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Chlorophyll, bacteria and picophytoplankton in ecological provinces of the North Atlantic

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Abstract

A comparative ecology of chlorophyll, bacteria and picophytoplankton is presented for seven ecological provinces in the North Atlantic. Depth-integrated standing stocks of these biota were measured from boreal polar to subtropical gyral regions. Averaging over all sampling times and locations within each province, it appeared that the integrated biomass of bacteria did not exceed that of phytoplankton in any province. Although this biomass ratio often exceeded unity in surface waters of the subtropical gyral provinces, the ratio for the upper water column as a whole was lowered by the subsurface chlorophyll layer. Bacteria and picophytoplankton, as the potential food resource of micrograzers, appeared to complement each other such that their total biomass did not vary much more than 2-fold amongst the seven provinces. Characteristic parameters of the biotic depth profiles, namely surface concentrations, integrated stocks and depth of maximum, were used to cluster the provinces. The original classification of provinces based on surface chlorophyll fields and characteristic regional physics was reinforced by the inclusion of bacteria and picophytoplankton.

1. Introduction

The rational partition of the ocean into ecological biomes and provinces by Longhurst (1995, 1998) is a masterly organization of pelagic ecosystems (Smith, 1999). This global biogeography is constructed from the seasonal evolution of phytoplankton growth and takes into account the regional diversity of ecologically significant physical processes in the upper ocean. This scheme has been successfully applied to the computation of regional and global phytoplankton production (Sathyendranath et al., 1995; Longhurst et al., 1995), improving upon a simpler partition based on

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latitude and depth (Platt et al., 1991). More generally, this framework points towards a new organization of in situ measurements for comparative, geographic oceanography (Banse, 1998).

The specification of provinces by Longhurst relied on the surface chlorophyll field given by remotely sensed images, this being the only available comprehensive indicator of plankton distribution on a global basis. The ability to validate these specifications using the distribution of other biota sampled by traditional methods is a daunting, if not impossible task. As surface chlorophyll concentration is variously related to the biomass of other plankton components (Vinogradov et al., 1999), first-order estimates can be made of the latter for each province. These estimates, being statistical derivations from an ecological continuum, cannot be used to validate the integrity of the discrete provinces. However, it is possible to distribute existing in situ measurements of biota into the proposed provinces (as suggested by Banse, 1998) with the aim of discerning differences in community structure.

In plankton communities, an important indicator of ecological dynamics is the relative balance between the biomass of heterotrophic bacteria and autotrophic phytoplankton (Odum, 1971). Generally, the ratio of bacterial biomass of phytoplankton biomass increases *down* a gradient of productivity, and equals or exceeds unity in waters of low chlorophyll concentration (Fuhrman et al., 1989; Cho and Azam, 1990; Li et al., 1993; Buck et al., 1996). This leads by inference to the unresolved question of whether the large expanse of open ocean is net heterotrophic or autotrophic (del Giorgio et al., 1997; Geider, 1997; Duarte and Agustí, 1998; Williams, 1998). These studies also indicate that the biomass ratio of heterotrophs to autotrophs does not bear a simple, universal relationship to the continuum of chlorophyll levels: the relationship differs amongst the open ocean, coastal ocean and lakes (Simon et al., 1992; del Giorgio and Gasol, 1995; Gasol et al., 1997). Thus, with the partition of the ocean into ecological provinces, we sought to refine the geographic distribution of the balance between bacteria and phytoplankton.

In the past ten years, we have measured the biomass of bacteria and phytoplankton across seven ecological provinces of the North Atlantic. Discrete sampling from ships naturally failed to provide complete temporal coverage for the annum and complete spatial coverage for each province. However, the quantity of data at hand appears sufficient for an initial inter-province comparison. We accept the premise and definition of provinces: we thus distribute our measurements accordingly, then average them over depth, time and location so that a single value of each biological variable is assigned to each province. This integration at large spatial and temporal scales offers a macroecological view (Brown, 1995) of the North Atlantic.

2. Methods

From 1989 to 1998, we conducted 14 cruises in the North Atlantic (Fig. 1, Table 1). In total, the data represent 270 days of sampling at sea distributed unevenly amongst seven provinces, as specified by Longhurst (1998), belonging to the Polar biome: ARCT (Atlantic Arctic province), BPLR (Boreal Polar province); the Westerlies biome: GFST (Gulf Stream province), NADR (North Atlantic Drift province), NASE (North Atlantic Subtropical Gyral East province), NASW ((North Atlantic Subtropical Gyral West province); and the Coastal biome: NWCS (Northwest Atlantic Shelves province).

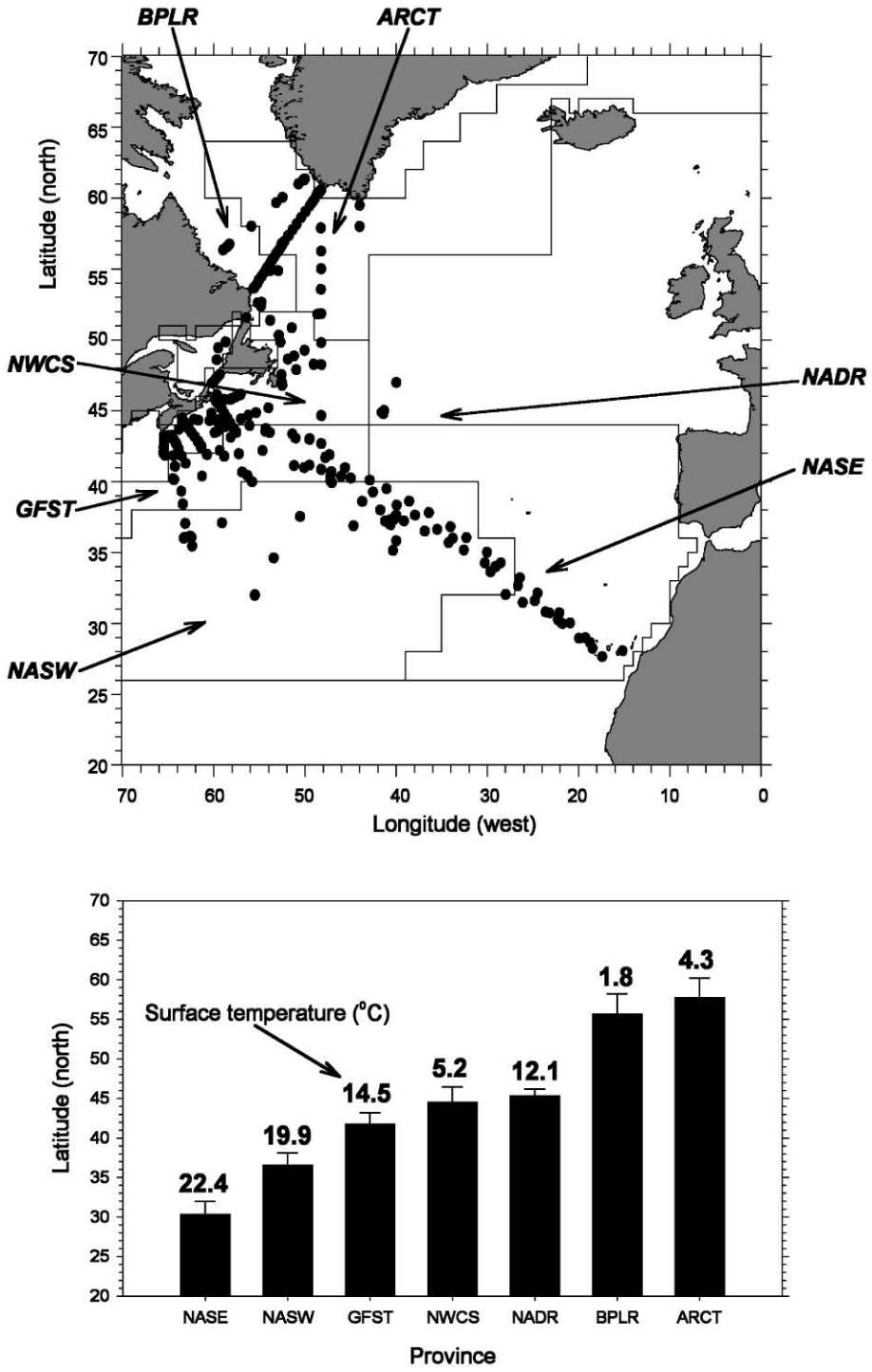

Fig. 1. Map of sampling locations in the North Atlantic. For each province, the average latitude of sampling stations is indicated, together with the average surface temperature at those stations.

Table 1
The seasonal and geographic distribution of 419 stations sampled in the North Atlantic. The numerical entry referenced by mission (rows) and province (columns) is the number of depth profiles for that time and place

Mission #	Season	Start date	End date	# of days	ARCT	BPLR	GFST	NADR	NASE	NASW	NWCS	All provinces
89-003	Spring	20-Apr-89	15-May-89	26			9	5		5		19
90-001	Spring	09-Apr-90	27-Apr-90	19			5			22	8	35
91-001	Spring	04-Apr-91	19-Apr-91	16			11			9		20
92-037	Fall	18-Sep-92	19-Oct-92	32			9		12	14		35
93-002	Spring	20-May-93	06-Jun-93	18			7		6	7		20
94-008	Spring	26-May-94	08-Jun-94	14	6	4					2	12
95-016	Summer	06-Jul-95	23-Jul-95	18	12	7	5				16	40
96-006	Spring	12-May-96	30-May-96	19	5	11	1				18	35
96-026	Fall	20-Oct-96	17-Nov-96	29	7	5						12
97-003	Spring	18-Apr-97	28-Apr-97	11			2				42	44
97-009	Spring	19-May-97	01-Jun-97	14	13	9					7	29
98-002	Spring	08-Apr-98	26-Apr-98	19			6				46	52
98-023	Summer	22-Jun-98	08-Jul-98	17	3	8					10	21
98-050	Fall	03-Oct-98	20-Oct-98	18			5				40	45
	Spring			156	24	24	41	5	6	43	123	266
	Summer			35	15	15	5	0	0	0	26	61
	Fall			79	7	5	14	0	12	14	40	92
	Total			270	46	44	60	5	18	57	189	419

ARCT was mostly sampled on the WOCE transect AR7W in the central Labrador Sea between South Wolf Island, Labrador and Cape Desolation, Greenland. BPLR stations were located in the Labrador and Greenland coastal current systems at the ends of AR7W. GFST was fairly well-sampled in the Scotian and Newfoundland Basins. On the other hand, NADR was very poorly represented: only five stations were occupied in the southwest corner of the province very close to GFST. NASE and NASW were sampled on transects between the Canary islands and Nova Scotia; but NASW also included many stations at 40°W within the subtropical gyre, and also some stations north of Bermuda. NWCS was the most intensely studied province with stations located in the Nova Scotian and Newfoundland shelves. The seasonal bias in the dataset is evident from Table 1, which indicates that 63% of all the samples were collected in spring, 15% in summer, 22% in fall, and none in winter.

