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The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems

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Abstract

We analyzed published rates of extracellular release (ER) of organic carbon to determine the primary constraints on this process and its importance to bacteria. From 16 studies we extracted observations of ER, particulate primary production (PP), and phytoplankton biomass. In a regression model based on 225 observations, PP explained 69% of the variance in ER. From this model we estimate the average percent extracellular release (PER) to be 13% of total fixation. The slope of this relationship does not support the hypothesis that the PER declines with increasing productivity. Differences exist between marine and freshwater systems. In lakes, ER increases nonlinearly with productivity, resulting in very low PER in very eutrophic systems. In coastal marine and estuarine systems, ER increases linearly with productivity and the PER does not vary systematically. ER is not primarily related to phytoplankton biomass as predicted by passive diffusion models. Instead, ER appears to be constrained by the total availability of photosynthates. By comparing our model to an existing model of bacterial production and assuming a 50% growth efficiency, we estimate that ER amounts to less than half the C required for bacterial growth in most pelagic systems.

The release of dissolved organic substances by phytoplankton has long been recognized as an important source of high quality carbon to bacteria (Cole et al. 1982), as well as a frequently significant loss of photosynthate from pelagic algae (Fogg et al. 1965). As a consequence, this extracellular release (ER) has been studied widely, both within systems over depth and time and across production gradients. Unfortunately, results have often conflicted, making generalization concerning ER difficult.

One point of disagreement concerns the

relationship between total primary production (TPP) and the percentage of production lost as dissolved organic matter (percent extracellular release or PER). Since Fogg et al. (1965) first documented the prevalence of ER in natural communities of phytoplankton, a common observation has been that PER is inversely related to TPP. This pattern has been noted both within systems (Berman 1976) and across systems of different productivity (e.g. Anderson and Zeutschel 1970). However, some cross-system studies (Lancelot 1979; Sellner 1981) and some within-system studies (e.g. Riemann et al. 1982; Brock and Clyne 1984; Bell and Kuparinen 1984) have failed to detect this pattern. An important question is, therefore, how general is the widely accepted inverse relationship between PER and TPP?

Much research and discussion has centered on the causal basis for the relationship between PER and TPP. Very high PER has been associated with both supersaturating light intensities (Fogg et al. 1965) and very low light levels (Berman and Holm-Hansen

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1974), although exudates released under both of these conditions probably represent a small fraction of system ER (Mague et al. 1980). Observation and experiment also suggest a linkage between nutrient stress and enhanced release in oligotrophic systems (Jensen 1984). In opposition to these physiological explanations, Bjørnsen (1988) argued that ER should be constrained by passive diffusion of organics across phytoplankton cell membranes. He predicted that ER should, as a consequence, be related primarily to phytoplankton community cell surface area and the geometrically related variable, biomass. The relative impact of physiological and passive diffusion processes on natural variability in ER has not been assessed with reference to a general data set.

In most cases, ER is used rapidly by bacteria (e.g. Cole et al. 1982). Given the supposed inverse relationship between PER and TPP, it is tempting to postulate decreased importance of ER to bacteria as TPP increases. The fraction of bacterial C requirements which ER can meet varies between 4 and >100% (Riemann et al. 1982; Cole et al. 1982; Bell and Kuparinen 1984). However, no attempt has been made to determine if a pattern with respect to TPP exists. Direct estimates of the contribution ER can make to bacterial C requirements are relatively few, vary widely in methodology, and cover a restricted range in overall system productivity. In contrast, a wider empirical base exists in the literature for independent estimates of both system-averaged ER and bacterial productivity (Cole et al. 1988). A comparison of the relationships between ER and TPP, and bacterial production and TPP (Cole et al. 1988) would show indirectly whether the importance of ER to bacteria declines as system TPP increases.

In this paper, we summarize data from published studies containing observations on ER, particulate production (PP), and phytoplankton biomass. We describe the variability in ER relative to PP and address five questions. Do differences in methodology account for variability in ER? Does the fraction of total production released as extracellular compounds vary along a productivity gradient? Does ER obey the predictions of Bjørnsen's (1988) passive dif-

fusion model? What is the average fraction of bacterial C requirements that can be met by ER? Does this fraction vary systematically with productivity?

Methods

A sample data set comprising individual observations of ER and PP was derived from 16 studies (summarized in Table 1) encompassing both freshwater and marine habitats and covering a wide range in productivity. We avoided data from manipulation experiments and diel studies because such data are often closely spaced in time and might severely violate assumptions of independence implicit in the analyses. In addition, a minimum interval of 4 d between observations from seasonal or annual studies of single systems was set to further promote independence. A second data set comprised of system means was also derived (Table 2). These means were intended to characterize a lake or, in marine systems, a fixed station over an annual scale. When possible, we used means provided by the investigators. Otherwise, means were calculated from all the available data before logarithmic transformation. To test for biomass effects we derived two smaller data sets from the sample data set. One of these contained biomass estimates calculated from biovolume measurements, and the other contained Chl estimates.

