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Sea Ice Microbial Communities (SIMCO)

9. Effects of Temperature and Salinity on Rates of Metabolism and Growth of Autotrophs and Heterotrophs

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Summary. Sea ice microbial communities (SIMCO) grow luxuriantly within several microhabitats of sea ice, indicating that the microorganisms comprising these communities are well adapted to the physicochemical gradients which characterize sea ice. We used SIMCO obtained from the bottom of congelation ice in McMurdo Sound, Antarctica, to test the hypothesis that low temperature limits microbial productivity in polar oceans and also to investigate the effect of salinity on rates of autotrophic and heterotrophic metablism. Substantial rates of carbon fixation, incorporation of thymidine, and uptake of glutamate occurred at the in situ temperatures of −1.9 °C, with maximum rates at temperatures considerably warmer but below 15 °C. Microalgae and bacteria of SIMCO are thus indicated to be psychrophiles. The relative rates of autotrophic and heterotrophic microbial growth (based on rates of fixation of $^{14}CO_2$ by microalgae and incorporation of ^{3}H-thymidine by bacteria, respectively) were similar and overlapped from 4 ° and 7 °C. These data suggest that a recent hypothesis proposing the uncoupling of primary production and bacterial production in cold water, due to differential growth of phytoplankton and bacterioplankton at low temperatures, is refuted with respect to SIMCO. Maximum rates of carbon fixation by autotrophs of SIMCO occurred at salinities which characterized the ice from which the SIMCO were collected. In contrast, heterotrophs of SIMCO exhibited a more stenohaline response to variable salinity, with maximum incorporation of thymidine and uridine from 20‰ to 30‰. Adaptations by autotrophs and heterotrophs of SIMCO that permit substantial metabolism and growth at very low temperatures and variable salinities are significant when considering production and trophodynamics in polar oceans. Actively growing microorganisms in these unique communities contribute to overall production in polar oceans, provide carbon for food webs associated with sea ice, and upon release from melting ice may contribute to microbial blooms in marginal ice edge zones, which in turn support cryopelagic food webs.

Introduction

Metabolism and growth of phytoplankton and bacterioplankton are hypothesized to be limited in part by the low temperatures of polar oceans (Holm-Hansen et al. 1977; Noeri and Holm-Hansen 1982; Jacques 1983; El-Sayed 1984; Harrison and Platt 1986; Pomeroy and Deibel 1986; Tilzer et al. 1985, 1986). Sea ice microbial communities (SIMCO), composed of microalgae, bacteria, and protozoans, are ideal sources of microorganisms which can be used to test this hypothesis and also to investigate the effect of salinity on microbial metabolism and growth because of the physicochemical extremes which characterize their habitat. These microorganisms may be exposed to a marked temporal range and gradient of temperature and salinity during the cycle of formation, growth, and decay of the ice. In McMurdo Sound, Antarctica, the highest southern latitude where sea ice exists (77 °51′S), microbial cells are bathed initially in seawater at temperature close to −1.9 °C and salinity close to 34‰ (Littlepage 1965) and are incorporated into the growing fast ice sheet by a variety of physical and biological mechanisms (Bunt 1968; Ackley et al. 1979; Garrison et al. 1983; Sullivan 1985). Following formation of sea ice, SIMCO are distributed along physicochemical gradients of temperature and salinity that span the ice column (Whitaker 1977; Ackley et al. 1979; Sullivan 1985; Grossi and Sullivan 1985; Palmisano and Sullivan 1985; Palmisano et al. 1985a). SIMCO may be exposed to temperatures at the surface of congelation ice that range from −42 °C in winter to about 4 °C in summer (Littlepage 1965; Anonymous 1984, 1985; Grossi and Sullivan 1985; Palmisano et al. 1985a; Kottmeier et al. 1985). SIMCO are also found in brine chambers within congelation ice where temperatures may reach those of underlying seawater (−1.9 °C) before onset of melting and salinities have been observed to range from greater than 150‰ to 34‰ (S. T. Kottmeier and C. W. Sullivan, unpublished observation). The salinities of sea ice brine are known to be strictly a func-

