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Microbial processes in cold oceans. I. Relationship between temperature and bacterial growth rate

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ABSTRACT: Despite the obvious relevance of the high latitude oceans to models and budgets of biogenic carbon, the seasonal patterns of energy flow through the lower food web in this region are poorly understood. It has been suggested that, in high latitude and cold oceans, the rates of bacterial metabolism and growth are low and are depressed to a much greater degree than those of co-occurring phytoplankton and metazoan heterotrophs. The low-temperature suppression of bacterial growth would reduce microbial food web activity, bacteria would consume and recycle less primary production and more phytoplankton carbon would be available to metazoan grazers. The implications of this scenario for models of oceanic carbon flow are profound. In this paper, we present an analysis of 66 published studies on temperature and growth rate for bacteria from the World Ocean, including polar regions, and examine the results of a field investigation of bacterioplankton growth in seasonally cold Newfoundland (eastern Canada) coastal waters. Based upon the analysis of published data, where approximately 50% of the observations were from environments ≤4°C, we report a weak (r^2 = 0.058, n = 231) relationship between specific growth rate (SGR) and temperature with a Q_{10} = 1.5. The mean (0.39 to 0.41 d^{-1}) and median (0.25 to 0.29 d^{-1}) SGR of bacteria from cold (≤4°C) and warm (>4°C) waters were not significantly different. For both the published data as well as for the field study in Conception Bay, Newfoundland, the SGR was significantly greater ($p < 0.01$) when computed from empirical thymidine conversion factors than from theoretical or literature derived thymidine conversion factors. Our analysis suggests that the growth rates of bacterioplankton from cold and temperate oceans are similar at their respective ambient temperatures, when the appropriate conversion factors are used to compute growth. We propose that bacteria-based food webs and microbial trophic pathways are as important in overall energy and material cycling in high latitude oceans as they are at lower latitudes.

KEY WORDS: Bacteria · Cold ocean · Growth rate · Microbial trophic level · Polar · Temperature · Thymidine conversion factor

INTRODUCTION

It has been recognized for over 2 decades that heterotrophic bacteria are a crucial component of marine food webs (Pomeroy 1974, Azam et al. 1983). Although it is generally accepted that the microbial trophic pathways (e.g. phytoplankton → DOC → bacteria → protozoa → metazoa) will consume and recycle 20 to 60% of primary production in temperate and tropical marine ecosystems (Cole et al. 1988, White et al. 1991), recent investigations show that bacterially mediated elemental fluxes are highly variable in rate and composition (Azam et al. 1994). Carbon fluxes can vary from 0 to >100% of local primary production (Findlay et al. 1991, Pomeroy et al. 1991, Hoch & Kirchman 1993 and references cited therein) and, depending on the composition of the available substrates, bacteria can switch roles as net remineralizers or consumers of inorganic and organic nitrogen and phosphorus (Wheeler & Kirchman 1986, Goldman et al. 1987, Kirchman 1994). Because the rates and patterns of nutrient utilization can be highly variable, elucidating the factors regulating bacterial growth and metabolism and their concomitant influence on elemental fluxes is central to understanding biogeochemical cycles in the sea (Ducklow & Fasham 1992, Fasham et al. 1993, Ducklow 1994).

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The principal factors regulating bacterial growth and abundances are temperature, substrate supply, predation and mortality due to viruses (Li & Dickie 1987, White et al. 1991, Ducklow & Carlson 1992, Fuhrman 1992, Shiah & Ducklow 1994a, b, 1995, Kirchman et al. 1995 and references cited therein). Surprisingly, however, the qualitative and quantitative relationships among these factors are poorly understood. In low to middle latitudes, bacterial activities are normally at a minimum when water temperatures are low (Findlay et al. 1991, Hoch & Kirchman 1993, Shiah & Ducklow 1994b, 1995, and others). For example, in 2 estuaries on the east coast of North America, significant correlations between bacterial growth or production and temperature were observed only during the colder months, approximately November to May (<12°C in the Delaware Bay, Hoch & Kirchman 1993; and <20°C in the Chesapeake Bay, Shiah & Ducklow 1994b, 1995). During the warmer periods, bacterial activity was controlled by substrate supply, grazer predation, or viruses rather than temperature.