At each of the 419 stations, samples at various depths were collected by a rosette of Niskin-type bottles. Our methods for analyzing chlorophyll *a* (Chl), bacteria and picophytoplankton have been previously described in detail (Harrison et al., 1993; Li, 1995, 1998; Li et al., 1993, 1995). Briefly, Chl was measured from acetone extracts of particulate matter collected on glass fibre filters (Whatman GFF) using a Turner Designs fluorometer. Preserved bacteria were either stained with DAPI and enumerated by epifluorescence microscopy; or stained with TO-PRO-1, TOTO-1 or SYTO-13 and enumerated by flow cytometry. Picophytoplankton were enumerated by flow cytometry on the basis of chlorophyll autofluorescence. We analyzed 5962 samples for Chl, 2965 for bacteria, and 3948 for picophytoplankton. For each station, the areal standing stock was computed from discrete depth measurements using trapezoid integration from the sea surface to the greatest depth at which a sample was collected, which was usually between 100 and 200 m except where the ocean bottom was shallower. The average integration depths are indicated for each province (see Figs. 2–8), and these were always greater than the mixed layer depth averaged from spring to fall as compiled by Longhurst (1998).

Phytoplankton carbon was computed using a carbon to Chl ratio of 40 (Li et al., 1993). Bacterial carbon was computed assuming a cellular content of 30.2 fg C bacterium^{-1} in the coastal province of NWCS and 12.4 fg C bacterium^{-1} in all other provinces that were oceanic (Fukuda et al., 1998). Picophytoplankton include *Prochlorococcus*, *Synechococcus* and eukaryotic autofluorescent cells less than 2 μm in equivalent spherical diameter (ESD). For *Prochlorococcus*, a carbon content of 59 fg C cell^{-1} was assumed as in earlier work (Li et al., 1993): this value is very close to more recent estimates (Partensky et al., 1999a, b). For other picophytoplankton, we used 115 fg C cell^{-1}: the value for a cell of 1 μm ESD assuming a conversion factor of 220 fg C μm^3.

Cluster analysis of data was performed by the hierarchical Euclidean distance centroid method (Statgraphics Plus, Manugistics Inc).

3. Results

3.1. Depth profiles

The complete dataset is presented as depth profiles of biotic concentration (Figs. 2–8). Although there is much variability in the individual profiles belonging to each province, the averages give

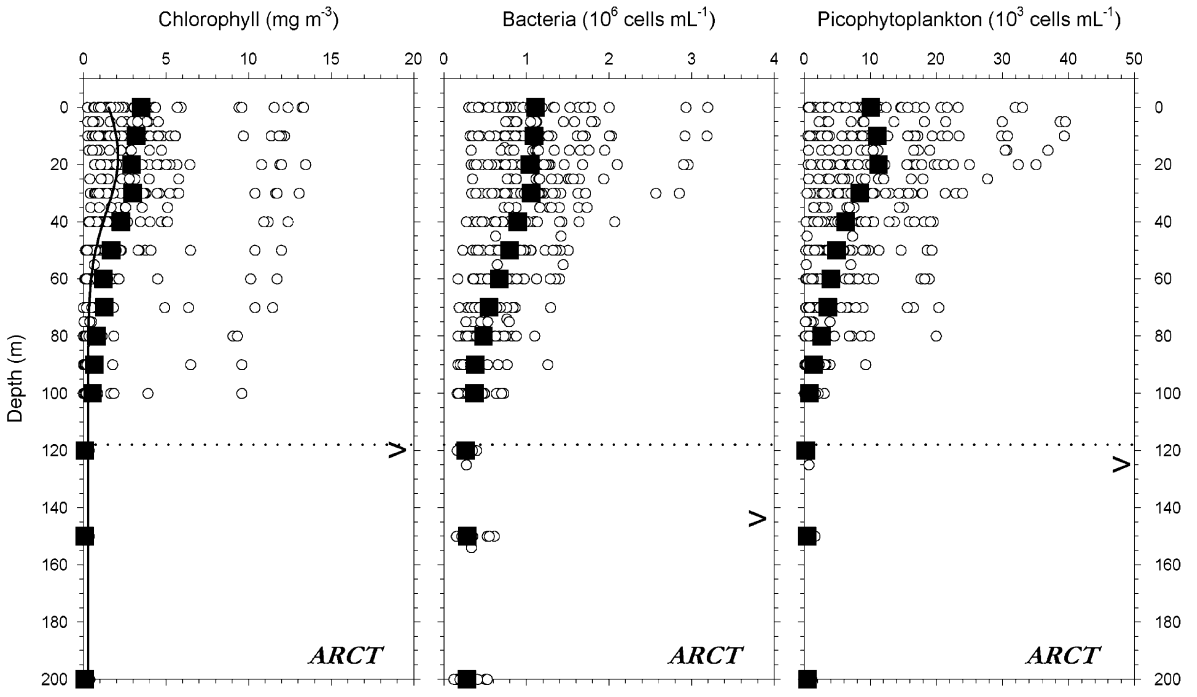

Fig. 2. Depth profiles of chlorophyll, bacteria and picophytoplankton for all stations in ARCT. The averages at 10 m depth intervals are indicated by solid square symbols. For chlorophyll, the smooth curve depicts the exemplary profile established by Longhurst (1998). Horizontal dashed line indicates the mixed layer depth based on density, averaged from spring to fall. Arrowhead indicates the depth to which integration of the property was made, averaged over all stations in the province.

a clear indication of the vertical distribution and abundance of the three biotic components: Chl, bacteria and picophytoplankton.

For Chl, comparisons can be made to the exemplary profiles computed from a shifted Gaussian distribution (Platt et al., 1988) using annual parameters for each province as specified in Longhurst's biogeography. As evident from the curves superimposed on the data (Figs. 2–8), the depth profiles of average Chl were reasonably close to the exemplary distributions, except at NASE (Fig. 6). There, the measured values peaked at 90 m but the Gaussian model parameter Z_m (i.e. depth of Chl maximum) is significantly shallower at 56 m. We examined this discrepancy by inspecting the archival Chl profiles used by Longhurst (Sathyendranath et al., 1995; Caverhill, personal communication), which extended over a geographic area in NASE much wider than we sampled. It appears that our measurements in NASE are much closer to the exemplary situation in fall than the annual mean.

The depth of maximum concentration (Z_m) for Chl (Table 2) compared well against archival records (Sathyendranath et al., 1995) everywhere except in the subtropical gyre. Our results indicate a general coherence (but not equivalence) in Z_m amongst Chl, bacteria and picophytoplankton. For each biotic group, Z_m was deepest in NASE and shallowest in NADR (Table 2).

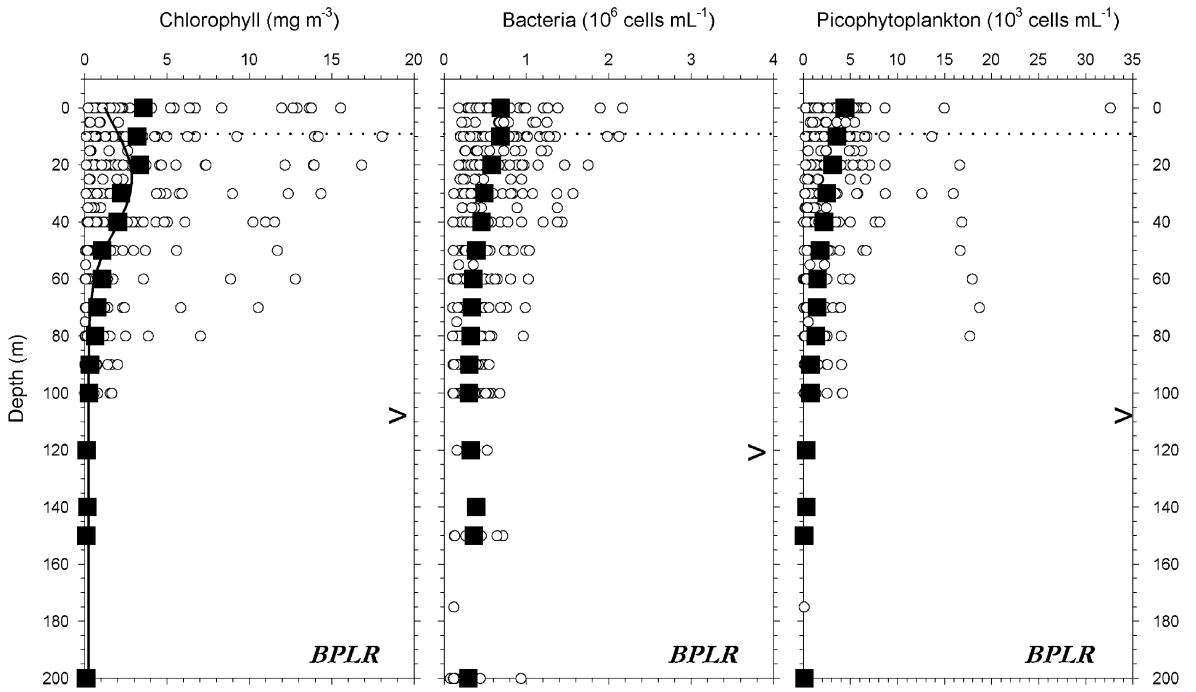

Fig. 3. Same as Fig. 1, except for all stations in BPLR.

