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Vertical distribution and activity of bacteria in the Central Arabian Sea

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Abstract

During the RV "Meteor" expedition in the Central Arabian Sea (MINDIK 87) the vertical distribution of particulate organic carbon and nitrogen, bacterial abundance, heterotrophic activity for glucose and the bacterial production determined by [^{3}H-methyl]-thymidine incorporation were surveyed. At the time of observation (April-May) the study area was characterized by a stable pycnocline at 35 m and a nutricline at 50 to 55 m depth. Maxima for all biomass measurements were observed in the nutricline, whereas highest rates were detected in the nutrient-depleted surface layer above the nutricline. Based on these hydrographic conditions, a double vertical zonation was established also for microbiological and planktological events in the water column. The integrated bacterial production in the mixed surface layer (0-30 m) was half that in the layer underneath (30-100 m). This upper zone can be considered as a more or less closed sub-system and a significant amount of primary production (approximately 30 %) was channelled through the bacteria. Corresponding to the higher biomass in the lower zone the turnover of organic material was somewhat slower. This observation together with the presence of nutrients in the chemocline indicated a subsystem of more open character for exchange processes with underlying waters.

Introduction

Due to new microbiological methodologies developed during the seventies and eighties the significance of bacterioplankton among the trophic levels of diverse aquatic environments as a major pathway of organic matter flux has become increasingly recognized (WRIGHT and HOBBIE 1966, FUHRMAN and AZAM 1982, AZAM et al. 1983, SCAVIA et al. 1986). Especially in stratified oligotrophic surface waters bacterioplankton may play a major role for the internal dynamics of a 'steady state system' by initiating the recycling of biologically important molecules within the 'microbial loop' which results in a minimized vertical flux of organic material to underlying waters (AZAM 1984).

This paper reports the vertical distribution and activity of bacteria in the Central Arabian Sea, measured during the 5th "Meteor" cruise (leg 3b; 27th April to 12th May, 1987). Of particular interest was the division of the euphotic zone into two sub-systems (according to DUGDALE and GOERING 1967) and the role of bacteria within these two production systems.

Material and methods

Data were collected on five stations in the Central Arabian Sea (19°N, 65°E; 17°N, 66°E). The water column was surveyed in a series of vertical profiles (5 to max. 150 m) following the track of a free-drifting sediment trap (100 m) in order to carry out all investigations within the same waterbody. All samples were taken with 30 l watersamplers (Hydro-Bios, Kiel) and were immediately processed aboard.

For the POC and PON determinations 2 to 4 l seawater were filtered onto pre-combusted (2 h, 550 °C) Whatman GF/F filters. The filters were frozen at - 18 °C and then analyzed ashore with a Perkin - Elmer CHN - Analyzer Type 240C.

Direct counts of bacteria were performed on black stained (irgalan black) 0.2 µm Nuclepore filters using the fluorescent dye acridin orange (ZIMMERMANN and MEYER-REIL 1974). Bacterial dimensions were determined after a photographic and magnification process with the aid of a digitizer board (MOP AM02, Fa. Kontron, FRG). For the bacterial biomass calculations the factor of 0.38 pg C μm^{-3} (LEE and FUHRMAN 1987) was used.

The turnover rate (T_r) of glucose was determined according to GOCKE (1977). 0.245 µg C dm^{-3} of uniformly labelled D-[C_6-^{3}H]-glucose were added to 50 ml sample water. According to pre-experiments triplicates and one control were incubated for 0.5 h at 22 °C in the dark.

The bacterial productivity was estimated by the incorporation of [^{3}H-methyl]-thymidine (TdR) as described by FUHRMAN and AZAM (1980). According to uptake kinetic and time series experiments, 5.4 nmol [^{3}H-methyl]-thymidine were added to 20 ml watersample and triplicates together with two controls were incubated for 2 h at 22 °C in the dark. Derived from conversion factor experiments cell production was calculated with a conversion factor of $9.7 \cdot 10^{18}$ cells mol^{-1} incorporated thymidine.

Results and discussion

Ranges and vertical distribution patterns of hydrophysical and chemical as well as biological variables were very similar at all stations. Characteristic distribution patterns for the measured hydrophysical and microbiological data are demonstrated for Stn. 494 (Fig. 1 and Fig. 2 a-e, resp.).

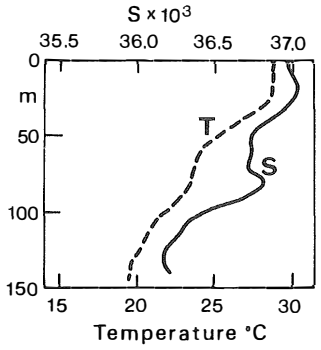

Fig. 1. Vertical distribution of temperature (T) and salinity (S) at drift station 494.

During the whole investigation period a strong pycnocline at about 35 m depth was recorded (Fig. 1). In the upper water column (0 to 50 m) nitrate and nitrite were below the detection limit (<0.1 and <0.01 µmol dm^{-3}, resp.), whereas concentrations for silicate and phosphate were about 1.5 and 0.24 to 0.56 µmol dm^{-3}, respectively. Below 50 m all measured nutrient concentrations increased, except nitrite with a weak maximum at about 60 m.

