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Abstract

A recently published evaluation of bacterioplankton abundance and productivity in the bathypelagic North Pacific suggests that these properties are generally coupled with particulate organic carbon (POC) fluxes. In that analysis, bacterial biomass and productivity were several-fold greater in subarctic than subtropical waters, consistent with the basin-scale distribution of POC flux and suggestive of a sinking POC $\rightarrow$ DOC $\rightarrow$ bacteria transformation of the carbon. To test this hypothesis, we sought to determine whether the very strong spatial and temporal gradients in POC flux in the Arabian Sea would force similar deep-ocean gradients in bacterial variables. On both a within- and between-cruise basis, there was variability in bacterial abundance and thymidine incorporation in the deep Arabian Sea, but correspondence was equivocal between these variables and several correlates to export: flux of biogenic carbon from the euphotic zone, state of the monsoon, and proximity to productive coastal upwelling zones. However, when annual mean bacterial abundance at 2,000 m was compared with annual POC flux at that depth, a strong correspondence emerged: high annual flux supported high bacterial abundance (such a correspondence was not found for bacterial productivity). This finding suggests that bathypelagic bacterial abundance responds to the long-term mean input of organic matter and less to episodic inputs. A comparative evaluation of the North Pacific revealed that although the bathypelagic bacteria there showed correspondence to deep POC flux, that variable alone would not account for the wide meridional variations in bacterial abundance that have been reported.

The nutrition and sustenance of organisms in the deep sea has been a classic problem in oceanography since the discovery of life on the sea floor by the Challenger Expedition in 1872–1876 (Mills 1983). With the advent of deep-ocean sediment traps, sedimentation of particulate organic matter became recognized as the principal agent of deep-sea food supply (Moseley 1880; Tyler 1988). Subsidy with dissolved organic matter has long been invoked as a potential nutritional and energy source (Jørgensen 1976). Bacteria dominate the metabolism of deep waters below the euphotic zone (Pomeroy and Johannes 1968), but the mechanism of their nutrition is not clear. The proximal sources of organic matter for bacteria are dissolved, low-molecular-weight substances because bacterial uptake systems are restricted to transporting molecules $<$500 Da across cell membranes (Williams 2000). However, the ultimate sources of the substances actually transported into bacterial cells are not well characterized, even at a crude operational level.

Karl et al. (1988) showed that sediment trap contents collected from 30–600 m depths did not support bacterial growth, concluding that the organic matter lost from particles by dissolution or fragmentation was oxidized by free-living cells. Cho and Azam (1988) observed that particle-associated bacteria were rare in the 0–1,000 m water column ($<$5% of total) but also found a general correspondence of vertical profiles of total bacterial biomass, bacterial production, and estimated sediment trap fluxes. These authors simultaneously advanced the hypothesis that free-living bacteria are the agents of mineralization of the organic matter transported into the deep sea in (or on) sinking particles, leading to the concept that sinking particles are the principal source of bacterial nutrition in the oceanic mesopelagic zone.

These studies led to the prediction that bacterial rates and stocks might covary with particle fluxes measured by sediment traps. Ducklow (1993) compared vertical profiles of bacterial production (100–1,000 m) with the supply of sinking particulate organic carbon (POC) in the Arabian Sea and concluded that the POC flux was insufficient to meet the bacterial carbon demand. Simon et al. (1992) made the same comparison for the subarctic Pacific, estimating that bacterial metabolism accounted for 41–172% of the sinking POC flux over 80–600 m. Similarly, H.-G. Hoppe (pers. comm.) estimated from later studies in the Arabian Sea that sinking POC could support only a minor part of the bacterial carbon demand. The results of these studies implicate the large reservoir of suspended organic particles as a potential additional source of bacterial nutrition and demonstrate intense exoenzymatic hydrolysis rates by carbon-limited bacteria in the mesopelagic and deep zones. Of these studies only the last

Acknowledgments

This analysis included data collected as part of the U.S. JGOFS Arabian Sea Expedition, archived at the Data Management Office (http://usjgofs.whoi.edu/research/arabian.html). H.W.D. in collaboration with F. Azam generated the bacterial data as part of that program with support from OCE 9600601. POC flux data collected in the US JGOFS Arabian Sea program and used in this analysis were generated by S. Honjo and J. Dymond. Analysis of these data for this manuscript was supported by NSF OCE 0097237 (to H.W.D.) and OCE 9726091 (to D.A.H.) as part of the US JGOFS Synthesis and Modeling Program.