Clearly, in much of the World Ocean, bacteria and bacteria-based food webs process a large fraction of local organic production and the rates and temporal patterns of microbial activity are frequently regulated by temperature (Ducklow & Carlson 1992, Pomeroy & Wiebe 1993). However, the role of bacteria in mediating the flux of dissolved organic carbon to protozoan and metazoan grazers in high latitude and other persistently cold environments is still unresolved. Pomeroy and coworkers (Pomeroy & Deibel 1986, Pomeroy et al. 1990, 1991, Pomeroy & Wiebe 1993) have put forward the 'cold ocean paradigm': '...the rates of bacterial metabolism and growth are depressed to a much greater degree than those of phytoplankton at low (<4°C) seawater temperatures...'. These authors reported low bacterioplankton growth rates (0.002 to 0.033 d^{-1}) and inferred that the low-temperature suppression of bacterial growth also reduces microbial loop activity. Hence bacteria consume less primary production and more phytoplankton carbon would be available to metazoan grazers. Low-temperature suppression of bacterial growth has not been universally observed. For example in Antarctica, bacterial growth rates of ca 0.01 to 2 d^{-1} have been reported at −1.5°C (Hanson et al. 1983, Kottmeier et al. 1987, Kottmeier & Sullivan 1988, Cota et al. 1990, Rivkin 1991, Rivkin et al. 1991). In the North Bering and Chukchi Seas, bacteria grew at 0.1 to 0.54 d^{-1} at <1°C (Anderson 1988) and in Resolute, NWT, Canada, sea ice bacterial growth rates were 0.02 to 0.25 d^{-1} at −1.7°C (Smith et al. 1989, Smith & Clement 1990).

Accurately quantifying bacterioplankton growth rates and knowing how these rates compare to those of bacterioplankton from lower latitude oceans is fundamental to understanding the role of microbial trophic pathways in mediating carbon flow in high latitude and cold ocean ecosystems. Other crucial questions concern whether the large differences in growth rates reported in the literature are due to seasonal or spatial phenomena, a consequence of localized substrate enhancement or temperature limitation or whether differences are the result of different methodologies. In this paper, we present an analysis of published data on temperature and growth rate for bacteria from the World Ocean, including polar regions, and examine the results of a field investigation of bacterioplankton growth in seasonally cold Newfoundland (eastern Canada) coastal waters. From these data, we suggest possible explanations for the wide discrepancy in the published data on bacterial growth.

METHODS

Analysis of published data on temperature dependent bacterial growth rates. Data were obtained from 66 separate published studies representing a wide diversity of marine environments, depths (≤200 m) and seasons (Table 1). The data set consists of 231 observations of specific growth rate (SGR) and incubation temperature (Temp). These were distributed nearly equally between ≤4°C (108 observations from 23 studies) and >4°C (123 observations from 45 studies). In 228 cases, SGR was estimated from [*methyl*-^{3}H] thymidine (^{3}H-TdR) incorporation, and the remaining 3 were by frequency of dividing cells or changes in abundance. Bacteria were normally enumerated by epifluorescence microscopy after staining with acridine orange or DAPI (4',6-diamidino-2-phenylindole) and all stained bacteria were considered to be physiologically active. Only studies which included temperature, SGR and thymidine conversion factors (TCF), or which had information from which SGR and TCF could be calculated, were included in the statistical analyses. Where necessary, bacterial carbon production was converted into increases in cell number using factors of 8 and 20 fg C $cell^{-1}$ for studies carried out at ≤4 and >4°C, respectively (Fuhrman & Azam 1980, Bratbak & Dundas 1984, Lee & Fuhrman 1987).

The relationship between Temp and SGR was examined by least-square regression after log-transforming SGR. The difference among data subsets (e.g. SGR ≤4°C and >4°C) was tested using both parametric and non-parametric methods, as appropriate. All statistical analyses were performed using SAS/STAT.

Field studies in Newfoundland coastal waters. Sampling was carried out in Conception Bay, Newfoundland between early 1992 and late 1993. Conception Bay is a deep (>300 m) fjord-like bay with a sill at

Table 1. Sources of data for statistical analysis. Some references provide data for more than one condition

Permanently cold (≤4°C)	Seasonally cold (≤4°C)	Warm (>4°C)	
Anderson et al. (1990)	Anderson (1988)	Admiraal et al. (1985)	Jonas & Tuttle (1990)
Bjørnsen & Kuparinen (1991)	Ducklow & Kirchman (1983)	Anderson (1988)	Kirchman & Hoch (1988)
Cota et al. (1990)	Hoch & Kirchman (1993)	Billen & Fontigny (1987)	Kirchman et al. (1982)
Fuhrman & Azam (1980)	Kirchman et al. (1982)	Borsheim (1990)	Kirchman et al. (1989)
Grossmann & Dieckmann (1994)	Kuosa & Kivi (1989)	Chin-Leo & Kirchman (1988)	Kirchman et al. (1991)
Gustafson et al. (1990)	Pomeroy et al. (1991)	Chin-Leo & Benner (1991)	Kirchman et al. (1993)
Hanson et al. (1983)		Chrzanowski & Zingmark (1989)	Kuuppo-Leinikki (1990)
Helmke & Weyland (1995)		Douglas et al. (1987)	Laanbroek & Verplanke (1986)
Karl et al. (1991)		Ducklow (1982)	Li et al. (1993)
Kottmeier et al. (1987)		Ducklow (1986)	Malone et al. (1986)
Kottmeier & Sullivan (1990)		Ducklow (1993)	Malone & Ducklow (1990)
Pomeroy et al. (1990)		Ducklow & Kirchman (1983)	Moriarty et al. (1985)
Rivkin et al. (1989)		Ducklow et al. (1992)	Moriarty et al. (1990)
Rivkin (1991)		Fuhrman & Azam (1980)	Newell & Fallon (1982)
Sullivan et al. (1985)		Fuhrman et al. (1980)	Painting et al. (1989)
Sullivan et al. (1990)		Fuhrman et al. (1985)	Pedros-Alio & Newell (1989)
Thingstad & Martinussen (1991)		Fuhrman et al. (1989)	Peele et al. (1984)
		Griffith et al. (1990)	Rosenberg et al. (1990)
		Hanson et al. (1986)	Sand-Jensen et al. (1990)
		Hanson et al. (1988)	Sherr et al. (1989)
		Hoch & Kirchman (1993)	van Duyl et al. (1990)
		Joint & Pomeroy (1983)	Wikner et al. (1990)
		Joint & Pomeroy (1987)	

