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Bacterial production in fresh and saltwater ecosystems: a cross-system overview

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ABSTRACT: Heterotrophic bacteria are thought to be important components of aquatic ecosystems in several ways. These bacteria remineralize organic materials and convert some organic material into bacterial biomass. We examined data from 70 studies in which estimates of production of heterotrophic bacterial biomass (bacterial production) were reported for fresh- and saltwater ecosystems. In sediments, bacterial production was significantly ($p < 0.001$), positively correlated to sediment organic C content. Systems which had high rates of benthic primary production (such as coral reefs) had rates of bacterial production greater than those predicted by sediment organic C content alone. In the photic zone of lakes and the ocean, bacterial production was significantly correlated with planktonic primary production, chlorophyll *a*, or numbers of planktonic bacteria. For all planktonic systems analysed, bacterial production ranged from 0.4 to 150 $\mu g\ C\ l^{-1}\ d^{-1}$ and averaged 20 % (median 16.5 %) of planktonic primary production. On an areal basis for the entire water column, bacterial production ranged from 118 to 2439 $mg\ m^{-2}\ d^{-1}$ and averaged 30 % (median 27 %) of water column primary production. Heterotrophic bacterial production is, thus, a large component of total secondary production and is roughly twice as large as the production of macrozooplankton for a given level of primary production.

INTRODUCTION

In both the water column and sediments of aquatic ecosystems, bacteria are thought to be the major decomposers of organic matter (Fenchel & Blackburn 1979, Wetzel 1982). The rapid growth rates and potentially high growth efficiencies of aquatic bacteria have suggested to many researchers that the production of particulate heterotrophic bacterial biomass represents an important link between detritus, dissolved organic matter, and higher trophic levels (Pomeroy 1974, Paerl 1978, Porter et al. 1979, Williams 1981; but see Ducklow et al. 1986). What regulates this bacterial production is a matter of considerable speculation. The microbial literature contains the notion that it is controlled by, or directly related to, the supply of decomposable organic matter but little quantitative data exist to support this notion (Hobbie & Rublee 1977, Cole 1982). If this idea is correct, bacterial production in different systems should be correlated with the supply or standing stock of decomposable organic matter in those systems. Although it is presently impossible to quantify precisely a supply of labile organic matter to any system, it is possible to estimate variables, such as primary production, which would be related to that supply. To our knowledge, the hypothesis of an increase in bacterial production as a function of organic matter supply has not been directly tested. Thus, we do not know to what extent bacterial production is a predictable property of aquatic ecosystems. If we expect rates of bacterial production to vary predictably across systems of differing trophic status, it is also reasonable to ask whether the contribution of bacteria to total secondary production is also consistent across systems.

Williams (1981), on the basis of the rather limited data available at that time, suggested that bacterial production averaged about 20 % of primary production. Many new measurements have been made since Williams' review, largely due to the introduction of the ^{3}H-thymidine technique (Fuhrman & Azam 1980). Although the accurate measurement of bacterial production still involves numerous problems (Karl & Winn 1984, Fuhrman et al. 1986), there are now a large number of estimates of bacterial production, by a variety of techniques, in a variety of marine and freshwater environments. How does the oft-cited estimate that bacterial production is 20 % of primary production apply in a general cross-system relationship? Are there exceptional systems in which bacterial production is considerably higher or lower than 20 % of primary production?

Using the substantial data from the recent literature,

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we sought to address the following questions: (1) Can bacterial production be predicted from measurements of the supply or standing stock of organic matter? (2) What is the importance of bacterial production in comparison to other components of secondary production (e.g. zooplankton)? (3) Are there particular methods or particular classes of systems (e.g. freshwater versus saltwater) which yield results different from the general trend?

METHODS

Selection and conversion of pelagic data. To obtain an unbiased set of the data from the literature, we selected cases on the basis of 4 criteria: (1) both algal and bacterial production estimates were reported; (2) the estimates extended for some period of time so that seasonal, regional or annual values could be readily obtained – we specifically excluded single-date, single-site observations; (3) the method of measurement was stated or explained; and (4) it was possible to extract data for the photic zone alone – we specifically excluded measurements for the aphotic zone alone for the volumetric relationships. (The whole water column was included in the areal relationships, below.) We did not exclude any studies on the basis of the methods used or the values reported. For studies meeting the above criteria, we also recorded data on chlorophyll *a* and bacterial abundance, where available.

