———, M. Macek, J. Pernthaler, V. Straskrabova, and R. Psenner. 1996. Can freshwater planktonic ciliates survive on a diet of picoplankton? J. Plankton Res. **18:** 597–613.

———, J. Vrba, J. Pernthaler, T. Posch, P. Hartman, J. Nedoma, and R. Psenner. 1997*b*. Morphological and compositional shifts in an experimental bacterial community influenced by protists with contrasting feeding modes. Appl. Environ. Microbiol. **63:** 587–595.

Stockner, J. G. 1988. Phototrophic picoplankton: An overview from freshwater and marine ecosystems. Limnol. Oceanogr. **33:** 765–775.

Vaulot, D., D. Marie, R. J. Olson, and S. J. Chisholm. 1995. Growth of *Prochlorococcus*, a photosynthetic prokaryote in the equatorial Pacific Ocean. Science **268:** 1480–1482.

Veldhuis, M. J. W., G. W. Kraay, J. D. L. Van Bleijswijk, and M. A. Baars. 1997. Seasonal and spatial variability in phytoplankton biomass, productivity and growth in the northwestern Indian Ocean: The southwest and northeast monsoon, 1992–1993. Deep-Sea Res. **44:** 425–449.

Weisse, T. 1993. Dynamics of autotrophic picoplankton in marine and freshwater ecosystems. Adv. Microb. Ecol. **13:** 327–369.

Zhukov, B. F. 1991. The diversity of bodonids, p. 177–184. *In* D. J. Patterson and J. Larsen [eds.], The biology of free-living heterotrophic flagellates. Claredon.

Zubkov, M. V., and M. A. Sleigh. 1995. Bacterivory by starved marine heterotrophic nanoflagellates of two species which feed differently, estimated by uptake of dual radioactive-labelled bacteria. FEMS Microb. Ecol. **17:** 57–65.

Received: 2 October 1997
Accepted: 19 January 1998
Amended: 6 March 1998

Limnol. Oceanogr., 43(7), 1998, 1746–1753

Annual average abundance of heterotrophic bacteria and *Synechococcus* in surface ocean waters

Abstract—Global abundance of marine bacteria was investigated at the annual climatological scale. In surface waters of diverse marine habitats, the annual average abundances of heterotrophic bacteria and the photosynthetic cyanobacterium *Synechococcus* are directly related to annual average temperature below 14°C. Notably, average nitrate concentrations at the surface are never high where the temperature is above 14°C. These results suggest that, over the course of a year, temperature is the dominant factor affecting bacterial growth and loss in colder waters. Other factors, such as substrate supply, may be important in warmer waters.

Heterotrophic bacteria and the photosynthetic cyanobacterium *Synechococcus* are found almost everywhere in the upper ocean. In temperate waters, the annual cycle of their abundance may be quite regular. Generally, both groups are most abundant in summer and least so in winter. More particularly, cell abundance at individual locations can evidently track water temperature throughout the year. A broader issue, however, is whether temperature exerts a significant influence on cell abundance across a biogeographical range. In other words, is there a relationship between climatological averages of abundance and temperature in diverse marine habitats? If so, the large-scale distribution of these cells could conceivably be mapped by temperature. I addressed this question by compiling annual average abundances of bacteria and *Synechococcus* from seasonal cycles with wide geographic coverage reported in the literature, combined with new observations made in Bedford Basin, Canada.

My aim was to establish the annual average abundances of heterotrophic bacteria and *Synechococcus*, together with annual average temperature, from as many locations as possible using the published literature. For this purpose, the ideal data sets were multiyear records of frequently sampled sea surface temperature and cell abundance. Some data sets extended to slightly less than a full year; in these cases, I assumed that the annual cycle was symmetrical about the peak at mid-year. Studies in freshwater or hypereutrophic systems and those in which bacteria were assessed as colony-forming units were not included.

Where authors did not directly report average values from their time series data, they were computed as follows: Published figures of seasonal cycles were image-scanned and stored as bitmap files. Images were analyzed by Scion ImagePC software to compute annual areas representing the number of degree-days for temperature and the number of cells per milliliter-day for abundance. Annual averages were calculated by dividing the annual areas by 365 d. Where abundance was expressed in logarithmic units, the data were digitized, expressed as antilogarithms, and then replotted to calculate arithmetic averages. Where the results were presented as three-dimensional surface plots (i.e., abundance versus time versus depth), the data could not be extracted; such studies were left out of consideration. Data from the U.S. Joint Global Ocean Flux Study (JGOFS) were downloaded from the agency's World Wide Web site (http://usjgofs.whoi.edu).

Where temperatures were not reported, annual averages were taken from one of three sources: (1) a database from the Bedford Institute of Oceanography (http://dfomr.dfo.ca/science/ocean/ocean_data.html#oceansst); (2) the *World Ocean Atlas* (U.S. Department of Commerce et al. 1994) maintained by the International Research Institute for Climate Prediction and the Lamont-Doherty Earth Observatory at Columbia University (http://ingrid.ldgo.columbia.edu/sources/.levitus94/); and (3) other published papers describing areas such as Narragansett Bay (Karentz and Smayda 1984) and Villefranche Bay (Buecher et al. 1997).

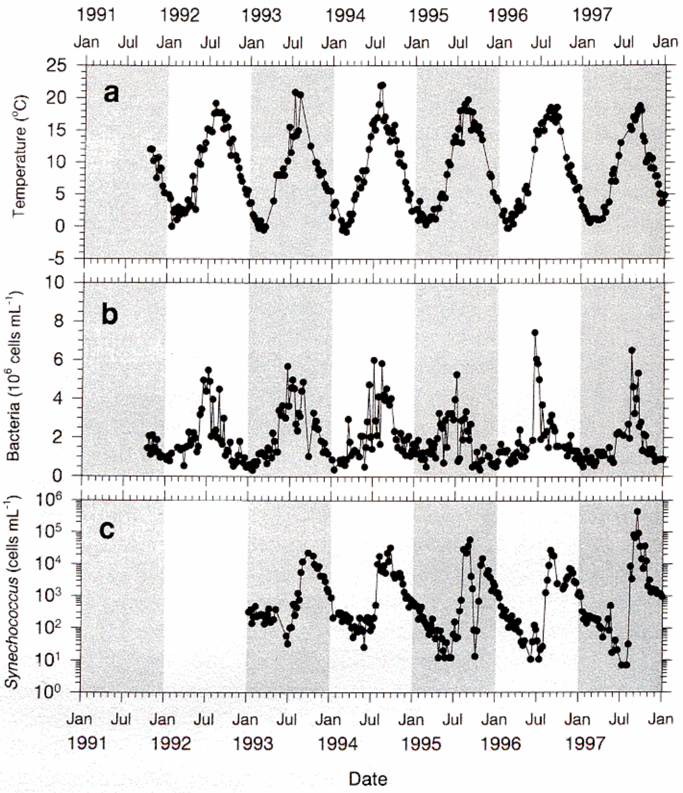

Fig. 1. Weekly observations in Bedford Basin: (a) water temperature, (b) heterotrophic bacteria, and (c) *Synechococcus*. Alternate years are shaded for clarity.

