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Benthic studies of the Northwest African upwelling region: bacteria standing stock and ETS-activity, ATP-biomass and Adenylate Energy Charge

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ABSTRACT: During the 'Meteor' expedition SUBTROPEX '82, sediment samples were taken at 14 stations in different water depths at 35, 29, 25, 21 and 17 °N, and measurements of bacterial biomasses and activites were carried out in these different upwelling-intensity areas. Highest densities and biomasses by AODC (2.2×10^8 cells, corresponding to 14.8 µg C g^{-1} sediment dry wt) were recorded at 21 °N, year-round upwelling, at 1200 and 800 m, but at 500 m biomass was still 4.3 µg C g^{-1} dry wt. Relatively high densities and biomasses (6.5 and 6.8 µg C g^{-1} dry wt) were found at 17 °N, upwelling mostly in winter and spring, at 1200 and 800 m. AODC were 2 to 3 orders of magnitude higher than viable counts, incubation at 2 or 20 °C. For deep-water sediments, counts at 2 °C were higher than at 20 °C. Biomass and ATP concentrations were highest in the 0 to 2 cm sediment layers; they decreased with sediment depth. Bacterial biomasses were correlated with organic carbon and ATP concentrations. The fractions of Bacterial ATP were calculated to be 2 to 24 % of ATP-biomass. On the basis of organic carbon, however, fractions of Bacterial Organic Carbon were only 0.02 to 0.06 ‰. For microbial communities, the conversion factor 0.004 for BOC to BATP seems 2 orders of magnitude too high. Maximum AEC ratios of 0.53 to 0.70 were found at 21 and 17 °N; the other stations had AEC ratios of 0.21 to 0.47. Numbers of bacteria with respiratory ETS were between 0.5 and 10.5 % of AODC. An exception was the shelf station at 35 °N with 34.2 % of AODC.

INTRODUCTION

The Northwest African upwelling region is characterized by a front near Cape Blanc, where North Atlantic Central Waters and South Atlantic Central Waters mix (Minas et al. 1982). Here, upwelling takes place the whole year round, with the highest primary productivity rates found in the Cape Barbas–Cape Blanc area around 21 °N. To the south, upwelling occurs mostly in winter and spring. North of Cape Bojador, about 26 °N, upwelling is strongest in summer. During active upwelling seasons, very nutrient rich waters and high primary productivity rates may be observed close to the coast. In the African upwelling region, nutrients and primary production are closely related (Minas et al. 1982); sediments also reflect the processes in the overlying waters (Diester-Haass 1978, Seibold 1982).

Sediment metabolism from the Northwest African coast was assayed by measurements of the respiratory Electron Transport System (ETS); a correlation was found between ETS-activities and depth of the water column (Christensen & Packard 1977). Watson (1978) determined bacterial biomass and heterotrophic activity in sediments and overlying waters between 21 and 22 °N off Northwest Africa.

Studies of benthic macro- and meiofauna standing stocks and chloroplastic pigment equivalents off the Northwest African coast at 17, 21 and 25 °N revealed that macrofauna and chloroplastic pigment equivalents were related to primary productivity in surface waters, whereas the meiofauna was not (Thiel 1982). These investigations were extended by respiration measurements of the benthic community under an area of low upwelling intensity off Morocco (Pfannkuche et al. 1983).

From these earlier studies it is known that benthic standing stocks and ETS-activities are related to primary production in upwelling systems. Further meas-

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urements of benthic biomasses and activites in this region of the Canary Current with different upwelling intensities and water depths were carried out during the 'Meteor' expedition in 1982. The interdisciplinary biology programme consisted of bacteria, meio- and macrofauna standing stock determinations, measurements of respiration, ETS-activity, chloroplastic pigment equivalents, ATP-biomass and Adenylate Energy Charge (AEC), and investigations of the benthic bacterial communities and nitrogen transformation processes. Some of our results concerning the distribution of psychrophilic bacteria and the catabolic potentials of bacterial communities have been reported (Rüger 1982, 1985). Results of bacterial biomass and activity determination are reported here.

MATERIALS AND METHODS

Sampling methods and station locations. During the cruise SUBTROPEX '82 in January and February 1982 on board RV 'Meteor' in the Northwest African upwelling region, sediment samples were taken with a box-grab-sampler (surface area: 50 × 50 cm). Two subsamples were drawn from the box with a 15 × 2 cm corer, each about 10 cm deep. The first core was used for determinations of viable counts, acridine orange direct counts (AODC), bacteria cells with respiratory ETS, organic carbons and dry weights. The second core was used for extractions required for adenine nucleotides determinations. Cores were divided horizontally into 2 cm sections, and sediments from 0–2, 2–4 and 4–6 cm sections were each collected in sterile 100 ml flasks. Sediments in the flasks were thoroughly mixed with a spatula and kept in a refrigerator until further processing within 6 h.