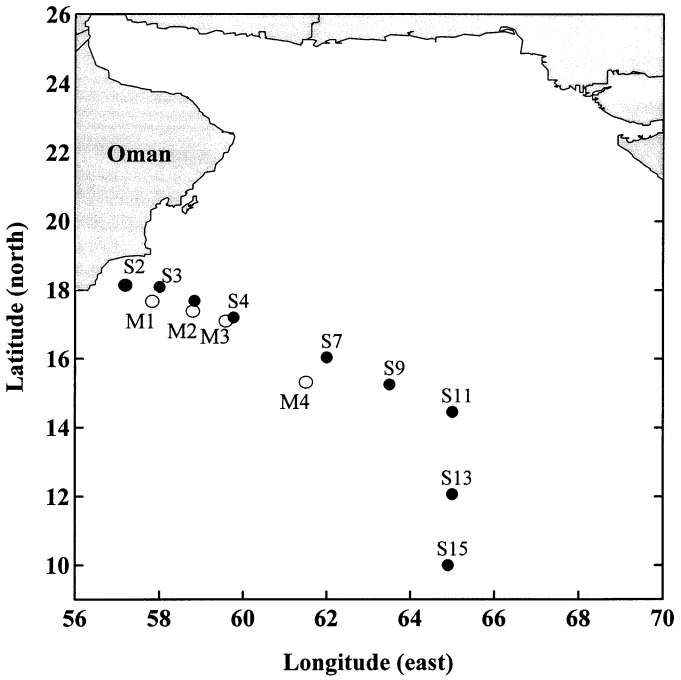

Fig. 1. Map of the Arabian Sea depicting the nominal locations of hydrographic stations (S series; solid symbols) and moored sediment traps (M series; open symbols).

focused on depths below 1,000 m. Thus, the balance of evidence to date is inconclusive on the importance of sinking POC as a carbon source for bacterial production in bathypelagic waters.

Recent work has been focused on the question of bottom-up (substrate limitation) versus top-down (limitation by removal of bacterioplankton by processes such as grazing) controls on deep-ocean bacteria. Dufour and Torréton (1996) evaluated this question with bacterial biomass and production data taken at sites described as eutrophic (>2,000 m depth), mesotrophic (>3,000 m), and oligotrophic (>4,000 m) on a zonal section off northwestern Africa. Bacterial abundance varied by an order of magnitude at depths >1,000 m, with highest values under the eutrophic waters. Their findings suggested a moderate but increasing bottom-up control from eutrophic to oligotrophic conditions and from the surface to the deep ocean. Supporting the concept of bottom-up control are the results of Patching and Eardly (1997), who evaluated bacterial abundance at oligotrophic (28°N) and eutrophic (50°N) sites in the northeastern Atlantic. Bacterial abundance at >1,000 m was several-fold greater at the eutrophic than at the oligotrophic site.

Nagata et al. (2000), presenting data on bacterial biomass and production rates in the deep North Pacific, suggested that bacterial production and carbon consumption in the bathypelagic zone (water depths >1,000 m) are largely coupled with sinking fluxes of POC. They reported 2–4-fold greater bacterial biomass and 3–7-fold greater bacterial production in the subarctic than in the subtropical North Pacific. The authors indicated that the meridional gradients are consistent with the basin scale distribution of export production: low export flux in the subtropics (F_{100} = 5–10 gC m^{-2} yr^{-1}) and high flux in the subarctic gyre (F_{100} = 10–50 gC m^{-2} yr^{-1}), where F_{100} is the export flux at 100 m. Their findings suggest that a substantial transformation of organic carbon occurs via a sinking POC → DOC → bacteria route.

Table 1. Details about cruises aboard the RV *T.G. Thompson* during the U.S. JGOFS Arabian Sea Expedition in 1995.