Data were taken directly from tables or digitized from graphs by triplicate measurements. Points for which the C.V. was >10% were not included in the sample data set. If available, measured corrections for bacterial uptake were included to get the best estimate of ER unless the investigators suggested that these corrections were suspect (e.g. Larsson and Hagström 1982).

Data were expressed in hourly volumetric units. For the sample data, depth profiles were integrated and divided by the maximum sampling depth, thereby generating a volumetric average ER for the water column. Such an integration was not performed on the data used in the tests of biomass control of ER because we felt that depth-related variability in fixation due to light provides a particularly good test of Bjørnsen's (1988) hypothesis. Hourly units

Table 1. Summary of studies used in sample data set. PP and ER in $\mu\text{g C liter}^{-1} \text{h}^{-1}$.

Code	Source	Site	n	PP		ER		PER (Mean)	Study type
				Min	Max	Min	Max		
1	Anderson and Zeitschel 1970	Pacific Ocean, coast of Washington	7	0.24	19.8	0.09	1.79	14.5	X-system
2	Bell and Kuparinen 1984	Lake Erken, Sweden	12	1.86	19.1	0.60	7.94	30.9	System
3	Berman and Holm-Hansen 1974	Southern California Bight	11	0.52	11.2	0.19	3.18	15.2	X-system
4	Blauboer et al. 1982	Lake Vechten, The Netherlands	20	1.21	6.20	0.08	3.48	18.6	System
5	Brock and Clyne 1984	Lake Mendota, Wisconsin	12	0.69	10.5	0.25	9.12	41.4	System
6	Chróst and Faust 1983	Rhode River estuary, Chesapeake Bay	18	3.09	30.2	1.29	123	25.2	System
7	Cole unpubl. data	Mirror Lake, New Hampshire	12	0.28	1.03	0.04	0.53	21.8	System
8	Coveney 1982	Bysjön, Sweden	7	14.1	79.4	0.32	1.78	3.4	System
9	Tilzer and Horne 1979	Lake Tahoe, California/Nevada	4	0.10	0.24	0.01	0.03	12.48	System
10	Lancelot 1979	North Sea and North Atlantic	10	0.54	35.5	0.22	16.2	31.7	X-system
11	Larsson and Hagström 1982	Coastal Baltic Sea, Sweden	18	0.41	3.89	0.02	0.52	11.2	System
12	Larsson and Hagström 1982	Himmersjärden Fjord, Sweden	18	1.38	8.91	0.06	0.66	8.3	System
13	Mague et al. 1980	Gulf of Maine	21	0.60	36.3	0.21	2.75	11.3	System
14	Riemann et al. 1982	Lake Mossø, Denmark	13	19.1	120	0.49	10.2	4.5	System
15	Vadstein et al. 1989	Nesjøvatn, Norway	13	1.35	18.2	0.08	2.95	19.0	System
16	Williams and Yentsch 1976	Tropical Atlantic, Bahamas	7	0.17	0.65	0.003	0.04	6.7	System
17	Wolter 1982	Kiel Bight, Germany	23	4.17	105	0.41	40.7	18.7	System

were used because of uncertainties of extrapolation to daily rates from incubations of <24 h (Saunders 1972). When necessary, daylength was estimated to the nearest 0.5 h with sunrise and sunset times determined from an almanac.

The sample data consisted of 225 observations from 16 studies, seven of which were from freshwater and the remainder from marine or estuarine systems. Of the 16 observations making up the system means data, 10 were from lakes and the other six from marine or estuarine systems. No rivers or brown-water lakes were included in either data set. Most of the marine systems were coastal sites. ER ranged over 6 orders of magnitude in the sample data and 4 orders of magnitude in the system means data. PP ranged over 4 orders of magnitude in both the sample and system means data. PER varied from <1 to 75% in the sample data and 3 to 40% in the system means data.

The methodology used to measure ER varied considerably across studies. Because the measurement of ER is subject to a wide array of possible errors (Søndergaard and Jensen 1986), we classified the data into methodological categories according to the length of the ^{14}C incubation period, the use of factors correcting for bacterial uptake, and the pressure of sample filtration (Table 3). This classification was not intended to encompass all the potential methodological errors in ER measurements, but simply to allow us to detect systematic errors due to methodology as best we could.

To check the robustness of our original findings, we collected additional data free of the constraints imposed on the original data set. Data were culled from seven additional freshwater studies (Berman and Gerber 1980; Rai 1984; Søndergaard et al. 1985; Robarts and Sephton 1989; Sundh 1989; Sundh and Bell 1991) and three additional marine studies (Thomas 1971; Sellner 1981; Lignell 1990) for this purpose.

All linear regression models are of the form $\log(Y) = a + b \times \log(X)$. Logarithmic transformation was necessary to attain normality and homoscedasticity. All logarithms are base 10. The effects of noncontinuous variables were evaluated by means of ANCOVA to detect whether the regres-

Table 2. Summary of system means data set. PP and ER in $\mu\text{g C liter}^{-1} \text{ h}^{-1}$.

