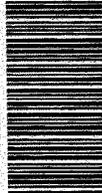


ILLiad TN: 409913



OKS Document Delivery

Journal Title: Microbial Ecology

Volume: 21

Issue: 1

Month/Year: December
1991

Pages: 99-118

Article Author: Paul A. White Jacob Kalff,
Joseph B. Rasmussen and Josep M. Gasol

Article Title: The effect of temperature and algal
biomass on bacterial production and specific
growth rate in freshwater and marine habitats

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The Effect of Temperature and Algal Biomass on Bacterial Production and Specific Growth Rate in Freshwater and Marine Habitats

Paul A. White, Jacob Kalff, Joseph B. Rasmussen, and Josep M. Gasol

Limnology Research Centre, Department of Biology, McGill University, Montréal, Québec H3A 1B1, Canada

Received: August 22, 1990; Revised: December 14, 1990

Abstract. We analyzed heterotrophic, pelagic bacterial production and specific growth rate data from 57 studies conducted in fresh, marine and estuarine/coastal waters. Strong positive relationships were identified between 1) bacterial production and bacterial abundance and 2) bacterial production and algal biomass. The relationship between bacterial production and bacterial abundance was improved by also considering water temperature. The analysis of covariance model revealed consistent differences between fresh, marine and estuarine/coastal waters, with production consistently high in estuarine/coastal environments. The log-linear regression coefficient of abundance was not significantly different from 1.00, and this linear relationship permitted the use of specific growth rate (SGR in day^{-1}) as a dependent variable. A strong relationship was identified between specific growth rate and temperature. This relationship differed slightly across the three habitats. A substantial portion of the residual variation from this relationship was accounted for by algal biomass, including the difference between marine and estuarine/coastal habitats. A small but significant difference between the fresh- and saltwater habitats remained. No significant difference between the chlorophyll effect in different habitats was identified. The model of SGR against temperature and chlorophyll was much weaker for freshwater than for marine environments. For a small subset of the data set, mean cell volume accounted for some of the residual variation in SGR. Pronounced seasonality, fluctuations in nutrient quality, and variation of the grazing environment may contribute to the unexplained variation in specific growth.

Introduction

Over the past 20 years we have become much more aware of the significant role that heterotrophic bacteria play in aquatic systems. This is, to a large

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degree, the result of improvements in methods used for assessing bacteria biomass and production. It is now clear that bacteria have a somewhat dual role in aquatic ecosystems. They are not only the major decomposers of organic matter in the water column and sediments [30, 50, 96], but are increasingly recognized as important producers of particulate organic carbon, through the consumption and assimilation of dissolved organic carbon [9, 27]. Bacteria can convert large amounts of organic matter, both autochthonous and allochthonous, into bacterial biomass and can sustain high specific growth rates [12, 52]. Thus they may provide a route for the assimilation of dissolved organic carbon into the classical food chain [46, 51, 80].

It is evident that a thorough understanding of the flow of nutrients and carbon in the aquatic ecosystem will require knowledge of the parameters that regulate microbial production and specific growth. Both production and specific growth are likely affected by a panoply of environmental factors in both fresh and saltwater ecosystems. These factors have long been a matter of considerable speculation. Laboratory and in situ research suggests that substrate quantity and quality, as well as temperature, are important regulators of production and specific growth [48, 64, 72, 100]. Recent research has described broad-scale empirical relationships between bacterial abundance and algal biomass [2, 11, 20], between bacterial production and bacterial abundance, as well as between bacterial production and net primary production [20]. Empirical relationships such as these reveal those parameters which are important regulators of bacterial growth and production, and are extremely useful in directing future research efforts.

Here we describe several empirical models that relate bacterial production and specific growth rate in fresh and salt waters to several variables, including bacterial abundance, water temperature, and algal biomass (expressed as concentration of chlorophyll *a*).

Methods

Data Collection

Simultaneous observations of pelagic bacterial production, bacterial abundance, in situ temperature, chlorophyll *a* concentration and salinity in fresh and saltwater ecosystems were assembled from the recent literature. Chlorophyll and salinity data were not always available but were collected whenever possible. When available, data on mean cell size (in μm^3) at time of sampling was also noted. The data were obtained from 57 separate studies conducted in a wide range of aquatic environments (Table 1). Data were selected using the following criteria: 1) bacterial production or ^3H -thymidine uptake rate (when this method had been used), bacterial abundance and temperature were reported; 2) production (or ^3H -thymidine uptake) estimates were measured at in situ temperature. Saltwater habitats were classified on the basis of salinity, with marine environments defined as those with a salinity $\geq 33\text{‰}$, and estuarine/coastal environments as those $< 33\text{‰}$ [88]. Ten of the freshwater studies were conducted in eutrophic lakes (chlorophyll *a* $\geq 15 \mu\text{g/liter}$ [96]), fourteen were conducted in mesotrophic lakes (chlorophyll *a* between 2 and 15 $\mu\text{g/liter}$), and the remaining two were conducted in rivers. A wide range of seasonal conditions and depths were represented. The number of data points obtained from each study varied from 3 to 50, with a mean of 13. Studies with one single observation were avoided. When large quantities of time series data were present in one study, monthly means were used. Where in situ temperature was not

Table 1. Sources of data for regression analysis: a qualitative description. Note: eutrophic denotes chlorophyll *a* concentrations $\geq 15 \mu\text{g liter}^{-1}$; mesotrophic denotes a chlorophyll concentration between 2 and $15 \mu\text{g liter}^{-1}$. Some references provide data for more than one system