ca 170 m. The mouth of the bay opens onto the east coast of Newfoundland. A tongue of the inshore branch of the Labrador Current enters Conception Bay, and below ca 100 m, water temperatures are always <−1.0°C (deYoung & Sanderson 1995). Most of our sampling was carried out from the Department of Fisheries and Oceans vessels CSS 'Shamook' or CSS 'Marinus' at our regular sample site, Stn BRLP5 (47° 32.5' N, 53° 07.8' W). When our sample site was ice covered, samples were collected at a nearby deep water site. Water samples were collected with acid cleaned 5 l Niskin samplers equipped with silicon elastic closures. Prior to water sampling, a Seabird CTD was deployed and the density and temperature characteristics of the 238 m water column were determined.

Bacterial growth was calculated from the bacterial abundances and incorporation rate of radiolabelled thymidine (Fuhrman & Azam 1980, Kirchman et al. 1982). Water was collected from 4 to 6 depths in the upper 150 m. Samples for enumerating bacteria were drawn from Niskin bottles and immediately preserved with glutaraldehyde (2% final concentration). Cells were filtered onto Poretic pre-stained black 0.2 µm polycarbonate filters, post stained with acridine orange (Hobbie et al. 1977) and counted using epifluorescent microscopy. For each sample, duplicate filters were prepared and at least 300 cells per filter were counted. Preliminary studies showed that TdR uptake ([*methyl*-^{3}H]thymidine: ICN, 60 to 90 Ci mmol^{-1}) was saturated and isotopic dilution of internal pools was negligible at 5 nmol TdR l^{-1}. Samples were incubated with ^{3}H-TdR (final concentration of 5 nmol) in the dark at the ambient temperature (±0.2°C) of the depth of collection, and the total radioactivity available for uptake was assessed from aliquots collected from each replicate 100 ml polycarbonate incubation bottle, at both the beginning and the end of the incubation. Triplicate 10 to 20 ml aliquots were removed immediately after adding the isotope (t = 0) and at the end of a 3 to 4 h incubation. Particulate material was collected onto 0.2 µm Poretics filters, serially rinsed 2× with filtered seawater, 3× with 3 ml of ice cold 5% trichloroacetic acid (TCA), 1× with filtered seawater. Filters were placed into liquid scintillation vials and counted on shore.

The conversion factors relating cell production to substrate uptake were empirically determined (Kirchman et al. 1982) for bacterial populations in the surface mixed layer (usually 5 m) and from 125 m. This deep sample was always below the seasonal pycnocline. Seawater dilution cultures were prepared by diluting, at a ratio of 1:5, a <1.0 µm filtrate (1 part) with 0.2 µm membrane filtered seawater (4 parts). ^{3}H-TdR was added to 1 l acid cleaned polycarbonate bottles containing 900 ml of the dilution culture and the time course of change of cell abundances and the incorporation of TdR were determined at ca 6 to 12 h intervals for 36 to 48 h. All incubations were carried out in the dark at the temperature from the depth of collection. Conversion factors determined using the integrative (Riemann et al. 1987, Kirchman & Hoch 1988) and cumulative (Bjørnsen & Kuparinen 1991) methods were similar.

Radioactivity was counted using a Packard Tricarb 2500TR liquid scintillation spectrometer with Biofluor as a scintillant. All counts were corrected for quench by the external standards method and for background radiation.

RESULTS

Temperature dependent bacterial growth rate

The descriptive statistics (minimum, maximum, median, mean and standard deviation) for SGR, Temp and TCF calculated for the entire temperature range of −1.9 to 30.5°C as well as for the temperature ranges ≤4 and >4°C are summarized in Table 2. There were approximately equal numbers of observations above and below 4°C. Over the entire temperature range and at low seawater temperatures (e.g. −1.9 to 4°C), SGR varied by 10^4 (0.0002 to 2.1 d^{-1}), whereas at higher seawater temperatures (e.g. 4.01 to 30.5°C), SGR varied by ca 10^3 (0.003 to 2.2 d^{-1}). Although the minimum SGR in the ≤4°C group was 10 fold smaller than in the >4°C group, the median and mean SGR for the 2 groups were not significantly different (Wilcoxon rank sum test, $Z = -1.56$, prob > $Z = 0.122$).

