Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems

Paul A. del Giorgio*, Jonathan J. Cole* & André Cimbleris†

* Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545-0129, USA
† Department of Biology, McGill University, 1205 Dr Penfield, Montreal, Quebec H3A 1B1, Canada

PLANKTONIC bacteria are a fundamental component of the organic carbon cycle in aquatic systems[1]. Organic carbon consumption by planktonic bacteria is the sum of bacterial production (BP) and bacterial respiration (BR). It is now estimated that 30–60% of phytoplankton production (the amount of inorganic carbon fixed by phytoplankton photosynthesis, corrected for phytoplankton respiration) in marine and freshwater systems is processed by bacteria[1–3]. These estimates of carbon flow through bacteria are conservative, however, because losses due to bacterial respiration are seldom directly measured[4,5]. We report here that bacterial respiration is generally high, and tends to exceed phytoplankton net production in unproductive systems (less than 70 to 120 μg carbon per litre per day). A large proportion of the world's aquatic systems have phytoplankton productivities below this value[6]. Bacterial growth efficiency (BGE) is the result of BP and BR[BGE = BP/(BR + BP)]. Comparisons of our models of bacterial respiration with published models of bacterial secondary production[1,7] show that bacterial growth efficiency must range from less than 10% to 25% in most freshwater and marine systems, well below the values commonly assumed in many current ecological models[1,2,8,9]. The imbalance between

bacterial respiration and phytoplankton production suggests that in unproductive aquatic systems, the biological system is a net source of CO_2.

Bacterial production is routinely measured in aquatic studies, but bacterial respiration is not[5]. Instead, most current ecological models of aquatic carbon flow assume bacterial growth efficiencies in the range of 40 to 60%[1,2,8–11], mostly on the basis of the uptake and efficiency of conversion of simple ^{14}C-labelled organic compounds[12]. There is now indication that growth efficiencies of bacteria using natural substrates are substantially lower than these assumed values[5,13,14], so ecological models may greatly underestimate the total amount of carbon flowing through bacterioplankton. We surveyed the literature for direct measurements of planktonic bacterial respiration from marine, estuarine and freshwater systems, and assessed how these rates varied with increasing bacterial abundance and planktonic primary production, with a twofold purpose. First, we compared organic carbon consumed through bacterial respiration to organic supplied by net primary production (NPP); if bacterial respiration exceeds net primary production, bacteria must use external sources of organic matter, and the system is net heterotrophic. Second, we estimated bacterial growth efficiencies and assessed how these vary across aquatic systems. A better knowledge of bacterial growth efficiencies is needed to improve our estimates of carbon flow through aquatic microbial food webs.

Using the data averaged per site and study, we observed a strong relation between bacterial abundance and bacterial respiration, lending credibility to this collection of *in situ* measurements of respiration (Fig. 1*a*). Although there is much scatter in this relation, both bacterial abundance and respiration varied by three orders of magnitude, so the log–log least-squares slope (o.l.s.) was not significantly different from unity (Table 1). The structural (r.m.a.) slope was significantly higher than unity (Table 1). Bacterial respiration was also positively related to net primary production across a wide range of primary productivities, from ultraoligotrophic oceans to highly eutrophic lakes and estuaries (Fig. 1*b*). Bacterial respiration was almost two orders of magnitude less variable than net primary production among systems, and both the o.l.s. and r.m.a. slopes of this log–log relationship were significantly lower than unity (Table 1), indicating that increases in net primary production are followed by proportionately smaller increases in bacterial respiration. The analysis of the individual data rather than the means revealed essentially the same patterns in bacterial respiration and is not included here.

Bacterial abundance has been shown to be remarkably constant among aquatic systems[1–3], and our data show that planktonic bacterial respiration is at least as uniform as bacterial abundance. Interestingly, 51% of our average observations (and 63% of the individual points) had NPP/BR < 1, including marine, estuarine and freshwater data, and none of these cases occurred with NPP > than 120 $\mu g\,C\,l^{-1}\,d^{-1}$ (Fig. 1*b*). Bacterial respiration thus tended to exceed net primary production in aquatic systems with net primary production below 100 $\mu g\,C\,l^{-1}\,d^{-1}$, suggesting that the degree of heterotrophy varies systematically with system productivity. This conclusion is further supported by the strong positive correlation

