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Adenosine triphosphate in the North Atlantic Ocean and its relationship to the oxygen minimum

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Abstract—Measurements were made of the vertical distribution of microbial biomass in the water column and sediments for two mid-Atlantic stations. Biomass estimates were based on measurements of total adenosine triphosphate (ATP) concentration. Both profiles indicate a large viable microbial population in near-surface waters (> 50 μg C l^{-1}), followed by a characteristic decrease with depth. A second maximum (> 20 μg C l^{-1}) occurred in both locations between 700 and 1000 m and corresponded to the depth of the oxygen minimum. Below 2200 m, the biomass remained relatively constant with depth (0·125 μg C l^{-1}). Both profiles exhibited a six-fold increase in biomass 10 m above the sediment–water interface (4165, 6339 m), with an additional increase in the uppermost sediment layer (2·24 to 2·58 μg C g^{-1}). The biomass rapidly decreased in the sediments to less than 0·5 μg C g^{-1} at a depth of 4 to 5 cm. Dissolved organic carbon (DOC) values ranged from 0·2 to 0·6 mg C l^{-1} for the water samples. At the sediment–water interface values increased two-fold. Pore water DOC values ranged from 0·8 to 2·3 mg C l^{-1}, decreasing with core depth.

INTRODUCTION

BIOLOGICAL activity has long been recognized as a major influence on the chemistry of seawater and the interstitial water of sediments. Of special interest are the relationships between the distributions of living biomass carbon, oxygen, nitrate, and phosphorus. The vertical distribution of dissolved oxygen in the ocean is characterized by an intermediate depth oxygen minimum (reviewed by RICHARDS, 1957). Observed vertical variations in dissolved oxygen concentrations have been explained by mixing of opposing water masses (MENZEL and RYTHER, 1968; MENZEL, 1970), *in situ* microbial decomposition of organic matter (SVERDRUP, 1938; ZOBELL, 1946; RILEY and CHESTER, 1971; SOROKIN, 1971) and by a combination of the two (REDFIELD, 1942; CRAIG, 1971). MENZEL and RYTHER (1971) argued that because oxygen concentrations may be predicted from salinity in easily identified water masses, little or no measurable influence is exerted on the dissolved oxygen concentration through decomposition of organic matter or by *in situ* respiration of organisms. They further concluded that the behavior of oxygen and the vertical homogeneity of organic matter suggest that the cycling of organic matter is restricted to the relatively shallow surface water. Below 200 m both carbon and oxygen should behave as conservative properties of seawater. More recently (CRAIG and WEISS, 1970; CRAIG, 1971) it has been demonstrated that a simple diffusion–advection model predicted the behaviour of the carbonate alkalinity system only when an *in situ* biological consumption term was included. RAKESTRAW, RUDD and DOLE (1951) observed that the $^{18}O/^{16}O$ ratio reached a maximum value at a depth corresponding to the minimum in dissolved oxygen, and further concluded that the ^{16}O was preferentially consumed over the ^{18}O by biological processes at depth. An explanation of the oxygen minimum on a physical basis (MENZEL and RYTHER, 1968, 1971) fails to explain the related phosphate and nitrate maxima that have also been observed.

FOURNIER (1966, 1971) observed large concentrations of small, biflagellated, pigmented cells

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living heterotrophically throughout the aphotic zone of the North Atlantic Ocean. These cells have a maximum concentration at a depth of between 300 and 500 m, and they may play an integral role in the oxygen–phosphate levels of the North Atlantic. PACKARD, HEALY and RICHARDS (1971) measured the activity of respiratory electron transport systems (ETS) to estimate *in situ* biological oxygen consumption rates. Their observations indicated that ETS activity in seawater was related to both the concentration of oxidizable organic matter and total living biomass.

Different methods have been described for the enumeration of microorganisms in natural waters (JANNASCH and JONES, 1959); however, in recent years adenosine triphosphate (ATP) has been used extensively as an indicator of environmental microbial biomass (HOLM-HANSEN and BOOTH, 1966; HOLM-HANSEN and PAERL, 1972; HOLM-HANSEN, 1973 a, b). This type of biochemical enumeration will only yield information concerning the total amount of living carbon and will not differentiate between classes of organisms. It does, however, avoid nutritional constraints involved with cultural enumeration methods.

