

Concentrations and uptake of neutral monosaccharides along 140°W in the equatorial Pacific: Contribution of glucose to heterotrophic bacterial activity and the DOM flux

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Abstract

We examined concentrations and uptake of dissolved neutral monosaccharides (DNMS) in order to determine the contribution of DNMS to heterotrophic bacterial production and to the flux of dissolved organic matter (DOM) in the equatorial Pacific. DNMS concentrations were greater during El Niño-affected months of February–April 1992 than during August–October 1992; in contrast, glucose turnover was the opposite—turnover was faster in August–October than in February–April. The variation in sugar concentrations and turnover probably resulted from El Niño-induced changes in primary production; as El Niño waned primary production increased, which appeared to stimulate bacterial activity, especially glucose turnover, that in turn forced down DNMS concentrations. In all months, however, DNMS concentrations were low, especially compared with total dissolved organic carbon concentrations (<1%). Glucose was the dominant neutral monosaccharide and alone supported 15–47% of bacterial production. Other monosaccharides apparently did not support much bacterial growth; concentrations of other sugars were low, as probably was turnover. Respiration of glucose (30–60% of uptake) and mannose (60–90%) was relatively high, suggesting that DNMS supported a large fraction of bacterial respiration as well as biomass production. These results point to the importance of DNMS and glucose in particular in supporting bacterial growth and in contributing to the flux of labile DOM.

The concentration of labile dissolved organic matter (DOM) in aquatic ecosystems is usually low, but rates of bacterial activity and biomass production (Cole et al. 1988; Ducklow and Carlson 1992) indicate that DOM fluxes can be quite high. In spite of the recognized importance of DOM, we have few direct measures of DOM fluxes and know little about the composition and uptake of specific components of the labile DOM pool. Nearly all previous studies on labile DOM have focused on dissolved free amino acids (DFAA) and on the support of bacterial production by DFAA.

Free amino acids can provide much C and N for bacterial growth, which in turn suggests that the DFAA is a large component of the labile DOM flux in at least some marine environments. In estuaries, DFAA seems to support a large fraction (if not all) of bacterial production (Billen and Fontigny 1987; Jørgensen et al. 1993; Hoch and Kirchman 1995). Dissolved combined amino acids

(DCAA) have been shown to support some bacterial growth in Lake Constance (Rosenstock and Simon 1993), but in other environments, DCAA uptake seems to be low compared with bacterial production and DFAA uptake (Keil and Kirchman 1993; Jørgensen et al. 1993). In contrast, in the few open-ocean studies completed to date, the DFAA flux is insufficient to supply much C or N for bacterial production (Kirchman et al. 1994; Suttle et al. 1991); hence the labile DOM flux must be dominated by other compounds.

Of the many DOM components in natural waters, dissolved sugars seem important to examine next after amino acids. Mopper et al. (1992) provided an HPLC method for measuring the low concentrations of neutral monosaccharides (DNMS) expected in marine waters. Using this HPLC method, Jørgensen (1990) and Jørgensen and Jensen (1994) found that glucose supported 6–49% of bacterial production in three lakes. Other studies provide indirect evidence that DNMS could potentially support much bacterial production in marine waters. Burney (1986) used the MBTH method and observed large changes in sugar concentrations over time, suggestive of high fluxes. Kirchman et al. (1990) hypothesized that uptake of dissolved inorganic nitrogen (DIN) (principally NH_4^+) by heterotrophic bacteria is driven by monosaccharide uptake, but it is difficult to extrapolate from their enrich-

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ment experiments to in situ processes. Finally, although they did not measure fluxes, Pakulski and Benner (1994) did find high concentrations of mono- and polysaccharides in equatorial Pacific waters. Other studies point to the importance of polysaccharides in supporting bacterial growth and in contributing to DOM fluxes (Amon and Benner 1994; Benner et al. 1992; Hanisch et al. 1996).

The main goal of our study, which was part of the JGOFS Equatorial Pacific Program, was to estimate DNMS concentrations and turnover and to compare glucose uptake and bacterial production in equatorial Pacific waters. This region is an important biogeochemical province to examine because of its large area and high rates of new production (Barber and Chavez 1991; Murray et al. 1994). In addition, El Niño-Southern Oscillation (ENSO) events during our four cruises in 1992 allowed us to examine how DNMS concentrations and uptake varied over large temporal scales. We show here that glucose is the main DNMS component and that it can support a substantial portion (~40%) of bacterial production and respiration, which points to the importance of glucose and DNMS in the labile DOM flux.

Methods and materials

Study site and experimental conditions—The data reported on here were from four cruises in 1992: 4 February–10 March (survey 1), 22 March–9 April (time-series 1), 10 August–24 September (survey 2), and 2–20 October (time-series 2). Water was collected from three to five depths within the euphotic zone from 12°N to 12°S along 140°W using either 10-liter Niskin bottles with silicone tubing (survey 1) or 20-liter Teflon-lined GoFlo bottles (all other cruises). Measurements were always started within 0.5 h after collection. For survey 1 and 2, samples for carbohydrate analysis were collected in precombusted 20-ml vials, immediately desalted (*see below*), and rapidly frozen. For time-series 1 and 2, samples were filtered through Acrodiscs (0.22 μm) and then frozen in combusted vials. These samples were desalted just prior to HPLC analysis. All incubations were at ambient temperature (15–28°C) in the dark.

