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# The bacterial component of the oceanic euphotic zone

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**Abstract**

Bacteria in the open sea remote from land are sustained strictly on local sources of organic production which should make understanding their nutrition and growth regulation easier than in nearshore systems, estuaries and lakes. Until now, a paucity of data from geographically isolated oceanic sites prevented ready interpretation. In the past decade investigation of bacterial properties in oceanic systems has increased rapidly, stimulated in part by large oceanographic programs like the Joint Global Ocean Flux Study. Here I review comprehensive investigations of bacterial biomass and production dynamics in the subarctic north Atlantic and north Pacific, oligotrophic gyres in both oceans, upwelling provinces in the equatorial Pacific and northwest Arabian Sea, and in the Ross Sea, Antarctica. Euphotic zone bacterial stocks are remarkably similar across all except the last regime, averaging about 1 g C $m^{-2}$. Production and growth rates vary more widely, suggesting independent regulation of biomass and production. The seasonal to annual mean ratio of bacterial to primary production is usually below 20%. 

*Keywords:* Bacterioplankton; Open ocean; Phytoplankton; Carbon; Biogeochemistry; Plankton

## 1. Introduction

A decade ago Cole et al. [1] published a seminal analysis of bacterioplankton biomass and productivity in freshwater and marine systems. Synthesizing data from about 70 published studies, they showed that bacterial production (BP) was significantly and positively correlated ($r^2 = 0.55$, $n = 59$) with primary production (PP) rates across a wide range of aquatic ecosystems including streams, lakes, marshes, estuaries, and the coastal and open ocean. They concluded that on an areal basis and over the seasonal to annual time scale, BP averaged 30% of the local PP rate. They also concluded that bacterial abundance was correlated with chlorophyll concentration ($r^2 = 0.75$), indicating that over all systems, BP was sustained ultimately by the flow of organic matter from primary producers, dominated by phytoplankton. This study and several previous [2] and subsequent [3,4] analyses finally provided solid empirical underpinning for the current paradigm of aquatic bacterioplankton ecology, suggested originally by Pomeroy [5] and then Williams [6].

Largely because of its enormous geographical extent the open ocean dominates global aquatic metabolism [4]. In many ways open ocean systems provide the simplest and most straightforward systems in which to analyze the relationships among bacterial and phytoplankton biomass and production rates. Oceanic systems seaward of continental shelves and

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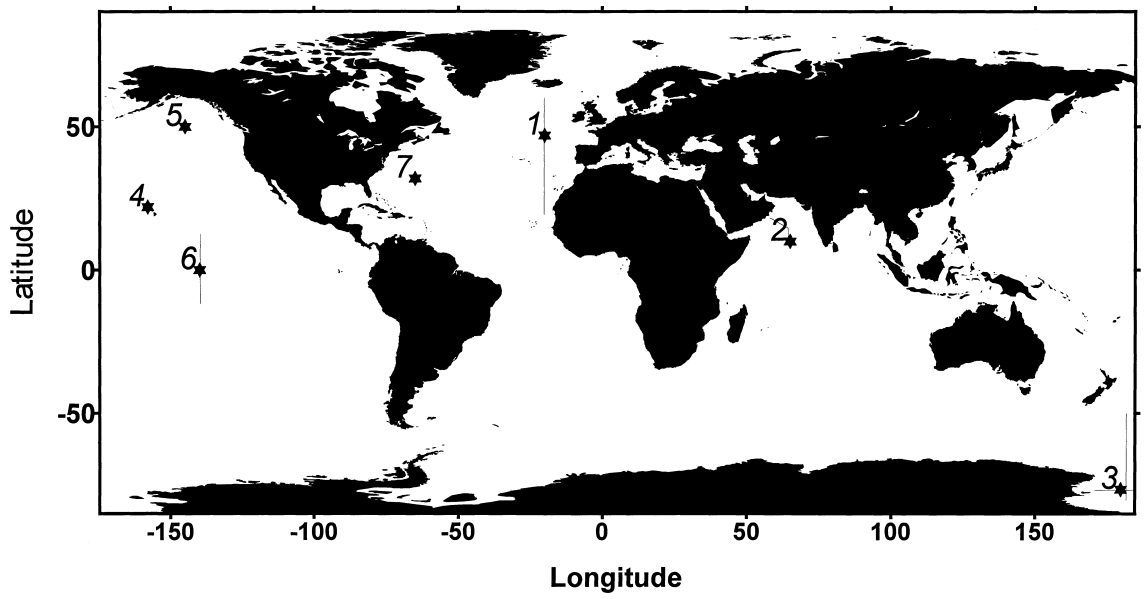