We converted all data to units of $\mu g\ C\ l^{-1}\ d^{-1}$ for the photic zone. This conversion required several assumptions in some cases. When only daylight hourly values were available, we assumed that daily bacterial production was 24 times the hourly rate and that primary production was 10 times the hourly rate. Although diurnal variation in bacterial production has been reported, the magnitude of these variations is relatively small in comparison to bacterial production (Riemann et al. 1984). Some data were originally reported on an areal basis for the photic zone. For these studies we divided by the depth of the photic zone to obtain volumetric estimates. This manipulation tends to overestimate the importance of the darker, less productive waters in lakes because lake volume usually decreases with depth; this would have a negligible effect in the ocean or in large lakes.

A significant subset of the data (36 observations) was also expressed, by the original authors, on an areal basis for the entire water column (mg $C\ m^{-2}$ $time^{-1}$). For these data we made the same assumptions as above concerning time but made no assumptions about depth.

The data reported in the literature were obtained using different methods, assumptions and conversions. We made no attempt to standardize the data in these aspects. Instead, we used the data as they were reported, except for the unit corrections explained above.

Selection and conversion of benthic data. The literature on benthic bacterial production is very limited. We therefore relaxed our criteria on long-term averages and considered only 2 requirements: (1) both bacterial production and sediment organic matter had been measured; and (2) the methods of measurement were stated or explained. Bacterial abundance and benthic primary production were also recorded where available.

In order to arrive at a consistent set of units, we assumed that organic carbon was 50 % of ash-free dry weight and that bulk density of sandy sediments was 1.8 $g\ cm^{-3}$. The variability in these figures in nature is likely to be small in comparison to the vast changes in bacterial production within the data set. We also assumed no diel variation in bacterial production. In 2 cases where diel variation was known, the authors also reported daily averages (e.g. Moriarty & Pollard 1982).

Statistical analysis. Equations relating bacterial production to measures of standing stocks or supplies of organic matter were established with ordinary least-squares regression analysis. For functional interpretation of these regressions (Model II analysis), we used the geometric mean method (GM; Ricker 1973). Because variance tended to increase with mean estimates of bacterial production, the data were log-transformed to stabilize the variance and meet the normality assumptions of regression analysis. The data were fit to the model $\text{Log } Y = a + b \times \text{Log } X$. In particular cases, we also calculated multiple regressions to determine if additional independent variables improved models to predict bacterial production. To compare the univariate and multivariate models, we used the adjusted coefficients of determination (R^2) which accounts for differences in the number of parameters in the models and allows their comparison in terms of the relative improvement in prediction (Gujarti 1978). Regression statistics were computed with STATPRO (Penton Software 1985).

RESULTS AND DISCUSSION

Pelagic data

Unit volume relationships

Primary production ranged from 4.5 to 1834 $\mu g\ C\ l^{-1}\ d^{-1}$ and averaged 184 ± 286 $\mu g\ C\ l^{-1}\ d^{-1}$ (SD); the median was 72 $\mu g\ C\ l^{-1}\ d^{-1}$. Bacterial production

ranged from 0.4 to 153 μg C l^{-1} d^{-1} and averaged 26.4 ± 33.1 μg C l^{-1} d^{-1}; the median was 11.5 μg C l^{-1} d^{-1}. In the data set we summarized, 24 studies were freshwater and 30 studies were marine (Table 1). We encountered 7 different methods for measuring bacterial production: ^{3}H-thymidine uptake (n = 32, see Fuhrman & Azam 1980 for an example of the method); ^{14}C-flux with differential filtration (n = 5, Møller-Jensen 1983); the uptake of labelled organic substrates (n = 10, Bolter 1981); frequency of dividing cells (n = 4, Hagström et al. 1979); decomposition (n = 3, Linley et al. 1983); dark CO_2 uptake (n = 2, Coveney 1982); and uptake of ^{35}S-SO_4 (n = 1, Jordan & Likens 1980). Of the 54 studies we reviewed, 49 were published during or after 1981, the date of Williams' review.

For all the data, bacterial production was significantly ($p < 0.001$) and positively related to algal primary production, the standing stocks of chlorophyll *a*, and to the numbers of bacteria in the water column and may be reasonably well predicted from any of these variables (Table 2). The best relation was between bacterial production (BP) and primary production (PP). The overall equation for this relation (Fig. 1) is:

$$\text{Log BP} = 0.8 \text{ Log PP} - 0.46$$

which explains about 57 % of the variance in bacterial production. Converting to linear terms, and correcting for the statistical bias introduced by antilog transformation (Sprugel 1983, Land 1972) the equation becomes:

$$\text{BP} = \text{CF} [0.347 \text{ PP}^{0.8}]$$

where CF = the correction factor, and is equal to 1.56. Using the same form of equation, similar relationships at similar levels of significance were found when either chlorophyll *a* or bacterial numbers were used as the independent variable (Table 2).