Freshwater			Marine and estuarine	
Eutrophic	Mesotrophic	Salinity < 33‰	Salinity $\geq 33‰$	
L. Tystrup [75]	Little Crooked L. [57]	Bothnian Sea [97, 98]	Pebble Beach, New York [35]	
L. Nesjøvatn [91, 92]	L. Mahoney [40]	Baltic Proper [97]	Nova Scotia Coast [24]	
L. Norrviken [9]	L. Erken [10]	Mediterranean Sea [97]	Gulf Stream [4, 26]	
L. Bysjön [21]	L. Constance [36, 37, 39, 84]	Chesapeake Bay [25, 58]	Hudson River Plume [27, 28]	
L. Häljasjön [21]	L. Biwa [63]	Howe Sound [3]	McMurdo Snd., Antarctica [32, 53]	
L. Mossø [78]	L. Kvernvatnet [14, 15]	Saline Aquaculture Ponds [61]	California Coast [32]	
L. Hylke [77]	L. Oglethorpe [79]	Elbrí Lagoon, Ivory Coast [89]	British Columbia Coast [32]	
L. Arlington [19]	L. Dalnee [87]	Oosterschelde Basin [54]	Gulf of Carpentia [62]	
Fredriksborg Slottssø [74]	L. Vechten [12, 13]	Long Island Sound [47]	North Sea [68]	
L. Toolik (fert. limnocorals) [45]		Subtrop. Estuary, Georgia [65, 70, 81, 82]	Upwelling Zone [59]	
Rimov Reservoir [83]		Subtrop. Estuary, Florida [69]	New York Bight [28]	
		Danish Coastal Estuary [67]	Arctic Ocean [71]	
Riverine data:			Red Sea [95]	
Blackwater Rivers [29]			Southern California Bight [34]	
Mississippi River [42]			Drake Passage, Antarctica [41]	
			Subtropical Atlantic [5]	
			Gulf of Aden [95]	

reported, the data were in some cases obtained from the principal author. Bacterial abundance in the data set was determined by epifluorescence direct counts, employing either acridine orange or diamidinophenyl indole (DAPI). Bacterial production was measured by four methods: uptake of [*methyl*-³H] thymidine (n = 48), dark ¹⁴C (HCO₃⁻ or labelled organic C) uptake (n = 4), frequency of dividing cells (n = 4), and increase in cell number upon dilution and incubation (n = 2). For studies where only [*methyl*-³H] thymidine uptake rates were reported (n = 12), estimates of bacterial production were obtained using a conversion factor that is a mean of those reported in the literature, i.e., 2.1×10^{18} cells mole⁻¹ thymidine. Values of this magnitude have been shown to be an approximate baseline conversion factor over a wide range of ³H-thymidine concentrations [8, 76]. To convert increase in cell number to production, the conversion factor 2.9×10^{-14} g C cell⁻¹ [65] was applied. While higher than the conversion factor used by some authors, it lies well within the published range of 1.0×10^{-14} to 5.8×10^{-14} g C cell⁻¹ [16, 17, 25, 31, 55, 63, 73]. Primary productivity data for three studies were converted to chlorophyll *a* concentrations using the model of Smith [85]. Phytoplankton biomass values for one study were converted to chlorophyll *a* concentrations according to Banse [7]. Values expressed on the basis of area were divided by the sampling depth to obtain volumetric equivalents. Studies for which in situ temperature could not be provided were excluded from the analysis.

Data Analysis

The data were analyzed by ordinary least squares regression and analysis of covariance (ANCOVA) using SYSTAT [99] and GLIM 3.12 [1]. The data were fit to the model $Y = \beta_0 + \beta_1 \cdot (X) + \epsilon$ for simple linear regressions and $Y = \beta_0 + \beta_1 \cdot (X_1) + \beta_2 \cdot (X_2) + \dots + \beta_k \cdot (X_k) + \epsilon$ for multiple regressions. The error term ϵ was assumed to be independent and normally distributed with mean zero and variance σ^2 . Where necessary, the data were log transformed to equalize the variance over the range of observations and meet the normality assumptions of least squares regression analysis [74]. To compensate for inherent bias in log transformed equations, correction factors were calculated (CF = antilog $1.1513 \times \text{RMS}$, where RMS is the residual mean square of the regression) [66]. To account for the possibility of underestimating the regression coefficient (slope) when there was error in the independent variable, a model II or geometric mean slope was calculated as recommended by Ricker [74]. Cross-validation and model selection employed the prediction sum of squares (PRESS) [1, 6]. The method involves omitting each observation in turn from the data set, fitting the model to the remaining observations, predicting the value of the omitted observation, and comparing the prediction with the observed value. The sum of the squared differences between the omitted observations and their predicted values provides the PRESS. When this is minimized, one selects the model with the greatest predictive value [1]. For multiple regressions, standardized partial regression coefficients (beta coefficients) were calculated to provide an indication of the relative impact of each independent variable on the dependent variable [101]. Normality of the residual values from each model was assessed using the Komogorov-Smirnov test [101], and visual inspection of a normal probability plot [99].

The following abbreviations are used in the text: PROD = bacterial secondary production ($\mu\text{g C liter}^{-1} \text{ day}^{-1}$), ABUND = bacterial abundance (10^9 cells liter⁻¹), TEMP = water temperature (°C), SGR = specific growth rate (day⁻¹), CHLA = chlorophyll *a* concentration ($\mu\text{g liter}^{-1}$), G = doubling time (days), SAL = salinity (‰), and VOL = cell volume (μm^3). All confidence intervals are 99%. Log values are base 10.