Station locations at 35, 29, 25, 21 and 17 °N and at different water depths were chosen for these investigations (Fig. 1). The numbers of the grab-samplers employed for obtaining subsamples are presented in Table 2. Viable count determinations were made using the spread-plate-method on seawater agar. For seawater agar composition as well as sample pretreatment and processing see Rüger (1982).

Acridine orange direct counts. A spoonful (1 ml) of sediment sample was suspended in 4.5 ml of sterile water (750 ml seawater + 250 ml distilled water) in a 20 ml polypropylene vial. The sediment suspension was homogenized with an Ultra Turrax 18 KG blender (Janke & Kunkel, IKA-Werk, Staufen, FRG) for 1 min at about 20 000 rpm. The shaft was then cleaned twice in each 4.5 ml of sterile seawater by rotating the blender for about 10 s at full speed, to remove remaining cells and sediment particles. Both cleaning suspensions were combined with the sediment suspension in one vial. Cells were then preserved with formaldehyde at a final concentration of 2 % and samples stored in a refrigerator at 4 °C. The Ultra-Turrax shaft was thoroughly rinsed in 70 % ethanol and sterile seawater before treating the next sample. A second sediment sample was homogenized in the same manner for determination of bacteria cells with respiratory ETS (10 ml), and the rest of this suspension was preserved with formaldehyde and taken as duplicate sample for AODC.

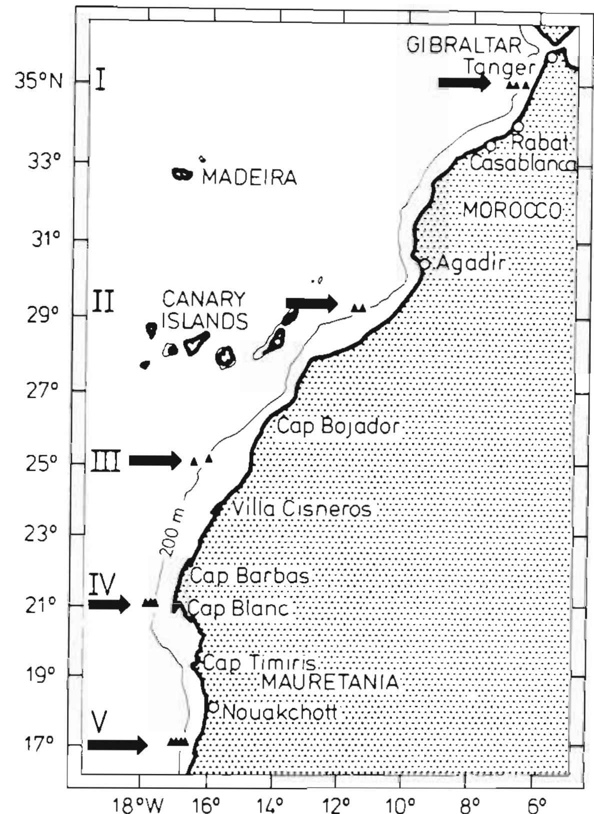

Fig. 1. Map of Northwest African coast showing station locations at approximately 35, 29, 25, 21 and 17 °N, i.e. Transects I, II, III, IV and V

Samples were further processed not later than 6 mo after preservation. The sediment suspension was mixed with an Ultra-Turrax for a few seconds, and sediment particles were then allowed to settle for 10 min. The bacterial suspension above the sediment was carefully pipetted and further diluted with sterile seawater to a final dilution of 100-fold.

The method of acridine orange staining and fluorescence microscopy (Hobbie et al. 1977) was used, but 5.7 ml of the diluted suspension was stained with 0.3 ml of a 0.1 % acridine orange solution in phosphate buffer, pH 8.0 (Tan 1983)

Bacteria were morphologically differentiated into 5 groups and each group counted quantitatively for biovolume determinations:

Group 1: Small coccoid cells, diameter about 0.2 μm, volume 4.187×10^{-3} μm^3.

Group 2: Large coccoid cells, diameter about 1 μm, volume 523.33×10^{-3} μm^3.

Group 3: Short rods, size 0.4 by 0.7 μm, volume 87.92×10^{-3} μm^3.

Group 4: Long rods, size 0.4 by 1.5 μm, volume 188.4×10^{-3} μm^3.

Group 5: Filamentous cells, 0.4 by 2.5 μm or longer (up to 50 μm), volume 314×10^{-3} μm^3.

