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Deep-Sea Research I 51 (2004) 1529–1540
DEEP-SEA RESEARCH PART I
www.elsevier.com/locate/dsr

Macroecological limits of heterotrophic bacterial abundance in the ocean

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Received 12 February 2004; accepted 29 June 2004

Abstract

The global association between heterotrophic bacteria and phytoplankton in the open ocean was examined to identify the macroecological limits of bacterial abundance. A consolidated dataset was constructed using 13,973 paired measurements of bacterial abundance and chlorophyll concentration from 15 years of observation in various biogeochemical provinces covering the Atlantic, Pacific, Arctic and Antarctic Oceans as well as the Arabian Sea. The bivariate relationship between bacteria and chlorophyll is a filled polygon whose upper boundary undergoes a change in slope from positive to negative at about 1 mgChl m^{-3}, suggesting a transition from bottom-up to top-down control of bacteria along a resource supply gradient. The upper limit of bacterial abundance in the ocean is everywhere set by phytoplankton, but the limit is not realized in productive waters because of mortality losses. A carrying capacity of about 7 trillion bacteria for 1 mg of chlorophyll is indicated by empirical observations, consistent with theoretical considerations and predictions from food web modelling.

Keywords: Bacterioplankton; Chlorophyll; Comparative analysis; Macroecology; Phytoplankton

1. Introduction

Bacteria and Archaea are the smallest free-living marine organisms. Yet, by virtue of exceedingly large numbers (Whitman et al., 1998), they shape the biology and chemistry of the oceans. Assessing the global influence of these microbes requires, amongst other information, knowledge of their abundance at the largest possible spatial scale. Comparative analysis of statistical patterns (Cole et al., 1991) from different ecosystems is a useful start, but the ideal is to have a dataset so large as to allow the emergence of a common pattern from seemingly diverse relationships (Gasol and Duarte, 2000). Sufficient data now exist to formulate a comparative ecology of heterotrophic bacterioplankton in different ocean provinces (Ducklow and Carlson, 1992; Ducklow, 1999,2002), but an emergent common pattern has yet to be identified from diverse conditions.

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0967-0637/$ - see front matter
doi:10.1016/j.dsr.2004.06.012

A trophic coupling exists between phytoplankton, which is the autochthonous source of labile dissolved organic substrates in the open ocean, and bacteria that utilize those molecules for heterotrophic growth (Nagata, 2000; Morán et al., 2002). The coupling processes include exudation of photosynthates by healthy phytoplankters, the release of dissolved organic matter in the egesta of protozoans and metazoans that have consumed the phytoplankters, and the liberation of phytoplankton cell contents by viral lysis or autolysis (Nagata, 2000). To greater or lesser degrees, the biomasses of heterotrophic bacteria and phytoplankton therefore covary; but the statistical relationship between them is not universal (Simon and Azam, 1992; Gasol and Duarte, 2000). A power slope of less than 1 is indicated from individual studies, signifying that the biomass ratio of bacteria to phytoplankton increases at low levels of phytoplankton. However, there is large scatter about the mean expectations in each case, and the slopes range widely depending on system conditions.

Here we compile a global dataset of 13,973 paired measurements of heterotrophic bacterial abundance and chlorophyll concentration, allowing an examination of large scale associations that subsume local contingencies (Lawton, 1999). We present a macroecological pattern (Li, 2002) that delimits the abundance of heterotrophic bacteria in the open ocean, unifies divergent comparative analyses, and evidences the hypothesized transition of bottom-up to top-down control along trophic gradients.

2. Materials and methods

Data from the Bedford Institute of Oceanography (BIO) were compiled from 28 oceanographic cruises in the North Atlantic Ocean during 515 sea-days that spanned 15 years from 1989 to 2003 (Table 1). Altogether, 8,072 paired measurements of heterotrophic bacterial abundance and chlorophyll concentration were collected from 999 hydrocasts in 7 biogeochemical provinces (Longhurst, 1998): mainly in the Atlantic Arctic (ARCT), Boreal Polar (BPLR), Northwest Atlantic Shelves (NWCS) and Gulf Stream (GFST); to a much lesser extent in the North Atlantic Subtropical Gyre East (NASE), North Atlantic Subtropical Gyre West (NASW) and the North Atlantic Drift (NADR). Analytical methodologies have been described previously (Li and Harrison, 2001).

Data from the International Joint Global Ocean Flux Study (Conkright et al., 2003) were assembled from contributions of the United States, France, Germany, Spain, New Zealand, and United Kingdom (Table 2). The US-JGOFS data were 4,765 paired measurements from the Arabian Sea Expedition, Bermuda Atlantic time-series Study (BATS), equatorial Pacific Ocean process study, Hawaii Ocean time-series (HOT) Program, the Southern Ocean process study and the North Atlantic bloom experiment (NABE). Other JGOFS data were 1145 paired measurements from the French programs in the Mediterranean Sea (DYFAMED, DYNAPROC) and the Pacific Ocean (OLIPAC); the German expeditions in the eastern North Atlantic (M10-1, M10-2), the Arabian Sea (SO120), the South Atlantic (ANT-X/6); the Spanish Antarctic program (Fruela); the international program in the Southern Ocean (SOIREE); and the UK. Biogeochemical Ocean Flux Study (BOFS) contribution in the eastern North Atlantic (NABE). Many research publications have arisen from the JGOFS program (e.g. Ducklow and Harris, 1993; Murray, 1995; Karl and Michaels, 1996; Smith and Anderson, 2000), but there are fewer syntheses of the consolidated data (e.g. Hanson et al., 2000; Fasham, 2003).