Results

Mean, minimum, and maximum values of bacterial production, temperature, bacterial abundance, specific growth rate, chlorophyll *a* concentration, doubling time, salinity, and cell volume are summarized in Table 2. Some extreme values

are worth noting. The highest freshwater chlorophyll and bacterial production values are from eutrophic Lake Nesjøvatn in central Norway [91]. The highest marine chlorophyll concentrations are from an upwelling zone off the coast of Chile [59]. Extremely low (almost unbelievable) marine abundance and productivity values are from marine snow in the subtropical Atlantic [5]. Production values are consistently high in the estuarine/coastal habitat. Extremely high estuarine/coastal abundance, production, and chlorophyll values are from eutrophic Biétri Bay (Elbrié Lagoon, Ivory Coast) [89]. Specific growth rates in the data set ranged from a low of 0.0003 day^{-1} to a high of 30.8 day^{-1} , with a mean of 0.9 day^{-1} . Extremely low values, equivalent to doubling times of well over 1 year, occurred in Drake Passage, Antarctica [41]. Extremely high values of 30.8 day^{-1} , equivalent to a doubling time of 47 minutes, occurred in eutrophic Biétri Bay, at a chlorophyll concentration of approximately $78 \mu\text{g liter}^{-1}$ and a temperature of 30°C [89]. The relationships between the major variables of interest are summarized in Fig. 1. The scatter plot matrix demonstrates linear relationships between specific growth rate or production and several variables including temperature, bacterial abundance, and algal biomass (concentration of chlorophyll *a*). Pearson correlation coefficients are provided for each scatterplot.

Bacterial Production

For the entire data set, a significant relationship was identified between bacterial production and bacterial abundance. The overall relationships for model (1) is:

$$\log \text{PROD} = 0.88 + 1.19 \log \text{ABUND} \quad r^2 = 0.63, n = 723 \quad (1)$$

Comparison of the studentized residuals from this model to a *t* distribution with the appropriate Bonferonni correction [60] revealed several extreme outliers at $\alpha = 0.05$. Two values were from Antarctic data [32], and the remainder (21 observations) were riverine data [29, 42]. Leverage values (h_i) [94] associated with these observations revealed undue influence on the regression estimates. These observations were removed from subsequent analyses. The revised model (model (2)) with slightly changed coefficients and r^2 is:

$$\log \text{PROD} = 0.89 + 1.22 \log \text{ABUND} \quad r^2 = 0.68, n = 700 \quad (2)$$

The slope estimate is not significantly different from the one published by Cole et al. [20]. In addition, a consistent relationship was identified between bacterial production and chlorophyll *a* concentration:

$$\log \text{PROD} = 0.86 + 0.71 \log \text{CHLA} \quad r^2 = 0.36, n = 412 \quad (3)$$

The slope estimate (model (3)) is also not significantly different from the one published by Cole et al. [20]. It should be noted that the intercepts of the models published by Cole et al. [20] fall well below our lower 99% confidence limit. The above relationships differed slightly among the different habitats examined. Regression equations for each habitat are summarized in Table 3.

The analysis of the relationship between bacterial production and abundance was significantly improved by the inclusion of in situ temperature as an ad-

Table 2. Summary statistics. Mean, minimum, and maximum values of bacterial production ($\mu\text{g C liter}^{-1} \text{ day}^{-1}$), bacterial abundance (10^9 cells liter^{-1}), temperature ($^{\circ}\text{C}$), chlorophyll *a* concentration ($\mu\text{g liter}^{-1}$), specific growth rate (day^{-1}), doubling time (days), salinity (‰) and cell volume (μm^3) for fresh, marine, and estuarine/coastal waters. For sample size (*n*) see Table 3. NA = not available or applicable

	Fresh			Marine
	Mean	Min	Max	Mean
PROD	43.33	0.45	302.40	17.96
ABUND	3.76	0.32	13.90	1.39
TEMP	13.94	2.10	32.00	14.35
CHLA	16.60	0.40	103.70	4.39
SGR	0.56	0.017	8.69	0.44
G	7.41	0.12	59.65	57.64
SAL	NA	NA	NA	34.66
VOL	0.119	0.083	0.185	0.468

ditional independent variable. The following model (model (4)) was identified for the entire data set:

$$\log \text{PROD} = 0.11 + 1.07 \log \text{ABUND} + 0.05 \text{TEMP} \quad (4)$$

$$r^2 = 0.79, n = 700$$

Analysis of covariance revealed a significant habitat effect and temperature-habitat interaction. The differences between the relationships in each habitat are slight, but significantly different at $\alpha = 0.05$. Regression models for each habitat are summarized in the top half of Table 4. The analysis of covariance model (model (5)) ($r^2 = 0.81, n = 700, F$ significance < 0.00001), identified by minimizing the prediction sum of squares, is as follows (values associated with regression coefficients are 99% confidence intervals):

$$\log \text{PROD} = \begin{bmatrix} \text{Fresh: } 0.43 \\ \text{Marine: } -0.08 \\ \text{Estuarine} \\ \text{\& Coastal: } 0.165 \end{bmatrix} + 1.00 \pm 0.08 \log \text{ABUND}$$

$$+ \begin{bmatrix} \text{Fresh: } 0.031 \pm 0.015 \\ \text{Marine: } 0.052 \pm 0.005 \\ \text{Estuarine} \\ \text{\& Coastal: } 0.046 \pm 0.008 \end{bmatrix} \cdot \text{TEMP} \quad (5)$$

The regression coefficients indicate that the temperature-habitat interaction is primarily due to the difference in the effect of temperature between fresh and saltwater habitats (i.e., little difference exists between marine and estuarine/coastal habitats). The standardized regression coefficients indicate that in fresh and estuarine/coastal habitats the impact of temperature on production is greater than that of abundance, but that the reverse is true for the marine data.

