Vol. 25: 43–53, 2001 | AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol | Published August 10

Short-term temporal and spatial dynamics of bacterioplankton near Barbados in the Caribbean Sea

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ABSTRACT: To investigate temporal (ca 1 mo) and spatial dynamics of bacterioplankton in the Caribbean Sea, time-series measurements of chlorophyll *a* concentration, bacterial abundance, and thymidine incorporation rate were performed at 6 stations near Barbados. In addition, a series of incubation experiments was carried out with seawater samples collected from various depths and stations to determine bacterial growth rates and removal rates by bacterivory. Vertically integrated phytoplankton and bacterioplankton biomasses averaged 1290 and 1200 mg C m^{-2}, respectively, and heterotrophic bacterial production was 106 mg C m^{-2}, with *in situ* bacterial growth of 0.1 d^{-1}. Approximately halfway through the sampling period, surface salinity dropped by as much as 4 following the arrival of water from the Amazon River. No subsequent change, however, was noted in chlorophyll *a* concentration, bacterial abundance, or bacterial production. Averaged bacterial growth and bacterivory determined from bottle incubation experiments were 0.6 and 0.5 d^{-1}, respectively, suggesting that predation was a major sink of daily bacterial biomass production. Both regression analysis of bacterial biomass and production and measurements of growth and bacterivory from incubation experiments suggest that top-down processes control bacterioplankton dynamics to a greater degree than bottom-up processes.

KEY WORDS: The Caribbean Sea · Bacterial growth · Bacterivory · Amazon River discharge

INTRODUCTION

Bacterioplankton is one of the key constituents of planktonic food webs. It frequently comprises a significant fraction of planktonic biomass in oceanic waters (Ferguson & Rublee 1976, Cho & Azam 1988, Fuhrman et al. 1989) and bacterial metabolism may exceed that of phytoplankton in oligotrophic environments (del Giorgio et al. 1997). Bacteria utilize dissolved organic carbon, incorporate it into particulate biomass, and thereby help to mediate cycling of nutrients and materials in seawater (Azam et al. 1983, Cho & Azam 1988, Fuhrman 1992). In addition to this energetic view of bacteria in planktonic food webs, bacterial growth represents the ultimate microbial response to the ambient environmental condition (Cooper 1991). Thus, to understand the function and structure of the planktonic food web, it is necessary to quantify *in situ* bacterial growth and removal by bacterivory and viral lysis (Wright & Coffin 1984, Ducklow & Hill 1985a, Fuhrman 1999).

The majority of oceanic waters is characterized by low nutrient concentrations; thus, bacterial growth in these environments is consistently limited by substrate supply (Morita 1997). Sanders et al. (1992) proposed that planktonic biomass and production in oligotrophic waters are more likely substrate-limited, whereas predation more likely controls them in eutrophic environments. In a more complicated scenario, Ducklow (1992) proposed that substrate-limited control of oceanic bacterioplankton growth in spring shifts to

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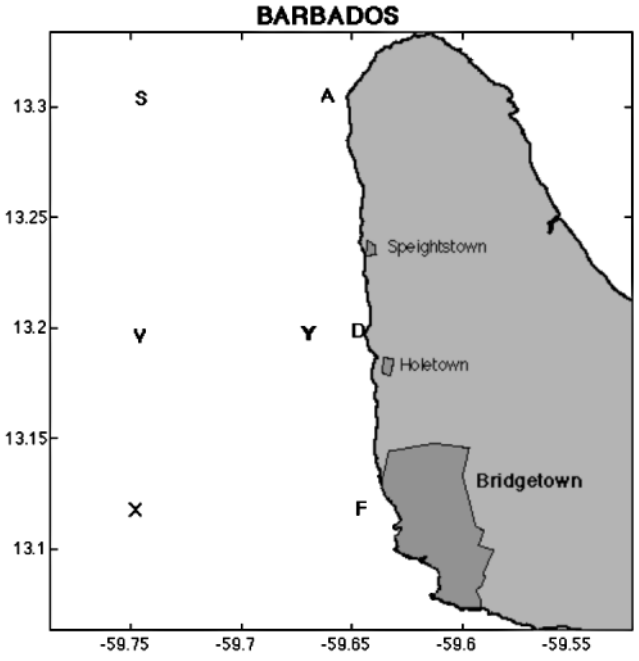

Fig. 1. Map showing sampling sites, indicated by letters, nearby and to the west of Barbados (courtesy of Peter Kelly, MSRC SUNY Stony Brook, New York, USA)

top-down control in summer. In spite of their low nutrient concentrations in the open ocean, however, high bacterial biomass and production relative to phytoplankton biomass, and bacterial growth rates comparable to those in estuarine and coastal waters have often been reported (Ducklow & Carlson 1992 and references therein). This phenomenon of relatively high bacterial growth can be explained by the fact that nutrient limitation can be relieved in part by regeneration of nutrients through *in situ* grazing (Ducklow 1983, Fuhrman 1992 and references therein), although resource supply will be set by primary production. Unusually low rates of bacterivory, however, have been observed occasionally in oceanic waters (Ducklow & Carlson 1992, Ducklow et al. 1992). Research on bacterial growth and bacterivory is less well-articulated in nutrient-limited environments as opposed to eutrophic environments (Ducklow & Carlson 1992, Morita 1997).

The Caribbean Sea comprises a significant fraction of the western North Atlantic Ocean and generally fluctuates little in its hydrographic conditions except for periods of freshwater discharge from the Orinoco and Amazon Rivers (Muller-Karger 1988, Muller-Karger et al. 1989). The freshwater input to the study area causes a steady decrease of surface salinity and increased nutrient concentration (Borstad 1982a,b). In addition, the freshwater discharge causes oscillatory variations of phytoplankton biomass, with about a 4 mo periodicity driven by the blooming and waning of *Trichodesmium* sp., a nitrogen-fixing cyanobacterium found at the base of the euphotic zone off Barbados (Steven & Glombitza 1972, Muller-Karger et al. 1989). On a shorter temporal scale, the biomass of heterotrophic bacterioplankton and protists varies several-fold over a diel cycle in the Caribbean Sea, driven by bacterial utilization of organic materials released by phytoplankton (Burney et al. 1982).