In this paper we report on finding a large, subsurface ATP maximum between 650 and 1040 m and its relation to the oxygen minimum in the North Atlantic Ocean. We also present our findings on ATP and dissolved organic carbon (DOC) in deep-sea marine sediments.

METHODS AND MATERIALS

Before the collection of water or sediment samples for ATP determinations, all sampling equipment was washed with 95% ethanol to reduce the possibility of bacterial contamination, and then rinsed thoroughly with membrane filtered (0·45 μm) seawater. All water samples were collected in 5-liter Niskin bottles (General Oceanics) and shipboard analysis was begun immediately after retrieval of samples. A pinger was positioned directly above the hydrowire weight to allow deep water sample collection within 5 m of the sediment–water interface. Sediment samples were obtained using a hydroplastic (PVC) 2-m gravity coring device. Cores were stored for 24 h before analysis at *in situ* temperature (2°C) to insure re-equilibration of certain parameters.

Microbial biomass in the water column was determined on 1- to 1·5-liter samples by the ATP technique of HOLM-HANSEN and BOOTH (1966), modified by KARL and LAROCK (1975). Sediment microbial biomass was determined by measuring the total ATP concentration using the sulfuric acid–EDTA extraction procedure outlined by KARL and LAROCK (1975; and KARL and LAROCK, 1974, *Abstracts of the Annual Meeting, American Society for Microbiology*, G 202).

Before the collection of interstitial water for DOC analysis, glass fiber filters (Gelman) and the 10-ml glass ampoules were precombusted at 500°C for 20 h to eliminate any organic matter that may have been present. Interstitial water was collected using a hydraulic sediment press with internal glass fiber filter. One milliliter of the pore water was used for carbon analysis. Sample volume for the water column DOC determinations was 5 ml of glass fiber-filtered seawater. Sample material was added to the ampoules along with sodium persulfate and phosphoric acid. The ampoule was then purged with oxygen, sealed and autoclaved. The DOC was analyzed according to the method of MENZEL and VACCARO (1964) as modified by STRICKLAND and PARSONS (1972) using a non-dispersive infra-red analyzer (Oceanography International).

Dissolved oxygen, temperature, salinity, density, and phosphate measurements were compiled from data supplied by the National Oceanographic Data Center (NODC), Washington, D.C. The measurements used were those data obtained during various research cruises of the R.V. *Crawford* and R.V. *Atlantis II*. The curves generated from these data represent mean values for each parameter, calculated from four different sample stations taken at various times of the year, all within a 1° square area surrounding the actual coordinates of our sample stations.

RESULTS

Mid-Atlantic Ridge station

Samples from the Mid-Atlantic Ridge were collected at 26°18·0′N, 44°44·3′W, in water overlying the central rift valley and from ponded sediments within the rift valley, near the Trans-Atlantic Geotraverse (TAG) hydrothermal field (Scott, Scott, Swanson, Rona and McGregor, 1974).

The vertical distribution of ATP, dissolved oxygen, and phosphate are presented in Fig. 1A to C. The ATP rapidly decreased from a near-surface maximum of 400 ng l^{-1}, to a value of 3 ng l^{-1} at about 280 m. Below 300 m, the ATP increased and a subsurface maximum of 225 ng ATP l^{-1} occurred at 650 m. With increasing depth, the ATP gradually decreased to a value of 0·8 ng l^{-1} at 2000 m and to 0·3 ng l^{-1} at 4100 m. Between 3 and 5 m above the bottom, the ATP concentration increased 8-fold to a value of 3·2 ng l^{-1}. The secondary ATP peak extended from 400 to 2000 m, and was determined by at least five data points. No ATP was detected in the sediment cores taken from the hydrothermal field. The lower limit of detectability for our ATP analysis was 0·1 ng ATP per g wet weight of sediment.