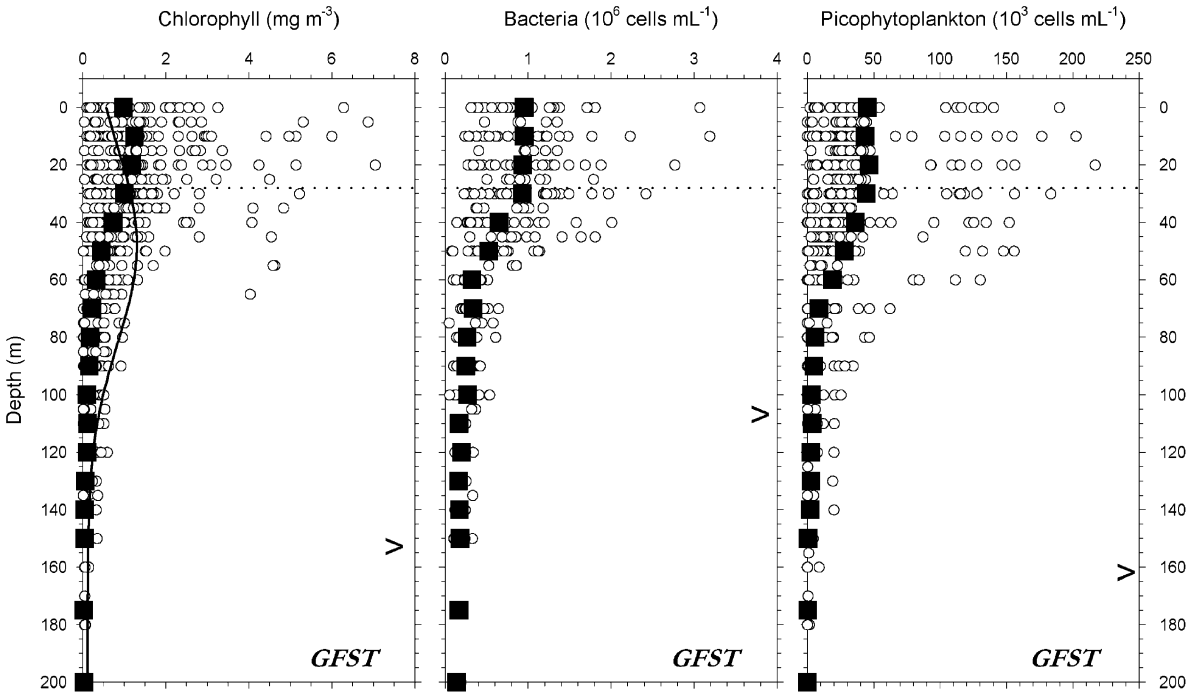

Fig. 4. Same as Fig. 1, except for all stations in GFST.

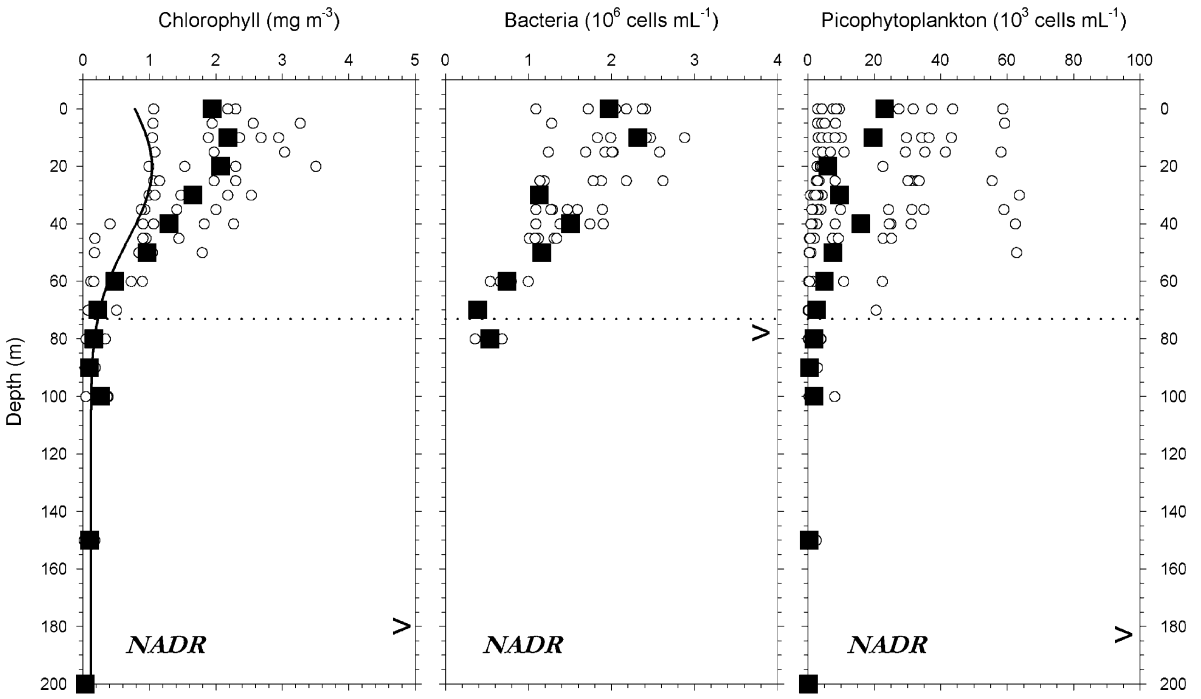

Fig. 5. Same as Fig. 1, except for all stations in NADR.

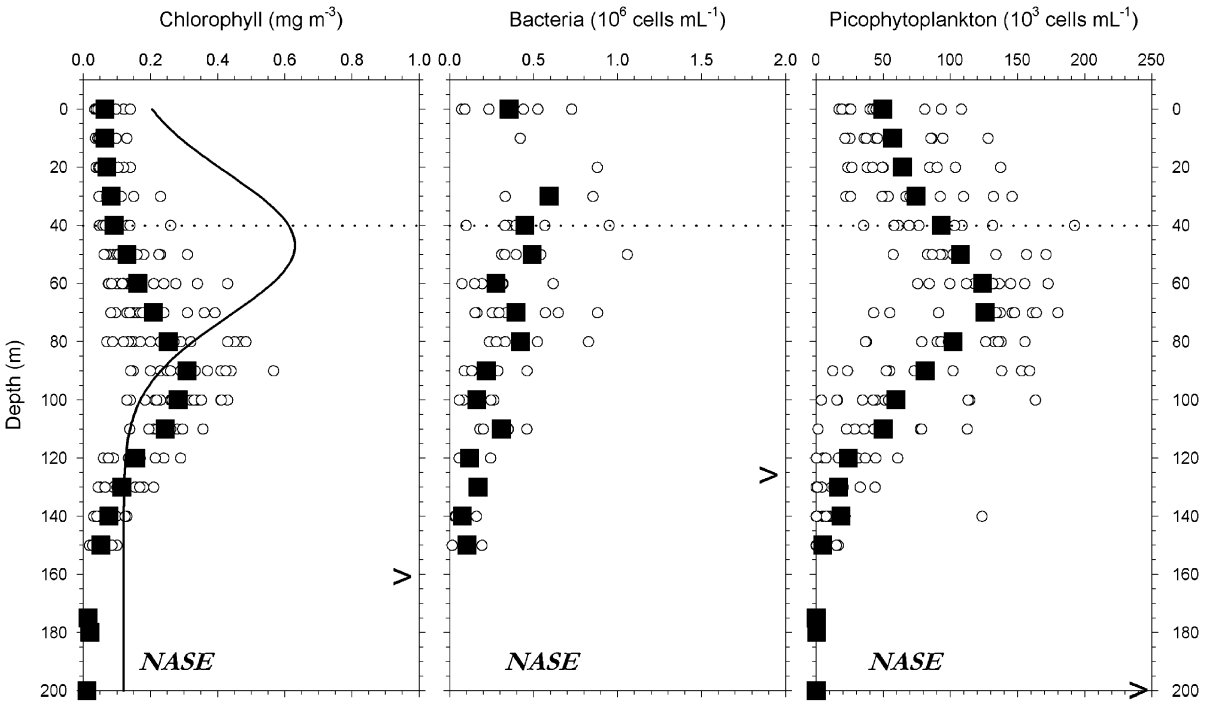

Fig. 6. Same as Fig. 1, except for all stations in NASE.