For the entire data set (Eq. 1; n = 231, $F = 14.2$, p = 0.0002), as well as for the >4°C group (Eq. 2; n = 123, $F = 6.04$, p = 0.015), there were significant relationships between Temp and log SGR (Fig. 1).

Table 2. Summary of descriptive statistics for specific growth rate (SGR, divisions d^{-1}), temperature (°C) and thymidine conversion factor (10^{18} cells produced per mole thymidine incorporated) from the publications in Table 1. For the >4°C subgroup, n = 120 for the TdR conversions factors. nd: not determined

	SGR	Temp	TdR conversion factor
All data (n = 231)			
Minimum	0.0002	−1.9	0.1
Maximum	2.2	30.5	30.0
Median	0.26	6.0	nd
Mean	0.40	9.3	3.4
SD	0.43	10.9	5.4
≤4°C (n = 108)			
Minimum	0.0002	−1.9	0.1
Maximum	2.1	4.0	30.0
Median	0.25	−1.0	nd
Mean	0.39	−0.8	5.1
SD	0.42	1.4	7.2
>4°C (n = 123)			
Minimum	0.003	4.2	0.7
Maximum	2.2	30.5	17.0
Median	0.29	17.7	nd
Mean	0.41	18.1	1.9
SD	0.42	7.5	2.2

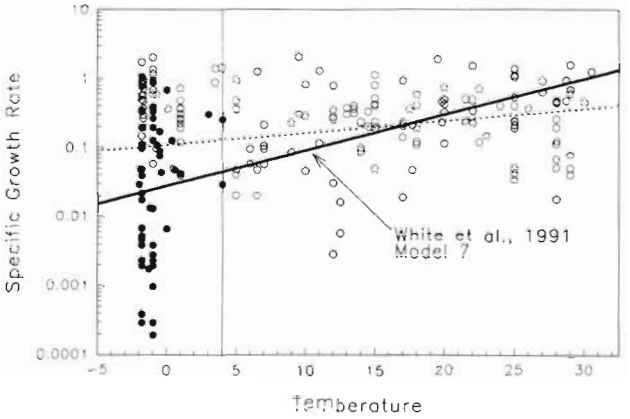

Fig. 1 Relationship between bacterial specific growth rate (SGE, divisions d^{-1}) and temperature (°C). The regression line (dashed line) represents the linear least square fit of the log SGR vs Temp. The equation for the regression is log SGR = −0.949(± 0.0669) + 0.0176(± 0.0047)Temp, $r^2 = 0.058$ (value in parentheses is the standard error of the estimate). Open symbols in the temperature range ≤4°C represent growth rates calculated using E-TCF (empirical thymidine conversion factor); filled symbols in the temperature range ≤4°C represent growth rates calculated using T-TCF (theoretical thymidine conversion factor). For comparison, the temperature dependent growth rate model for marine systems (model 7; White et al. 1991) has been superimposed on our data

$$\log SGR = -0.949(\pm 0.0669) + 0.0176(\pm 0.0047)Temp \quad (r^2 = 0.058) \quad (1)$$

$$\log SGR = -0.918(\pm 0.1252) + 0.0157(\pm 0.0063)Temp \quad (r^2 = 0.047) \quad (2)$$

In contrast, for temperatures ≤4°C, the relationship between Temp and log SGR was not significant ($F = 2.67$, p = 0.105). In Eqs. (1) and (2), the values in parentheses are the standard errors of the intercepts and slopes, respectively.

Computing rates of growth from ^{3}H-TdR incorporation requires that cell production be related to TdR uptake by a thymidine conversion factor (TCF). Despite the fact that the empirically determined thymidine conversion factors (E-TCF) can vary >500 fold (Kirchman et al. 1982, Coveney & Wetzel 1988, Smits & Riemann 1988, Ducklow & Carlson 1992, Ducklow et al. 1992), the E-TCF is not routinely measured during most field studies. Instead, a theoretical thymidine conversion factor (T-TCF), or average value derived from the literature (typically 1 to 4 × 10^{18} cells produced per mole TdR incorporated) is normally used to convert TdR uptake into cell production. To determine if there was a systematic difference between SGR calculated using E-TCF or T-TCF, the low temperature range (≤4°C) was partitioned into

Table 3. Summary of descriptive statistics for specific growth rate (SGR, divisions d^{-1}), temperature (°C) and thymidine conversion factor (10^{18} cells produced per mole thymidine incorporated) from the publications in Table 1. The ≤4°C group was partitioned into subgroups based upon use of an empirical thymidine conversion factor or a theoretical or an assumed thymidine conversion factor to calculate growth rate. nd: not determined