Determinations of bacteria cells with respiratory ETS. Homogenization of the sediment sample was done as described under AODC. To 5 ml of sediment suspension in a 20 ml vial were added solutions of succinic acid, NADH, $NADPH_2$ and INT (Rüger 1984). After incubation at 20 °C for 1.5 h samples were preserved with 1 ml of 37 % formaldehyde and stored in a refrigerator. Preserved samples were stained and bacteria cells with respiratory ETS counted not later than 3 mo after storage. The sediment suspension was shaken vigorously and after 10 min of sedimentation the supernatant was diluted 1 : 10 or 1 : 50 with distilled water, and 4 ml of the diluted suspension were filtered on a 0.2 μm polycarbonate filter. Staining the bacteria cells with molybdatophosphoric acid and methylgreen was done according to Iturriaga & Rheinheimer (1975), but the methylgreen solution had to be diluted 40-fold and staining time was 5 s. Then the remaining dye was rinsed with 5 ml of distilled water and the wet filter mounted in immersion oil, Type A (Cargille Laboratories, Cedar Grove, N. J., USA) on a slide. The slide was immediately inspected with a Standard RA microscope (Carl Zeiss, Oberkochen, FRG) at a magnification of 1250-fold.

Dry weight and organic carbon determinations. The sediment sample (1 ml) was filled in a polypropylene 25 ml container and dried at 60 °C for 3 d. Hydrogen chloride was added to the dried and ground sediment sample to remove the inorganic carbon fraction (Ernst 1975). The organic carbon was subsequently oxidized to carbon dioxide in a furnace and carbon dioxide determined with an Infrared-Analyzer IR 215 (Beckman Instruments, Munich, FRG).

Extractions of adenine nucleotides. ATP, ADP and AMP standard solutions, each at a concentration of 0.5 mg ml^{-1}, were made from ATP-disodium salt, ADP-di-monocyclohexylammonium salt and AMP-sodium salt (Sigma Chemie, Deisenhofen, FRG). From these standards an AMP + ADP + ATP standard (1 : 1 : 1) was mixed. Amounts of 1 ml standard solutions were sealed in glass ampoules and sterilized in an autoclave at 121 °C for 20 min.

Sediment samples (1 ml portions) were extracted in boiling Tris-buffer pH 7.7 according to Holm-Hansen (1973), or in boiling $NaHCO_3$ pH 8.5 (Christian et al. 1975) in a sand-bath (Gerhardt, Bonn, FRG). Six 250 ml Erlenmeyer flasks, fitted with condensing glass stoppers, could be heated simultaneously in the sand-bath. Per sediment section and buffer solution the following extractions and additions of ATP, ADP and AMP + ADP + ATP standards were done according to Graf (1979):

Extractions Nos. 1 to 5: Sediments without additions of standards.

Extractions Nos. 6 to 8: Sediments with additions of AMP + ADP + ATP standards, each 20 μl.

Extractions Nos. 9 to 11: Sediments with additions of ADP standards, each 10 μl.

Extractions Nos. 12 to 14: Sediments with additions of ATP standards, each 10 μl.

The extracts were adjusted to initial volumes, filled into centrifuge tubes and cooled in an ice-bath. Subsequently the extracts were centrifuged at 5000 rpm for 10 min (Hettich centrifuge 1200, Tuttlingen, FRG) to precipitate the sediment particles. The clear extract was filled into two 2.2 ml Eppendorf-containers, the rest discarded. Extracts were stored at −25 °C until further enzymatic conversions.

Determinations of adenine nucleotides. After thawing, the bicarbonate extracts were diluted in 0.1 *M* Hepes-buffer to get a total dilution of 50-fold. The same enzyme preparations and enzyme solutions as given by Falkowski (1977) were taken for quantitative conversions of ADP and AMP to ATP, but half the amounts of pyruvate kinase and myokinase were sufficient. Samples for ATP determinations and for enzymatic conversions of ADP and AMP to ATP were incubated at 30 °C in a shaking water bath for 30 min. Standards ATP, ADP and AMP + ADP + ATP in 0.1 *M* Hepes-buffer, ranging from 5 to 50 ng ml^{-1}, were treated in the same manner as the samples. Heat denaturation in a thermoblock at 120 °C for 2 min was necessary to inactivate the remainder enzyme pyruvate kinase (Karl & Holm-Hansen 1978).

ATP (or ADP and AMP converted enzymatically to ATP) was assayed using ATP-luciferase test combinations CLS and HS (Boehringer, Mannheim, FRG). For AMP converted to ATP the HS enzyme had to be used. The sample or standard (50 μl) was mixed with CLS enzyme (50 μl) or with HS enzyme (200 μl) in a 4 ml scintillation vial and light emission was recorded with an ATP-Biophotometer, model 3000 (SAI, San Diego, California, USA), equipped with a flatbed recorder (Kipp & Zonen, Delft, Netherlands). Measurements with CLS enzyme were made using the integration mode (20 s assay period), whereas peak height measurements were necessary for the HS enzyme. The ATP contents of the samples were determined from the linear calibrations obtained with the 3 different standards. Recovery rates for ATP, ADP and AMP were

determined from extraction Nos. 6 to 8 and 12 to 14, Nos. 6 to 11 and Nos. 6 to 8, respectively.