The vertical distribution of all biomass measurements, chlorophyll **a** (data from planktological working group), POC and PON, bacterial abundance and biomass, showed at all stations a similar pattern. Maximum values were about 1 µg dm^{-3} for chlorophyll a, about 125 µg C dm^{-3} for POC and 28 µg N dm^{-3} for PON. For bacterial abundance they were about $0.2 \cdot 10^{12}$ cells dm^{-3} and for bacterial biomass approximately 2.4 µg C dm^{-3}. These maxima were always detected within or at the top of the nutricline.

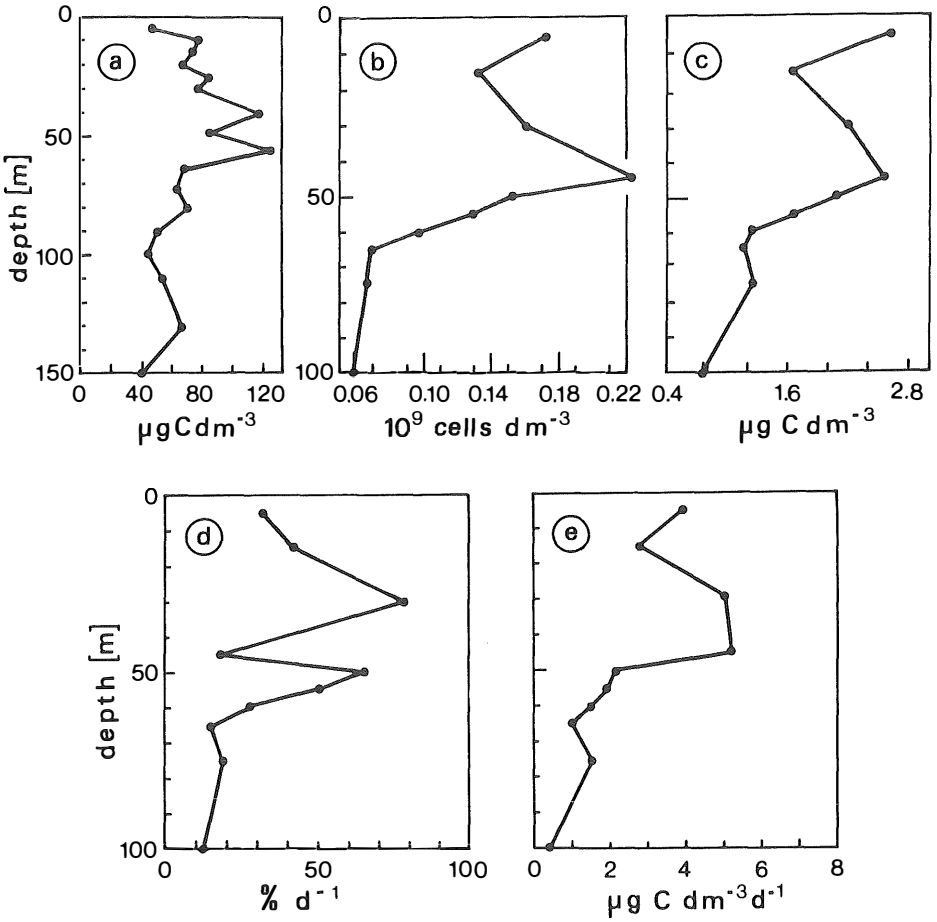

Fig. 2. Vertical distribution of a) POC: mg C dm^{-3}; b) total bacterial number: 10^9 cells dm^{-3}; c) total bacterial biomass: µg C dm^{-3}; d) Turnover rate glucose: % d^{-1}; e) bacterial production: µg C dm^{-3} d^{-1} at drift station 494.

In contrast to bacterial stock measurements, the distribution of bacterial activity showed a different vertical pattern. Highest rates were always detected above the nutricline. Maximum values for the glucose turnover rate were mostly found at about 30 and 50 m depth and ranged from 54 to 78 % d^{-1} of the *in situ* glucose concentration. Below the euphotic zone turnover rates decreased to about 10 % d^{-1} at 100 m depth. Highest bacterial production rates were also measured above 50 m with about 5.2 µg C dm^{-3} d^{-1}. In contrast to the turnover rate of glucose a sharp decrease of the production rates occurred within the deeper part of the euphotic zone; production values at 100 m depth averaged about 0.7 µg C dm^{-3} d^{-1}.

Table 1. Integrated values from all drift stations calculated relative to 1 m^3. POC: mg C m^{-3}; PON: mg N m^{-3}; PB: phytoplankton biomass (assumed is a ratio of C : Chl. a of 35) mg C m^{-3}; PP: primary production mg C m^{-3} d^{-1} (data from F. JOCHEM); TBB: total bacterial biomass mg C m^{-3}; BP: bacterial production mg C m^{-3} d^{-1}.