	SGR	Temp	TdR conversion factor
≤4°C; empirical thymidine conversion factor (n = 50)			
Minimum	0.04	−1.9	0.7
Maximum	1.44	4.0	30.0
Median	0.48	−1.0	nd
Mean	0.55	−0.5	8.9
SD	0.38	1.6	9.2
≤4°C; theoretical thymidine conversion factor (n = 58)			
Minimum	0.0002	−1.9	1.0
Maximum	2.1	4.0	4.0
Median	0.05	−1.0	nd
Mean	0.26	−0.9	1.9
SD	0.44	1.3	1.0

subgroups based upon whether an E-TCF (n = 50) or a T-TCF (n = 58) was used to compute SGR. The descriptive statistics (minimum, maximum, median, mean and standard deviation) for SGR, Temp and TCF for these groups are presented in Table 3. The SGR varied by factors of ca 36 and 10^4 in the E-TCF and T-TCF groups, respectively. The mean SGR was 2 fold and the median SGR was 10 fold greater when calculated using the E-TCF than a T-TCF (Table 3). The differences between the SGR in the E-TCF and T-TCF groups were highly significant (Wilcoxon rank sum test, $Z = -5.17$, prob > $Z = 0.0001$).

The frequency distribution of SGR for the temperature ranges (a) ≤4°C, (b) >4°C, (c) ≤4°C where SGR was calculated from the E-TCF, and (d) ≤4°C where SGR was calculated from the T-TCF is shown in Fig. 2. The distribution in all temperature ranges was non-normal and skewed to the lower growth rates. Except for group (c), the highest frequency of occurrence was for growth rates of ≤0.15 d^{-1}. Over 65% of the observations were ≤0.15 d^{-1} in group (d) compared with ca 40% and 15% in groups (a) and (c), respectively.

Seasonal patterns of bacterioplankton growth in Newfoundland coastal waters

The rates of bacterioplankton growth were measured in Conception Bay, Newfoundland over a 15 mo period. Here we report on the patterns in the surface mixed layer (typically collected at 5 to 10 m) and from 125 m. This deep sample was 110 m above the bottom

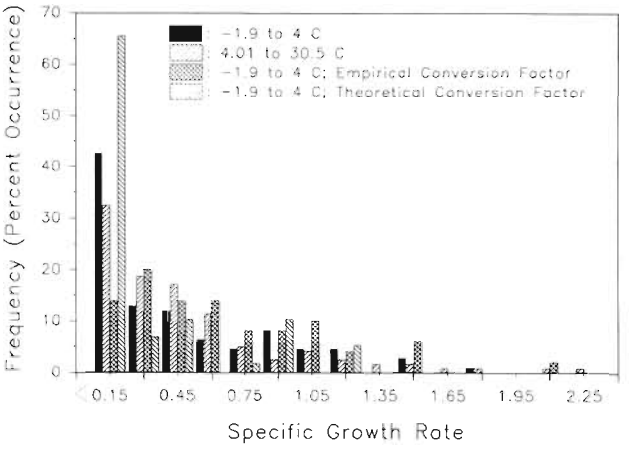

Fig. 2. Frequency distribution of bacterial specific growth rate (SGR, divisions d^{-1}) for the temperature ranges ≤4°C; >4°C; ≤4°C where SGR was calculated from the E-TCF (empirical thymidine conversion factor); and ≤4°C where SGR was calculated from the T-TCF (theoretical thymidine conversion factor)

and thus was not influenced by benthic resuspension. The samples collected at 125 m were within the subsurface tongue of Labrador Current water, hence water temperatures were always below −1.0°C. In contrast, temperatures in the mixed layer ranged from a minimum of −1.8°C in January and February to a maximum of ca 13°C in August and September (Table 4). The seasonal variation in the E-TCF was about 10 fold both in the mixed layer (1.1 to 9.5 × 10^{18} cells mol TdR^{-1}; mean ± SD = 4.4 ± 2.6) and at 125 m (5 to 49 × 10^{18} cells mol TdR^{-1}; mean ± SD = 20.3 ± 11.8) with the seasonal maxima occurring in January and February in the mixed layer and in October and November at 125 m. The E-TCF was significantly greater (Student's *t*-test, p = 0.0005) at 125 m than in the mixed layer (Table 4).

Growth rates were computed using both the E-TCF, and a T-TCF of 2 × 10^{18} cells mol TdR^{-1} incorporated. The SGR was significantly greater (Student's *t*-test, p = 0.004) when calculated from the E-TCF than the T-TCF (Table 4). When SGR was computed from the E-TCF, growth rates were significantly greater (Student's *t*-test, p = 0.03) at 125 m (mean ± SD = 0.32 ± 0.14, n = 14) than in the mixed layer (mean ± SD = 0.21 ± 0.10, n = 15). In contrast, when SGR was computed from the T-TCF, growth rates were significantly greater (Student's *t*-test, p = 0.01) in the mixed layer (mean ± SD = 0.13 ± 0.06, n = 15) than at 125 m (mean ± SD = 0.04 ± 0.02, n = 14). For SGR computed from E-TCF, seasonal maxima occurred in August through October in the mixed layer and in October, November, and May through August at 125 m. For SGR computed from T-TCF, seasonal maxima occurred in April through August both in the mixed layer and at 125 m.