Cruise designation	Dates	Monsoon status
TTN 043	08 Jan–05 Feb 1995	Late NE monsoon
TTN 045	14 Mar–10 Apr 1995	Spring intermonsoon
TTN 049	17 Jul–15 Aug 1995	Middle SW monsoon
TTN 050	18 Aug–15 Sep 1995	Late SW monsoon
TTN 053	29 Oct–26 Nov 1995	Fall intermonsoon
TTN 054	30 Nov–29 Dec 1995	Early NE monsoon

We assessed the generality of these findings by evaluating data collected in the Arabian Sea, where a strong gradient in the annual export flux exists from onshore to offshore (Buesseler et al. 1998; Lee et al. 1998; Honjo et al. 1999). In 1995, at stations adjacent to the Oman coast (Stations S2, S3, and S4; Fig. 1) annual average F_{100} ranged from 6.7 to 9.4 mmoles C m^{-2} d^{-1} (29.5–41.4 gC m^{-2} yr^{-1}), whereas in the central Arabian Sea (Station S15), F_{100} was 2.7 mmoles C m^{-2} d^{-1} (11.9 gC m^{-2} yr^{-1}) (annual average F_{100} reported by Lee et al. [1998] as determined by ^{234}Th activity distributions of Buesseler et al. [1998]). This is a 2.5–3.5-fold range in flux, similar to that reported by Nagata et al. (2000) for the subtropical/subarctic gradient in the North Pacific. If the rationale for the gradients of bacterial variables provided by Nagata et al. (2000) is correct for the North Pacific, then similar gradients should be found in the Arabian Sea. We posed two specific questions. Are there gradients in deep bacterioplankton abundance and production corresponding to the gradient and temporal variability in export production in the Arabian Sea? What is the relationship between deep bacterioplankton abundance in the Arabian Sea and deep POC flux? We also investigated how relationships in the Arabian Sea compared with such a relationship in the North Pacific, the region of the Nagata et al. (2000) study.

Methods

With the vast data available through U.S. JGOFS, the Arabian Sea can be evaluated for spatial and temporal trends in bacterial variables and vertical fluxes. Stations at fixed locations were occupied several times in 1995 (Table 1), and the section on which the stations were located was approximately normal to the coast (Fig. 1). As a result, gradients in biological and biogeochemical variables can be assessed both by distance from shore and over time. If POC flux controls bathypelagic bacterial abundance and productivity via DOC as suggested for the North Pacific, then spatial gradients in the deep Arabian Sea from the Oman coast to the central basin should be present. Temporal gradients may also be present from times of high flux to times of low flux in specific regions.

Spatial gradients can be assessed using data from each cruise, whereas temporal variability can be assessed across

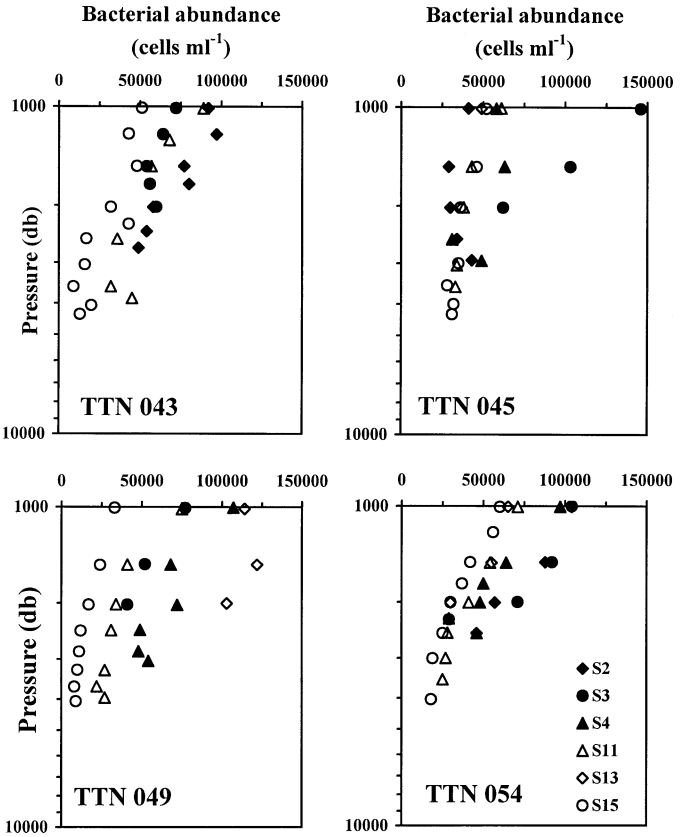

Fig. 2. Plot of BA (cells ml^{-1}) versus log depth (>1,000 m) during four cruises in the Arabian Sea. Coastal upwelling influenced (inshore) station symbols are solid; offshore station symbols are open.

