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Impact of macroalgal dredging on dystrophic crises and phototrophic bacterial blooms (red waters) in a brackish coastal lagoon

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Abstract – The Prévost lagoon (Mediterranean coast, France), was subject to annual dystrophic crises caused by the biodegradation of opportunistic macroalgae (*Ulva lactuca*) in the past. These crises result in anoxic waters with subsequent blooms of Purple Sulphur Bacteria (red waters) which, by oxidizing sulphide, contribute to the reestablishment of oxic conditions in the water column. Mechanical dredging of the macroalgal biomass has been carried out in the lagoon since 1991 with the aim of preventing the ecological and economic disturbances caused by such crises. Dredging began just before the phototrophic bloom when the water was already hypoxic (O_2 = 0.7 mg·L^{-1}) and contained sulphilde (H_2S = 7.3 mg·L^{-1}) and purple patches of phototrophic bacteria (*Thiocapsa sp.*) that were beginning to develop on decaying macroalgae at the sediment surface. The dredging prevented red water formation and drastically modified both phototrophic community structure and activity and biogeochemical sulphur cycling. The dredging permitted the reestablishment of oxic conditions for a short period only (1–13 August). Resuspension of the superficial sediment layers disturbed the phototrophic bacterial community, whose numbers decreased by one order of magnitude (from 2×10^6 to 3.9×10^5 CFU.mL^{-1}). The phototrophic community was no longer effective in reoxidizing the reduced sulphur compounds remaining in the sediments, as shown by a drastic sulphate depletion in the superficial sediment layers. Moreover, the increase in the specific bacteriochlorophyll *a* concentration of the phototrophic purple bacteria and the rapid development of Green Sulphur Bacteria (*Prosthecochloris*-like microorganisms) indicated that the phototrophic community was growing under severe light-limiting conditions due to the resuspension of sediment particles in the water. These conditions did not allow the phototrophic bacterial community to efficiently reoxidize the reduced sulphur compounds originating from the sediments. In consequence, hypoxic conditions (O_2 = 4.7 to 4.8 mg·L^{-1}) and low sulphide concentrations (H_2S = 0.4 to 0.7 mg·L^{-1}) were detected in the water column until September. The ecological balance in the lagoon was reestablished only in October, whereas, in previous years it had been restored in August. © Elsevier, Paris

lagoons / macroalgae / dystrophic crisis / red waters / phototrophic bacteria

Résumé – Impact du dragage des macroalgues sur une crise dystrophique avec formation d'eaux rouges (bactéries phototrophes) en milieu lagunaire (étang du Prévost, France). L'étang du Prévost (côte méditerranéenne française) a été soumis périodiquement à des crises dystrophiques estivales provoquées par la biodégradation de grandes quantités de macroalgues (*Ulva lactuca*). Ces crises se traduisent par l'anoxie des eaux et la formation d'eaux rouges (malaïgues) dues au développement des bactéries phototrophes sulfureuses rouges ; par leur activité de réoxydation des composés soufrés toxiques, ces microorganismes contribuent à la restauration de conditions oxiques. Depuis 1991, afin d'éviter les nuisances

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écologiques et économiques causées par ces phénomènes, un programme de dragage des macroalgues a été mis en place dans l'étang. Le ramassage des algues est entrepris juste avant le développement de l'eau rouge, lorsque les eaux sont déjà hypoxiques (O_2 = 0,7 mg·L^{-1}) et contiennent du sulfure (H_2S = 7,3 mg·L^{-1}). Les bactéries phototrophes (*Thiocapsa sp.*) forment déjà des biofilms sur les macroalgues en décomposition à la surface des sédiments. Le dragage évite la formation de l'eau rouge et influe largement sur la communauté de bactéries phototrophes et donc sur le cycle du soufre. Le dragage ne restaure des conditions oxiques dans les eaux de l'étang que pour une courte durée. La mise en suspension des sédiments superficiels affecte la communauté de bactéries phototrophes dont les nombres ont chuté d'un facteur 10 (de 2 × 10^6 à 3,9 × 10^5 CFU.mL^{-1}). Le déficit en sulfate des sédiments superficiels montre que cette communauté n'est plus capable de réoxyder les composés soufrés issus des sédiments. De plus, l'augmentation du contenu spécifique en Bchl.*a* des bactéries phototrophes rouges ainsi que le développement rapide des bactéries phototrophes vertes sulfureuses (*Prosthecochloris sp.*) indiquent que la lumière constitue un facteur limitant l'activité de ces microorganismes ; facteur limitant par suite de la mise en suspension de particules sédimentaires. Cette communauté ne pouvant plus jouer son rôle dans la réoxydation des composés soufrés, les eaux redeviennent hypoxiques (O_2 = 4,7 à 4,8 mg·L^{-1}) alors que de faibles concentrations en sulfures y sont détectées (H_2S = 0,4 à 0,7 mg·L^{-1}). Les conditions normales ne sont rétablies dans l'étang du Prévost qu'en octobre alors que les années précédentes elles étaient atteintes plus tôt en été.

milieu lagunaire / macroalgues / crise dystophique / eaux rouges / bactéries phototrophes

1. INTRODUCTION

Many coastal lagoons of the French Mediterranean coast undergo annual dystrophic crises [5]. The Prévost lagoon, located 10 km south of Montpellier close to Palavas, is a typical example of such environments [2, 3]. It is influenced both by freshwater inputs containing organic material (urban sewage) and mineral nutrients (nitrate and phosphate) and by marine influences through exchanges with the sea. As a result, it is highly eutrophic, with a high primary production of macroalgae (mainly *Ulva lactuca*) in springtime [26].