Because of the high variances for all of these relations, the confidence limits are wide and slopes were not statistically different from 1.0, with the exception of the relationship with chlorophyll *a* (t-test; $p < 0.05$; Table 2). Further, since the measurement of the independent variables are all associated with uncertainties, it is correct to interpret our regressions in terms of a Model II analysis (Ricker 1973; Table 2). In no case is the Model II functional slope significantly different from 1.0. Thus, our regressions suggest that bacterial production is significantly correlated to primary production, chlorophyll *a*, and bacterial numbers, and that this relation is essentially linear across differing levels of primary production, chlorophyll *a*, and bacterial numbers.

Despite the apparent fit of all the data to one regression (Fig. 1), significant differences exist for components of the data (Table 2). For example, the variance of the freshwater data alone ($r^2 = 0.375$) is greater than for marine data ($r^2 = 0.77$). This greater variance may be caused by the importance of allochthonous carbon inputs or macrophyte production in some freshwater systems.

The thymidine method has a more variable relationship to primary production ($r^2 = 0.49$; n = 31) than do all other methods combined ($r^2 = 0.67$; n = 23; Table 2). Given the considerable uncertainties in these methods, it is possible that any organic substrate may be transported to some extent by both heterotrophs and autotrophs leading to a spurious correlation. The thymidine method, perhaps, suffers less from this problem than other methods (Fuhrman et al. 1986). It is conceivable that some of the other methods, especially dark CO_2 uptake or differential filtration after ^{14}C-HCO_3 addition, may measure both bacterial production plus some fraction of algal picoplankton production (Cole et al. 1982), and would therefore tend towards better correlation with primary production. It is also possible that different assumptions or approaches to the conver-

Table 1. Sources of data for regression analyses. Note that some references provide data for more than one system

Pelagic data		Benthic data
Freshwater systems	Marine and estuarine systems	
Bell et al. 1983	Albright & MacCrae 1987	Bott & Kaplan 1985
Bell & Kuparinen 1984	Bolter 1981	Ducklow et al. 1986
Cole et al. 1984	Chrost & Faust 1983	Fallon et al. 1983
Coveney 1982	Ducklow 1986	Findlay et al. 1986
Hobbie & Helfrich 1988	Ducklow & Kirchman 1983	Meyer-Reil 1983
Jordan & Likens 1980	Fuhrmann et al. 1985	Moriarty et al. 1985
Lovell & Konopka 1985	Fuhrman & Azam 1980, 1982	Moriarty & Pollard 1982
Pedros-Alio & Brock 1982	Hagström et al. 1979	
Riemann 1983	Hitchcock et al. 1985	
Riemann et al. 1982	Hobbie & Cole 1984	
Riemann & Sondergaard 1986	Lancelot & Billen 1984	
Scavia et al. 1986	Linley et al. 1983	
Simon & Tilzer 1987	Møller-Jensen 1983	

Table 2. Regression statistics for volumetric relations in pelagic systems. Variables are NPP (net primary production; μg C l^{-1} d^{-1}), BP (bacterial production; μg C l^{-1} d^{-1}), CHL (chlorophyll *a*; μg l^{-1}), BNUMS (bacterial numbers; cells ml^{-1}). All values were log-transformed to compute regression statistics. Confidence limits around predicted values of Y can be calculated using mean X and corrected sums square X (SSX). The residual mean square can be calculated from the correction factor (CF). The correction factor must be used when converting from log to arithmetic scales; this factor corrects for an inherent bias of log-transformed regressions (see text). The Model II slope is an estimate of the true relation between X and Y when there is error in the independent variable

Data	Y, X	n	Slope (90 % conf.)	Y-int.	r^2	F	Mean X	SSX	CF	Signif. (F-test)	Model II slope
All points	BP, NPP	54	0.814 (0.162)	−0.483	0.593	75.7	1.89	17.6	1.43	<0.0001	1.06
Excluding validation set	BP, NPP	46	0.804 (0.173)	−0.461	0.566	58.7	1.86	15.9	1.56	<0.0001	1.07
Validation set	BP, NPP	8	0.897 (0.475)	−0.64	0.900	54.2	2.08	1.38	1.05	<0.0001	1.06
Thymidine method for BP	BP, NPP	31	0.787 (0.251)	−0.339	0.494	28.3	2.02	7.9	1.58	<0.0001	1.12
Other methods for BP	BP, NPP	23	0.753 (0.272)	−0.784	0.670	42.7	1.74	8.7	1.30	<0.0001	0.92
Freshwater all methods	BP, NPP	24	0.683 (0.243)	−0.135	0.375	13.2	2.04	6.94	1.76	<0.0015	1.11
Marine all methods	BP, NPP	30	0.860 (0.152)	−0.627	0.767	92.3	1.79	9.8	1.23	<0.0001	0.98
All data	BP, CHL	41	0.618 (0.146)	0.346	0.618	51.7	0.87	24.0	1.59	<0.0001	0.82
All data	BP, BNUMS	40	1.124 (0.273)	−6.08	0.627	63.8	6.45	7.4	1.46	<0.0001	1.41
All data	BNUMS, CHL	35	0.524 (0.091)	5.96	0.753	100.5	0.96	17.8	1.14	<0.0001	0.60