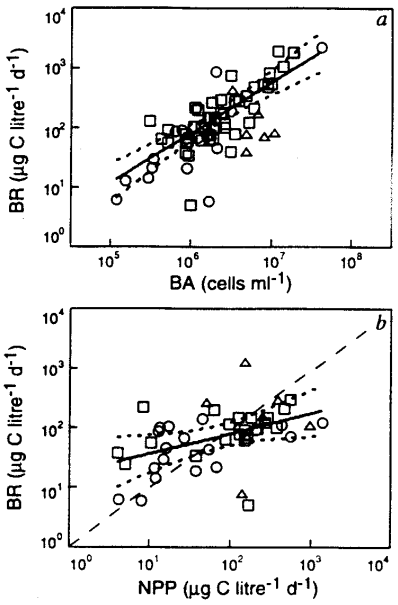

FIG. 1 Planktonic bacterial respiration (BR) as a function of *a*, bacterial abundance (BA), and *b*, net primary production (NPP). Symbols represent data from marine (circles), freshwater (squares) and estuarine (triangles) systems. Plots show data averaged per site for each study, and the solid line is the least-square regression with 95% confidence intervals. The dashed line represents equality. The least-squares regression and structural regression parameters for both relationships are shown in Table 1.

found between the NPP/BR ratio and both chlorophyll concentration and phytoplankton biomass in two subsets of the data set (not shown). A large proportion of the world's aquatic systems have primary productivities below 100–120 $\mu g\,C\,l^{-1}\,d^{-1}$ (ref. 6).

Can we confidently conclude that bacterial respiration exceeds phytoplankton production in many unproductive aquatic systems, based on these heterogeneous estimates of bacterial respiration and primary production from the literature? The conclusions of the analysis are similar irrespective of whether o.l.s. or r.m.a. slopes are considered (Table 1), and an unrealistically high error (coefficient of variation >250%) in the independent variables would be required to modify these conclusions. Most of the primary production data are measures of ^{14}C uptake made using standard techniques within the past ten years, so these data should be reliable, but the bacterial respiration data are more difficult to judge. One way to assess the overall validity of the bacterial respiration data is to determine whether the resulting growth efficiencies are within reasonable ranges. We calculated bacterial

TABLE 1 Parameters of linear regression models relating bacterial respiration to bacterial abundance and net primary production

Model	*X*	*Y*	Intercept	Slope	r^2	s.e.	*N*	CF
o.l.s.	BA	BR	−3.51 ± 1.26	0.67 < 0.88 < 1.09	0.53	0.41	72	1.56
r.m.a.	BA	BR	−5.21	0.98 < 1.15 < 1.35	0.53		72	
o.l.s.*	NPP	BR	1.21 ± 0.38	0.16 < 0.34 < 0.52	0.30	0.43	47	1.63
r.m.a.	NPP	BR	0.86	0.48 < 0.62 < 0.78	0.30		47	

Parameters of linear regression models, of the form $\log Y = a(\log X) + b$, relating bacterial respiration (BR, $\mu g\,C\,l^{-1}\,d^{-1}$) to bacterial abundance (BA, $\mu g\,C\,l^{-1}\,d^{-1}$) and net primary production (NPP, $\mu g\,C\,l^{-1}\,d^{-1}$). Ordinary least squares (o.l.s.) and reduced major axis (r.m.a.) models are provided, for the averages per site and study (means), together with the 95% confidence intervals for the regression parameters, the standard error of the estimate (s.e.), significance of the regression (*P*) and a factor (CF) to correct for bias introduced by log transformation[7]. All the equations are highly significant ($P < 0.001$). Confidence limits for the r.m.a. slope allow for the asymmetry of the distribution of the r.m.a. estimator[30].

* This is equation 1 (see text) used to estimate BK from NPP.

growth efficiencies by combining our bacterial respiration data with estimates of bacterial production for each site (Fig. 2). Roughly similar ranges and median values of bacterial growth efficiencies for each type of system were obtained when bacterial production was estimated from bacterial abundance or from net primary production, suggesting that the patterns in bacterial growth efficiency shown in Fig. 2 are robust.