During summertime, aerobic biodegradation of the macroalgal deposits leads to a high oxygen demand in the water column. Depending on hydrological and meteorological conditions, this aerobic biodegradation can result in anoxic conditions in the water column [2]. In the sediments, sulphate reduction is enhanced by the simple organic compounds originating from the incomplete aerobic and anaerobic degradation of the macroalgal biomass. Their activity contributes to the production of large quantities of hydrogen sulphide, mainly trapped in the sediments as FeS and FeS_2 [3].

When the lagoon becomes anoxic, sulphide spreads through the water column by convective mixing. Such conditions lead to red water formation due to the development of mass blooms of anoxygenic phototrophic purple sulphur bacteria. These bacteria participate in the reoxidation of reduced sulphur compounds and allow the rapid restablishment of normal biotic conditions in the water [2, 3].

Such red waters have been described in many Mediterranean lagoons [5, 6, 8, 10, 12, 29]. The most common phototrophic sulphur bacteria found in these red waters usually belongs to the genera *Thiocapsa* and *Chromatium*. Due to their versatile metabolic capacities [18, 31, 32], these microorganisms are well adapted to such environments with fluctuating conditions in oxygen and sulphide.

The dystrophic crises triggered by intense eutrophication processes in the Prévost lagoon cause both ecological and economic problems for aquaculture production in the lagoon and tourism-oriented economy of Palavas. Therefore, since July 1991, mechanical dredging of the macroalgal deposits (*Ulva lactuca*) has been carried out in the Prévost lagoon in an effort to avoid anoxic conditions with the presence of toxic hydrogen sulphide in the water. This paper describes the impact of this coastal lagoon management on dystrophic crisis development, phototrophic bacterial community activity and structure, and biogeochemical sulphur cycling.

2. MATERIAL AND METHODS

2.1. Sampling site description

The shallow brackish Prévost lagoon (43° 30' N, 3° 54' E) is located on the French Mediterranean coast, 10 km south of Montpellier (*figure 1*). This lagoon has a mean depth of about 0.8 m. It receives both fresh water, which is polluted by urban sewage, through the small river "le

Lez", and sea water through the connecting channel "le Grau du Prévost". The sampling site (Station 3) is located in the eastern part of the lagoon where the collection of decaying macroalgae was undertaken. Station 3 was selected for this study because previous studies have demonstrated that the main dystrophic crisis phenomena of the past were most pronounced at this station [2, 3, 5]. This station is slightly affected by the water streams (inflow of sea water or fresh water, depending on tidal and meteorological influences) between the Arnel lagoon and the sea [2]. Morever, because of the dominant winds, large amounts of macroalgae accumulate in this part of the lagoon [4].

2.2. Sampling procedures

All samples were collected between 10.00 a.m. and 11.00 a.m. from March to December 1991. Sediment samples were obtained by manually inserting plexiglass cores 6 cm in diameter. Water samples were collected using sterile screw-capped bottles. Water samples (5, 10 and 50 mL) for the determination of sulphide were fixed by adding 10 mL of 2 % zinc-acetate solution. Samples were kept in a coolbox at 4 °C and brought to the laboratory for further analyses. Cores for chemical analyses were frozen at –18 °C, and samples for bacteriological analyses were kept at + 4 °C and analysed within 12 h.

2.3. Analytical procedures

2.3.1. Bacteriological methods

Purple and green phototrophic bacteria were enumerated as colony-forming units (CFU) using the deep agar dilution method [23]. The basal medium, prepared according to Pfennig and Trüper [25], contained, per litre of dis-