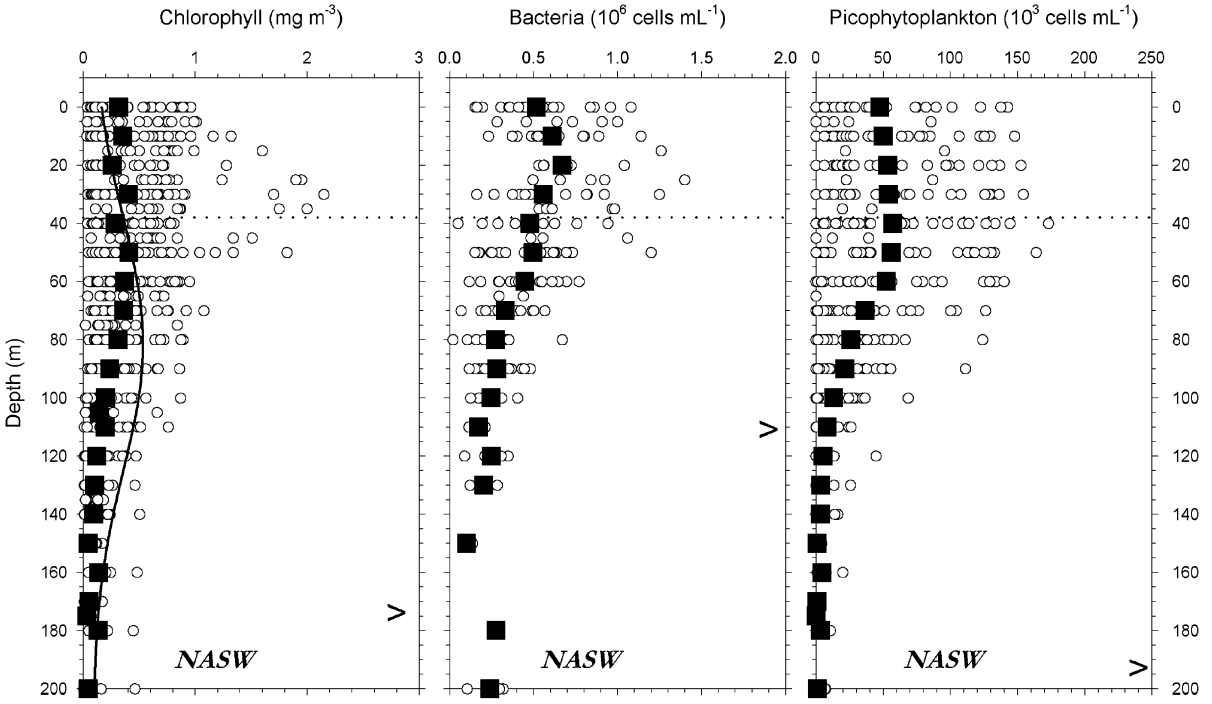

Fig. 7. Same as Fig. 1, except for all stations in NASW.

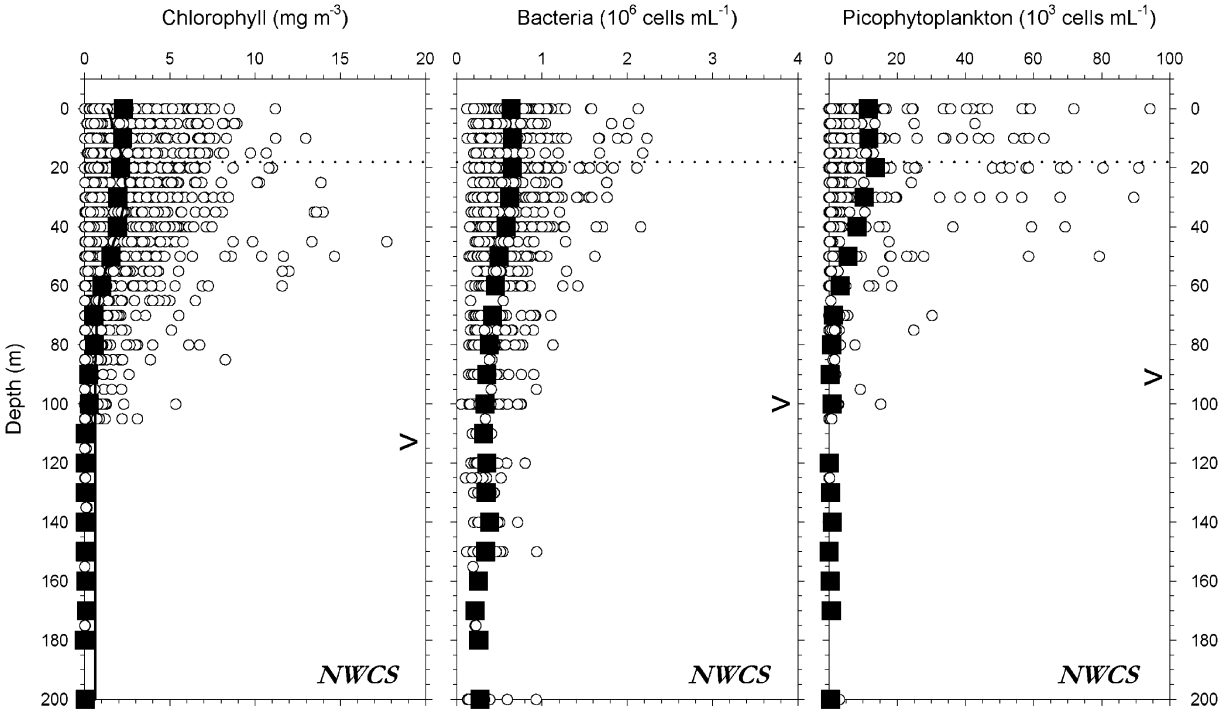

Fig. 8. Same as Fig. 1, except for all stations in NWCS.

Table 2
Average properties measured in North Atlantic provinces. The carbon standing stock of total phytoplankton (derived from chl), bacteria and picophytoplankton are given in volumetric units ($mg\,C\,m^{-3}$) for surface samples, and in areal units ($mg\,C\,m^{-2}$) for samples integrated through the upper water column. The depth of maximum occurrence is Z_m (m). Average ratios of integrated bacterial and picophytoplankton carbon to integrated phytoplankton carbon are also indicated ($mg\,C\,m^{-2}$: $mg\,C\,m^{-2}$). Note that these are averages of the ratios within each province (Fig. 13b); they are not the ratios of the average standing stocks as one might be tempted to calculate using the entries lines 4–6

	NASE	NASW	GFST	NWCS	NADR	BPLR	ARCT
Surface phytoplankton ($mg\,C\,m^{-3}$)	2.6	12.6	39.2	91.6	77.8	143.1	139.8
Surface bacteria ($mg\,C\,m^{-3}$)	4.4	6.4	11.8	19.3	24.4	8.5	13.8
Surface picophytoplankton ($mg\,C\,m^{-3}$)	5.7	5.5	5.2	1.3	2.7	0.5	1.2
Integrated phytoplankton ($mg\,C\,m^{-2}$)	840	1660	3366	6173	5450	7415	8099
Integrated bacteria ($mg\,C\,m^{-2}$)	501	474	641	1510	819	597	1166
Integrated picophytoplankton ($mg\,C\,m^{-2}$)	753	361	334	59	275	56	71
Z_m, phytoplankton	92	52	31	28	16	17	22
Z_m, bacteria	42	33	22	31	13	16	25
Z_m, picophytoplankton	64	48	24	26	11	16	19
Bacteria: phytoplankton ($mg\,C\,m^{-2}$: $mg\,C\,m^{-2}$)	0.50	0.41	0.27	0.46	0.15	0.19	0.32
Picophytoplankton: phytoplankton ($mg\,C\,m^{-2}$: $mg\,C\,m^{-2}$)	0.80	0.34	0.25	0.03	0.06	0.02	0.02

3.2. Areal standing stocks

Within each province, the standing stocks of Chl ($mg\,m^{-2}$), bacteria ($cells\,m^{-2}$) and picophytoplankton ($cells\,m^{-2}$) varied substantially with time and place (Figs. 9a, 10a, 11a). However, broad trends in the averages were evident in relation to increasing latitude (Figs. 9b, 10b, 11b). Chlorophyll increased significantly from provinces at low latitudes to high latitudes; the range was almost 10-fold from NASE to ARCT. Bacteria also increased in the same direction, but the range was only slightly more than 2-fold. Picophytoplankton was abundant in the westerly winds biome (NASE, NASW, NADR, GFST), but not in the coastal (NWCS) or polar biomes (ARCT, BPLR); the range was more than 20-fold from NASE to BPLR (Table 2).

Total picoplankton, that is the sum of bacteria and picophytoplankton expressed in common carbon units $mg\,C\,m^{-2}$ was less variable across provinces than either bacteria or picophytoplankton separately (Fig. 12).

3.3. Ratio of bacterial carbon to phytoplankton carbon

At each station where we measured both bacteria and Chl, we calculated the ratio of depth-integrated bacterial carbon ($mg\,C\,m^{-2}$) to phytoplankton carbon ($mg\,C\,m^{-2}$). Of 267 such ratios, only 27 were of a value 1 or higher (Fig. 13a). This subset was confined almost exclusively in NWCS, where bacteria are assumed larger than elsewhere (Fukuda et al., 1998), and included two