tion of ice temperature (Pounder 1965). At the bottom of congelation ice and in the unconsolidated platelet ice layer beneath, SIMCO are exposed to temperatures averaging −1.9 °C and salinities close to 34‰ (Bunt and Wood 1963; Kottmeier et al. 1985). During summer, temperatures can rise above −1.9 °C in this region and salinity may drop to near 0‰ with the onset of ice and snow melting and formation of freshwater lenses (Bunt 1968; Grossi 1985; Palmisano and Sullivan 1985; Kottmeier et al. 1985; Grossi et al. 1987). During melting of ice, SIMCO may be released into the underlying seawater to complete the cycle (Horner 1976; Ackley et al. 1979; Legendre et al. 1981; Sullivan et al. 1983, 1985; Grossi 1985; Sasaki and Hoshiai 1986; Grossi et al. 1987) or alternatively be retained and "refrozen" into ice that survives summer melting to yield multi-year communities (Ackley et al. 1979; Hoshiai 1981; Palmisano and Sullivan 1985; S. T. Kottmeier and C. W. Sullivan, unpublished observation).

Here we present the effects of temperature and salinity on the rates of metabolism and growth of autotrophs and heterotrophs in SIMCO collected from the bottom of congelation ice in McMurdo Sound, Antarctica, during the austral spring and summer of 1983 and 1984. The study was designed to determine what limitations temperature and salinity place on microbial metabolism and growth in sea ice and seawater. This information is important not only in characterizing the physiological ecology of a poorly known community of microorganisms, but also in defining conditions that influence microbial blooms in sea ice and seawater of marginal ice edge zones (Smith and Nelson 1985, 1986; Wilson et al. 1986), which support the ice and cryopelagic food webs of polar oceans (Ainley et al. 1986; Garrison et al. 1986).

Methods

Sample Collection

Samples of annual sea ice, predominantly congelation ice (Gow et al. 1981), were taken during the austral summers of 1983–84 by SIPRE auger (7.6 cm dia) from several locations in McMurdo Sound, Antarctica, (Fig. 1) for use in temperature and salinity experiments. Snow cover was less than 5 cm at all of the sites sampled. Microalgae accumulated in "bloom" proportions, coloring the bottom 5 cm of the ice brown with chlorophyll *a* concentrations ranging from 280 to 1580 $\mu g\, l^{-1}$ of ice meltwater. The diatom species *Nitzschia stellata*, *Pleurosigma* sp., *Amphiprora kufferathii*, and *Pinnularia quadratarea* in various proportions were the dominant microalgae at these sites, similar to that described earlier for sea ice of McMurdo Sound (Bunt and Wood 1963; Grossi 1985; Grossi and Sullivan 1985). These diatoms live on ice crystals and in brine chambers/ interstitial water of congelation ice (S. T. Kottmeier and C. W. Sullivan, unpublished observation). Tube diatoms of the *Amphipleura/Berkeleya* group were rarely observed suggesting that "mat-strand" were either not sampled by our coring or not present in significant numbers. Although numerous epibacteria and free-living bacteria were observed, flagellates and ciliates were rarely observed, as we have reported previously for this time of year (Sullivan and Palmisano 1984; Kottmeier et al. 1987). The bottom 5 cm of up to 5 ice cores were removed in the field by aluminum ice saw in dim light and placed immediately into large volumes (1–2 l) of cold (0 °C) 0.2 µm pore size (Nuclepore) filtered seawater (FSW) of 34‰. This procedure was followed to minimize short-term, osmotic