Monosaccharide concentrations—Neutral monosaccharides were analyzed on a high-pressure anion exchange column (Dionex Carbopac PA1) using pulsed amperometric detection (HPLC-PAD) as described by Mopper et al. (1992). The system was isocratic, with NaOH as the solvent. With 12 mM NaOH, monosaccharides were separated adequately, but the sensitivity was relatively low. Conversely, with 30 mM NaOH, important compounds were not well separated, but sensitivity was enhanced. We used 12 mM NaOH as the solvent and found that glucose was often the only monosaccharide present (*see results*), allowing us to use the higher solvent concentration which gave better sensitivity. Samples that contained coeluting sugars were run at both concentrations. The use of two solvent concentrations also reduced the risk of misidentification of peaks because it is less

likely that two sugars would coelute at both solvent concentrations. Solvents were continuously purged with helium in order to minimize the buildup of carbonates on the column. Because purging also removes oxygen from the solvents, it was necessary to purge the samples in order to avoid a large trough in the chromatograms.

Prior to injection, salts were removed from the samples by ion exchange using a mixed anion and cation resin, which was prepared from AG 2-X8 anion exchange resin (20–50 mesh) and AG 50W-X8 cation exchange resin (50–100 mesh) (Bio-Rad). The prepared mixed resin was added to a clean plastic column as a slurry. Excess water was then blown out of the column with high-purity nitrogen. The column was then rinsed three times with 500 μl of sample. Each rinse was blown through with high-purity nitrogen. A 1-ml sample was added, and the column was capped and allowed to react for 7 min. The sample was blown out of the column, collected in a precombusted glass vial, and rapidly frozen. Salinity of samples was checked periodically with a refractometer to ensure that the samples were adequately desalted; salinity was always 0‰. The resins were regenerated according to the manufacturer's instructions and used repeatedly with no loss of ion exchange capacity.

The desalting procedure appeared to remove most of the bacterial cells as observed with epifluorescence microscopy. However, to ensure that bacteria would not affect sugar concentrations during storage, we tested the effects of filtering the sample before desalting. Samples were gently filtered through a 0.2- μm syringe filter (Acrodisc), which was cleaned with two rinses of deionized water and then one of sample water. For all samples, filtration increased the concentrations of several monosaccharides (Table 1). This increase could be due to known effects of filtration on cells as demonstrated by Fuhrman and Bell (1985) for dissolved free amino acids. The properly cleaned syringe filters were not the source of the contamination.

Monosaccharide standards were used to confirm identification of the peaks. Standard monosaccharide solutions were prepared in deep seawater (>2,000 m), in which the concentrations of naturally occurring monosaccharides were below detection. Sample peaks were identified by retention time as compared to these standards. The limit of detection was found to be around 3 nM. Rhamnose was added to each sample as an internal standard to a concentration of either 25 or 50 nM prior to desalting. Periodically, samples were run without the internal standard to confirm that in situ concentrations of rhamnose were below detection.

Several experiments were run on the two survey cruises to check for the recovery of sugars by this method. Recovery of monosaccharides was estimated by adding sugars to deep seawater and treating these as regular samples. Percent recoveries varied from $22 \pm 8\%$ for rhamnose to $87 \pm 9\%$ for glucose (Table 2). All reported concentrations were corrected for these recoveries by using an internal standard.

Monosaccharides concentrations were measured at three (February–March) to five depths (August–September) at

Table 1. Effects of gentle filtration through a syringe filter on concentrations of neutral monosaccharides. Samples were frozen immediately after filtering. Sample depth was 40 m.

Lat	Sugar	Filtered (nM)	Unfiltered (nM)	Filtered/unfiltered
2°S	Fucose	6	≤3*	≥2
	Glucose	57	7	9
	Fructose	24	4	6
5°S	Fucose	≤3	≤3	≥1
	Glucose	23	9	3
	Fructose	6	≤3	≥2

* Below the limit of detection which was 3 nM.

each latitude during survey 1 and 2. All data were averaged over these depths because there were no clear patterns in the depth profiles. Standard deviations reported here thus include variation due to depth. Samples taken below the euphotic zone (>120 m) did not have detectable levels of monosaccharides (<3 nM).

Uptake and respiration—Uptake of D-[6-³H]glucose (DuPont NEN) was measured in duplicate for each sample. The added concentration was 0.5 nM. After 0.5–1-h incubations, uptake was stopped by filtration through 0.45- μ m Millipore filters or 0.22- μ m Sartorius filters (rates determined with these two filter types did not differ), which were then rinsed twice (3 ml) with filtered cold seawater, dissolved in ethyl acetate, and radioassayed. The scintillation cocktail was Ultima-Gold (Packard Instr.). At the same time, controls were run in which samples were killed with trichloroacetic acid (TCA) prior to incubation. Radioactivity from these killed samples was subtracted from the other samples.

Percent respiration was determined by using the filtrate from the uptake measurements. The filtrate was vacuum distilled at 60°C, and the distillate was collected in a scintillation vial immersed in an acetone and ice mixture. The distillate that contained respired ³H water was radioassayed. Blue food coloring was added to the filtrate in order to see it and thus avoid carryover of the sample without distillation. Respiration was measured with killed controls and used to correct the live samples.

Bacterial production—Bacterial production was measured by the [³H]thymidine method (Fuhrman and Azam 1980). Details on the method were given by Kirchman et al. (1995). The following conversion factors were used: 2.15×10^{12} cells per mole of thymidine incorporated and 20 fg carbon per bacterial cell (Kirchman et al. 1995). The depth profiles discussed by Kirchman et al. (1995) were based on 3–10 depths, and bacterial production was based on both thymidine and leucine incorporation. In the depth profiles from the survey cruises discussed here, only thymidine incorporation was measured. However, both methods appeared to give the same estimate of production. For the time-series data, bacterial production was estimated from both thymidine and leucine incorporation (Ducklow et al. 1995).