The Adenylate Energy Charge ratios of the microbial sediment populations were calculated from the following equation according to Chapman & Atkinson (1977):

$$AEC = \frac{|ATP| + 1/2\,|ADP|}{|ATP| + |ADP| + |AMP|}$$

RESULTS

Bacterial cell numbers and biovolumes

The results of bacterial cell number and biovolume determinations of the 3 sediment layers are presented in Table 1. The bacterial densities were highest in the upper sediment layers (0 to 2 cm) and decreased with sediment depth. AODC were 2 to 3 orders of magnitude higher than the viable counts at incubation temperatures of 20 or 2 °C. For shallow-water sediments higher counts were obtained after incubation at 20 °C, whereas for the deep-water sediments the numbers of CFU were higher at the incubation temperature of 2 °C. The highest bacterial cell numbers and biovolumes were found at 21 °N at water depths of 780 and 1198 m, but bacterial cell numbers and biovolumes were also high at 17 °N for water depths of 827 and 1205 m.

Organic carbon and bacterial biomass concentrations

A good correlation was found between organic carbon and bacterial biomass concentrations in sediments (Fig. 2). Correlation coefficients for the 3 sediment layers are 0.78 (0 to 2 cm), 0.55 (2 to 4 cm) and 0.72 (4 to 6 cm). Bacterial organic carbon (BOC) contents were calculated from biovolumes using the conversion factor of 5.6×10^{-13} gC μm^{-3} (Bratbak 1985). Fig. 2 shows maximum bacterial biomasses at 21 °N for 800 and 1200 m, but relatively high biomasses were also found at 17 °N (800 and 1200 m) and at 25 °N (800 m). The highest concentrations of organic carbon, however, were at 17 °N (800 and 1200 m); almost the same concentrations were recorded in sediments at 21 °N for 800 and 1200 m. The organic carbon concentration in 400 m at 21 °N was still 12.6 mg C per g sediment dry weight.

Adenosine triphosphate and bacterial adenosine triphosphate concentrations

Fig. 3 shows the results of adenosine triphosphate (ATP) and bacterial adenosine triphosphate (BATP) determinations. Only the bicarbonate extracts of the sediments gave correct ATP, ADP and AMP results that were in good agreement with the additions of adenylate standards. Therefore, results of ATP analyses with Tris-buffer extracts are not taken into consideration. ATP concentrations are presented as mean values from 5 replicates by considering the respective recovery rates. ATP recovery rates between 45 and 109 % were found for sediments of the upwelling region. BATP was calculated from BOC using a conversion factor of 0.004 (Karl 1980). A correlation between ATP and BATP was found only for the 0 to 2 cm sediment layer; the correla-

Table 1. Bacterial cell numbers and biovolumes per g sediment dry weight in the Northwest African upwelling region. Sediment layers: 0 to 2, 2 to 4, 4 to 6 cm

Water depth (m)	CFU at 20 °C $\times 10^5$	CFU at 2 °C $\times 10^5$	AODC $\times 10^7$	Biovolume $\times 10^6$ μm^3	Latitude (N)
0138	9.21/6.90/4.11	1.65/1.54/1.05	04.42/4.07/3.29	04.06/03.55/3.89	
0423	3.50/2.53/1.58	1.05/0.32/0.33	03.45/2.80/2.31	03.68/02.91/2.02	35°
0811	2.73/0.96/1.20	2.79/5.51/1.18	06.44/3.07/2.94	08.53/03.70/2.96	
0529	1.26/0.29/0.22	0.90/0.29/0.12	07.35/4.40/3.83	07.94/05.03/5.62	29°
0823	0.72/0.26/0.22	3.24/0.89/0.15	06.79/4.31/3.74	06.58/05.08/4.89	
0772	1.26/0.11/0.11	2.97/0.90/0.78	06.50/4.41/4.11	10.07/05.98/5.69	25°
1138	0.31/0.42/0.08	2.35/0.53/0.10	06.00/3.99/3.76	06.06/04.12/3.63	
0495	7.11/0.82/0.33	0.28/0.07/0.06	06.48/5.44/5.22	07.63/07.26/5.19	
0780	6.80/0.97/0.25	2.26/0.26/0.09	17.17/9.72/5.73	22.28/12.43/7.02	21°
1198	3.07/0.23/0.13	5.18/0.24/0.12	21.71/6.83/6.84	26.49/06.64/6.84	
0084	8.94/5.85/2.29	0.12/0.05/0.07	04.74/3.85/3.72	05.01/04.81/5.50	
0418	3.26/2.69/1.02	2.81/1.81/0.28	02.52/2.11/2.12	03.39/02.91/2.74	17°
0827	7.09/1.03/0.19	6.02/1.92/0.61	09.94/4.94/4.54	12.13/06.95/5.64	
1205	3.21/0.66/0.79	7.94/2.39/0.86	10.32/8.13/5.40	11.64/07.50/6.91	