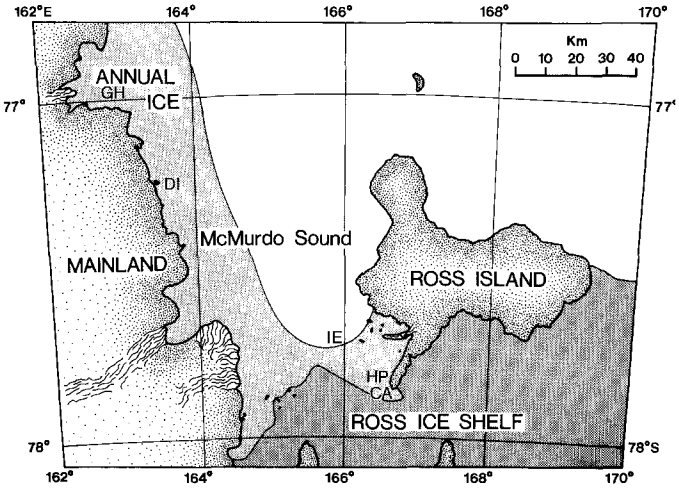

Fig. 1. Map of McMurdo Sound, Antartica showing sites where samples of congelation ice were taken to obtain SIMCO used in experiments. Legend: *GH* = Granite Harbor, *DI* = Dunlop Island, *IE* = edge of fast ice, *HP* = Hut Point, and *CA* = Cape Armitage

(Palmisano et al. 1985b, 1987b; Bates and Cota 1986; Garrison and Buck 1986) and thermal "shock" of SIMCO during transport in darkened Freezesafes (Polyfoam Packers) to the Eklund Biological Center and subsequent melting of the ice. Cores were allowed to melt into the FSW contained in 8 l jars (Nalgene) in the dark at 0 °C overnight prior to use in the experiments described below. Salinity of the final meltwater was determined by refractometer (Bausch and Lomb) and ranged from 19‰ to 26‰ for the temperature experiments. Nuclepore filters were used in all filtrations unless noted differently.

Temperature Experiments

Rate of carbon fixation versus temperature experiments were initiated by dispensing 20 ml suspensions of ice meltwater into triplicate light and one dark (wrapped with electrical tape) scintillation vials, which were covered with Parafilm (American Can) and then capped. Vials were allowed to equilibrate at each temperature in the experiment for $\frac{1}{2}$ h prior to addition of 60–100 µl of 40 $\mu Ci\, ml^{-1}$ $NaH^{14}CO_3$ (New England Nuclear). Vials were capped again, inverted several times to mix the radiolabel uniformly, and placed into a thermostatically controlled (±0.1 °C), circulating glycol bath (Braun) at an irradiance of 40 $\mu Einsteins\, m^{-2}\, s^{-1}$, saturating irradiance for photosynthesis of sea ice microalgae (Palmisano et al. 1985b), for 1 h incubation at each temperature. After incubation, vials were removed, placed on ice (0 °C) in the dark. Total $NaH^{14}CO_3$ in each assay vial was determined first on duplicate 100 µl samples placed in scintillation vials with 10 ml of Aquasol II (New England Nuclear), neutralized with the addition of NaOH, for radioassay by a Beckman LS 100C scintillation counter. Next, 10 ml from each assay vial were filtered through a 1.0 µm pore size filter, which was rinsed twice with cold (0 °C) FSW, fumed over concentrated HCl for 1 min, and placed in a scintillation vial with 10 ml of Aquasol II for radioassay of $^{14}CO_2$ fixed by microalgae. Last, dissolved extracellular organic carbon (EOC) was determined on a filtrate obtained by filtering a separate 5 ml sample from each assay vial through a 1.0 µm pore size filter. The filtrate was acidified to pH 2 by addition of concentrated HCl and shaken in a scintillation vial on a rotary shaker overnight. Duplicate 1 ml samples of acidified filtrate were radioassayed as described above. Each data point represents the mean radiochemical uptake of triplicate live assays plus EOC from which the dark assay plus EOC was subtracted. Replicate assays were within ±10% of one another.