Source	System	PP	ER	PER
Bell and Kuparinen 1984	Lake Erken, Sweden	8.16	3.06	27.2
Berman 1976	Lake Kinneret, Israel	21.6	0.82	3.7
Blaauboer et al. 1982	Lake Vechten, The Netherlands	3.34	0.87	20.7
Brock and Clyne 1984	Lake Mendota, Wisconsin	4.59	3.34	42.1
Chróst and Faust 1983	Rhode River, Chesapeake Bay	109	32.8	23.0
Cole 1985	Mirror Lake, New Hampshire	0.58	0.18	23.7
Coveney 1982	Bysjön, Sweden	34.2	0.99	2.82
Larsson and Hagström 1982	Baltic Sea, coast of Sweden	1.53	0.29	16.0
Larsson and Hagström 1982	Himmersfjärden Fjord, Sweden	3.94	0.54	12.0
Mague et al. 1980	Gulf of Maine	14.4	1.29	8.2
Riemann et al. 1982	Lake Mossø, Denmark	63.4	3.18	4.8
Tilzer and Horne 1979	Lake Tahoe, California/Nevada	0.16	0.02	12.8
Vadstein et al. 1989	Nesjøvatn, Norway	6.28	1.25	16.6
Wetzel et al. 1972	Lawrence Lake, Michigan	1.44	0.09	5.7
Williams and Yentsch 1976	Coast of Bimini, Bahamas	0.32	0.02	5.9
Wolter 1982	Kiel Bight, Germany	14.4	3.16	18.0

sion of ER on PP differed in the y -intercept among groups. All statistics were computed in SAS (version 6.03).

Results and discussion

General relationship between PP and ER—The relationship between ER and PP is of interest for two reasons. First, we expect ER to be constrained by the amount of C fixed and available for leakage. Constructing a model relating ER to PP would allow us to assess the importance of this fundamental constraint relative to factors affecting the fraction of photosynthate leaked. Second, the slope of the log-log regression of ER on PP should have a slope < 1.0 if PER were inversely related to TPP. Literature values actually suggest a probable slope between 0.6 and 0.8 (Anderson and Zeutschel 1970; Berman and Holm-Hansen 1974; Mague et al. 1980).

Both the sample and system means re-

gressions of ER on PP were highly significant ($P < 0.0001$, Table 4, Fig. 1). The system means slope is indistinguishable from 1.0 whereas the sample regression slope is significantly < 1.0 ($P = 0.0098$), but still higher than the upper expectation of 0.8. Both of these slopes are model 1 regression estimates and may be conservative given the conditions of the data (Ricker 1973). Model 2 slope estimates are > 1.0 in both cases (Table 4).

Predicted PER values are similar for the two models. For example, a PP value of $6 \mu\text{g C liter}^{-1} \text{ h}^{-1}$, which is close to the mean for both data sets, has a predicted PER of 13.5 and 12% for the sample and system mean regressions. There is a large degree of error about the predicted means. For both regressions, 95% C.I. for individual predictions in terms of PER range from ~ 2 to 55%. Despite having only half the residual variance as the sample regression, the sys-

Table 3. Class variable summary. Studies are referred to according to Table 1.

Variable	Group	n	Grouping criteria	Studies included
Incubation length	0	205	0–10 h	1, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17
	1	53	12–24 h	2, 3, 7, 16
Filtration pressure	0	96	Max ≤ 125 mm of Hg	3, 6, 10, 13, 15, 17
	1	65	Max ≥ 200 mm of Hg	1, 2, 4, 8, 14, 16
	2	48	Syringe filtered	5, 11, 12
Correction factor	0	140	No correction	1, 2, 3, 4, 7, 9, 10, 11, 12, 13, 16
	1	95	Correction used	5, 6, 10, 14, 15, 17
Habitat	0	133	Estuarine and marine	1, 3, 6, 10, 11, 12, 13, 16, 17
	1	92	Lacustrine	2, 4, 5, 7, 8, 9, 14, 15

Table 4. Summary of regressions fit to the model $\log(Y) = a + b \times \log(X)$. *P*-values are for two-tailed *t*-tests of the hypothesis that slopes are equal to either 0 or 1 ($\alpha = 0.95$). Model 2 slopes are $b \div r$ where r is the square root of R^2 .

Data set	<i>Y</i>	<i>X</i>	Intercept <i>a</i>	Slope <i>b</i>	R^2	<i>P</i> for <i>b</i> = 0	<i>P</i> for <i>b</i> = 1	Model 2 slope
Sample data								
All data	ER	PP	-0.73	0.89	0.69	0.0001	0.0098	1.08
All data	ER	TPP	-0.86	0.96	0.78	0.0001	0.18	1.08
All data	PER	TPP	1.14	-0.04	0.01	0.18	—	—
Marine-estuarine	ER	PP	-0.88	1.03	0.78	0.0001	0.5	1.16
Freshwater	ER	PP	-0.52	0.66	0.52	0.0001	0.0001	0.92
Within studies	ER	PP	—	0.70	0.85	0.0001	0.0001	0.76
System means data								
All data	ER	PP	-0.80	0.92	0.79	0.0001	0.6	1.04
All data	ER	TPP	-0.90	0.96	0.84	0.0001	0.7	1.04
All data	PER	TPP	1.10	-0.04	0.01	0.66	—	—

tem mean regression is no more precise at predicting ER, due to the low number of observations as well as large differences in the average PER among systems (Table 2).