Depth range	0 - 30 m	> 30 - 75 m	> 75 - 100 m
POC	62.25	89.45	58.61
PON	11.84	16.88	11.62
PB	5.28	17.93	9.14
PP	10.74	8.47	-
TBB	1.52	1.30	0.92
BP	2.33	1.75	0.89

Table 1 summarizes the depth-integrated values relative to 1 m^3 for all drift stations. Average standard deviations in percent for the variables and different depth horizons (0 to 30 m = mixed layer; > 30 to 75 m = bottom of euphotic zone; > 75 m to 100 m = beginning of disphotic zone) covered a range from 6.7 to 60.9 % (mean = 26.6 %). For estimating the phytoplankton biomass a C : Chl. a ratio of 35 was assumed. Except for the bacterial biomass the different vertical distributions of biomass and rate variables are also well reflected by integrated values relativated to 1 m^3.

The hydrophysical and chemical data from the drift stations indicated that all investigations were carried out within the same waterbody. Also biological variables showed no significant changes in their range and vertical distribution. This leads to the conclusion that the surveyed ecosystem remained at steady state during the investigation period.

A stable pycnocline divided the epipelagic system in two compartments. The upper system was characterized by warm temperatures (about 28 °C), high light intensities and depleted nitrogen nutrients. Below the pycnocline temperature (25 to 22.5 °C) and light dropped down towards the bottom of the euphotic zone and nitrogen nutrient concentrations recovered. So most of the primary production in the mixed layer was mainly dependent on 'regenerated forms' of nitrogen whereas below the pycnocline with increasing depth the growth of phytoplankton was supplied also by nitrogen sources from the aphotic zone ('new forms').

The zonation of microbial biomass was closely related to the vertical pattern of autotrophic biomass. In the open sea the majority of dissolved organic matter

(DOM) for bacterial growth must be directly and indirectly derived from the activity of phytoplankton. Mechanisms responsible for the supply of the DOM pool are exudation (FOOG 1977), autolysis (SHARP 1977) as well as grazing and excretion from zooplankton (BURNEY et al. 1979, TAYLOR et al. 1985) and bacterial hydrolysis of POM (HOPPE et al. 1988).

The relatively low bacterial biomass in the mixed layer exhibited in comparison with the underlying part of the euphotic zone high turnover rates of glucose and bacterial production rates. This suggests a higher specific activity per cell probably due to higher surface temperatures and a lower percentage of inactive bacteria cells. Although highest bacterial and primary production rates were measured in the lower sub-system, due to the relatively high standing stocks, the turnover of biomass in this system was somewhat slower. The higher flux of energy in the mixed layer points to the fact that this sub-system can be considered more or less closed. The presence of nitrogen nutrients in the lower subsystem together with the slower turnover of biomass indicates a pelagic structure of more open character for exchange processes with underlying waters. Derived from sediment trap investigations, sedimentation almost entirely originated from this zone (PEINERT, pers. communication).

The mixed layer was dominated by pico- and nanoplankton. 70 to 85 % of the primary production was synthesized by the autotrophic picoplankton fraction (JOCHEM 1990) and the majority of the zooplankton respiration was measured in the size fraction of 2 to 20 µm (FLECKNER, pers. communication). In these size classes very high metabolic rates per unit of volume can be expected and the sedimentation rates are extremely low (TAKAHASHI and BIENFANG 1983). This suggests two essential mechanisms to keep and remineralize organic material within the mixed layer. In this sub-system bacteria provide a major route for transfer of - otherwise lost - dissolved organic carbon (DOC) into the food web. Bacterial net production amounted 22 % of the primary production (bacterial gross production: 30 %). Assuming a C:N-ratio of 6 for primary production and 4.5 for bacterial production approximately 29 % of the nitrogen remineralization through the food web was initiated by the activity of bacteria. Adapting a bacterial C production efficiency of 60 % (CALOW 1977) also for N, the bacterial nitrogen demand would require maximal 11.5 % (relative to the particulate primary production), which would be remineralized via bacterial respiration. However, data available from nitrogen limited systems strongly suggest that bacteria under these conditions are rather net consumers of inorganic nutrients (for example, GOLDMAN et al. 1985). Therefore this part of nitrogen remineralization was probably re-utilized by bacteria via external uptake or internal metabolism. Despite all uncertainties involved with the determination of bacterial production this reported nitrogen remineralization rates fitted well in calculations carried out independently for the nitrogen mass balance in this subsystem (POLLEHNE, pers. communication).

In the upper part of the lower sub-system the contribution of bacteria to the N-cycle was similar to that in the mixed layer. Only within the nutricline bacterial productivity sharply decreased, probably due to a lesser supply with organic substrates and to lower temperatures. In this sub-system the calculated nitrogen remineralization via the 'microbial loop' amounted 25 % of the particulate primary production. Also for this system the amount of nitrogen remineralization (10 % according to the above mentioned assumptions) via bacteria was probably low at least in the N-depleted upper part of this sub-system.

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