Rate of thymidine incorporation versus temperature experiments were conducted in parallel with the carbon fixation experiments and initiated by dispensing 30 ml suspensions of ice meltwater into duplicate

60 ml glass stoppered bottles. The bottles were allowed to equilibrate at each temperature in the experiment for $\frac{1}{2}$ h prior to addition of 30 µl of 200 µCi ml^{-1} [methyl-^{3}H] thymidine to yield a final concentration of 10 nM thymidine. [Methyl-^{3}H] thymidine (ICN) (sp act 72 Ci mmole^{-1}) was initially taken to dryness and rehydrated according to Kottmeier et al. (1987) to eliminate any volatile ^{3}H by-products that might have resulted from the high specific activity [methyl-^{3}H] thymidine. Bottles were gently swirled to mix the radiolabel and samples were incubated for 12–24 h in incubators set at various temperatures in the light and dark. The rate of ^{3}H-thymidine incorporation by SIMCO is linear for 48 h at −1.9 °C and 30‰ (S. T. Kottmeier and C. W. Sullivan, unpublished observation). After incubation total ^{3}H-thymidine was first determined by radioassay of duplicate 100 µl samples. Duplicate 10 ml samples were then filtered through 0.2 µm pore size filters and incorporation of ^{3}H-thymidine into cold (0 °C) trichloroacetic acid (TCA) insoluble material on the filters determined according to the method of Fuhrman and Azam (1980). Each data point represents radiochemical incorporation of a live assay from which a formalin killed (1% final concentration) assay is subtracted.

We conducted experiments to determine rates of glutamate uptake versus temperature in a manner similar to thymidine, except as follows. Additions of 15 µl of [3,4-^{3}H] L-glutamic acid (ICN) (sp act 50 Ci mmole^{-1}) were made to duplicate light and one dark bottle to yield a concentration of 5 nM ^{3}H-glutamate. Concentrations of glutamate have been measured as high as 3 µM at the sea ice-seawater interface (D. Manahan and C. W. Sullivan, unpublished observation). Thus, addition of 5 nmolar ^{3}H-glutamate made only a slight change in the concentration of glutamate available to SIMCO. Bottles were incubated for 1 h in parallel with the carbon fixation experiment. Filters were rinsed twice with FSW instead of being extracted with TCA.

Measurement of Temperature

Profiles of temperature in sea ice were determined by strings of thermocouples frozen into the ice in early September 1984. Each thermocouple was constructed of type T wire (copper constantan) with Teflon insulation and oversheath, covered with a 3 in stainless sheath held in place with epoxy cement, and a male connector attached to the opposite end (B. J. Wolfe Enterprises, Inc., N. Hollywood, Calif.). Strings of thermocouples were positioned on a 5.1 cm×5.1 cm×2.4 m wooden pole in order to measure profiles of temperature in air 25 cm above the surface of the snow or congelation ice, at the surface of the congelation ice, and at various depths in the congelation ice, platelet ice, and surface seawater. The stainless sheath of each thermocouple was pressed into a hole drilled through the wood pole such that 2 in of the sheath extended outside the hole. Wire from the thermocouples was secured to the wood by wraps of electrical tape. The wooden pole was frozen into a 12.7 cm (dia) hole drilled through the congelation ice by Jiffy Drill (Geotest). Male connectors from the thermocouples were enclosed above the surface of the snow or congelation ice in a gallon size Nalgene jar. This arrangement protected the connectors from corrosion and allowed for sequential reading of temperature using a single digital thermometer (Fluke Model 2175A), with a resolution of ±0.1 °C. Each temperature was read from the digital thermometer 1 min after mating the two connectors to allow for thermal equilibration.

Profiles of temperature in seawater beneath the ice were determined by lowering a 4 wire, resistance temperature detector (RTD) through the dive hole of a fish hut, located close to the strings of thermocouples. The RTD was constructed of copper constantan wire with Teflon insulation and oversheath, covered with a stainless sheath held in place with epoxy cement (B. J. Wolfe Enterprises, Inc.) and hard-wired to a digital thermometer (Fluke Model 2180), with a resolution of ±0.01 °C. The RTD was lowered by hand through the water column to the bottom, 19 m from the surface, on a weighted and marked line. At 1 m intervals, the RTD was allowed to equilibrate for 1 min before the temperature was read from the digital thermometer.