CFU: Colony forming units; AODC: Acridine orange direct counts

tion coefficient is 0.64. Data for the sediment layer 4 to 6 cm are not available for the shelf station at 35 °N . Generally, ATP concentrations were highest in the upper sediment layers (0 to 2 cm). ATP concentrations in sediments at 35, 29 and 25 °N showed a decreasing tendency with increasing water depth, but at 21 and 17 °N , ATP concentrations at greater water depths were higher than at the shallower stations. An exception was the ATP concentration of the shelf station at 17 °N, which was higher compared to the concentration at 400 m water depth.

Total adenylate concentrations and percent fractions of BOC to organic carbon and BATP to ATP

The concentrations of total adenylate (At), presented in Table 2, are correlated only with ATP concentrations in the sediment layer 0 to 2 cm. The correlation coefficient is 0.82. Total adenylate concentrations were highest in the 0 to 2 cm sediment layers, but At concentrations in the deeper sediment layers were not always decreasing. By assuming that ATP-biomass is identical to living biomass, we calculated the fractions of BATP

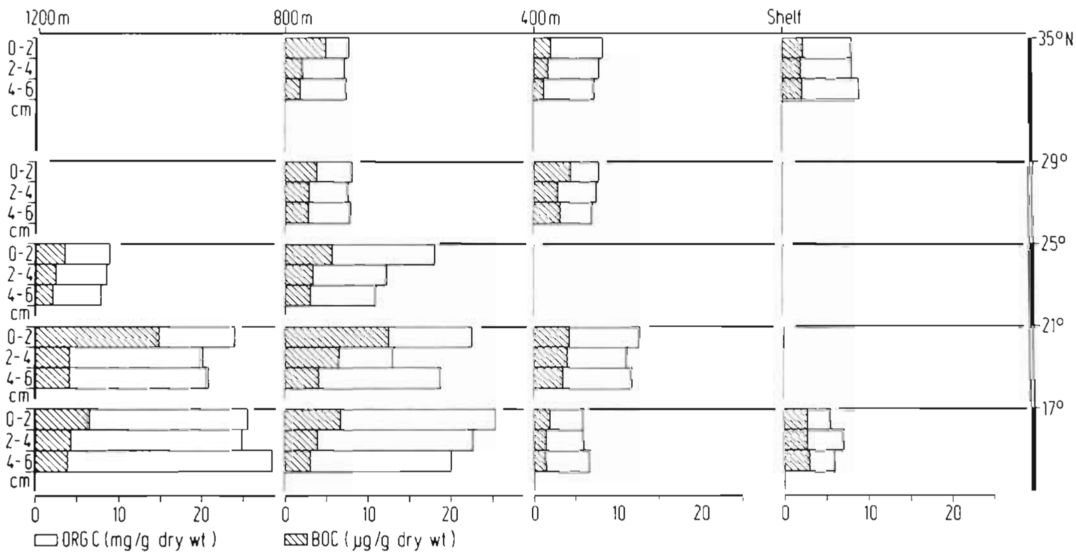

Fig. 2. Bacterial Organic Carbon and Organic Carbon concentrations in the sediments of the Northwest African upwelling region. Sediment layers: 0 to 2, 2 to 4, 4 to 6 cm