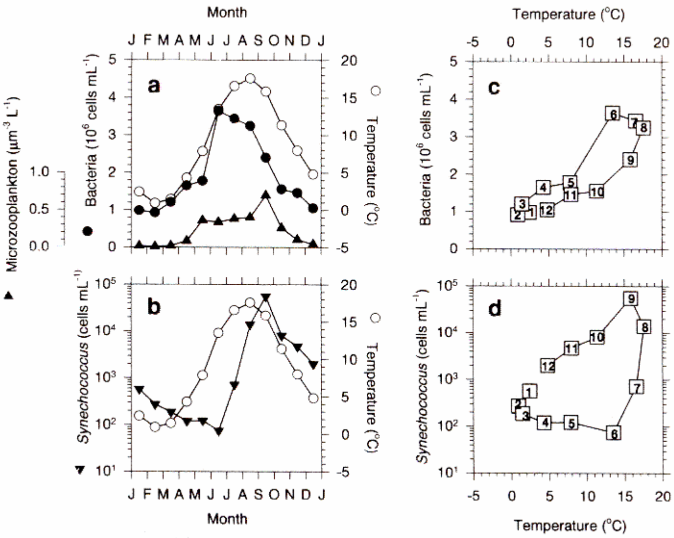

Fig. 2. Monthly averages (1992/93–1997) in Bedford Basin. (a) Annual progression of bacteria, microzooplankton (Taguchi and Platt 1978), and temperature. (b) Annual progression of *Synechococcus* and temperature. (c) Bacteria versus temperature. (d) *Synechococcus* versus temperature. Boxed numbers in (c) and (d) indicate months.

In each study, where applicable, data were compiled separately for each 12-month period and for each station monitored. These sets were then combined to give a grand mean representing the study area. Only data from the shallowest depth were considered. For this reason, the ensuing analyses are not as robust as they would be if the entire population in the upper mixed layer were considered, especially where subsurface maxima occur. In some cases, 12-month time series were not available. Most notably, these are oceanic locations such as the Labrador Sea (Li unpubl.), the Equatorial Pacific (Ducklow et al. 1995; Kirchman et al. 1995; Landry et al. 1996), the Arabian Sea (http://usjgofs.whoi.edu/jg/dir/jgofs/arabian/), and the northwest Indian Ocean (Veldhuis et al. 1997; Wiebinga et al. 1997). Annual averages for such areas were based on data much less highly resolved over a complete cycle.

Where necessary, bacterial carbon (C) was converted to bacterial abundance, assuming 20 fg C per bacterium (Lee and Fuhrman 1987). Data for *Synechococcus* in the Indian Ocean reported by Veldhuis et al. (1997) in units of red fluorescence were converted to cell carbon using the authors' stated regression equation and then re-expressed as abundance (cells ml^{-1}), assuming 294 fg C cell^{-1} (Veldhuis et al. 1993).

New measurements from Beford Basin are presented here for comparison to published datasets from other temperate waters, reinforcing the stereotype of high abundances in summer and low abundances in winter. Bedford Basin (44°41.3′N, 63°38.3′W) is a semienclosed temperate coastal inlet having a surface area of 17 km^2, a maximum depth of 70 m, and a sill depth of 20 m. Plankton was sampled weekly for 6 yr over the deepest point of the basin (Li et al. 1998). Bacteria were either stained with 4′6-diamidino-2-phenylindole (DAPI) and enumerated by epifluorescence microscopy or stained with TO-PRO-1, TOTO-1, or SYTO-13 (Molecular Probes Inc.) and enumerated by flow cytometry (Li et al. 1995; del Giorgio et al. 1996; Guindulain et al. 1997). *Synechococcus* were detected as orange autofluorescing picoplankters and enumerated by flow cytometry (Li 1995).

The time scale at which bacteria and *Synechococcus* respond on a mechanistic level to regulating factors (temperature, light, grazing, substrate supply, and viral lysis) is on the order of days or less. Weekly observations in Bedford Basin (Fig. 1) show that short-term responses of cell abundance to presumed shifts in the controlling factors do not obscure the underlying annual cycles. From 1992 to 1997, temperature ranged from −0.8 to 22.0°C and averaged 8.7°C. Bacteria counts ranged from 0.32 × 10^6 to 7.45 × 10^6 cells ml^{-1}, averaging 1.95 × 10^6 cells ml^{-1}. *Synechococcus* ranged from 7 to 445,000 cells ml^{-1}, averaging 6,150 cells ml^{-1}. An exceptional crash and recovery of *Synechococcus* was documented from September to October 1995 (Fig. 1c), but the cause of this event was not investigated.

High-frequency fluctuations can be smoothed by averaging over time periods longer than the sampling interval. At the seasonal scale, temperature emerges as the dominant influence of heterotrophic bacterial processes in winter and spring (Hoch and Kirchman 1993; Shiah and Ducklow 1995). In Bedford Basin, monthly averages of bacteria and temperature were tightly correlated from January to June (Fig. 2a). The monthly average temperature of 14°C in June marked the start of bacterial decline, presumably because of

Table 1. Annual average abundance of heterotrophic bacteria (10^6 cells ml^{-1}) and annual average temperature (°C) in surface marine waters.