Salinity Experiments

SIMCO suspensions of 10 different salinities, ranging from 5‰ to 90‰, were made over 24 h by adding distilled water or brine of 113‰ to original ice meltwater of 30‰ as follows. Slow dropwise addition of 80 ml was made initially. This was followed by four additions of 80 ml over 24 h to yield 400 ml of SIMCO suspension of each salinity. Last, concentrated, filter sterilized (0.22 µm pore size Millex, Millipore) F/2 nutrients and vitamins (Guillard and Ryther 1962) were added to each suspension to assure that nutrient limitation would not occur during the short duration of the experiment. These were added in small volumes to yield F/2 enrichment for all suspensions without changing their volume or salinity significantly.

To evaluate rates of carbon fixation versus salinity, experiments were conducted using 20 ml SIMCO suspensions of each salinity as described above for temperature experiments except as follows. $NaH^{14}CO_3$ (ICN) was added to each vial to yield 0.36–0.45 µCi ml^{-1} final concentration and the sample incubated for 2–2.4 h at −1.9±0.1 °C and 50 µ Einsteins m^{-2} s^{-1} in a circulating glycol bath. After incubation, 18.5 ml subsamples were removed and filtered through GF/C filters (Whatman) to determine rate of carbon fixation as described above.

Experiments to determine rates of thymidine and uridine incorporation versus salinity were conducted in parallel with the carbon fixation experiments. [Methyl-^{3}H]-thymidine (ICN) (sp act 50–88 Ci/mmole) or [5,6-^{3}H]-uridine (ICN) (sp act 34–47 Ci/mmole) were injected into scintillation vials containing 20 ml of sample to yield a final concentration of 60 nM and samples incubated at −1.9±0.1 °C and 50 µEinsteins m^{-2} s^{-1} for 21–48 h in the circulating glycol bath. The rate of ^{3}H-uridine incorporation by SIMCO is linear for 34 h at −1.9 °C and 30‰ (S.T. Kottmeier and C. W. Sullivan, unpublished observation). After incubation, 18 ml subsamples were removed, filtered through 0.2 µm pore size filters, and TCA insoluble material radioassayed to determine rate of incorporation as described above.

Brine Collection

Brine was collected for use in salinity experiments as follows. A mobile drill was used to drill a 1 m dia hole, 1 m deep in approximately 1.75 m thick annual sea ice north of Hut Point (Fig. 1). The hole was carefully cleared of ice chips and snow by hand, and a 1.2 m×1.2 m piece of 1.3 cm thick plywood placed over the opening. Brine was allowed to drain from chambers and channels in the congelation ice for 24 h and then collected by dipping sterile, 1 l polycarbonate flasks (Nalgene) into the pool that formed at the bottom of the hole. Brine was filtered through a 0.2 µm pore size filter and stored in the dark at −1.9 °C until use in salinity experiments. Salinity of the brine, collected at ambient temperatures of −9.2 °C, was 113‰ as determined by refractometer (Bausch and Lomb).

Determination of Chlorophyll a

Samples of ice meltwater were filtered through 1.0 µm pore size (Nuclepore) and GF/C (Whatman) filters depending upon the experiment; filters were frozen at −20 °C until extraction. Although GF/C filters are routinely used to determine chlorophyll *a* content of seawater, 1.0 µm pore size Nuclepore filters have been shown to retain 100% of the total chlorophyll *a* in SIMCO (Palmisano et al. 1985a). Filters were extracted in 90% acetone and analyzed fluorometrically following the method of Strickland and Parsons (1972).

Calculation of Q_{10}

Q_{10} values were calculated from microalgal assimilation numbers according to the following modification of the van Hoff't equation:

$$\log Q_{10} = \left(\frac{10}{t_1 - t_2}\right) \log \left(\frac{k_1}{k_2}\right)$$

where t_1 = higher temperature in °C, t_2 = lower temperature in °C, k_1 = mg C mg Chl a^{-1} h^{-1} at higher temperature, and k_2 = mg C mg Chl a^{-1} h^{-1} at the lower temperature.