Table 2. Recovery of monosaccharides (mean \pm SE) after desalting and analyzing by the HPLC-PAC method.

Monosaccharide	Recovery (%)	N
Arabinose	62 \pm 7	8
Fucose	55 \pm 6	8
Fructose	70 \pm 6	4
Galactose	46 \pm 8	4
Glucose	87 \pm 9	8
Rhamnose	22 \pm 8	8

Results

Particulate primary production is typically high at the equator because of the upwelling of nutrient-rich waters (Barber and Chavez 1991). Enhanced primary production was observed even in El Niño-affected months (February–March, Fig. 1). Bacterial production somewhat followed primary production along the 12°N to 12°S transect, although there was much variation in the ratio of bacterial to primary production (Kirchman et al. 1995).

Concentrations of DNMS also varied greatly with latitude and did not seem to follow bacterial production or primary production (Fig. 2). In February–March, DNMS concentrations were lowest within the upwelling region between 3°N and 3°S (58 ± 8 nM), with higher concentrations north (115 ± 62 nM) and south (93 ± 5 nM) of the equator (Fig. 2). The high concentrations at 5°N in February–March are most prominent. The DNMS pool at 5°N included high amounts of glucose (Fig. 3A) as well as unusually high concentrations of arabinose (Table 3).

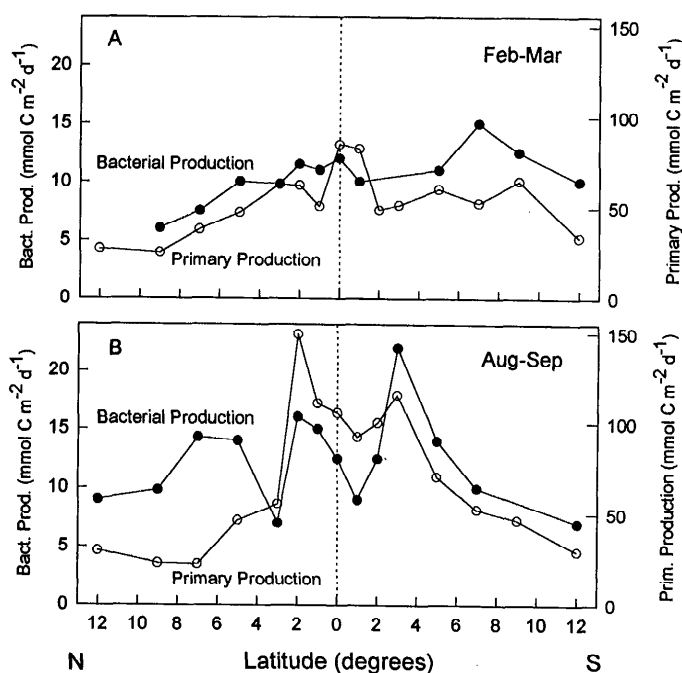


Fig. 1. Primary and bacterial production during survey cruise 1 (A) and 2 (B) along 140°W. (Modified from Kirchman et al. 1995.)

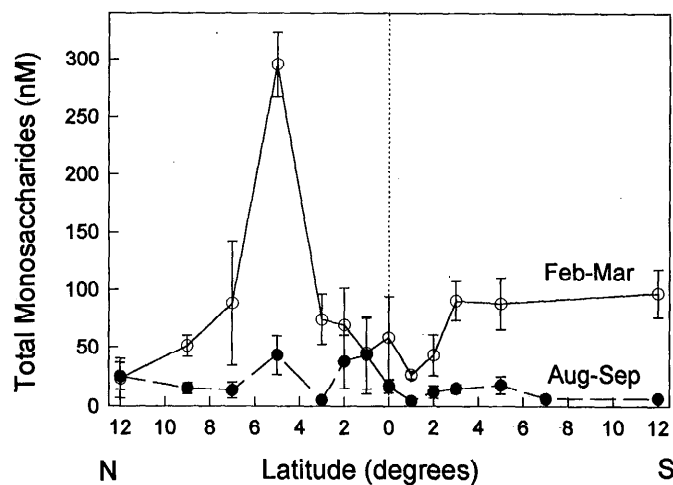


Fig. 2. Total monosaccharides (DNMS) in February–March (survey 1) and August–September (survey 2) along 140°W. Three (survey 1) or five (survey 2) depths were sampled over 0–80 m. Because there was no obvious pattern with depth, the average (\pm SE) of all samples was calculated and is given here.

In August–September, there was little difference among the northern, southern, and equatorial regions; total concentrations were uniformly low along the 12°N–12°S transect.

Glucose was the most abundant monosaccharide observed during all cruises (Table 3). It comprised 47 and 79% of the total pool during survey 1 and 2, although it was proportionally lower (24–36%) during the two time-series cruises (Table 4). Fructose was 16–18% of total DNMS, with the other monosaccharides contributing <10% to the total; the exceptionally high arabinose concentrations at one station were already noted. Except for arabinose, there were no obvious patterns or remarkable exceptions in the relative amount of different monosaccharides with latitude (Rich 1994).

Effect of El Niño on monosaccharide concentrations—

Of more interest than the variation with latitude is the variation in total sugar concentrations and glucose turnover among the different cruises. In brief, sugar concentrations were high but turnover slow during El Niño-affected months of February–April, but the opposite was the case when El Niño had subsided during August–October; during those months, concentrations were low and turnover fast.

