A deep profile of some biologically Circulation anticyclonique important properties in the central North Pacific gyre



North Pacific Profil

Pacifique Nord

Biological properties

Propriétés biologiques

Profile

Gyre

	P. M. Williams, A. F. Carlucci, R. Olson Institute of Marine Resources, A-018, University of California, San Diego, La Jolla, California 92093, USA.				
	Received 12/12/79, in revised form 12/5/80, accepted 20/5/80.				
ABSTRACT	A vertical profile of dissolved and particulate organic carbon and nitrogen, dissolved organic phosphorus, adenosine triphosphate, total adenylates and total bacteria was taken from the surface to 5680 m, 15 m above the bottom, at a station in the central North Pacific gyre. The prominent feature of these non-conservative properties was an increase in dissolved organic carbon and nitrogen from 5000 to 5680 m, as compared to no significant gradients in the other properties measured in that depth interval. Also discussed is an <i>in situ</i> filtration system used to collect the particulate organic carbon and nitrogen, adenosine triphosphate and total adenylates.				
	Oceanol. Acta, 1980, 3 , 4, 471-476.				
RÉSUMÉ	Un profil vertical profond de quelques propriétés biologiquement importantes au centre de la circulation anticyclonique du Pacifique Nord.				
	Un profil vertical des paramètres suivants : carbone et azote organiques particulaires et dissous, phosphore organique dissous, adénosine triphosphate, adénylates totaux, nombre total de bactéries, a été réalisé de la surface à 5 680 m, 15 m au-dessus du fond, à une station au centre de la circulation anticyclonique du Pacifique Nord. Le trait marquant de la distribution de ces propriétés non conservatives fut une augmentation du carbone et de l'azote organiques dissous de 5 000 à 5 680 m, en l'absence de gradients significatifs des autres propriétés mesurées dans le même intervalle de profondeur. Un système de filtration <i>in situ</i> utilisé pour la collecte du carbone et de l'azote organiques 'particulaires, de l'adénosine triphosphate et des adénylates totaux, est également discuté.				
	Oceanol. Acta, 1980, 3, 4, 471-476.				
INTRODUCTION	Whatman GF/C glass fiber filter), organic carbon (POC) and nitrogen (PON) was taken at 10-12 depths over a 2-				

In conjunction with natural radiocarbon analyses of the organic matter in red-clay sediments collected in the central North Pacific gyre, cruise Indopac-15, June 1977, at $28^{\circ} \pm 30'$ N, $155^{\circ} \pm 30'$ W (Williams *et al.*, 1978), a vertical profile of dissolved (dissolved connotes truly dissolved, colloidal and particulate organic matter, which passes a Whatman GF/C glass fiber filter), organic carbon (DOC), nitrogen (DON) and phosphorus (DOP), and particulate (particulate organic matter is that which passes a 35 or 183 µm nylon net and is retained by a

week period, to detect possible gradients in these parameters above the sediment-seawater interface. At the same time, samples were collected for analyses of particulate adenosine triphosphate (ATP) and total adenylates (ATP, AMP and ADP), and for free and attached total bacteria. The slurry (water plus sediment) from a box core taken in this same area was also analyzed for DOC, DON, DOP and total bacteria. No deep profiles of the above properties have been taken from the surface to within 15-30 m of the ocean floor in any abyssal waters, at least to our knowledge.

The vertical distributions of DOC, POC, PON, ATP and total bacteria at depths up to 5550 m in the central North Pacific as reported in the literature, are given in the Table. The only comparable DON analyses (P. M. Williams, unpublished results), were for a 5900 m profile taken July 7, 1970, in the central North Pacific gyre. The only deep profiles of total adenylates that have been reported were taken in the Black Sea from the surface to 2 200 m, where the waters were anoxic below 200 m (Karl, 1978). Deep profiles of DOP in abyssal waters are not available. These above literature studies are amplified in the Discussion section.

METHODOLOGY

The main sampler used in this work for the determination of POC, PON, ATP and total adenylates was an in situ pumping system, modified from one described earlier by Laird et al. (1967), and referred to here as the "Yentsch pump". It consisted of a Pelagic Electronics Model 5010 in situ pump, powered by a 12-volt storage battery, which pulls water through a 26.5 cm diameter glass-fiber filter (Whatman GF/C, previously ignited at 450°C to oxidize organic matter), supported in a polyvinyl chloride housing connected in series with a Corad Series CM flowmeter. The pump is activated by calibrated pressure switches (Whitman General, Series P7505) or a clocktimer relay and gives initial flow rates of 15 l/mn. through a clean filter. Contamination from the pumping system is made minimal by coating all metal parts with heat-cured epoxy resin.