Although these earlier studies provide a general picture of phytoplankton and bacterial populations in the Caribbean Sea, quantitative information concerning microbial growth rates, especially of heterotrophic bacteria, and their controlling factors, is scarce. In this study, we expand upon earlier works and focus on a series of stations in the vicinity of Barbados. We present short-term (approximately 1 mo) temporal and spatial variations of chlorophyll *a* (chl *a*), bacterial abundance, and bacterial production, together with concomitant measurements of bacterial growth and bacterivory.

MATERIALS AND METHODS

Study site and water collection. Six stations (Stns A, D, F, S, V, and X) were occupied from April 30 through May 25, 1997, to the west of Barbados in the Caribbean Sea (Fig. 1; for details on Stn Y, refer to 'Bacterial growth and bacterivory from bulk incubation' section). Seawater samples for chl *a*, bacterial biomass, and bacterial production were collected every 3 or 4 d during the study period. Samples were collected using 12 l Go-Flo bottles during CTD casts through the upper 100 to 120 m at Stns A, D, and F or upper 160 m at Stns S, V, and X. Six to 9 water samples were obtained along a depth profile at each station and at each sampling time. Seawater samples were collected from Stns A, D, and F (defined hereafter as nearshore stations) during the day and from Stns S, V, and X (defined as offshore stations) at night. Upon recovery, seawater was transferred to opaque 1 l Nalgene bottles via non-toxic Teflon tubing. All incubation bottles and tubing had been rinsed with 5% HCl, then Milli-Q water, and finally with seawater.

Measurements of plankton biomass and production. To quantify chl *a* concentration, 150 ml of seawater was filtered onto 25 mm GF/F filters, then measured fluorometrically following an acetone extraction method corrected for the presence of pheophytins (Parsons et al. 1992).

For bacterial enumeration, 10 ml seawater samples were fixed with 1% (final concentration) formaldehyde and stored at 4°C. Bacterial counts were made following a standard 4′6′-diamidino-2-phenylindole (DAPI) staining technique (Porter & Feig 1980). The samples were filtered onto 0.2 µm black Poretic filters, stained with 1 µg l^{-1} DAPI (final concentration), and mounted

onto glass slides using Cargille type F immersion oil. Slides were prepared within a few days of sampling and stored at −20°C on board ship and at −85°C in the laboratory until examination. Bacteria were enumerated by examining 20 fields at 1250× magnification using epifluorescence microscopy. An Olympus BX50 microscope was used with a mercury lamp, BP 330–385 excitation filter and BA 420 barrier filter.

Bacterial production was measured by the incorporation of [methyl-^{3}H]thymidine (TdR, specific activity 80.3 Ci mmol^{-1}, Amersham Inc.) into bacterial macromolecules. Seawater samples of 20 to 40 ml were transferred to glass vials or 50 ml plastic tubes and amended with 10 nM (final concentration) of ^{3}H-thymidine. Samples were incubated in containers filled with seawater collected from the corresponding depths, in reduced light for water samples from depths <60 m, and in the dark for water samples collected below 60 m. Formaldehyde-killed control samples were used to determine abiotic and other effects. Incubation of samples was terminated by adding formaldehyde (final concentration, 1%). Samples were kept at 4°C until they were filtered onto 0.2 µm cellulose-nitrate membrane filters. The filters were washed 3 times with 5% ice-cold trichloroacetic acid (TCA), and 3 times with 80% ice-cold ethanol. The filters were dissolved in 1 ml of ethyl acetate, scintillation cocktail (Fisher Scientific Inc.) was added, and radioactivity was counted with a LS 5000 TD scintillation counter (Beckman Inc.).

Bacterial growth and bacterivory from bulk incubation. For bacterial growth experiments, seawater samples were collected using 12 l Go-Flo bottles at various times from several depths at Stns A, S, and Y (Table 1, Fig. 1). Freshly collected seawater was transferred to a 20 l carboy or 2 l polycarbonate bottles via Teflon tubing. All incubation bottles and tubing were previously rinsed with HCl (5%), copious Milli-Q water, and finally seawater. Particle-free seawater (0.2 µm filtrate) was obtained using sequential filtering through 3 and 0.2 µm Gelman Versapor filters and the first 2 l of filtrate was discarded. One part of whole water (undiluted) was diluted with 4 parts of particle-free seawater to make 2 l water samples. Diluted and whole water samples collected from 40 m depth were incubated in reduced light in a deck incubator overflowing with ambient surface seawater (ca 30°C). The water samples collected from 100 and 160 m were incubated in the dark at 2 to 3°C elevated temperatures relative to *in situ* temperatures (ca 27°C for 100 m samples and ca 22°C for the samples from 160 m). Subsamples were withdrawn over a period of up to 56 h to determine bacterial counts.

On one occasion, bacterial cell volumes were measured using samples taken for bacterial counts in a growth-rate experiment. These samples were collected on May 12 at Stn Y from depths of 40, 100, and 160 m.

Table 1. Summary of water sampling and treatments for bacterial growth experiments

Date	Stn	Depth (m)	% inoculum diluted with particle-free water	Incubation temp. (°C)	Incubation duration (h)
May 4	Y	40	0	29.5	48
May 4	Y	40	80	29.5	48
May 12	A	40	0	29.8	49
May 12	A	40	80	29.8	49
May 12	Y	40	0	30.0	56
May 12	Y	40	80	30.0	56
		100	0	26.5	56
		100	80	26.5	56
		160	0	22.0	56
		160	80	22.0	56
May 13	S	40	0	29.3	56
May 13	S	40	80	29.3	56
May 19	Y	40	0	30.5	56
May 19	Y	40	80	30.5	56

Cell volumes were determined at the beginning (0 h) and at the end (56 h) of the incubation. Bacteria were stained with acridine orange (AO), and photographed at 1000× magnification using print film (Kodak 400 ASA). The prints were examined under a stereo microscope and approximately 150 bacterial cells were sized; only the bright inner edge was measured. The final magnification was about 10000×. Bacterial size was calibrated using various sizes of fluorescently labeled beads (Molecular Probes, Inc.).