Bacterial growth efficiencies ranged from less than 5% to more than 60% across systems (Fig. 2). The median BGE for marine sites was 0.24 (0.23s.d.) when BP was calculated from BA, and 0.20 (0.17s.d.) when BP was calculated from NPP, and for lakes the medians were 0.17 (0.12s.d.) and 0.23 (0.17s.d.), respectively (Fig. 2). For estuaries, the median BGE calculated based on NPP was 0.21 (0.27s.d.), and much higher when calculated based on BA (0.46, 0.21s.c.). Except for this last estimate, all these values are in good agreement with direct measurements of growth efficiency of bacterial assemblages utilizing natural dissolved organic matter[13-18], suggesting that our data on bacterial respiration are realistic. Furthermore, these results support previous reports that bacterial growth efficiencies in aquatic food webs are generally lower than normally assumed in many current ecological models[1,2,8,9]. One important consequence is that many contemporary models of organic carbon cycling for both freshwater and marine aquatic systems do not balance if the median bacterial growth efficiencies reported here are applied.

How do these patterns in bacterial respiration among systems relate to published models of bacterial secondary production? Comparisons of the above models of bacterial respiration with existing large-scale empirical relationships[1,7] further show that bacterial respiration increases far more slowly than bacterial production along gradients of both bacterial abundance[7] and primary production[1] in freshwater and marine systems. We simulated bacterial growth efficiency along a gradient of net primary production, by calculating bacterial respiration ($\mu g\,C\,l^{-1}\,d^{-1}$) from NPP ($\mu g\,C\,l^{-1}\,d^{-1}$) using equation (1) in Table 1, and bacterial production ($\mu g\,C\,l^{-1}\,d^{-1}$) from NPP using the model of Cole *et al.*[1]. For each NPP point, BGE was then calculated as BP/(BP + BR). This calculation suggests that bacterial growth efficiency increases as a power function of NPP ($BGE = 0.02 \pm NPP^{0.41}$).

Although there is considerable uncertainty associated with these large-scale empirical models, an interesting consequence of the diverging trends in bacterial production and respiration is that there appears to be a general trend of increasing bacterial growth efficiencies along gradients of system enrichment, from <10% in oligotrophic sites to a plateau at ~40% in the most productive systems. Similar trends have been reported in BGE for specific sites[17,18], and the increase in BGE with system productivity may be linked to systematic changes in both the rate of supply and nutritional quality of organic carbon substrates available for bacteria[14,18]. The availability of organic carbon substrates, however, is only one of the factors regulating growth efficiencies: for example, low overall bacterial growth efficiencies in open oceans may be linked to low iron availability[19].

Our results support the observations that many unproductive lakes and estuaries are net heterotrophic systems[20,21], where the total carbon processed by bacteria exceeds the carbon fixed by phytoplankton. Allochthonous organic carbon of terrestrial origin is likely to play a major role in this metabolic imbalance. Lakes, for example, are often supersaturated with CO_2 (refs 22, 23), and bacterial degradation of allochthonous organic carbon is thought to be one of the main causes for high CO_2 partial pressure[20]. Likewise, estuaries and coastal oceans are often heavily subsidized with organic carbon from land and wetland ecosystems[21,24,25].

Our results also concur with microbial observations for the open ocean that suggest a large role for bacteria in the organic carbon flow[8,11], and further indicate that parts of the ocean are net heterotrophic, at least during certain periods. Methodological uncertainties may be partly responsible for these patterns, but our study only deals with volumetric rates of bacterial respiration and phytoplankton production measured either in the mixed layer or, more often, in the euphotic zone of the water column. Bacterial activity in the deep waters of the ocean is low compared to that in surface waters[2], but photosynthesis is effectively zero, so if these rates were integrated over the entire water column, the imbalance between bacterial respiration and phytoplankton production would be much greater than shown here.

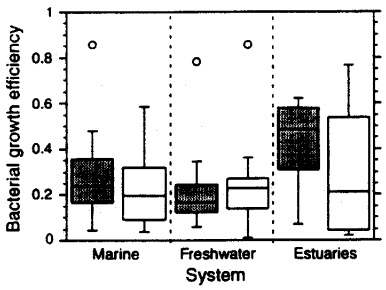

FIG. 2 Box-and-whisker plots showing the range and the median bacterial growth efficiency (BGE) by system. BGE was calculated using the measured rates of bacterial respiration culled from the literature, and rates of bacterial production estimated either from the accompanying bacterial abundance data using the model in ref. 7 (grey boxes) or from net primary production data using the model in ref. 1 (white boxes).