Water volumes filtered ranged from 895 to 21221 (mean = 1420 l), except at 5680 m, where only 2231 were pumped. Below 1000 m, the pump was generally run 3 to 4 hours, the effective life of the battery. A 51 Niskin bottle was used for all DOC, DON, DOP and total bacteria analyses, and for some ATP, total adenylates, POC and PON determinations above 500 m. The Niskin bottle was cleaned initially and between lowerings with methanol, 10% HCl and distilled water. This cleaning procedure was necessary to prevent contamination from organic matter, and has also been found to be suitable for bacteriological sampling. A 301 Niskin bottle was used for determinations of POC and PON below 100 m, to compare these analyses with those done on the filter pad from the "Yentsch pump".

The array on the wire for the deepest sample (5680 m) consisted of the pump attached to the end of the hydrowire 15 ± 2 m off the bottom, a depth transducer 5 m above the pump, a 30 l Niskin bottle 2 m above the transducer, and a 5 l Niskin bottle 5 m above the 30 l Niskin. For the other deep samples (> 500 m), the array consisted of the pump, a Nansen bottle 5 m above the pump (for thermometric depths), the 30 l Niskin bottle 5 m above the Nansen bottle, and the 5 l Niskin bottle 10 m above the 30 l Niskin. The Niskin bottle flushed the length of time the pump was running (1-4 hours below 100 m), before being closed by messengers.

The sampling was done in the following order: (1) Seawater in the 5 l Niskin bottle was shaken and sampled immediately in the ship's laboratory after filtration throught a 35 µm nylon net fastened over the outlet valve. The first 150 ml was taken for metal ion activities (not reported here), and then 200 ml was drawn and immediately pickled with 5 ml of borate-buffered formalin for bacterial enumeration. Next, a 400 ml sample for DOC and DON was drawn, and finally, a 1-21 sample was taken for ATP, POC and PON determinations at depths above 500 m. The DOC and DON sample was filtered through a 47 mm diameter Whatman GF/C glass fiber filter (ignited), and immediately frozen. Samples for POC, PON, ATP and total adenylates were filtered through 24 mm diameter GF/C glass fiber filters (ignited). (2) Seawater in the 30 l Niskin was shaken, passed through a 183 µm nylon net fastened over the outlet valve, and then through a 24 mm diameter GF/C glass fiber filter (ignited) for POC and PON analyses. (3) The filter pad from the "Yentsch pump" was placed on combusted aluminum foil, and 19 mm circles were cut with an acid-cleaned cork borer from the pad in triplicate midway between edge and center, and in the center of the filter. One set of circles was used for analyses of ATP and total adenylates, and another set for POC and PON. All the ATP and total adenylate samples were fixed immediately in boiling Tris buffer and frozen, and the POC and PON circles from both the "Yentsch pump", and the 5 and 301 Niskin samples were put into aluminum combustion boats and frozen for subsequent analyses. It should be pointed out that the seawater samples taken from the Niskin bottle were subject to possible wall effects (adsorption of particulates, solubles, and/or bacteria) during the time between bottle closures and sampling in the laboratory. This time ranged from 2 minutes for surface samples up to 100 minutes for the 5673 m water. Bacterial growth in cleaned 51 Niskin bottles is not a problem, due to the long doubling times (>10 hours) for bacteria collected at these depths (Williams, Carlucci, 1976; Carlucci, Williams, 1978).

The POC and PON were analyzed using a Hewlett-Packard Model 185B CHN Analyzer, and the ATP and total adenylates by the methods of Karl and Holm-Hansen (1978). The total bacteria were enumerated by epifluorescent microscopy (Hobbie et al., 1977), and the DOC, DON and DOP were run in triplicate by the techniques of Menzel and Vaccaro (1964), and Armstrong et al. (1966), respectively (see also Strickland, Parsons, 1972). The coefficient of variation for each determination where samples were run in triplicate were: DOC, 3%; DON, 9%; DOP, 10%; POC, 20%; PON, 30%; ATP, 25%; and total adenylates, 30%. Calculation of a coefficient of variation for total bacteria was not applicable since only one aliquot of the original preserved sample was counted. However, each value (count) reported varies by $\pm 20\%$.