In all cases, we compiled paired measurements of bacterial counts (cells m^{-3}) and chlorophyll concentrations (mg m^{-3}). Bacteria are defined operationally as small unicells detected upon nucleic acid staining, either by epifluorescence microscopy or flow cytometry. The protocol presumably includes *Archaea* and recently reported bacteria with novel metabolic capabilities, but these would only be a small percentage of total bacteria in the euphotic zone (Karner et al., 2001; Karl, 2002). Phycoerythrin-containing cyanobacteria (*Synechococcus*) are specifically excluded by their characteristic orange fluorescence. Data

Table 1
The seasonal and geographic distribution of 999 hydrocasts in the North Atlantic from Bedford Institute of Oceanography cruises

Cruise	Season	Start date	End date	Days	ARCT	BPLR	GFST	NADR	NASE	NASW	NWCS	All provinces
89-003	Spring	20-Apr-1989	15-May-1989	26			9	5		5		19
90-001	Spring	9-Apr-1990	27-Apr-1990	19			5			22	8	35
91-001	Spring	4-Apr-1991	19-Apr-1991	16			11			9		20
92-037	Fall	18-Sep-1992	19-Oct-1992	32			9		12	14		35
93-002	Spring	20-May-1993	6-Jun-1993	18			7		6	7		20
94-008	Spring	26-May-1994	8-Jun-1994	14	6	4					2	12
95-016	Summer	6-Jul-1995	23-Jul-1995	18	12	6	5				15	38
96-006	Spring	12-May-1996	30-May-1996	19	5	10	1				18	34
96-026	Fall	20-Oct-1996	17-Nov-1996	29	9	6						15
97-003	Spring	18-Apr-1997	28-Apr-1997	11			2				42	44
97-009	Spring	9-May-1997	1-Jun-1997	24	8	4					6	18
98-002	Spring	8-Apr-1998	26-Apr-1998	19			6				46	52
98-023	Summer	22-Jun-1998	8-Jul-1998	17	3	8					10	21
98-050	Fall	3-Oct-1998	20-Oct-1998	18			5				40	45
99-003	Spring	8-Apr-1999	18-Apr-1999	11			1				36	37
99-022	Summer	27-Jun-1999	12-Jul-1999	16	7	15					10	32
99-054	Fall	23-Oct-1999	12-Nov-1999	21			3				49	52
00-002	Spring	6-Apr-2000	23-Apr-2000	18			3				60	63
00-009	Spring	20-May-2000	8-Jun-2000	20	8	6					3	17
00-050	Fall	30-Sep-2000	16-Oct-2000	17			2				50	52
01-009	Spring	1-May-2001	25-May-2001	25			4				60	64
01-022	Spring	30-May-2001	15-Jun-2001	17	6	20					11	37
01-061	Fall	24-Oct-2001	7-Nov-2001	15			4				58	62
02-032	Summer	23-Jun-2002	16-Jul-2002	24	9	12					37	58
02-064	Fall	18-Oct-2002	31-Oct-2002	14			5				39	44
02-075	Fall	1-Dec-2002	9-Dec-2002	9	11	9						20
03-005	Spring	12-Apr-2003	19-Apr-2003	8			3				22	25
03-038	Summer	13-Jul-2003	1-Aug-2003	20	7	13					8	28
	Spring			265	33	44	52	5	6	43	314	497
	Summer			95	38	54	5	0	0	0	80	177
	Fall			155	20	15	28	0	12	14	236	325
	Total			515	91	113	85	5	18	57	630	999

The numerical entry referenced by cruise (rows) and province (columns) is the number of hydrocast profiles for that time and place

from microscopy can be expected to include *Prochlorococcus*, but the error would be generally small and not confound our results (Gasol et al., 1997). Chlorophyll is defined operationally as the pigment biomass detected from particles retained on glass-fibre membranes, either by fluorometry or by high-performance liquid chromatography. We did not consider any datum reported without its matching variable, which included all the bacterial counts below the euphotic zone where chlorophyll was essentially nil.

3. Results

3.1. General description

The data were from the open ocean and over continental shelves, excluding nearshore and estuarine environments. An overview of the consolidated dataset is given by the frequency distribution of the 2 variables (Fig. 1). Both chlorophyll and bacteria appeared lognormally distributed, with respective geometric medians of

Table 2
The distribution of chlorophyll-bacteria data-pairs collected during the international JGOFS program extracted from Conkright et al. (2003), excluding Canadian data

Country	JGOFS Program	Area	Cruise	Start date/station	End date/station	Chl-Bacteria data-pairs
USA	US-JGOFS	Arabian Sea	ttn043			144
USA	US-JGOFS	Arabian Sea	ttn045			155
USA	US-JGOFS	Arabian Sea	ttn049			178
USA	US-JGOFS	Arabian Sea	ttn050			270
USA	US-JGOFS	Arabian Sea	ttn054			294
USA	BATS	Bermuda		21-Oct-1988	18-Oct-2000	1495
USA	EQPAC	Equatorial Pacific	tt007			323
USA	EQPAC	Equatorial Pacific	tt008			75
USA	EQPAC	Equatorial Pacific	tt011			233
USA	EQPAC	Equatorial Pacific	tt012			92
USA	HOT	Hawaii		1-Feb-1991	24-Sep-1995	519
USA	NABE	North Atlantic	atlantis			175
USA	NABE	North Atlantic	endeavor			24
USA	AESOPS	Southern Ocean	nbp96-4A			98
USA	AESOPS	Southern Ocean	nbp97_1			65
USA	AESOPS	Southern Ocean	nbp97_3			65
USA	AESOPS	Southern Ocean	nbp97_8			136
USA	AESOPS	Southern Ocean	rr-kiwi_6			19
USA	AESOPS	Southern Ocean	rr-kiwi_7			164
USA	AESOPS	Southern Ocean	rr-kiwi_8			38
USA	AESOPS	Southern Ocean	rr-kiwi_9			203
France	OLIPAC	Equatorial Pacific		18-Nov-1990	20-Nov-1990	65
France	DYFAMED	Mediterranean Sea		16-Jun-1998	20-Feb-2001	196
France	DYNAPROC	Mediterranean Sea		10-May-1991	30-May-1991	41
Germany	German-JGOFS	Northeast Atlantic	Meteor10/1			8
Germany	German-JGOFS	Northeast Atlantic	Meteor10/2			143
Germany	German-JGOFS	Arabian Sea	Sonne120			12
Germany	German-JGOFS	South Atlantic	ANTX6	857C1	972C2	454
New Zealand	SOIREE	Southern Ocean		T1141	T1171	56
Spain	FRUELA	Southern Ocean		5	225.1	73
United Kingdom	BOFS	North Atlantic				98
Total						*5910*