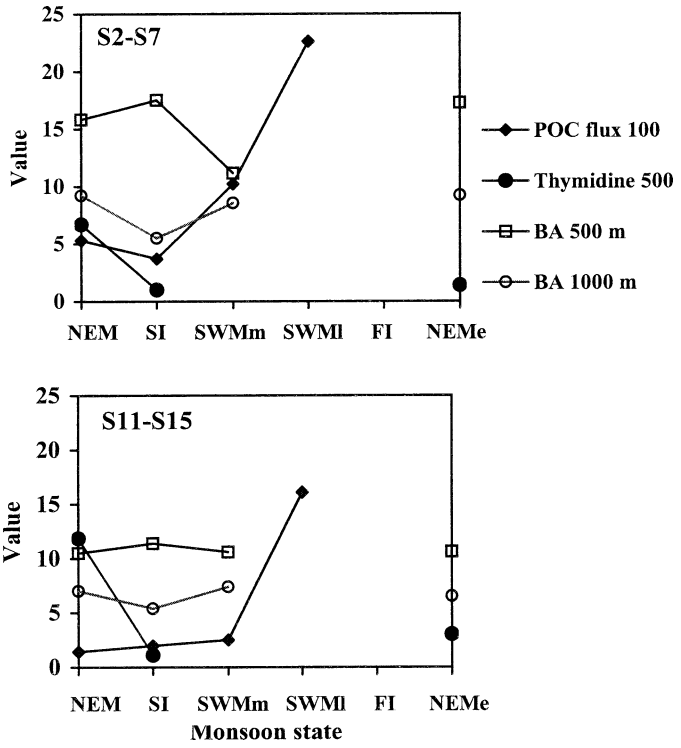

Fig. 3. Values of relevant variables in waters highly impacted by coastal upwelling (means of stations S2–S7) and in waters that are characterized as being more oligotrophic and weakly influenced by coastal upwelling (means of stations S11–S15). The values are plotted against time, delineated as the state of the monsoon (northeast monsoon, NEM; spring intermonsoon, SI; middle southwest monsoon, SWMm; late southwest monsoon, SWMl; fall intermonsoon, FI; early northeast monsoon, NEMe). Variables shown are sinking POC flux (mmol C m^{-2} d^{-1}) at 100 m, thymidine incorporation (pmol L^{-1} h^{-1}) at 500 m (shown as true value × 10), and BA (cells ml^{-1}) at 500 and 1,000 m (shown as true value × 10^{-5}). Not all variables were sampled during all cruises, hence the gaps in coverage.

the cruises with data from specific (groups of) stations. Station S15 (and those near it, such as stations S11 and S13) represents the most oligotrophic water occupied during the Arabian Sea project. This location was the most remote from the influence of coastal upwelling during the southwest (SW) monsoon (>1,200 km from the Oman shore). Surface concentrations of nitrate were <0.2 μmol L^{-1} throughout the year (Morrison et al. 1998). In this analysis, S15 is the oligotrophic end member (analogous to the subtropical end member in the Nagata et al. (2000) analysis of the North Pacific and the southern station of Patching and Eardly [1997]). Stations near the coast of Oman (S2–S4), where export production is high because of strong nutrient inputs during the SW monsoon (>10 μmol L^{-1} surface nitrate), are the eutrophic end members in this analysis. To compare directly to the findings of Nagata et al. (2000), we focused this analysis on depths >1,000 m.

Results

Bacterial abundance—Within-cruise spatial variability of bacterial abundance (BA) at depths >1,000 m is depicted in Fig. 2. The offshore (S11, S13, S15) and inshore (S2–S4) stations demonstrated overlap in BA, although throughout most of the year (cruises TTN 043, TTN 049, and TTN 054) BA at S15 was consistently lower than that at all other stations. During the spring intermonsoon (TTN 045), BA at S15 was indistinguishable from that at the other stations. This general finding for S15 would support the Nagata et al. (2000) hypothesis if not for the fact that S11 and S13 had BA values indistinguishable from those at the coastal influenced stations (S2–S4). As with S15, S11, and S13 are located in the central Arabian Sea basin and thus similar to S15 in terms of phytoplankton productivity and export.