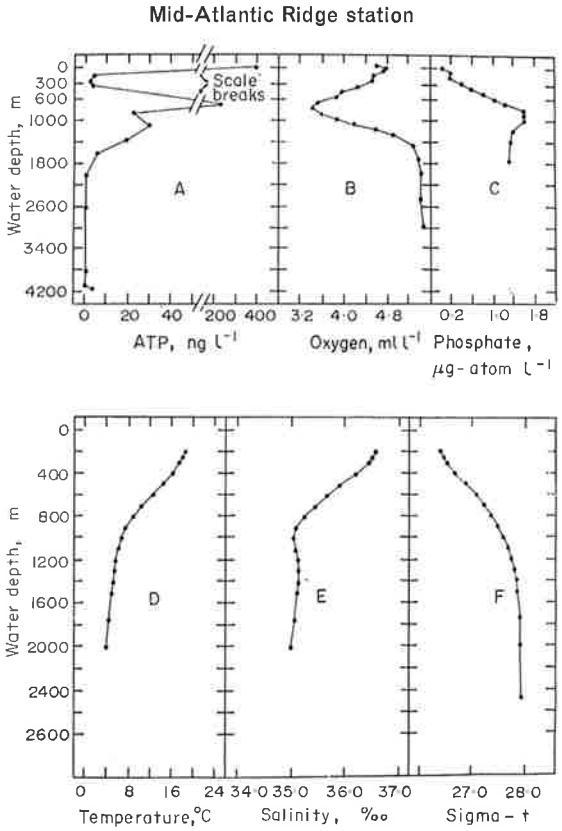


Fig. 1. Vertical distribution of selected chemical, biochemical and physical variables at the Mid-Atlantic Ridge station. A. ATP. B. Oxygen. C. Phosphate. D. Temperature. E. Salinity. F. Density.

The dissolved oxygen concentration increased in the upper portion of the euphotic zone from a surface value of 4·6 ml l^{-1} to 4·75 ml l^{-1} at 50 m. This was followed by a steady decrease below 50 m to a minimum of 3·38 ml l^{-1} at 800 m. Below this depth there was a uniform increase in dissolved oxygen to 5·36 ml l^{-1} at 2000 m. The oxygen concentration then remained uniform between 2000 and 3000 m and increased slightly to 5·42 ml l^{-1} at 3000 m.

Orthophosphate-phosphorus was detected in the surface waters (0·02 µg-atoms l^{-1}) and increased rapidly with depth to a maximum of 1·58 µg-atoms l^{-1} at 800 m. Below this depth, the orthophosphate concentration decreased slightly and then appeared to level off at a value of between 1·28 and 1·32 µg-atoms l^{-1} at 1800 m.

The vertical profiles of temperature and salinity (Fig. 1D and E) were constructed using mean values from four different data observations. The upper 200 m were omitted to exclude seasonal temperature and salinity variations. Below 200 m, the temperature decreased rapidly from 18·7 to 6·8°C at 1000 m. Below this depth the temperature decreased much less rapidly than in the permanent thermocline, and reached a minimum of 3°C at 2500 m. The vertical variation in salinity is slightly more complex than the temperature distribution. The salinity decreased with depth from 36·57‰ at 200 m to a minimum of 35·05‰ (Antarctic Intermediate Water) at 1000 m. Below this depth it increased slightly to 35·11‰ at 1400 m, and gradually decreased again to 34·72‰ at about 2500 m. In the density profile, expressed as σ_t (Fig. 1F), there is a rapid increase in σ_t below 200 m to 27·55 at 1000 m. The density continues to increase below this depth, but at a much slower rate, to a maximum of 27·88 at 2500 m.

Abyssal Plain station

Samples from the abyssal plain were collected at 26°50·8′N, 60°13·6′W in a relatively flat portion of the Nares Abyssal Plain.

