial numbers are usually greater in silts than in sands, there is approximately double the iron content in silts that can either regulate the redox potentials of sediments or be a component of nitrification and respiration enzymes and, lastly, it is possible that ammonia concentrations are higher in pore waters of silt sediments. Despite the low rates of nitrification in silt sediments, practically all of the ammonia evolved during ammonification can be oxidized to nitrites and nitrates at the sediment surface layer.

Nitrogen fixation. Nitrogen fixation was found in all samples investigated and fixation intensity drops sharply in deeper sediment layers (Table 7). However, the rate of nitrogen fixation possible is rather low, e.g., 1-3 times lower than the possible rate of ammonification. These values are close to those measured earlier in sand and silt sediments of coastal waters off Vietnam (Propp et al. 1988). Extremely low rates of nitrogen fixation were found in sandy sediments of the *Thalassodendron ciliatum* community near African Banks (Table 7) in the present study. The same levels of nitrogen fixation were found for pure sandy sediments off the Vietnamese coast where the organic matter content was less than 0.2%. Because of its low intensity, nitrogen fixation in sediments can compensate for nitrogen losses during ammonification and due to diffusion of ammonia only to a very limited degree.

Sediments in nitrogen balance in coastal waters of the Seychelles Islands. The extremely low concentrations of natural chlorophyll in surface layers of sandy and silty sediments shows that the photosynthetic intensity of benthic microalgae at the bottom-water interface is very low, at least during the period of investigation (in spring 1989). Destruction of organic matter in sediments prevailed though it also was not intensive, probably related to the small amount of organic matter at sediment surfaces and on its low concentration in all sediments.

Both the sandy sediments of atolls and the silt sediments of Mahé Island, Victoria Harbor, are the major sources of ammonia that is produced during ammonification in the anaerobic layer of sediments. Production of organic nitrogen combinations due to nitrogen fixation is considerably smaller (1-3 times). Since nitrification in sandy sediments of the carbonate atolls is not prevalent, ammonia is not converted into nitrogen due to denitrification. Sediments can denitrify only small quantities of nitrates from the bottom-water boundary layer because the nitrate concentration in this layer is very low and the gradient between the bottom layer waters and the sediment pore waters may be quite small.

Nitrate and nitrite concentrations in the pore waters of silt sediments of Victoria Harbor were somewhat higher. These two nitrogen forms may be partially denitrified both by diffusion into sediment anaerobic zones and due to denitrification during suboxic and aerobic conditions. Processes in such sediments represent mechanisms of molecular nitrogen formation from its various compounds, but their intensity is low due to small concentrations of nitrate and nitrite in both bottom and pore waters. As a whole, the role of sediments in the nitrogen cycle, as a possible

regulator of the overall total supply, is not predominant because of low rates of nitrogen transformation. In the reef ecosystems of the Seychelles Islands, nitrogen cycle processes in very deep waters are probably more important.

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Table 1. Rates of nitrate and nitrite uptake, nitrate ammonification and nitrification in a flow-through system at different oxygen input levels ($ml \cdot l^{-1}$). The difference of nutrient input/output concentrations, μM; Victoria Harbor silt was initially in reduced form; NH_4, NO_2, NO_3 input concentration was 20 μM.

Step	O_2 conc. $ml \cdot l^{-1}$ input	output	Uptake NO_2^-	NO_3^-	Nitrate-reduction $NO_3^- \rightarrow NO_2^-$	Nitrate ammonification $NO_3^- \rightarrow NH_4^+$	Nitrification $NH_4^+ \rightarrow NO_2^-$	$NH_4^+ \rightarrow NO_3^-$
1	0.3	0.1	-10.5	-10.8	2.05	1.13	0	0
2	0.3	0.1	-10.2	-9.9	2.03	0.8	0	0
3	2.02	0.1	-6.2	-7.5	1.18	0	0	0
4	1.9	0.3	-5.2	-6.8	1.1	0	0	0
5	4.8	0.6	-1.8	-6.0	0.6	0	0.3	0.21
6	4.6	0.9	-1.2	-5.8	0.5	0	0.17	0.30
7	15	9.0	-1.0	-4.5	0	0	0.48	0.58
8	15	11.0	-0.5	-4.0	0.05	0	0.47	0.61

Table 2. Common features and photosynthetic pigment contents of sediments (number of measurements given in parenthesies).