Table 4. Seasonal patterns of temperature (°C), empirical thymidine conversion factors (E-TCF; 10^{18} cells produced per mole of TdR incorporated) and specific growth rate (SGR, divisions d^{-1}) of bacterioplankton collected in the surface mixed layer (typically 5 to 10 m) and from 125 m at or near Station BRLP5 (Conception Bay, Newfoundland, Canada). SGR was computed from ^{3}H-TdR incorporation using the E-TCF (E-SGR) and theoretical thymidine conversion factor (T-SGR) of 2×10^{18} cells produced per mole of TdR incorporated. nd: not determined

Date	Mixed layer				125 meters			
	Temp	E-TCF	E-SGR	T-SGR	Temp	E-TCF	E-SGR	T-SGR
Jun 1992	6.5	2.2	0.26	0.24	−1.6	26	0.32	0.028
Jul 1992	7.8	1.2	0.11	0.19	−1.6	15.6	0.21	0.029
Aug 1992	12.3	3.3	0.20	0.13	−1.4	9.8	0.11	0.023
Sep 1992	12.9	4.3	0.24	0.11	−1.5	11.4	0.23	0.045
Oct 1992	6.8	4.8	0.42	0.19	−1.2	22.7	0.28	0.028
Nov 1992	3.0	5.2	0.22	0.09	−1.4	37.4	0.57	0.039
Dec 1992	1.3	nd	nd	nd	−1.5	nd	nd	nd
Jan 1993	−1.7	9.5	0.16	0.03	−1.7	11.1	0.17	0.032
Feb 1993	−1.7	8.8	0.18	0.04	−1.8	9.8	0.20	0.044
Mar 1993	−1.2	4.5	0.11	0.05	−1.8	4.8	0.12	0.051
Apr 1993	−1.0	3.7	0.18	0.10	−1.7	nd	nd	nd
May 1993	1.2	2.8	0.21	0.15	−1.7	19.5	0.63	0.086
Jun 1993	5.6	2.4	0.18	0.16	−1.6	22.0	0.44	0.048
Jul 1993	7.2	1.7	0.17	0.20	−1.6	25.0	0.29	0.026
Aug 1993	12.2	8.5	0.47	0.13	−1.5	19.9	0.56	0.073
Sep 1993	12.8	nd	nd	nd	−1.4	nd	nd	nd
Oct 1993	6.5	3.5	0.13	0.08	−1.2	48.7	0.49	0.026

DISCUSSION

If the cold ocean paradigm is correct, and temperature suppression of bacterial metabolism and of microbial food web activity are general characteristics of high latitude oceans, the implications for global carbon flow models would be profound. Firstly, approximately 25% of global marine primary production occurs above 50° latitude. Although net photosynthesis sets the upper limit of the magnitude of the biological pump that transfers atmospheric CO_2 into the ocean interior, it is the sinking or advection of dissolved and particulate inorganic and biogenic carbon below the pycnocline which is one of the principal factors controlling the flux of atmospheric CO_2 into the upper mixed layer. Bacteria and bacteria-based food webs influence the magnitude and composition of sinking fluxes by altering both the size of sinking particles and the equilibrium between the particulate and dissolved phases (Cho & Azam 1988, 1990). Thus, heterotrophic microbes play a key role in material processing within, and export from, the surface layer of the ocean. Secondly, if the low-temperature suppression of metabolic activity and growth is greater for bacterioplankton than for co-occurring autotrophs and metazoan heterotrophs, a potentially large proportion of phytoplankton carbon would be diverted from the microbial into metazoan food webs. Moreover, since a large fraction of the primary production grazed by mesozooplankton will be rapidly exported in the form of sinking faeces, the suppression of bacterial activities at high latitudes could enhance the carbon export from the upper ocean and potential carbon sequestration into the deep ocean. Thirdly, a consequence of depressed bacterial growth would be low abundances of bacterivorous flagellates and their ciliate predators. This could alter the feeding strategies of metazoan grazers in high latitudes and cold oceans. For example, during periods when incident irradiances are nil or low, or when appropriate phytoplankton prey are scarce, algae-based food webs would be of negligible importance. At these times, mesozooplankton would be omnivorous and ingest ciliates and flagellates (Gifford 1991, Sanders & Wickham 1993, Ohman & Runge 1994). However, a prerequisite for omnivory on flagellates and ciliates is the presence of an active microbial trophic level.

The relationship between temperature and bacterial growth has been studied in specific environments (Li & Dickie 1984, 1987, Kottmeier & Sullivan 1988, Billen & Becquevort 1991, Hoch & Kirchman 1993, Shiah & Ducklow 1994a, b, Kirchman et al. 1995 and references cited therein) and examined in several general reviews (White et al. 1991, Jumars et al. 1993, Pomeroy & Wiebe 1993). Temperature is clearly an important regulator of microbial growth, however it is not the only one. Based upon both statistical analyses (White et al. 1991) and empirical studies (Pomeroy et al. 1991, Wiebe et al. 1992, 1993, Kirchman et al. 1993, Shiah & Ducklow 1994a, b, and others), interactions between substrate availability and temperature have been inferred (from chlorophyll *a* concentrations; Pomeroy et al. 1991, White et al. 1991) or measured directly