Location	Station	Temperature	Abundance	Reference
McMurdo Sound, Antarctica	Cape Armitage/Tent Island	−1.9	0.13	Rivkin 1991
Signy Island, Antarctica	Borge Bay	−0.1	0.13	Clarke and Leakey 1996
Labrador Shelf	WOCE-AR7/W line	2.0	0.74	Li, unpublished
Barents Sea, Russia	Dal'nezelenetskaya Inlet	3.3	1.37	Baitaz et al. 1996
Greenland Shelf	WOCE-AR7/W line	4.2	0.50	Li, unpublished
Labrador Sea	WOCE-AR7/W line	5.5	0.91	Li, unpublished
Gulf of Bothnia, Baltic Sea	Near Norrby, Sweden	5.8	1.45	Andersson et al. 1994
Gulf of Bothnia, Baltic Sea	Ore estuary, Sweden	6.5	1.26	Wikner and Hagström 1991
Baltic Sea	Near Asko, Sweden	6.6	0.88	Hagström et al. 1979
Baltic Sea	Many	6.6	2.59	Kuparinen and Kuosa 1993
Bedford Basin, Canada	Compass Buoy	8.6	1.95	Li et al. 1998
Humber Estuary, U.K.	Hull (free bacteria)	9.1	2.74	Bent and Goulder 1981
Subarctic Pacific	OWS–PAPA	9.2	0.91	Kirchman et al. 1993
Gulf of Maine, U.S.A.	Essex Estuary/Ipswich Bay	9.5	2.18	Wright and Coffin 1983
Kiel Bight, Baltic Sea	Central bight	9.7	1.57	Kirstein 1991
Kiel Bight, Baltic Sea	Kiel fjord and bight	9.7	1.98	Zimmermann 1977
Narragansett Bay, U.S.A.	Graduate School Oceanography dock	10.7	2.58	Davis et al. 1985
Buzzards Bay, U.S.A.	Central bay, Cape Cod canal, various harbor	11.5	3.09	Turner and Borkman 1993
Wadden Sea, Netherlands	Ems-Dollard estuary	11.8	2.97	Admiraal et al. 1985
Clyde Estuary, U.K.	Upper to lower estuary	12.1	4.99	Rogerson and Laybourn-Parry 1992
Delaware Estuary, U.S.A.	Upper to lower estuary	13.9	3.33	Hoch and Kirchman 1993
Chesapeake Bay, U.S.A.	Near Chesapeake Beach	14.3	7.92	Tabor and Neihof 1984
Galicia, Spain	Ria de Vigo	14.5	2.12	Zdanowski and Figueiras 1997
Onagawa Bay, Japan	Inner bay	14.9	1.35	Tanaka et al. 1997
Chesapeake Bay, U.S.A.	Mid bay	15.0	6.38	Ducklow and Shiah 1993
Chesapeake Bay, U.S.A.	Mid "Chop-Pax" transect	15.0	5.60	Malone et al. 1991
Yellow Sea, Korea	Kunsan Estuary	16.2	11.63	Lee and Lee 1991
Ligurian Sea, Mediterranean	Villefranche Bay	16.7	0.73	Mostajir et al. 1995
South California Bight, U.S.A.	Harbor and Channel	16.9	1.34	McGrath and Sullivan 1981
South California Bight, U.S.A.	San Pedro Channel	16.9	1.09	Krempin and Sullivan 1981
North Atlantic	WCR82B and surrounding area	17.0	1.00	Ducklow 1984, 1986
Mediterranean coast, Spain	Bay of Blanes	17.4	0.48	Satta et al. 1996
Chesapeake Bay, U.S.A.	Horn Point	17.8	7.68	Shiah and Ducklow 1995
Ria Formosa, Portugal	Inner to outer lagoon	18.5	6.75	Barbosa 1991
Patos Lagoon, Brazil	Marinheiros Island	19.2	2.10	Abreu et al. 1992
Natal, South Africa	ORI reef	22.4	2.01	Schleyer 1981
Gulf of Mexico	Laguna Madre/Baffin bay	22.5	7.73	Chin-Leo and Benner 1991
Bermuda	Core—JGOFS BATS	23.5	0.42	www.bbsr.edu/bats
Hawaii	ALOHA—JGOFS HOT	24.8	0.48	hahana.soest.hawaii.edu/hot
Tampa Bay, U.S.A.	St. Petersburg pier	24.9	3.42	Jiang and Paul 1994
Tampa Bay, U.S.A.	Inner to outer bay	24.9	2.48	Paul et al. 1988
Indus River delta, Pakistan	Isaro creek	27.3	2.70	Bano et al. 1997
Equatorial Pacific	140°W, 12°N to 12°S: JGOFS expeditions	27.3	0.73	usjgofs.whoi.edu/jg/dir/jgofs/eqpac
Arabian Sea	Oceanic and neritic stations of JGOFS expeditions	27.3	1.10	usjgofs.whoi.edu/jg/dir/jgofs/arabian
Indian Ocean	Red Sea, Gulf of Aden, Somali Basin	27.4	1.60	Wiebinga et al. 1997

the dominating effects of some other factor. An earlier study (Taguchi and Platt 1978) showed that microzooplankton biomass in Bedford Basin was low through the winter, then increased from May to a peak in September (Fig. 2a). Bacteria may therefore decline in the summer because of grazing. The role of substrate supply to bacteria was not investigated, but we can assume its importance increases in the summer, when metabolic rates rise with temperature (Shiah and Ducklow 1994*a,b,* 1995).

In contrast to heterotrophic bacteria, *Synechococcus* decreased in average numbers from January to June (Fig. 2b). However, a rapid cell increase of more than 700-fold in 3 months led to a peak in September. Although *Synechococcus* was most abundant at high temperatures, they were not least abundant at low temperatures (Fig. 2b,d). The role of temperature in setting the net seasonal abundance of *Synechococcus* is therefore less clear than it is for bacteria.