Approximately 70% of the collected saltwater data included salinity values. Salinity accounts for some of the residual variation in the relationship between

Table 2. Continued

Marine			Estuarine & Coastal	
Min	Max	Mean	Min	Max
4.0E-06	336.19	355.56	0.03	23767
3.0E-06	11.40	4.93	0.12	31.70
-2.00	38.00	21.40	-1.70	35.00
0.04	62.00	12.34	0.08	78.20
0.0003	10.17	1.75	0.007	30.81
0.10	2,900	15.41	0.032	1,353
33.00	39.20	22.69	4.50	32.80
0.033	1.00	NA	NA	NA

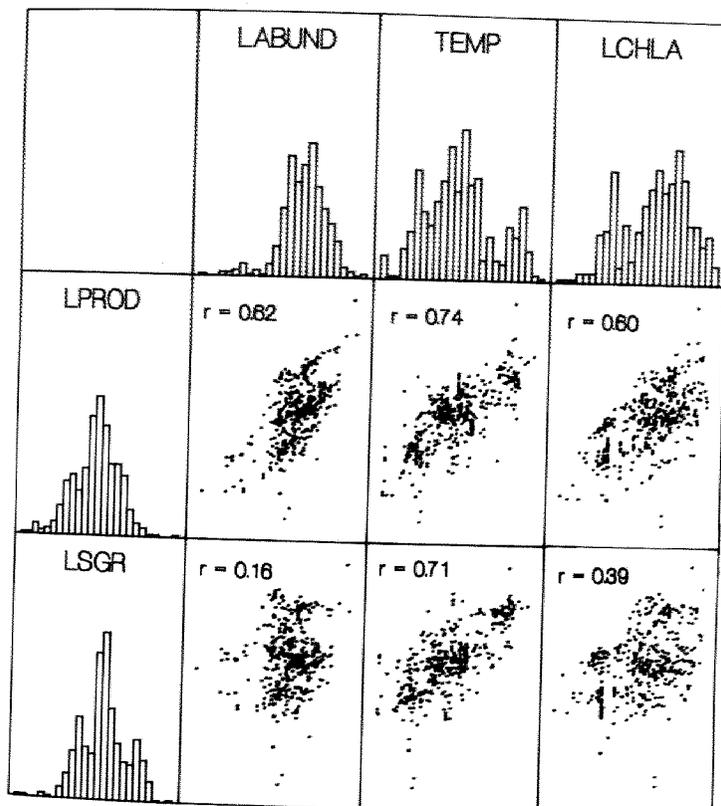


Fig. 1. Scatterplot matrix of the major variables of interest: LPROD, log bacterial production ($\mu\text{g C liter}^{-1} \text{ day}^{-1}$); LSGR, log specific growth rate (day^{-1}); LABUND, log bacterial abundance ($10^9 \text{ cells liter}^{-1}$); temperature ($^{\circ}\text{C}$) and LCHLA, log chlorophyll a concentration. Values associated with scatterplots are Pearson correlation coefficients (r); values greater than 0.164 are significant at $P = 0.001$. Frequency distributions are also provided for each variable.

Table 3. Linear regression statistics. All values, except temperature, were log transformed. Confidence limits around an individual prediction can be calculated using mean \bar{x} , Σx^2 , and the residual mean square of the regression (contained in the correction factor; see text). Predictions converted to arithmetic scale must be multiplied by CF, the correction factor. The model II (geometric mean) slope is provided as an estimate of the functional slope when there is error in the independent variable. In all cases P values from F test are <0.00001 . TdR Method for Prod indicates that bacterial production was measured by the ^3H -thymidine method only

Data	Y, X	n	Slope (99% conf)	Y-int (99% conf)	r^2	Mean \bar{x}	Σx^2	CF	Model II slope
All data	PROD, ABUND	700	1.22 (± 0.08)	0.89 (± 0.07)	0.68	0.24	439.32	3.33	1.48
Fresh water	PROD, ABUND	275	0.81 (± 0.25)	0.95 (± 0.16)	0.21	0.47	28.95	2.01	1.77
Marine	PROD, ABUND	207	1.12 (± 0.11)	0.71 (± 0.14)	0.77	-0.37	268.37	3.74	1.28
Estuarine & coastal	PROD, ABUND	218	1.52 (± 0.30)	1.04 (± 0.20)	0.44	0.52	34.12	3.48	2.29
TdR Method For Prod	PROD, ABUND	621	1.23 (± 0.08)	0.88 (± 0.07)	0.70	0.21	426.76	3.38	1.47
All data	PROD, LCHLA	412	0.71 (± 0.12)	0.86 (± 0.12)	0.36	0.68	205.12	3.23	1.18
Fresh water	PROD, LCHLA	219	0.49 (± 0.17)	0.90 (± 0.19)	0.20	0.95	59.51	2.04	1.09
Marine	PROD, LCHLA	88	0.50 (± 0.25)	0.75 (± 0.17)	0.23	-0.02	40.24	2.79	1.04
Estuarine & coastal	PROD, LCHLA	105	1.23 (± 0.26)	0.92 (± 0.25)	0.60	0.68	46.92	3.42	1.59
TdR Method For Prod	PROD, LCHLA	346	0.76 (± 0.13)	0.86 (± 0.12)	0.39	0.60	172.94	3.44	1.60

Table 4. Multiple regression statistics. All values, except temperature, were log transformed. In all cases *P* values from *F* tests are <0.00001. See Table 3 legend for description of CF. TEMP·CHLA indicates an interaction between temperature and chlorophyll concentration (i.e., an increase in the temperature effect at increased chlorophyll concentration). Std Coeff refers to the standardized regression coefficient or beta coefficient