Fig. 1. The global ocean, showing locations of comprehensive bacterial sampling discussed in this review. 1: North Atlantic spring phytoplankton bloom. 2: Arabian Sea. 3: Ross Sea, Antarctica. 4: Hawaii Ocean time series. 5: Subarctic north Pacific. 6: Central equatorial Pacific. 7: Bermuda Atlantic time series. Oceanographic sections were run along transect lines in regions 1, 2, 3, 6.

slopes are often separated from coastal waters by frontal systems or major ocean currents, and thus isolated from terrestrial sources of organic matter. Fluxes of organic matter from terrestrial and benthic sources sustain some fraction of BP in estuaries and coastal waters [7,8], complicating construction of nutritional budgets for bacterioplankton. In the open sea, bacterial metabolism is supported entirely by planktonic primary producers, directly or indirectly, conforming to the 'Cole model' of bacterial trophodynamics. Thus the ultimate sources and physiological processes supplying organic matter used by oceanic bacterioplankton can be specified with increasing detail, and are being incorporated in increasingly sophisticated models [9].

Especially in oligotrophic regimes, the concentrations of labile organic matter and reduced nitrogen compounds supporting bacterial nutrition are remarkably low. Concentrations of individual monosaccharides are amino acids are just a few nanomolar. Oceanic bacterioplankton present the unique example of a globally significant biomass (see below) sustained on relatively small fluxes and standing stocks of organic matter, quite unlike the bacterial species studied in the laboratory.

There are, however, several factors which still complicate better understanding of oceanic bacterial ecology. Levels of bacterial abundance and production rates are low, with the latter often being near detection limits for radioisotopic productivity assays. Methodological limitations constrain the number of samples which can be analyzed, as long incubations need to be performed to boost signal to noise ratios for each determination. In addition, the open sea is remote from most labs and opportunities to sample it in detail are expensive and relatively infrequent. For example, Cole et al. [1] included just a single data set taken exclusively from an oceanic location [10]. Even the most recent review [4] included just 15 reports, of which just a few had extensive coverage and/or employed more widely adopted methods. A severe lack of data has been perhaps the foremost barrier to understanding of the nature of oceanic bacterial ecology.

This latter situation is now being remedied to some extent. In the decade following Cole et al.'s [1] analysis there have been many additional open sea expeditions which included high quality bacteriological programs, and the consequent appearance of new publications and accumulating data in acces-

sible archives. Considerable limitations still exist. Bacteriological assays will seemingly be limited to discrete samples for some time to come, if not indefinitely. This constraint contrasts starkly with remote sensing capability for gaining information about phytoplankton biomass and production [11] and even grazing patterns [12]. Longhurst [11,12] provides the first global synthesis of satellite data on surface chlorophyll, its patterns in time and space, and derived photosynthetic rates in 51 oceanic biogeochemical provinces distinguished by both physical oceanographic and ecological structures. The resulting annual cycles of phytoplankton stocks, production and removal provide a context in which bacterial as well as other plankton dynamics can be explored. Bacteriologists will probably never have the amounts of data synthesized by Longhurst (and even more is on the way), but sufficient observations are now available to make some tentative generalizations. The purpose of this short review is to provide a synthetic overview of some of the newer data and characterize the stocks and production rates of bacterioplankton in the open sea. Rather than providing a new regression analysis akin to [1], I concentrate on bacterial dynamics as observed in the ocean at selected sites. I suggest that bacterial production in the open sea is somewhat lower a fraction of primary production than the canonical 30% found by Cole [1], and suggest that lower conversion efficiencies are a likely reason. A more comprehensive analysis will follow in future publications.

## 2. Methods and data sources

Here I present data on bacterial abundance and leucine incorporation rates from studies conducted between ca. 1986 and 1996 in the open Atlantic, Pacific, Indian and Southern Oceans (Fig. 1). Most data were collected on cruises of the Joint Global Ocean Flux Study (JGOFS), and obtained from: http://www1.whoi.edu/jg/dir/jgofs/. Bacterial abundance was determined by epifluorescence microscopy using acridine orange or DAPI. In most cases BP rates were assayed using both [$^3$H]thymidine and [$^3$H]leucine incorporation. Here I present BP estimates from leucine incorporation derived using the conversion factor 3 kg C mol$^{-1}$ [13]. The leucine factor has been better constrained, and may vary less than the thymidine factor [14]. In a similar vein, I present standing stocks as the integrated bacterial abundance (cells m$^{-2}$) to avoid reliance on any single carbon conversion factor [14]. Data considered here were, however, extrapolated to biomass using 20 fg C cell$^{-1}$ for consistency with published reports [15]. This review concentrates on the euphotic zone as determined from in situ light penetration and primary productivity measurements. Primary production and chlorophyll were determined using standard techniques [16].