Locality	Depth m	Porosity %	Content, % of dry wt. $C_{org.}$	N	P	Total Fe	Pigments, $mg \cdot m^{-2}$ chlorophyll a	pheophytin a
Cöetivy	26	61/12/	0.46/2/	0.046/2/	0.04/2/	0.154±0.016(3)	47±10/4/	67±11/4/
Desroches	27	67/12/	0.40/1/	0.037/1/	0.08/1/	0.2±0.01(2)	3.5±1.5/5/	5±1/5/
St. Joseph	3	49/8/	0.40/1/	0.04/1/	0.084/1/	0.15±0.018(4)	0.23/2/	0.36/2/
Mahé, Victoria Harbor	14	45/12/	0.42/4/	0.035/5/	0.032/5/	0.245±0.014(10)	1/2/	11/2/

Table 3. Redox potential (corrected for nitrogen electrode), total H_2S content in pore water, μM; pH in sediments.

Layer	Cöetivy			Desroches			St. Joseph			Mahé		
cm	Eh	H_2S	pH	Eh	H_2S	pH	Eh	H_2S	pH	Eh	H_2S	pH
0-3	-43	0.07	7.76	87	0	7.7	225	-185	-	99	-720	7.62
3-6	-48	21	7.64	-3	-0.6	7.68	130	-210	-	13	-19	7.40
6-9	-33	36	7.59	-13	-9	-	90	-238	-	-6	-30	7.63
9-12	-53	-22	7.49	-33	-14	-	70	-369	-	27	-15	7.60
12-15	-53	155	-	-	-	-	70	-343	-	-	-	-
15-18	-63	-155	-	-	-	-	60	-380	-	-	-	-
18-21	-33	150	-	-	-	-	60	-	-	-	-	-

Table 4. Nutrient (PO_4, NH_4, NO_2, NO_3) concentrations, μM, in bottom and pore waters of Victoria Harbor sediments.

	PO_4	NH_4	NO_2	NO_3
bottom waters	0.52	7.3	0.29	0.93
pore waters, 0-3cm	12.4	108	0.7	0.83
pore waters, 3-6cm	15.8	148	-	-

Table 5. MM equation parameters for processes of nitrogen reduction in anoxic conditions in Seychelles Island sediments (ammonia mineralization - $\mu M \cdot cm^{-3} \cdot h^{-1}$; numerator - V_{max}, $\mu M \cdot cm^{-3} \cdot h^{-1}$; denominator - K_m, μM; in parenthesis - number of measurements)

Processes	Cöetivy	Desroches	St. Joseph	Mahé
Ammonia mineralization	0.08±0.008/6/	0.02±0.03/6/	0.02±0.003/6/	0.055±0.01/6/6/
Uptake of NH_4	0	0.1/0.571/10/	0	0
Uptake of NO_3	0.436/9.93/6/	0.398/12.8/14/	0.551/20.3/14/	0.946/13.6/12/
Uptake of NO_2	-/15/8/	0.281/6.1/14/	0.37/14.5/14/	1.23/19.5/12/
Nitrate-reduction $NO_3 \rightarrow NO_2$	0.16/7.73/10/	0.227/29.1/14/	0.337/69.5/14/	0.46/104/8/8

Table 6. MM equation parameters for ammonia uptake and nitrification in Victoria silt sediments (numerator - Vmax, $\mu M \cdot cm^{-3} \cdot h^{-1}$; denominator - K_m, μM; NMM - not MM kinetics + traces of a process; 14 measurements).

Conditions	Uptake			Oxidation		
	NH_4	NO_2	NO_3	$NH_4 \rightarrow NO_2$	$NH_4 \rightarrow NO_3$	$NO_2 \rightarrow NO_3$
Normoxic	0.814/10.8	0.347/54.6	0.246/3.5	0.08/12.6	0.104/15.4	+
Hyperoxic	0.22/1.53	0.216/1.7	-	0.02/-0.2 NMM	0.03/-0.6 NMM	+

Table 7. Nitrogen fixation rates in some sediment samples.

Locality	Sediment	Depth, m	Layer, cm	Nitrogen fixation rate
Desroches	sand	27	0 -3	0.16±0.06(7)
			4 - 7	0.09±0.02(7)
			8 - 11	0.08±0.02(7)
African Banks	sand	11	0 - 10	0.02±0.02(13)
			0 - 3	0.202±0.016(5)
			3 - 6	0.090±0.004(3)
Mahé	silt	14	6 - 9	0.038±0.001(3)
			8 - 12	0.004±0.000(3)
			12 - 15	0.002±0.002(3)

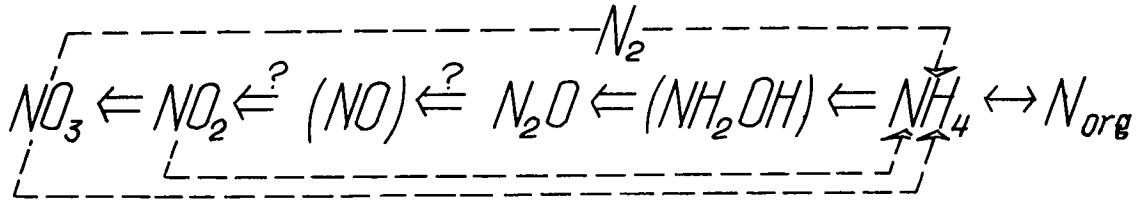

Fig. 1. Nitrogen cycle; in parentheses - nitric oxide and hydrohylamine, which probably are converted in a cell without significant release to the water; continuous line indicates processes with constant nitrogen valency; dotted line - reduction; double line - oxidation.