0.28 mgChl m^{-3} and 4.5×10^{11} bacteria m^{-3}. The maximum values were 24.6 mgChl m^{-3}, recorded in the Southern Ocean during the Spanish program Fruela in February 1996; and 4.94×10^{12} bacteria m^{-3} recorded in the Arabian Sea during the USA cruise ttn-050 in September 1995. The abundance of bacteria was remarkably constrained in the ocean, with 92% of the observations within 1 order of magnitude around the mean value. Chlorophyll values spanned 4.4 orders of magnitude, a much wider range than the bacterial values (Fig. 1).

Phytoplankton have an obligate requirement for light whilst heterotrophic bacteria do not. The data were therefore separated into 2 groups using a nominal depth of 50 m to distinguish between the upper strongly lit zone, and the lower dimly lit zone of the water column. Geometric medians for both chlorophyll and bacteria were higher in the upper than the lower zone (Fig. 1). For chlorophyll, the medians were 0.59 and 0.13 mgChl m^{-3}, respectively; for bacteria, the medians were 6.0×10^{11} and 3.3×10^{11} cells m^{-3}, respectively.

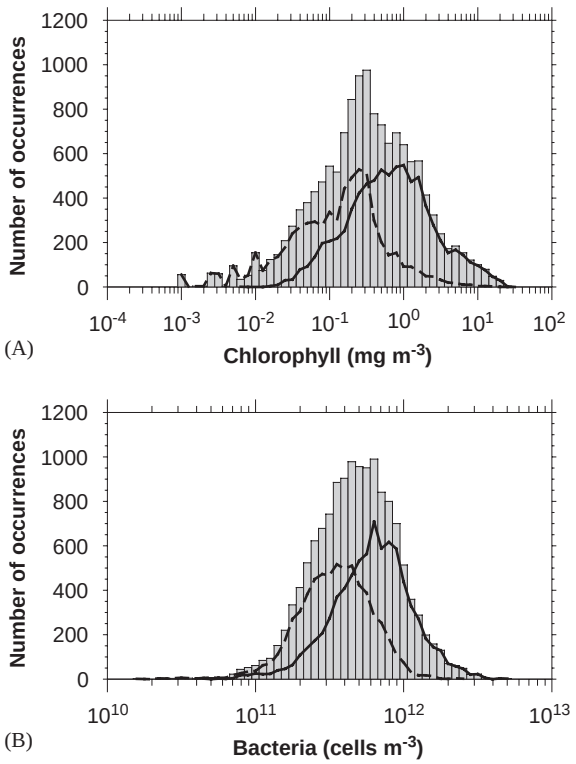

Fig. 1. Frequency distribution of the variables. (A) Chlorophyll in the consolidated dataset (bars, $n=13{,}973$), in the subset of samples $\leqslant 50$ m depth (solid line, $n=7728$), and in the subset of samples >50 m depth (dashed line, $n=6245$). (B) Bacteria, symbols and sample numbers as for chlorophyll.

3.2. Bivariate relationship between bacteria and chlorophyll

Taking a comparative approach to the relationship between bacteria and chlorophyll in various biogeochemical provinces (Fig. 2), we confirm that the power slope between these variables was positive and less than 1. The model 2 regression slope ranged from 0.34 to 0.59, and averaged 0.46 ± 0.09 over the provinces examined (Table 3).

In a departure from comparing diverse ecosystems, we consolidated all the data in a macroecological approach to seek a common pattern (Fig. 3). In this way, the bivariate relationship between bacteria and chlorophyll can be visualized as a filled polygon whose boundaries are the upper (99 percentile) and lower (5 percentile) limits of bacterial distributions within binned intervals of chlorophyll. In the upper 50 m of the water column where autotrophic–heterotrophic coupling can be expected to be most intense, there was a convergence of bacterial maxima and minima at both the low and high end of the chlorophyll range (Fig. 3B). The interior of the polygon was completely filled with data expressing the realizations of oceanic conditions at 7728 space-time coordinates. Conversely, combinations outside the boundary limits were rarely observed in the open ocean.

A significant feature of the upper boundary was the inflection of slope at about 1 mgChl m^{-3}. The slope changed from positive at low chlorophyll to negative at high chlorophyll. The same was true of the line depicting median bacterial values. Thus, in most low chlorophyll regimes (0.01–1 mgChl m^{-3}), bacterial abundance increased with phytoplankton biomass, but not in direct proportion, as indicated by power slopes of less than unity, namely 0.44 for the upper limit and 0.22 for the median (Fig. 3B). Conversely, in most high chlorophyll regimes in the open ocean (>1 mgChl m^{-3}), bacteria decreased with phytoplankton biomass. This was most evident in 3 North Atlantic provinces that sustain high chlorophyll levels in the spring and summer (ARCT, BPLR, NWCS); however, a decreasing bacterial upper boundary at high chlorophyll was somewhat discernible even in provinces with fewer observations exceeding 1 mgChl m^{-3} (ANTA + APLR, GFST) (Fig. 2). Other provinces at lower latitudes (NASW, NPTG, PEQD, ARAB) did not have many observations exceeding 1 mgChl m^{-3} (Fig. 2). The upper boundary of bacterial abundance was well-defined by the numerous observations in just the single province of NWCS (Fig. 2), but the boundary appeared to be common across all provinces (Fig. 3), indicating a universal pattern.