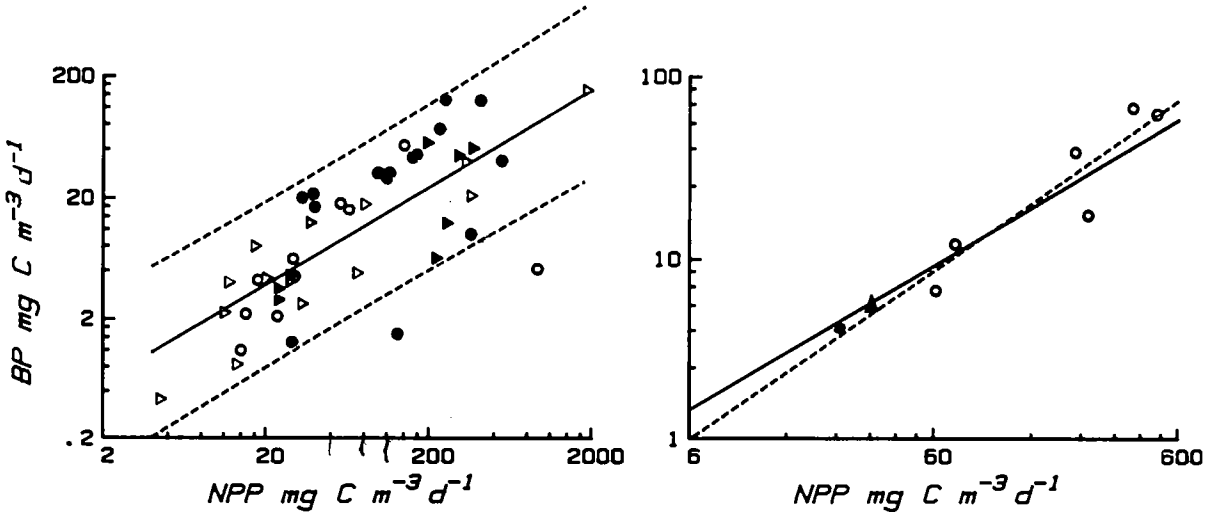

Fig. 1. Relation between bacterial production (BP; Y-axis) and net primary production (NPP; X-axis), both expressed on a volumetric basis for the photic zone. Each point represents a different system. Circles (●: freshwater; ○: marine systems) represent systems in which BP was measured by the thymidine method. Triangles (▲: freshwater; △: marine systems) represent systems in which other methods were used to measure BP (see text). Left panel shows the regression Log BP = 0.8 Log PP − 0.46 for all data excluding the points in the validation set, which are shown in right panel. Curved lines represent 90 % confidence limits for the individual predicitions of BP from the regression; confidence limits for the relation (not shown) are much narrower. Right panel shows the validation set; the solid line is the regression from the left-hand panel; the dotted line is the regression for the validation set (Log Y = 0.89 Log X − 0.64)

sion factor in the thymidine method lead to greater variance. However, slopes for regressions based on methodology were not significantly different (Table 2; Fig. 1).

There are several obvious 'outliers' on Fig. 1. Two points fall below the 90 % confidence interval; one comes from a study of a Swedish lake (Bell & Kuparinen 1984) and the other from a Danish lake (Riemann et al. 1982). Both studies used the thymidine method and the points represent averages for early spring, April–May. Perhaps bacterial production is relatively lower in cold water under spring bloom conditions (Pomeroy & Deibel 1986); we have insufficient data to test this idea. At any rate, neither of these studies are from especially unusual systems or used unusual measurement methods.

We combined the variables for the systems for which we had data and tested primary production, chlorophyll *a*, and bacterial abundance in a series of multiple regressions to predict bacterial production. The best equation was:

$$\text{Log BP} = -4.62 + 0.465\,\text{Log PP} + 0.748\,\text{Log BNUM}$$

where BNUM = number of bacteria in cells ml^{-1}. This regression explained 73 % of the variance in bacterial production. In comparison to the best univariate model using PP as the independent variable, the multiple model had a higher adjusted R^2 (0.73 *vs* 0.56) indicating that this model would provide improved predictions of bacterial production where data on both primary production and bacterial abundance are available. A multiple regression employing chlorophyll in combination with bacterial abundance ($R^2 = 0.58$) was not superior to the univariate equation.