Results

Vertical profiles of temperature in sea ice exhibited considerable variation depending on snow cover and time of

year. In early October, temperature was −18 °C in air 25 cm above the surface of congelation ice, −24 °C at the surface of congelation ice, and −1.9 °C at the bottom of the congelation ice (Fig. 2A). Beneath the congelation ice, the temperature was −1.9 °C at the interface of the congelation/platelet ice, in platelet ice, and in seawater beneath the sea ice. Temperatures in sea ice covered with 1 m of snow were consistently warmer than those in snow-free sea ice, demonstrating the insulating effects of snow cover (Fig. 2A, closed circles). Two months later in mid-December, there was no apparent temperature gradient as air, ice, and seawater temperatures were isothermal near −1.9 °C (Fig. 2B). Underlying seawater temperatures were isothermal down to 19 m and gradually increased from −1.91 °C in October to −1.76 °C in mid-December (Kottmeier et al. 1985).

Since the majority of SIMCO biomass in McMurdo Sound congelation ice is found in the bottom 20 cm of ice (Palmisano and Sullivan 1983; Sullivan and Palmisano 1984), significant growth and metabolism of SIMCO occur at temperatures close to −1.9 °C during the spring and summer. These data measured in situ agree with the profile of temperature estimated for congelation ice by Grossi and Sullivan (1985), who suggested a gradient of less than 2 °C over the bottom 20 cm of ice. We used the temperature from our profiles to estimate the salinity of brine chambers in the bottom 5 cm of ice from the phase diagram of Pounder (1965) for a binary system consisting of NaCl and H_2O. The bottom 5 cm layer of congelation ice with a temperature near −1.9 °C would contain brine ca. 35‰, which is close to 34‰, the average salinity of surface seawater in McMurdo Sound (Littlepage 1965).

Rates of carbon fixation versus temperature for seven experiments performed on SIMCO from several sites are shown in Fig. 3A (as assimilation numbers) and Fig. 3B (as percent of maximum carbon fixation). Carbon fixa-