Relationship between PER and TPP—In neither the sample nor the system means data does PER vary systematically with TPP (Table 4, Fig. 2). This result is surprising considering how often PER is observed to decrease with increasing TPP within studies. An ANCOVA of the sample data revealed that the within-studies slope of the

relationship between ER and PP did not vary significantly across studies (Table 5) and averaged 0.7 (Table 4). In contrast to the overall regression slope, the within-studies slope differed significantly from 1 ($P < 0.001$), suggesting strongly that within studies the expectation of an inverse relationship between PER and TPP is borne out.

This discrepancy in the relationship of ER to PP at different hierarchical levels of the data does not seem to be a statistical artefact resulting from the use of model 1

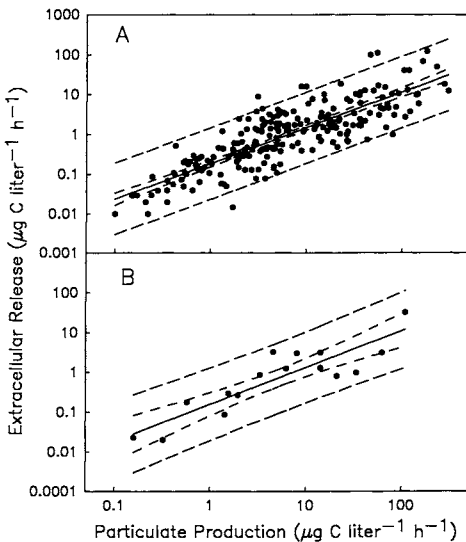


Fig. 1. Regressions of ER on PP. Solid lines—regression; inner broken lines—95% C.I. for the mean prediction; outer broken lines—95% C.I. for individual predictions. A. Regression for the sample data set. B. Regression for the system means data set.

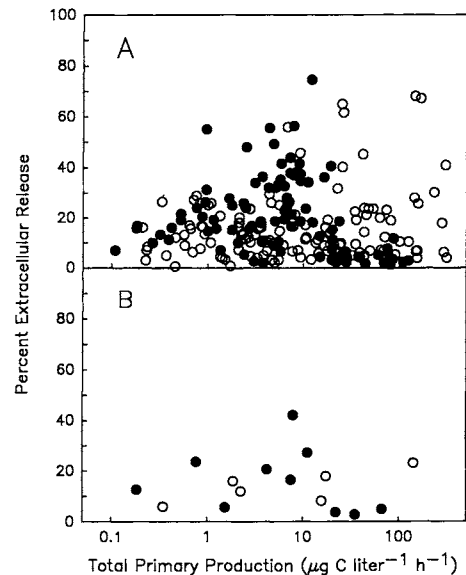


Fig. 2. Plot of percent ER against total primary production. Lacustrine data—●; marine-estuarine data—○. A. Sample data set. B. System means data set.

Table 5. Summary of ANCOVA of methodological and habitat effects. *P*-values are from *F*-tests of the hypothesis that intercepts and slopes are the same. R^2 improvement is the increase in R^2 due to class effects compared to a simple regression of ER on PP.

Variable	<i>n</i>	<i>P</i> -value for intercepts	<i>P</i> -value for slopes	R^2 improvement
Incubation length	258	0.0251	0.4203	0.007
Filtration pressure	209	0.0015	0.4200	0.021
Correction factor	235	0.0002	0.0004	0.034
Habitat	225	<0.0001	<0.0001	0.030
Study	225	<0.0001	0.6898	0.172

regression estimates because the model 2 slopes also disagree. Another, more mechanistic explanation may be that observations within systems over time may not be strictly independent. Over the seasonal cycle PP may be correlated with other variables which might affect the percent of primary production that is released. For example, periods of low primary production following blooms might be characterized by high nutrient stress which can cause high PER (Jensen 1984). If so, slopes of the within-studies regression of ER on PP would be influenced by this correlated variable as well as by PP. However, by averaging all the observations from a system, the effect of temporal dynamics is eliminated. Therefore, any correlations between predictors of ER that arise because of temporal dynamics would be removed from the system means data. Likewise, the elevated slope of the sample regression of ER on PP would result from the large influence of among-system differences which are independent of within-system dynamics.

Methodological effects—Incubation length and filtration pressure had small but significant effects on the regression of ER on PP (Table 5). Longer incubations are associated with elevated ER. More complete labeling of intracellular C pools with time can lead to higher measured ER (Hama and Handa 1987). This effect is apparently more important in these data than the uptake and respiration of radiolabel by bacteria which results in the opposite pattern (e.g. Wolter 1982). The relatively high ER observed in

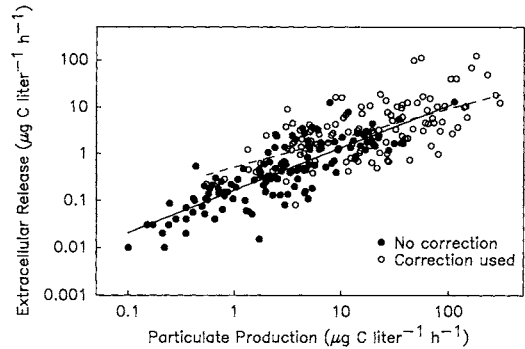


Fig. 3. Comparison of ER measurements with and without correction for bacterial uptake of exudates. Broken line—regression for the corrected data; solid line—regression for the uncorrected data.

studies with low pressures of filtration contradicts any expectation. Both incubation length and filtration pressure are of small magnitude and explain relatively little of the variability (Table 5).