Extrapolating local studies to wider generalizations, a global annual climatology of heterotrophic bacterial abundance was developed based on 45 separate studies covering the full range of prevailing annual temperatures (Table 1). Investigations in neritic waters greatly outnumber those in oceanic waters, but the two JGOFS oceanic datasets in Bermuda and Hawaii are among the most comprehensive time series. Below 14°C, annual average abundance of bacteria is directly related to annual average temperature; above 14°C, no relationship is discernible (Fig. 3a). In other words, on an annual worldwide basis, the abundance of bacteria is predicted with reasonable accuracy by temperature in regions where the average is less than 14°C. This extends the view, developed at shorter time scales, that in cold waters, temperature is the dominant factor influencing the processes that set bacterial abundance (Hoch and Kirchman 1993; Shiah and Ducklow 1995). At higher temperatures, other factors apparently become dominant and reduce abundance by varying degrees in different habitats, giving rise to the wide variance of results above 14°C (Fig. 3a). For example, temperatures at Tampa Bay, Hawaii, and Bermuda are very similar, but bacterial abundance is about seven times higher in Tampa Bay, an eutrophic estuary receiving high phosphate loads, than in Hawaii and Bermuda, both oligotrophic oceanic sites (Table 1). It is a prevailing notion that typical bacterial abundances, measured in cells ml^{-1}, in eutrophic lagoons and estuaries (10^7), coastal zones (10^6), and the open ocean (10^5) are set by the magnitude of the flux of dissolved organic matter—a manifestation of the dominance of bottom-up over top-down control factors at large scales (Ducklow 1992). This notion may now be refined: It appears that at the annual scale, the role of substrate supply in setting the net bacterial abundance is manifest only where average temperatures exceed 14°C.

The global annual climatology of *Synechococcus* abundance is based on fewer studies, which nevertheless adequately span the full temperature range (Table 2). For phytoplankton as a whole, the annual average distribution of pigment measured by remote sensing of ocean color does not match average sea surface temperatures. Explanations for this lie in considerations of water-column stability, nutrient supply, illumination, and loss processes (Longhurst 1995). From an analysis of 28 studies (Table 2), *Synechococcus* also appear to be directly related to temperatures below, but not above, 14°C (Fig. 3b). A conspicuous departure from this trend, previously noted by Weisse (1993), occurs in the Baltic Sea (Kuosa 1991; Andersson et al. 1994), where very high abundances were recorded (Table 2). At the high end of the temperature range, in the Indian Ocean, the recent studies of Veldhuis et al. (1997) and the United States

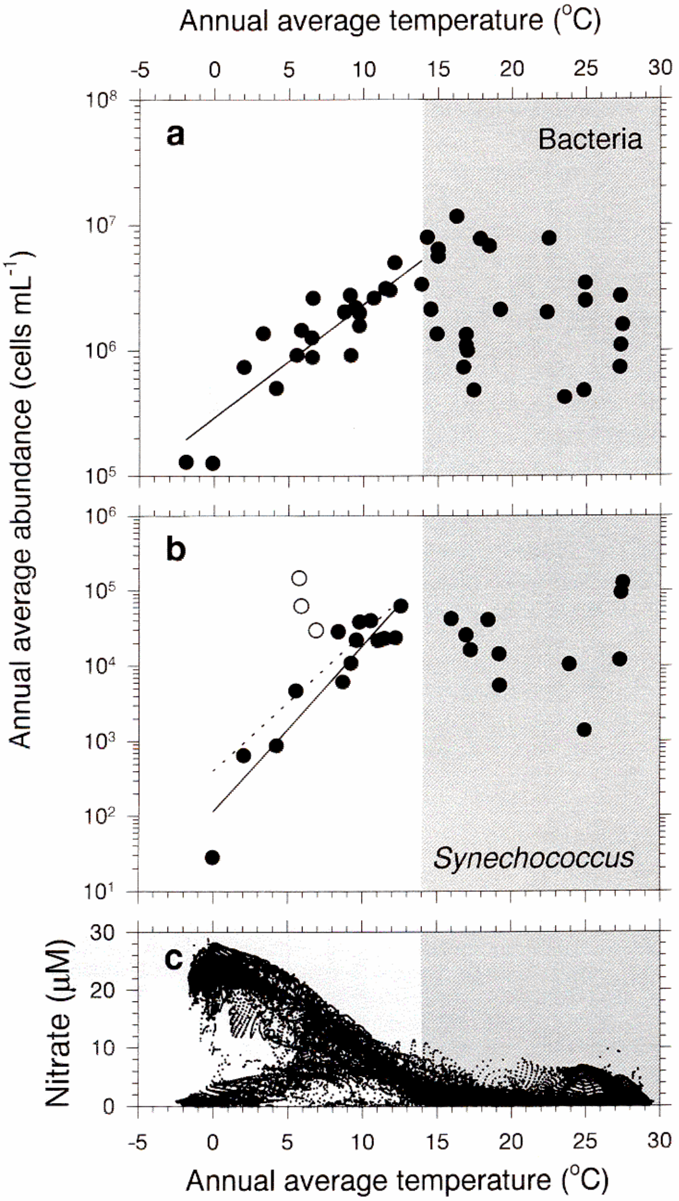

Fig. 3. Annual average abundance (AAA) versus annual average temperature (AAT). (a) Bacteria, from Table 1. Linear regression for temperatures $<$14°C is log AAA = 5.46 + 0.090 AAT (r^2 = 0.79). (b) *Synechococcus,* from Table 2. Baltic Sea data are indicated by open symbols. Linear regression for temperatures $<$14°C, excluding Baltic Sea data, is log AAA = 2.07 + 0.221 AAT (r^2 = 0.87), indicated by solid line. Linear regression for temperatures $<$14°C, including Baltic Sea data, is log AAA = 2.62 + 0.181 AAT (r^2 = 0.53), indicated by dashed line. (c) Nitrate at sea surface, from the *World Ocean Atlas* (U.S. Department of Commerce et al. 1994). Shading indicates temperatures above 14°C.

Table 2. Annual average abundance of *Synechococcus* (cells ml^{-1}) and annual average temperature (°C) in surface marine waters.