Concentrations of total DNMS were 4-fold higher during February–March (81 ± 19 nM; mean \pm SE) than during August–September (19 ± 4 nM) (ANOVA $P < 0.001$, $n = 100$) (Fig. 2). In the equatorial region, DNMS concentrations differed by \sim 2-fold (50 ± 8 nM vs. 19 ± 9 nM; significant at $P < 0.05$), although glucose concentrations were about the same during the two survey cruises (30 ± 6 nM vs. 19 ± 5 nM; $P > 0.05$) (Fig. 3).

As during the survey cruises, sugar concentrations were much higher in El Niño-affected months of March–April than in October during the time-series cruises at the equator. Concentrations were \sim 4-fold higher during time-se-

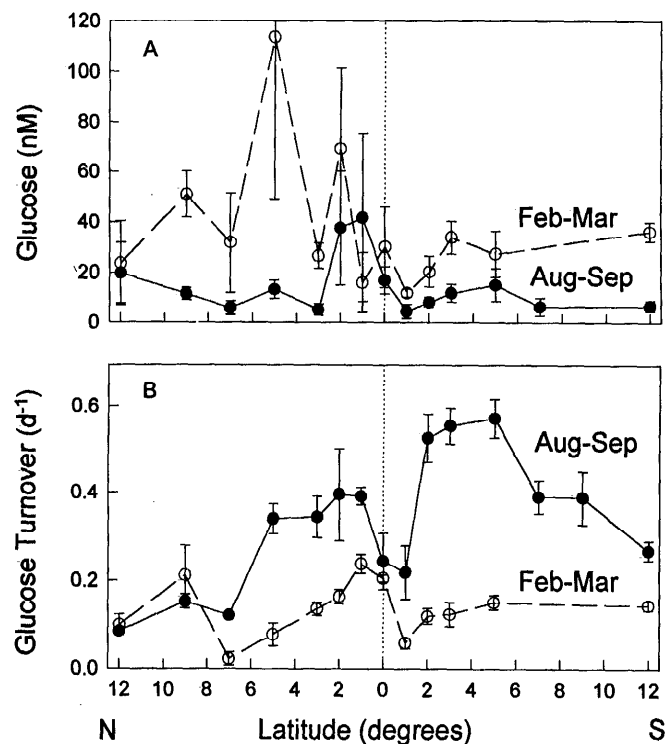


Fig. 3. As Fig. 2, but of glucose concentrations (A) and glucose turnover rate constants (B).

ries 1 than during time-series 2 (Table 4), similar to the difference observed in the two survey cruises. The measured DNMS concentrations were generally higher during the time-series cruises than during the survey cruises, which were a month earlier, but this difference may be a methodological artifact. Unlike the survey cruises, samples for concentrations during the time-series cruises were first filtered and frozen before the desalting step, which experiments showed can lead to contamination (Table 1). Unlike total DNMS concentrations, however, glucose

Table 3. Summary of neutral monosaccharide concentrations during the two survey cruises in the equatorial Pacific, 12°S–12°N along 140°W. All latitudes and depths were averaged together.

Sugar	Feb–Mar		Aug–Sep	
	Concn (nM)	%*	Concn (nM)	%
Arabinose	$12 \pm 29^\dagger$	15	1 ± 2	5
Fructose	15 ± 12	18	3 ± 7	16
Fucose	0	0	0 ± 1	0
Galactose	2 ± 5	2	0	0
Glucose	38 ± 27	47	15 ± 12	79
Mannose	4 ± 8	5	0	0
Unknown	9 ± 10	11	0	0
Total	81 ± 69		19 ± 14	

* Percent of total concentration.

† Mean \pm SD of 13 (February–March) or 14 latitudes (August–September), each sampled at three (February–March) or five (August–September) depths (0–80 m).

Table 4. Concentrations of dissolved neutral monosaccharides (DNMS) and glucose (mean \pm SD) during the two time-series cruises at the equator, 140°W.

Cruise	N	Depth (m)	DNMS (nM)	Glucose (nM)	% of total*
Mar–Apr	5	15	137 \pm 233	33 \pm 42	24
	7	30	133 \pm 124	34 \pm 38	26
Oct	17	15	28 \pm 40	10 \pm 11	36
	17	30	43 \pm 63	11 \pm 10	26

* Percent of total DNMS contributed by glucose alone.

concentrations at the equator did not differ significantly between survey 1 and time-series 1 or between survey 2 and time-series 2 (Fig. 4). Also, glucose concentrations were lowest on time-series 2, which argues against large contamination during the two time-series cruises.

Regardless of possible artifacts, when all the data at the equator for the four cruises are considered together, glucose concentrations clearly decreased from El Niño-affected months (February–April) to August–October by 2–3-fold (Fig. 4).

Effect of El Niño on glucose turnover—Rate constants for glucose turnover were relatively high from 3°N to the equator and then decreased to a local minimum at 1°S during both survey cruises (Fig. 3B). The other striking feature in the meridional variation was that the mean rate constant was lower north ($0.26 \pm 0.02 \text{ d}^{-1}$) than south of the equator ($0.43 \pm 0.02 \text{ d}^{-1}$) (Fig. 3B). These turnover rates constants do not include respiration (*see below*).

Like concentrations, turnover varied more consistently among the different cruises than across the latitudes. During the survey cruises, turnover of glucose was significantly slower (Student's *t*-test; $P < 0.001$, $n = 103$) in El Niño-affected months than in August–September (Fig.