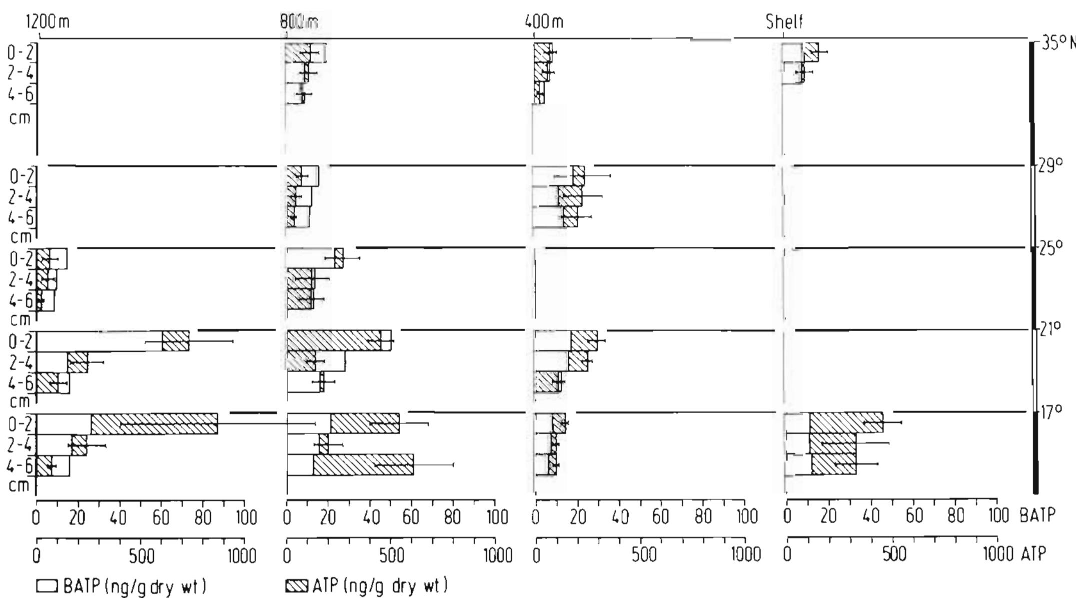

Fig. 3. Bacterial Adenosine Triphosphate and ATP concentrations in sediments of the Northwest African upwelling region. ATP concentrations are mean values of 5 replicates. Bars: standard deviations. Sediment layers: 0 to 2, 2 to 4, 4 to 6 cm

to be between 2 and 24 % of the total living biomasses (Table 2). On the basis of organic carbon contents of the sediments, however, the BOC concentrations were only between 0.02 and 0.06 % of the organic carbon concentrations. The BATP to ATP fractions are 50 to 600 times higher than the corresponding fractions of BOC to organic carbon.

Adenylate energy charge and numbers of bacteria with respiratory ETS

Adenylate energy charge (AEC) ratios and numbers of bacteria with respiratory ETS (percent of AODC) for sediment populations are presented in Fig. 4. Our results indicate that the microbial communities at 21° and also at 17 °N (depths of 84 and 827 m), with AEC ratios of 0.53 to 0.7 for the upper sediment layers, comprised of cells like those in the stationary phase of growth in pure cultures (Wiebe & Bancroft 1975). The physiological conditions of the other investigated microbial communities – AEC ratios of 0.21 to 0.48 – were much worse.

The numbers of bacteria with respiratory ETS ranged only between 0.5 and 10.5 % of AODC. An exception was the number of bacteria with respiratory ETS at the shelf station (35 °N) with 34.2 % AODC. Respiratory ETS cell numbers in the 0 to 2 cm sediment layer of the 17 °N shelf station were not determined, but in deeper sediment layers the numbers did not exceed 10 % of the AODC.

A negative correlation between AEC ratios and numbers of bacteria with respiratory ETS can be seen in Fig. 4 for the 0 to 2 cm sediment layer. The correlation coefficient is 0.63. However, more data on AEC ratios and numbers of bacteria with respiratory ETS should be available before this presumption can be verified.

DISCUSSION

Our investigations of benthic bacterial biomass revealed the highest amounts at 21 °N, the centre of the upwelling, but relatively high amounts were still found at 17 and 25 °N. The results coincided with primary productivity rates found in the overlying waters, dependent on upwelling intensities and seasons (Minas et al. 1982). Bacterial biomasses by AODC were in the range of 2 to 15 µg C per g sediment dry weight for surface layers (0 to 2 cm). This bacterial biomass represents only 0.03 to 0.06 % of the sediment organic carbon content. The values found were in the same range as reported by Wood (1970) with his method of erythrosine staining. With the AODC technique, however, fractions of bacterial biomass were found between 0.2 and 2 % of the organic carbon or organic matter contents, depending on grain size and organic carbon content of the sediments, as reviewed by Meyer-Reil (1984). Our biomass determinations are probably 2 to 3 times too low, because an Ultra-Turrax mechanical stirrer was used to disrupt cell aggregates from sediment particles, whereas in counting bacteria from sediment samples ultrasonication is the method chosen by most workers (Ellery & Schleyer 1984). The direct

Table 2. Total adenylate (At) concentrations and percent fractions of Bacterial Organic Carbon and Bacterial Adenosine Triphosphate to Organic Carbon and Adenosine Triphosphate in sediments of the Northwest African upwelling region. Sediment layers: 0 to 2, 2 to 4, 4 to 6 cm