If POC flux forces deep bacterial responses, then periods of high export could be anticipated to correspond with increased BA. Temporal variability of BA, however, was inconclusive relative to the Nagata hypothesis (Fig. 2). BA was lowest at S15 during TTN 049, when export associated with the SW monsoon was near its annual maximum. BA at 1,000 m, taken as a point of reference, in the central basin stations (S11, S13, S15) during all cruises was generally in the range of 50 × 10^3 to 100 × 10^3 cells ml^{-1}. Variability in BA at 1,000 m did not track the variability in export flux at 100 m in the coastal group of stations (S2–S4 and S7) or in the offshore stations (S11, S13, S15) (Fig. 3), although variability decreased with increasing depth (Fig. 2). A BA

response to the high export may have been missed (in Fig. 3, data for BA were not available during the period of highest flux). Patching and Eardly (1997), however, reported the absence of variability in deep BA at their eutrophic site through the period of expected maximum export in the North Atlantic. Nagata et al. (2000), in contrast, reported a 2.3-fold increase in bacterial biomass (1,000–4,000 m) at a subarctic site visited 2 yr apart, even though both occupations were in the same month (October). The Nagata et al. (2000) observations of meridional gradients in bacterial properties were made without consideration of the timing of export. Thus, the gradients may reflect the long-term inputs of sinking material rather than short-term responses to the seasonality of inputs.

Thymidine incorporation—BA response to episodic flux events might not be detected if predation removes the bacteria as fast as they grow, i.e., strong top-down control. However, the removal processes would not mask the growth response itself. As with BA in the Arabian Sea, spatial trends in thymidine incorporation rates (an index of bacterial cell division) are not obvious (Fig. 4), although fewer data exist as compared with BA. For the two cruises on which coverage was greatest (TTN 043 and TTN 054), the eutrophic inshore (S2–S4) and oligotrophic offshore (S11, S13, S15) station groups are indistinguishable from one another. As for temporal variability, uptake rates during TTN 043 were consistently higher than those during TTN 054. These two cruises took place in January 1995 and December 1995, respectively, both during the northeast (NE) monsoon period. The reason for the variability in samples that were collected so near to each other in a seasonal time frame is unknown. The fact that the temporal variability occurred uniformly for both the in- and offshore station groups suggests a systematic offset in the rate determinations. Thymidine incorporation rates at 500 m (a depth selected because of its higher data coverage than that for greater depths) did not covary with F_{100} (Fig. 3). The rates remained rather uniform at 500 m throughout the year, apparently independent of export flux. Bacterial production may be underestimated by half in decompressed samples collected from depths >1,000 m (Bianchi et al. 1999), so the rates shown in Fig. 4 may underestimate true values and may not show actual variability.

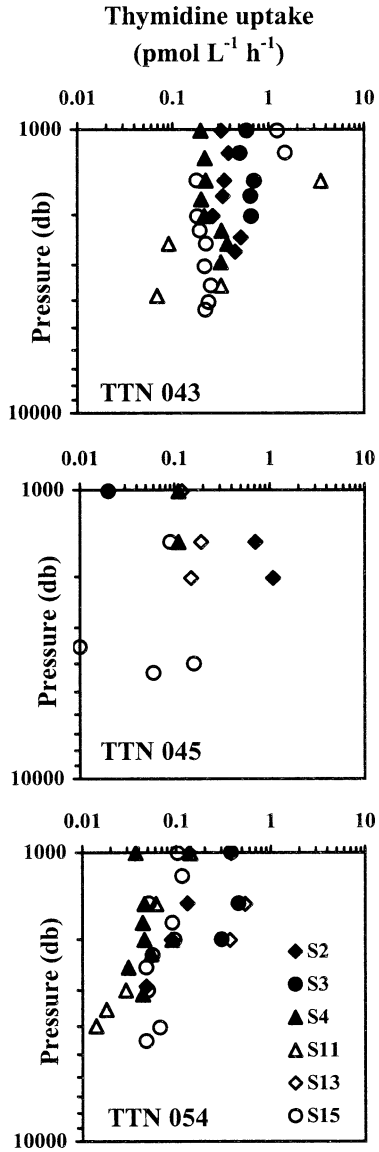

Fig. 4. Plot of thymidine incorporation rates (pmol L^{-1} h^{-1}) versus log depth (>1,000 m) during three cruises in the Arabian Sea. Coastal upwelling influenced station symbols are solid; offshore station symbols are open.

