Zooplankton and bacterioplankton of an abyssal benthic boundary layer: *in situ* rates of metabolism

Maccrozooplankton
Bacterioplankton
Metabolism
Abyss
Panama Basin

Macrozooplancton
Bactérioplancton
Métabolisme
Gouffre
Bassin de Panama

K.L. SMITH Jr.[a], A.F. CARLUCCI[b], P.M. WILLIAMS[b], S.M. HENRICHS[c], R.J. BALDWIN[a], D.B. GRAVEN[b]

[a] Marine Biology Research Division A-002, Scripps Institution of Oceanography, La Jolla, California 92093, U.S.A. ·

[b] Food Chain Research Group, Institute of Marine Resources A-018, Scripps Institution of Oceanography, La Jolla, California 92093, U.S.A.

[c] Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99701, U.S.A.

ABSTRACT

Metabolism of macrozooplankton and bacterioplankton was measured *in situ* between the sediment and 100 m above the bottom in the Panama Basin at a depth of 3 850 m using the submersible "Alvin". Mixed macrozooplankton were collected at depths of 1, 5, 10, 20, and 50 m altitude with a 4-chambered slurp gun respirometer on 4 dives and incubated *in situ* for one day with continuous measurements of oxygen consumption. Bacterioplankton samples were collected at seven depths (0.5, 1, 5, 10, 20, 50, and 100 m altitude) with a 4-syringe array, inoculated with ^{3}H-glutamic acid, incubated for four hours at the depth of collection and poisoned prior to recovery. Although respiration of macrozooplankton per m^3 generally decreased with increasing distance above the bottom, the correlation was not statistically significant ($p > 0.05$). Utilization rates of glutamic acid, as a measure of bacterial respiration and incorporation, were highest at 0.5 m and decreased an order of magnitude at one meter above the bottom with no significant correlation between utilization and altitude ($p > 0.05$). Macrozooplankton respiration rate, integrated over 50 m was $111 \, ul \, O_2 \, m^{-2} d^{-1}$ or equivalent to $0.05 \, mg \, C \, m^{-2} d^{-1}$. Bacterioplankton respiration estimated from glutamic acid uptake rates and extrapolated to total dissolved free amino acid (TDFAA) uptake was equivalent to $0.30 \, mg \, C \, m^{-2} d^{-1}$ when integrated over the 50 m water column of the benthic boundary layer (BBL), six times greater than the macrozooplankton respiration. Respiration rates of macrozooplankton ($0.05 \, mg \, C \, m^{-2} d^{-1}$) combined with incorporation + respiration rates for bacterioplankton ($1.25 \, mg \, C \, m^{-2-1}$) account for 11% of the estimated input of organic carbon to the BBL in the fall ($11.5 \, mg \, C \, m^{-2} d^{-1}$) and reveal the importance of the plankton in carbon cycling in the BBL at abyssal depth.

Oceanol. Acta, 1986, **9**, 1, 47-55.

RÉSUMÉ

Métabolisme du zooplancton et du bactérioplancton dans la couche au-dessus de l'interface avec le benthos abyssal

Le métabolisme du macrozooplancton et celui du bactérioplancton ont été mesurés *in situ* entre le sédiment et 100 m au-dessus du fond (3 850 m) dans le bassion de Panama. Un mélange de macrozooplancton a été prélevé au cours de quatre plongées du submersible Alvin à 1, 5, 10, 20 et 50 m au-dessus du fond avec un aspirateur à quatre chambres. Les échantillons ont été incubés *in situ* pendant une journée, avec mesure en continu de la consommation d'oxygène. Les échantillons de bactérioplancton ont été prélevés à 0,5, 1, 5, 10, 20, 50 et 100 m au-dessus du fond avec une batterie de quatre seringues, inoculés à l'acide glutamique et incubés pendant 4 heures à la profondeur de prélèvement. Bien que la respiration du macrozooplancton par mètre cube décroisse en général lorsque la distance au fond augmente, la corrélation n'est

pas significative (p > 0,05). Le taux d'utilisation de l'acide glutamique comme indicateur de la respiration et de l'assimilation bactérienne est maximal à 0,5 m et se réduit au 1/10 à 1 m au-dessus du fond, sans corrélation significative entre l'utilisation et l'altitude (p > 0,05). Le taux de respiration intégré sur 50 m est de $111 \, \mu l \, O_2 \, m^{-2} j^{-1}$, équivalent à $0,05 \, mg \, C \, m^{-2} j^{-1}$. La respiration du bactérioplancton, estimée par les taux d'assimilation de l'acide glutamique extrapolés à la quantité totale des acides aminés libres dissous est égale à $0,03 \, mg \, C \, m^{-2} j^{-1}$, après intégration sur une colonne d'eau de 50 m dans la couche d'interface benthique BBL (benthic boundary layer). Le taux de respiration du bactérioplancton est donc six fois plus grand que celui du macrozooplancton. Le taux de respiration du macrozooplancton $(0,05 \, mg \, C \, m^{-2} j^{-1})$, combiné avec le taux d'incorporation et le taux de respiration du bactérioplancton $(1,25 \, mg \, C \, m^{-2} j^{-1})$ s'élève à 11 % de la production de matière organique dans la BBL en automne $(11,5 \, mg \, C \, m^{-2} j^{-1})$. Ces résultats montrent l'importance du plancton dans le recyclage du carbone dans la couche à l'interface avec le benthos abyssal.

INTRODUCTION

The mixed layer associated with the deep-sea floor is biologically enriched compared to the overlying water column. Plankton biomass increases in the bottom mixed layer and the benthic boundary layer (BBL) at bathyal and abyssal depths (Karl et al., 1976; Wishner, 1980 b). Smith (1982) estimated that this BBL plankton was an energetically important component of the BBL community with food energy demands equivalent to that of the sediment community at a bathyal station. In partitioning the BBL plankton by size, Smith estimated that the bacterioplankton had the highest energy demands.