We also tested our data set for the relationship between bacterial numbers and chlorophyll *a* and obtained the regression:

$$\text{Log (bacterial nos.)} = 5.97 + 0.53\,\text{Log (chl } a\text{)};\ r^2 = 0.75$$

This is similar to regressions developed for Japanese lakes (Aizaki et al. 1981; slope = 0.63) and Quebec Lakes (Bird & Kalff 1984; slope = 0.57), but differs from a previous review of the overall literature (Bird & Kalff 1984; slopes range from 0.78 to 0.84) in that our slope is less steep (Fig. 2). Based on the available information, we cannot explain this difference.

Validation of volumetric relations

To test the validity of some of the relations we obtained, we used an independent data set, not included in the regressions. This set consisted of observations from Mirror Lake, New Hampshire, USA (Cole et al. unpubl.) and from a coastal mesocosm experiment at the MERL facility in Rhode Island, USA (Hobbie & Cole 1984). These data sets were chosen because of our familiarity with them and because they spanned a fairly large range of bacterial production values. For both of these data sets the thymidine method was used to estimate bacterial production. Additionally, we included data from Lake Constance, Germany (Simon & Tilzer 1987) that we simply had not seen until after we had completed the analysis of the bulk of the studies. The Lake Constance data was the only volumetric-based data that we received after completing the initial analysis. In the case of PP, chlorophyll and bacterial numbers, the regression from the literature was a good predictor of the data in the validation set (Fig. 1B). The regressions from the validation set alone, while not significantly different from the regressions from the overall literature, had lower variances ($r^2 = 0.90$; Table 2). This lower variance may, in part, be the result of consistency of methods within the more limited data set. Including the 8 points from the validation set with the other data did not change the overall relation significantly but improved the fit slightly ($r^2 = 0.59$; Table 2). As with the larger data set, the Model II slope of the validation set was essentially 1.0, implying a linear relation between BP and PP across the trophic gradient.

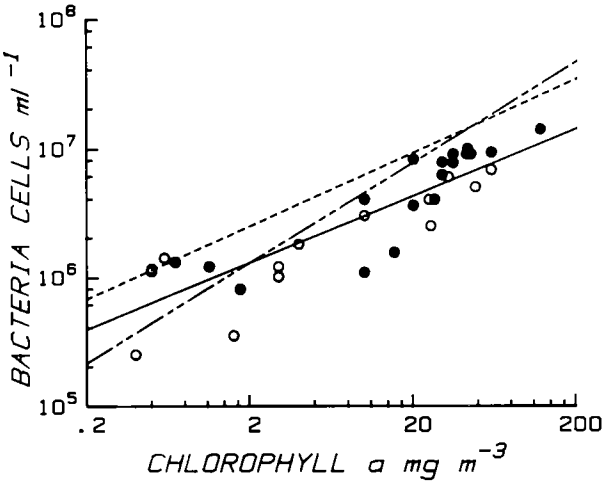

Fig. 2. Relation between chlorophyll *a* and bacterial direct counts (both on volumetric basis) for the data we reviewed (solid regression line and all points). Regression equation is Log Y = 0.52 Log X + 5.96. (●) Freshwater; (○) marine systems. (- - - - -) Regression lines for Quebec Lakes (from Bird & Kalff 1984); (——·——) overall review of the literature (from Bird & Kalff 1984)

Areal relations: bacteria

For the systems in which the data could be expressed on an areal basis, primary production ranged from 118 to 2439 mg C m^{-2} d^{-1} and averaged 861 ± 673 mg C

Table 3. Regression statistics for areal relations in pelagic and benthic systems. Variables are NPP (net primary production; mg C m^{-2} d^{-1}), BP (bacterial production; mg C m^{-2} d^{-1}), ZP (zooplankton production; mg C m^{-2} d^{-1}), SOC (sediment organic content; mg C [g DW]$^{-1}$), SBP (sediment bacterial production; µg C [g DW]$^{-1}$ d^{-1}), SBM (sediment bacterial biomass; mg C [g DW]$^{-1}$). See Table 2 for explanation of statistics