Location	Station	Temperature	Abundance	Reference
Antarctica	Davis Bay	0.0	28	Walker and Marchant 1989
Labrador Shelf	WOCE-AR7/W line	2.0	655	Li, unpublished
Greenland Shelf	WOCE-AR7/W line	4.2	881	Li, unpublished
Labrador Sea	WOCE-AR7/W line	5.5	4,751	Li, unpublished
Baltic Sea	Tvarminne Langskar	5.7	148,288	Kuosa 1991
Gulf of Bothnia, Baltic Sea	Near Norrby	5.8	62,635	Andersson et al. 1994
Baltic Sea	Swedish archipelago	6.8	29,733	Larsson and Hagström 1982
Boothbay Harbor, U.S.A.	Dock	8.3	28,621	Shapiro and Haugen 1988
Bedford Basin, Canada	Compass Buoy	8.6	6,150	Li et al. 1998
Subarctic Pacific	OWS—PAPA	9.2	10,900	Booth et al. 1993
Skagerrak, North Sea	Kristineberg MBS	9.5	22,057	Kuylenstierna and Karlson 1994
Kiel Bight, Baltic Sea	Kiel fjord and bight	9.8	38,342	Jochem 1988
Funka Bay, Japan	Central bay	10.5	39,905	Odate 1989
Menai Straits, U.K.	Menai Bridge Pier	11.0	21,507	El Hag and Fogg 1986
Skagerrak, North Sea	Kosterfjorden	11.2	22,352	Karlson and Nilsson 1991
Woods Hole, U.S.A.	Harbor	11.4	23,029	Waterbury et al. 1986
Northwest Atlantic	Shelf-Slope, off Cape Cod, U.S.A.	12.2	23,511	Waterbury et al. 1986
Long Island, U.S.A.	Carmans Estuary/Crane Neck Beach	12.5	62,119	Campbell and Carpenter 1987
Adriatic Sea	Cesenatico coast	15.9	42,193	Vanucci et al. 1994
South California Bight, U.S.A.	San Pedro Channel	16.9	25,597	Krempin and Sullivan 1981
Suruga Bay, Japan	Shimizu Harbour	18.4	40,767	Shimada et al. 1995
Mediterranean Sea	Bay of Naples	19.1	14,380	Modigh et al. 1996
Mediterranean Sea	South Gilla Lagoon, Sardinia	19.2	5,543	Andreoli et al. 1989
Bermuda	OFP	23.8	10,518	Chisholm 1992
Hawaii	ALOHA—JGOFS HOT	24.9	1,400	Campbell et al. 1997
Equatorial Pacific	140°W, 12°N to 12°S: JGOFS expeditions	27.3	12,063	usjgofs.whoi.edu/jg/dir/jgofs/eqpac
Arabian Sea	Oceanic and neritic stations of JGOFS expeditions	27.3	94,157	usjgofs.whoi.edu/jg/dir/jgofs/arabian
Indian Ocean	Red Sea, Gulf of Aden, Somali Basin	27.4	127,704	Veldhuis et al. 1997

JGOFS Arabian Sea expeditions confirm the extremely high abundances of *Synechococcus* reported earlier by Burkill et al. (1993). These findings stand in distinct contrast to the low abundances found near Hawaii in the Pacific Ocean (Campbell et al. 1997), which has an annual average temperature only slightly lower than the Indian Ocean sites.

Previous comparisons of *Synechococcus* from different latitudes have shown that abundance is generally least at low temperatures and greatest at high temperatures (Murphy and Haugen 1985), but with notable exceptions (Joint 1986; Booth et al. 1993). We can now refine this generalization to say that at the annual scale, *Synechococcus* abundance is directly related to temperatures below 14°C; however, even within this range, large differences exist between systems that differ only slightly in temperature (i.e., Baltic Sea versus Labrador Sea). Chisholm (1992) made the insightful suggestion that the two prokaryotic picoplankters *Synechococcus* and *Prochlorococcus* complement each other: Their relative abundance in time and space is different, but their combined biomass is rather constant when the two populations are considered together. Recent observations in the Pacific Ocean (Campbell et al. 1997) and the Indian Ocean (Veldhuis et al. 1997) seem to confirm Chisholm's insight. Unfortunately, there are not enough seasonal datasets of *Prochlorococcus* suitable for inclusion in the present analysis.

Finally, I must emphasize that for both heterotrophic bacteria and *Synechococcus,* the stated relationships between annual average abundance and annual average temperature do not necessarily hold at shorter time scales. For example, Antarctic bacteria may be extremely abundant at the particular moment in the seasonal cycle when, say, primary production is high.

The temperature of 14°C marks a transition in the climatology of both heterotrophic bacteria (Fig. 3a) and *Synechococcus* (Fig. 3b). The same temperature is significant with respect to the global distribution of nitrate (Levitus et al. 1993), as shown by a plot of 42,164 points extracted from the surface depth horizon of the recent *World Ocean Atlas* (Fig. 3c). It appears that nitrate concentrations are never high where the temperature is above approximately 14°C. This intriguing coincidence prompts the question of whether the annual regime above 14°C is dominated by the influence of nutrient limitation on phytoplankton (*Synechococcus* included), and that there follows a diminished supply of organic substrates to bacteria from phytoplankton. Rivkin and Anderson (1997) recently suggested that inorganic phosphate may directly limit heterotrophic bacteria. The plot of sea-surface phosphate concentrations from the *World Ocean Atlas* versus average temperature (data not shown) resembles the nitrate plot (Fig 3c), but phosphate concentrations are limited above a temperature of approximately 19°C. At the global annual scale, it remains an open question as to what factor exerts dominant control on bacteria at high temperatures.

The importance of temperature as a positive regulator of marine bacterial growth rate is well recognized (White et al. 1991), although the strength of this regulation is perhaps uncertain (Rivkin et al. 1996). In their study of the Delaware estuary, Hoch and Kirchman (1993) made the intriguing observation that as temperature varies over an annual cycle, bacterial growth rate is directly related to temperatures below, but not above, 12°C. In Delaware, bacteria responded to the supply of organic substrates associated with the spring phytoplankton bloom, which occurs at temperatures below 12°C.

Here, though, I turn the focus away from seasonal events such as the spring bloom toward broader biogeographic patterns. In the world oceans, 49% of all 1° latitude–longitude grid boxes, representing a global ocean area of 32%, exhibit an average surface temperature below 14°C. For these regions which extend toward the north and south poles from approximately 40° latitude in each hemisphere, it appears that marine bacteria may have a surface distribution that largely reflects the poleward decrease in temperature. This pattern in observable cell abundance is the net manifestation of the underlying processes of growth and loss upon which the direct physiological effects of temperature are exerted. Further progress in the ecological geography of marine bacteria can be expected when climatological averages are compiled for the rates of growth and loss and when due consideration is given to the entire population in the upper mixed layer.

W. K. W. Li

Biological Oceanography Section
Bedford Institute of Oceanography
P.O. Box 1006
Dartmouth, Nova Scotia B2Y 4A2
Canada

References

ABREU, P. C., B. B. BIDDANDA, AND C. ODEBRECHT. 1992. Bacterial dynamics of the Patos Lagoon estuary, southern Brazil (32°S, 52°W): Relationship with phytoplankton production and suspended material. Estuar. Coast. Shelf Sci. **35:** 621–635.