RESULTS

The results are presented in Figures 1 and 2, where the DOC, DON, DOP and total bacteria analyses are from the 5 l Niskin samples, and the POC, PON, ATP and

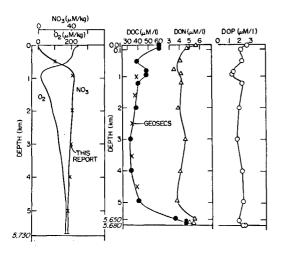


Figure 1

Profiles of: (1) O_2 and NO_3 at 30° O'N, 159° 50'W. Data from Geosecs Operations Group/NSF, 1976, station 212, September 18, 1973, bottom depth = 5731 m. Smooth curves drawn by hand. The "X" values on the NO_3 profile are from this work. (2) DOC (\oplus), DON (\triangle), and DOP (\bigcirc), this work. The "X" values on the DOC profile are from Geosecs TOC results, station 206, 29° 9.7'N, 153° 50.7'W, September 3, 1973, bottom depth = 5408 m (L. I. Gordon, pers. comm.). Concentrations are reported as µmoles per liter or per kilogram (µM/l, µM/kg).

total adenylate analyses are from the "Yentsch pump" samples. The O₂ and NO₃ profiles (Fig. 1) are drawn from Pacific Geosecs results (Geosecs Operation Group/NSF, 1976) at station 212, 30° 0'N, 159° 50'W, September 18, 1973. The "X" values on the Geosecs NO₃ curve are NO₃ values resulting from DON determinations in this work. Some total organic carbon (TOC) results from Geosecs station 206, 29° 9.7'N, 153° 50.7'W, September 3, 1973, are also plotted (X) on the DOC curve (Fig. 1). The precision at $\pm 1 \sigma$ for all results (excepting the bacteria) are indicated by the size of the symbols or by horizontal straight lines through the data points. The notation μ M stands for μ moles.

Results for the slurry waters from the box core are as follows: total bacteria (unfiltered sample which contained 45 mg dry sediment/90 ml seawater), 10^{10} cells/l; DOC, DON and DOP (filtered through GF/C glass fiber filters), 130, 8.1 and 0.29 μ M/l, respectively.

DISCUSSION

.The central North Pacific gyre is a region of low phytoplankton production in the euphotic zone where production is limited by available nitrogen (Eppley et al., 1977), and to some extent by available phosphorus (Perry, 1972). The area has been studied extensively in the upper several hundred meters, with respect to standing stocks of phyto - and zooplankters, chlorophyll a, nutrients, ATP and temperature – salinity profiles (Beers et al., 1975; Eppley et al., 1977; McGowan, Hayward, 1978). The profiles of POC, PON and ATP measured in this paper for the upper 100 m are qualitatively similar but quantitatively lower than the results reported by the above workers. Since sampling of the euphotic zone in this work was limited and nonsynoptic, this discussion is primarily directed to the 500-5680 m water colum.

Geosecs Pacific expeditions I and II made deep profiles of the non-conservative substances: NO₃, PO₄, SiO₃, O₂ and Σ CO₂ in the gyre area, but did not measure POC, PON, DON, ATP, total adenylates or any "biological" properties other than TOC. The Geosecs TOC values (Table) include DOC plus POC since the water samples were not filtered. In the central gyre, maximum POC concentrations are less than 5 µg C/l below 100 m and hence the contribution of POC is within the precision of the DOC determination (±0.03 mg C/l). The Geosecs TOC results below 500 m are in good agreement with the DOC values reported in this paper (Fig. 1).