3.3. Relationship of bacteria to temperature

The frequency distribution of bacteria in the upper 50 m shifted towards higher abundance from -2 to 15 °C, then towards lower abundance from 15 to 25 °C (Fig. 4). An analysis of variance

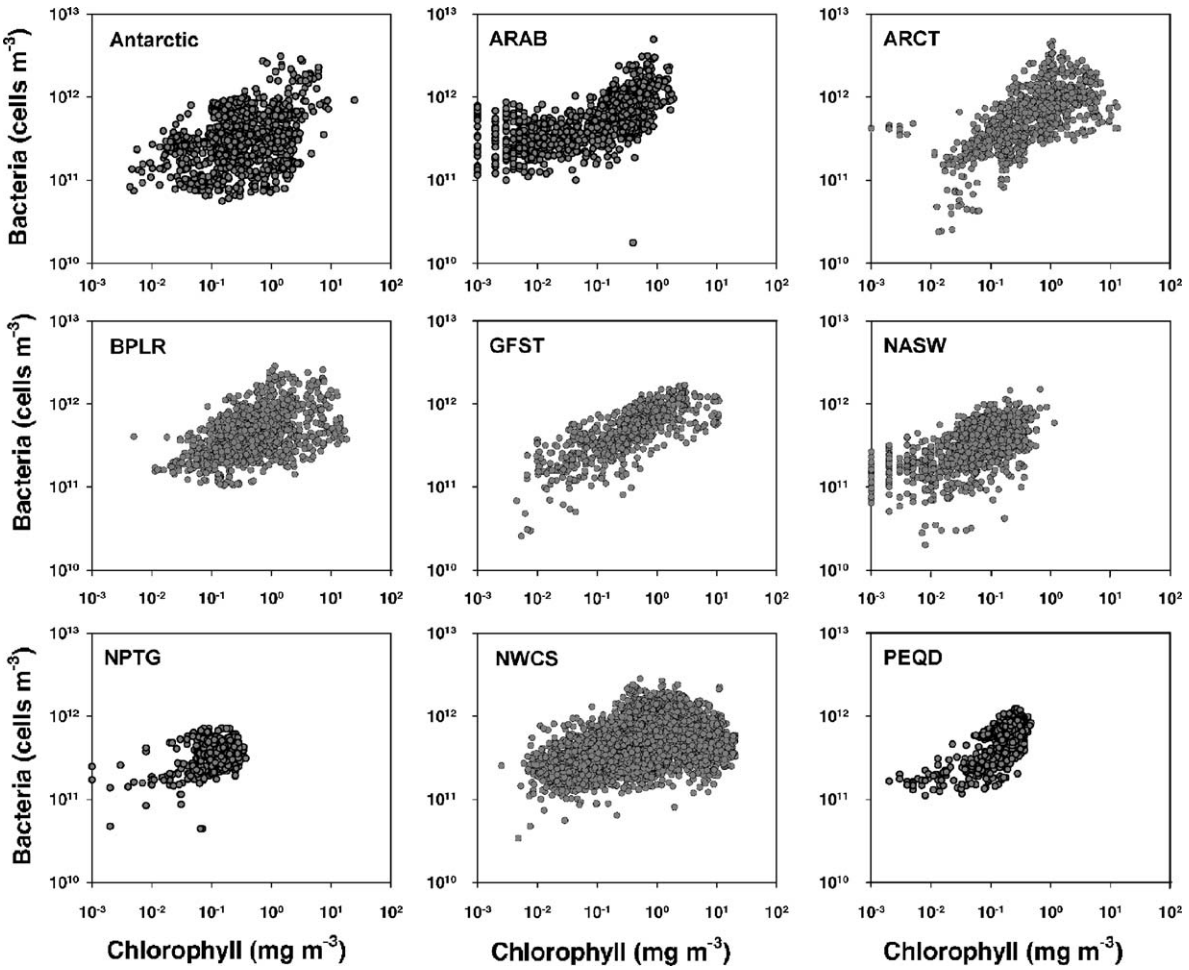

Fig. 2. Comparative analysis of the relationship between bacterial abundance and chlorophyll concentration in biogeochemical provinces: Antarctic, combining ANTA and APLR (US Southern Ocean process study, Spain FRUELA program, international SOIREE program, Table 2), ARAB (US Arabian Sea expedition, Table 2), ARCT (Canada, Table 1), BPLR (Canada, Table 1), GFST (Canada, Table 1), NASW (US Bermuda Atlantic time-series study, Table 2), NPTG (US Hawaii Ocean time-series program, Table 2), NWCS (Canada, Table 1), PEQD (US Equatorial Pacific Ocean process study, France OliPac study, Table 2).

of log bacterial abundance classified into 5 successive temperature intervals (of approximately 5 °C width) indicated a highly significant effect of temperature on mean abundance ($F_{[4,5142]} = 191$, $p \ll 0.001$). However, the range from minimum to maximum abundance overlapped greatly amongst the successive temperature intervals (Fig. 4). We found that the limits of bacteria were not indicated by temperature alone, but rather in conjunction with chlorophyll. In fact, multiple regression of log bacterial abundance versus temperature and log chlorophyll concentration was highly significant ($F_{[2,4797]} = 539$, $p \ll 0.001$) and indicated very similar standardized strengths of the independent variable effects, namely beta coefficients of 0.35 for temperature and 0.38 for chlorophyll.