## 3. Bacterioplankton biomass and net production at selected sites

### 3.1. North Atlantic spring phytoplankton bloom

A multinational, multi-ship experiment conducted in 1989 investigated the biogeochemical consequences of the oceanic, basin-scale phytoplankton bloom in the eastern North Atlantic Ocean [17]. This bloom is seen regularly in satellite imagery [11], with surface Chl *a* concentrations reaching 3–5 mg m$^{-3}$ at the surface [18] (Fig. 2A). Besides supporting a massive flux of phytodetritus to the benthos 5000 m below [19], which in turn supports active mesopelagic activity [20] and a deep microbial flora [21], the phytoplankton bloom also fuels a subsequent bacterial bloom (Fig. 2A). In 1989 bacterial standing stocks grew by a factor of three over a month following the inception of the bloom in late April [22,23], averaging about 20% of the phytoplankton stocks (Table 1). BP varied in parallel with, though slightly lagging PP (Fig. 2B), and amounted to an average of about 25% of the net particulate PP[1]. Bacteria contributed up to 90% of the measured total nitrogen uptake by phytoplankton and bacteria during the latter phases of the bloom, with amino acids and ammonium contributing about equally to the bacterial nutrition [24].

[1] All the primary production estimates quoted here are routine $^{14}$C measurements of particulate primary production, excluding DOC production. Thus when BP:PP ratios are reported, no direct flux of the photosynthetically fixed carbon to bacteria is implied. Ratios are reported for scaling and comparison, not mechanistic conclusions.

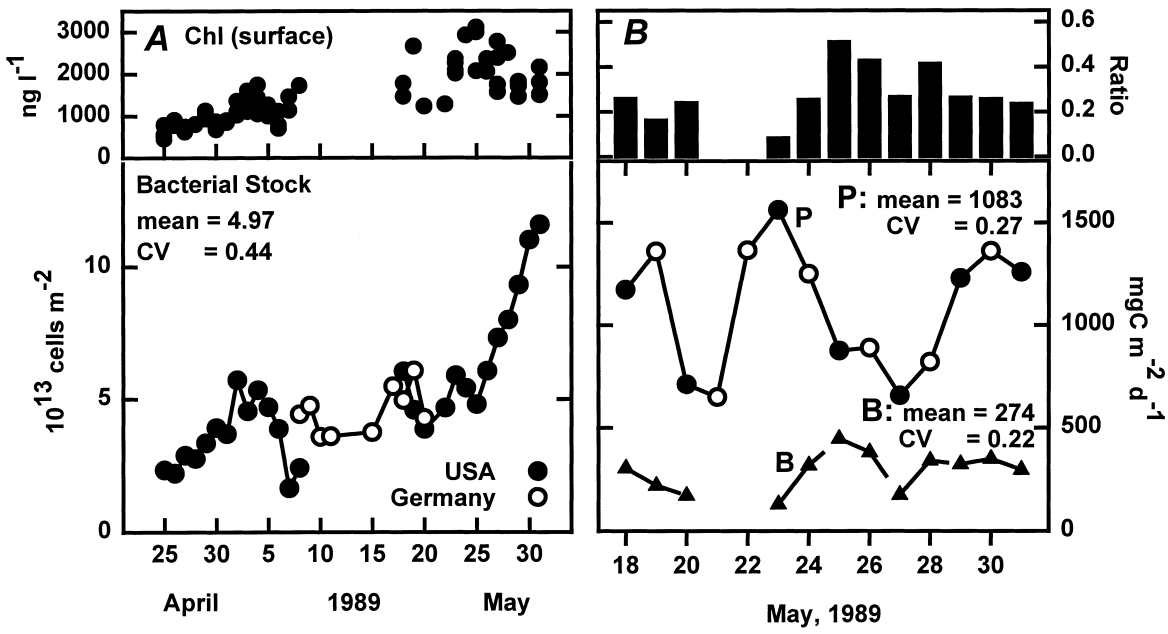


Fig. 2. Bacteria and phytoplankton during the North Atlantic spring phytoplankton bloom at 47°N, 20°W, April–May, 1989. A: Surface chlorophyll (upper panel) and euphotic zone bacterial stock (lower panel). B: Primary and bacterial production (lower panel) and their ratio (upper panel). Means and coefficients of variation (S.D./mean) are also shown.