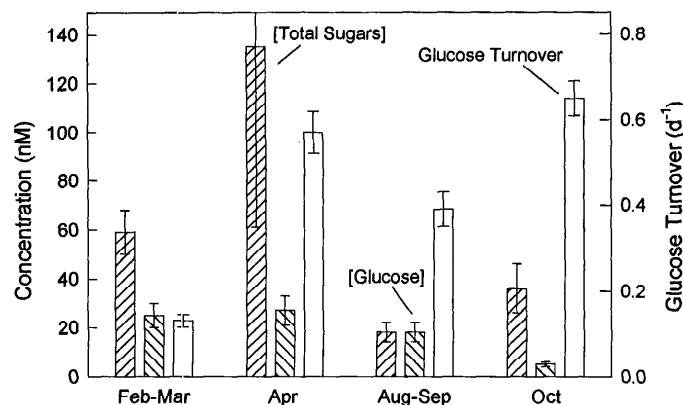


Fig. 4. Concentrations of total sugar (DNMS) and glucose and turnover rate constants of glucose in the equatorial region. Data from February–March and August–September (the survey cruises) include samples from 3°N to 3°S. Average (\pm SE) include all samples (i.e. all depths, dates, and latitudes). Numbers of samples are given in Tables 4 and 5 for the time-series cruises and Table 6 for the survey cruises.

Table 5. Glucose turnover, uptake, bacterial production (BP), and percent of BP supported by glucose uptake during the two time-series cruises at the equator, 140°W. Mean \pm SD.

Cruise	Depth* (m)	Turnover (d^{-1})	Glucose uptake	BP	% of BP
			(nmol C liter $^{-1}$ d $^{-1}$)	(nmol C liter $^{-1}$ d $^{-1}$)	BP
Mar–Apr	15	0.49 \pm 0.16	107 \pm 137	310 \pm 36	32 \pm 42
	30	0.61 \pm 0.18	132 \pm 125	281 \pm 31	51 \pm 51
Oct	15	0.63 \pm 0.18	41 \pm 48	271 \pm 58	14 \pm 16
	30	0.65 \pm 0.19	47 \pm 38	71 \pm 62	17 \pm 15

* Number of samples at each depth was 9 for March–April and 18 for October.

3B). This difference was as much as 5-fold and was observed at every latitude except 0, 9, and 12°N. Averaged over the entire equatorial region (3°S to 3°N), glucose turnover was >2-fold slower in February–March than in August–September when El Niño had waned (Fig. 4).

Similarly, turnover rate constants for glucose were significantly lower during time-series 1 than during time-series 2 at the equator (Table 5; Fig. 4). Contamination of DNMS, which cannot be ruled out for the time-series cruises, would not affect these turnover estimates because rate measurements were handled separately from the samples for DNMS concentrations, and the same procedures were used for all cruises.

Figure 4 summarizes the four cruises that examined sugar concentrations and glucose turnover in equatorial waters (3°N–3°S). This figure shows that total sugar (DNMS) and specifically glucose concentrations were higher during El Niño-impacted months than during August–October. The pattern for glucose turnover is not as clear. As indicated by the more detailed analysis given above, turnover was faster for survey 2 than for survey 1 and was somewhat faster for time-series 2 than for time-series 1. However, the rate constants for glucose turnover in March–April complicate any simple explanation based on El Niño for examining how turnover varied over the year. The fast glucose turnover in March–April was accompanied by the highest average bacterial growth rates of the four cruises (0.21 d^{-1} vs. the next highest average of 0.016 d^{-1} during survey 2). Even given this complication, it appears that El Niño had a large effect on sugar concentrations and turnover, probably because of its effect on primary production and, in turn, bacterial production.

Coupling among primary production, bacterial production, and glucose turnover—Time-series 2 provided an opportunity to examine our hypothesis that changes in primary production over time cause changes in bacterial production and in glucose turnover and concentrations. During this cruise, a tropical instability wave passed through the equatorial station, evident from changes in sea surface temperature (Fig. 5A). When temperature was nearly the lowest, specifically on year-day 284, primary production was highest, and it then declined as temper-

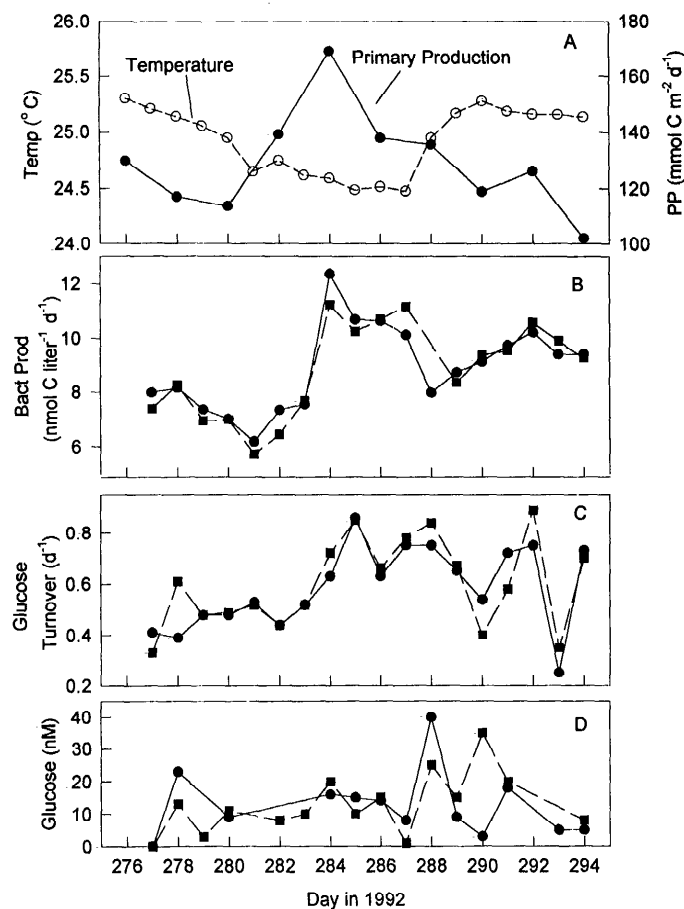


Fig. 5. Response of microbial production and glucose parameters to the passage of the tropical instability wave during time-series 2 (October). A. Sea surface temperature and primary production. B. Bacterial production at 15 m (●) and 30 m (■). C. Turnover rate constants for glucose at 15 m (●) and 30 m (■). D. Glucose concentrations at 15 m (●) and 30 m (■).