Bacteria incorporate labeled photosynthate during ^{14}C incubations. As expected, studies with a correction factor for this bacterial uptake had significantly higher ER estimates (Fig. 3). However, the slope of the relationship between ER and PP differed for the corrected and uncorrected data, indicating that the effect varies in magnitude across the range of the data (Table 5, Fig. 3). The average difference between the corrected and uncorrected data is twofold. This difference agrees well with measured correction factors from the literature, which suggests that on average half of the radioactivity released during ^{14}C incubations is found in the bacteria (Table 6). Although this correction is not trivial to accurate measurement of ER, it also does not account for a large fraction of the residual variance from the regression of ER on PP. Considering this factor, and because the calculated correction for bacterial uptake of ER varied greatly depending on PP, we did not apply a correction to the uncorrected data.

Comparison of freshwater and marine data—There are significant differences between the regressions with data from freshwater lakes and the combined estuarine-marine data (Table 4). The estuarine-marine regression has a slope of 1.03 and R^2 of 0.78. The lacustrine model slope is

Table 6. Literature estimates of bacterial uptake of ^{14}C -labeled exudates during measurements of photosynthesis.

Study	PER incorporated by bacteria	Methods
Chróst and Faust 1983	32.3	Differential filtration (1.2 μm , 0.2 μm) and incubation of exudates with bacteria
Larsson and Hagström 1982		Differential filtration (3.0 μm , 0.2 μm), corrected for photosynthesis <3.0 μm and bacteria >3.0 μm
No respiration	57.0	
Including respiration	68.0	
Nalewajko et al. 1980	36.0	Comparison of xenic and axenic culture exudates
	71.0	
Nalewajko et al. 1976	~70.0	Comparison of xenic and axenic culture exudates
Chróst 1978	67.0	Comparison of exudates with and without antibiotics
Lancelot 1979	16.0	Kinetic analysis of time-series data
Wolter 1982		Differential filtration (3.0 μm , 0.2 μm), corrected for photosynthesis <3.0 μm and bacteria >3.0 μm
6 h	21.7	
24 h	16.3	
Riemann et al. 1982	45.0	Differential filtration (1.0 μm , 0.2 μm), corrected for bacteria >1.0 μm
Coveney 1982	54.6	Differential filtration (GFC, 0.2 μm)
Jensen 1984	37.2	Comparison of exudates with and without antibiotics
Brock and Clyne 1984	55.0	Differential filtration (3.0 μm , 0.2 μm)
Cole et al. 1982	40.0	Differential filtration (0.4 μm , 0.2 μm), corrected for uptake and respiration >0.4 μm
Mean	45.8	

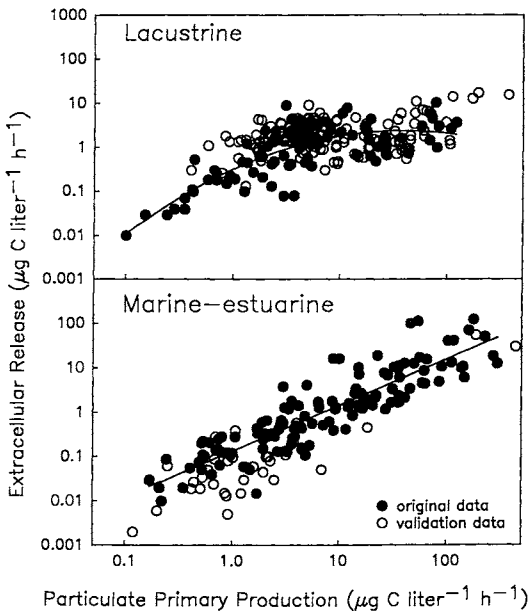


Fig. 4. Comparison of lacustrine and marine-estuarine patterns. Validation data are included but were not used to calculate the regression lines. Lacustrine data fit to the binomial regression model $\log(\text{ER}) = a + b \times \log(\text{PP}) + c \times [\log(\text{PP})]^2$. Marine-estuarine data are fit to a simple linear model.

significantly <1 and the model R^2 is only 0.52. Inspection of the lacustrine data revealed that ER appears to increase with PP to a certain level after which it remains fairly constant. Consequently, a binomial model provides a better fit to the lacustrine data ($R^2 = 0.80$, Fig. 4). This curvilinearity is attributable to the influence of a cluster of observations of very low PER at high productivity (Fig. 2A).