This study also provided the first demonstration of direct utilization of dissolved organic carbon (DOC) by oceanic bacteria [25]. In particular it was concluded that bacteria converted DOC into biomass with just ca. 5–10% efficiency. If both this estimate and the BP:PP ratios are accurate, bacterial gross production (net production plus respiration, or total carbon utilization) was in excess of the daily PP. This is not impossible during a bloom, when the accumulated biomass could serve as a supplement to the flux of recently produced DOM [26]. Billen and Fontigny [27] invoked extracellular hydrolysis of macromolecular polymers to explain a similar lag between phytoplankton and bacteria blooms in the Belgian coastal zone. Billen et al. [28] hypothesized that significant regressions of BP (as an index of DOM supply) on bacterial biomass could be used to indicate whether bacterial stocks were predominantly controlled by resource supply (bottom-up) or removal (top-down) control mechanisms. The BP and abundance observations shown in Fig. 2 have a exponential regression slope of 0.45, suggesting moderate bottom-up control [29]. Clearly the bacterial blooming phenomenon itself signals a lack of strong top-down control. In the tropical Atlantic (at the southern end of the transect line in Fig. 1), bottom-up control was also moderate, but increased from eutrophic upwelling sites toward the oligotrophic 'EUMELI' station of France-JGOFS [30]. This oligotrophic-to-eutrophic gradient presents a good opportunity to test the factors regulating bacterial growth in the open sea. Greater bottom-up control in oligotrophic regions suggests resource limitation rather than grazing limits biomass and activity, but specific limiting compounds (e.g., inorganic nutrients vs. organic matter) have not been investigated.

### 3.2. *HNLC regimes: equatorial and subarctic north Pacific*

Like the better-studied eastern tropical Pacific, the central basin (Station 6 and transect in Fig. 1) is strongly influenced by upwelling which supplies the euphotic zone with limiting nutrients $NO_3$, $PO_4$ and iron [31], driving high rates of PP [32]. In spite of high surface macronutrients and productivity, phytoplankton biomass is low (Fig. 3A, top), hence the region is one of the major oceanic 'high-nutrient,

Table 1
Bacterioplankton and phytoplankton properties in the open sea[a]

| Property | North Atlantic | Equatorial Pacific, spring | Equatorial Pacific, fall[b] | Sub north Pacific[c] | Arabian | Hawaii | Bermuda[d] | Ross Sea[e] |
|---|---|---|---|---|---|---|---|---|
| Euphotic zone (m) | 50 | 120 | 120 | 80 | 74 | 175 | 140 | 45 |
| Biomass (mg C $m^{-2}$) | | | | | | | | |
| Bacteria | 1000 | 1200 | 1467 | 1142 | 1448 | 1500[f] | 1317 | 217 |
| Phytoplankton | 4500 | 1700 | 1940 | 1274 | 1248 | 447 | 573 | 11450 |
| Ratio (B:P) | 0.2 | 0.7 | 0.75 | 0.9 | 1.2 | 3.6 | 2.7 | 0.02 |
| Production (mg C $m^{-2}$ $day^{-1}$) | | | | | | | | |
| Bacteria | 275 | 285 | 176 | 56 | 257 | nd | 70 | 55 |
| Phytoplankton | 1083 | 1083 | 1548 | 629 | 1165 | 486[g] | 465 | 1248 |
| Ratio (B:P) | 0.25 | 0.26 | 0.11 | 0.09 | 0.22 | nd | 0.18 | 0.04 |
| Growth rates ($day^{-1}$) | | | | | | | | |
| Bacteria | 0.3 | 0.13 | 0.12 | 0.05 | 0.18 | nd | 0.05 | 0.25 |
| Phytoplankton | 0.3 | 0.64 | 0.8 | 0.50 | 0.93 | 1.1 | 0.81 | 0.11 |
| Ratio (B:P) | 1 | 0.2 | 0.15 | 0.1 | 0.19 | nd | 0.06 | 2.3 |