A notable pattern emerged when the ratio of bacteria to chlorophyll (cells mg^{-1}) was examined in relation to temperature (Fig. 5A). This ratio was almost always near its maximum value at high

Table 3
Comparative analysis by Model II linear regression of the relationship between log bacterial abundance (Y) and log chlorophyll concentration (X) in various biogeochemical provinces

Abbreviation	Province	Y-intercept	Slope	SE of slope	r^2
ANTA + APLR	Antarctic + Austral Polar	11.777	0.530	0.016	0.137
ARAB	Northwestern Arabian Upwelling	12.087	0.339	0.008	0.440
ARCT	Atlantic Arctic	11.944	0.546	0.014	0.422
BPLR	Boreal Polar	11.769	0.456	0.012	0.254
GFST	Gulf Stream	11.863	0.423	0.011	0.581
NASW	North Atlantic Subtropical Gyre West	12.062	0.441	0.009	0.383
NPTG	North Pacific Tropical Gyre	11.971	0.456	0.019	0.128
NWCS	Northwest Atlantic Shelves	11.786	0.345	0.004	0.233
PEQD	Pacific Equatorial Divergence	12.195	0.592	0.016	0.438
Average		*11.939*	*0.459*		

temperatures, but the ratio could assume much lower values at low temperatures (Fig. 5A). By binning the observations into successive 1° temperature intervals, we found that the logarithm of this ratio at percentile p, ($\boldsymbol{Y_p}$) was approximately linear with temperature, $\boldsymbol{T}$:

$$\boldsymbol{Y_{99}} = 12.79 + 0.0046T (r = 0.33,\ p > 0.05),$$

$$\boldsymbol{Y_{50}} = 11.66 + 0.033T (r = 0.92,\ p < 0.01),$$

$$\boldsymbol{Y_{5}} = 10.83 + 0.054T (r = 0.90,\ p < 0.01).$$

Since the regression of $\boldsymbol{Y_{99}}$ was not statistically significant, we took its average value independent of temperature, which was 12.85. In other words, everywhere in the open ocean, bacteria were constrained to be no more abundant than about 7×10^{12} cells m^{-3} (antilog 12.85) for every 1 mgChl m^{-3} of prevailing phytoplankton biomass.

4. Discussion

The covariation between bacterial abundance and phytoplankton biomass has been described as one of the few undisputed patterns in aquatic microbial ecology (Gasol and Duarte, 2000). It manifests the dependence of bacteria on resources supplied to them by phytoplankton, either directly through exudation of labile organic photosynthates or cell lysis, or indirectly through egestion from phytoplankton grazers. An assessment of this linkage requires measuring the extent to which primary production satisfies bacterial carbon demand (Morán et al., 2002). These measurements indicate a strong coupling in open ocean environments away from coastal inputs of dissolved organic carbon. Alternatively, the extent to which bacteria are controlled by resource supply can be examined by the relationship between bacterial biomass and bacterial production rate (Billen et al., 1990). Here, the production rate is a surrogate for the substrate supply rate, with which it is assumed to be in balance. This approach indicates that at large scales, resource limitation indeed regulates bacterial biomass, but there is modulation by loss processes at other scales (Ducklow, 1992). However, the most widely used surrogate for resource supply to bacteria is chlorophyll biomass. Although chlorophyll is not a robust indicator of organic matter flux, its extensive pragmatic use in comparative analyses has provided many testable inferences on microbial food webs (Ducklow and Carlson, 1992; Gasol and Duarte, 2000).

There is already a wealth of information on the bacteria-chlorophyll relationship in many ecosystems. Our comparative analysis of data partitioned into biogeochemical provinces (Fig. 2) confirmed the significance of this relationship on a global basis. In fact, the slope averaged across numerous provinces, namely 0.46 ± 0.09 (Table 3), was

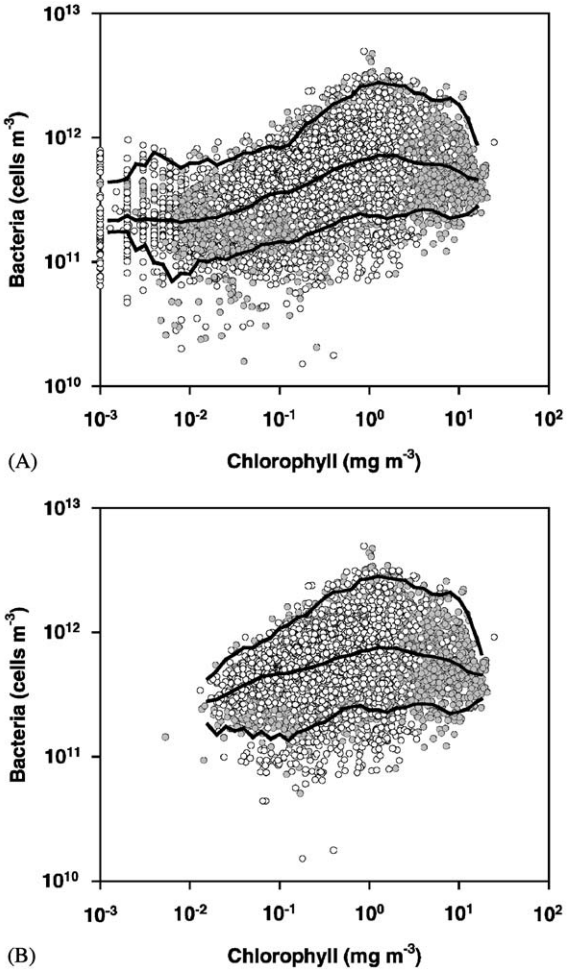

Fig. 3. Macroecological analysis of the relationship between bacterial abundance and chlorophyll concentration in the entire consolidated dataset (A), and the subset of samples at depths $\leqslant 50$ m (B). Quantile lines are constructed from bacterial distributions within successive binned chlorophyll intervals of 0.1 logarithmic unit (99 percentile = upper; 50 percentile = middle; 5 percentile = lower). Data from Bedford Institute of Oceanography (grey) and from international JGOFS programs (white).