ADMIRAAL, W., J. BEUKEMA, AND F. B. VAN ES. 1985. Seasonal fluctuations in the biomass and metabolic activity of bacterioplankton and phytoplankton in a well-mixed estuary: The Ems-Dollard (Wadden Sea). J. Plankton Res. **7:** 877–890.

ANDERSSON, A., P. HAECKY, AND Å. HAGSTRÖM. 1994. Effect of temperature and light on the growth of micro-, nano-, and picoplankton: Impact on algal succession. Mar. Biol. **120:** 511–520.

ANDREOLI, C., N. RASCIO, F. DALLA VECCHIA, AND L. TALARICO. 1989. An ultrastructural research on natural populations of picoplankton from two brackish water environments in Italy. J. Plankton Res. **11:** 1067–1074.

BAITAZ, V. A., O. N. BAITAZ, AND I. E. MISHUSTINA. 1996. Cell morphometry, abundance, and biomass of the main morphological groups of the Barents sea bacterioplankton. Oceanology **36:** 833–836.

BANO, N., M.-U. NISA, N. KHAN, M. SALEEM, P. J. HARRISON, S. I. AHMED, AND F. AZAM. 1997. Significance of bacteria in the flux of organic matter in the tidal creeks of the mangrove ecosystem of the Indus River delta, Pakistan. Mar. Ecol. Prog. Ser. **157:** 1–12.

Acknowledgements

I thank Paul Dickie for sampling the Bedford Basin. Glen Harrison and Alan Longhurst offered many ideas that underlie this work. Erica Head, Shubha Sathyendranath, and Trevor Platt commented on an early version of the manuscript. I appreciate the constructive criticism offered by Ian Joint, Hugh Ducklow, and David Kirchman.

BARBOSA, A. 1991. Spatial and temporal variation of bacterioplankton abundance and biomass in a coastal lagoon (Ria Formosa, southeastern Portugal). Kiel. Meeresforsch. Sonderh. **8:** 66–73.

BENT, E. J., AND R. GOULDER. 1981. Planktonic bacteria in the Humber estuary: Seasonal variation in population density and heterotrophic activity. Mar. Biol. **62:** 35–45.

BOOTH, B. C., J. LEWIN, AND J. R. POSTEL. 1993. Temporal variation in the structure of autotrophic and heterotrophic communities in the subarctic Pacific. Prog. Oceanogr. **32:** 57–99.

BUECHER, E., J. GOY, B. PLANQUE, M. ETIENNE, AND S. DALLOT. 1997. Long-term fluctuations of *Liriope tetraphylla* in Villefranche Bay between 1966 and 1993 compared to *Pelagia noctiluca* pullulations. Oceanol. Acta **20:** 145–157.

BURKILL, P. H., R. J. G. LEAKEY, N. J. P. OWENS, AND R. F. C. MANTOURA. 1993. *Synechococcus* and its importance to the microbial foodweb of the northwest Indian Ocean. Deep-Sea Res. II **40:** 773–782.

CAMPBELL, L., AND E. J. CARPENTER. 1987. Characterization of phycoerythrin-containing *Synechococcus* spp. populations by immunofluorescence. J. Plankton Res. **9:** 1167–1181.

———, H. LIU, H. A. NOLLA, AND D. VAULOT. 1997. Annual variability of phytoplankton and bacteria in the subtropical north Pacific Ocean at station ALOHA during the 1991–1994 ENSO event. Deep-Sea Res. I **44:** 167–192.

CHIN-LEO, G., AND R. BENNER. 1981. Dynamics of bacterioplankton abundance and production in seagrass communities of a hypersaline lagoon. Mar. Ecol. Prog. Ser. **73:** 219–230.

CHISHOLM S. W. 1992. Phytoplankton size, p. 213–237. *In* P. G. Falkowski and A. D. Woodhead [eds.], Primary productivity and biogeochemical cycles in the sea. Plenum.

CLARKE, A., AND R. J. G. LEAKEY. 1996. The seasonal cycle of phytoplankton, macronutrients, and the microbial community in a nearshore Antarctic marine ecosystem. Limnol. Oceanogr. **41:** 1281–1294.

DAVIS, P. G., D. A. CARON, P. W. JOHNSON, AND J. MCN. SIEBURTH. 1985. Phototrophic and apochlorotic components of picoplankton and nanoplankton in the North Atlantic: Geographic, vertical, seasonal and diel distributions. Mar. Ecol. Prog. Ser. **21:** 15–26.

DEL GIORGIO, P. A., D. F. BIRD, Y. T. PRAIRIE, AND D. PLANAS. 1996. Flow cytometric determination of bacterial abundance in lake plankton with the green nucleic acid stain SYTO 13. Limnol. Oceanogr. **41:** 783–789.

DUCKLOW, H. W. 1984. Geographical ecology of marine bacteria: Physical and biological variability at the mesoscale, p. 22–31. *In* M. J. Klug and C. A. Reddy [eds.], Current perspectives in microbial ecology. American Society of Microbiology.

———. 1986. Bacterial biomass in warm-core Gulf Stream ring 82-B: Mesoscale distributions, temporal changes and production. Deep-Sea Res. **33:** 1789–1812.

———. 1992. Factors regulating bottom-up control of bacteria biomass in open ocean plankton communities. Arch. Hydrobiol. Beih. **37:** 207–217.

———, H.L. QUINBY, AND C.A. CARLSON. 1995. Bacterioplankton dynamics in the equatorial Pacific during the 1992 El Niño. Deep-Sea Res. II **42:** 621–638.

———, AND F.-K. SHIAH. 1993. Bacterial production in estuaries, p. 261–287. *In* T. E. Ford [ed.], Aquatic microbiology: An ecological approach. Blackwell.

EL HAG, A. G. D., AND G. E. FOGG. 1986. The distribution of coccoid blue-green algae (cyanobacteria) in the Menai Straits and the Irish Sea. Br. Phycol. J. **21:** 45–54.

GUINDULAIN, T., J. COMAS, AND J. VIVES-REGO. 1997. Use of nucleic acid dyes SYTO-13, TOTO-1, and YOYO-1 in the study of *Escherichia coli* and marine prokaryotic populations by flow cytometry. Appl. Environ. Microbiol. **63:** 4608–4611.