Bacterial growth rates and removal rates by grazing were calculated based on the equations of Landry & Hassett (1982), as modified by Ducklow & Hill (1985a):

$$R_n = \mu - g$$
$$R_d = \mu - Xg$$

where R_n and R_d represent net bacterial growth rate within whole and diluted water, respectively, μ is gross growth rate, g is grazing rate, and X is the dilution factor, 0.2 here, since the whole water was diluted 5-fold with particle-free water. R_n and R_d were obtained from the slopes of time versus natural-log-transformed bacterial abundance (Ducklow & Hill 1985a). Since R_n, R_d, and X were known, the values of μ and g could be calculated. Bacterial growth rates and removal rates were also calculated using biovolume (abundance × mean cell volume) data (Ducklow et al. 1992).

RESULTS

Hydrographic conditions

Mean water temperature at the surface was about 28°C, changed little (generally <2°C) down to 80 m

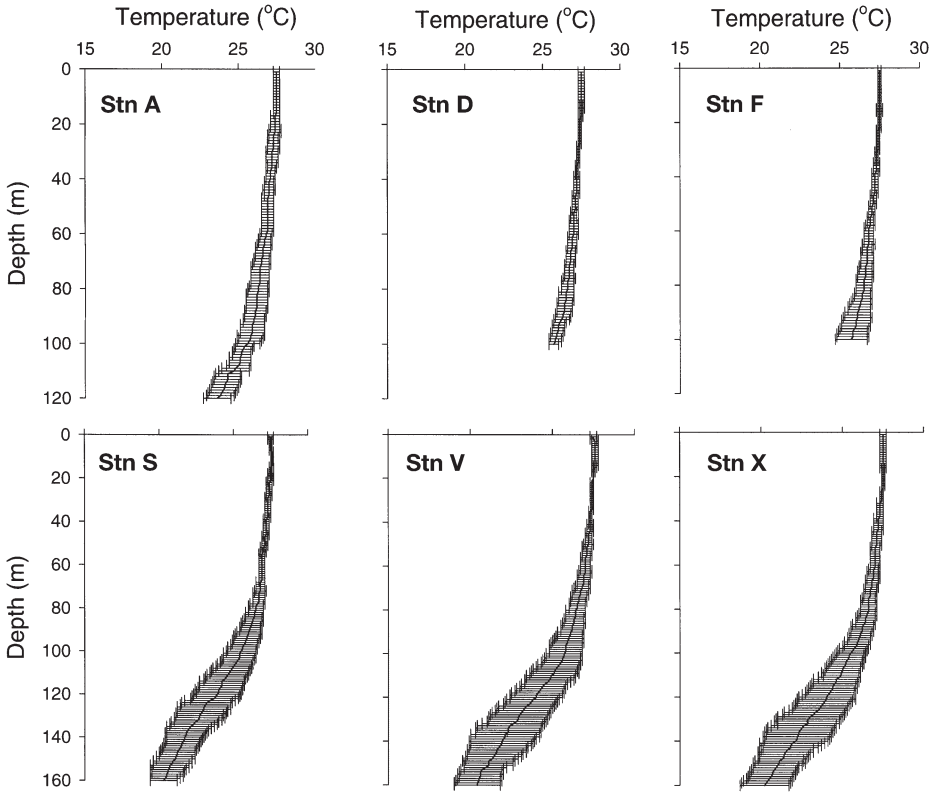

Fig. 2. Vertical profile of temperature at each station. A total of 8 casts for temperature were made at each station during the study period. Horizontal bars represent 1 standard deviation (courtesy of Peter Kelly, MSRC SUNY Stony Brook, New York, USA)

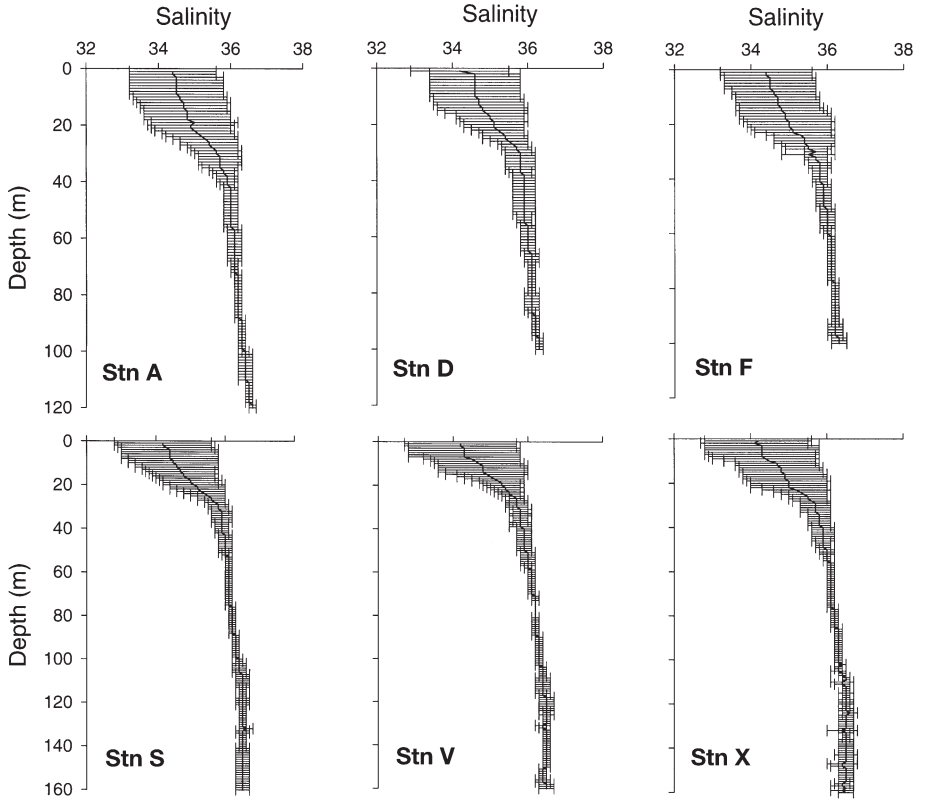

Fig. 3. Vertical profile of salinity at each station. A total of 8 casts for salinity were made at each station during the study period. Horizontal bars represent 1 standard deviation (courtesy of Peter Kelly, MSRC SUNY Stony Brook, New York, USA)

depth, and then rapidly decreased to 20°C at 160 m depth (Fig. 2). Inter-station variation of water temperature was minimal (Fig. 2). Water temperature exhibited little temporal variation in the upper 80 m depth, whereas temporal variation below 80 m ranged nearly 5°C during the study period (Fig. 2).