ature increased (Fig. 5A). Bacterial production increased from ~ 9 mmol C liter⁻¹ d⁻¹ to 15 mmol C liter⁻¹ d⁻¹ at the peak of primary production. Bacterial production then remained at or near the high level, in spite of a decrease in primary production (Fig. 5B).

Changes in turnover rate constants of glucose mirrored the increase in primary and bacterial production, although the maximum glucose turnover was 1 d later than the production maxima (Fig. 5C). Glucose concentrations varied sporadically in no clear pattern during this period (Fig. 5D). In short, primary production did seem to affect bacterial production on this time scale, but the two processes are obviously not totally coupled. Glucose turnover followed bacterial production, although we could not see any effect on sugar concentrations on this time scale.

Respiration and mannose turnover—Mannose respiration was consistently high, ranging from 60 to 90% of total uptake along the transect from 12°N to 12°S (Fig. 6A). Percent mannose respiration was always higher than percent respiration of glucose (Fig. 6A). Percent respi-

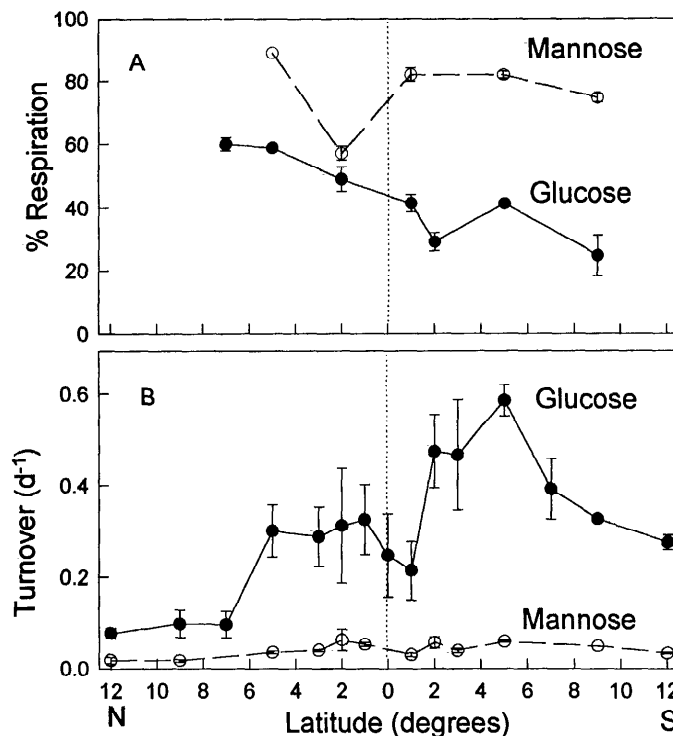


Fig. 6. Glucose and mannose utilization during survey 2 (August–September) along 140°W. Averages (\pm SE) of 5 replicates taken over 0–80 m. A. Percent respiration of glucose and mannose. B. Turnover rate constants for glucose and mannose.

ration of glucose decreased along the N–S transect, from 60% at 7°N to 30% at 9°S (Fig. 6A).

Turnover of mannose was always substantially lower than glucose turnover (Fig. 6B). The rate constants were uniformly low at ~ 0.02 d⁻¹, which is 4–25-fold lower than turnover rate constants of glucose (Fig. 6B).

Bacterial production supported by glucose—Glucose uptake, which is the product of glucose concentrations and turnover rate constants, was roughly similar during survey 1 and 2 (Table 6). The rates were similar for the two cruises because concentrations were high and turnover slow during survey 1 (El Niño) whereas concentrations were low and turnover fast during survey 2 (non-El Niño). As expected from the variation in concentration and turnover, glucose uptake rates varied greatly and had no obvious pattern along the 12°N–12°S transect (Table 6).

In equatorial waters, glucose uptake was about the same on average during three of the four cruises, the exception being time-series 1 (Fig. 7). During that cruise, glucose uptake was 2–5-fold higher than during the other cruises; we also observed high bacterial production and growth rates during time-series 1 (Ducklow et al. 1995).

We compared glucose uptake with bacterial production in order to assess the importance of glucose as a C source for bacterial growth and to estimate the contribution of glucose to the total DOM flux. Respiration was not included in this analysis because we did not measure total

Table 6. Heterotrophic bacterial production (BP, nmol C liter⁻¹ d⁻¹) and glucose uptake (nmol C liter⁻¹ d⁻¹) during the two survey cruises along 140°W.