HAGSTRÖM, Å., U. LARSSON, P. HÖRSTEDT, AND S. NORMARK. 1979. Frequency of dividing cells, a new approach to the determination of bacterial growth rates in aquatic environments. Appl. Environ. Microbiol. **37:** 805–812.

HOCH, M. P., AND D. L. KIRCHMAN. 1993. Seasonal and inter-annual variability in bacterial production and biomass in a temperate estuary. Mar. Ecol. Prog. Ser. **98:** 283–295.

JIANG, S. C., AND J. H. PAUL. 1994. Seasonal and diel abundance of viruses and occurrence of lysogeny/bacteriocinogeny in the marine environment. Mar. Ecol. Prog. Ser. **104:** 163–172.

JOCHEM, F. 1988. On the distribution and importance of picocyanobacteria in a boreal inshore area (Kiel Bight, Western Baltic). J. Plankton Res. **10:** 1009–1022.

JOINT, I. R. 1986. Physiological ecology of picoplankton in various oceanographic provinces. Can. Bull. Fish. Aquat. Sci. **214:** 287–309.

KARENTZ, D., AND T. J. SMAYDA. 1984. Temperature and seasonal occurrence patterns of 30 dominant phytoplankton species in Narragansett Bay over a 22-year period (1959–1980). Mar. Ecol. Prog. Ser. **18:** 277–293.

KARLSON, B., AND P. NILSSON. 1991. Seasonal distribution of picoplanktonic cyanobacteria of *Synechococcus* type in the eastern Skagerrak. Ophelia **34:** 171–179.

KIRCHMAN, D. L., R. G. KEIL, M. SIMON, AND N. A. WELSCHMEYER. 1993. Biomass and production of heterotrophic bacterioplankton in the oceanic subarctic Pacific. Deep-Sea Res. I **40:** 967–988.

———, J. H. RICH, AND R. T. BARBER. 1995. Biomass and biomass production of heterotrophic bacteria along 140°W in the equatorial Pacific: Effect of temperature on the microbial loop. Deep-Sea Res. **42:** 603–619.

KIRSTEIN, K. O. 1991. Annual variation of bacterial number, production and activity in central Kiel bight. Kiel. Meeresforsch. Sonderh. **8:** 8–13.

KREMPIN, D. W., AND C. W. SULLIVAN. 1981. The seasonal abundance, vertical distribution, and relative microbial biomass of chroococcoid cyanobacteria at a station in southern California coastal waters. Can. J. Microbiol **27:** 1341–1344.

KUOSA, H. 1991. Picoplanktonic algae in the northern Baltic Sea: Seasonal dynamics and flagellate grazing. Mar. Ecol. Prog. Ser. **73:** 269–276.

KUPARINEN, J., AND H. KUOSA. 1993. Autotrophic and heterotrophic picoplankton in the Baltic Sea. Adv. Mar. Biol. **29:** 73–128.

KUYLENSTIERNA, M., AND B. KARLSON. 1994. Seasonality and composition of pico- and nanoplanktonic cyanobacteria and protists in the Skagerrak. Bot. Mar. **37:** 17–33.

LANDRY, M. R., J. KIRSHTEIN, AND J. CONSTANTINOU. 1996. Abundances and distributions of picoplankton populations in the central equatorial Pacific from 12°N to 12°S, 140°W. Deep-Sea Res. II **43:** 871–890.

LARSSON, U., AND Å. HAGSTRÖM. 1982. Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. Mar. Biol. **67:** 57–70.

LEE, G.-H., AND D.-M. LEE. 1991. Seasonal distribution and character of heterotrophic marine bacteria in the intertidal zone of the Yellow Sea near Kunsan, Korea. Kiel. Meeresforsch. Sonderh. **8:** 81–85.

LEE, S., AND J. A. FUHRMAN. 1987. Relationships between biovolume and biomass of naturally derived marine bacterioplankton. Appl. Environ. Microbiol. **53:** 1298–1303.

LEVITUS, S., M. E. CONKRIGHT, J. L. REID, R. G. NAJJAR, AND A. MANTYLA. 1993. Distribution of nitrate, phosphate and silicate in the world oceans. Prog. Oceanogr. **31:** 245–273.

LI, W. K. W. 1995. Composition of ultraphytoplankton in the central north Atlantic. Mar. Ecol. Prog. Ser. **122:** 1–8.

———, J. F. JELLETT, AND P. M. DICKIE. 1995. DNA distributions in planktonic bacteria stained with TOTO or TO-PRO. Limnol. Oceanogr. **40:** 1485–1495.

———, P. M. DICKIE, AND J. A. SPRY. 1998. Plankton monitoring programme in the Bedford Basin, 1991–1997. Can. Data Rep. Fish. Aquat. Sci. **1036:** vii + 342 p.

Longhurst, A. 1995. Seasonal cycles of pelagic production and consumption. Prog. Oceanogr. **36:** 77–167.

Malone, T. C., H. W. Ducklow, E. R. Peele, and S. E. Pike. 1991. Picoplankton carbon flux in Chesapeake Bay. Mar. Ecol. Prog. Ser. **78:** 11–22.

McGrath, S. M., and C. W. Sullivan. 1981. Community metabolism of adenylates by microheterotrophs from the Los Angeles Harbor and southern California coastal waters. Mar. Biol. **62:** 217–226.

Modigh, M., V. Saggiomo, and M. R. d'Alcalà. 1996. Conservative features of picoplankton in a Mediterranean eutrophic area, the Bay of Naples. J. Plankton Res. **18:** 87–95.

Mostajir, B., J. R. Dolan, and F. Rassoulzadegan. 1995. Seasonal variations of pico- and nano-detrital particles (DAPI Yellow Particles, DYP) in the Ligurian Sea (NW Mediterranean). Aquat. Microbiol. Ecol. **9:** 267–277.

Murphy, L. S., and E. M. Haugen. 1985. The distribution and abundance of phototrophic ultraplankton in the North Atlantic. Limnol. Oceanogr. **30:** 47–58.

Odate, T. 1989. Seasonal changes in cell density of cyanobacteria and other picophytoplankton populations in Funka Bay, Japan. Bull. Plankton Soc. Jpn. **36:** 53–61.