Box No.	Water Depth (m)	At (ng g^{-1} dry wt)	BOC/ORG.C (%)	BATP/ATP (%)	Latitude (N)
882	0138	1298/1369/nd	0.027/0.024/0.025	05.76/08.59/nd	
888	0423	0440/0268/0224	0.025/0.021/0.015	12.20/12.17/17.85	35°
895	0811	0312/0315/0315	0.064/0.030/0.022	16.54/07.74/07.83	
909	0529	1371/1534/1352	0.058/0.038/0.044	07.61/05.03/06.25	29°
899	0823	0835/0791/0528	0.046/0.038/0.036	22.45/29.62/42.54	
915	0772	1259/0394/0707	0.031/0.027/0.029	08.43/11.28/10.90	25°
968	1138	0581/0886/1148	0.038/0.029/0.027	23.91/19.90/70.00	
937	0495	0765/0679/0795	0.034/0.036/0.025	05.80/06.59/10.55	
925	0780	1148/0495/0320	0.055/0.053/0.021	11.09/20.23/08.99	21°
971	1198	2242/1487/0369	0.061/0.019/0.018	08.12/06.20/15.46	
962	0084	0988/0890/0864	0.051/0.041/0.052	02.45/03.30/03.74	
941	0418	0572/0478/0355	0.032/0.027/0.023	05.50/06.93/06.49	17°
947	0827	1121/0473/0941	0.027/0.017/0.016	05.03/07.89/02.07	
955	1205	4467/3612/0750	0.026/0.017/0.013	02.99/07.19/20.93	

nd: not determined

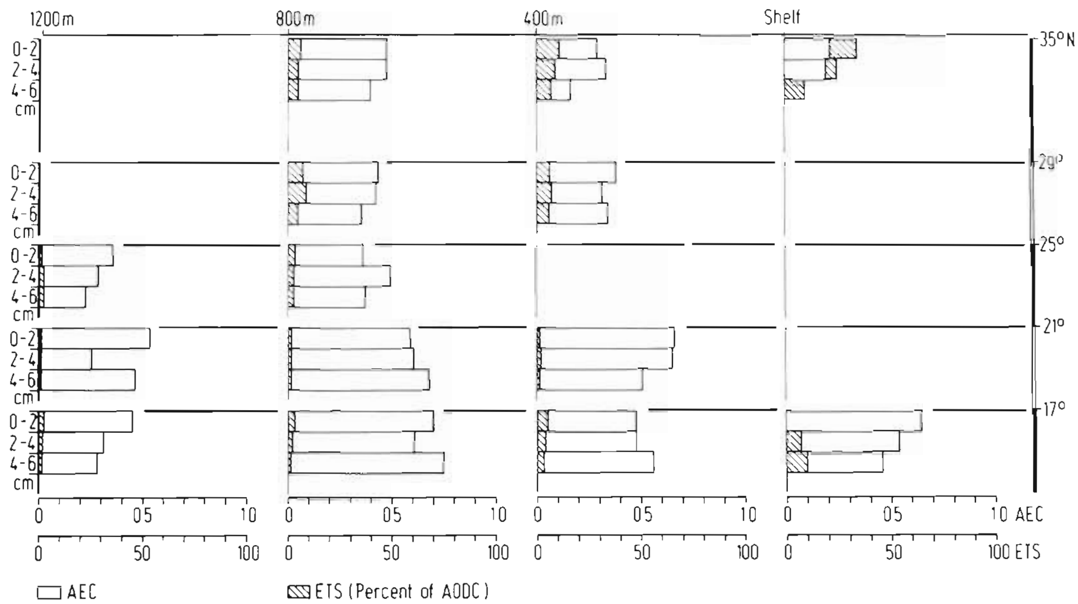

Fig. 4. Adenylate Energy Charge ratios versus numbers of bacteria with respiratory ETS (percent of AODC) for the sediments of the Northwest African upwellig region. Sediment layers: 0 to 2, 2 to 4, 4 to 6 cm

counts with acridine orange staining have been compared with DAPI, a highly specific DNA fluorochrome (Porter & Feig 1980), but for sediment samples the final concentration used was 2 µg ml^{-1}. The DAPI counts were in good agreement with our reported AODC. It is quite difficult to differentiate in sediment samples between bacteria with red fluorescence and detritus or organic matter fluorescing red too. With the method of acridine orange staining applied (Tan 1983), between 91 and 98 % of the sediment bacteria fluoresced green or yellow-green. We therefore have taken into account only cells with green and yellow-green fluorescence for biomass determinations.

Watson (1978) compared the bacterial biomass and heterotrophic activity in sediments from shallow and deep stations between 21 and 22 °N off Northwest Africa and found higher biomass and activity in shallow water than in slope sediments from the deeper stations. Unfortunately, specific growth rate estimates, e.g. with the 'Frequency of Dividing Cells' method (Hagström et al. 1979, Meyer-Reil 1983) or the adenine turnover method (Karl et al. 1987, Novitsky 1987) were not performed for our benthic investigations off Northwest Africa.

Availability of dead microbial biomass from a marine sand sediment to degradation and mineralization was examined with labeled cells, and biochemical components like DNA and RNA were monitored. Labeled RNA was degraded more rapidly than labeled DNA, but both nucleic acids were degraded to 60 to 70 %. Respiration was completed in 3 d, whereas nucleic acid degradation continued throughout the 10 d incubation period (Novitsky 1986). Not much is known about the grazing rate of benthic meio- and macrofauna feeding on bacteria, but grazing stimulates the metabolic activity of the bacteria (Gerlach 1978).