Salinities were typical of the open ocean (ca 35) and increased slightly with depth down to 40 m, then were almost constant with depth (Fig. 3). Almost no inter-station variation in salinity was detected. Salinity displayed substantial temporal variation (~3) in the upper 40 m of the water column. This variation was caused by the introduction to the area, beginning around May 15, of relatively low salinity water from the Amazon River, indicated by a $^{228}Ra/^{226}Ra$ ratio of approximately 1, characteristic of the Amazon River mixing zone (Kelly et al. 2000).

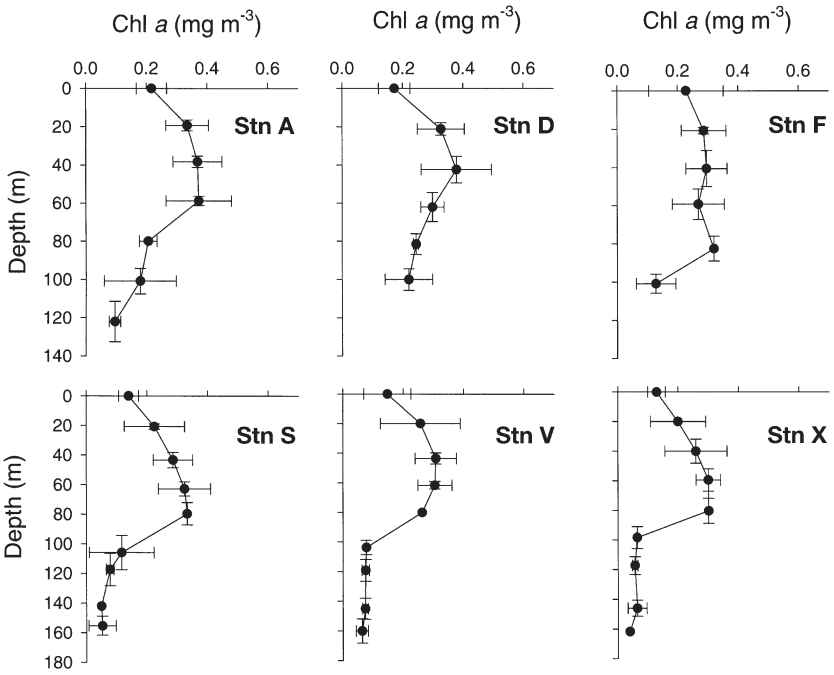

Fig. 4. Vertical profile of chlorophyll *a* concentration at each station. A total of 5 casts for chlorophyll were made at each station during the study period. Vertical and horizontal bars represent 1 standard deviation

Spatial variation of biomass, production, and growth

Average chl *a* concentrations were <0.4 mg m^{-3} at all stations during the period of the study. Chl *a* concentrations showed subsurface maxima and those maxima were relatively shallower, between 40 and 60 m, at 2 nearshore stations (Stns A and D) than at offshore stations (Fig. 4).

Mean bacterial abundance was greatest at the surface (0.7×10^9 cells l^{-1}) and decreased to minimum values (0.2×10^9 cells l^{-1}) at 160 m depth (Fig. 5). Depth-integrated bacterial C biomass was equivalent to about 73 to 111% of phytoplankton POC (Table 2). Neither depth-integrated phytoplankton biomass nor bacterioplankton biomass exhibited significant inter-station differences (Table 2). The ratio of bacterioplankton to phytoplankton biomass, however, was significantly higher at Stn X than at Stns A and D.

Thymidine incorporation rate either decreased slightly with depth (Stn A) or showed no discernable change with

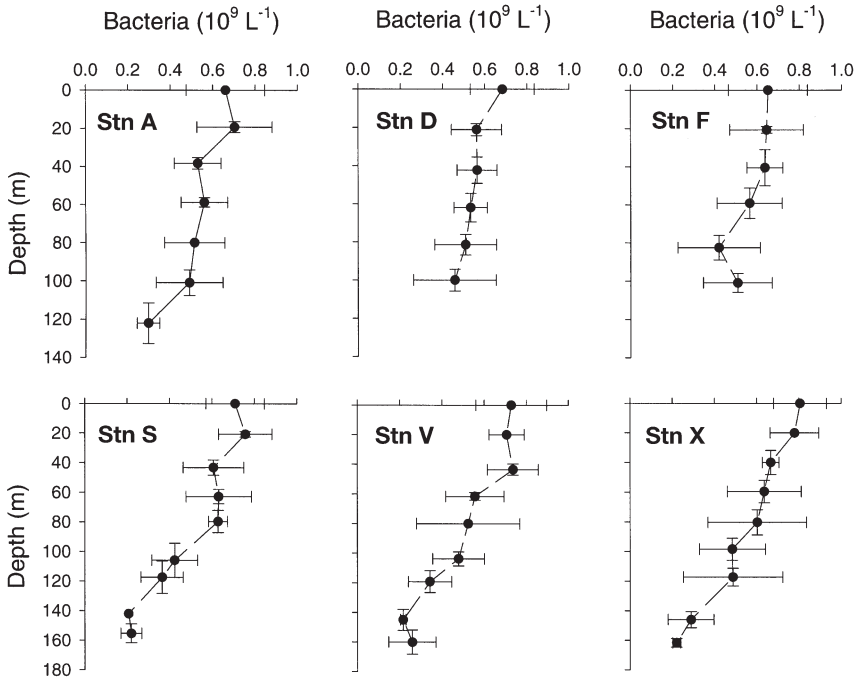

Fig. 5. Vertical profile of bacterial abundance at each station. A total of 8 casts for bacterial abundance were made at each station during the study period. Vertical and horizontal bars represent 1 standard deviation