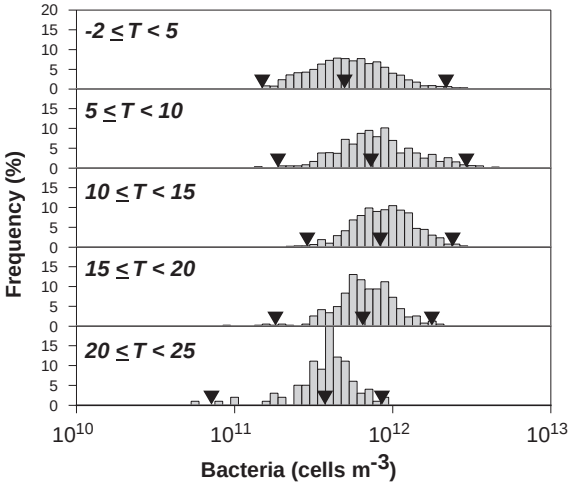

Fig. 4. Normalized frequency distribution of bacterial abundance in 5 temperature intervals. Data of BIO samples at depths $\leqslant 50$ m. Quantiles are marked by triangles (99 percentile = right; 50 percentile = middle; 1 percentile = left).

statistically identical to the average of 0.47 ± 0.03 compiled from other earlier studies (Gasol and Duarte, 2000). We have possibly now arrived at the state where "the empirical basis for the relationship is so substantial as to suffer little change from the investigation of additional ecosystems" and where the limitation of non-random sampling is "surpassed once the data sets and comparative analyses become so large as to allow the emergence of a common pattern from the seemingly diverse relationships" (Gasol and Duarte, 2000).

A new perspective of the bacteria-phytoplankton relationship emerged when the data were consolidated as a whole (Fig. 3). Instead of comparing ecosystems according to their different responses, we recognize that local contingencies inevitably lead to variability. At the biological community level, there are thousands of case histories and overwhelming details of ecological interactions that complicate any general relationship (Lawton, 1999). However, at the macroecological scale, detail-free patterns may be revealed quite clearly. Thus, whereas the positive power slope between bacteria and chlorophyll has been confirmed in many cases, a negative slope has not.

This negative slope, contra-indicating the trophic coupling of bacteria with phytoplankton (Fig. 3) suggests top-down control on bacteria, say by bacterivores and viruses. Usually, strong mortality is inferred by a less positive, or even zero slope in the relationship between bacterial biomass and resource gradient (Pace and Cole, 1994). However, the possibility is admitted that the

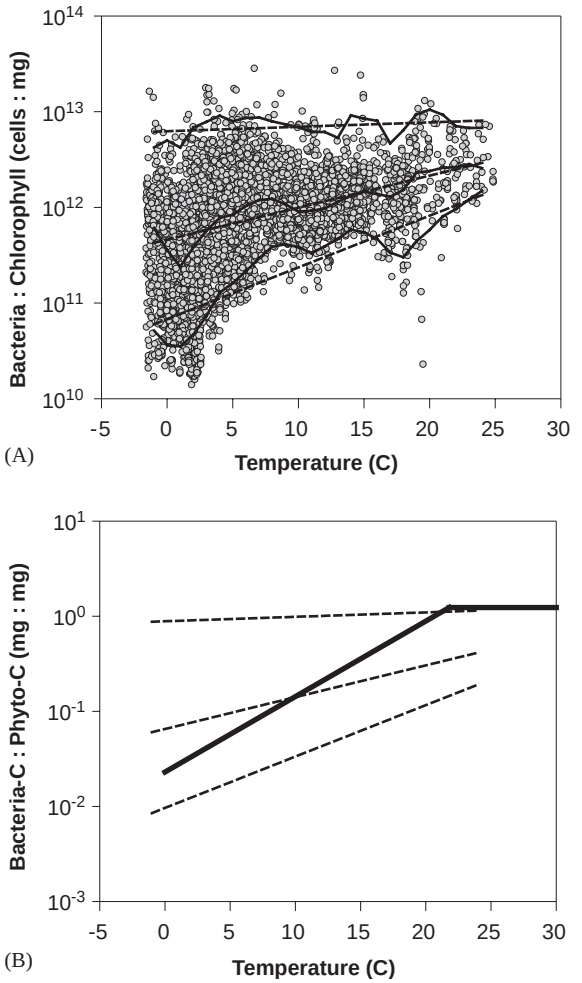

Fig. 5. (A) Temperature dependence of the ratio of bacterial abundance to chlorophyll concentration. Data of BIO samples at depths $\leqslant 50$ m. Quantile lines are constructed from ratio distributions within successive binned temperature intervals of 1 °C (99 percentile = upper; 50 percentile = middle; 5 percentile = lower). Dashed lines are linear regressions as described in the text. (B) Temperature dependence of the ratio of bacterial carbon biomass to phytoplankton carbon biomass. Quantile regression lines (dashed lines) are converted from panel A using factors described in the text. Model output from Laws et al., 2000 (solid line).

response of bacteria might be nonlinear especially at higher resource levels (Pace and Cole, 1994). The observed nonlinearity in bacterial slope, from positive at low chlorophyll levels to negative at high chlorophyll levels (Fig. 3), can thus be taken as a transition from bottom-up to top-down control. Along a resource or productivity gradient, there is an intermediate point where the decreasing intensity of autotrophic–osmoheterotrophic coupling is matched by the increasing intensity of phagotrophic–osmoheterotrophic coupling (Cotner and Biddanda, 2002). We infer that this cross-over point is marked by the inflection of slope evident in the macroecological upper bound and median (Fig. 3). In high chlorophyll regimes, the extent of grazing or viral loss is presumably the difference between the actual bacterial abundance and a presumed maximum (loss-free) abundance that is represented by a straight line extrapolation from the low chlorophyll regime. This follows the suggestion by Gasol (1994) that the same might be true for the bacterivores themselves: that is, along a gradient of bacteria, which is the resource for nanoflagellate grazers, the distance between the maximum possible concentration of these nanoflagellates and their actual concentration is a measure of top-down control on these bacterivores.