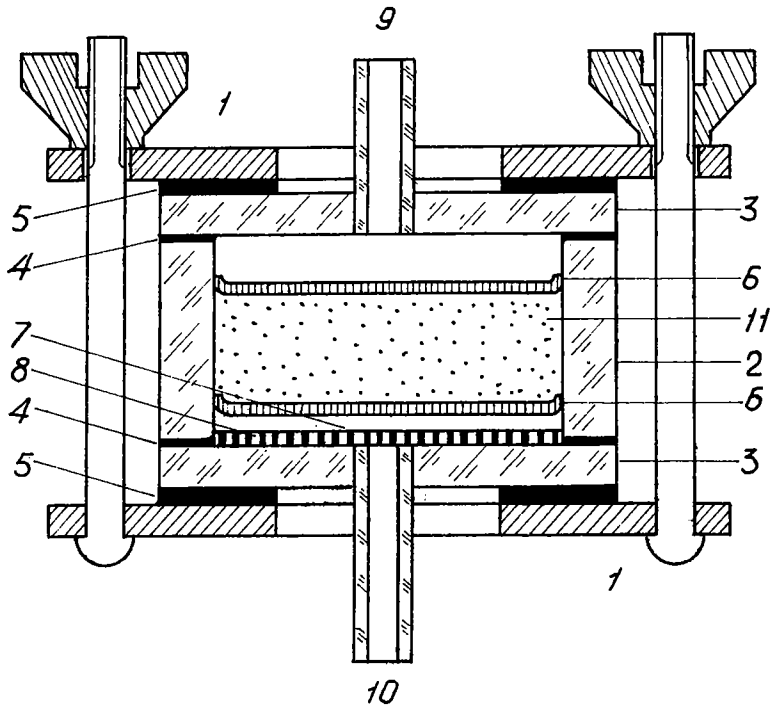

Fig. 2. Flow-through cell; 1 - compression casing; 2 - glass cylinder; 3 - glass lids; 4 - hermetic stoppers; 5 - rubber stoppers; 6 - filters; 7 - porous teflon lining; 8 - nylon net; 9 - solution input; 10 - solution output.