Data	Y, X ₁ , X ₂	n	Partial Coeff X ₁ (99% conf)	Std Coeff X ₁	Partial Coeff X ₂ (99% conf)	Std Coeff X ₂	Y-int (99% conf)	r ²	CF
All data	PROD, ABUND TEMP	700	1.07 (±0.07)	0.72	0.050 (±0.008)	0.30	0.11 (±0.12)	0.79	2.15
Fresh water	PROD, ABUND TEMP	275	0.52 (±0.24)	0.30	0.041 (±0.013)	0.43	0.52 (±0.18)	0.37	1.75
Marine	PROD, ABUND TEMP	207	1.06 (±0.09)	0.83	0.051 (±0.013)	0.30	-0.04 (±0.20)	0.86	2.28
Estuarine & coastal	PROD, ABUND TEMP	218	0.81 (±0.28)	0.35	0.060 (±0.013)	0.57	0.14 (±0.25)	0.66	2.11
TdR Method For Prod	PROD, ABUND TEMP	621	1.06 (±0.07)	0.72	0.052 (±0.008)	0.37	0.05 (±0.12)	0.82	2.08
All data	SGR, TEMP TEMP·CHLA	412	0.046 (±0.008)	0.54	0.015 (±0.005)	0.29	-1.34 (±0.12)	0.56	1.67
Fresh water	SGR, TEMP TEMP·CHLA	219	0.027 (±0.02)	0.31	0.017 (±0.01)	0.28	-1.15 (±0.20)	0.26	1.58
Saltwater	SGR, TEMP TEMP·CHLA	193	0.052 (±0.01)	0.61	0.013 (±0.008)	0.28	-1.42 (±0.20)	0.69	1.73
TdR Method For Prod	SGR, TEMP TEMP·CHLA	346	0.050 (±0.008)	0.60	0.013 (±0.005)	0.27	-1.41 (±0.13)	0.63	1.57

production and temperature. It was found to have a small, but significant, negative influence on production (F significance <0.00001) (model (6)):

$$\log \text{PROD} = 0.45 + 0.095\text{TEMP} - 0.039\text{SAL} \quad n = 298, r^2 = 0.46 \quad (6)$$

(± 0.64) (± 0.02) (± 0.02)

Values associated with regression coefficients are 99% confidence intervals. A model including abundance, temperature, and salinity was not possible due to the collinear nature of abundance and salinity. Collinearity inflates the standard error of the regression coefficients and can obscure a relationship which exists in the population.

The model of production as a function of abundance and temperature (model (5)) demonstrates that the effect of bacterial abundance on productivity is equivalent in each of the three environments. Since the coefficient is not significantly different from 1.00, the relationship between bacterial production and abundance is linear once the effect of temperature is accounted for. Assuming a steady state between population growth and mortality, this linear relationship permits the computation of a dependent variable which is the ratio of production to biomass, the specific growth rate. The use of specific growth rate as a dependent variable eliminates the problem of collinearity between the independent variables in models 4, 5, and 6. Thus it permits the isolation of the effect of temperature on bacterial growth.

Growth Rate

A strong relationship was identified between specific growth rate and temperature in both fresh and saltwater habitats. The analysis of covariance model revealed a slight but significant difference between the three habitats. The model (model (7)) ($r^2 = 0.44$, $n = 700$, F significance <0.00001) is summarized below:

$$\log \text{SGR} = \begin{bmatrix} \text{Fresh: } -1.04 \\ \text{Marine: } -1.54 \\ \text{Estuarine} \\ \text{\& Coastal: } -1.30 \end{bmatrix} + \begin{bmatrix} \text{Fresh: } 0.031 \pm 0.015 \\ \text{Marine: } 0.052 \pm 0.005 \\ \text{Estuarine} \\ \text{\& Coastal: } 0.046 \pm 0.008 \end{bmatrix} \cdot \text{TEMP} \quad (7)$$

A substantial portion of the residual variation from this relationship can be accounted for by algal biomass expressed as concentration of chlorophyll a . The analysis of covariance model ($r^2 = 0.57$, $n = 412$, F significance <0.00001), is summarized below in model (8):

$$\log \text{SGR} = -1.30 + \begin{bmatrix} \text{Freshwater: } 0.037 + 0.016 \log \text{CHLA} \\ (\pm 0.005) \quad (\pm 0.005) \\ \text{Saltwater: } 0.052 + 0.016 \log \text{CHLA} \\ (\pm 0.008) \quad (\pm 0.005) \end{bmatrix} \cdot \text{TEMP} \quad (8)$$

Once variation in algal biomass is accounted for, there is no longer a significant difference between the different saltwater habitats. However, a small but significant difference remained between the log-linear temperature coefficients in