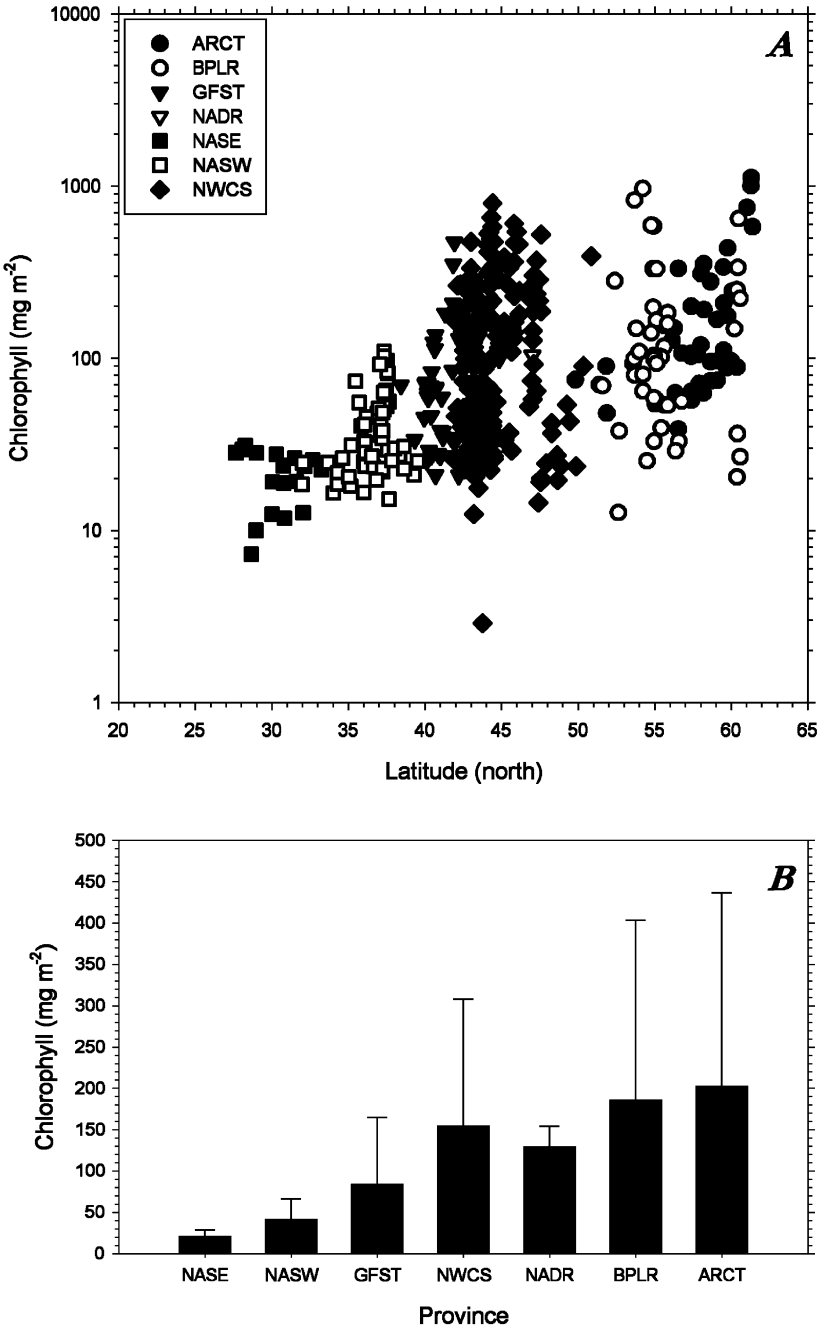

Fig. 9. Depth-integrated standing stock of chlorophyll. (A) Station-by-station plot versus latitude. (B) Average of all stations within each province.

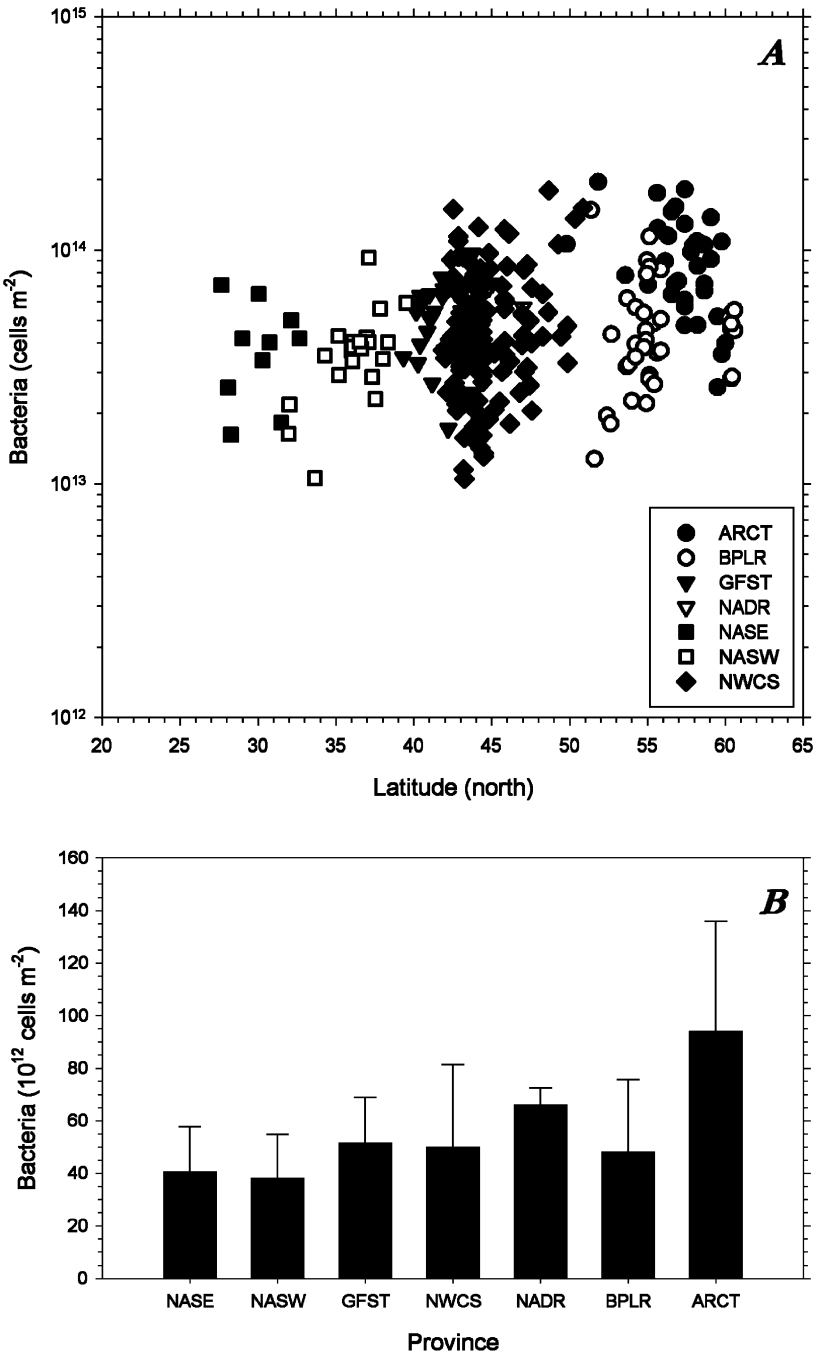

Fig. 10. Same as Fig. 9, except for depth-integrated abundance of bacteria.

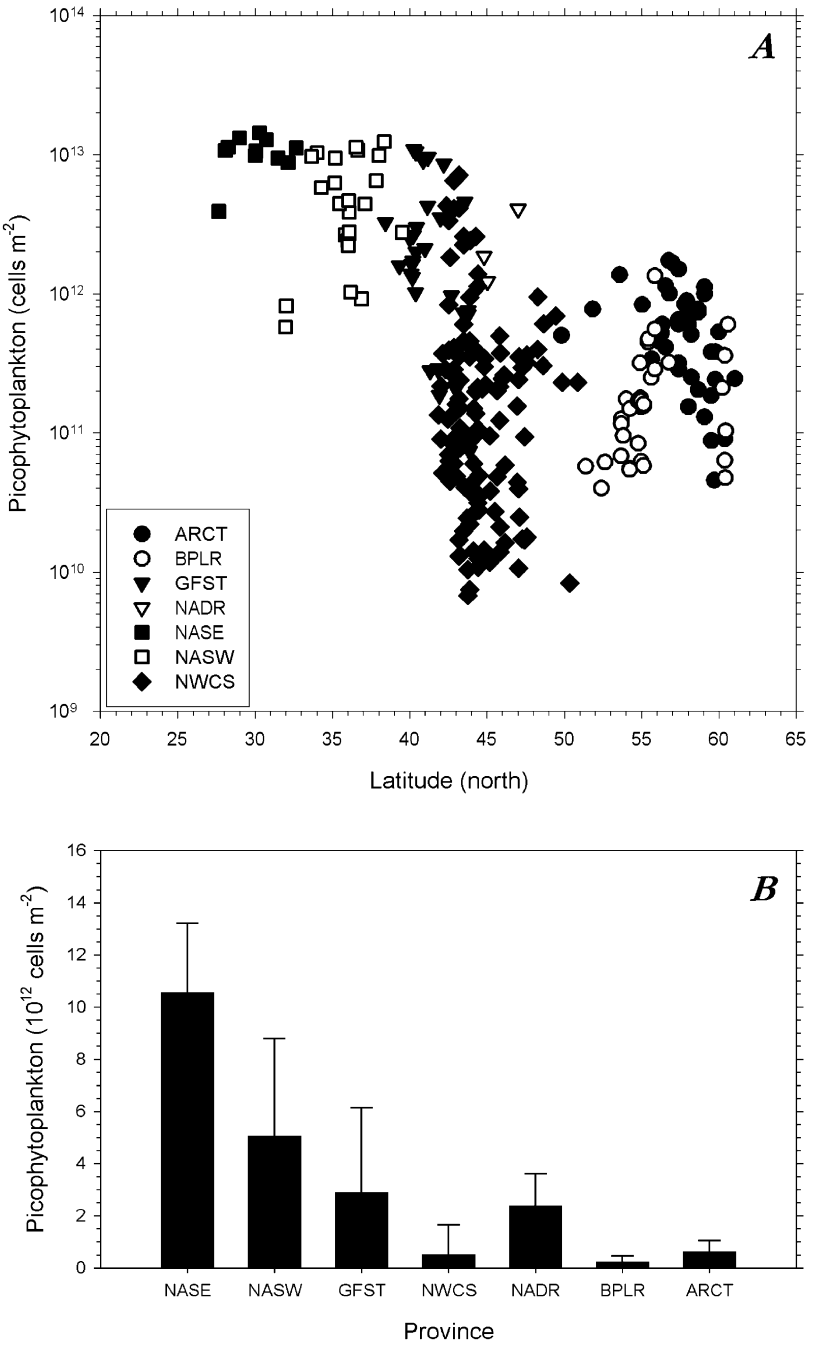

Fig. 11. Same as Fig. 9, except for depth-integrated abundance of picophytoplankton.

apparent outliers with incredibly low Chl values. The average of such ratios were calculated for each province (Fig. 13b, Table 2) and none exceeded unity, ranging from 0.15 in NADR to 0.50 in NASE.