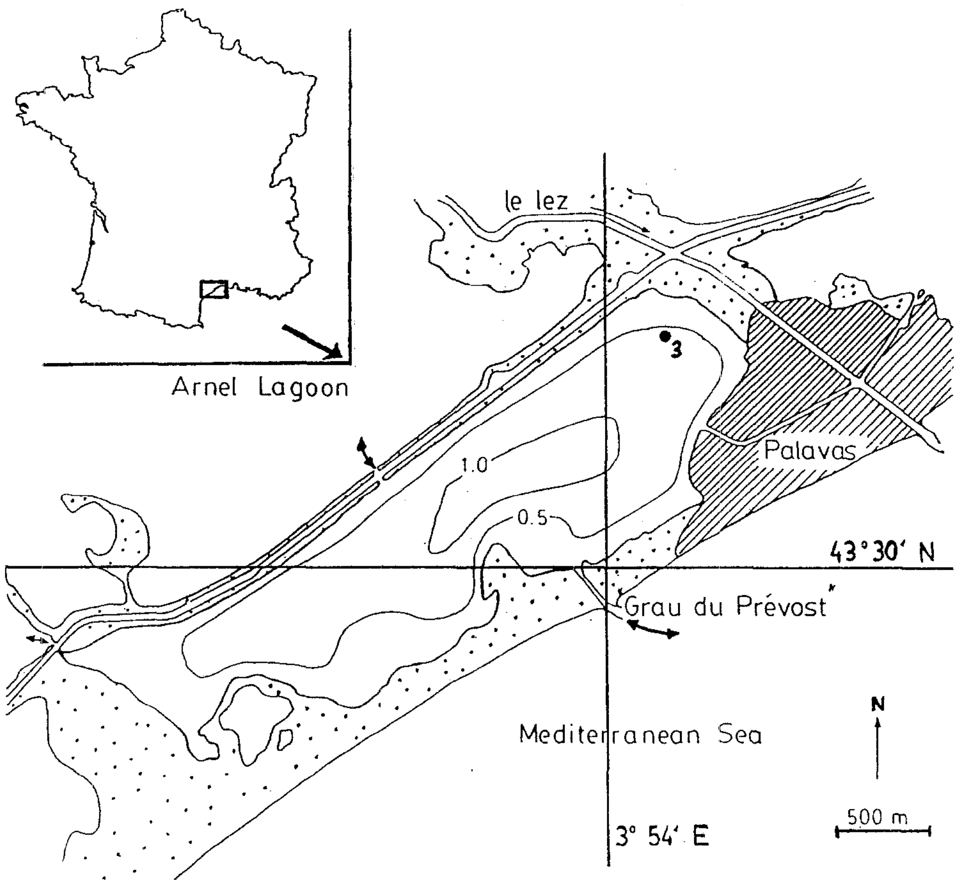

Figure 1. Map of the Prévost lagoon on the western French Mediterranean coast. Bathymetric profiles (m) and location of sampling station 3 (redrawn after Caumette, [3]).

tilled water: KH_2PO_4, 0.3 g; NH_4Cl, 0.5 g; $CaCl_2.2H_2O$, 0.05 g; $MgCl_2.6H_2O$, 1 g; $MgSO_4.7H_2O$, 0.5 g; NaCl, 20 g; trace element solution SL12 [19], 1mL; vitamin V_7 solution [25], 1mL; $NaHCO_3$, 1.5g; $Na_2S.9H_2O$, 0.5g; final pH 7.2. Prior to utilization, Na-Acetate (5 mM) and $Na_2S_2O_3.5H_2O$ (2.5 mM) were added as additional substrates.

Sediment samples were diluted in sterile anoxic sea water using decimal dilution series up to 10^{-10}. Aliquots (1 mL) from each dilution were transferred into deep agar medium (duplicates). The culture tubes were incubated at 30 °C under a 16 h light – 8 h dark cycle. Illumination was provided by incandescent lamps (30 $\mu E \cdot m^{-2} \cdot s^{-1}$). After one month of incubation, CFU were enumerated and assigned to the following main taxonomic groups: Purple Sulphur Bacteria, Purple Nonsulphur Bacteria and Green Sulphur Bacteria. Identification of the different phototrophic bacterial colonies counted was done on the basis of colony colour, presence of elemental sulphur surrounding the colonies and by microscopic observation of the microorganisms forming the different colonies (cell morphology, type of cellular division, motility, intracellular or extracellular accumulation of elemental sulphur globules).

2.3.2. Physicochemical methods

Salinity in the water was determined in situ with an ATAGO S-10 refractometer. Chloride was measured on diluted sediment samples and on water samples using the Mohr method [21]. pH measurements were made in situ with an Ingold pH-electrode coupled to a portable pH-meter (Bioblock scientific 93301). Dissolved oxygen and temperature were determined polarographically in situ using an YSY 57 oxymeter.

Sulphide was determined colorimetrically (Beckman Model 54 spectrophotometer), using the methylene blue method [7]. Sediment samples were acidified with 10 M HCl (pH 1) and purged with nitrogen which was passed through a zinc acetate trap to collect acid-volatile sulphides [14].

Sulphate concentrations were measured using a turbidometric method [30]. The sulfate/chloride molar ratio was compared with the conservative value for sea water, which is 0.051 [13].

Concentrations of bacteriochlorophyll *a* (Bchl.*a*) were determined spectrophotometrically (Kontron Uvikon Model 860 spectrophotometer) after methanol extraction and methanol-n-hexane phase separation [28]. Sedimentary organic matter content was determined by weight losses of dried sediment core sections after calcination at 500 °C [15].

3. RESULTS

3.1. Water column processes

The lagoon was sampled from March to December 1991. The dredging of the macroalgae started from mid-July (after 12 July) and continued up to the beginning of August. *Figures 2a* and *2b* show the concentrations of oxygen and sulphide, pH, temperature, salinity, and the Sulphate/Chloride molar ratio in the water column. The phototrophic bacterial numbers and community structures are presented in *figure 2c*.