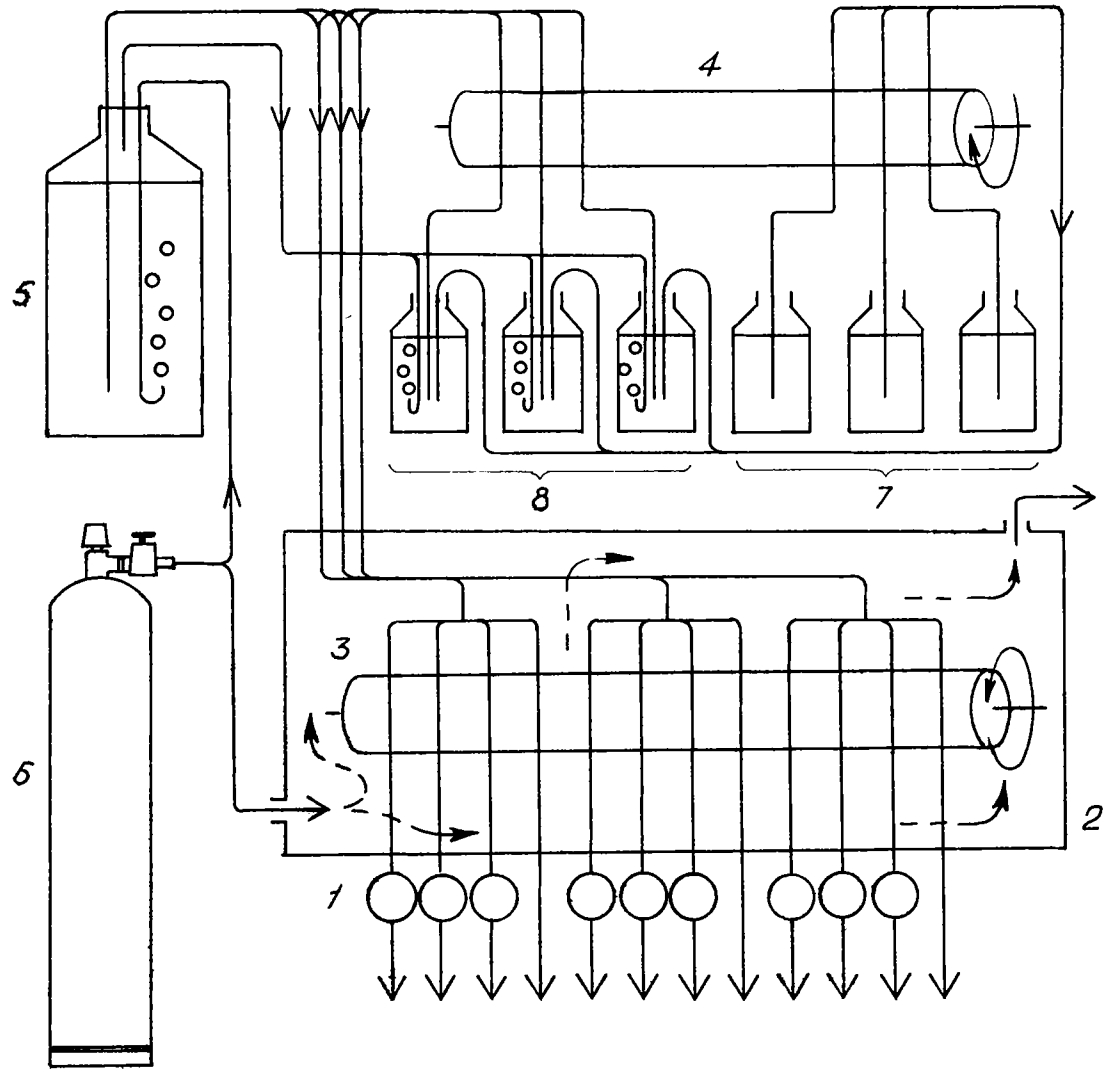

Fig. 3. Flow-through experimental system. 1 - flow-through cells; 2 - metal-glass casing; 3 - main peristaltic pump; 4 - auxiliary peristaltic pump; 5 - main seawater supply; 6 - oxygen or helium tank; 7 - nutrient supply solution bottles; 8 - intermediate mixing vessels.

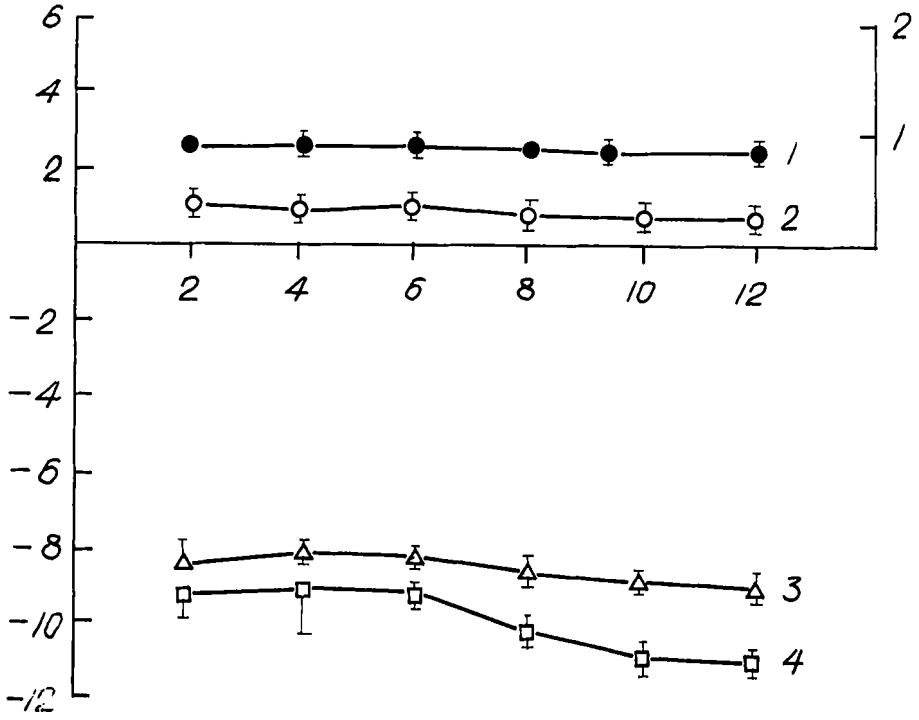

Fig. 4. The dynamics of nitrate and nitrite uptake rates and nitrate reduction at a stable biotic content (20 μM) and oxygen concentration (0.1 $ml \cdot l^{-1}$) at flow-through system input (μM); horizontally - period from biotic addition (h).