The reasons for the difference of several orders of magnitudes observed between AODC and viable counts were treated in detail by Van Es & Meyer-Reil (1982). Moreover, the viable counts proved to be dependent on the incubation temperature applied for the samples. From shallow-water sediments with temperatures of about 15 °C, the highest counts were obtained after incubation at 20 °C. The numbers of CFU from deeper sediments incubated at 2 °C were up to 1 order of magnitude higher than the numbers obtained at 20 °C (Rüger 1982).

The organic carbon concentrations found in the sediments were correlated with bacterial biomass and ATP concentrations. ATP concentrations ranging from 60 to 900 ng per g sediment dry weight were found for the surface sediments (0 to 2 cm layers), depending on water depth and upwelling intensity. These values are in good agreement with the values reported for ATP contents from Northeast Atlantic sediments (Ernst & Goerke 1974). Ernst & Goerke also reported decreasing ATP contents of the sediments with increasing water depth. In general, ATP concentrations of 2 to 5 ng g^{-1} were found in deep-sea sediments (Karl et al. 1976, Thistle et al. 1985), whereas in marine coastal sediments ATP concentrations from 300 to 8000 ng g^{-1} were recorded (Aller & Yingst 1980, Christensen & Devol 1980, Delmas & Romano 1980, Pamatmat et al. 1981, Novitsky 1987).

Total adenylate concentrations (At) were used to determine the heterotrophic-photoautotrophic index, defined as the concentration of total adenylates divided by the concentration of active chlorophyll *a* (Campbell et al. 1979). For the sediments off Northwest Africa, however, only chloroplastic pigment equivalents were determined.

Fractions of BATP to ATP were between 2.5 and 24 % for surface sediment layers (0 to 2 cm). These fractions are 50 till 600 times higher than the corresponding BOC to organic carbon fractions; the average value is 250. BATP was calculated from BOC using the conversion factor of 0.004, estimated as average from laboratory grown bacterial cultures (Karl 1980). Algal ATP/C ratios decreased with nutrient deficiency, to a greater extent with phosphorous than with nitrogen deficiency (Hendzel & Healy 1984). For the bacterial population from the water of a salt-marsh creek near Georgetown, South Carolina, Wilson et al. (1981) also reported an ATP/cell content 2 orders of magnitude lower than the ATP/cell content from laboratory-grown cultures. For calculations of BOC to BATP contents of microbial populations from nutrient-limited environments, we therefore recommend the conversion factor of 16×10^{-6} according to our results of BATP/ATP fraction determinations.

The AEC ratio to measure growth states of natural microbial communities was first applied by Wiebe & Bancroft (1975) for salt-marsh sediments at Sapelo Island, Georgia. They found that the AEC ratio rose during February to July, 1973 from 0.3 to about 0.6, which coincides with the ratio characteristic of a stationary phase of growth for pure cultures of bacteria. Others have since used the AEC ratio to determine the physiological state of microbial communities (Christensen & Devol 1980, Romano & Daumas 1981, Klinken & Skjoldahl 1983). Thus microbial communities at 21 and 17 °N, with AEC ratios of 0.53 to 0.70, were comparable with bacteria cells in the stationary phase of growth in pure cultures. Investigations of sediment-water interface communities in Halifax Harbor, Canada, revealed that this community, supporting high bacterial biomass and activity, consisted mostly (over 90 %) of non-growing cells (Novitsky 1983, 1987).

Numbers of bacteria cells with respiratory ETS ranged only between 0.5 and 10.5 % AODC. An exception was the shelf station at 35 °N with 34.2 % AODC. In water samples from coastal areas of the Baltic Sea, 6 to 12 % of the bacterial population consisted of cells with respiratory ETS (Zimmermann et al. 1978). The percentage of active respiring bacteria in activated sludge was 16 % (Dutton et al. 1983), and less than 25 % was found in stream sediments (Bott & Kaplan 1985). By determining INT-formazan formation photometrically, we found low ETS-activities at 4 °C in mesophilic and psychrophilic bacteria from sediments of the same upwelling areas (Rüger 1984). Temperatures for optimal ETS-activities – even in extremely psychrophilic bacteria with maximum growth temperatures between 4 and 12 °C – were between 18 and 40 °C. In can be deduced from the sediment temperatures between 6 and 16 °C (Rüger 1982) and the low ETS-activities of the isolates at the corresponding temperatures, that respiratory electron transport systems are of minor importance in the sediments investigated.

Maximum bacterial densities and biomasses were found at 21 and 17 °N, the centers of the upwelling off Northwest Africa. Microbial activities were also highest at 21 and 17 °N with AEC ratios of between 0.53 and 0.70. Our results again showed the dependance of microbial biomasses and activities in sediments of upwelling regions on the primary productivity rates of the overlying waters.

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