(Christian & Wiebe 1974, Billen & Becquevort 1991, Wiebe et al. 1992, Shiah & Ducklow 1994a, b). The strong positive correlation between phytoplankton and bacterial biomass and production usually observed in field and enclosure studies suggests that phytoplankton exudates may be an important autochthonous source of bacterial substrates (Cole et al. 1988, Williams 1990, Wood & Van Valen 1990, White et al. 1991). However, there are other sources. Viral lysis of both bacteria and algae may also be a significant mechanism for the production of dissolved organic material (DOM) in the sea (Fuhrman 1992, Bratbak et al. 1994). In addition, both micro- and mesozooplankton rapidly recycle and regenerate both dissolved organic and inorganic nutrients through sloppy feeding, excretion and leaching of faecal pellets (Azam et al. 1983, Hagström et al. 1988, Jumars et al. 1989, 1993, Roy et al. 1989, Caron & Goldman 1990, Pomeroy & Wiebe 1993). Indeed, zooplankton rather than phytoplankton may be the principal autochthonous source of bacterial substrates.

Based upon correlations between bacterial activity and phytoplankton biomass, Pomeroy et al. (1990, 1991) suggested that at low temperatures, bacteria require higher concentrations of DOM than are normally present except in regions of elevated phytoplankton biomass, such as at subsurface chlorophyll maxima. Furthermore, laboratory culture studies with psychrotrophic bacteria isolated from the Arctic Ocean and Newfoundland coastal waters have clearly demonstrated reciprocal interactions between substrate concentration and temperature (Wiebe et al. 1992). Bacteria could grow rapidly at low (<0°C) temperatures and high (micromolar) substrate concentrations, or at high (>10°C) temperatures and low (nanomolar) substrate concentrations, but not at low temperatures and low substrate concentrations. Although growth rates of these psychrotrophic bacteria were significantly enhanced when temperature or substrate concentrations were increased, their growth rate was ≥ 0.6 d^{-1} at −1.5°C and the lowest substrate concentrations. This was ca 40 times faster than the rates reported for the bacterioplankton population (Pomeroy et al. 1990, 1991) from which the strains of bacteria which Wiebe used were isolated, and are similar to growth rates of bacteria from temperate and tropical regions (White et al. 1991, Ducklow & Carlson 1992). Since Wiebe determined growth rates from changes in cell numbers and biovolume rather than TdR uptake (Wiebe et al. 1992), his reported growth rates were not confounded by the uncertainties associated with converting substrate uptake into cell production using a T-TCF (Pomeroy et al. 1990, 1991).

In a comprehensive analysis of temperature dependent bacterial processes reported by White et al. (1991), observations from cold and polar environments were under-represented relative to temperature distribution in the World Ocean. Only 3 of the 33 studies analyzed from estuarine and marine environments were from polar regions and <10% of the 425 observations were from temperatures <5°C. By contrast, 70% of the ocean is always <5°C and 90% is seasonally <5°C (Baross & Morita 1978, Levitus 1982). The temperature dependent bacterial growth model reported here (Eq. 1) was developed from a data set where >35% of the studies and >45% of the observations were from cold (≤4°C) oceans. We found a weak but significant temperature dependence of SGR with an explained variance of <6%. For comparison, the temperature dependent growth rate model reported by White for marine systems (model 7; White et al. 1991) has been superimposed on our data in Fig. 1. The marked difference in the 2 models may reflect the much larger number of observations at low temperatures and the fact that the median SGR for our ≤4°C group (Table 2) is higher than any of White's observed growth rates below 5°C. The Q_{10} for our models are 1.4 to 1.5, which is 2 to 3 fold lower than reported by White et al. (1991) and Shiah & Ducklow (1994a, b), but is similar to the Q_{10} reported by Hoch & Kirchman (1993).

In Conception Bay, the spring phytoplankton bloom typically occurs in mid-April when the water temperatures are −1.0 to 0°C. At this time of year, bacterial growth rates were ca 0.20 d^{-1} in the surface layer to ca 0.40 d^{-1} at 125 m. These are similar to the average annual SGR (0.21 d^{-1} for the mixed layer and 0.32 d^{-1} at 125 m). The average annual bacterial growth rates computed from T-TCF (0.13 d^{-1} for the mixed layer and 0.04 d^{-1} at 125 m) are similar to those reported by Pomeroy et al. (1991) for Conception Bay. It is important to note that the subsurface chlorophyll *a* maximum typically occurs between 25 and 50 m, hence our measurements of bacterial growth (Table 4) were not associated with elevated phytoplankton biomasses and substrate concentrations. Based upon these results, and assuming an invariant growth efficiency, 2 to 8 times more dissolved organic carbon would be required to sustain bacterioplankton when growth is computed from E-TCF compared to the T-TCF.