Lat	BP		Glucose uptake		% of BP*	
	(mean ± SD)	N	(mean ± SD)	N	(mean ± SD)	N
Survey 1 (Feb–Mar 92)						
12°N	94±37	5	24±12	6	44±23	3
9	111±49	5	46±40	5	41±30	5
7	64±31	3	8±2	3	13±5	3
5	150±49	6	51	1	39	1
3	89±15	6	24±12	3	25±12	3
2	89±32	6	41±21	2	54±6	2
1	94±21	6	33±30	5	36±30	5
0	100±34	14	29±38	3	25±33	3
1°S	51±36	6	5±1	3	27±18	3
2	93±25	9	17±12	3	17±14	3
3	66±24	6	23±1	3	55±36	3
5	65±19	3	30±21	3	53±46	3
12	81±51	5	21±7	3	25±22	3
Overall mean					35%	
Survey 2 (Aug–Sep 92)						
12°N	74±45	11	3±2	9	5±4	9
9	76±49	7	15±13	3	15±13	3
7	77±40	14	8±5	9	10±4	9
5	165±90	11	39±41	6	31±42	6
3	70±53	8	14±8	3	17±6	3
2	118±56	11	56±15	3	48±16	3
1	126±62	8	148±199	3	85±102	3
0	141±102	11	33±32	5	22±15	5
1°S	76±49	8	7±2	2	12±11	2
2	110±54	11	28±22	6	22±15	6
3	158±91	8	59±35	3	30±5	3
5	151±64	11	42±26	5	27±16	5
7	74±35	8	24±13	3	29±17	3
12	79±31	11				
Overall mean					27%	

* (glucose uptake/BP) × 100. Calculated for samples for which uptake and production were measured simultaneously. Overall mean %BP is the mean of individual ratios, which will not equal the ratio of the averages for production and glucose uptake.

bacterial respiration. We are justified in comparing uptake of glucose into biomass and bacterial biomass production because both exclude respiration.

Our most important observation is that glucose usually supported a large fraction of bacterial production. The highest average percentage of bacterial production supported by glucose (32–51%, depending on the depth) was observed during time-series 1 when glucose uptake was the highest of the four cruises (Fig. 7). The lowest percent (14–17%) was during time-series 2 (Table 5; Fig. 7). Both glucose uptake and bacterial production decreased in October compared to the previous two cruises, but uptake decreased more. Even though turnover rate constants during time-series 2 were the highest of the four cruises, glucose uptake decreased in October due to a decrease in concentrations. The 2-fold difference in turnover was not enough to offset the 5-fold decrease in concentrations.

Discussion

Bacterial production and growth efficiency can be used to estimate the flux of labile DOM because heterotrophic bacteria are the main sinks of DOM and direct use of particulate organic matter is very low relative to DOM, especially in coastal and oceanic environments (Kirchman 1993). Even though the ratio of bacterial production to primary production (BP:PP) is low in equatorial Pacific waters (~0.15 vs. the average of 0.30 for aquatic systems; Cole et al. 1988; see also Ducklow and Carlson 1992), the labile DOM flux in these waters could still be substantial (Ducklow et al. 1995; Carlson and Ducklow 1995) and perhaps is even greater north and south of the equator (Kirchman et al. 1995). The few direct measures of this flux in any aquatic environments are restricted to DFAA. Progress in understanding other labile DOM components has been hampered by the lack of techniques to measure the expected low concentrations. Given the complexity of the DOM pool, it is noteworthy to observe here that a single DOM component, glucose, can support a substantial fraction (15–45%) of bacterial production and by implication is a large component of the labile DOM flux.

Glucose and to a lesser extent the other DNMS components probably fuel a large fraction of bacterial respiration, which is usually a larger sink for labile DOM than is bacterial production. The large contribution of sugars to bacterial respiration is indicated by the large percent respiration of glucose and mannose (usually >40%). Our estimates of the percent respiration of glucose were often higher than those observed previously (e.g. Hobbie and Crawford 1969; Azam and Hodson 1981; Griffiths et al. 1984), although the other estimates are from waters very different from those we studied. We could directly estimate the contribution of sugars to bacterial respiration,

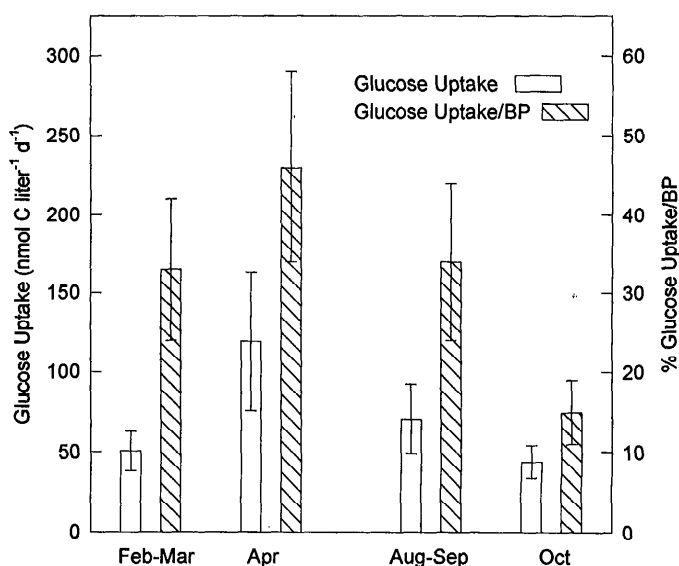


Fig. 7. Glucose uptake and percent bacterial production supported by glucose (% glucose uptake/BP) during February–April (El Niño-affected months) and August–October (waning of El Niño) in the equatorial region. Averages (±SE) were calculated as described in Fig. 4; Number of samples given in Tables 4–6.

but it is sufficient to compare percent DNMS respiration and growth yield (expressed as a percentage). If percent DNMS respiration were much lower than 100% minus the growth yield, then DNMS uptake would not support much bacterial respiration and these data would have little relevance for understanding the labile DOM flux. But it appears that the "conversion efficiency" (i.e. 100% minus % respiration) of DNMS (this study) and of other individual compounds (Jahnke and Craven 1995) is similar to estimates of growth yield. Thus, the DOM components important in supporting bacterial production, such as glucose and DFAA, are also highly likely to be important in fueling bacterial respiration. We base our discussion on biomass production and uptake because we have many more estimates of production and uptake than of growth yield and conversion efficiencies; also, respiration of only bacteria is difficult to estimate directly (Cole and Pace 1995).