To examine the energetic importance of the BBL plankton at greater depths, we measured in situ the metabolism of the macrozooplankton and bacterioplankton at an abyssal station in the Panama Basin in the fall of 1981. These measurements were designed to test two hypotheses: 1) plankton metabolism/m³ significantly decreases with increasing distance above the bottom (p < 0.05); and 2) metabolic rates/m³ of the bacterioplankton component of the BBL plankton are significantly higher (p < 0.05) than those of the macrozooplankton.

AREA OF INVESTIGATION

A Panama Basin study site was selected in the trough at the base of the Coiba Ridge (5°20'N, 81°55'W; 3 850 m depth) where extensive investigations of the water column and sediments have been made. Productivity of the surface water overlying this basin is influenced by strong seasonal upwelling activity to the north and east in winter and spring (Forsbergh, 1969) and by deep mixing due to storms in fall (Bishop, Marra, 1984). Mean primary productivity over the basin is estimated at $261 \, mg \, C \, m^{-2} d^{-1}$, with a range of 163 to $528 \, mg \, C \, m^{-2} d^{-1}$ (Bishop, Marra, 1984). Correlated with the seasonal changes in primary production, there are seasonal pulses in particulate organic matter (POM) flux at this site. Particulate organic carbon (POC) fluxes to the bottom are highest in spring and summer with peaks up to $23.1 \, mg \, C \, m^{-2} d^{-1}$ (Honjo, 1982), fluxes which are considerably higher than those

measured at other open ocean stations not influenced by upwelling (Honjo et al., 1982 a).

An extensive nepheloid layer existed from 900 m to the bottom where particle concentration increased with depth (Gardner et al., 1984). These authors attributed this thick layer to resuspension and advection of material from the basin walls. This material is believed to be largely lithogenic in composition (Honjo et al., 1982 b). The bottom water comes north from the Peru Basin via the Ecuador Trench (Lonsdale, 1977) and flows westward through the study site with a mean velocity of $0.5 \, cm \, s^{-1}$ (Gardner et al., 1984). The sediments in the Panama Basin are a silty clay (van Andel, 1973) with an organic carbon content of 1.7 % (Honjo et al., 1982 a).

METHODS

A series of nine dives were made with the submersible DSRV "Alvin" (dives 1135 - 1143) from 24 September to 3 October, 1981 in the Panama Basin to characterize the habitat of the benthic boundary layer and measure in situ the metabolism of the macrozooplankton and bacterioplankton. Sample collection and measurements were made at 6 arbitrarily selected distances above the bottom (1, 5, 10, 20, 50, 100 m). In addition, bacterioplankton were sampled at 0.5 m above the sediment-water interface.

Chemical characterization of environment

Dissolved nutrients and concentrations of POM were measured on water samples taken with 2 and 5 l Niskin bottles attached to "Alvin" and trippled by the manipulator arm at the desired depths on each of 9 dives. The elapsed time between collection and recovery on the support ship was 2 hours.

Immediate shipboard analyses of inorganic nitrogenous nutrients and dissolved oxygen were performed on subsamples form the 2 l Niskin bottles. Ammonium and nitrite were analyzed using the methodology of Strickland and Parsons (1972) on quadruplicate 5ml samples. Nitrate analysis was conducted with the copper-coated cadmium wire methods (Gardner et al.,

1976) on quadruplicate 2ml samples. Oxygen content was determined on duplicate samples using the modified Winkler method (Carpenter, 1965).

Organic matter analyses were performed on the water collected in 5 l Niskin bottles and included both dissolved and particulate fractions. The Niskins were washed thoroughly with residue-free laboratory detergent, rinsed with distilled water and enclosed in plastic bags before each deployment. For the determination of dissolved free amino acids, duplicate subsamples of 25 ml were collected; one was filtered (BioRad unipore polycarbonate filters, $0.2 \mu m$ pore size, pre-rinsed with 100 ml water distilled from an acidic persulfate solution in a glass still) under a pressure of 8 psi while the other was unfiltered. Both filtered and unfiltered samples were placed in ignited glass prescription bottles and frozen at $-20°C$ for later transfer to a $-70°C$ freezer ashore. These samples were then thawed within one month of collection and analyzed for dissolved free amino acids following the procedure of Lindroth and Mopper (1979). The remaining water from the 5 l samplers (4.5 liters) was filtered on board ship through precombusted GF/C filters and the filters frozen for later analyses of POC and total nitrogen (Sharp, 1974) using a Perkin-Elmer model 240-C CHN analyzer.

Macrozooplankton

Macrozooplankton were collected, concentrated, and the oxygen consumption rates measured using a 4-chambered slurp gun respirometer (SGR) mounted on "Alvin". This instrument is fully described by Smith (1982) and Smith and Baldwin (1983). Macrozooplankton were collected on four dives (1136, 1138, 1141, 1143). The SGR pump was activated at the six discrete sampling depths and mixed macrozooplankton from volumes of 3.18 to $4.24 m^3$ were concentrated behind a $297 \mu m$ mesh screen in each chamber while "Alvin" traversed the study site at 18-21 cm s $^{-1}$ for approximately one hour. Once the first chamber was filled in this manner, the valves were closed and the other two chambers were filled sequentially at other altitudes. The fourth chamber served as a control without macrozooplankton and was filled at a depth intermediate to the sampling depths for that particular dive. When all the chambers were filled and sealed, the SGR was tethered by "Alvin" to a free vehicle mooring line, released from the submersible, and allowed to incubate 22.5 to 26.0 h at the intermediate depth. During the incubation, the dissolved oxygen tension in each chamber was monitored continuously with a polarographic oxygen sensor (Smith, Baldwin, 1983). Dissolved oxygen tensions in each chamber over the period of incubation were never depleted more than 5.9% of the initial tension which ranged from 7.59 to 8.03 kPa. After incubation, the mooring line was acoustically released from the bottom and recovered by the support ship. The contents of each SGR chamber were immediately removed and frozen at $-20°C$ for transfer to a $-70°C$ freezer and analyses in the laboratory. The two attempted measurements of macrozooplankton respiration at 100 m failed due to incomplete chamber closure and the samples were discarded.