Data	Y, X	n	Slope (90 % conf.)	y-int	r^2	F	Mean X	SSX	CF	Signif. (F-test)	Model II slope
Pelagic relations											
All data	BP, NPP	36	0.746 (0.194)	0.093	0.559	43.2	2.80	4.84	1.15	<0.0001	0.99
All IBP data	ZP, NPP	24	1.074 (0.250)	−1.26	0.706	52.9	2.21	9.64	1.74	<0.0001	1.28
Benthic relations											
All data	SBP, SOC	24	0.444 (0.283)	0.42	0.240	7.08	0.96	15.22	3.08	<0.0143	0.91
Excluding high benthic NPP sites	SBP, SOC	18	0.698 (0.213)	−0.15	0.698	30.9	1.12	13.3	1.73	<0.0001	0.86
All data	SBP, SBM	24	1.08 (0.356)	2.05	0.53	25.1	−1.12	5.65	1.99	<0.0001	1.48

m^{-2} d^{-1}; the median was 627 mg C m^{-2} d^{-1}. Bacterial production ranged from 18 to 576 mg C m^{-2} d^{-1} and averaged 213 ± 149 mg C m^{-2} d^{-1}; the median was 167 mg C m^{-2} d^{-1}. Using these data we also obtained a highly significant regression, explaining 56 % of the variation in bacterial production (Table 3; Fig. 3). The slope of the Model II regression is not significantly different from 1.0, again suggesting a linear response.

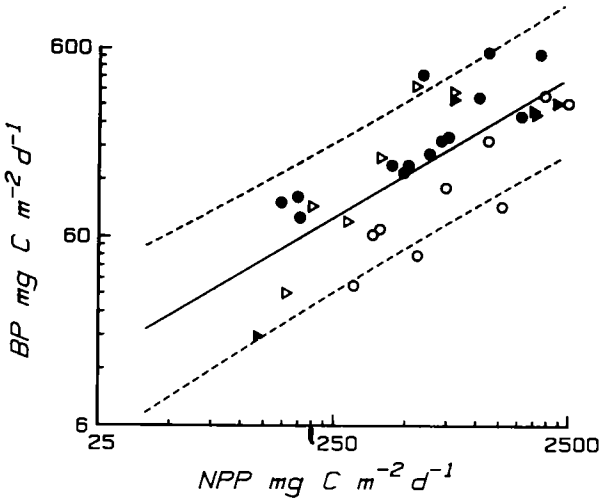

Fig. 3. Areal relation between primary production (NPP; X-axis) and bacterial production (BP; Y-axis) expressed per unit area for the entire water column. Symbols are as in Fig. 1. Regression line (Log Y = 0.75Log X + 0.093) is shown with 90 % confidence limits for the individual predictions of BP

Areal relations: zooplankton

We wanted to compare planktonic bacterial production to other forms of secondary production. Unfortunately there are rather few data sets for which both zooplankton and bacterial production have been estimated. Instead we compared our bacterial and primary production relation to a relation for zooplankton and primary production developed from the lakes studied as part of the International Biological Programme (IBP; LeCren & Lowe-McConnel 1980). This study presented annual data on both zooplankton production and primary production and we performed regression analysis on these data. Unfortunately, this data set has measurements only for freshwater. In these IBP data primary production averaged 324 ± 288 mg m^{-2} d^{-1} and ranged from 5.9 to 929 mg m^{-2} d^{-1} while zooplankton production averaged 34 ± 40 mg m^{-2} d^{-1} and ranged from 0.1 to 132 mg m^{-2} d^{-1}. Zooplankton secondary production (herbivores plus carnivores) was significantly correlated to primary production. The log-log regression explained 71 % of the variation in zooplankton production (Fig. 4). Based on this regression, bacterial production tends to be almost twice as large as zooplankton production across systems.

Benthic data

In the data set, benthic bacterial production ranged from 0.14 to 51.4 µg C (g DW)$^{-1}$ d^{-1} and averaged 14.3 µg C (g DW)$^{-1}$ d^{-1}. Sediment organic carbon content ranged from 0.33 to 460 mg C g^{-1} and averaged 55 mg C (g DW)$^{-1}$ d^{-1}. Ideally we would have used the input of organic C to the sediments as the independent variable, but these data were not available. There was a significant ($p = <0.015$) but highly variable relation between benthic bacterial production and sediment organic content. This regression, however, explained