In springtime, from March to June, the increase in temperature and solar irradiation led to massive development of macroalgae throughout the water column. During daylight periods, highly alkaline conditions (pH higher than 9.5) occurred and dissolved oxygen was supersaturated (10 to 12 $mg \cdot L^{-1}$/ 105 to 130 % saturation). The biomass of macroalgae at station 3 amounted to 3.3 $kg \cdot m^{-2}$ fresh weight (760 g dry $weight \cdot m^{-2}$). At the end of June, the macroalgae began to deposit at the sediment surface and the oxygen concentration decreased to 6.1 $mg \cdot L^{-1}$ (approx. 80 % saturation). Nevertheless, sulphide was still not detected in the water column. Purple Nonsulphur Bacteria and Purple Sulphur Bacteria could be detected in the water (approx. 10^3 $CFU \cdot mL^{-1}$). No Green Sulphur Bacteria were detected.

In mid-July (12 July), the pH decreased in the water column while the temperature increased up to 30 °C. Hypoxic conditions (O_2 = 0.7 $mg \cdot L^{-1}$) and free sulphide (H_2S = 7.3 $mg \cdot L^{-1}$) were found in the water column, indicating the onset of the dystrophic crises (*figure 2b*). The Sulphate/Chloride molar ratio reached 0.0585 in the water, indicating sulphate enrichment. Red patches of phototrophic Purple Sulphur Bacteria were observed on the surface of decaying macro-algae deposited at the sediment surface. In the samples collected from these red patches, the Sulphate/Chloride molar ratio attained 0.0822 (data not shown). Direct microscopic observations of such biofilms revealed the presence of bacteria ressembling representatives of the genus *Thiocapsa*. Within these red patches, the Bchl.*a* contents of the phototrophic bacterial biofilms was 38.5 $\mu g \cdot g^{-1}$ of fresh algae material. In the water, the total number of phototrophic bacteria reached 5×10^3 $CFU \cdot mL^{-1}$ and Green Sulphur Bacteria could be detected in the water (*figure 2c*).

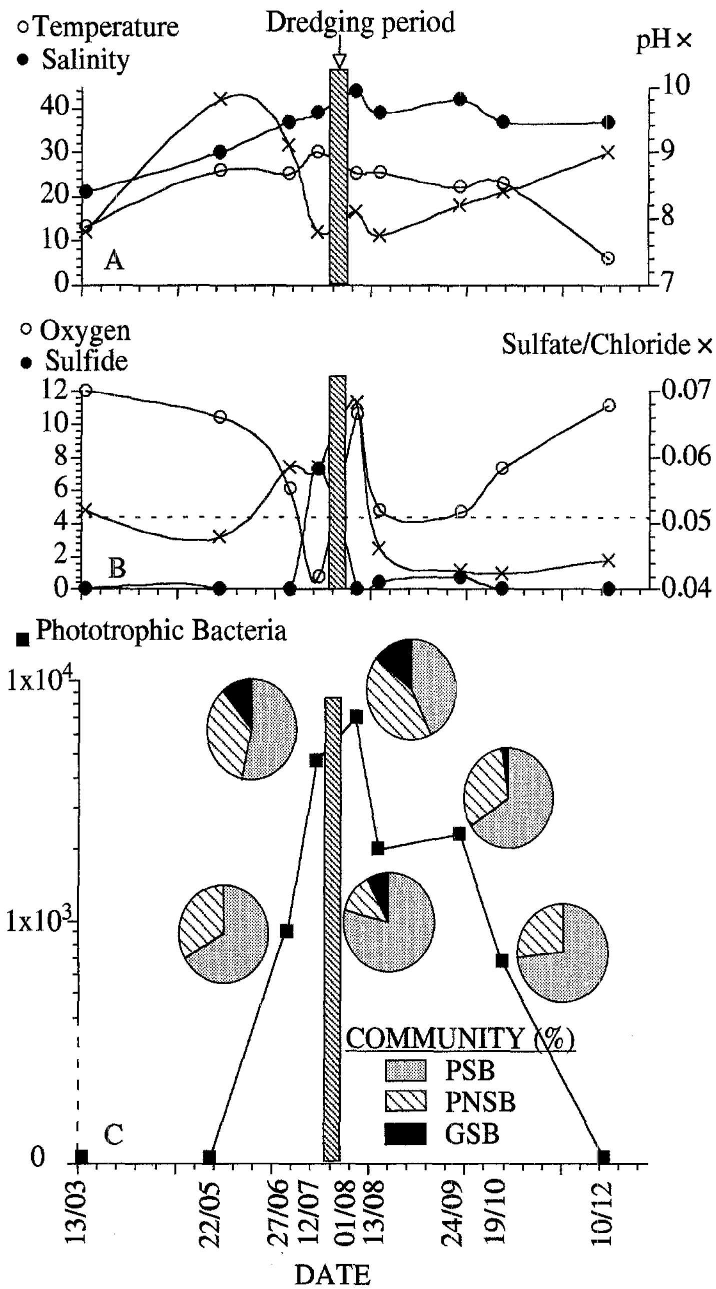

Figure 2. Physico-chemical parameters and phototrophic bacterial numbers in the water at station 3 during the period studied in 1991. A: temperature (°C), salinity (PSU) and pH; B: Oxygen and sulphide ($mg \cdot L^{-1}$) and Sulphate/Chloride molar ratio (dotted line represents the conservative value in sea water); C: Numbers of phototrophic bacteria ($C.F.U \cdot mL^{-1}$) and community structure (PSB, Purple Sulphur Bacteria; PNSB, Purple Nonsulphur Bacteria; GSB, Green Sulphur Bacteria).