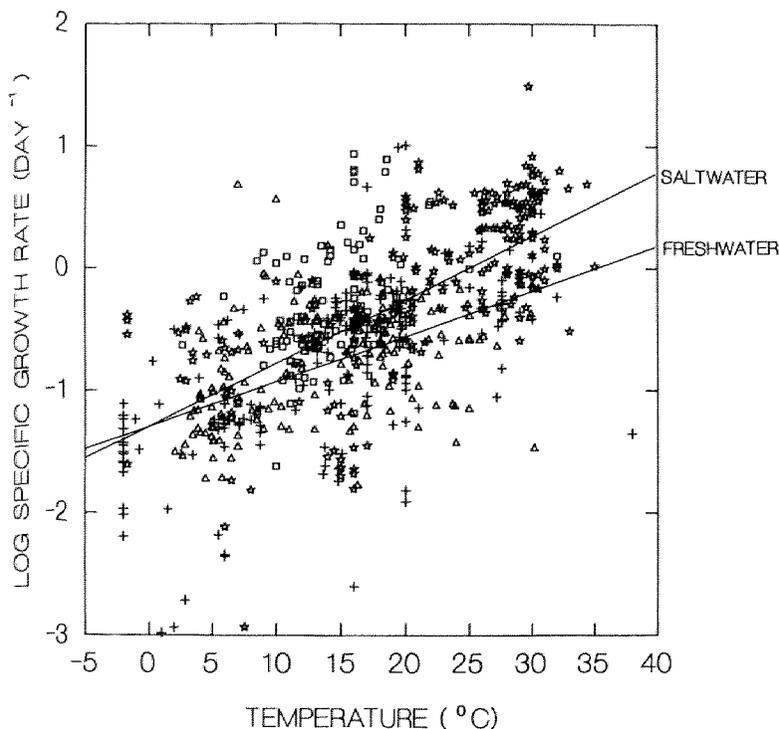


Fig. 2. The relationship between bacterial specific growth rate (day^{-1}) and temperature ($^{\circ}\text{C}$) in fresh- and saltwater habitats. The fitted lines represent the ANCOVA fit for fresh- and saltwater habitats at a constant concentration of chlorophyll a . The difference in the effect of temperature between the two habitats is represented by the difference in slope. Squares represent eutrophic lakes, triangles—mesotrophic lakes, crosses—marine habitats, and stars—estuarine and coastal habitats.

fresh- and saltwater habitats (Fig. 2). No significant difference between habitat was revealed for the chlorophyll effect. A strong interaction was identified between chlorophyll concentration and temperature. Thus the effect of temperature on specific growth rate rises with increasing chlorophyll concentration (Fig. 3). The standardized regression coefficients indicate that temperature consistently has greater impact on the specific growth rate than chlorophyll concentration. The separate regression statistics for the fresh and saltwater data are summarized in the bottom half of Table 4.

The relationship between SGR and temperature can alternatively be expressed as a Q_{10} , the increase in growth rate associated with a 10°C increase in temperature. The values obtained are 3.3 for the entire data set, 3.9 for saltwater, and 2.1 for fresh water.

None of the above models take differences in bacterial cell size into account. When this is done for the minority of studies that report cell volume data, a highly significant trend is revealed in the freshwater data set (Fig. 4). The addition of cell size to the freshwater model results in a 15% increase in the coefficient of determination. The two freshwater models, with (eq. (9)) and without (eq. (10)) a cell size variable, are summarized below (F significance < 0.00001):

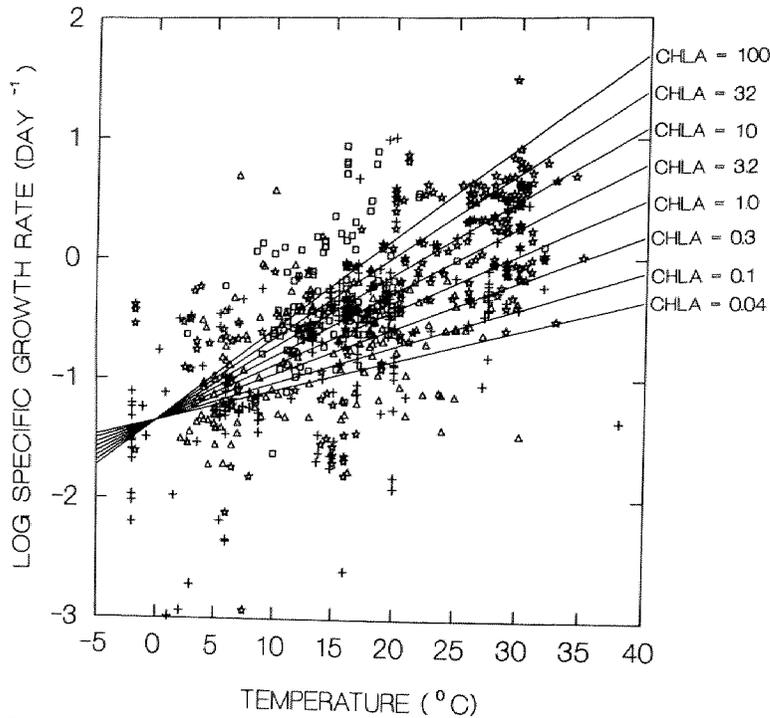


Fig. 3. The relationship between bacterial specific growth (day^{-1}) and temperature ($^{\circ}\text{C}$) at various concentrations of chlorophyll *a* (CHLA in $\mu\text{g liter}^{-1}$) in fresh and saltwater habitats. The fitted lines represent the best ANCOVA model, ignoring the effect of habitat. The interaction between CHLA and TEMP results in a slope increase as the concentration of chlorophyll *a* increases. The lines span chlorophyll concentrations from 0.04 to 100 $\mu\text{g liter}^{-1}$, the full range encountered in the data set. Squares represent eutrophic lakes, triangles—mesotrophic lakes, crosses—marine habitats, and stars—estuarine and coastal habitats.

$$\log \text{SGR} = -1.91 + 0.049\text{TEMP} + 0.024\text{TEMP} \cdot \log \text{CHLA}$$

(± 0.018) (± 0.016)

$$\log \text{SGR} = -2.22 + 0.036\text{TEMP} + 0.018\text{TEMP} \cdot \log \text{CHLA} + 7.28\text{VOL}$$

(± 0.013) (± 0.012) (± 3.01)

$$r^2 = 0.69, n = 51 \quad (9)$$

$$r^2 = 0.84, n = 51 \quad (10)$$

The standardized regression coefficients from the above model indicate that the impact of cell size and temperature on bacterial growth in fresh waters is almost equal. No significant cell volume effect was identified in the saltwater data.