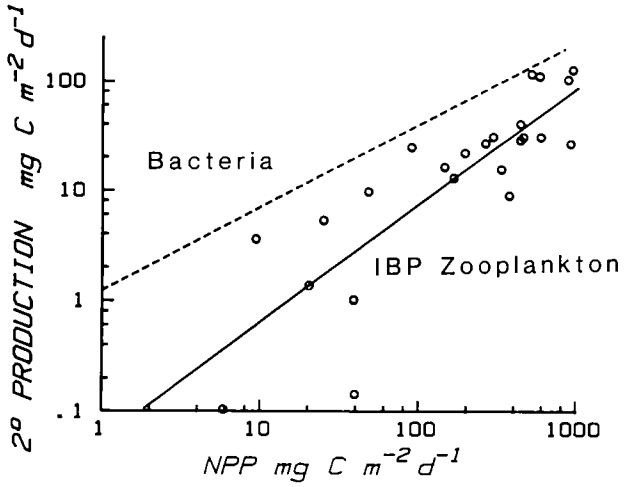

Fig. 4. Areal relation between primary production and zooplankton secondary production for a series of lakes studied by the IBP (all points, solid regression line). Regression is Log Y = 1.07 Log X − 1.26. (-----) Regression from Fig. 3 for bacterial production

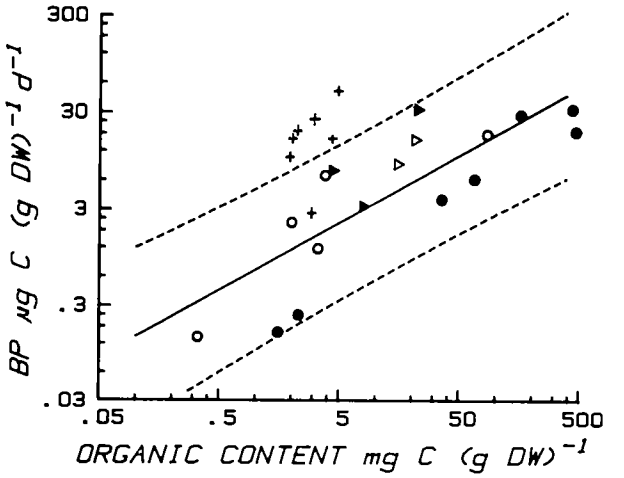

Fig. 5. Relation between sediment organic content (X-axis) and benthic bacterial production (Y-axis). Each point represents a different site; symbols follow Fig. 1. (+) points from Moriarty et al. (1985) with high rates of benthic algal production (not included in the regression). Regression equation is Log Y = 0.69 Log X − 0.15. The 90 % confidence limits are shown for the individual predictions of BP

only 24 % of the variance (Table 3). Data from a study of coral reef sediments (Moriarty et al. 1985), an environment which has high benthic algal production, were above the general trend (Fig. 5). We re-examined the original regression of bacterial production against organic content, eliminating data from those systems with high rates of benthic algal production, and obtained a significant relation between benthic bacterial production and organic content, which explained 66 % of the variation in benthic bacterial production (Fig. 5). If we 'correct' the high values from Moriarty et al. (1985) by extrapolating to zero primary production, we expect a rate of bacterial production of 1.0 µg C (g DW)$^{-1}$ d^{-1}, very close to the value predicted from our revised regression (1.53 µg C (g DW)$^{-1}$ d^{-1}). The actual mean of the high values was 21.4 µg C (g DW)$^{-1}$ d^{-1}, suggesting that benthic systems with primary production can support much higher bacterial production than systems supported only by the existing pool of sediment organic matter. We do not know if this support is direct, via carbon supply, or indirect via enhancement of benthic nutrient recycling.

There was also a significant ($p < 0.05$) regression between bacterial production on an areal basis (mg C m^{-2} d^{-1}) and sediment organic matter (OM; g C m^{-2}). The equation was:

$$\log BP = -0.057 \log OM$$

and explained 47 % of the variance.

Benthic bacterial production could also be predicted from benthic bacterial biomass (B; Table 3). For the entire data set the regression was Log P = 2.054 + 1.08 Log B and explained 53 % of the variance.

A multiple regression including both benthic organic matter and bacterial biomass explained the highest fraction of the variance (76 %) and both independent variables were significant. The regression was:

$$\text{Log BP} = 0.64 + 0.54 \text{Log OM} + 0.516 \text{Log B}$$

This regression ($R^2 = 0.72$) was an improvement over the regressions for organic matter ($R^2 = 0.64$) or biomass ($R^2 = 0.46$) alone.

IMPLICATIONS FOR AQUATIC FOOD WEBS

In a broad, cross-system sense, bacterial production is a predictable property of aquatic ecosystems. In the plankton, we obtained highly significant relations between bacterial production and the individual variables, primary production, chlorophyll *a*, or bacterial numbers, all expressed on a volumetric basis. In sediments, either the organic content or bacterial biomass were reasonable predictors of bacterial production; however, in this environment benthic primary production tended to also increase bacterial production. In both pelagic and benthic environments, predictions of bacterial production are improved by multiple regressions including a measure of the supply of organic matter and a measure of bacterial abundance or biomass. In view of the differences in the array of techniques that have been applied to various environments, it is satisfying that even rather coarse prediction is possible. Nevertheless, the residual variance in all of these

relations is large, indicating that other factors are important in explaining bacterial production. We point out, however, that the relation between bacterial production and primary production is no worse than the relation between chlorophyll *a* and primary production from the same data set.