After mid-July, the mechanical collection of macro-algae interrupted the phototrophic bacterial bloom. Fully-saturated oxygen conditions were reestablished in the water (O_2 = 10.6 $mg \cdot L^{-1}$), while sulphide was undetectable (*figure 2b*). The Sulphate/Chloride molar ratio increased to 0.0684. Although oxygen was present in the water, phototrophic bacteria were still present (7×10^3 $CFU \cdot mL^{-1}$). However, the community structure had changed, with a relative increase in Purple Nonsulphur Bacteria and a decrease in Purple Sulphur Bacteria (*figure 2c*).

From 13 August to 24 September, hypoxic conditions occurred again (O_2 = 4.7 to 4.8 mg·L^{-1}), together with low sulphide concentrations (H_2S = 0.4 to 0.7 mg·L^{-1}). The Sulphate/Chloride molar ratio (0.0461 to 0.0429) decreased below the conservative value. During this period, phototrophic bacterial numbers were 2 × 10^3 CFU·mL^{-1}. Normal conditions were only reached in October samples (19 October), when sulphide was undetectable in the water column. Oxygen concentration increased to 7.3 mg·L^{-1}, due to the development of *Enteromorpha sp.* at the sediment surface. Phototrophic bacterial numbers decreased to 7 × 10^2 CFU·mL^{-1} and representatives of the Green Sulphur Bacteria were not present in the water column.

3.2. Benthic processes

Organic matter contents (*figure 3*) were relatively constant during May and June from the water-sediment interface (3.8 to 4.9 % dry weight) to 10 cm depth (data not shown). Later, in mid-July, an organic matter enrichment (7.2 % dry weight) due to the deposition of macroalgal debris at the sediment surface was found in the first centimetre of the sediments. The organic material amount increased drastically following the start of dredging (1 August), where it represented 15.8 % of dry weight in the first cm. Afterwards, this amount decreased from mid-August (7.6 % dry weight) to December (*figure 3*).

Acid volatile sulphilde concentrations (AVS) and Sulphate/Chloride molar ratio within the sediment depth are presented in *figure 4*. AVS concentrations gradually increased from springtime to summertime throughout the sediments. In mid-July, AVS concentrations reached 37 µmol·cm^{-3} between 2 and 4 cm depth. The Sulphate/Chloride molar ratio was above the conservative value throughout the sediments in March (ranging from 0.0526 to 0.0781). In May, sulphate depletion extended progressively to the deeper sediment layers, and in July the entire sediment was sulphate-depleted (0.0061 to 0.0074), except for the first centimetre where the Sulphate/Chloride molar ratio was close to the conservative value (0.0514). After dredging (1 August), the entire sediment column was strongly sulphate-depleted, and high AVS amounts were still present. The sediment remained sulphate-deficient until October, when the Sulphate/Chloride molar ratio became higher than the conservative value. Acid volatile sulphide concentrations also decreased in October and December, with the highest concentrations ranging from 8 to 13 µmol·cm^{-3}.

The numbers of phototrophic bacteria (*figure 5a*) and the Bchl*a* concentrations (*figure 6a*) in the superficial sediment layers increased from March to mid-July (from 7 × 10^4 to 2 × 10^6 CFU·cm^{-3} and from 2.0 to 6.8 µg·cm^{-3} respectively). Microscopic observations of colonies obtained in agar media (*figure 5b*) revealed Purple Sulphur Bacteria (mainly *Chromatiaceae* from the genera *Thiocapsa* and *Chromatium*) as the dominant group among the phototrophic bacterial community (60 to 80 %). The Purple Nonsulphur Bacteria and the Green Sulphur Bacteria were minor components of the phototrophic community. Shortly after dredging began (1 August), phototrophic bacterial numbers decreased by about one order of magnitude (3.9 × 10^5 CFU·mL^{-1}) in the sediments, reflecting the mechanical impact of the mac-

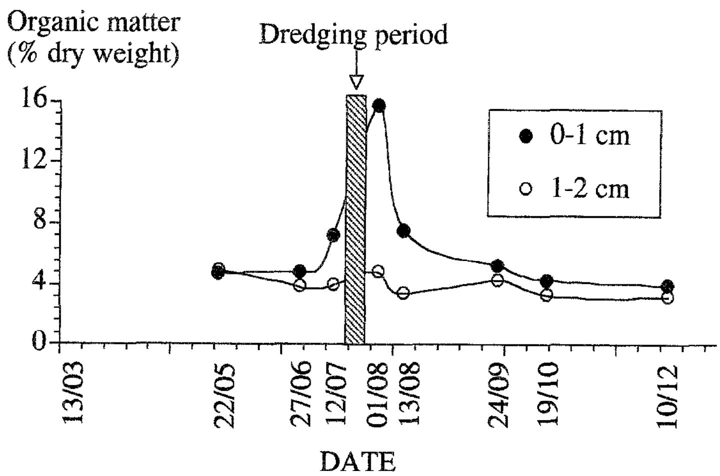

Figure 3. Organic matter contents in the 0–1 and 1–2 cm depth layers of the sediments at station 3 during 1991.