The vertical distribution of ATP, dissolved oxygen, and total phosphorus are presented in Fig. 2A to C. The ATP concentrations at this site were lower, but had a distribution pattern similar to the Ridge station. The ATP rapidly decreased from a near-surface value of 188 ng l^{-1} to a minimum of 3 ng l^{-1} at 750 m, and then increased to a maximum of 80 ng l^{-1} at 1040 m. Below the secondary maximum, ATP decreased to 0·5 ng l^{-1} at about 2300 m. The entire secondary maximum feature was well defined, extending vertically for 1500 m. Below 2300 m, the ATP concentration was uniform with increasing depth, but exhibited a 6-fold increase to 3·0 ng l^{-1} 5 m above the water–sediment interface (6011 m). The topmost sediment layer (0 to 2 cm) had an ATP concentration of 2·5 ng g^{-1} wet weight of sediment, an increase of nearly three orders of magnitude over the ATP concentration of the deepest water sample. Between 4 and 6 cm, the ATP concentration decreased to 0·3 ng g^{-1} sediment and was below the limit of detection (0·1 ng g^{-1} sediment wet weight) at greater sediment depths.

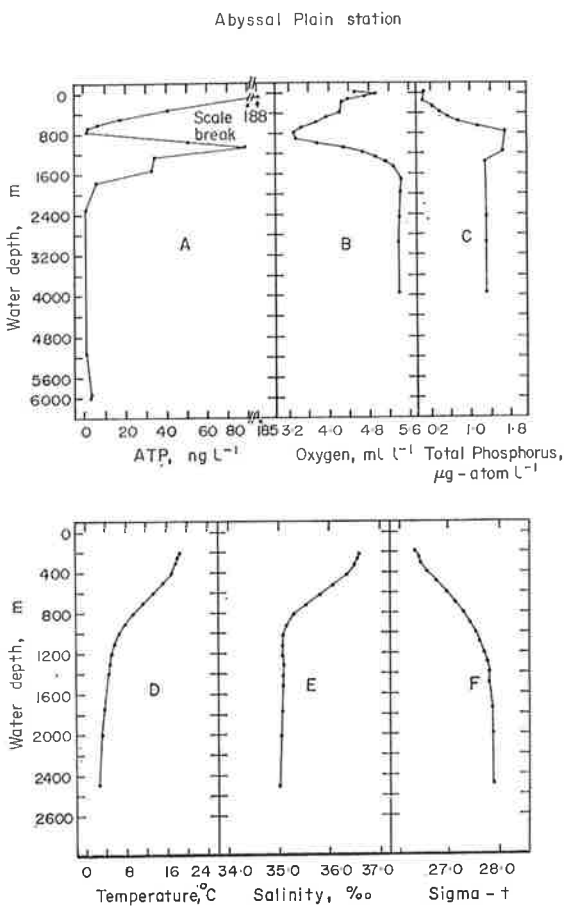


Fig. 2. Vertical distribution of selected chemical, biochemical, and physical variables at the Abyssal Plain station. A. ATP. B. Oxygen. C. Total phosphorus. D. Temperature. E. Salinity. F. Density.

The concentration of dissolved oxygen increased from 4·5 ml l^{-1} at the surface to a maximum of 5·0 ml l^{-1} at about 40 m, and then decreased steadily with depth to a distinct minimum of 3·34 ml l^{-1} at 800 m. This minimum was followed by a uniform increase to 5·50 ml l^{-1} at 1800 m and remained relatively constant to at least 4000 m (deepest data available).

The total phosphorus concentration increased uniformly from 0·15 μg-atoms l^{-1} at 200 m to a maximum of 1·75 μg-atoms l^{-1} between 800 and 1000 m. Below the phosphorus maximum, the concentration decreased slightly with depth to 1·35 μg-atoms l^{-1} at 1400 m.

The water overlying the core had a mean DOC value of 0·75 ± 0·18 mg C l^{-1}, and the topmost sediment layer (0 to 4 cm) had nearly a 4-fold increase from the overlying water to a value of 2·34 ± 0·10 mg C l^{-1} (Fig. 3). Within the upper sediment layer, the pore water DOC decreased uniformly with sediment depth to a mean value of 0·74 ± 0·11 mg C l^{-1} at the 12- to 16-cm depth interval. These interstitial DOC values are lower than have been reported by STARIKOVA (1970) for a similar sediment type; however, her water column values are also several times higher than found in other recent investigations. The ATP and DOC concentrations for the lower portion of the water column and the upper 14 cm of the sediment column are presented in Fig. 3.