Table 2. Comparison among stations of vertically integrated, average values (standard deviation) in the euphotic zone. (The actual euphotic depth was between 110 and 120 m. However, no biological measurements were performed below 100 m at nearshore stations. To facilitate comparisons between nearshore and offshore stations, measures shown here represent values integrated over only the upper 100 m). Phytoplankton biomass (calculated assuming 50 µg C µg^{-1} chl *a*, Ducklow 1999) (Phyto C, mg C m^{-2}), bacterioplankton biomass (computed assuming 20 fg C cell^{-1}, Lee & Fuhrman 1987) (Bac C, mg C m^{-2}), ratio of bacterial biomass to phytoplankton biomass (Bac C/Phyto C), bacterial production (calculated from thymidine incorporation rate assuming 1.6 × 10^{18} cells mol^{-1}, Ducklow 1999) (Bac P, mg C m^{-2} d^{-1}), and bacterial growth (Bac G, d^{-1}). Superscripted letters represent results of Tukey's HSD test; values with the same letter are not significantly different at a family error rate of 0.05

Parameter	Stn						Grand mean
	A	D	F	S	V	X	
Phyto C	1523^{a} (191)	1411^{a} (291)	1192^{a} (162)	1250^{a} (209)	1264^{a} (206)	1112^{a} (205)	1291 (238)
Bac C	1138^{a} (211)	1047^{a} (210)	1142^{a} (204)	1270^{a} (217)	1265^{a} (112)	1331^{a} (188)	1199 (208)
Bac C/Phyto C	0.73^{a} (0.15)	0.76^{a} (0.07)	0.92^{ab} (0.06)	1.02^{ab} (0.30)	0.98^{ab} (0.18)	1.11^{b} (0.09)	0.93 (0.21)
Bac P	20^{a} (3)	50^{ab} (59)	67^{bc} (21)	139^{c} (68)	148^{c} (67)	147^{c} (52)	101 (67)
Bac G	0.02^{a} (0.00)	0.06^{ab} (0.08)	0.07^{bc} (0.03)	0.11^{c} (0.06)	0.12^{c} (0.05)	0.11^{c} (0.04)	0.08 (0.05)

depth (Fig. 6). Average thymidine incorporation rates were 0.1 to 1.5 pmol l^{-1} h^{-1} at nearshore stations and 1.2 to 2.4 pmol l^{-1} h^{-1} at offshore stations. Both bacterial production (estimated from thymidine incorporation rate) and growth rates (computed from bacterial production divided by bacterial biomass) were significantly greater at offshore stations than at nearshore stations A and D (Table 2).

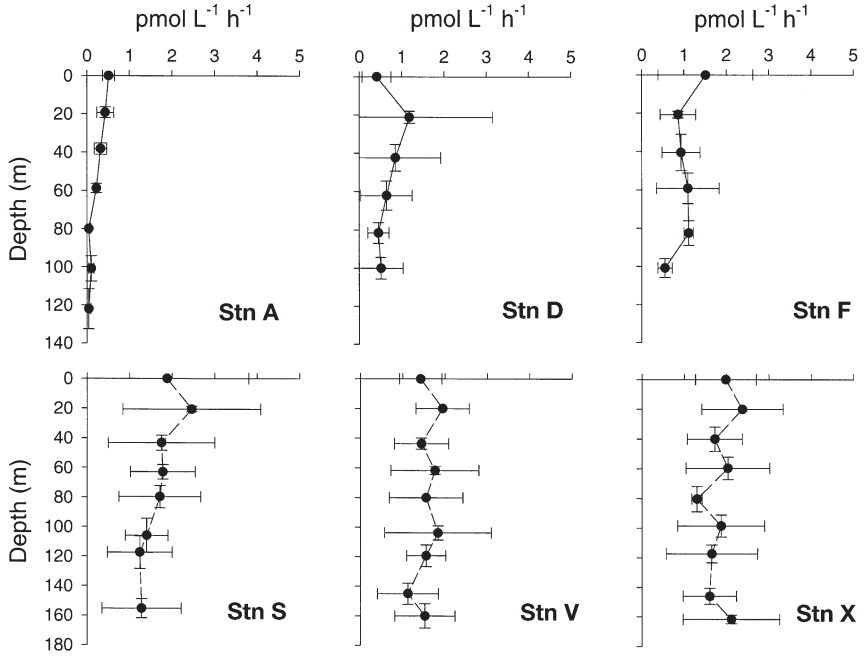

Fig. 6. Vertical profile of [methyl-^{3}H]thymidine incorporation rate at each station. A total of 5 casts at nearshore stations and 8 casts at offshore stations were made during the study period. Vertical and horizontal bars represent 1 standard deviation

Temporal variation of biomass, production, and growth

There were temporal variations in plankton biomass, production, and growth rates at all stations (Fig. 7). Phytoplankton biomass and bacterioplankton biomass varied as much as 2-fold, exhibited tight or slightly delayed couplings (Fig. 7), and yielded a positive linear regression when the latter was regressed on the former (r^2 = 0.13, regression slope = 0.41, $p < 0.05$, n = 26). Bacterial production was coupled to phytoplankton biomass with a greater time lag, yielding a negative regression of production on biomass (r^2 = 0.31, regression slope = –0.56, $p < 0.01$, n = 28). Bacterial growth tracked the pattern of bacterial production more so than that of bacterial biomass.