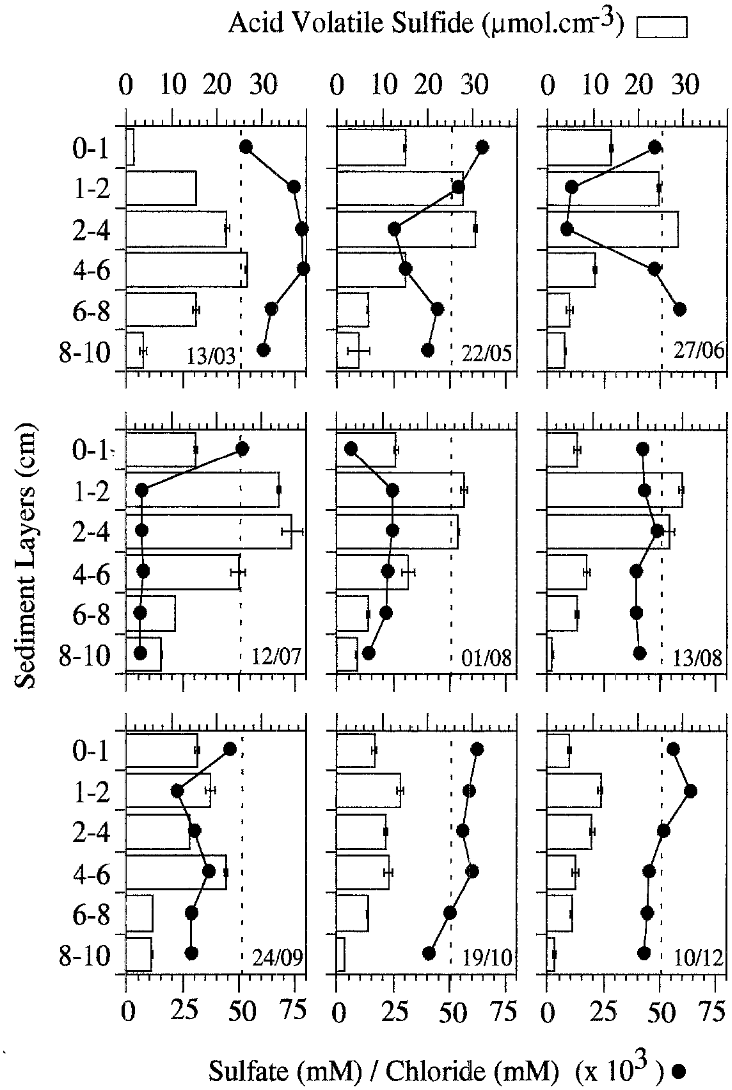

Figure 4. Acid volatile sulphide concentrations and Sulphate/Chloride molar ratio within the depth in the sediments of station 3 in the Prévost lagoon in 1991. Sampling dates are given in each of the graphs; the dotted line represents the conservative value of the Sulphate/Chloride ratio in sea water. Error bars for sulphide determination represent 95 % confidence intervals of the method assay.

roalgal removal on the whole phototrophic community (*figure 5a*). This impact is also shown (*figure 6a*) by the decrease in Bchl.*a* content of the sediment surface to 2.4 µg·cm^{-3} in early August.

In mid-August, the Green Sulphur Bacteria population was 1.4×10^5 CFU·mL^{-1}, similar to that detected before the dredging (2×10^5 CFU·mL^{-1} on 12 July). This phototrophic bacterial group was mainly composed of microorganisms morphologically related to the genus *Prosthecochloris*, which accounted for more than 50 % of the phototrophic community on 13 August (*figures 5a, 5b*). During the same period, purple phototrophic bacteria numbers did not increase, although the Bchl*a* concentration increased to 12.7 µg·cm^{-3} in mid-August (*figure 6a*). This increase in Bchl.*a* was due to an increase in the average Bchl*a* content of the purple phototrophic bacteria (*figure 6b*). The classic community structure of phototrophic bacteria in the Prévost lagoon, with a dominance of Purple Sulphur Bacteria, was only reestablished in September (*figure 5b*).