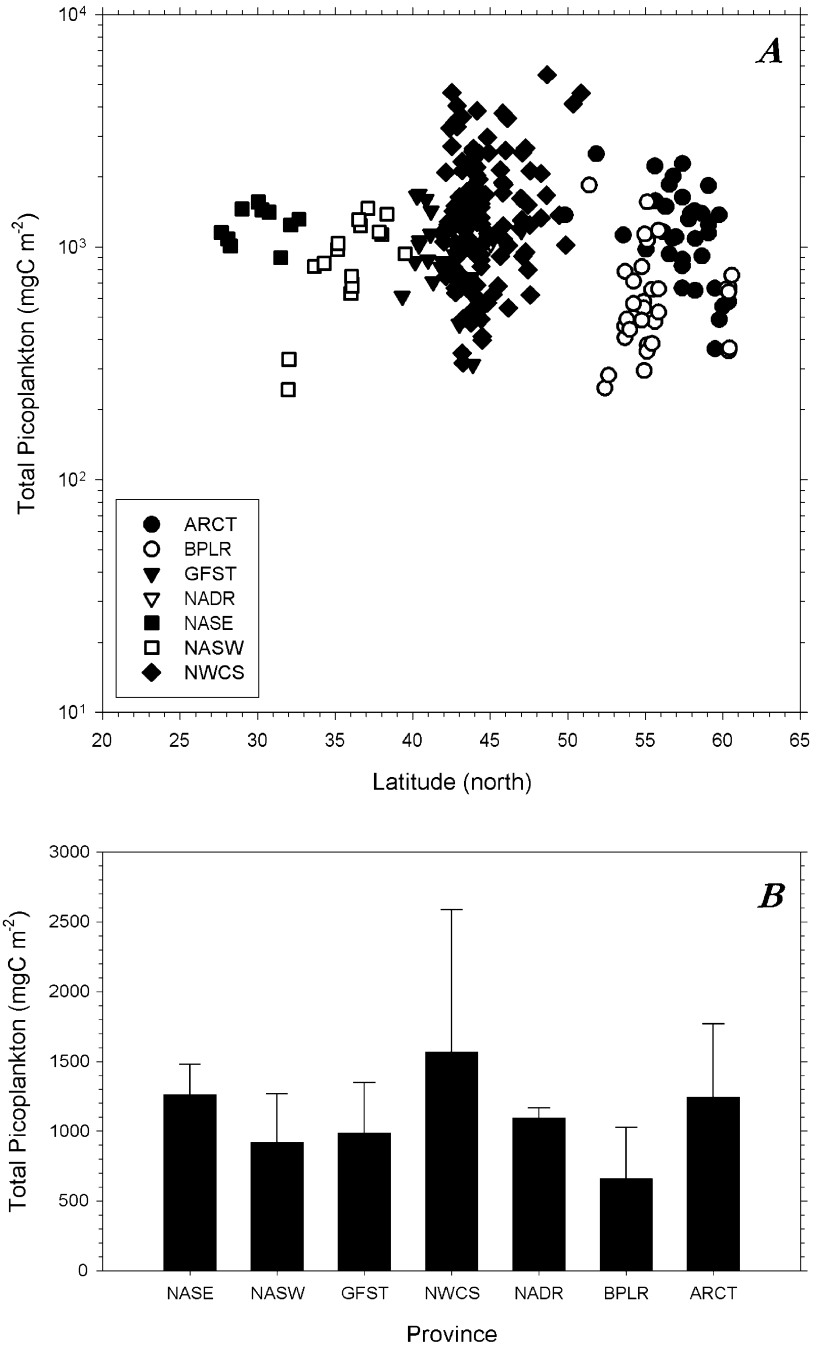

Fig. 12. Same as Fig. 9, except for depth-integrated carbon standing stock of total picoplankton.

We confirmed a different conclusion by considering only the surface samples (results not shown). Because the vertical distribution of Chl and bacteria were not identical, the biomass ratio of bacteria to phytoplankton in surface waters exceeded unity in waters where most of the Chl was in

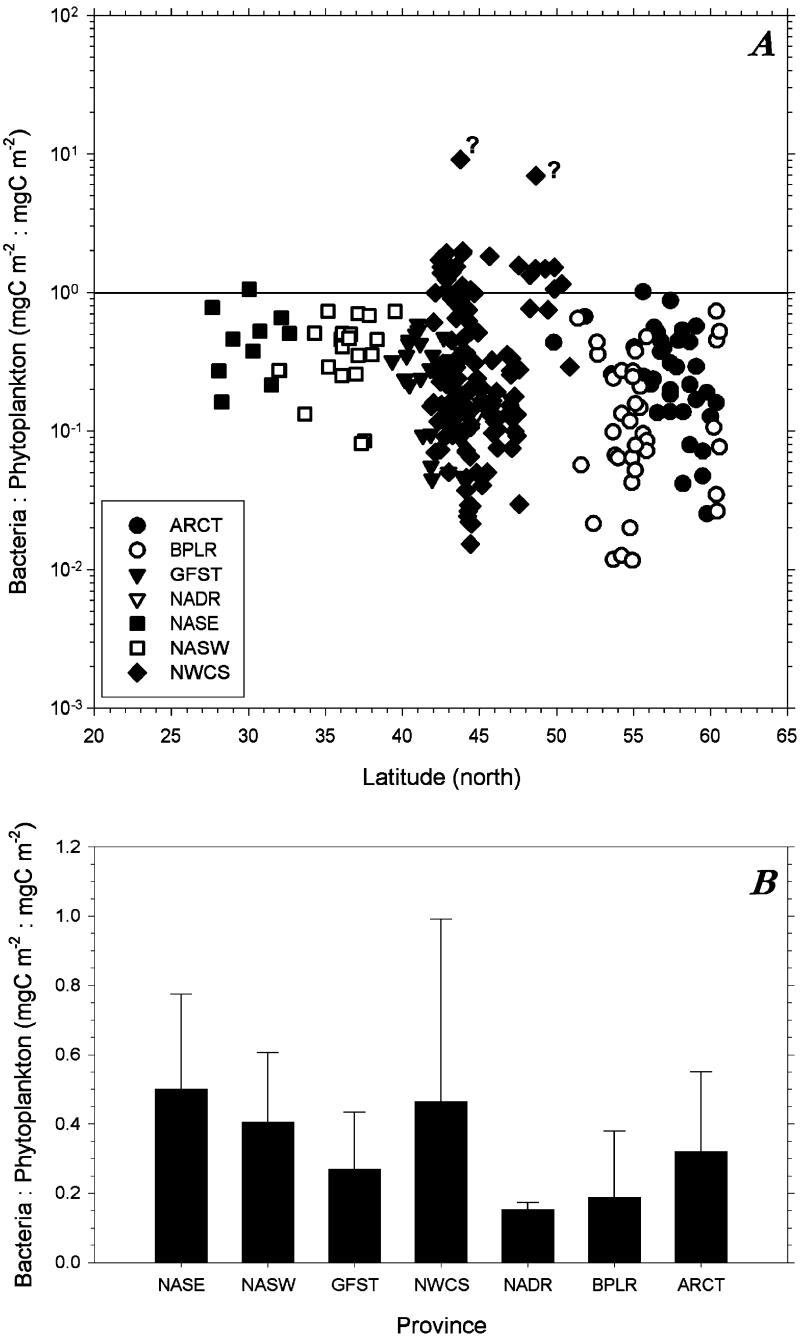

Fig. 13. The ratio of integrated bacterial carbon standing stock to integrated phytoplankton standing stock. (A) Station-by-station plot versus latitude. (B) Average of all stations within each province. At NWCS, the 2 apparent high outliers identified by question marks were excluded from averaging.

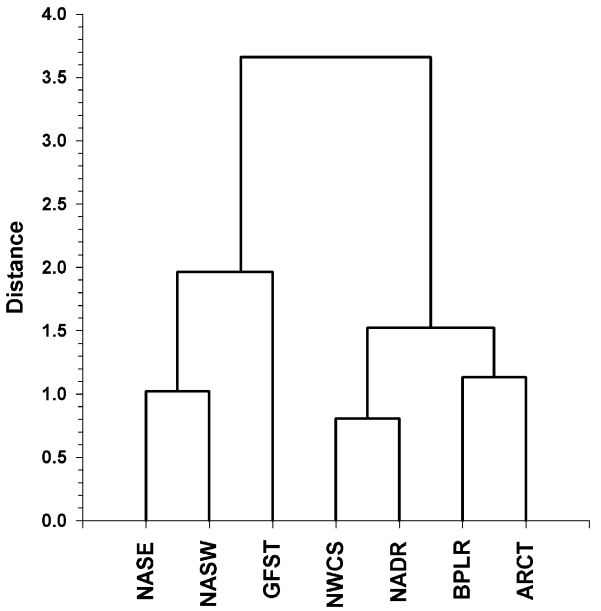

Fig. 14. Cluster analysis of provinces using surface concentrations, integrated stocks and depth of maximum for each of phytoplankton, bacteria and picophytoplankton (Table 2).

deep subsurface layers. At NASE, the average of this ratio in surface waters was 1.7; at NASW, the average was 1.1. Out of 26 stations at these two subtropical provinces, 16 surface samples contained more bacterial biomass than phytoplankton biomass.