[a]Means derived from data shown in Figs. 2–5 unless noted. All bacterial stock estimates based on 20 fg C $cell^{-1}$. Data may overestimate actual heterotrophic eubacterial biomass as a consequence of lower C contents and/or interference by *Prochlorococcus* and *Archaea*.
[b]Sept.–Oct., 1992, $n = 19$ [36].
[c][33].
[d]1991–1998, $n = 106$ paired comparisons; for BP and phytoplankton biomass calculations [41]. The ratios are means of the ratios, not ratios of the means. BP calculated from TdR* $1.6 \times 10^{18}$ cells $mol^{-1}$.
[e][51]; Ducklow, unpublished data.
[f]1995–1997, $n = 19$. HOT data system, http://hahana.soest.hawaii.edu/hot/methods/pprod.html
[g]1989–1996, $n = 64$. Data source as above.

low-chlorophyll' (HNLC) provinces [11]. A previous study of bacterial dynamics and regulation in the HNLC regime of the subarctic north Pacific [33] (Fig. 1, Station 5; Table 1) showed that the BP:PP ratio was relatively low (5–15%) but bacterial biomass was about equal to the phytoplankton (85–104%). Bacterial activity, like phytoplankton, may be iron-limited in this region [34]. The production and biomass ratios in the equatorial Pacific are similar (Table 1). BP:PP was nearly constant at 12% on three of four cruises in 1992 [35,36], except near the peak of the El Niño in March (Fig. 3B). The reason for the low BP:PP ratio in these HNLC systems is still unknown. Dissolved monosaccharide concentrations were greater during the El Niño (spring), when glucose supported 30–50% of BP, compared to just 15% in the fall [37]. But comparison with the high-biomass North Atlantic suggests the possibility that BP is controlled more by phytoplankton biomass than production per se. Note the exactly similar (and coincidental) levels of PP in the two systems during the respective sampling periods. In contrast to the variable North Atlantic, oceanic HNLC regimes have high bacterial biomass relative to phytoplankton. Reflecting the phytoplankton stocks, the bacterial biomass is very uniform in time and space. The bacterial biomass seems to be more grazer- than resource-controlled in these regions. In general, the most striking aspect of the equatorial Pacific bacterial assemblage is its constancy. Coefficients of variation (CV) for stocks and production were about 1/4–1/2 the corresponding values in the North Atlantic (Figs. 2 and 3). The simplest explanation is that bacterial variability is directly coupled to phytoplankton variability. The similarity of phytoplankton and bacterial CV support this hypothesis, although the biological mechanisms of the coupling are not known.

### 3.3. The oligotrophic gyres: Hawaii and Bermuda

Detailed biweekly to monthly time series observations were initiated at oceanic sites near Hawaii and Bermuda in 1988 [38] (Fig. 1, Stations 4, 7). Both these regions are considered oligotrophic, with persistent nutrient depletion throughout the euphotic zone, and severe nutrient limitation of PP. Primary productivity is low, but not as low as once thought.