4. DISCUSSION

The dystrophic crises in the Prévost lagoon were the consequence of eutrophication, which resulted in a very high

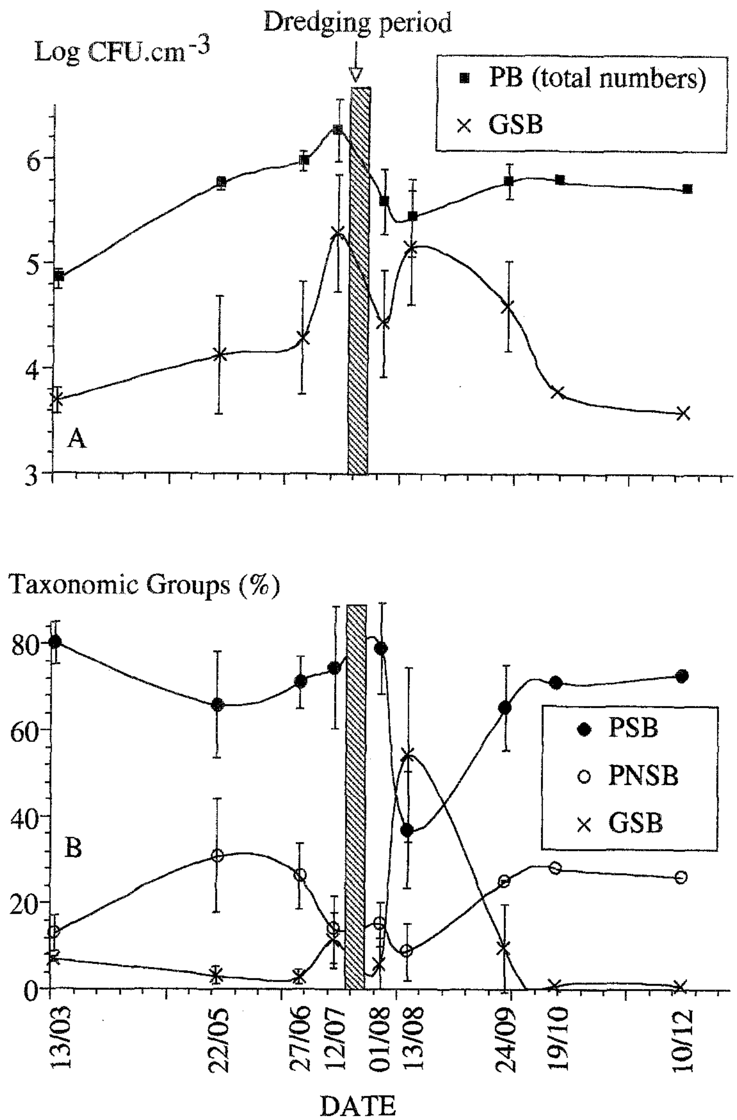

Figure 5. Phototrophic bacterial numbers (A) and community structure (B) in the 0–2 cm layer of the sediments at station 3 during 1991. A: Enumerations of total phototrophic bacteria and Green Sulphur Bacteria (error bars indicate standard deviation); B: Phototrophic community structure, the major taxonomic groups including PSB (Purple Sulphur Bacteria), GSB (Green Sulphur Bacteria) and PNSB (Purple Nonsulphur Bacteria) are represented as percentages of total counts (error bars indicate standard deviation).

primary production of macroalgae. In 1991, we estimated a fresh weight macroalgal biomass of 3300 g·m^{-2} at station 3, similar to those previously found at this station [26].

In 1991, from springtime to summertime, chemical and bacteriological analyses showed the typical development of the dystrophic crisis as described earlier [2, 3], with degradation of the accumulated macroalgal material in July. Subsequently, hypoxic conditions and hydrogen sulphide were found in the water column. The development of purple patches of Purple Sulphur Bacteria on moribund macroalgae deposited at the sediment surface indicated the imminent onset of the red water. The high Sulphate/Chloride molar ratio analysed in the vicinity of these patches revealed sulphide oxidation activity by the phototrophic bacteria. Many physiological studies carried out on *Thiocapsa roseopersicina* [27, 31, 32] have demonstrated the very versatile metabolism of this bacterium, which is able to grow phototrophically and

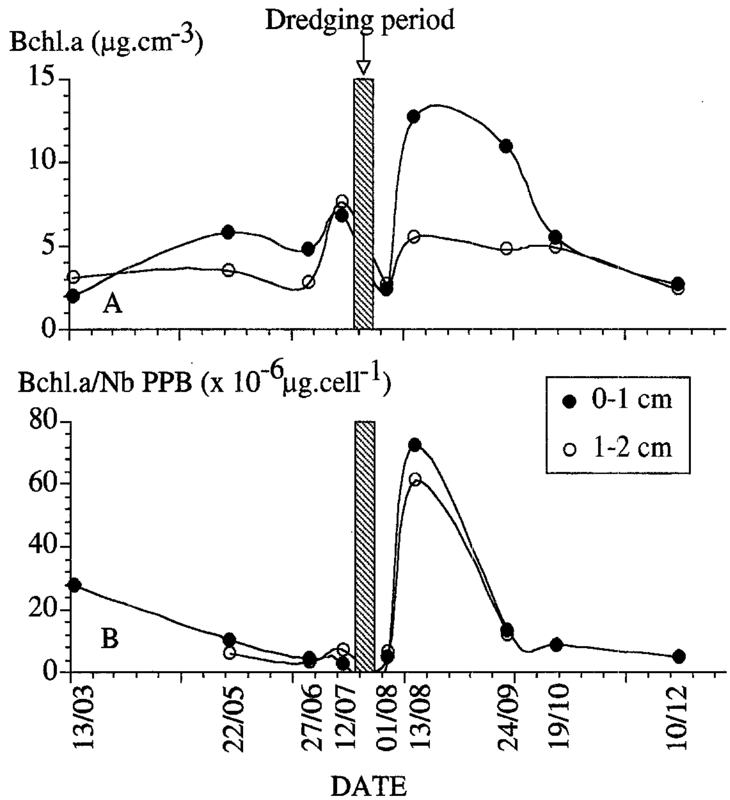

Figure 6. Bacteriochlorophyll *a* (A) and Bchl.*a* /Purple Phototrophic Bacteria Numbers (PPB) ratio (B) in the 0–1 and 1–2 cm depth layers of the sediments at station 3 during 1991.