The relation between bacterial production and primary production suggests 2 possibilities: either (1) that both bacteria and phytoplankton grow in response to common factors (nutrient load, temperature, etc.); or (2) that phytoplankton or material produced by phytoplankton are important substrates for bacterial growth (Larsson & Hagström 1979, Fallon & Brock 1980, Cole et al. 1984). On average, for the pelagic data, bacterial production was 20 % (median = 16.5 %) of primary production on a volumetric basis. If bacteria grow at 50 % growth efficiency (Cole 1982), then about 40 %, on average, of primary production fluxes through bacteria in the photic zone. (If bacteria grow at a lower efficiency, as implied by some studies, e.g. Newell et al. [1981], Bjørnsen [1986], this percentage of PP utilized by bacteria would be even larger.) This value of bacterial production as 20 % of primary production agrees extremely well with Williams' (1981) earlier assessment and with other direct studies of carbon cycling in lakes and marine systems.

When we consider the entire water column, bacterial production is even more significant, averaging 30.6 % (median = 27.1 %) of primary production on an areal basis. Again, considering both the assimilation and respiration terms, 60 % of primary production would be expected to flux through bacteria for an average water column. As our data are biased towards lakes and coastal marine systems, we may be underestimating the importance of bacterial production in deep water columns where the depth is many times greater than the photic zone.

Our regressions also allow comparison of bacterial production in the sediments versus bacterial production in the overlying water column. For an eutrophic lake (Lake Mendota, Wisconsin, USA), bacterial production in the water column (288 mg C m^{-2} d^{-1}) was much greater than in the sediments (83.5 mg C m^{-2} d^{-1}) implying that the water column could support a larger bacterivore population. For an oligotrophic lake (Mirror Lake), benthic bacterial production (57.6 mg C m^{-2} d^{-1}) was much greater than in the overlying water (17.4 mg C m^{-2} d^{-1}). The average depth of Lake Mendota (12.4 m) is only twice the average depth of Mirror Lake (5.75 m) so this difference could not completely explain the changing importance of the water column versus sediments in supporting bacterial growth. We expect that a pattern will be found in the relative contributions of the 2 habitats, perhaps based on trophic status, mixing depth, presence/absence of an anaerobic hypolimnion or other factors. At present, the relationship between water column variables and sediment characteristics is not clear enough to make any predictions.

In the water column, bacterial production is of comparable or larger magnitude than zooplankton secondary production, both expressed on an areal basis. For the IBP data, the sum of herbivorous plus carnivorous zooplankton production averaged 12 % of primary production and this fraction was essentially independent of trophic status (Fig. 4). Thus, on average we would expect planktonic bacterial production to be roughly twice zooplankton production. Since zooplankton are less efficient than bacteria and have growth efficiencies of about 25 % (Conover 1978, Comita 1972 in Wetzel 1982, Omori & Ikeda 1984), zooplankton respiration would average about 36 % of primary production while bacterial respiration would average 29 %. Thus, on average, we would expect zooplankton respiration to be about as large as or larger than planktonic bacterial respiration.

Given a complex food web in which the same organic molecules may be consumed and recycled several times, secondary production, especially of efficient organisms such as bacteria, could be nearly as large as primary production. Respiration, however, is constrained and must be less than the inputs of organic C from primary production and allochthonous sources. For our data, on an areal basis, planktonic bacterial respiration plus zooplankton respiration accounts for about two-thirds of planktonic primary production. Since some carbon is exported to the sediments and respired or buried there, the respiration of protozoa or other unmeasured planktonic organisms is also constrained and must be relatively small. If protozoa consumed all bacteria and only bacteria, and if they grew at a 40 % growth efficiency (Fenchel 1982), protozoan production could be as large as 12 % of primary production, about as large as the production of macrozooplankton. The respiration of these protozoa would account for 17 % of primary production. This added respiration would leave only 16 % of primary production for sedimentation. These simple calculations suggest that respiration within the water column by microbes (bacteria plus protozoa) is probably not larger than 50 % of net primary production.

CONCLUSIONS

(1) Bacterial production in both the water column and in the sediments is broadly predictable. The best predictor appears to be some measure of the supply or standing stock of organic matter.

(2) Bacterial production is a large component of total

secondary production in the plankton and is roughly twice the production of macrozooplankton.

(3) There do not seem to be consistent differences between marine and freshwater systems in these relationships.

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