The E-TCF is highly variable over depth and season in Conception Bay (Table 4). Cross-system variability in the TCF has been reported (mean = 2×10^{18} cell mol TdR^{-1}, range = 0.1 to 60×10^{18} cell mol TdR^{-1}; Ducklow & Carlson 1992). Clearly, using the appropriate conversion factor will have considerable influence on the computation of the growth rate and ultimately the relationship between microbial processes and environmental variables. In Conception Bay, there are times of year when the E-TCF = T-TCF, however for most of the year E-TCF $\gg$ T-TCF. Thus SGR computed from T-TCF

would be systematically underestimated relative to SGR computed from E-TCF. For example, the average TCF of 2×10^{18} cell mol TdR^{-1} for oceanic bacteria (Ducklow & Carlson 1992) is similar to the mean TCF for the >4°C group (Table 2), however it is 4.5 fold smaller than the mean E-TCF for cold regions (i.e. ≤4°C; Table 3) and is 10 fold smaller than the mean E-TCF measured at 125 m in Conception Bay (Table 4). Thus, we propose that using an average TCF determined for bacteria from temperate regions, or the T-TCF, would underestimate the rates of growth and production of bacteria from both persistently cold environments and from seasonally cold oceans when water temperatures are low.

How will our models of heterotrophic processes be influenced if the rates of bacterial growth are underestimated from T-TCF when seawater temperatures are low? Firstly, the SGR in the ≤4°C group determined from T-TCF are shown in Fig. 1 as filled circles. When these values are not included in the regression analysis between Temp and log SGR, the relationship for the entire temperature range of −1.9 to 30.5°C is no longer significant ($F = 3.12$, $p = 0.079$, $n = 193$). Secondly, the mean SGR in the ≤4°C and >4°C groups are not significantly different (Table 2). However, when the SGR in the ≤4°C group is calculated only from E-TCF (Table 3), the SGR of the ≤4°C group (mean = 0.55 d^{-1}; Table 3) is significantly greater (Wilcoxon rank sum test, $Z = 2.731$, prob > $Z = 0.006$) than for the >4°C group (mean = 0.41 d^{-1}; Table 2). Clearly, bacteria from cold oceans grow as fast as bacteria from warmer waters, when the appropriate conversion factors are used. This conclusion is supported by the observations from Conception Bay showing generally higher growth rates of bacteria from 125 m compared to the mixed layer. Hence the paradigm of slow bacterial growth in cold water may be incorrect.

In persistently cold environments, such as polar oceans and the deep sea, what regulates bacterial activity? Substrate availability undoubtedly interacts with temperature. For example, in Conception Bay, bacterioplankton from 125 m show a 6 and 10 fold annual variation in SGR and E-TCF, respectively, yet water temperatures are constant (Table 4). Based upon substrate amendment studies, carried out at approximately bimonthly intervals (Rivkin unpubl.), ambient concentrations of dissolved organic carbon and nitrogen can limit bacterial growth during certain times of year (Rivkin & Matthews 1993, Rivkin unpubl.). Preliminary studies suggest that the E-TCF is not temperature dependent, rather it appears to be influenced by both substrate availability and nutritional status of the bacterioplankton. Initial studies suggest that nutrient-limited bacteria may catabolize TdR as a carbon or nitrogen source, hence the TCF is lower than would be anticipated than when TdR was used primarily for DNA synthesis. This relationship is currently being studied.

It should not be inferred from the above models that the maximum growth rate of bacteria in cold and warm waters is the same. Indeed, the SGR of nearly 31 d^{-1} reported from a warm (>30°C) tropical lagoon (Torreton et al. 1989) is >20 fold higher than the observed maximum growth rate of bacteria from cold waters. Furthermore, growth rate is not the same as production rate. Growth is an intrinsic cellular characteristic whereas production is the product of growth and the standing stock of bacterial biomass. The latter reflects the balance between growth and mortality. Bacterial abundances in polar and other cold ocean regions can be up to 10 fold lower than in warm temperate and tropical oceans. Hence, although average growth rates of bacteria in cold and warm oceans may be similar, rates of bacterial carbon production in seasonally and permanently cold ocean environments would be lower, by virtue of lower standing stocks.

The average growth rates of bacterioplankton from cold and temperate oceans appear to be similar, at their respective ambient temperatures. However, it is generally observed that in polar seas, despite high rates of growth, bacterial abundances are relatively low and constant (Billen & Becquevort 1991, Rivkin 1991, Thingstad & Martinussen 1991). Since the steady-state abundance is the balance between growth and mortality, the magnitude of grazing losses, due to bacterivory (Anderson et al. 1990, Rivkin 1991) and perhaps viral lysis (Maranger & Bird 1995), must be similar to that of cell divisions. Based upon the observed high rates of bacterial growth and grazer mortality (Laurion et al. 1995, Anderson & Rivkin unpubl.), we propose that bacteria-based food webs and microbial trophic pathways are as important in overall energy and material cycling in high latitude oceans as they are at lower latitudes. It is clear that simple temperature dependent models of growth, developed from observations in temperate systems, where there are seasonal cycles in temperature and phytoplankton production (which are often correlated), may not be appropriate for cold environments without careful consideration of the physiology of the cold water microbial community.

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