Other sugars—Monosaccharides other than glucose are less important in supporting bacterial growth for two reasons. First, turnover rate constants for glucose are higher than those for other sugars. That conclusion is based on our work with [³H]mannose, and also on experiments with other monosaccharides (Rich 1994). The important exception is fructose. In seawater culture experiments, depletion rates of fructose and glucose were similar, and both sugars were taken up much faster than other monosaccharides in equatorial waters (Rich 1994). A second reason glucose is the most important monosaccharide is that usually its concentration is much higher than that of other monosaccharides (this study; also Mopper et al. 1992; Jørgensen 1990; Jørgensen and Jensen 1994). Uptake of monosaccharides other than glucose could support perhaps another 10% of bacterial production. Additional bacterial growth could be supported by polysaccharides, but concentrations and turnover rate constants for the labile components of this pool are unknown in oceanic waters. Hanisch et al. (1996) found that total dissolved carbohydrates, as measured by the MBTH method, supported much bacterial growth in Lake Constance.

HPLC vs. MBTH estimates of monosaccharide concentrations—Concentrations of DNMS, as measured by HPLC-PAD, were low in equatorial waters (usually $\ll 1 \mu\text{M C}$). Similar low concentrations were observed in the only other published study of monosaccharides in oceanic waters using HPLC-PAD (Mopper et al. 1992). The few lakes examined to date also have nanomolar levels of these sugars (Jørgensen 1990; Jørgensen and Jensen 1994). In an estuary, Hanson and Snyder (1980) also measured nanomolar levels with an enzymatic method. Higher concentrations (low micromolar) of monosaccharides have been observed in some oceanic waters (Mopper et al. 1980; Ittekkot et al. 1981), although it is not clear whether these high concentrations can occur occasionally (e.g. during and after phytoplankton blooms; Ittekkot et al. 1981) or whether they are artifacts of early HPLC methods. Using the MBTH method, Pakulski and Benner (1994) found rather high ($> 1 \mu\text{M C}$) concentrations of mono-

saccharides in the same waters in which we found much lower concentrations of DNMS. Differences in methodology explain this contradiction.

The MBTH method used by Pakulski and Benner (1994) includes a variety of sugars, amino sugars and sugar alcohols, for example, that are not detected by the HPLC-PAD method. A critical difference is the desalting step required by the HPLC-PAD method. This step removes charged sugars that are included in the MBTH assay. We suspect that the large pool of monosaccharides measured by the MBTH assay includes many compounds, each of which is present in low concentrations (nanomolar) as we measured here for the neutral monosaccharides.

Variation in sugar concentrations and turnover due to El Niño—The time-series data directly and the meridional data indirectly indicate that there are at best weak interactions among the processes governing glucose concentrations, glucose uptake, and biomass production on short time (days) and spatial (kilometers) scales. However, we can see some correlations among parameters when larger scales are examined. The main factor affecting all processes during the four cruises (time scale of months) was El Niño-Southern Oscillation (ENSO). Equatorial primary production was lower in El Niño-affected months of February–April than in August–October, when El Niño had waned (Murray et al. 1994). For the most part, bacterial production followed primary production and was lower in February–April than in August–October (Kirchman et al. 1995; Ducklow et al. 1995).

Sugar concentrations and utilization were also affected by El Niño. Although there is much variation, it seems that glucose and total DNMS concentrations were higher and turnover rate constants lower for El Niño-affected months of February–April than for August–October, when El Niño had waned. One hypothesis is that the supply of inorganic nitrogen increased as El Niño waned, which in turn caused glucose turnover to increase from February–April to August–October. The problem with the nitrogen hypothesis, however, is that heterotrophic bacterial production in equatorial waters (Kirchman and Rich in press) and in at least some other open oceanic regions (Kirchman 1990) seems to be limited by carbon, not nitrogen, and so one would expect sugars to limit DIN uptake, not DIN to limit sugar uptake (Kirchman et al. 1990).

Another, perhaps more plausible, scenario is that El Niño caused an increase in primary production which led to increases in DOM fluxes and ultimately bacterial production. This increase in bacterial activity caused glucose to be utilized more rapidly, which drove down glucose concentrations. This scenario suggests that bacterial activity determines sugar concentrations, not vice versa.

We can now identify a large fraction of the organic compounds that support bacterial growth and thus comprise the flux of labile DOM in the open ocean. Assuming that free amino acids support as much bacterial production in the equatorial Pacific as in the North Atlantic (Kirchman et al. 1994), we are able to account for about two thirds of the carbon required for bacterial production; DFAA supply about a third in addition to the third sup-

plied by glucose. The "missing" third may come from combined amino acids (proteins) and sugars (polysaccharides). Hydrolysis of these combined forms could produce low molecular by-products, such as DNMS, which would contribute to the fluxes we measured here. However, if hydrolysis and uptake are tightly coupled, then hydrolysis by-products may not necessarily be routed through the free monomer pools and thus would not be included in our DFAA and DNMS measurements. Thus, direct use of proteins and polysaccharides could easily account for the missing carbon. In short, although the labile DOM pool may be very complex chemically, we hypothesize that the list of compounds used by bacteria to support daily bacterial production is relatively short. If so, we should now be able to directly examine the DOM used by bacteria in order to understand more completely than before the controls of bacterial production and the role of bacterial processes in a variety of biogeochemical processes.

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