The POC and PON concentrations reported by Gordon (1971) in the Table, are for a 4000 m profile at a location 700 km south of the station sampled in this work (essentially in the same central gyre waters). Gordon's procedure involved gravity filtration of water samples collected in 30 l Niskin bottles through silver (Selas Flotronic), filters and analyses of POC and PON with an F and M Model 185 CHN analyzer. Gordon's results from 210 samples collected on 13 cruises showed a

Table

Comparison of literature values with results from this report for DOC, POC, ATP, and total bacteria in waters of the central North Pacific below 500 m(*)

	Properties	Location	Depth range (m)	Concentration range	Reference	Concentration range (this work)
· · · · · ·	DOC (µM/l)(**)	29° 9.7'N 153° 50.7'W	490-4 600	48-37	Geosecs/ L. I. Gordon, pers. comm.	47-30
	POC (µg/l)	22° 10′N 158° 00′W	500-4 000	3.2-2.9	Gordon, 1971	- 5-1
	PON (µg/l)	22° 10′N 158° 00′W	500-4 000	0.34-0.19	Gordon, 1971	0.5-0.1
	ATP (ng/l)	22° 10′N 158° 00′W	500-4 200	3.6-0.2	Holm-Hansen, 1973	2.5-0.3
•	Bacteria (cells/l×10 ⁻⁶)	21° 00′N 155° 00′W	575-5 341	5.8-2.3	Taga and Matsuda, 1974	316-10
		30° 38'N 155° 22'W	500-5 550	20-5	Carlucci and Williams, 1978	

(*) To our knowledge, there are no published values for DON, DOP and total adenylates for deep waters in the central North Pacific gyre. (**) The Geosecs values are for TOC (see text). decreasing concentration of POC and PON from the surface to 1000 m, and constant values (mean POC=2.68 μ g/l, mean PON=0.20 μ g/l, and C:N by weight=13.4) from 1000 to 4000 m. The results reported here using the "Yentsch pump" filters, show a similar decrease in POC and PON down to 1200 m, and relatively constant values from 500 to 5680 m (mean POC=2.57 μ g/l, mean PON=0.24 μ g/l; and C:N by weight=10.7). Thus the "Yentsch pump" results for POC and PON agree well with Gordon's mean values for water taken from 30 1 Niskin bottles.

A comparison of POC and PON concentrations ($\mu g/l$) measured on samples collected by the 30 l Niskin bottles with pumped samples taken at 500-5 680 m, showed fair agreement (mean C, N and C:N by weight from 500-5 680 m for the 30 l Niskin=3.00, 0.30 and 10.0, respectively), although there was less analytical precision and more scatter in the Niskin bottle results. At the surface, 10, and 100 m, the two sampling techniques could not be directly compared, since the 5 l Niskin bottle samples were not taken synoptically with the pumped ones.

The concentrations of ATP reported here for samples taken from 500 to 5680 m essentially agree with earlier results of Holm-Hansen (1973), who found that ATP decreased from 3.6 ng/l at 500 m to 0.2 ng/l at 4200 m at a station in the central gyre (Table). It is important to note that ATP determinations on a single seawater sample, where different water volumes are filtered, do not after normalization. Karl agree and Holm-Hansen (1978) found $\sim 25\%$ less ATP in 500 ml aliquots of coastal, surface seawater than in 50 ml aliquots of the same seawater, and concluded that these discrepancies were due to partial conversion of ATP to AMP and ADP.

These authors suggested that total adenylates are a more accurate measurement of microbial biomass; consequently, total adenylates, in addition to ATP, were measured in this study since large volumes of water were filtered, and processing times were relatively long. For the surface, 10 and 100 m samples, taken with the 51 Niskin bottle, the ratio of total adenylates to ATP averaged 2.2, while in the deep, pumped samples (500 m and below), the ratio averaged 3.2. These values are higher than the mean ratio of 2.0 found by Karl (1978), for all samples from the Black Sea profiles. The "Yentsch pump" samples from the euphotic zone contained very low ATP concentrations compared to the 51 Niskin samples, so that the ratios of total adenylates to ATP were 2 to 3 times higher for the pumped samples. However, in the samples from 500 m and below, no large differences were seen between the ratios of total adenylates to ATP for samples collected by the in situ pump and the 51 Niskin bottles. The most plausible explanation of the low ATP values for the pumped samples taken in the euphotic zone, is that organisms other than bacteria (phytoplankters, microflagellates, etc.) are subject to stress, lysis and loss of ATP during the pumping process.

The numbers of bacteria in deep water profiles taken in the central North Pacific gyre, have been reported by Taga and Matsuda (1974) and Carlucci and Williams (1978) (Table). Sorokin (1964) also determined numbers of bacteria in two deep profiles taken at approximately 8-10°N, 153°W. Both Taga and Matsuda's and Sorokin's total bacteria counts were obtained by direct microscopy of stained cells and were up to two orders of magnitude lower than those determined by the epifluorescent microscopic technique used in this study. About 10^7 - 10^9 cells/l were found throughout the water column (this work, Fig. 2), where the cell numbers below 900 m did not change significantly with depth. This uniformity in bacterial populations is reflected in the ATP and total adenylate profiles below 900 m (Fig. 2).