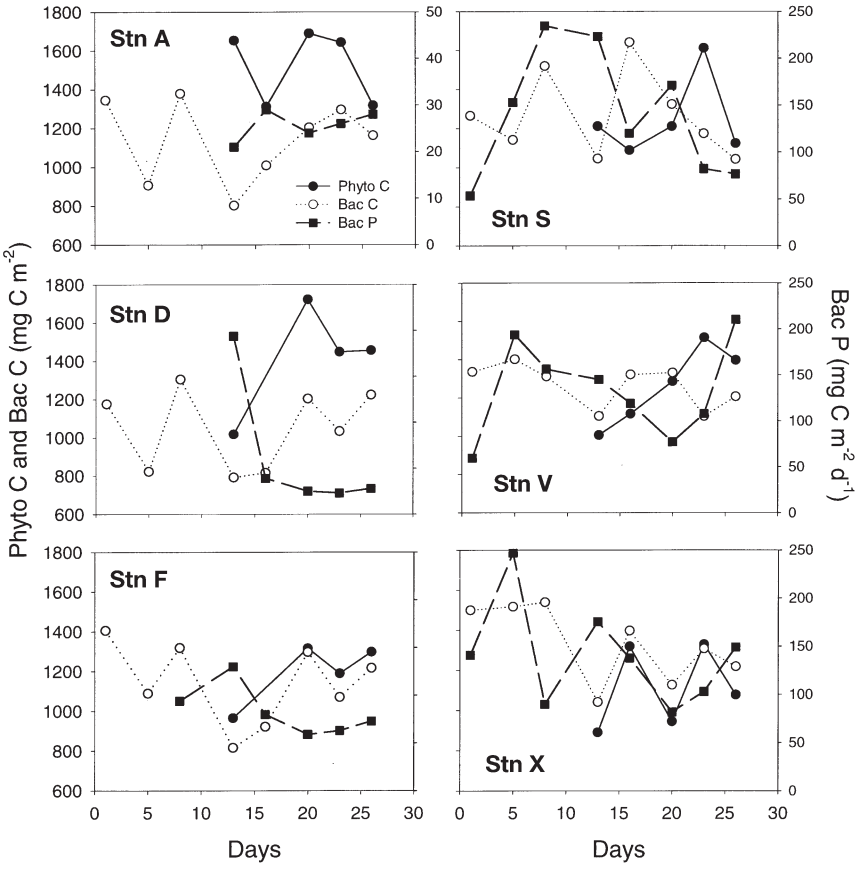

Fig. 7. Temporal variation of phytoplankton biomass (Phyto C), bacterioplankton biomass (Bac C), and bacterioplankton production (Bac P), expressed as values integrated through the euphotic zone. Note that the scale of bacterial production at Stn A has a lesser range than at other stations

The effect of the Amazon River plume on planktonic biomass and production

To assess the effect of the Amazon River plume on the biomass of phyto- and bacterioplankton as well as on bacterial production, the relationship of chl *a*, bacterial abundance, and bacterial production to salinity was examined. Surface salinity dropped from 36 to 32 after the lower salinity water arrived. However, there was no subsequent increase or decrease in chl *a* concentration, bacterial abundance, or bacterial production following the introduction of low salinity water through the upper 40 m surface layer (Fig. 8).

Bacterial growth and bacterivory in incubation experiments

Based on cell abundance, bacteria grew at rates of 0.38 to 0.85 d^{-1} with generation times of 28 to 63 h. Bac-

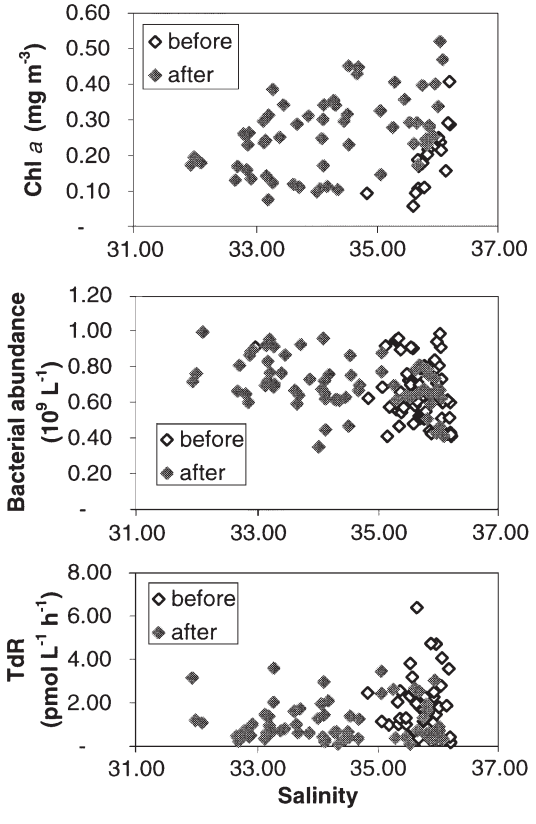

Fig. 8. Effect of the Amazon River plume on chl *a* concentration, bacterial abundance, and bacterial production (TdR) in the upper 40 m of the study area. Before: before arrival of the saline water, After: after arrival of less saline water

Table 3. Bacterial growth (μ) and removal rates (g) estimated by the dilution approach. Cell: rates based on bacterial abundance; Biovolume: based on bacterial biovolume

Date	Stn	Depth (m)		μ (h^{-1})	μ (d^{-1})	g (h^{-1})	g (d^{-1})
May 4	Y	40	Cell	0.016	0.38	0.010	0.23
May 12	A	40	Cell	0.028	0.66	0.025	0.61
	Y	40	Cell	0.020	0.47	0.038	0.92[b]
			Biovolume	0.013	0.32	0.013	0.27
	Y	100	Cell	0.035	0.85	0.032	0.77
			Biovolume	0.051	1.21	0.052	1.26
	Y	160	Cell	0.022	0.52	0.013	0.31
			Biovolume	0.061	1.46	0.029	0.69
May 13	S	40	Cell	0.026	0.63	0.021	0.49
May 19[a]	Y	40	Cell	0.007	0.16	−0.001	−0.02
			Mean[b]		0.61		0.48

[a]Estimates of growth and grazing rates for this experiment are not valid because the net growth rate of the whole sample was greater than that of the diluted sample