In the laboratory, the plankton were identified to major taxa, weighed, lyophilized at $-50°C$, and reweighed. Weight specific rates of oxygen consumption were calculated from continuous recordings of the voltage outputs from each oxygen sensor and corrected for drift and pressure effects. Oxygen consumption was undetectable in the controls on each dive.

Bacterioplankton

Bacterial utilization of organic substrates consists of 1) substrate incorporation into cellular materials; 2) substrate respiration, or oxidation, to the final products of carbon dioxide and water; and 3) excretion of intermediates. When ^3H-labeled compounds are employed, the measurement of ^3H_2O may be used as an estimate of respiration (Carlucci et al., 1984, and references therein). Although ^3H_2O may also be produced in metabolic processes other than respiration (Karl, in press), comparisons of respiration using ^3H-glucose and ^{14}C-glucose with plankton samples differed by only 10% (Kuparinen, Tamminen, 1982). We therefore will refer to ^3H_2O production as respiration.

Bacterioplankton were collected using a syringe sampling array manipulated by "Alvin" at 7 sampling depths. This array consisted of 4-50 ml syringes (Plastipak) with 18 gauge needles mounted in two parallel banks in an aluminum rack. The two facing banks of syringes were held in a cocked position with the syringe plungers secured to the top plate and the syringe barrels held in a closed position against the plunger by a spring-loaded arm. A similar device for single syringe withdrawal sampling was described by Smith and Baldwin (1983). Upon initial release of the spring-loaded arm by the "Alvin" manipulator, the syringe barrels were driven down, filling each syringe with 47.5 ml of ambient water. At this stage the barrels were held by a second spring-loaded arm which prevented complete filling to 50 ml and the needles from penetrating stoppered bottles containing formalin under each syringe. After incubation the second arm was released by the "Alvin" manipulator which allowed all the syringes to take up 2.5 ml of formalin and poison each syringe sample prior to surfacing. Final formalin concentration in each syringe was 5%. As a control, one syringe was poisoned with the 2.5 ml of formalin during the initial filling at depth.

Immediately prior to each deployment, the sterile syringes were inoculated with 3 uCi of ^3H-glutamic acid ([3,4-^3H]-label, 42 Ci mmol^{-1}, New England Nuclear, Boston, MA). This amount of added glutamic acid is equivalent to 1.4 nM for a 50 ml syringe (ambient glutamic acid concentration ranged from 1.9-7.0 nM). The syringe sampling array was mounted on Alvin and filled with ambient water at the desired depth on 7 dives (# 1135-1138, 1140-1142). After filling, the array was attached to a mooring line and incubated for 4 h at the collection depth. The second release was then activated, poisoning the samples with formalin, and the entire array was detached from the mooring line and returned to the surface. Immediately after recovery, the syringes were removed from the array and held at 2°C during the following analysis.

For the measurement of glutamic acid incorporation, 40 ml from each syringe was filtered through a millipore filter (PH, 0.3 μm pore diameter) under low vacuum. Filter edges were carefully rinsed, and each filter was placed in a glass scintillation vial and frozen. Filtrates were frozen for subsequent measurement of ^3H_2O. The remaining 10 ml of sample in each syringe was placed in a clean vial and stored for subsequent determination of bacterial abundances by epifluorescent microscopy.

In the laboratory, 8 ml Betaphase (WestChem, San Diego) was added to each of the scintillation vials containing filtered particulates and radioactivity was measured in a Beckman LS 100C scintillation counter, using external standard ratios to correct for quenching. Aliquots of the filtrates were vacuum-evaporated and ^3H_2O was measured in the condensates. Incorporation (particulate) and respiration (filtrate) were normalized to the recovery of added isotope for each incubation. Calculations of substrate specific activity and utilization were made as described by Carlucci et al. (1984).

Bacterial abundances were determined with acridine orange epifluorescence microscopy (Hobbie et al., 1977), following the modifications detailed by Carlucci et al. (1984). A minimum of 20 fields or 300 cells were counted for each sample replicate.

The measure of correlation between altitude and abundance, biomass, and oxygen consumption for the macrozooplankton and abundance, incorporation, and utilization rates of ^3H-glutamic acid for the bacterioplankton was determined using the Spearman rank test with p=0.05 (Siegel, 1956). The Mann-Whitney U Test (Tate, Clelland, 1957) was used to compare data sets from 2 areas and to compare macrozooplankton and bacterioplankton respiration in the Panama Basin.

RESULTS

Chemical characterization of environment

Most parameters measured at the study site were relatively constant up to 100 m above the bottom, with the exception of total dissolved free amino acids (TDFAA), particulate organic carbon (POC) and particulate organic nitrogen (PON; Tab. 1).

The concentration of unfiltered TDFAA revealed considerable variation with no trend related to altitude (Tab. 1). Filtered samples were erratic and generally higher than the unfiltered samples which may have resulted from variable release of amino acids from the particulate material (Liebezeit et al., 1980; Mopper, Lindroth, 1982; Fuhrman, 1984) abundant in all of the samples. We have used unfiltered TDFAA concentrations in our data analyses because these are most comparable with our bacterial uptake experiments which used unfiltered ambient water in the syringes and because of the erratic nature of the filtered data.

Quantitatively, the most important amino acids were serine and glycine+threonine, each of which comprised about 25% of the TDFAA. Of lesser importance were alanine and valine which constituted 12 and 8% respectively of the total amino acid composition over all depths. The proportions of each of these dominant amino acids and glutamic acid changed little with distance above the bottom.

POC and total nitrogen concentrations peaked at 10 m with an order of magnitude decrease above and below this altitude (Tab. 1). In contrast, TDFAA concentrations were low at 10 m above the bottom. The C: N ratio was highest at 1 m and lowest at 20 m above the bottom (Tab. 1).

Macrozooplankton

Copepods were the numerically and gravimetrically dominant taxa collected. They occurred at all sampling depths at densities of 10-40 individuals m^{-3}; $x=19\pm9$, $n=10$. The other 3 dominant taxa (isopods, ostracods and polychaetes) were collected less frequently and were most prevalent near the bottom.