PER is unrelated to TPP in marine-estuarine systems, averaging ~12% with 95% C.I. ranging between 2 and 50%. By contrast, in lakes we predict a decrease in PER from 40 to 5% as productivity increases when a linear model relating ER and PP is used. The actual relationship between PER and TPP in freshwater is not simple, so we must be cautious with such predictions. Nonetheless, the observed pattern seems to be general, which suggests that PER is negatively related to TPP in lacustrine but not estuarine or marine systems.

We collected additional data to determine if the habitat-specific differences we detected initially were robust. When plotted with the original data, the validation data uphold

the general patterns (Fig. 4). The freshwater validation data exhibit somewhat higher average PER than the original data, but still tend to approach a maximum value for extracellular release. The average PER of the marine-estuarine validation data is much lower than for the original data, especially at low TPP. The lack of a negative trend in PER as production increases in marine systems is thus reinforced. Although only two points represent the highly productive end of the marine-estuarine spectrum, they do indicate that ER does not seem to level off at high ER, as in freshwater systems.

Why does ER increase nonlinearly with PP in our lacustrine data set? The taxonomic composition of the phytoplankton in the eutrophic lakes Mossø and Bysjön does not appear to differ systematically from other lakes in the data set nor does it appear overly similar to the eutrophic communities in Lake Kinneret or Hartbeespoort Dam. Culture (Mykkestad 1977), and field observations (Lancelot 1983; Søndergaard and Jensen 1986) have demonstrated that the onset of nutrient stress is related to high excretion rates. There is some evidence that PO_4^{3-} limitation may stimulate more excretion than does N limitation (Mykkestad 1977). P primarily limits phytoplankton biomass in lakes (Dillon and Rigler 1974), with N becoming increasingly important in more productive systems (McCauley et al. 1989). In lakes, phytoplankton growth can be limited by N, P, or both (e.g., Elser et al. 1990). In contrast, P limitation is not widely observed in marine systems (Hecky and Kilham 1988). A shift in the critical nutrient limiting algal growth as productivity increases across lakes could cause the differences we see between marine and lacustrine systems.

Even when differences between marine and freshwater systems are considered, there is considerable residual variability in the data (Table 5). A large part may result from the inexact nature of ER measurements. The standard assumptions regarding isotopic equilibrium and linear release with time may be violated to varying degrees depending on environment and physiology (Søndergaard and Jensen 1986). Bottle effects, filtration artifacts, and sample storage time may also

be important in some circumstances. Our methodological categories would not detect random variability resulting from such sources of error.

Much of the variability is also likely to reflect natural differences in ER among communities. It has long been known that rates of excretion can differ dramatically between taxa (Hellebust 1965). Also, differences in the ability of a phytoplankton community to store C in excess of growth capacity and respiratory demand could account for differences in the response of communities to nutrient stress (Mykkestad 1977). Studies directly addressing the impact of nutrient stress and the physiological traits of different taxa upon ER in situ are sorely needed.

Passive diffusion hypothesis—Bjørnsen (1988) hypothesized that ER was the result of passive diffusion across cell membranes. Given this model, he argued that total cell surface area of the phytoplankton community and the geometrically related variable, phytoplankton biomass, should better predict ER than does PP. If Bjørnsen were correct, PP would be acting as a surrogate for biomass in our models. It is therefore important to evaluate the possible role of biomass.

To test the effect of phytoplankton biomass, we evaluated alternative models by means of a stepwise model selection procedure with PP, biomass-specific PP (PP/phytoplankton biomass), and biomass or Chl as potential predictors of ER. Depending on which processes are responsible for ER, there are three possible extreme outcomes. First, biomass would be the only predictor if Bjørnsen's passive diffusion model were correct. Second, if the steepness of the cross-membrane gradient of photosynthate were to drive ER by influencing passive or enzyme-facilitated diffusion, then PP would be the best predictor. Bjørnsen argued explicitly against this possibility. Third, if ER were constrained primarily by the availability of photosynthates to release processes, then PP should be the best predictor. Variability about the regression of ER on PP would reflect differences in species-specific excretion rates and the physiological status of the various communities. Com-

Table 7. Summary of regressions testing for the effects of biomass. For both data sets, model 1 represents the stepwise selection best model. Partial R^2 -values and slopes for the bivariate models (2) are reported to the right of their corresponding independent variables. SPP—Biomass-specific primary production; PB—phytoplankton biomass. All P -values are for two-tailed tests.

Model	Dependent variables	Independent variables	Intercept a	Slope b	R^2	P -value $b = 0$
Biomass data: studies 9, 10, 12, 13, 15						
1	ER	PP	0.86	0.85	0.62	0.0001
2	ER	PB	0.85	0.85	0.35	0.0001
		SPP		0.85	0.27	0.0001
3	PP	PB	1.60	0.97	0.56	0.0001
4	PP	SPP	2.40	0.96	0.40	0.0001
5	PB	SPP	2.40	-0.04	0.00	0.7
Chlorophyll data: studies 1, 2, 5, 6, 8						
1	ER	PP	0.56	0.87	0.70	0.0001
2	ER	PB	0.56	0.87	0.58	0.0001
		SPP		0.65	0.13	0.0001
3	PP	PB	0.24	0.86	0.69	0.0001
4	PP	SPP	0.59	0.70	0.10	0.002
5	PB	SPP	0.70	-0.41	0.05	0.03

binations of the variables would represent some form of mixed model.