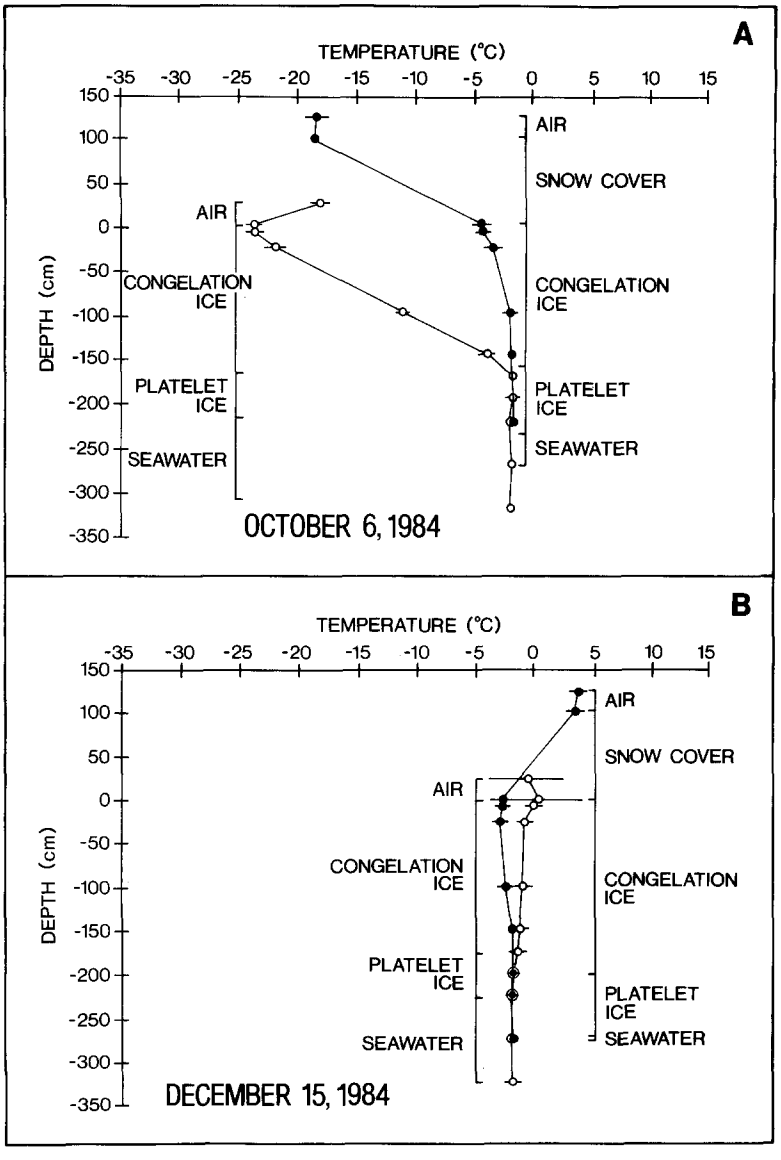

Fig. 2. Seasonal changes of temperature in the air, at the ice surface, in sea ice (congelation and platelet), and in underlying seawater at Cape Armitage for **(A)** Oct. 6, 1984 and **(B)** December 15, 1984, determined from copper constantan thermocouples frozen into the congelation ice. Legend: ● = 1 m snow-covered and ○ = snow-free sea ice of 1.6 to 2.0 m thickness; *horizontal bars* represent the range of duplicate thermocouples

tion increased several-fold from −1.9 °C up to a maximum temperature ranging from 8° to 14 °C. This was followed by a marked decline in carbon fixation from 14° to 30 °C, with rates from 20° to 30 °C less than those at −1.9 °C. Maxima for carbon fixation thus correspond to temperatures 9° to 16 °C above the in situ temperature of −1.9 °C found at the bottom of congelation ice.

In Fig. 4 the temperature dependence of assimilation numbers from Fig. 3A are expressed in an Arrhenius plot. Assimilation numbers increased at a diminishing rate with rising temperature up to 8° to 14 °C, then declined at higher temperatures. Q_{10} values, based on assimilation numbers, also declined with rising temperature, reflecting the declining slopes of the carbon fixation versus temperature relationship (Table 1). Our Q_{10}'s for SIMCO fell below 1.0 at temperatures above 8 °C and differed from Q_{10}'s we calculated from assimilation numbers reported recently for Antarctic phytoplankton by Tilzer and Dubinsky (1987), which fell below 1.0 from 2° to 8 °C.

Figure 5 illustrates the temperature dependence of incorporation of thymidine by SIMCO. Similar to carbon fixation, incorporation of thymidine increased several-fold at temperatures above ambient −1.9 °C. Maximum

Table 1. Comparison of Q_{10} values, calculated from assimilation numbers, for Antarctic phytoplankton and sea ice microalgae. ND = no data

Range of temp. (°C)	Phytoplankton (Tilzer et al. 1986; Tilzer and Dubinsky 1987)	Sea ice microalgae	
		Congelation Ice (this study)	Congelation (C) and Platelet (P) Ice (Palmisano et al. 1987b)
−1.9 to 0	1.1 to 8.6	2 to 4	6 (C) to
0 to 2	1.1 to 4.8	2 to 5	28 (P)
2 to 8	0.7 to 1.6	1 to 5	1 (P) to 3 (C)
8 to 14	ND	<1 to 1	