Although abundance of mixed macrozooplankton generally decreased with increasing distance above the bottom up to 20 m, a local maximum occurred at 50 m

Table 1

Benthic boundary layer of Panama Basin: chemical characterization at seven altitudes from 0.5 to 100 m. TDFAA = total dissolved free amino acids, POM = particulate organic matter. The detection limits of the nitrite and ammonium assays were 0.01 and 0.1 μM respectively (N.D. = not determined).

Altitude above bottom (m)	Dissolved				TDF AA n mol liter^{-1} Unfiltered	POM μg liter^{-1}		
	Temp. °C	O_2 μM	NO_3^- μM	NO_2^- μM	NH_4^+ μM		Carbon	Nitrogen	Total C: N
0.5	N.D.	N.D.	N.D.	N.D.	N.D.	134.3	N.D.	N.D.	
1	1.8	113.8 ± 2.2	37.31 ± 1.25	<0.01	<0.1	120.9	43.0 ± 2.6	1.0 ± 0.1	43.0
5	1.8	116.5 ± 2.7	31.38 ± 0.27	<0.01	<0.1	147.9	50.0 ± 3.4	5.0 ± 0.5	10.0
10	1.8	116.5 ± 1.8	36.38 ± 2.40	<0.01	<0.1	62.6	240.0 ± 50.0	20.0 ± 20.0	12.0
20	1.8	115.6 ± 2.2	40.42 ± 0.55	<0.01	<0.1	154.2	27.0 ± 5.1	8.0 ± 0.9	3.4
50	1.8	115.6 ± 2.2	38.59 ± 0.41	<0.01	<0.1	92.1	31.0 ± 2.7	3.4 ± 1.4	9.1
100	1.8	116.1 ± 1.8	35.68 ± 2.24	0.21	<0.1	25.2	N.D.	N.D.	

Table 2

Abundance, biomass and oxygen consumption rates of macrozooplankton collected with the SGR at five altitudes above the bottom in the Panama Basin (macrozooplankton $\geqslant 297\,\mu m$). Numbers in parentheses for sample 1141-B represent values corrected for weight of one decapod (see text for explanation).

| Sample | Altitude above bottom (m) | Vol. sampled (m^3) | No. Animals (m^{-3}) | Macrozooplankton Biomass ($mg.m^{-3}$) | | | | O_2 Consumption | | |
				wet wt	dry wt	% water	(mg wet wt^{-1})	($\mu l\ O_2 . d^{-1}$) (mg dry wt^{-1})	(m^{-3})
1136-D	1	3.18	42.6	13.54	2.04	84.9	0.24	1.59	3.25
1138-D	1	4.17	23.0	8.11	1.06	86.9	0.28	2.14	2.27
1143-D	1	4.24	29.2	14.14	1.81	87.2	0.37	2.89	5.23
1138-C	5	4.24	18.6	4.42	0.79	82.1	0.48	2.67	2.12
1136-C	10	3.11	19.0	8.80	1.44	83.6	0.36	2.18	3.13
1138-B	10	4.24	10.4	5.95	0.88	85.2	0.37	2.51	2.20
1141-C	20	4.24	15.3	12.91	2.43	81.2	0.33	1.75	4.26
1141-D	20	4.24	10.9	4.30	0.67	84.4	0.33	2.10	1.42
1141-B	50	4.24	30.7	28.81 (30.4)	3.92 (3.08)	86.4 (0.53)	0.26	1.91	7.49
1143-C	50	4.24	19.3	2.45	0.44	82.0	0.42	2.35	1.03

(Tab. 2). Thus, there was no significant correlation between altitude and abundance ($p_{.05} = 0.56$, $r_s = 0.26$). A clearer trend occurred in biomass. Wet and dry weight biomass were significantly correlated with distance above the bottom and decreased with increasing altitude if the one large decapod from 1141-B chamber at 50 m is deleted (Tab. 2) ($p_{.05} = 0.56$, $r_s = -0.70$; $r_s = -0.57$, respectively). The dominant taxa, copepods, decreased in size at 50 m contributing to the observed reversal between abundance and biomass at the upper sampling depth.

Wet weight specific oxygen consumption rates of the plankton revealed no significant correlation with altitude ($p_{.05} = 0.56$, $r_s = -0.33$) and ranged from 0.24 to 0.48 ul O_2 mg wet wt^{-1} d^{-1} (Tab. 2). Dry weight specific oxygen consumption was also relatively consistent in magnitude, 1.59 to 2.89 ul O_2 mg dry wt^{-1} d^{-1}. Oxygen consumption of the macrozooplankton per m^3 exhibited no correlation with distance above the bottom ($p_{.05} = 0.56$, $r_s = -0.15$) (Tab. 2). However, if the measurement from chamber 1141-B at 50 m which contained the large decapod was deleted from analysis, there was a general, although not a statistically significant, decrease in oxygen consumption rate with increasing distance above the bottom ($p_{.05} = 0.60$, $r_s = -0.58$; Tab. 2).

Bacterioplankton

Both free-living and attached cells comprised the BBL bacterial population (bacterioplankton), with attached forms being more prevalent closer to the sediment where increased numbers of particles of largely amorphous detritus occurred. The dominant free-living bacteria were small cocci; less abundant were vibrios and spirilli. Attached bacteria were predominantly cocci of larger size than the free-living cells. We have included both free-living and attached bacteria in the category of bacterioplankton, since the two populations were incubated and analyzed as a single group.

Bacterioplankton abundance was negatively correlated with distance above the bottom ($p_{.01} = 0.94$, $r_s = -0.94$), decreasing with increased altitude from 1 to 100 m (Tab. 3). After a slight but insignificant increase ($p > 0.05$) in cell number between 0.5 and 1 m altitude, abundance decreased precipitously from 1 to 10 m then leveled off up to 100 m altitude above the bottom.

Incorporation of ^{3}H-glutamic acid by bacteria was nearly an order of magnitude higher at 0.5 m than at all other sampling depths above the interface (Tab. 3). There was no significant correlation between incorporation rate and distance above the bottom ($p_{.05} = 0.83$, $r_s = -0.36$).