[b]Mean values shown here are based solely on bacterial abundance. Furthermore, they exclude data from Stn Y 40 m on May 12, because in that sample the ratio of grazing rate to bacterial growth rate was exceptionally high

terial growth rates calculated from biovolume data were 0.32 to 1.46 d^{-1}, with corresponding generation times of 16 to 77 h (Table 3). In 8 out of 9 incubations, bacteria increased in abundance at a rate greater in diluted samples than in whole water samples (Fig. 9). In the incubation incorporating measurements of bac-

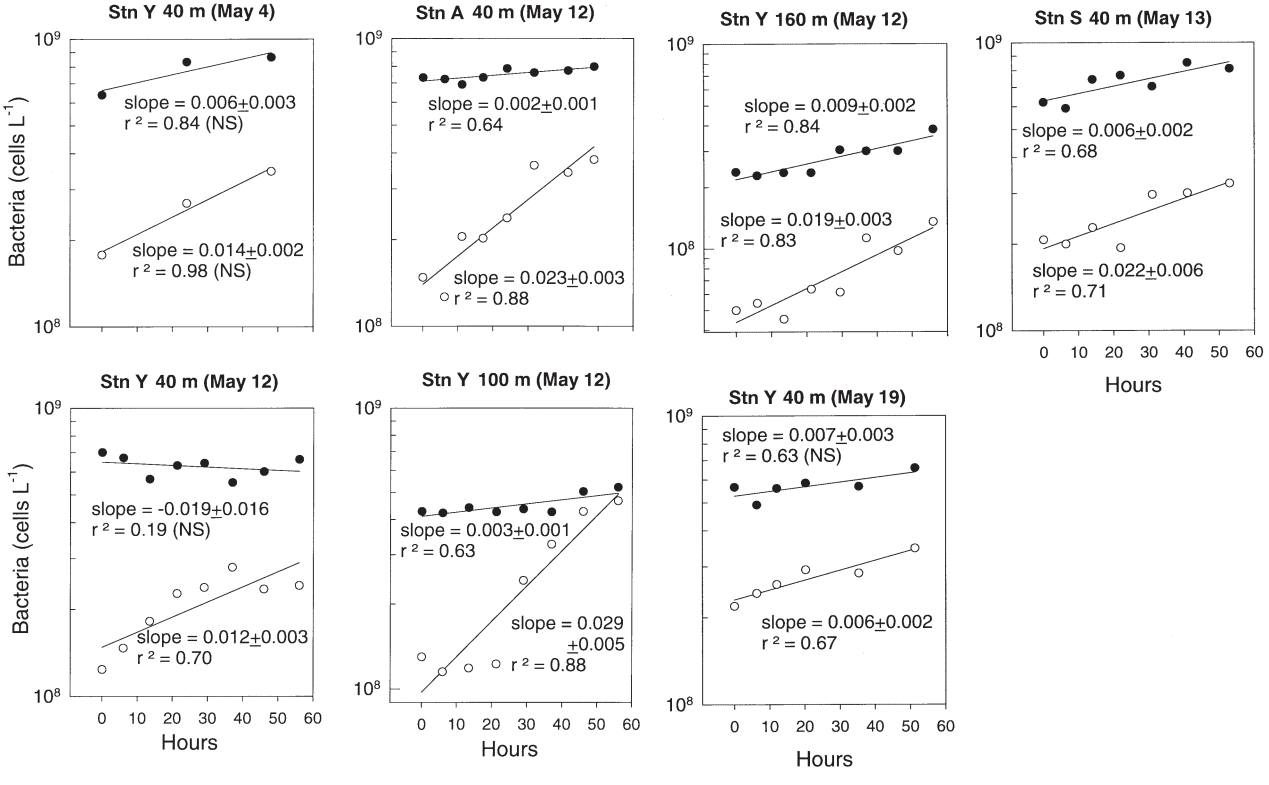

Fig. 9. Changes in bacterial abundance during incubation of seawater samples from various stations and depths. (●) Whole water samples; (○) diluted water samples. (NS: regression coefficient is not significant [$p > 0.05$]. The small number of subsamples [n = 3] from incubation of diluted water collected at 40 m from Stn Y on May 4 rendered the regression not significant despite the increase in cell abundance)

terial cell volumes, significant biovolume increases occurred over time in both whole and diluted water from 160 m and in diluted water from 100 m (Fig. 10). Taken together, these results suggest that grazing by microzooplankton significantly affected bacterial abundance and, in water 100 m and deeper, bacterial biovolume.

The estimated rates of bacterial removal due to grazing varied across depths and sampling time and ranged from 0.23 to 0.77 d^{-1} (cell abundance data) and 0.27 to 1.26 d^{-1} (biovolume data) (Table 3). Overall, these removal rates indicate that an average of 80% of bacterial biomass produced daily could be removed by bacterivory.

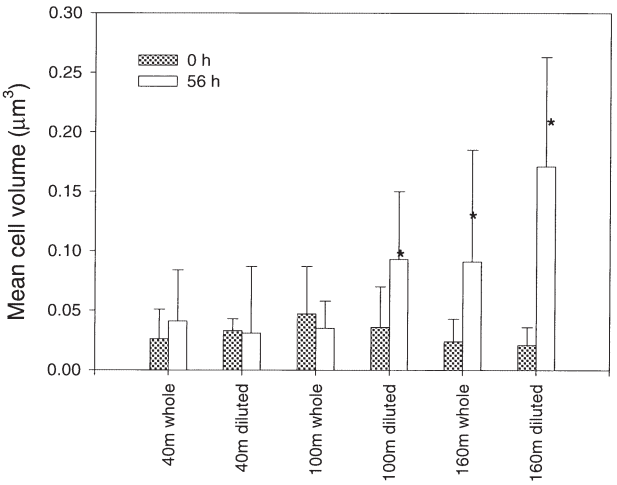

Fig. 10. Changes in mean bacterial cell volumes before and after incubation of seawater samples for 56 h. Vertical lines represent 1 standard deviation. *Significant differences within a pair of samples (ANOVA, $p < 0.05$)

DISCUSSION

Before discussion of the results, it is important first to assess the possibility that the study area's proximity to Barbados substantially affected the observations. In fact, the influence of the island on plankton biomass was indiscernible, as evidenced by similarities in chl *a* concentration and bacterial abundance between nearshore and offshore stations (Table 2). Furthermore, there was no evidence for any anthropogenic effect on plankton biomass, since no increased levels of chl *a* or bacterial abundance were detected at Stn F, near the waste-water outflow from the city of Bridgetown (Figs. 4 & 5). Concentrations of chl *a*, on average less than 0.4 µg m^{-3} in the water column down to 100 m, were quite similar to values obtained 25 yr previously by Steven & Glombitza (1972).