DISCUSSION

The most significant features of the ATP measurements are:

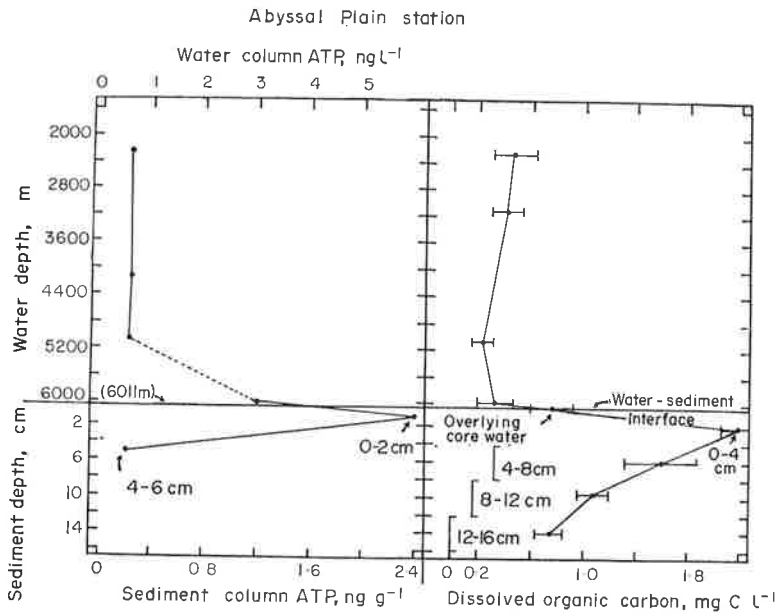


Fig. 3. Dissolved organic carbon and ATP concentrations for the lower portion of the water column and the top 16 cm of the sediment column at the Abyssal Plain station.

1. the large subsurface peak centered at 800 to 1000 m and extending over a vertical distance of 1200 m. The maximum subsurface ATP concentrations were nearly half those found at the surface.
2. An increase in the ATP concentration 3 to 5 m above the sediment–water interface.
3. An ATP concentration in the top 2 cm of sediment that was three orders of magnitude greater than in the overlying water.

The surface ATP peak and the magnitude of he surface and deep water (below 2200-m) ATP; values were comparable to values reported for otther locations (HOLM-HANSEN and BOOTH, 1966 HOLM-HANSEN, 1970, 1973a, b). The presence of the large subsurface ATP peak at two stations separated by 1600 km, suggests that for the North Atlantic elevated ATP values at depth may be a regular feature.

HOLM-HANSEN and BOOTH (1966) found a similar sub-euphotic ATP maximum in the Pacific Ocean, which corresponded to values between 34 and 66 ng ATP l^{-1}. This increase in ATP at 600 m was attributed to some biological process, probably the result of actively migrating zooplankton populations (HAMILTON, HOLM-HANSEN and STRICKLAND, 1968). In this report, the ATP feature is broader and better defined (Figs. 1A and 2A).

Bacterial populations have been reported to be directly proportional to the concentration of organic matter (ZOBELL and GRANT, 1943; KRISS, 1953, cited by JANNASCH and JONES, 1959), especially at the low organic carbon levels found in seawater. Any large increase in the microbial population density would be expected to reflect a corresponding increase in the POC levels at that same depth interval, but no POC measurements for these two hydrographic stations are available. WANGERSKY and GORDON (1965) obtained large POC values in waters beneath the Guinea Current at depths of 400 to 1200 m. DALPONT and NEWELL (1963) noted increases in the POC concentration associated with an intermediate salinity minimum in the South Pacific, and HOLM-HANSEN, STRICKLAND and WILLIAMS (1966) reported a maximum in the POC concentration at the depth of the oxygen minimum layer in a station off the California coast. The original claim of constancy

of POC below 200 m (MENZEL, 1967) may be an oversimplification (HOLM-HANSEN, 1970). It is possible that POC concentrations may increase by an order of magnitude as a result of isolated discontinuity layers in the depth profile (PARSONS and SEKI, 1970).