Integrated bacterial biomass and production—Total bacterial biomass and production (the latter from leucine incorporation rates), integrated between 1,000 m and the bottom at each station, were estimated using the same conversion factors as used by Nagata et al. (2000). Bottom depths varied from 2,415 m at S2 to 4,418 m at S15. We used integrals over 1,000–2,000 m and 1,000–4,000 m as a uniform basis for comparison among stations. The vertical fluxes delivering sinking POC to the bathypelagic zone varied consistently along the on- to offshore gradient (Fig. 5a). Neither bacterial production (Fig. 5b) nor biomass (Fig. 5c) showed correspondence to the sinking fluxes at 2,000 or 4,000 m. Between-cruise (seasonal) variability may have obscured trends, but production integrated through the year to yield annual rates also showed no trend consistent with coupling to the flux pattern.

Relationship between BA and deep POC flux—BA in the bathypelagic zone is perhaps the least ambiguous of the measurements reported here. Most importantly, it is not biased by decompression effects as can occur for bacterial productivity (Bianchi et al. 1999). Evidence for a difference in deep BA between the stations closest to the Oman coast (e.g., S3 and S4) and the most remote station (S15) is clear in Fig. 2.

We compared annual mean BA at 2,000 m (the most commonly sampled bathypelagic depth during the Arabian Sea Expedition) with annual POC flux at depths >2,000 m measured with moored sediment traps (data from Honjo et al. 1999). The sites of analysis were those where the moorings were located (Fig. 1; M series), thus providing a strongly contrasting set of environments (the upwelling influenced hydrographic stations S2, S3, S4, and S7, corresponding to

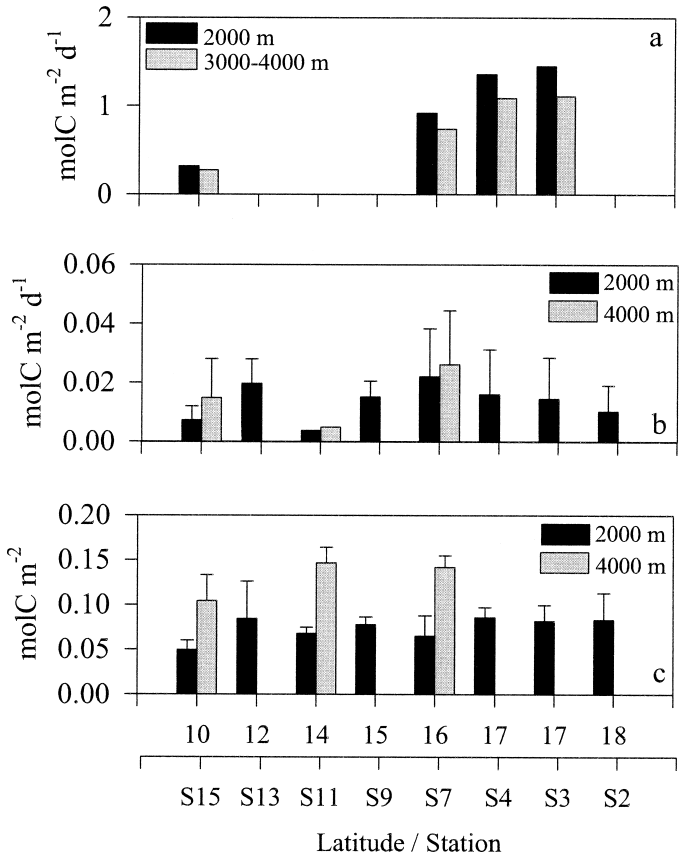

Fig. 5. POC fluxes into sediment traps at 2,000 m and at 3,000–4,000 m (a), integrated bacterial production between 1,000 and 2,000 m and between 1,000 and 4,000 m (b), and bacterial biomass integrated from 1,000 to 2,000 m and from 1,000 to 4,000 m (c). Bars in b and c are averages of two to four seasonal cruises. Not all stations are the full 4,000 m in depth.