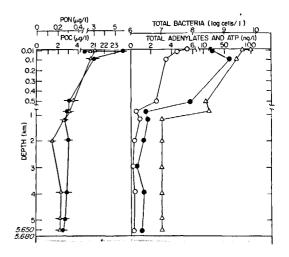


Figure 2 Profiles of POC ($- \bullet -$) and PON ($- \bigtriangleup -$), total hacteria (\bigtriangleup), total adenylates (\bullet) and ATP (\bigcirc), this work. Note scale changes at 0.5 km, and at 0.4 µg/l (PON), 4 µg/l (POC), and at 6 ng/l (ATP and total adenylates).

Note that the relation of total bacteria to ATP or total adenylates cannot be calculated since there is no reliable factor for converting ATP and total adenylates to bacterial carbon. Therefore, it is not possible to estimate the percentage of viable cells. By converting total bacterial cells to cell carbon, and comparing this value to the total POC, the percent of PQC attributable to the total bacteria can be determined. Assuming 10^7 cells/l from 1 210 to 5680 m, and 10^{-14} gm of carbon per cell (Williams, Carlucci, 1976), then the bacterial POC would be ~ 100 ng/l or less than 5% of the total POC in this depth interval.

The above results illustrate the utility of the *in situ*, selfcontained filtration system versus 30 l Niskin bottles, for collecting particulate samples below several hundred meters. The advantages of the *in situ* system are: (1) more representative samples and higher precision results are obtained due to the large volumes of water filtered; (2) there is less contamination from atmospheric particulates and from the handling of bulky water samplers on the ship; (3) formation of particulates by sample agitation is reduced; (4) there are no problems from the settling of larger particles as may occur with the Niskin bottles; and (5) there is the option of sampling the large filter pad for determinations of additional particulate components (e. g., the remainder of some of these filter pads have been analyzed for several radioactive isotopes, ²¹⁰ Pb, ²⁴¹ Am and ²³⁹⁺²⁴⁰ Pu). The disadvantages of the *in situ* system are (1) the possibility of ATP loss by conversion to AMP and ADP in samples taken above 500 m, and (2) the longer time periods (1 to 4 hours) and hence increased ship-time necessary for filtering 500-2000 l of seawater *in situ*.

Several descriptive features of these profiles from 500 to 5 680 m are apparent from Figures 1 and 2. One feature is the absence (within experimental and sampling errors) of significant gradients in any of the 8 properties measured other than DOC and DON, including no consistency of interrelated properties to the O₂ minimum and/or NO₃ maximum at 950 and 1000 m, respectively. The decrease in DON $(\sim 0.5 \, \mu M/l)$ and DOP (~0.05 μ M/l) at 900 m is inconsistent with the corresponding increase in DOC (~8 μ M/l) at this depth, assuming that the decrease in DON and DOP resulted from the oxidation of dissolved organic matter (DOM) in the O_2 minimum zone. Contamination of the 500 m sample with soluble organic matter low in DON and DOP, is one possible explanation of this inconsistency. A second feature is the overall correlation of DOC with DON from 500 to 5680 m and from 10 to 5680 m, where the correlation coefficients, r, are 0.805 and 0.754, respectively. Correlation of DOC with DOP. or DON with DOP, is not statistically significant, either from 500 to 5680 m or from 10 to 5680 m. The C/N ratios (by atoms) for DOC to DON are 10.5 and 12.5 at 10 and 100 m, respectively; 17.6 and 15.6 for duplicate samples at 5680 m, and have a mean value of 10.0 from 500 to 5000 m. The relatively high C/N ratios in the surface water above 500 m suggest a small contribution of DOM derived from recent production (C/N for phytoplankton \sim 7) to the total, more refractory pool of DOM. The mean N/P ratio (by atoms) of DON to DOP is 21.7 for all 13 samples, and does not show any depth dependence. This high N/P ratio for the DOM (N/P for phytoplankters ~ 16) results from the hydrolysis and subsequent loss of organic phosphate during the formation and "aging" of DOM.