Discussion

The goal of this work was to determine and quantify those environmental variables that are capable of regulating the production and specific growth rate of heterotrophic aquatic bacteria. To do this, data were collected from a wide

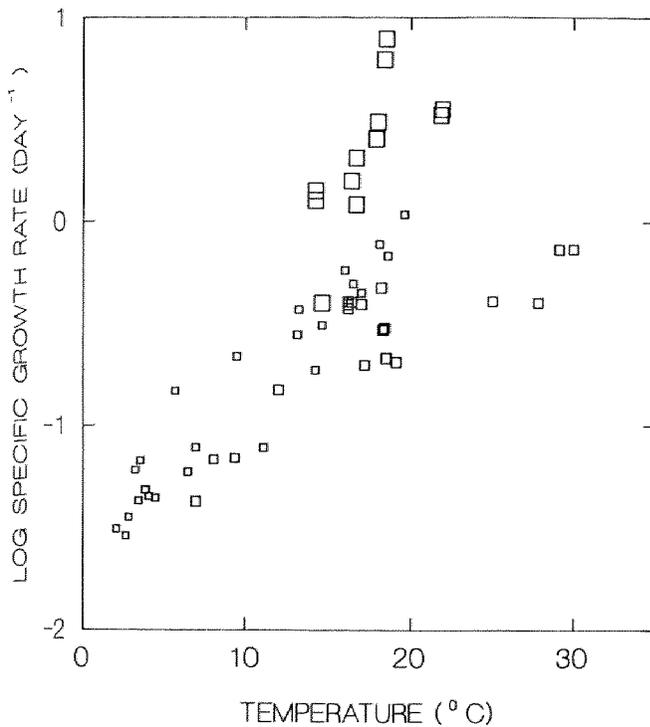


Fig. 4. The influence of mean cell volume on the relationship between specific growth rate (day^{-1}) and temperature ($^{\circ}\text{C}$) in freshwater. The size of the plotting symbol is proportional to the mean cell volume. The smallest symbol represents $0.083 \mu\text{m}^3$, the largest symbol represents $0.19 \mu\text{m}^3$.

variety of both fresh- and saltwater ecosystems (Table 1). Before discussing the implications of the results, it is appropriate to note constraints on the data used and any associated biases. The freshwater data include only temperate lakes, none of which are oligotrophic. The majority of the lakes (60%) are mesotrophic, dimictic lakes; the remaining (40%) are eutrophic. Only one lake in the data set is meromictic. The saltwater data cover an extremely wide range of habitats: temperate, subtropical, tropical, upwelling zones, Gulf stream, Arctic, and Antarctic. However, the estuarine/coastal data are somewhat restricted (slightly less than $\frac{2}{3}$) to temperate coastal regions, with the remainder obtained primarily from research conducted in subtropical U.S. coastal areas.

Bacterial Production

Using a much larger data set than that available to Cole et al. [20], we confirmed the relationship between bacterial abundance and production, as well as that between bacterial production and chlorophyll *a* concentration (Table 3). By considering water temperature as an independent variable we significantly increased the proportion of variation in bacterial production that could be explained. When the effect of temperature is accounted for, the relationship between abundance and production is linear and identical for the three habitats.

The effect of temperature on production is not equivalent in the three habitats studied, with the effect being most pronounced in the estuarine/coastal habitats, followed by the marine and freshwater habitats. The standardized regression coefficients indicate that for the entire data set, bacterial abundance has a more pronounced effect on production than does water temperature. However, when the three habitats are examined individually, temperature seems to be the more important factor in the freshwater and estuarine/coastal habitats only. However, this result is not robust due to the high correlation between abundance and temperature.

The saltwater data revealed a small, but significant, negative effect of salinity on bacterial production. Such a negative effect was previously noted by Ducklow and Kirchman [27], who reported a significant negative correlation (Pearson $r = -0.9$) between ^3H -thymidine uptake and salinity in the $<3.0 \mu\text{m}$ fraction of the Hudson River Estuary. This supporting evidence is biased by the fact that the data of Ducklow and Kirchman are included in the data set. However, the Ducklow and Kirchman data comprised only a small portion (slightly more than 1%) of the total data set used to derive the model (6).

Growth Rate

To isolate the effect of temperature, specific growth rate (SGR), a growth indicator familiar to microbial ecologists [18], was used as the dependent variable. The computed growth rate values, summarized in Table 2, range from 0.017 day^{-1} to 8.7 day^{-1} in fresh water and 0.0003 day^{-1} to 30.81 day^{-1} in saltwater habitats. These values are comparable to those described in the recent literature. Newell and Fallon [65] reported growth rates of 0.095 to 0.45 day^{-1} off the coast of Georgia at approximately 27°C , Tranvik and Hofle [90] reported rates of 0.30 to 0.75 day^{-1} in mixed lakewater batch cultures, and Ducklow [26] noted rates of 0.07 to 0.63 day^{-1} in warm core Gulf Stream rings. Extremely small specific growth rates ($<0.01 \text{ day}^{-1}$) were computed for some freshwater lakes at temperatures less than 6°C , shortly after ice melt. The lowest specific growth rates were found among the Antarctic data [32, 41], and are equivalent to doubling times of several years. Such low growth rates likely indicate a high fraction of dormant or nonviable cells. Alternatively, a large population of the Antarctic cells, presumably psychrophiles, may be unable to incorporate exogenous ^3H thymidine into DNA. Such a possibility finds support in a variable and sometimes very low degree of participation of cells in ^3H thymidine uptake experiments, as measured by autoradiography [24, 33].