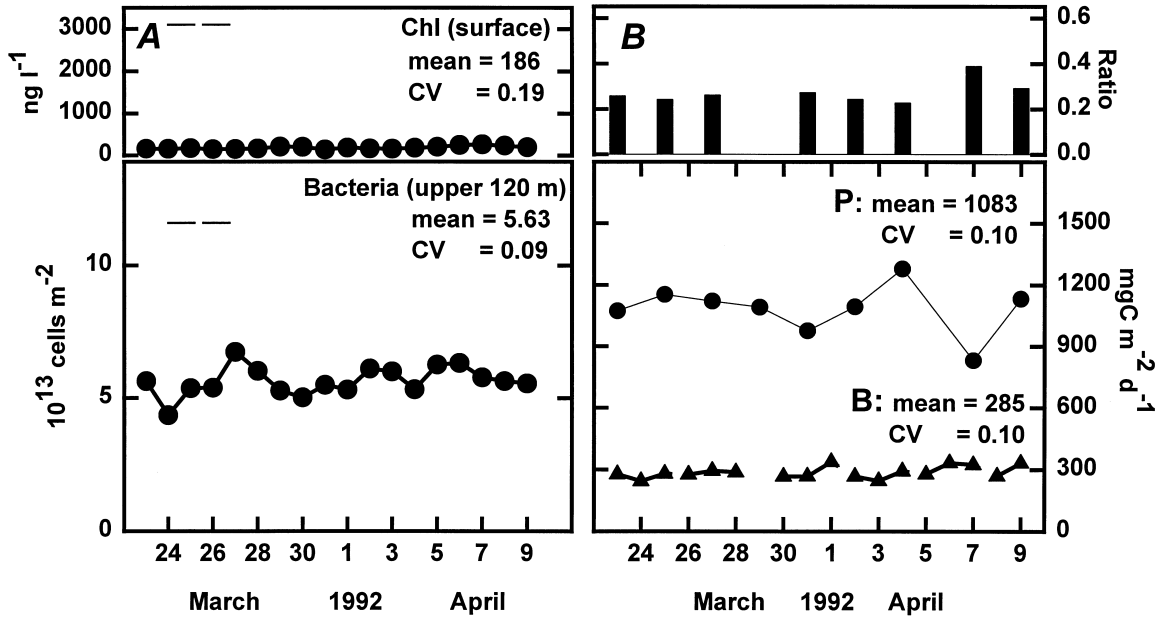


Fig. 3. Phytoplankton and bacteria in the equatorial Pacific at 0°N, 140°W, March–April, 1992. All scaling and data as in Fig. 2. The long dashed lines in A indicate peak levels of Chl and bacteria observed in the North Atlantic (Fig. 2).

Bacterial abundance in the surface is low, but euphotic zone stocks are surprisingly high, owing to the greater depth of the euphotic zone [14]. For example, the north central Pacific gyre off Hawaii is one of the most persistently oligotrophic regions of the planet. But bacterial stocks are about the same as in the equatorial Pacific and Arabian Sea (Table 1), where upwelling driven PP is 2–4 times greater. Similar biomass ratios have been documented in the Sargasso Sea [39–41] (Table 1). Bacterial conversion efficiency for bulk DOC was about 15%, so gross BP was high, amounting to over 50% of the daily particulate PP [41]. In these oligotrophic ocean systems more PP is stored in bacterial biomass than in more productive regions and euphotic zone processes must funnel organic matter efficiently toward the base of the foodweb. Although the bacterial assemblage as a whole turns over slowly, these gyre systems must now be viewed as intensely bacteria-dominated. This is exceptional, since these regimes occupy almost half the total area of the global ocean [12].

### 3.4. Monsoon-driven upwelling: the Arabian Sea

The northwest Arabian Sea (Fig. 1, Station 2) is a tropical basin, closed to the north and impacted by a strong atmospheric jet which drives intense coastal upwelling during the southwest monsoon [42,43]. Strong seasonal variation in physical forcing and PP in a tropical sea was expected to cause similar variation in bacterial dynamics. However, there was no significant variation in BP or stocks between the SW monsoon (June–Oct) and NE monsoon (Dec–Feb) in 1992–93 [42] or between the SW monsoon and following fall intermonsoon in 1994 [43]. BP:PP was high just following the 1986 SW monsoon [44], suggesting that unused 'slow-to-degrade' DOC stored during periods of high PP could sustain high BP:PP during the subsequent oligotrophic phase [45]. This hypothesis was tested during a comprehensive year-long expedition in 1995 [46], but it could not be unequivocally confirmed or rejected. Unexpectedly, bacterial stocks and production as well as PP remained high year round, during both monsoons and the spring intermonsoon season [46]. Fig. 4 depicts onshore–offshore distributions seen over all four seasons in 1995. It was expected that monsoon-driven coastal upwelling would cause higher stocks and BP onshore. Although there is a suggestion of an onshore-offshore gradient, there was no