The processes underlying the apparent net heterotrophy in oceans may be different from those in lakes and estuaries. It is problematic to invoke the influence of allochthonous organic matter to fuel excess heterotrophic activity, particularly in the central gyres of the oceans[4]. Organic carbon of terrestrial origin is a significant fraction of dissolved organic carbon (DOC) in marine coastal and shelf waters[26], but in open oceans only about 10% of the DOC is now estimated to be of terrestrial origin[27]. Much of this carbon may not even be biologically available, although photochemical breakdown of DOC may facilitate the utilization by bacteria of recalcitrant humic compounds[28]. Export of DOC from more productive coastal and upwelling areas to open oceans has also been proposed[25]. Also, our analysis may mask a succession of periods of net autotrophy in the open ocean, owing to time lags between peaks of primary production in the spring and heterotrophic utilization of the resulting organic carbon later on in the year[29]. The challenge will be to quantify the relative importance of these alternative processes to net heterotrophy in aquatic systems. □

Methods

Data collection. The relationship between bacterial respiration and bacterial abundance (Fig. 1*a*) was constructed with data from 20 published articles, and reports of several measurements for the same site were averaged (Fig. 1*a*) or analysed individually (data not shown). A total of 153 individual data points collected for the literature, which resulted in 62 average values, 20 for open ocean and coastal marine sites, 7 for estuaries and 35 lakes worldwide. Additional data from 10 southern Québec lakes were included (A.C., unpublished results). Most studies reported bacterial respiration measured as oxygen consumption in water filtered through small-pore-size filters (0.8–2 μm) and bacterial abundance measured with epifluorescence counts. Bacterial respiration reported as oxygen consumption per unit time were converted to $\mu g\,C\,l^{-1}\,d^{-1}$, assuming a respiratory quotient (RQ) of 1 (by mol), and that respiration per day was 24 times the hourly rate. All data, except temperature, were log-transformed to attain homoscedasticity and normality. For a subset of the data ($n = 38$), temperature was reported together with BR and BA and we could explore the effect of temperature on the rates of bacterial respiration (data not shown). The following least-squares multiple regression model of bacterial respiration as a function of bacterial abundance and temperature (T) explained 82% of the variance in BR in this subset of the data: $\log BR = -3.67\,(\pm 2.30) + 0.75\,(\pm 0.35)\log BA + 0.059\,(\pm 0.01)T$; $r^2 = 0.82$, $n = 38$, s.e. = 39, $P < 0.001$. The temperature coefficient for BR is not significantly different for the one reported by White *et al.*[7] for bacterial production, suggesting that temperature dependence of bacterial growth efficiencies is probably weak and should not influence the patterns in BGE among systems discussed here.

The relation between BR and NPP (Fig. 1*b*) was constructed with data extracted from 17 published articles, and reports of several measurements for the same site were averaged. A total of 81 individual data points collected from the literature resulted in 47 average values, 18 for open ocean and coastal marine sites, 7 for estuaries and 22 for lakes worldwide. Volumetric rates of net primary production per unit time were converted to $\mu g\,C\,litre^{-1}\,d^{-1}$, assuming 12 times the hourly rate. The complete data sets are available from the authors or from the Repository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ontario KIA 0S2.

Statistical analysis. All the data were analysed using ordinary least squares (o.l.s.) regression, for comparison with previously published empirical models. The o.l.s. slope will systematically underestimate the true slope, however, owing to error in both the dependent and the independent variables, so we also calculated the reduced major axis (r.m.a.) slopes for the structural relationship between BR–BA and BR–NPP[30]. the complete o.l.s. and r.m.a. regression parameters are shown in Table 1.

Calculation of BGE. For Fig. 2, bacterial growth efficiencies were calculated as BGE = BP/(BP + BR), where BR are bacterial respiration data collected from the literature and used in Fig. 1*a*, *b*. For each BR point, bacterial production (BP, in $\mu g\,C\,l^{-1}\,d^{-1}$) was calculated from either the accompanying net primary production data in Fig. 1*b* using the equation of Cole *et al.*[1], or from the accompanying bacterial abundance data in Fig. 1*a* using the equation of White *et al.*[7]. Data are presented as box-and-whisker plots showing the median and range of BGE for each system for the two methods for estimating bacterial production.

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CORRESPONDENCE and requests for materials should be addressed to P.A.d.G. (e-mail: c1434@er.uqam.ca).