3.4. Ratio of picophytoplankton carbon to phytoplankton carbon

Since Chl increased from provinces at low to high latitudes (Fig. 9), and conversely picophytoplankton decreased in the same direction (Fig. 11), the ratio of picophytoplankton to total phytoplankton biomass had a strong negative correlation with Chl (Table 2).

3.5. Cluster analysis

Each province was defined by nine property averages: the surface concentration, the integrated standing stock and the Z_m for each of the three biotic components (Table 2). Cluster analysis employing these properties (Fig. 14) confirmed the expected similarity between NASE and NASW of the subtropical gyre in the lower latitudes, and that between ARCT and BPLR of the polar biome in the high latitudes. In between, GFST clustered closer to the gyre provinces whereas NWCS and NADR clustered towards the polar provinces.

4. Discussion

The partition of the ocean into ecological provinces is perforce a view that plankton communities have discrete characteristics, notwithstanding the provision that boundaries between provinces

are dynamic in both space and time. Yet many prevailing concepts of marine microbial plankton ecology are expressed in terms of a continuum in characteristics, an approach that enjoys some favour (Dandonneau, 1999). Therefore the question, a longstanding one (Begon et al., 1990), arises whether communities have clear boundaries. Longhurst (1998) argues that the discrete and continuum views are not mutually exclusive and both are required for different purposes. For our observations of bacteria and picophytoplankton, an analysis that is referenced only to geographic latitude seems limited in its usefulness. The Longhurst provinces are a logical set of compartments that we have chosen to use, but other rational schemes (summarized by Longhurst, 1998) also might be appropriate. In particular, our detailed surveys on the Scotian Shelf were consolidated into a single province (NWCS), but in fact may profit from subdivision, perhaps according to regions of recognizable fisheries resources.

Much can be inferred about the distributions of heterotrophic bacteria and picophytoplankton from their positions along the continua of sea-surface temperature and Chl (Gasol et al., 1997; Li, 1998). Yet, there is convincing evidence that a different approach might yield additional insight. To illustrate this, we plot our data across the gradient of sea-surface temperature and note that the sea-surface abundance (Cells m^{-3}) of bacteria (Fig. 15a) and picophytoplankton (Fig. 15b) are rather well-arranged along the gradient. However, this is an incomplete representation since we have obviously not included many other waters for which data exist. A marked difference occurs at mid- to high temperatures (say $> 14^{\circ}C$) where a global survey indicates annual average abundance of bacteria often exceeds 1×10^{12} cells m^{-3} (Li, 1998), in contrast to the present data (Fig. 15a).

The partition of the North Atlantic into various provinces based on the seasonal growth of phytoplankton now provides a classification to examine the balance of bacterial and picophytoplankton biomass in relation to total phytoplankton biomass. We take some encouragement that

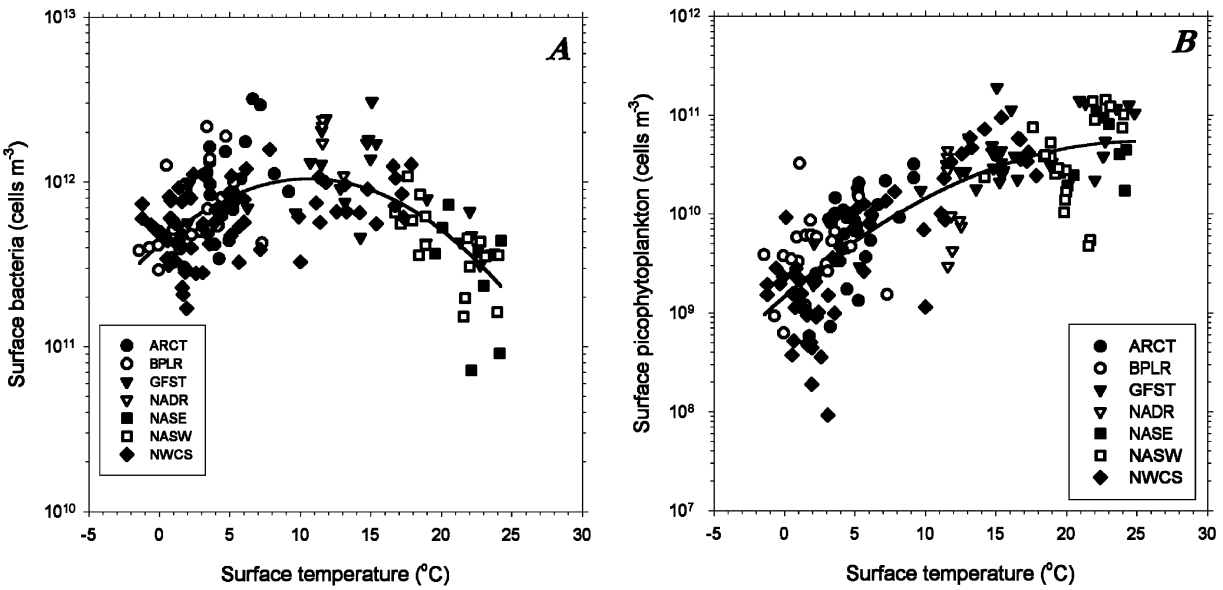

Fig. 15. Abundance of picoplankton at the sea surface versus temperature. (A) Bacteria (B) Picophytoplankton.

Longhurst's classification of the seven provinces appears to be reinforced with the inclusion of bacteria and picophytoplankton, given that the statistical clustering procedure produced no great surprises (Fig. 14). The northward progression in sequence from NASE, NASW, GFST, NWCS, NADR, BPLR to ARCT (Fig. 1b) is a general progression from low to high surface Chl, all seasons considered (http://seawifs.gsfc.nasa.gov/SEAWIFS/CZCS_DATA/global_full.html). However, more careful scrutiny of the progression indicates, as expected, that NWCS in the coastal biome had more Chl (Fig. 9b) and fewer picophytoplankton (Fig. 11b) than NADR, its closest cluster neighbour which is in the open ocean.

Bacteria, which are known to vary much less than Chl (e.g. Gasol et al., 1997) were indeed very similar across all provinces except in ARCT where they were twice as abundant on a depth-integrated basis (Fig. 10b). This organization of bacteria in the provinces at first appears inconsistent with the distribution of surface bacteria along the temperature gradient (Fig. 15a), but is in fact the outcome of depth-integration and averaging over time and location. As a check on the reliability of the surface concentrations of bacteria, we took the seven province averages (Figs. 2–8) together with the average surface temperatures (Fig. 1) and plotted the matched data-pairs (not shown) onto a global survey of annual average abundance versus annual average temperature (Li, 1998). The fit was well-acceptable. In discussing the balance of heterotrophy and autotrophy where the vertical distribution of the plankton components are not identical, generalizations are best made from the depth-integrated values (Williams, 1998).

The reliability of the surface measurements gives assurance that the integrated standing stocks of bacteria (in which we are here interested) are indeed exemplary of the respective provinces. The remarkable similarity in integrated bacteria between all the provinces is provocative (Fig. 10b). The coefficient of variation amongst the seven provinces was only 33%, and is reduced to 20% if ARCT is excluded. At these large time and spatial scales, Ducklow (1992) has suggested that the equilibrium level of bacteria is likely set by bottom–up (resource limitation) control. Further, if the limiting resource for bacteria is directly or indirectly from the resident phytoplankton, it becomes intriguing how the equilibrium is set by such different stocks of Chl as seen in say NASE and NWCS (Fig. 9b), especially since the growth efficiency of bacteria is thought to be positively related to phytoplankton production (del Giorgio and Cole, 1998). In other words, at NASE where phytoplankton production is low (Longhurst et al., 1995), bacteria are respiring a great deal and not growing very much; conversely at NWCS where phytoplankton production is high (Longhurst et al., 1995), bacteria channel their resources more equitably between respiration and growth. Yet, the total number of bacteria in the upper water column appears almost the same in these provinces.

Currently, it is believed that the proportion of metabolically active bacteria is quite small in oligotrophic waters but increases with system productivity (del Giorgio and Scarborough, 1995). If so, the relatively large pool of inactive bacteria accounts for the apparent invariance in total numbers. The concept and functional determination of active bacteria are gaining wider acceptance (Davey and Kell, 1996; Karner and Fuhrman, 1997), but we have not exhausted the useful information to be extracted from the existing store of measurements on total bacteria. At the same time, there is growing recognition that autocatalyzed cell death may be a natural process in phytoplankton (Berges and Falkowski, 1998). New fluorescent stains that permeate only compromised cell membranes suggest that, like bacteria, not all phytoplankton may be viable (Veldhuis and Kraay, 2000). A new biogeography of the active portions of autotrophic and heterotrophic biomass must await a coalescence of these ideas and an accumulation of different data.

Picophytoplankton are the smallest photoautotrophic cells in the ocean. Although much is known about the individual geographic distributions of *Prochlorococcus* and *Synechococcus* (Partensky et al., 1999a, b), we have focused our attention on the distribution of the picophytoplankton as a group because at least 2 of the 3 components (i.e. *Prochlorococcus*, *Synechococcus* and picoeukaryotes) appear to complement each other in the niche available to small marine photoautotrophs (Chisholm, 1992). Thus, whereas *Prochlorococcus* cannot physiologically tolerate low temperatures such as exist at the surface north of about 40°N (Partensky et al., 1999a, b), neither *Synechococcus* nor the picoeukaryotes are restricted in this way. It is evident that picophytoplankters occur in every province (Fig. 11) and their relative abundance contributes to the character of the province classification (Fig. 14). Their contribution to photoautotrophic biomass is very small except at NASE, NASW and GFST (Table 2), but this is not surprising in view of what is known from the large body of information on size-fractionated Chl and the resultant definitions of ecological domains that can be drawn therefrom (Tremblay and Legendre, 1994).