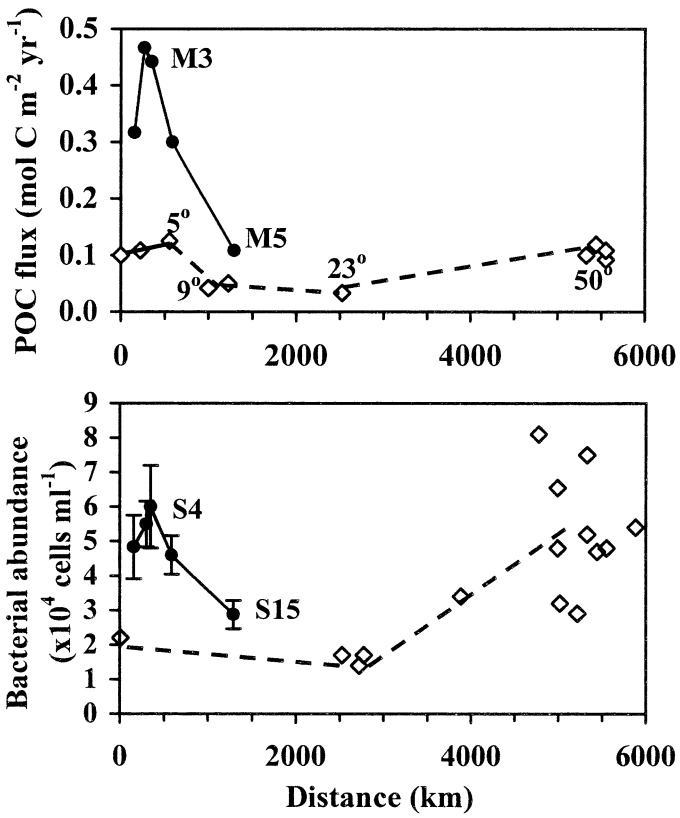

Fig. 6. POC fluxes (mol C m^{-2} yr^{-1}: upper plot) and BA ($\times 10^4$ cells ml^{-1}: lower plot) in the Arabian Sea (solid symbols) and the North Pacific (open symbols). POC fluxes in the Arabian Sea were taken from table 5 of Honjo et al. (1999), with fluxes combined from traps located at nominally 2 km depth and 500 m above the seafloor (the latter depths ranged from 2,871 to 3,915 m). POC fluxes in the North Pacific are largely from a compilation of data from the literature presented by Honjo et al. (1995), with traps ranging in depth from 2,100 to 3,800 m. The POC flux near 23°N (2,800 m trap at Station ALOHA) is from Karl et al. (1996) after estimating the average daily particulate carbon flux from their fig. 8 (0.21 mmol C m^{-2} d^{-1}) and assuming that half of this was organic carbon. Flux at 49°N is from Takahashi et al. (2000) with a trap at 4,800 m, and Wong et al. (1995) provided one of the POC flux values at 50°N with a trap at 3,800 m. Arabian Sea BA values were taken from the U.S. JGOFS Data Management Office. The values are the means of abundance at the hydrographic stations nearest the traps (i.e., S2, S3, S4, S7, and S15 for trap locations M1–M5, respectively) and from the sampling depth of 2,000 ± 30 m. The values are the mean abundance during 1995, with collections made during cruises TTN 043, TTN 045, TTN 049, and TTN 054 (BA data were not collected near 2,000 m at all relevant stations during all relevant cruises). BA at 2,000 m in the North Pacific was estimated using the regression results in table 2 of Nagata et al. (2000). Distance (*x* axes) is from the Oman coast in the Arabian Sea and from the equator in the North Pacific. Latitudes (°N) of a few of the POC flux sites in the North Pacific and station designations of a few flux sites in the Arabian Sea are included in the upper plot. Designations of selected hydrographic stations in the Arabian Sea are included in the lower plot. Trend lines were added to aid visual connection of the data clusters. Error bars in lower plot are ±SE.

mooring stations M1, M2, M3, and M4, vs. the highly oligotrophic hydrographic station S15, or mooring station M5). POC flux at mooring stations M1–M4 ranged from 0.30 to 0.47 mol C m^{-2} yr^{-1}, whereas at M5 POC flux was 2.7–4.3-fold less, at 0.11 mol C m^{-2} yr^{-1} (Fig. 6). Annual mean BA ranged from 4.6 to 6.0 $\times$ 10^4 cells ml^{-1} at S2, S3, S4, and S11, values 1.6–2.1 times greater than the 2.9 $\times$ 10^4 cells ml^{-1} found at S15 (Fig. 6). There is a clear relationship between POC flux at depth and the abundance of bacteria found at that depth (Fig. 7), supporting the Nagata et al. (2000) hypothesis that bacterial standing stocks reflect the levels of organic enrichment provided to the deep ocean by the vertical flux of particulate organic matter. Rates of bacterial production and integrated bacterial biomass did not show a correspondence with the POC flux gradient (Fig. 5).