Bacteria reached their maximum abundance in waters with an intermediate level of chlorophyll, and also in waters of intermediate temperature (Fig. 4). Earlier, we recognized that the annual average abundance of bacteria increased with the annual sea surface temperature up to about 14 °C, approximating the temperature of waters in the global ocean in which surface nitrate concentrations are usually low (Li, 1998). This trend is now confirmed by the median bacterial abundances of a much larger dataset (Fig. 4). In oceanic regions, temperature is often a suitable indicator for physical oceanographic processes that influence pelagic community structure (Bouman et al., 2003) and biogeochemistry (Laws et al., 2000). We have therefore examined the extent to which bacteria are supported by phytoplankton (by the ratio of bacterial abundance to chlorophyll concentration, cells mg^{-1}) across the global geographic continuum indexed by temperature. We found that in 99% of cases, bacteria appeared constrained to be no more abundant than about 7×10^{12} cells for every 1 mg Chl of prevailing phytoplankton biomass (Fig. 5A). This can be taken as the capacity of bacterial stocks supported by phytoplankton in

the open ocean. The median concentration of chlorophyll in the upper 50 m is 0.59 mg m^{-3} (Fig. 1A), implying a representative bacterial carrying capacity of 4.2×10^{12} cells m^{-3}. Theoretical estimates of this carrying capacity based on the flux of utilizable organic matter from primary production and cellular maintenance efficiency are from 4 to 8×10^{12} cells m^{-3} (Ducklow, 2001). The agreement between observation and theory is good. Nearshore and estuarine environments receiving significant allochthonous organic input to sustain high bacterial popluations would not necessarily be limited at this level. Inshore inlets influenced by anthropogenic inputs and shellfish aquaculture are examples where bacterial abundances frequently exceed the 99 percentile open ocean values (Harrison et al., 2004).

The ecological significance of the bacterial carrying capacity is highlighted by expressing bacteria and chlorophyll in common units of cellular carbon. Conversion factors must be selected from the literature. For oceanic bacteria, the encyclopedia gives a range from 7 to 15 fgC $cell^{-1}$ (Ducklow, 2001). We choose a value of 7.1 fgC $cell^{-1}$, which is the geometric mean value arising from recent X-ray microanalytical measurements of single cells from natural populations (Gundersen et al., 2002). For phytoplankton, the carbon to chlorophyll ratio ranges from about 20 to 150 (Laws et al., 2000). We choose a value of 50 mgC $mgChl^{-1}$, which is approximately the geometric mean of the observed extremes, and is also the value used in influential comparative analyses (Simon et al., 1992; Gasol et al., 1997). The ratio of bacterial carbon to phytoplankton carbon thus calculated is compared with predictions from a food web model in which bacteria are influenced by both bottom-up and top-down factors (Laws et al., 2000). The transformed observations and model predictions both indicate an upper limit for the biomass ratio (Fig. 5B). Below the upper limit, the biomass ratio falls with decreasing temperature, even though bacterial growth efficiency is thought to be inversely related to temperature (Rivkin and Legendre, 2001). These opposing trends can be reconciled if the relative production of extracellular photosynthate by phytoplankton increases with temperature, which would be consistent with the demonstrated increase of extracellular release in oligotrophic conditions (Morán et al., 2002).

The upper ratio of 7.08×10^{12} bacteria per 1 mg Chl (Fig. 5A) is equivalent to 50 mg bacterial carbon per 50 mg phytoplankton carbon. In other words, the equivalence of bacterial and phytoplankton carbon biomass is an upper constraint in the open ocean. Our earlier, less detailed work in the Sargasso Sea had indicated this possibility of bacteria–phytoplankton co-dominance (Li et al., 1992). Since it is an oversimplification to assume that bacteria and phytoplankton retain a fixed carbon quota everywhere in the ocean, this broad generalization might be expected to be contingent upon local conditions at smaller scales. Nevertheless, the use of average quantities to characterize macroecological processes at the global scale appears justified in view of their effective use at the scale of biogeochemical provinces (Ducklow, 2003).

In summary, the macroecological relationship between bacteria and chlorophyll (Fig. 3) unifies divergent comparative analyses of different ecosystems (Fig. 2). The upper limit of bacterial abundance in the ocean is everywhere set by phytoplankton (Fig. 5), but the limit is not realized in productive waters because of losses to grazers and viruses. A canonical upper limit of about 7 trillion bacteria for 1 mg of chlorophyll is suggested.

Acknowledgements

We thank all sea-going staff of the Biological Oceanography Section at Bedford Institute of Oceanography for collecting samples. We acknowledge the contributions from the International JGOFS project and all its multinational participants; their names are recorded in the JGOFS-DVD (Conkright et al., 2003). We especially thank Josep Gasol and Trevor Platt for their comments. Financial assistance was provided by the Department of Fisheries and Oceans Strategic Science Fund (SSF) and the Program of Energy Research and Development (PERD), Natural Resources Canada.

References

Billen, G., Servais, P., Becquevort, S., 1990. Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: bottom-up or top-down control? Hydrobiologia 207, 37–42.

Bouman, H.A., Platt, T., Sathyendranath, S., Li, W.K.W., Stuart, V., Fuentes-Yaco, C., Maass, H., Horne, E.P.W., Ulloa, O., Lutz, V., Kyewalyanga, M., 2003. Temperature as indicator of optical properties and community structure of marine phytoplankton: implications for remote sensing. Marine Ecology Progress Series 258, 19–30.

Cole, J., Lovett, G., Findlay, S. (Eds.), 1991, Comparative Analyses of Ecosystems: Patterns, Mechanisms and Theories. Springer, NewYork 375pp.

Conkright, M., Avril, B., Chandler, C., Griffiths, B., Herrmann, J., Lowry, R., Miyake, T., Sarupria, J., Spear, D., Torre, M.-P., 2003. JGOFS International Data Collection. DVD Vol. 1: discrete datasets, 1989–2000, http://www.uib.no/jgofs/Publications/datasets/DVDreadme.pdf.