Perhaps less obvious is that the sum of carbon biomass for bacteria and picophytoplankton (Fig. 12) is quite similar for all seven provinces. This sum represents the potential food resource for the micrograzer community of flagellated protists. For example, NASE, ARCT, and NWCS are distantly clustered but show very similar biomass for total picoplankton (heterotrophic plus photoautotrophic), namely $1261\,mg\,C\,m^{-2}$ at NASE, $1570\,mg\,C\,m^{-2}$ at NWCS and $1244\,mg\,C\,m^{-2}$ at ARCT. These three provinces display similar total picoplankton biomass in spite of substantial differences in composition: thus, in NASE, a significant contribution is made by *Prochlorococcus* (Li, 1995); in NWCS, the coastal bacteria are assumed to be more than twice the size of oceanic bacteria (Fukuda et al., 1998); and in ARCT, there is twice the number of bacteria as elsewhere (Fig. 10b).

The mean total picoplankton biomass over all provinces ($1105\,mg\,C\,m^{-2}$) had a coefficient of variation that was small, only 26%. The likelihood that there is grazing selection for different picoplankton prey, by whatever mechanism (Gasol et al., 1995), does not obscure the present conclusion that the heterotrophic and photoautotrophic components of the picoplankton tend to complement each other in a way that their total biomass is more conservative than either component alone.

So far, we have presented a case in which the seven provinces defined by the surface Chl field are shown to have large differences in integrated Chl but not in integrated bacteria. The biomass ratio of the latter to the former, although less informative of the functional nature of communities than the ratio of productivities (Odum, 1971), is related to factors such as the turnover rate of phytoplankton, the presence of detritus supporting heterotrophs, and the export of autotrophs reducing support of heterotrophs (Gasol et al., 1997). A recent analysis of published literature indicated a bacteria : phytoplankton ratio of 1.00 for the open ocean, and 0.62 for coastal waters (Gasol et al., 1997). Greater geographical resolution was given by Ducklow (1992) who reported ratios of 0.24 for the North Atlantic bloom, 0.43 for Gulf stream rings, 0.80 for the Indian Ocean and 0.94 for the subarctic North Pacific. Although the first 2 of these values are arguably similar to those for NADR and GFST respectively (Table 2), the comparisons should be tempered because Ducklow's analysis was based on volumetric (not areal) concentrations and different carbon : Chl ratios.

Whenever biomass is estimated from Chl and cell counts as in the present study, there is always some angst concerning the factors used for converting those measurements to carbon values. We

have previously explained our choice of 40 for the C : Chl conversion (Li et al., 1992, 1993). It is slightly less than values of 47–55 used by Cho and Azam (1990), Simon et al. (1992), Gasol et al. (1997) and Longhurst (1995, 1998), but much less than recent estimates of 87–172 published by Buck et al. (1996). The conversion factor of 40 is conservative because larger values would further strengthen our conclusion that the biomass ratio of bacteria to phytoplankton does not exceed unity.

The conversion of bacterial abundance to biomass is most often based on 20 fg C cell^{-1} (Lee and Fuhrman, 1987), but we have chosen the refined values of Fukuda et al. (1998) who distinguish between larger coastal cells and smaller oceanic cells. There appears to be growing evidence favouring 10 (or so) rather than 20 fg C cell^{-1} for oceanic bacteria (Christian and Karl, 1994). Nevertheless, for the sake of comparing against the large body of literature using the larger conversion factor, we have confirmed (calculations not shown) that none of the provinces would be dominated by bacteria even if they each contained 20 fg C.

We therefore conclude that on a seasonally averaged basis, in the upper water column of large areas in the North Atlantic, the integrated bacterial biomass does not generally exceed the integrated phytoplankton biomass. We have no data from the trade wind biome for the tropical provinces but it appears that autotrophs dominate there (Buck et al., 1996). Although the biomass ratio often exceeds unity in surface waters of the North Atlantic subtropical gyre (see Section 3), the subsurface Chl maximum lowers this ratio for the upper water column as a whole. The summer dominance of bacteria in the subtropical eastern North Atlantic (Buck et al., 1996) is likely not evident on an annual basis since Chl is low during the summer at both NASE and NADR (Longhurst, 1998). In three provinces where we have adequate seasonal data, the biomass ratio of bacteria to phytoplankton was indeed higher in the summer than spring or fall (Fig. 16); but the annual average ratio remained below unity (Fig. 13b). In ARCT, our most recent mission in the Labrador Sea (99-022), completed in July 1999, confirmed the high abundance of summer bacteria, up to 2×10^{14} cells m^{-2} in the upper 200 m at some stations along transect AR7W (unpublished); undoubtedly, this high standing stock is not sustained throughout the year.

An assessment can be made of the bias in our dataset due to uneven sampling over the four seasons (Table 1). For each province, Longhurst (1998) gives the standing stock of Chl on a month-by-month basis. From these, we made two calculations: an unweighted annual average, and an average that was weighted according to our schedule of sampling at each province. The errors due to uneven sampling were 9% at ARCT, 19% at BPLR, 17% at GFST, 5% at NADR, -2% at NASE, 7% at NASW and -4% at NWCS. Not surprisingly, errors tended to be lower in provinces with less seasonality. Thus, the errors were very slight in the subtropical provinces where the bacteria : phytoplankton biomass ratios were highest, though still less than unity (Table 2).

The view we present of the North Atlantic is one that is averaged over depth, time and location. At this level of integration, all details of vertical structure, seasonal variation and local forcing have been smoothed. Where in the continuum view we might record many instances in which the bacteria : phytoplankton biomass ratio is very high, the discrete partitioning of the ocean assigns only one value to each province. In none of the provinces we examined did this ratio exceed unity. This is not to say that autotrophs are necessarily dominant. With the inclusion of the other heterotrophic plankton components (protozoa and mesozooplankton), the hetrotroph to autotroph ratio obviously increases. Expectedly, the ratio is highest in the oligotrophic subtropical

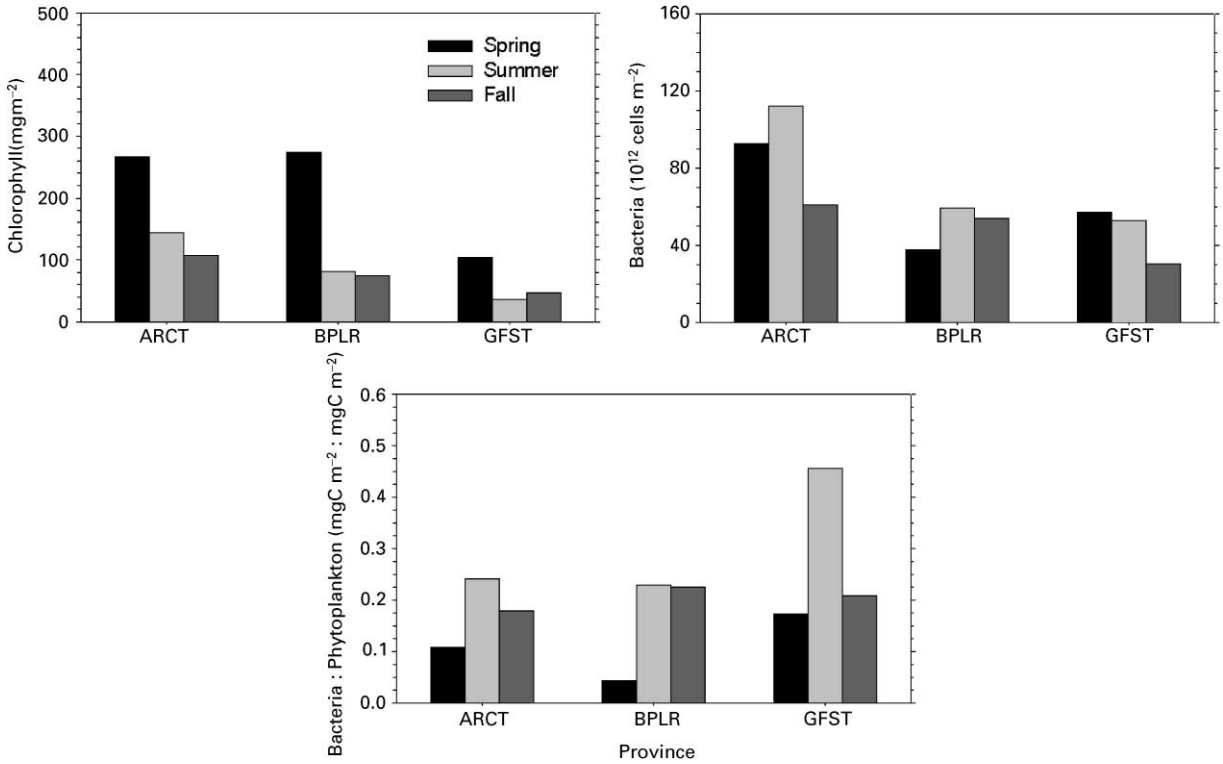

Fig. 16. Seasonal progression from spring to summer to fall of chlorophyll, bacteria and depth-integrated biomass ratio in ARCT, BPLR and GFST.

provinces of NASE and NASW. The ratio also appears high in NWCS, and this is because coastal bacteria are assumed to be larger than oceanic ones. Unexpectedly, the ratio is not as low as might be otherwise surmised in the polar province of ARCT. Here, one might speculate on the reason for the high bacterial standing stocks. Rivkin (unpublished) recently compiled evidence indicating that the growth efficiency of bacterioplankton is inversely related to temperature. If so, this means that bacteria respire less and grow more at low temperatures. Of course there are other possibilities such as reduced mortality but we cannot assess those at this time.

In summary, the partition of the ocean into provinces leads us to view the North Atlantic as a collection of regions where the overall biomass balance is in favour of the phytoplankton over bacteria, and also where the potential food resource for protozoan grazers, namely the picoplankton as a whole, is rather uniform.

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