PP was the only variable that entered the model in either case, which suggests that ER is primarily constrained by the total availability of photosynthate (Table 7). Phytoplankton biomass and specific PP seem to be only indirectly related to ER. We conclude, therefore, that our data are not consistent with current models of passive diffusion.

The failure of phytoplankton biomass to explain more of the variability in ER than did PP is probably not due to the activities of zooplankton. A significant amount of dissolved organic C can be released through the processes of sloppy feeding and excretion by zooplankton (Lampert 1978). However, the radioactivity of intracellular C does not equilibrate with ^{14}C in short-term (<24 h) primary production incubations (Storch and Saunders 1978). The incubation times in our data are mostly <6 h, so this effect should be even more pronounced. As a result, zooplankton-mediated release of dissolved organics probably represents only a small fraction of measured ER even when such release is significant. Eppley et al. (1981) reported no significant difference in measured ER between samples with and without zooplankton, despite evidence of significant zooplankton-mediated release. Similarly, we see no systematic difference in PER esti-

mates from studies where zooplankton were removed with nets before beginning primary production assays (studies 3, 10, 13, 14, Table 1) and those that did not remove zooplankton.

When the strong constraints imposed by cell membranes on passive diffusion of organic compounds are considered, the unexplained variability in ER is likely to reflect differences in the active release of organic compounds by communities. Although it is still possible that low molecular weight extracellular products may conform to the passive diffusion model, it is well known that large molecules are released and may even dominate exudate pools (Nalewajko and Schindler 1976; Chróst and Faust 1983; Sundh 1989). The inability of these molecules to passively diffuse through cell membranes explains the failure of passive diffusion models to explain rates of ER.

Contribution of ER to bacterial production—Cole et al. (1988) constructed an empirical function relating bacterial production (BP) and TPP across systems. Using our data, it is possible to construct an analogous relationship between ER and TPP which, when combined with the BP function, can be used to address two questions: what is the average contribution ER can make to bacterial C requirements, and does this contribution change with system productivity?

After conversion to daily units (assuming average daylength to be 13 h), the relationship developed here relating system ER and TPP is

$$\log(\text{ER}) = -0.946 + 0.955 \times \log(\text{TPP}). \quad (1)$$

Using a data set covering a range in TPP from 4.5 to 1,834 $\mu\text{g C liter}^{-1} \text{d}^{-1}$ and consisting of observations from 54 different systems, Cole et al. (1988) found that BP depended on TPP according to

$$\log(\text{BP}) = -0.483 + 0.814 \times \log(\text{TPP}). \quad (2)$$

In order to determine the bacterial C requirement (BCR) from BP, we need to know how efficiently bacteria convert assimilated C into biomass. The BCR is related to BP and bacterial growth efficiency (BGE) according to the identity

$$\log(\text{BCR}) = \log(\text{BP}) - \log(\text{BGE}). \quad (3)$$

BGE is usually assumed to be near 50% when C flux through bacteria is being calculated from production estimates (Cole et al. 1982; Bjørnsen 1986). Given this assumption and substituting Eq. 2 into 3, we get

$$\log(\text{BCR}) = -0.182 + 0.814 \times \log(\text{TPP}). \quad (4)$$

We assume that recycling of C within the bacterial compartment will not significantly affect the efficiency by which exudates are converted to bacterial biomass as considered by Strayer (1988).

Finally, the fraction (F) of the BCR that can be met by ER can be expressed as

$$\log(F) = \log(\text{ER}) - \log(\text{BCR}). \quad (5)$$

When we substitute Eq. 1 and 4 into 5, the resulting function relating F to TPP is

$$\log(F) = -0.764 + 0.141 \times \log(\text{TPP}). \quad (6)$$

Equation 6 predicts that on average ER provides up to half of the C required to support bacterial growth in natural systems (Fig. 5). F varies from 20% at TPP at 2.4 $\mu\text{g C liter}^{-1} \text{d}^{-1}$ to 50% at 1,850 $\mu\text{g C liter}^{-1} \text{d}^{-1}$, with a geometric mean of 32% (Fig. 5B). Because of the large error accrued as a result of combining models, the positive trend in F with TPP is only suggestive ($P = 0.35$, two-tailed *t*-test of slopes with different

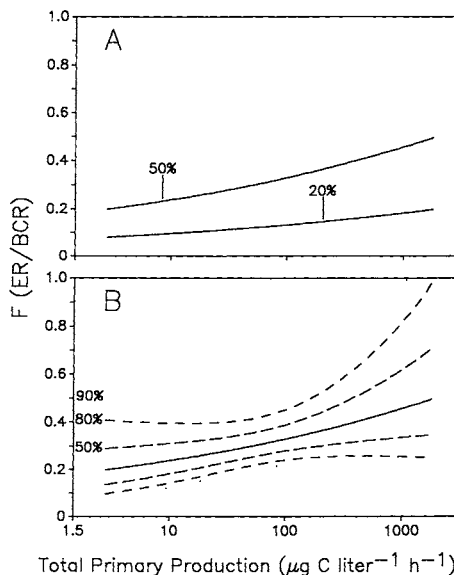


Fig. 5. Models for relating the potential contribution of dissolved production to BCR (F) to total primary production. A. Comparison of models assuming 50 and 20% BGE. B. The model assuming 50% BGE with 90, 80, and 50% C.I. for the median of the distribution. Confidence intervals were calculated by assuming that the variances of Eq. 1 and 2 are additive (i.e. no covariance among residuals of the regressions).