Table 3

Bacterioplankton abundance and glutamic acid incorporation and utilization at seven altitudes above the bottom in the Panama Basin. Samples for glutamic acid uptake analysis from 20 m were contaminated and are not given. Glutamic acid incorporation and utilization presented with mean and st. dev. (C.S. = contaminated sample).

Dive	Altitude above bottom (m)	Bacteria $\times 10^{10}\ m^{-3}$	Ambient glutamic acid conc. unfiltered (nM)	Glutamic acid incorporation n mol m^{-3} day^{-1}	Glutamic acid utilization Specific rate (n mol $\times 10^{-9}$ $cell^{-1}$ d^{-1})	n	Total rate (n mole m^{-3} d^{-1})	Glutamic acid Turnover time (d)
1142	0.5	7.46	7.0	130.8	2.31	1	172.1	41
1135	1	8.00	3.0	8.8 ± 4.6	0.15	3	11.6 ± 6.0	258
1136	5	5.00	3.4	15.8	0.42	1	20.8	164
1137	10	3.71	3.0	12.1 ± .3	0.43	2	15.9 ± .4	189
1138	20	C.S.	5.9	C.S.	C.S.		C.S.	C.S.
1140	50	3.56	6.9	23.6 ± 3.9	0.87	2	31.1 ± 5.3	222
1141	100	3.48	1.9	8.8 ± 2.0	0.33	3	11.6 ± 2.6	164

Due to malfunction of the evaporating apparatus, we measured ^3H_2O production (respiration) only on the 0.5 m sample. Respiration for the 0.5 m population of bacteria accounted for 24% of ^{3}H-glutamic acid utilization. This value is in reasonable agreement with a mean 30.8% respiration for bacteria found in other deep-sea nepheloid-layer environments (n = 20; Carlucci et al., unpublished data). We have therefore used the 0.5 m respiration percentage for our calculations, as it gives a conservative estimate of bacterioplankton respiration.

The calculated utilization (incorporation + respiration) of glutamic acid by bacterioplankton was highest at 0.5 m and decreased an order of magnitude at 1 m above the bottom (Tab. 3). A minor secondary peak in uptake rate occurred at 50 m above the bottom. There was no significant correlation between utilization rate and distance above the bottom ($p_{.05}$ = 0.83, r_s = −0.36). Rates of utilization per bacterial cell (specific rate) mirrored the total utilization rates with distance above the bottom.

Calculated glutamic acid turnover time was approximately five times shorter at 0.5 m (41 h) compared to all other depths sampled (163 − 258 h; Tab. 3). There was no correlation between turnover time and distance above the bottom ($p_{.05}$ = 0.83, r_s = 0.19).

DISCUSSION

Macrozooplankton

Copepods were the dominant taxa in the BBL of the Panama Basin as well as in other BBL studies of deep-sea plankton from a wide variety of areas (Wishner, 1980 a; Smith, 1982; 1985). Abundance of mixed macrozooplankton of the BBL in the Panama Basin (Tab. 2) falls within the range reported by Smith (1982) for the Santa Catalina Basin BBL (1 300 m; 1 - 36 animals m^{-3}) but an order of magnitude lower than those reported for a deep-sea hydrothermal vent area (2615 m) at 21°N on the East Pacific Rise (149 - 920 animals m^{-3}; Smith, 1985) using the same methodology. Macrozooplankton biomass measured in the Panama Basin (Tab. 2) is lower than that reported in the Santa Catalina Basin (44.6 − 261.8 mg wet wt m^{-3}) (Smith, 1982) but within the range of estimates made for deep-sea plankton between 1 000 and 4 000 m depth using a variety of methods (0.07 − 40 mg wet wt m^{-3}; summarized by Wishner, 1980 b).

Decrease in abundance of macrozooplankton with increased distance above the bottom in the Panama Basin agrees with previous findings of Smith (1982) to an altitude of 20 m. However, Smith recorded a continued decrease in abundance at 50 m whereas we found an increase at the same altitude. Smith (1982) stressed that the volume of water sampled in collections made with the SGR is small compared to those gathered with towed nets (Wishner, 1980 a; 1980 b). Given the known patchiness of surface-water zooplankton, our estimates of abundance may not be representative of the true values.

The trend of decreasing wet and dry weight biomass (corrected for weight of one decapod − see results) with increased altitude up to 50 m in the Panama Basin is similar to that reported by Smith (1982) over the same distance above the bottom for the 1 300 m Santa Catalina Basin.

Oxygen consumption rates of the Panama Basin plankton fall within the range of values previously measured for mixed macrozooplankton over a wide range of temperatures using a variety of methods. Dry weight specific oxygen consumption rates (Tab. 2) are of comparable magnitude to those measured for BBL plankton at 1 300 m (Smith, 1982; 1.44 − 3.16 μl O_2 mg dry wet^{-1}d^{-1}) and for hydrothermal vent plankton rates measured within one meter of the bottom at 2615 m (Smith, 1985; 1.68 − 4.26 μl O_2 mg dry wt^{-1}d^{-1}) using the same methodology.

Oxygen consumption rates/m^3 for the BBL plankton of the Panama Basin overlap with values measured for mixed macrozooplankton collected in a non-vent area on the East Pacific Rise at 21°N (Smith, 1985; 4.3 − 7.5 μl O_2 m^{-3}d^{-1}) and are comparable to those estimated at a mean depth of 2 500 m in midwater using the electron transport system method (King et al., 1978). There was a trend, although not a significant correlation, between oxygen consumption rates per m^3 and altitude above the bottom in the Panama Basin, with the elimination of decapod sample 1141-B (Tab. 2), which generally conforms to previous studies of BBL plankton metabolism in the Santa Catalina Basin where a definitive pattern of decreasing rates with increased altitude was found (Smith, 1982).