Paul, J. H., M. F. DeFlaun, W. H. Jeffrey, and A. W. David. 1988. Seasonal and diel variability in dissolved DNA and in microbial biomass and activity in a subtropical estuary. Appl. Environ. Microbiol. **54:** 718–727.

Rivkin, R. B. 1991. Seasonal patterns of planktonic production in McMurdo Sound, Antarctica. Am. Zool. **31:** 5–16.

———, M. R. Anderson, and C. Lajzerowicz. 1996. Microbial processes in cold oceans, I: Relationship between temperature and bacterial growth rate. Aquat. Microbiol. Ecol. **10:** 243–254.

———, and ———. 1997. Inorganic nutrient limitation of oceanic bacterioplankton. Limnol. Oceanogr. **42:** 730–740.

Rogerson, A., and J. Laybourn-Parry. 1992. Bacterioplankton abundance and production in the Clyde estuary, Scotland. Arch. Hydrobiol. **126:** 1–14.

Satta, M. P., S. Agustí, M. P. Mura, D. Vaqué, and C. M. Duarte. 1996. Microplankton respiration and net community metabolism in a bay on the NW Mediterranean coast. Aquat. Microbiol. Ecol. **10:** 165–172.

Schleyer, M. H. 1981. Microorganisms and detritus in the water column of a subtidal reef of Natal. Mar. Ecol. Prog. Ser. **4:** 307–320.

Shapiro, L. P., and E. M. Haugen. 1988. Seasonal distribution and temperature tolerance of *Synechococcus* in Boothbay Harbor, Maine. Estuar. Coast. Shelf Sci. **26:** 517–525.

Shiah, F.-K. and H. W. Ducklow. 1994*a*. Temperature regulation of heterotrophic bacterioplankton abundance, production, and specific growth rate in Chesapeake Bay. Limnol. Oceanogr. **39:** 1243–1258.

———, and ———. 1994*b*. Temperature and substrate regulation of bacterial abundance, production and specific growth rate in Chesapeake Bay, USA. Mar. Ecol. Prog. Ser. **103:** 297–308.

———, and ———. 1995. Multiscale variability in bacterioplankton abundance, production, and specific growth rate in a temperate salt-marsh tidal creek. Limnol. Oceanogr. **40:** 55–66.

Shimada, A., M. Nishijima, and T. Maruyama. 1995. Seasonal appearance of *Prochlorococcus* in Suruga Bay, Japan, in 1992–1993. J. Oceanogr. **51:** 289–300.

Tabor, P. S., and R. A. Neihof. 1984. Direct determination of activities for microorganisms of Chesapeake Bay populations. Appl. Environ. Microbiol. **48:** 1012–1019.

Taguchi, T. and T. Platt. 1978. Size distribution and chemical composition of particulate matter in Bedford Basin, 1973 and 1974. Fisheries and Marine Service Data Report No. 56, Canadian Department of Fisheries and Environment.

Tanaka, T., N. Fujita, and A. Taniguchi. 1997. Predator–prey eddy in heterotrophic nano-flagellate-bacteria relationships in a coastal marine environment: A new scheme for predator–prey associations. Aquat. Microbiol. Ecol. **13:** 249–256.

Turner, J. T., and D. G. Borkman. 1993. Plankton studies in Buzzards Bay, Massachusetts, USA, I: Hydrography and bacterioplankton, 1987 to 1990. Mar. Ecol. Prog. Ser. **100:** 17–26.

U.S. Department of Commerce; National Oceanic and Atmospheric Administration; National Environmental Satellite, Data, and Information Service; National Oceanographic Data Center; and Ocean Climate Laboratory. 1994. World ocean atlas: CD-ROM data sets. National Oceanic and Atmospheric Administration.

Vanucci, S., M. L. C. Acosta Pomar, and T. L. Maugeri. 1994. Seasonal pattern of phototrophic picoplankton in the eutrophic coastal waters of the northern Adriatic sea. Bot. Mar. **37:** 57–66.

Veldhuis, M. J. W., G. W. Kraay, and W. W. C. Gieskes. 1993. Growth and fluorescence characteristics of ultraplankton on a north–south transect in the eastern North Atlantic. Deep-Sea Res. II **40:** 609–626.

———, ———, J. D. L. van Bleijswijk, and M. A. Baars. 1997. Seasonal and spatial variability in phytoplankton biomass, productivity and growth in the northwestern Indian Ocean: The southwest and northeast monsoon, 1992–1993. Deep-Sea Res. I **44:** 425–449.

Walker, T. D., and H. J. Marchant. 1989. The seasonal occurrence of chroococcoid cyanobacteria at an Antarctic coastal site. Polar Biol. **9:** 193–196.

Waterbury, J. B., S. W. Watson, F. W. Valois, and D. G. Franks. 1986. Biological and ecological characterization of the marine unicellular cyanobacterium *Synechococcus*. Can. Bull. Fish. Aquat. Sci. **214:** 71–120.

Weisse, T. 1993. Dynamics of autotrophic picoplankton in marine and freshwater ecosystems. Adv. Microbiol. Ecol. **13:** 327–370.

White, P. A., J. Kalff, J. B. Rasmussen, and J. M. Gasol. 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microbiol. Ecol. **21:** 99–118.

Wiebinga, C. J., M. J. W. Veldhuis, and H. J. W. de Baar. 1997. Abundance and productivity of bacterioplankton in relation to seasonal upwelling in the northwest Indian Ocean. Deep-Sea Res. I **44:** 451–476.

Wikner, J., and Å. Hagström. 1991. Annual study of bacterioplankton community dynamics. Limnol. Oceanogr. **36:** 1313–1324.

Wright, R. T., and R. B. Coffin. 1983. Planktonic bacteria in estuaries and coastal waters of northern Massachusetts: Spatial and temporal distribution. Mar. Ecol. Prog. Ser. **11:** 205–216.

Zdanowski, M. K., and F. G. Figueiras. 1997. Relationships between the abundance of bacteria and other biota and the hydrographic variability in the Ría de Vigo, Spain. Mar. Ecol. Prog. Ser. **147:** 257–267.

Zimmermann, R. 1977. Estimation of bacterial number and biomass by epifluorescence microscopy and scanning electron microscopy, p. 103–120. *In* G. Rheinheimer [ed.], Microbial ecology of a brackish water environment. Springer-Verlag.

Received: 27 January 1998
Accepted: 29 April 1998
Amended: 12 May 1998