sample sizes and degrees of freedom, Moore and McCabe 1989). However, a negative slope for this relationship, which might be expected if there were a negative relationship between PER and system productivity, is unlikely [$P(\text{slope} < 0) = 0.18$]. Because PER is low in highly productive lakes, the contribution of ER to bacterial needs might decline with productivity when only freshwater systems are considered. We did not have enough observations of mean primary production to produce a freshwater-specific model. However, we note that the slope of the regression of BP on primary production with only freshwater data (0.688, Cole et al. 1988) is very similar to the slope of the freshwater regression of ER on TPP based on the sample data (0.665, Table 4).

The results of the analysis above are sensitive to the assumed BGE. Some studies have suggested that BGE values may fall in the range of 10–30%, thus increasing estimates of bacterial C demand by 2–5 times (Bjørnsen 1986). If we derive F assuming a BGE of 20% we get

$$\log(F) = -1.16 + 0.141 \times \log(\text{TPP}). \quad (7)$$

This model predicts that the contribution of ER to BCR increases from 8 to 20% as TPP increases, suggesting a much reduced importance of ER to bacteria compared to Eq. 6 (Fig. 5B). However, Eq. 7 also implies that the BCR exceeds system productivity at $\text{TPP} < 14.5 \mu\text{g C liter}^{-1} \text{d}^{-1}$. Thus, the assumption of a 20% BGE results in estimates of the BCR that seem high even given possible recycling of C within the bacterial compartment (Strayer 1988). We therefore consider Eq. 7 to represent a lower bound on the contribution of ER to the BCR. Maximum values of BGE on a variety of substrates (Bjørnsen 1986) show that the highest values fall between 50 and 60%. As a consequence, we feel that Eq. 6 and 7 probably bracket the true median trend for the contribution of ER to BCR.

Our models suggest that ER meets <50% of the BCR in most freshwater and coastal marine systems. This conclusion holds even when assuming the highest BGE (Eq. 6) and taking into account the error accrued by combining regression models. The error associated with mean predictions of Eq. 6 were estimated by assuming no covariance among residuals of the two regressions and adding variances of mean predictions from Eq. 1 and 2. Confidence intervals about the mean predictions were then derived (Fig. 5). Except at high TPP, the 80% prediction interval (two-tailed) does not include $F = 0.5$. When BGE is assumed to be <50%, this pattern is reinforced. Therefore, while ER in some systems may amount to >50% of bacterial needs, the contribution of ER in most lakes and coastal areas is clearly predicted to remain below this threshold.

General conclusions—The statistical analysis of the literature data on ER presented here serves several purposes. First, it provides general tests of hypotheses over scales which would be impossible to approach within the framework of a field study, particularly when the data are quite variable. Moreover, given large variability, it provides the easiest means of searching for systematic differences among systems, perhaps suggesting controlling factors not included in the analysis. Also, we can estimate

how much of the variability in ER remains unpredicted by our current understanding of the factors controlling ER. Finally, we can draw implications from the data which represent our best predictions about patterns of ecosystem structure and function in nature.

Several hypothesized patterns were not supported by our analyses. PER does not seem to be negatively related to TPP in either the sample data set or the system mean data set, although PER did decrease with TPP within studies. This apparent discrepancy may result from covariation of PP with other factors influencing ER over time within systems. PER also seems to be low in eutrophic lakes, but shows no trend across salt-water productivity gradients. These results suggest that the role often assigned to nutrient stress in determining large-scale patterns of ER is either incorrect or must be refined.

Passive diffusion models with phytoplankton biomass and specific primary production as explanatory variables for ER do not succeed. Instead, ER is constrained primarily by total fixation into the particulate fraction. PP explains 69 and 79% of the variance in individual and system mean ER respectively, the slope being close to one in both cases.

A large amount of residual variability in ER remains unexplained. Methodological artifacts arising from failure of the standard assumptions underlying calculations of ER or sample treatment may contribute to this variability. Real differences in ER among communities are also likely to contribute. Studies that control for methodological variability while directly addressing the bases for differences in ER between communities *in situ* are needed.

Contrary to expectation, the ratio of ER to BCR does not vary significantly along a production gradient. On average across lakes, estuaries, and coastal marine environments, ER amounts to 32 or 13% of BCR, if we assume values of BGE of 50 or 20% respectively. The true average value probably lies between these estimates. We conclude, therefore, that in most of these systems over half of the BCR is met by sources other than phytoplankton release. This re-

sult is in accordance with a general consensus emerging over the last decade that allochthonous C sources and such processes as sloppy feeding, zooplankton excretion, and phytoplankton senescence are needed to balance bacterial needs.

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