Bacterioplankton

TDFAA concentrations were measured in the Panama Basin to determine ambient concentrations of glutamic acid available for bacterial utilization. Limited information is available in the literature for comparing our TDFAA results with other areas and includes both filtered and unfiltered concentrations which can differ by as much as a factor of 2 on subsamples from the same collection (Fuhrman, 1984; Williams, Carlucci, unpublished data). For unfiltered samples, Liebezeit et al. (1980) reported a concentration of about 146 umoles m^{-3} for 6 major dissolved free amino acids at 65 m and 64 umoles m^{-3} at 1 500 m in the Sargasso Sea. Bottom water TDFAA concentrations greater than 100 umoles m^{-3} are reported only for unfiltered samples from the Baltic Sea (Mopper, Lindroth 1982). Lee and Bada (1975; 1977) measured filtered TDFAA concentrations of approximately 20 umoles m^{-3} at 4 500 m depth in the Sargasso Sea, and approximately 20 umoles m^{-3} at 4500 m depth in the Saragasso Sea, and approximately 40 umoles m^{-3} at 2700 m depth in the equatorial Pacific. Our unfiltered TDFAA concentrations (25.2 − 154.2 umoles m^{-3}) are within the range of concentrations reported above for both filtered and unfiltered samples.

We have compared the Panama Basin BBL bacterial abundance, TDFAA concentration, and utilization data to results obtained in two S. California Borderland Basins, San Pedro and Santa Monica (Carlucci et al.,

Table 4

Comparison of bacterioplankton abundance and glutamic acid utilization in the Panama Basin and Southern California Continental Borderland basins (San Pedro and Santa Monica Basins). *(Carlucci et al., unpublished data).

Site		Bacteria $\times 10^{10}$m^{-3}	TDFAA μmole m^{-3}	% Glutamic acid of TDFAA	Glutamic Acid Utilization		Turnover time (d)
					Specific rate (nmole $\times 10^{-9}$ cell^{-1} d^{-1})	Total rate (nmole m^{-3} d^{-1})	
Panama Basin (3750-3850 m)	$\bar{x}$	5.2	105.3	5.0	0.8	44	173
	range	3.5 − 8.0	25.2 − 154.2	2.3 − 7.7	0.2 − 2.3	12 − 172	41 − 258
	n	6	7	6	6	6	6
S. California Borderland Basins* (500-900 m)	$\bar{x}$	11.0	4.5	17.6	3.3	184	30
	range	3.7 − 29.0	1.4 − 15.0	7.3 − 29.8	0.4 − 10.2	48 − 720	4 − 60
	n	16	12	12	9	9	9

Table 5

Estimated utilization of total dissolved free amino acid (TDFAA) and respiration of bacterioplankton based on measured glutamic acid utilization and the concentration of glutamic acid and TDFAA at five altitudes in the BBL of the Panama Basin. See text for explanation of computations.

Altitude above bottom (m)	TDFAA μmole m^{-3}	% Glutamic acid of TDFAA	Glutamic acid utilization nmole m^{-3} d^{-1}	TDFAA utilization (m^{-3} d^{-1})			Respiration (m^{-3} d^{-1})		
				μmole	Joules	Carbon μg	μmole	Joules	Carbon μg
0.5	134.0	5.2	172.1	3.31	5.15	174.8	0.79	1.23	41.7
1	120.0	2.5	11.63	0.47	0.73	24.8	0.11	0.17	5.8
5	148.0	2.3	20.76	0.90	1.40	47.5	0.22	0.34	11.6
10	62.7	4.8	15.86	0.33	0.51	17.4	0.08	0.12	4.2
50	92.1	7.5	31.10	0.41	0.64	21.6	0.10	0.15	5.3

unpublished; Tab. 4). Unfiltered TDFAA concentrations in the Panama Basin were 2 orders of magnitude higher (T = 21, p < 0.01) than those found in filtered samples from the S. California Basins; comparable unfiltered samples were not collected. However, bacterial abundance and specific rate of glutamic acid utilization were not significantly different (T = 46 and T = 32, respectively, p > 0.05) between the two areas. The higher concentrations of TDFAA in the Panama Basin contribute to the significantly longer turnover times (T = 24, p < 0.01) when compared to the California basins.

Hypotheses

The purpose of our study was to test two hypotheses in an attempt to better define the energetic importance of plankton in the BBL community of the Panama Basin: 1) plankton metabolism/m^3 significantly decreases with increasing distance above the bottom (p < 0.05); and 2) metabolic rates of the bacterioplankton/m^3 are significantly higher (p < 0.05) than those of the macrozooplankton. There is no significant correlation (p > 0.05) between macrozooplankton or bacterioplankton metabolism and distance above the bottom in the Panama Basin. Hence, we can reject the first hypothesis. For comparison, a Spearman rank test was applied to the data of Smith (1982) on mixed macrozooplankton oxygen consumption at four distances above the bottom (1 − 50 m) in the Santa Catalina Basin. There was a significant negative correlation (p < 0.05) between macrozooplankton oxygen consumption and altitude. This contrasts our findings in the Panama Basin where neither mixed macrozooplankton, bacterioplankton or the combined metabolism revealed any significant corre-

lation (p > 0.05) with distance above the bottom up to 50 m and the rates are considerably lower. To address the second hypothesis concerning the comparative metabolic importance of the macrozooplankton and bacterioplankton, we integrated respiration rates/m^3 over a 50 m water column of the BBL. Macrozooplankton respiration was 111 μl O$_2$ m^{-2}d^{-1} which is equivalent to 2.22 J m^{-2} d^{-1} or 0.05 mg C m^{-2}d^{-1} assuming a respiratory quotient (RQ) of 0.80 and is an order of magnitude lower than a similar estimate from the 50 m BBL in the Santa Catalina Basin (Smith, 1982).