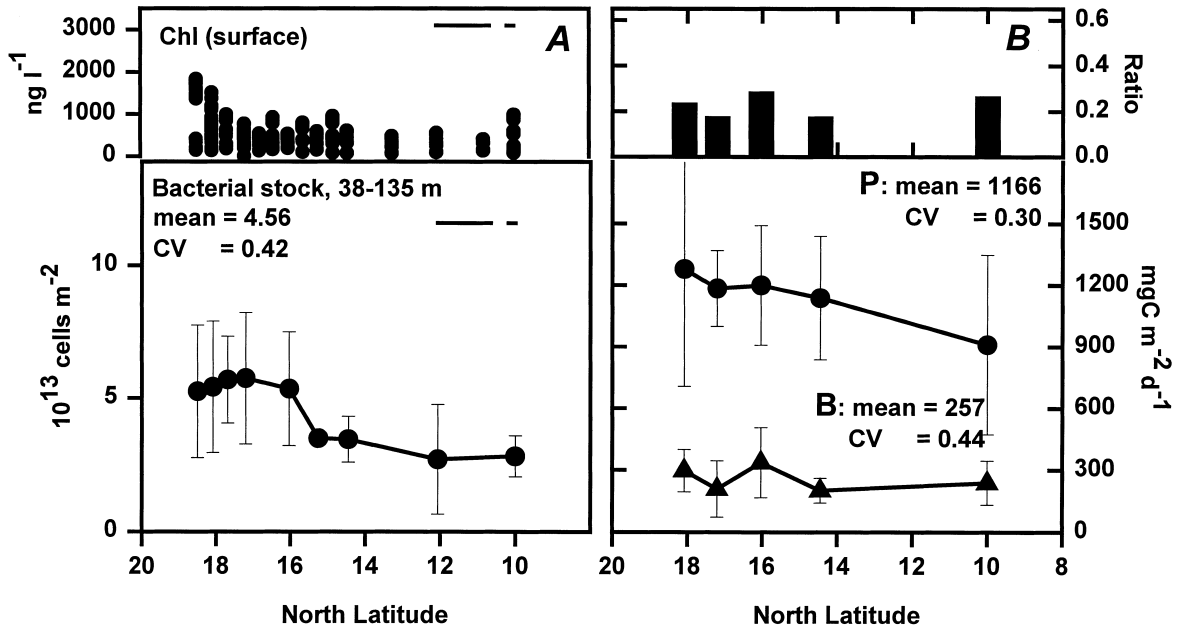


Fig. 4. Phytoplankton and bacteria along an onshore to offshore transect in the northwest Arabian Sea, Jan.–Dec. 1995. Scaling and data as shown in Fig. 2. Data are means and standard deviations (bars) of four seasonal occupations of each station. Dashed lines in A show peak North Atlantic levels.

significant trend in any season. BP:PP was a moderately high 22%, with no spatial or temporal pattern. The Arabian Sea appears to be a region where high bacterial abundance in shallow euphotic zones inshore and lower abundance in deeper euphotic zones offshore lead to similar levels for the integrated stocks. Finally, although the area has been intensively investigated in the past decade, use of different conversion factors [4,14,43] and interannual variability complicate comparisons and generalization.

### 3.5. Polar oceans: the Ross Sea

Antarctic coastal waters present an interesting regime for investigating bacterial dynamics. The continental shelf in the Ross Sea (Fig. 1, Station 3) is 300–700 m deep as a result of isostatic adjustment of the continental plates in response to the tremendous ice mass. Further, with no terrestrial production or landward sources of organic matter input, BP is supported by in situ production in these waters, like more remote oceanic locations. The combination of deep mixing and reliance on in situ sources makes the Ross Sea quasi-oceanic in nature. Conversely, water column stabilization from melting sea ice confers a more coastal, even estuarine character. Finally, Antarctic coastal waters are examples of persistently near-freezing environments in which bacterial growth must cope with the coldest liquid water on the planet. There has been considerable sampling effort in the Southern Ocean near Antarctica [47], but until recently, no comprehensive examinations in a single year, except in the immediate coastal zone near the Antarctic Peninsula [48] and in McMurdo Sound [49]. The Ross Sea is the site of Antarctica's most spatially extensive phytoplankton bloom, dominated by the colonial haptophyte *Phaeocystis antarctica*. This bloom reaches very high levels (Fig. 5A), with PP rates exceeding 4 g C $m^{-2}$ $day^{-1}$ (Fig. 5B). One would expect all this production and biomass might fuel a large bacterial bloom, which is indeed the case, measured in absolute terms: the bacterial bloom reaches levels comparable to the North Atlantic, but in persistently subzero water. But bacteria are just a minor component of the plankton in this region, reaching about 2–4% of the phytoplankton stock and PP, respectively (Table 1). An exception is the late austral autumn (March) when the polar