The relationship between specific growth rate and temperature was also expressed as a Q_{10} value. The calculated Q_{10} values, averaged over the entire temperature spectrum, range from 2.1 to 3.9, with a mean of 3.0. These values are comparable to Q_{10} 's of between 2.5 and 4.0 calculated by Hobbie and Cole [44] from enclosure experiments.

The relationship between specific growth rate and temperature accounts for almost half the variation in growth rate. Again, the model revealed a significant difference between the effect of temperature in the three habitats. Although the differences in the partial coefficients are slight, they are significant. The inclusion

of algal biomass (as concentration of chlorophyll *a*) increased the explained variation in growth rate by 12% overall, to 56%. When both temperature and algal biomass are considered, the difference between the marine and estuarine/coastal relationships disappears, leaving a significant difference only between fresh and saltwater habitats. The effect of algal biomass consistently had a pronounced interaction with temperature. Thus, as the algal biomass rises, temperature becomes increasingly important in regulating specific growth. This is not surprising since, at optimum levels of primary production, bacteria are likely to be constrained by physical parameters such as temperature and nutrient availability [23].

The standardized regression coefficients in the growth rate models (Table 4) reveal that temperature is consistently the more important variable in determining the specific growth rate. This finding is not surprising given that both in situ and laboratory observations have noted temperature as an important positive regulator of bacterial production and specific growth rate [44, 48, 56, 72, 93, 100]. The impact of temperature on specific growth rate may have profound implications for the aquatic ecosystem. The potential for temperature to regulate competition for nutrients in temperate freshwater habitats has been described [21, 23, 72]. Currie [23] discusses the possibility that temperature may regulate the timing of phytoplankton phosphorus limitation via regulation of bacterial growth. Pomeroy and Weibe [72] discuss the possibility that temperature may regulate nutrient competition between, not only bacteria and phytoplankton, but detritivores as well.

Although the effect of algal biomass on bacterial growth was found to be virtually identical in both fresh- and saltwater systems, the effect of temperature is consistently less in freshwater habitats. This may be due to the strong seasonal variability of temperature in temperate zone freshwater habitats. In addition, freshwater microbes are normally subjected to a dramatic variation in nutrient availability, with this variability confounding the effect of temperature. The relatively high supply of allochthonous dissolved organic carbon exported from drainage basins, compared to the more labile organic carbon from decaying algae which predominates in the marine system [43], may further confound the effect of temperature on the specific growth of lacustrine bacteria. The quite limited riverine data, of which approximately 80% were obtained from studies of blackwater rivers (extremely high in allochthonous dissolved carbon), did not fit the model at all. If this is due to a high concentration of allochthonous carbon, it would seem to suggest that it may be necessary to add a growth yield term to the freshwater models.

The seasonal and spatial variability of freshwater systems may also contribute to the low r^2 encountered in the freshwater models. Conversely, the higher r^2 encountered in the saltwater models may be the result of the apparent stability of saltwater systems, relative to temperate lakes. Alternatively, the inability of the model to explain growth rates in freshwater may be attributable to methodological problems. The large degree of spatial and temporal variation in dissolved organic carbon may affect the concentration of exogenous thymidine capable of diluting the labelled substrate [8]. Cole et al. [20] also noted a low r^2 for freshwater models relating bacterial production to net primary production. They suggested that some of this unexplained variation might be attrib-

utable to differences in conversion factors used to convert ^3H thymidine uptake to production in those studies that did not empirically determine their own conversion factor. These problems may be compounded by differences between the microbial communities of fresh- and saltwater systems. Johnstone and Jones [50] have demonstrated lack of incorporation of ^3H -thymidine by certain portions of the freshwater microbial community.

It does not appear that much of the unexplained variation in the models is attributable to differences in methods used to determine secondary production. Models using ^3H thymidine data only are almost indistinguishable from those including all data. Of course this is likely due to the fact that almost 90% of the data used the ^3H -thymidine technique. However, good agreement between ^3H -thymidine method and other methods such as dark ^{14}C uptake have been noted [86].

The model relating specific growth rate to temperature and algal biomass for freshwater (Table 4) was significantly improved by the inclusion of mean cell volume (μm^3). Neidhardt [64] states that small cells actually do grow more slowly, and this has also been observed in situ [22, 38]. Alternatively, the observed effect of cell size on specific growth may be due to the use of a constant carbon per cell conversion factor of 29 fg, leading to overestimation of small cell growth and underestimation of large cell growth. While these results are interesting, they are based on data from a small number of studies. No effect of cell volume could be identified in the saltwater data, which was even more limited. The conversion factor of 29 fg cell $^{-1}$, assumed for these analyses, may not be appropriate for some systems, though no consensus exists regarding a more appropriate value.

The models presented confirm that temperature is an important positive regulator of bacterial production and growth in aquatic systems. Therefore, realistic production estimates must be taken at in situ temperature. Consistent cell size measurements, taken in conjunction with production and biomass measurements, will clarify the relationship between cell size and growth. Further clarification of the effect of cell size on carbon content, and factors that contribute to methodological uncertainties, would allow more accurate measurements of specific growth rate. Moreover, the relationship of cell size and growth rate to seasonal factors, such as ice cover, nutrient pulses, allochthonous organic matter, and grazing, seems a promising area for investigation.

Acknowledgments. Special thanks to Marc Schallenberg for his helpful comments and advice. This paper is a contribution of the Limnology Research Centre, McGill University.

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