chemotrophically. The Oxygen/Sulphide molar ratio in mid-July in the water column was 0.096. A low supply of oxygen combined with a high supply of sulphide represents a competitive advantage for Purple Sulphur Bacteria compared to Colourless Sulphur Bacteria [9].

During the same period, high sedimentary AVS levels were found throughout the sediment and the Sulphate/Chloride molar ratio decreased progressively with sediment depth, indicating a progressive reduction of the sulphur compound pool. Remarkably, the Sulphate/Chloride molar ratio remained close to the conservative value only in the first centimetre of the sediments, demonstrating the activities of microorganisms involved in the reoxidation processes of reduced sulphur compounds. Among these microorganisms, phototrophic bacteria play a key role in the illuminated superficial layers of the sediments. In the Prévost lagoon, they were mainly represented by members of the species *Thiocapsa roseopersicina* and *Chromatium gracile* [11], which are common anoxygenic phototrophic microorganisms in brackish and marine sulphureta [24].

5. CONCLUSION

In the past, such physiochemical conditions in the water and the sediments were followed by the formation of red waters in the entire water column [3]. However, in order to prevent dystrophic crisis, a macroalgal dredging programme, beginning just before the red water formation, was launched in 1991. This management programme influenced the hydrodynamics of the lagoon and the biogeochemistry of both the water column and the upper sediment layers. At the beginning of August, sulphide had disappeared from the water column and oxygen reached levels close to saturation. This management programme appeared to be successful in preventing the bloom of Purple Sulphur Bacteria in the water. Total numbers of anoxygenic phototrophic bacteria remained at 10^3 CFU·mL^{-1}, instead of increasing to above 10^8 CFU·mL^{-1} as reported during red waters [3]. In the sediments, part of the resuspended mineral and organic material (upper layers of the sediments, uncollected macroalgal debris) was redeposited as an organic rich sediment layer. The dredging also affected sulphur cycling as shown by the residual high levels of AVS and the strong sulphate depletion in the first centimetre. The mechanical impact of the dredging on the phototrophic bacterial community resulted in a decrease in their abundance (approx. one order of magnitude). The phototrophic bacterial community was no longer effective in reoxidizing reduced sulphur compounds originating from sulphate reduction activity, which was probably enhanced by the incorporation of organic matter into the superficial sediments.

Due to the enhancement of sulphate reduction, the inhibition of photosynthetic sulphide oxidation and the resuspension of AVS-rich sediments, low sulphide concentrations were detectable in the water from mid-August to September. Moreover, the dissolved oxygen concentration decreased following the dredging (13 August). Nevertheless, phototrophic bacteria numbers did not increase in the water column. The Oxygen/Sulphide molar ratio in the water column was 11.3 and 6.6 in mid-August and September, respectively. A high supply of oxygen combined with a low supply of sulphide represents a competitive advantage for Colourless Sulphur Bacteria compared to Purple Sulphur Bacteria [9].

In the sediments, the phototrophic bacterial community slowly recovered from August to September. This regeneration began remarkably, with the development of the Green Sulphur Bacteria population, whose numbers increased from 2.7×10^4 $CFU{\cdot}mL^{-1}$ (1 August) to 1.4×10^5 $CFU{\cdot}mL^{-1}$ (13 August), whereas Purple Sulphur Bacteria and Purple Nonsulphur Bacteria numbers remained at nearly constant levels during this period. The Green Sulphur Bacteria mainly comprised representatives of the species *Prosthecochloris aestuarii* [11], commonly found in marine ecosystems [24]. The increase in the average specific Bchl*a* content in mid-August indicates that the purple bacteria were growing under severely light-limited conditions. The low light intensities due to the mechanical impact of the dredging (resuspension of sediment particles) may explain the rapid growth of the Green Sulphur Bacteria, which are able to grow at lower light intensities than purple bacteria [1, 17, 20]. Moreover, the development of *P. aestuari*-like bacteria can also be explained by the higher growth rates of the Green Sulphur Bacteria as compared to those of Purple Sulphur Bacteria [16, 22].

As a general statement, the lagoon management avoided the development of anoxic conditions in the water column and prevented the formation of red water. In 1991, dredging began in mid-July, when most of the moribund macroalgae were lying on the sediment surface. Since 1992, an extended dredging programme has been pursued, involving the collection of macroalgae during their active growth phase, from early springtime. This new management scheme reduces the impact of resuspension of the superficial sediment layers and thus the disturbance of the microbial communities. Consequently, long periods of anoxia and red water blooms have not been observed in the Prévost lagoon (station 3) since 1992.

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