SMAYDA (1970) indicated that the vertical distribution of nutrients will be influenced by the rate of decomposition and the rate of sinking of natural phytoplankton populations. There is little doubt that phytoplankton provide more than 90% of the basic stock of oceanic organic matter, and that the accumulated remains of non-living organic matter (DOC and POC) are much larger than the annual production (RILEY, 1970). Little quantitative information is available on sinking rates for organic detrital particles. Sinking rate depends on particle density and shape, as well as the density and viscosity of the fluid medium. These parameters can then be used to estimate sinking velocity, according to Stoke's law. Rapid changes in temperature and salinity with depth will alter density and decrease the sinking rate of organic detritus. The oceanic thermocline and halocline are not always smooth transitions between contrasting values of temperature and salinity, but in many cases they have been observed to represent a number of superimposed laminae, each layer nearly uniform in composition but interfaced between regions of strong temperature and salinity gradients (e.g. STOMMEL and FEDOROV, 1967). This rapid change in density slows the descent of sinking particles, causing a probable accumulation throughout the discontinuity layers of the pycnocline. BIGGS and WETZEL (1968) reported the effectiveness of the halocline as a barrier to particle sinking, and HARDER (1968) noted accumulation of organic detritus in both the thermocline and the halocline. RILEY (1970) reported that below the top of the permanent thermocline (about 200 m) the bulk of the POC is in the form of small particles or flakes, having an average density of 1·0272. For the two stations we surveyed, a sinking detrital particle would approach neutral buoyancy at 700 to 800 m (Figs. 1F and 2F). Discounting any increases in particle density that may result from decreasing temperature, a concentration of the particles should occur. The secondary ATP peaks are possibly the result of an increased concentration of assimilable organic matter in the permanent thermocline. These nearly neutrally buoyant particles may begin to aggregate via bacterial activity, resulting in a slow downward transport of oxidizable organic matter and the extension of the ATP secondary peak for 1200 to 1500 m (Figs. 1A and 2A).

The *in situ* concentration of dissolved oxygen represents a balance between vertical and horizontal diffusion, advection, and biological utilization (RILEY, 1951). Correlation coefficients of a plot of ATP versus dissolved oxygen concentrations between 400 and 2000 m are −0·80 and −0·82 for the Mid-Atlantic Ridge and abyssal plain stations, suggesting biological utilization of oxygen at these locations. The dissolved oxygen minimum in the North Atlantic Ocean is frequently located in the isopycnic surfaces (σ_t) = 27·2 to 27·3 (SEIWELL, 1937; SEIWELL and SEIWELL, 1938; BUBNOV, 1966), regardless of depth. The theoretical accumulation of oxidizable organic matter, the existence of an oxygen minimum layer, and a secondary peak in ATP all occur at the depth corresponding to a σ_t surface of 27·2 to 27·3 (Figs. 1A, B, F and 2A, B, F).

At the depth interval coincident with the dissolved oxygen minimum and ATP maximum, a phosphorus (orthophosphate) maximum is evident (Figs. 1A to C, and 2A to C). The microbial decomposition of accumulated organic matter proceeds with a utilization of oxygen, and a release of phosphate-phosphorus. RILEY and CHESTER (1971) reported that the phosphate maximum usually lies close to the oxygen minimum and carbon dioxide maximum.

The possibility of *in situ* microbial activity and its relation to the oxygen minimum and phosphate maximum has been suggested (SEIWELL, 1937; DAISLEY and FISHER, 1958; MENZEL and RYTHER, 1968; RILEY and CHESTER, 1971), but to our knowledge this is the first report of the presence of a large microbial population and sufficient evidence for *in situ* microbial decomposition of organic matter. This large population of hetero-

trophically growing microbial cells, besides performing an essential role in nutrient regeneration for phytoplankton, may also serve as a base for deep-water food chains (HOLM-HANSEN, 1970).

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