Discussion

For comparison to the Arabian Sea, BA and POC flux at 2,000 m in the North Pacific are plotted in Fig. 6 (data were not collected concurrently as was done in the Arabian Sea). The relationship between POC flux and BA in the North Pacific was similar to that found in the Arabian Sea (higher

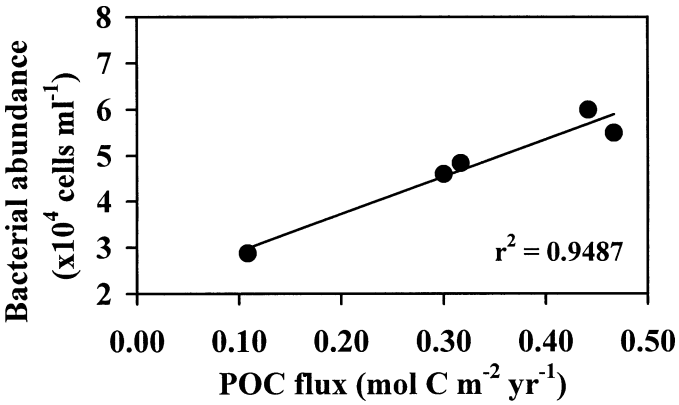

Fig. 7. Relationship between annual POC flux and mean annual BA at 2,000 m in the Arabian Sea during 1995 (*see* Fig. 6 for details on data sources). The highest four values for POC flux and BA are from stations highly impacted by upwelling during the SW monsoon. The lowest value point is from the offshore, oligotrophic station S15.

POC flux tends to correspond to higher BA), but the magnitude of the variability in the North Pacific was inconsistent within the basin and different from that in the Arabian Sea. For example, POC fluxes in the equatorial (0–5°N) and subarctic (near 50°N) regions were approximately equal, yet BA between the regions did not show a similar equality; BA at the equator was considerably lower than that in the subarctic. BA in the subarctic showed much higher variability, whereas POC flux in the region showed great uniformity. Apparently, POC flux is not the sole control on BA in the deep ocean. Bacterial growth rates may be significantly higher in the deep Pacific and/or removal by grazing or viral lysis might be lessened. The pattern of equatorial versus subarctic BA and POC flux in the North Pacific suggests that the relative strengths of top-down and bottom-up controls differ within this basin. In contrast, these processes seem to maintain their relative impacts over the enrichment gradient in the Arabian Sea, with a shorter geographic extent. Whatever the cause, the balance between organic matter delivery and net growth must be different between the basins to explain the high BA values found in the subarctic North Pacific, a region where POC flux at depth is not particularly high relative to the Arabian Sea.

We found a strong correlation between annual POC flux and the mean BA at 2,000 m in the Arabian Sea (Fig. 7). In contrast, POC export from the euphotic zone overlying a particular deep-water site did not show a similar trend, either spatially or temporally (Figs. 2, 3). BA appears to reflect the long-term mean of POC flux rather than episodic pulses. BA in the subarctic North Pacific, meanwhile, was at places equivalent to the highest values found in the most productive regions of the Arabian Sea, but deep POC flux was apparently much lower. The abundance of bacteria in the bathypelagic ocean must be controlled by factors beyond POC flux alone.

The apparently mixed signal for BA at oligotrophic sites other than S15 in the Arabian Sea (i.e., S11 and S13; Fig. 2) requires consideration. S11 and S13 often had BA values that were more like those of the inshore, highly productive stations than like those of the neighboring S15. Sinking POC created inshore of those stations may have moved considerable distances with, for example, mesoscale eddies. This mechanism could move slowly sinking and deep suspended POC into the region of S11 and S13, thereby supporting the bacteria in those deep waters. S15 may have received less lateral input. It is important, therefore, to link bacterial variables in the bathypelagic to POC flux at the depths of interest rather than to POC export from the surface ocean directly overhead. POC sinking from the euphotic zone can be carried long distances (Siegel and Deuser 1997) or be largely consumed in the mesopelagic, leaving little to reach bathypelagic depths directly below the site of formation.

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