A comparison of this deep profile with an earlier, more detailed profile taken to 1290 m in the San Clemente Basin, 100 km off the Southern California coast (33° 18.5'N, 118° 40'W) in May, 1965 (Holm-Hansen et al., 1966), can be made for the properties DOC, DON, DOP, POC and PON. Even though these two oceanographic regimes are quite dissimilar, the organic productivity at the shallow station in May, 1965, was only about twice that at the gyre station in June, 1977. The mean values of DOC, DON and DOP for the shallow station from 500 to 1 290 m, were approximately 40, 3, and 0.15 μ M/l, respectively, values almost identical to the mean concentrations of DOC, DON and DOP measured in the gyre profile from 500 to 5680 m (39, 4, and 0.2 μ M/l, respectively). However, the POC and PON (about 30 and $3 \mu g/l$ from 500 to 1 290 m in the shallow profile, were nearly 10 times that measured from 500 to 5680 m in the gyre (2.6 and 0.24 μ g/l). More recent, unpublished determinations of POC and PON in the San Clemente Basin for samples collected at 500 m and deeper give POC concentrations of 10 to $15 \,\mu g/l$ and PON concentrations of 0.5 to 1 μ g/l. The elevated POC and

PON concentrations for the 1965 station are now felt to have been due to contamination from insufficientlycleaned bottles, water-handling procedures and the less precise analytical methodology. The interesting point is the close agreement between the DOC, DON and DOP results for the two stations. This agreement emphasizes the ubiquitous occurrence of old, refractory DOM in coastal and open-ocean deep waters where the contribution of recent, labile DOM is small compared to the large pool of "old", recycled DOM.

The descriptive data reported in this paper, although limited in the number of depths sampled and sample replication, illustrates several important points concerning the abyssal water. One is the profile of DOC and of DON. The DOC (Fig. 1) increases nearly 100% from 5000 m to 20 m above the bottom (a 20% increase in DOC and a 10% increase in DON was also measured in 1970 [P. M. Williams, unpublished results, Institute of Marine Resources, Univ. California, IMR Rep. No. 71-10, p. 12, 1971], for Nansen bottle samples taken 20 m off the bottom at 30° 03.0'N, 156° 11.6'W). There is a lesser increase (40%) in DON in the bottom 700 m, a result leading to high atomic C/N ratios for the DOM just above the bottom. This high ratio (~ 17) implies a more refractory, carbon-rich, older component in the organic matter near the bottom, probably derived by vertical diffusion of relatively "old" DOM from the upper mixed layer in the sedimentary column into the overlying water; and in fact, the apparent mean radiocarbon age of the TOC in the upper 3 cm of this mixed sedimentary layer is 11×10^3 years before present (Williams *et al.*, 1978).

A second point is that no increasing concentrations of POC, PON, total bacteria, ATP or total adenylates were measured from 5000 m down to 15-30 m above the bottom. If these above properties increased similarly to the DOC (100%) and DON (40%), then gradients should have been detected, taking the maximum sampling and analytical errors to be approximately $\pm 30\%$, and assuming that the samples collected were representative ones. One explanation of the absence of increased total bacteria 30 m above the bottom where the concentrations of DOC and DON are high is that, as mentioned above, a large proportion of this DOM is derived from older, reworked particulates in the surface sediment. Labile, nitrogen-containing detritus of recent origin sinks from the surface to the seawater-sediment interface, and is then preferentially utilized (reworked) by the sedimentary microbial population, so that the residual, high C/N material becomes more resistant to further bacterial degradation. Since the total bacterial cells $(\sim 10^{10}/l)$ measured in the sediment-slurry from the box core were three orders of magnitude higher than in the overlying water, and since the \mathcal{C}/N ratio of the DOM in this same slurry was 16, relatively rapid bacterial utilization of the labile organic detritus sinking from the surface waters must occur at the seawater-sediment interface.

SUMMARY

A deep profile (0-5 680 m) of DOC, DON, DOP, POC, PON, ATP, total adenylates, and total bacteria in the central North Pacific gyre, indicated little vertical structure in these properties from about 900 m to the bottom, with the exception of DOC and DON, which increased from 5000 m to the bottom. There is apparently diffusion of dissolved (and/or colloidal), refractory organic matter upward from the sediments into the overlying waters. This increased concentration of DOM does not, however, support an increased bacterial population in the boundary layer. The advantages and disadvantages of using an *in situ*, self-contained pumping system for processing large volumes of seawater for analyses of particulate components were discussed.