Cotner, J.B., Biddanda, B.A., 2002. Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems. Ecosystems 5, 105–121.

Ducklow, H.W., 1992. Factors regulating bottom-up control of bacteria biomass in open ocean plankton communities. Archives in Hydrobiology Beih. 37, 207–217.

Ducklow, H.W., 1999. The bacterial component of the oceanic euphotic zone. FEMS Microbiology Ecology 30, 1–10.

Ducklow, H.W., 2001. Bacterioplankton. In: Steele, J.H., Thorpe, S.A., Turekian, K.K. (Eds.), Encyclopedia of Ocean Sciences. Academic Press, San Diego, pp. 217–224.

Ducklow, H.W., 2002. Bacterial production and biomass in the oceans. In: Kirchman, D.L. (Ed.), Microbial Ecology of the Oceans. Wiley-Liss, NewYork, pp. 85–120.

Ducklow, H.W., 2003. Biogeochemical provinces: towards a JGOFS synthesis. In: Fasham, M.J.R. (Ed.), Ocean Biogeochemistry: The Role of the Ocean Carbon Cycle in Global Change. Springer, Berlin, pp. 3–17.

Ducklow, H.W., Carlson, C.A., 1992. Oceanic bacterial production. Advances in Microbial Ecology 12, 113–181.

Ducklow, H.W., Harris, R. (Eds.), 1993. JGOFS North Atlantic bloom experiment. Deep-Sea Research II 40:1–641.

Fasham, M.J.R. (Ed.), 2003, Ocean Biogeochemistry: The Role of the Ocean Carbon Cycle in Global Change. Springer, Berlin.

Gasol, J.M., 1994. A framework for the assessment of top-down vs. bottom-up control of heterotrophic nanoflagellate abundance. Marine Ecology Progress Series 113, 291–300.

Gasol, J.M., del Giorgio, P.A., Duarte, C.M., 1997. Biomass distribution in marine planktonic communities. Limnology and Oceanography 42, 1353–1363.

Gasol, J.M., Duarte, C.M., 2000. Comparative analyses in aquatic microbial ecology: how far do they go? FEMS Microbiology Ecology 31, 99–106.

Gundersen, K., Heldal, M., Norland, S., Purdie, D., Knap, A.H., 2002. Elemental C,N, and P cell content of individual bacteria collected at the Bermuda Atlantic Time-series Study (BATS) site. Limnology and Oceanography 47, 1525–1530.

Hanson, R.B., Ducklow, H.W., Field, J.G. (Eds.), 2000, The changing ocean carbon cycle, a midterm synthesis of Joint Global Ocean Flux Study. Cambridge University Press, Cambridge.

Harrison, W.G., Perry, T., Li, W.K.W., 2004. Ecosystem indicators of water quality. I. Plankton biomass, primary production and nutrient demand. Handbook of Environmental Chemistry, vol. 5. Springer, Berlin accepted for publication.

Karl, D.M., 2002. Hidden in a sea of microbes. Nature 415, 590–591.

Karl, D.M., Michaels, A.F. (Eds.), 1996. Ocean Time Series:Results from the Hawaii and Bermuda Research Programs. Deep-Sea Research II 43, 127–685.

Karner, M.B., DeLong, E.F., Karl, D.M., 2001. Archaeal dominance in the mesopelagic zone of the Pacific Ocean. Nature 409, 507–510.

Laws, E.A., Falkowski, P.G., Smith Jr., W.O., Ducklow, H., McCarthy, J.J., 2000. Temperature effects on export production in the open ocean. Global Biogeochemical Cycles 14, 1231–1246.

Lawton, J.H., 1999. Are there general laws in ecology? Oikos 84, 177–192.

Li, W.K.W., 1998. Annual average abundance of heterotrophic bacteria and *Synechococcus* in surface ocean waters. Limnology and Oceanography 43, 1746–1753.

Li, W.K.W., 2002. Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. Nature 419, 154–157.

Li, W.K.W., Dickie, P.M., Irwin, B.D., Wood, A.M., 1992. Biomass of bacteria, cyanobacteria, prochlorophytes and photysnthetic eukaryotes in the Sargasso Sea. Deep-Sea Research 39, 501–519.

Li, W.K.W., Harrison, W.G., 2001. Chlorophyll, bacteria and picophytoplankton in ecological provinces of the North Atlantic. Deep-Sea Research II 48, 2271–2293.

Longhurst, A., 1998. Ecological Geography of the Sea. Academic Press, NewYork 398pp.

Morán, X.A.G., Estrada, M., Gasol, J.M., Pedrós-Alió, C., 2002. Dissolved primary production and the strength of phytoplankton-bacterioplankton coupling in contrasting marine regions. Microbial Ecology 44, 217–223.

Murray, J.W. (Ed.), 1995. A US JGOFS Process Study in the Equatorial Pacific; Deep-Sea Research II 42, 275–903.

Nagata, T., 2000. Production mechanisms of dissolved organic matter. In: Kirchman, D.L. (Ed.), Microbial Ecology of the Oceans. Wiley-Liss, NewYork, pp. 121–152.

Pace, M.L., Cole, J.J., 1994. Comparative and experimental approaches to top-down and bottom-up regulation of bacteria. Microbial Ecology 28, 181–193.

Rivkin, R.B., Legendre, L., 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291, 2398–2400.

Simon, M., Cho, B.C., Azam, F., 1992. Significance of bacterial biomass in lakes and the ocean: comparison to phytoplankton biomass and biogeochemical implications. Marine Ecology Progress Series 86, 103–110.

Smith Jr., W.O., Anderson, R.F., 2000. (Eds.), The US Southern Ocean Joint Global Ocean Flux Study (AESOPS); Deep-Sea Research II 47, 3073–3548.

Whitman, W.B., Coleman, D.C., Wiebe, W.J., 1998. Prokaryotes: the unseen majority. Proceedings of the National Academy of Sciences USA, vol. 95, pp. 6578–6583.