Bacterioplankton respiration was estimated from glutamic acid utilization rates at 0.5 m and for the four altitudes successfully examined for both plankton components (Tab. 5). This was done by calculating the percent of TDFAA (Tab. 1) represented by glutamic acid at each altitude and, given the rate of glutamic acid utilization (Tab. 3), estimating the utilization rate of TDFAA (Carlucci et al., 1984). In these calculations we assume that the bacterioplankton utilize all the TDFAA similarly (Carlucci et al., 1984; Dawson, Gocke, 1978; Williams et al., 1976). In addition, Ferguson and Sunda (1984) found a 1: 1 relationship between turnover rates of a mixture of 15 amino acids and glutamic acid indicating that the average turnover rate for seawater amino acids may be similar to that of glutamic acid. These utilization rates of TDFAA were converted: 1) to energy units using a composition value of 1 554.5 kJ mole^{-1} calculated from standard heats of combustion for the major amino acid components of the TDFAA; and 2) to organic carbon assuming 4.4 umoles C per umole TDFAA and 12 μg C per umole C (Tab. 5; Henrichs, Williams, 1985; Carlucci et al., 1984).

These bacterioplankton rates were then integrated over the 50 m water column yielding a total utilization rate of TDFAA of $36.79\,J\,m^{-2}\,d^{-1}$ ($1.25\,mg\,C\,m^{-2}\,d^{-1}$) with a component respiration rate of $8.84\,J\,m^{-2}\,d^{-1}$ ($0.30\,mg\,C\,m^{-2}\,d^{-1}$). The integrated respiration rates for the bacterioplankton were an order of magnitude higher than for the macrozooplankton with the bacterioplankton respiration being an underestimate since the uptake of other substrates such as sugars were not measured. In addition, estimated rates of bacterioplankton respiration were significantly higher ($p < 0.05$) than mean macrozooplankton respiration at comparable altitudes. Based on the above estimates, we can accept our second hypothesis that bacterioplankton respiration is significantly higher than macrozooplankton respiration in the 50 m water column of the BBL. Smith (1982) estimated a total bacterial carbon utilization of $30.1\,mg\,C\,m^{-2}\,d^{-1}$ for the BBL in Santa Catalina Basin. Since TDFAA represents $<5\%$ of the total dissolved organic carbon in the sea (usually $<1\%$ of total; Crawford et al., 1974; Lee, Bada 1977), our Panama Basin TDFAA utilization rates suggest a dissolved organic carbon utilization rate of $25\,mg\,C\,m^{-2}\,d^{-1}$ for the BBL bacterioplankton, assuming all dissolved organic carbon is labile and utilizable.

Respiration rates for the macrozooplankton and bacterioplankton combined are $0.35\,mg\,C\,m^{-2}\,d^{-1}$ which amounts to 3% of the particulate organic carbon flux ($11.5\,mg\,C\,m^{-2}\,d^{-1}$) measured in the basin at 3 560 m in the fall (Honjo, 1982). In the bacterioplankton, respiration accounts for a portion of the energy required and assimilation accounts for the majority of substrate utilization. We have no estimate of the energetic costs of growth in the macrozooplankton but even if it was equal to the respiration demand, it would not make an appreciable contribution compared to that of the bacterioplankton. Hence, if we disregard the growth component for the macrozooplankton, the combined utilization rate for the bacterioplankton (respiration + incorporation) and respiration rate for the macrozooplankton is $1.30\,mg\,C\,m^{-2}\,d^{-1}$ or 11% of the particulate organic carbon flux to the BBL in the Panama Basin. In such comparisons, we are assuming that the primary source of the non-refractory or utilizable carbon input to the BBL organisms in dissolved or particulate form is derived from particulate organic carbon. Bottom advection and chemolithotrophic production within the BBL cannot be discounted (Karl et al., 1984). We have also excluded other components of the BBL plankton in our calculations which may be important in estimating the energetic demands of the plankton and these include the organisms smaller than the macrozooplankton and larger than the bacterioplankton. No estimates of the importance of these organisms in the BBL have been made.

Our studies show that the plankton and especially the bacterioplankton are an important energetic component of the BBL community at abyssal depths and must be considered when modeling carbon and energy flow in the deep sea.

Acknowledgements

REFERENCES

Bishop J.K.B., Marra J., 1984. Variations in primary production and particulate carbon flux through the base of the euphotic zone at the site of the Sediment Trap Intercomparison Experiment (Panama Basin), J. Mar. Res., 42, 189-206.

Carlucci A.F., Craven D.B., Henrichs S.M., 1984. Diel production and microheterotrophic utilization of dissolved free amino acids in waters off southern California, Appl. Microbiol., 48, 165-170.

Carpenter J.H., 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method, Limnol. Oceanogr., 10, 141-143.

Crawford C.C., Hobbie J.E., Webb K.L., 1974. The utilization of dissolved free amino acids by estuarine microorganisms, Ecology, 55, 551-563.

Dawson R., Gocke K., 1978. Heterotrophic activity in comparison to the free amino acid concentrations in Baltic Sea water samples, Oceanol. Acta, 1, 1, 45-54.

Ferguson R.L., Sunda W.G., 1984. Utilization rates of amino acids by planktonic marine bacteria: importance of clean technique and low substrate additions, Limnol. Oceanogr., 29, 258-274.

Forsbergh E.D., 1969. On the climatology, oceanography and fisheries of the Panama Bight, Inter-Am. Trop. Tuna Comm. Bull., 14, 386 p.

Fuhrman J., 1984. Biological considerations in the measurement of dissolved free amino acids in seawater: implications for chemical and microbiological studies, Eos, 65, 926.

Gardner W.S., Wynne D.S., Dunstan W.N., 1976. Simplified procedure for the manual analysis of nitrate in seawater, Mar. Chem., 4, 393-396.

Gardner W.D., Bishop J.K.B., Biscaye P.E., 1984. Nephelometer and current observations at the STIE site, Panama Basin, J. Mar. Res., 42, 207-219.

Henrichs S.M., Williams P.M., in press. Dissolved and particulate amino acids and carbohydrates in the sea surface micro layer, Mar Chem.

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.

Honjo S., 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin, Science, 218, 883-884.

Honjo S., Manganini S.J., Cole J.J., 1982 a. Sedimentation of biogenic matter in the deep ocean, Deep-Sea Res., 29, 609-625.

Honjo S., Spencer D.W., Farrington J.W., 1982 b. Deep advective transport of lithogenic particles in Panama Basin, Science, 216, 516-518.