Acknowledgements

We gratefully acknowledge the generosity of K. Smith in providing ship-time, the shipboard assistance of R. Baldwin, and the laboratory assistance of K. J. Robertson and C. C. Price. This work was supported by U.S. Navy ONR Grant No. USN-N00014-75-C-0152 and U.S. Department of Energy Contract No. DE-AMO3-76-SF00010.

REFERENCES

Armstrong F. A. J., Williams P. M., Strickland J. D. H., 1966. Photooxidation of organic matter in seawater by ultra-violet radiation, analytical and other applications, *Nature*, 211, 481-483.

Beers J. R., Reid F. M. H., Stewart G. S., 1975. Microplankton of the North Pacific central gyre. I. Population structure and abundance, June 1973, Int. Rev. Gesamten Hydrobiol., 60, 607-638.

Carlucci A. F., Williams P. M., 1978. Simulated in situ growth rates of pelagic marine bacteria. Naturwissenschaften. 65, 541-542.

Eppley R. W., Sharp J. H., Renger E. H., Perry M. J., Harrison W. G., 1977. Nitrogen assimilation by phytoplankton and other microorganisms in the surface waters of the central North Pacific Ocean, *Mar. Biol.*, 39, 111-120.

Geosecs Operations Group/NSF, National Science Foundation, 1976. Geochemical Oceans Sections Study, Final Hydrographic Data Report, 1st Ed., 20 August, 1976.

Gordon D. C. Jr., 1971. Distribution of particulate organic carbon and nitrogen at an ocean station in the central Pacific, *Deep-Sea Res.*, 18, 1127-1134.

Hobbie J. E., Daley R. J., Jasper S., 1977. Use of nuclepore filters for counting bacteria by fluorescence microscopy, *Appl. Environ. Microbiol.*, 33, 1225-1228.

Holm-Hansen O., 1973. Determination of total microbial biomass by measurement of adenosine triphosphate, in: *Estuarine Microbial Ecology*, edited by L. H. Stevenson and R. R. Colwell, Univ. South Carolina Press, Columbia, 73-89.

Holm-Hansen O., Strickland J. D. H., Williams P. M., 1966. A detailed analysis of biologically important substances in a profile off Southern California, *Limnol. Oceanogr.*, **11**, 548-561.

Karl D. M., 1978. Distribution, abundance, and metabolic states of

microorganisms in the water column and sediments of the Black Sca, Limnol. Oceanogr., 23, 936-949.

Karl D. M., Holm-Hansen O., 1978. Methodology and measurement of adenylate energy charge ratios in environmental samples, *Mar. Biol.*, 48, 185-197.

Laird J. C., Jones D. P., Yentsch C. S., 1967. A submersible filtering unit, *Deep-Sea Res.*, 14, 251-252.

McGowan J. A., Hayward T. L., 1978. Mixing and oceanic productivity, Deep-Sea Res., 25, 771-793.

Menzel D. W., Vaccaro R. F., 1964. The measurement of dissolved organic and particulate carbon in seawater, *Limnol. Oceanogr.*, 9, 138-142.

Perry M. J., 1972. Alkaline phosphatase activity in subtropical Central North Pacific waters using a sensitive fluorometric method, *Mar. Biol.*, 15, 113-119.

Sorokin J. I., 1964. A quantitative study of the microflora in the central Pacific Ocean, J. Cons., 29, 25-40.

Strickland J. D. H., Parsons T. W., 1972. A practical handbook of seawater analysis, Fish. Res. Board Can., Ottawa, Bull. 167, 2nd ed.

Taga N., Matsuda O., 1974. Bacterial populations attached to plankton and detritus in seawater, in: *Effects of the ocean environment on microbial activities*, edited by R. R. Colwell and R. Y. Morita, Univ. Park Press, Baltimore, 433-448.

Williams P. M., Carlucci A. F., 1976. Bacterial utilization of organic matter in the deep sea, *Nature*, 262, 810-811.

Williams P. M., Stenhouse M. C., Druffel E. M., Koide M., 1978. Organic ¹⁴C activity in an abyssal marine sediment, *Nature*, 276, 698-701.