It has been of keen interest for marine microbiologists to ascertain whether bacterioplankton populations in seawater are controlled by bottom-up or top-down processes (Billen et al. 1980, Ducklow 1992, 1999, Shiah & Ducklow 1994). Billen et al. (1980, 1990) suggested a simple approach to address the relative magnitude of bottom-up (resource supply) and top-down (e.g. predation and viral lysis) control on bacterial biomass. If bacterial biomass were limited solely by resource supply, then a strong correlation would be observed between bacterial abundance and bacterial production, assuming bacterial uptake of resource equals the rate of resource input. Following the approach of Billen et al. (1980, 1990), bacterioplankton biomass in this study was significantly related to bacterial production ($r^2 = 0.10$, $p < 0.05$, $n = 40$) and the regression slope was 0.32, indicating moderate control by bottom-up processes. In contrast, bacterivory results indicate that approximately 80% of daily bacterial biomass production was removed by predation (Table 3), suggesting that top-down controls on bacterial dynamics were stronger than bottom-up processes.

It is not simple to compare bacterial growth rates among studies, due not only to temporal and spatial variability in bacterial growth rates, but also to the differences in methods employed, with each approach having advantages and disadvantages (Landry 1994). In the present study, 2 methods were employed to measure bacterial growth rates. In the first, using the P/B ratio based on *in situ* measures (Table 2), depth-integrated mean bacterial growth rate was 0.1 d^{-1}, precisely the value obtained by Rivkin & Anderson (1997) in the Caribbean Sea and well within the range of bacterial growth rates reported for the open ocean (Ducklow 1999).

Meanwhile, mean bacterial growth rates obtained from incubation experiments were 0.58 d^{-1} (range 0.38 to 0.85 d^{-1}) based on cell abundance and 0.75 d^{-1} (range 0.32 to 1.46 d^{-1}) based on cell volume data (Table 3). In both cases, rates were significantly higher than *in situ* growth rates. The dilution technique provides an advantage in that it requires less manipulation of seawater, growth and removal rates are measured concurrently with enumeration of bacteria or incorporation of radioprecursors into bacterial macromolecules, and it has been widely used to estimate bacterial growth and removal rate in oceanic waters (Ducklow & Hill 1985a,b, Ducklow et al. 1992, Landry et al. 1995).

It is not clear why in the present study there was a substantial discrepancy in estimating bacterial growth rates by these 2 approaches. One possible source of the difference is that since only 2 dilutions were used, as opposed to 5 to 10 dilutions as originally proposed by Landry & Hassett (1982), computation of growth and bacterivory rates might have been affected. Another

potential complication is that DOM might have been introduced into the diluted water during filtration, either by cell breakage or from contamination in the filtering system. We took care to minimize the introduction of DOM by adopting a standard protocol of cleaning and using gravity filtration to minimize cell breakage. It is not possible, however, to evaluate the possibility of any contamination or release of DOM because DOM measurements were not made before and after filtration. Using an approach similar to ours, however, Carlson & Ducklow (1996) observed no significant 'before-after' difference in DOM concentrations.

The relatively low salinity water introduced during the sampling period was from the Amazon River, translated into the study area in rings spawned from the North Brazil Current (Kelly et al. 2000), a phenomenon recognized for decades (Steven & Brooks 1972, Borstad 1982a,b). Recent studies, including remote sensing (Muller-Karger 1988), numerical models (Fratantoni et al. 1995), and tracking of the water's $^{228}Ra/^{226}Ra$ ratio (Moore et al. 1986, Moore & Todd 1993), suggest that the low salinity pools introduced to Barbados are mostly from the Amazon River mixing zone. It takes approximately 100 d or even more for the Amazon water to travel in residuals of North Brazil Currents to Barbados (Kelly et al. 2000). Elevated concentrations of nutrients and pigments in the Amazon River discharge (i.e. >1 order of magnitude greater than the ambient concentration) occur close to the plume or to the northwest part of the Caribbean Sea far from Barbados (Muller-Karger 1988, Muller-Karger et al. 1989). The long transitional time, in concert with stripping of labile nutrients during transport, may account for there being no apparent change in planktonic biomass and bacterial production in the study area when the low salinity water arrived.

In summary, there existed spatial and temporal variation of phytoplankton biomass and bacterioplankton biomass, production, and growth in the euphotic layer during a month-long period of study near Barbados. Temporal variation of these measures, however, was not associated with an input of low-salinity discharge from the Amazon River. Bacterial biomass and production were coupled tightly or with slight time lags to phytoplankton biomass. Analysis of bottom-up and top-down process studies suggested that predation on bacteria exerts more influence on bacterioplankton dynamics than does control by resource supply.

Acknowledgements. We thank David Burdige, Hugh Ducklow, David Karl, Arnoldo Valle-Levinson and 2 anonymous reviewers for their constructive comments on earlier versions of this manuscript. We are grateful to Peter Kelly at MSRC SUNY Stony Brook and Claire Paris at RSMAS/MBF University of Miami for providing hydrographic data. We also thank Curtis Hickman, Stephanie East, Teresa Rotunno, Graham Allen, and the captain and crew of the RV 'Seward Johnson' for their excellent assistance at sea and in the lab.

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Editorial responsibility: David Karl, Honolulu, Hawaii, USA

Submitted: May 11, 2000; Accepted: April 13, 2001
Proofs received from author(s): July 25, 2001