Karl D.M., in press. Determination of in situ microbial biomass, viability, metabolism and growth, in: Bacteria in nature: a treatise on the interactions of bacteria and their habitats: 2, edited by E. Ledbetter and J. Poindexter, Plenum Press, New York.

Karl D.M., LaRock P.A., Morse J.W., Sturges W., 1976. Adenosine triphosphate in the North Atlantic Ocean and its relationship to the oxygen minimum, Deep-Sea Res., 23, 81-88.

Karl D.M., Knauer G.A., Martin J.H., Ward B.B., 1984. Bacterial chemolithotrophy in the ocean is associated with sinking particles, Nature, 309, 54-56.

King F.D., Devol A.H., Packard T.T., 1978. Plankton metabolic activity in the eastern tropical North Pacific, Deep-Sea Res., 15, 689-704.

Kuparinen J., Tamminen T., 1982. Respiration of tritiated substrates in heterotrophic activity assays, Appl. Environ. Microbiol., 43, 806-809.

Lee C., Bada J.L., 1975. Amino acids in Equatorial Pacific Ocean Water, Earth Planetary Sci. Lett., 26, 61-68.

Lee C., Bada J.L., 1977. Dissolved amino acids in the Equatorial Pacific, the Sargasso Sea, and Biscayne Bay, Limnol. Oceanogr., 22, 502-510.

Liebezeit G., Bolter M., Brown I.F., Dawson R., 1980. Dissolved free amino acids and carbohydrates at pycnocline boundaries in the Sargasso Sea and related microbial activity, Oceanol. Acta, 3, 3, 357-362.

Lindroth P., Mopper K., 1979. High performance liquid chromatographic determination of subpicomole amounts of amino acids by precolumn fluorescence derivatization with ophthaldialdehyde, Anal. Chem., 51, 1667-1674.

Lonsdale P., 1977. Inflow of bottom water to the Panama Basin, Deep-Sea Res., 24, 1065-1101.

Mopper K., Lindroth P., 1982. Diel and depth variations in dissolved free amino acids and ammonium in the Baltic Sea determined by shipboard HPLC analysis, Limnol. Oceanogr., 27, 336-347.

Sharp J.H., 1974. Improved analyses for particulate organic carbon and nitrogen from seawater, Limnol. Oceanogr., 19, 984-989.

Siegel S., 1956. Nonparametric statistics for the behavioral sciences, McGraw-Hill, N.Y., 312 p.

Smith K.L. Jr., 1982. Zooplankton of a bathyal benthic boundary layer: in situ rates of oxygen consumption and ammonium excretion, Limnol. Oceanogr., 27, 461-471.

Smith K.L. Jr., 1985. Macrozooplankton of a deep-sea hydrothermal vent: in situ rates of oxygen consumption, Limnol. Oceanogr., 30, 102-110.

Smith K.L. Jr., Baldwin R.J., 1983. Deep-sea respirometry: in situ techniques, in: Handbook on polarographic oxygen sensors, edited by E. Gnaiger and H. Forstner, Springer, Berlin, 298-319.

Strickland J.D.H., Parsons T.R., 1972. A practical handbook of seawater analysis, 2nd ed. Bull. Fish. Res. Board Can., 167, 310 p.

Tate M.W. Clelland R.C., 1957. Nonparametric and shortcut statistics, Interstate Printers and Publishers, Inc. Danville, Ill. 171 p.

Williams P.J.leB., Berman T., Holm-Hansen O., 1976. Amino acid uptake and respiration by marine heterotrophs, Mar. Biol., 35, 41-47.

Wishner K.F., 1980a. Aspects of the community ecology of the deep sea, benthopelagic plankton, with special attention to gymnopleid copepods, Mar. Biol., 60, 179-187.

Wishner K.F., 1980b. The biomass of the deep-sea benthopelagic plankton, Deep-Sea Res., 27, 203-216.

Van Andel T.H., 1973. Texture and dispersal of sediments in the Panama Basin, J. Geol., 81,434-457.

LIEGE
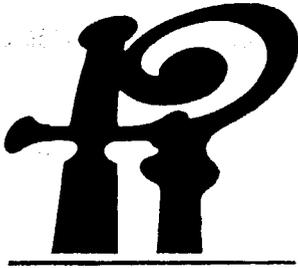
International Liège Colloquium on Ocean Hydrodynamics

IAPSO
IOC
AGU
EGS
IRMA

Prof. Jacques C. J. NIHOUL, *Modelenvironment*
University of Liège, B 5, Sart Tilman,
B-4000 LIEGE (Belgium)

18TH INTERNATIONAL LIEGE COLLOQUIUM
ON OCEAN HYDRODYNAMICS

Liège, May 5-9, 1986

"Three-dimensional models
of marine and estuarine dynamics"

The 18th International Liège Colloquium on Ocean Hydrodynamics will be held in Liège University, May 5-9, 1986, on the subject "Three-dimensional models of marine and estuarine dynamics".

The Colloquium will be devoted to the presentation, by eminent experts, of recent three-dimensional hydrodynamic models, to the critical survey of appropriate numerical methods and to the discussion of applications and case studies.

Without excluding a limited number of contributions on global models, applicable to general planetary ocean circulation and climate studies (which were the subject of the 16th Liège Colloquium), the emphasis will be laid on *regional* models designed for specific well-defined basins such as the North Atlantic, continental seas like the North Sea, the Mediterranean, ..., estuaries...

Papers are welcome on mesoscale and macroscale *general circulation models* (tides, storm surges, residuals...) as well as on *local circulation models* dealing with the formation and instabilities of fronts, coastal upwellings...

The Colloquium will be the occasion to compare and discuss respective approaches (multi-layer models, multi-mode models, vertical discretization,...), parameterization schemes (eddy viscosity, turbulent energy closure, ...), mathematical and numerical techniques (finite differences, finite elements, ...) and boundary conditions representations (in particular, open-sea boundary conditions).

A special attention will be given to the representation, in 3-D general circulation models, of boundary layers such as the bottom and surface layers which play an essential role in such important problems as the erosion and transport of sediments, air-sea interactions and the final disposal of telluric pollution in the marine system.