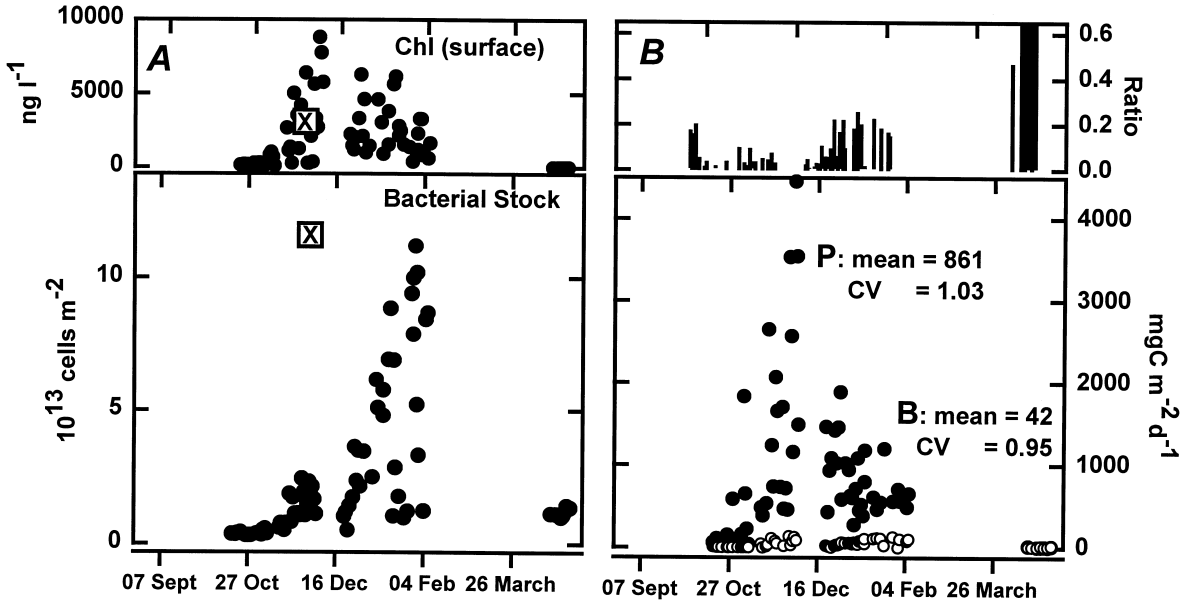


Fig. 5. Phytoplankton and bacteria along 76.5°S in the Ross Sea, Oct.–March, 1994–1997. Note that the scaling differs from previous figures. The boxed Xs show the amplitude and timing (offset by 182 days) of the bloom in the North Atlantic (Fig. 2). March BP:PP ratios are in excess of 1. In B, the March PP data are underneath the BP circles.

sun is above the horizon for just 1–4 h each day, net PP is vanishingly small (10–20 mg C $m^{-2}$ $day^{-1}$; Fig. 5B), and BP:PP is greater than 100%. This may reflect the carbon balance during the austral night (April–September) when very low BP is sustained by ambient DOC. The reason for the overall low BP:PP is not known. Bacteria are active, with mean specific growth rates about as high as in the North Atlantic (Table 1), even in −2°C water. A bacterial bloom clearly occurs, although it lags the phytoplankton bloom by about a month [50] (Fig. 5). There was little change in bulk DOC stocks during the 1994 *Phaeocystis* bloom suggesting that BP is limited by low fluxes of DOC from *Phaeocystis* colonies in the absence of macrozooplankton grazing [51]. These observations of a bacterial bloom in such cold water provoke questions about the role of temperature regulation of bacterial dynamics, which cannot be addressed in a review of this scope.

## 4. Conclusion

Investigation of oceanic bacterial ecology has expanded greatly in the past decade. Several of the major biomes (oligotrophic gyres, HNLC and upwelling regimes, polar and subpolar regions) have been studied and a range of distinct patterns (cf. Figs. 2 and 5 with Fig. 3) has been documented. However, as the shortage of good explanations for these patterns and contrasts indicates, our understanding and theories still lag behind data collection. A few conclusions can be drawn: standing stocks of bacteria are remarkably similar throughout the world ocean in euphotic zones ranging 35–135 m deep, at least outside the polar seas (Table 1). Production rates vary more widely. Taken together these two broad observations suggest varying degrees of bottom-up control of BP. At the same time, stocks appear to expand regardless of trophic state until removal processes cap them. Although production rates vary widely, the mean ratio BP:PP is generally less than 20% (Table 1). If bacterial conversion efficiencies ranging just 10–20% cited here [25,41] are accurate, this must be so. Apparent carbon requirements are about the same level as the PP. BP could hardly be larger in most cases. Finally it is interesting to note that bacterial variability closely mirrors that of phytoplankton properties (cf. CVs in Figs. 2–5 and ranges in Table 1). Phytoplankton variability

is transmitted without attenuation to bacteria. This is another way of stating the ultimate dependence of bacteria on phytoplankton processes in the open sea. As we gain increased power to look at the dynamics of individual species populations in the coming decade, perhaps better and more precise mechanistic explanations of these gross patterns will become clear.

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