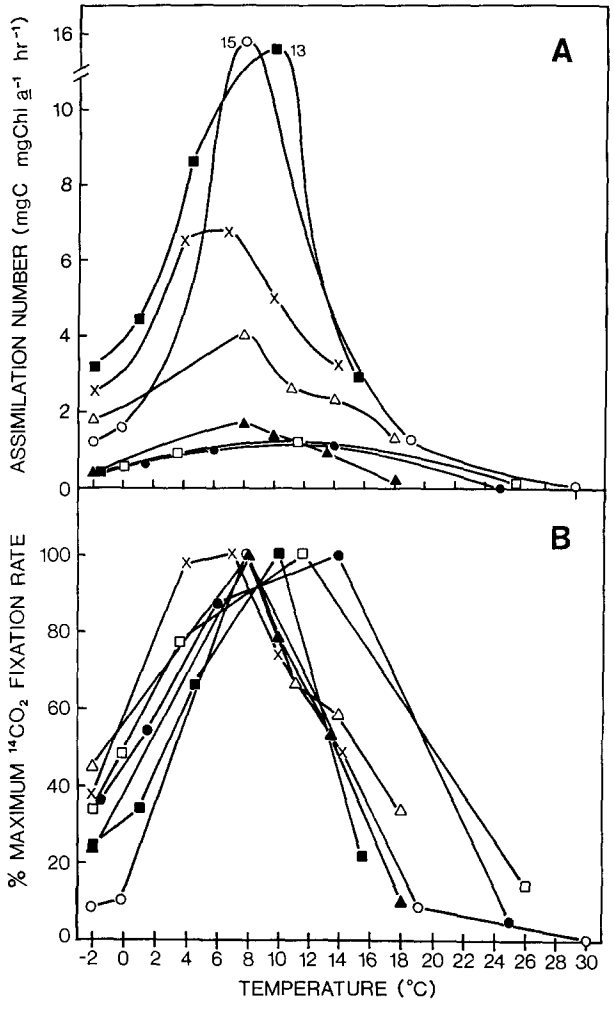

Fig. 3. Temperature dependence of carbon fixation by SIMCO expressed as (**A**) assimilation numbers and (**B**) percent of maximum carbon fixed. Legend: SIMCO obtained from congelation ice sampled from the following locations in McMurdo Sound, ○ = Hut Pt. (HP) Nov. 16, 1983; ● = edge of fast ice (IE) Nov. 18, 1983; □ = HP Nov. 30, 1983; ■ = IE Dec. 9, 1983; △ = Cape Armitage (CA) Dec. 27, 1983; ▲ = Dunlop Island (DI) Dec. 29, 1983; and × = DI Jan. 5, 1984

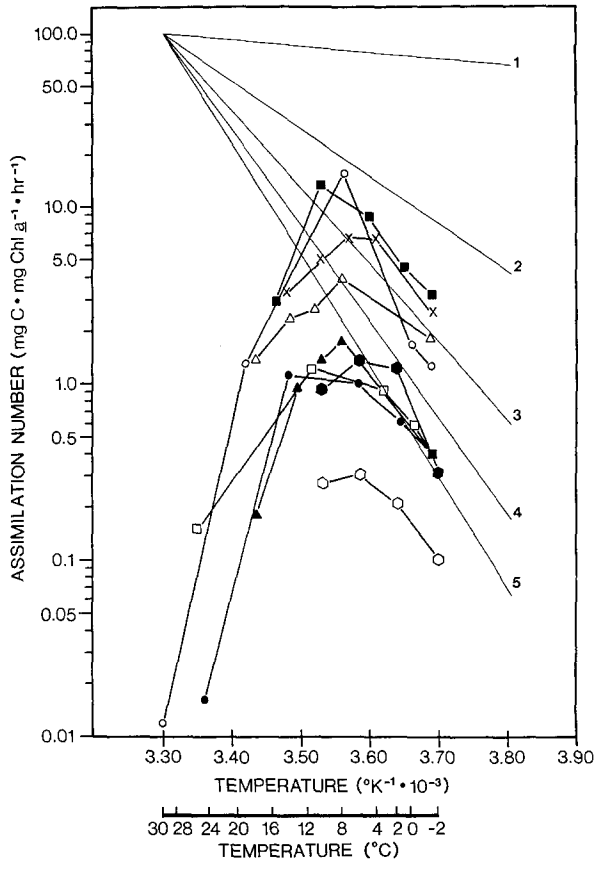

Fig. 4. Temperature dependence of assimilation numbers expressed as Arrhenius plots. Assimilation numbers are plotted logarithmically versus the reciprocal of absolute temperature. Numbered lines correspond to slopes of temperature quotients (Q_{10}s) from *1 to 5*. Legend as for Fig. 3 except ⬡ = congelation ice from HP Oct. 31, 1984 and ⬢ = platelet ice from CA Nov. 1, 1984; data from Table 2, Palmisano et al. (1987b)

incorporation of thymidine occurred however at lower temperatures (4–7 °C) than those found for carbon fixation.

The temperature dependence of glutamate uptake is shown in Fig. 6. Maximum uptake of glutamate in the light occurred at elevated temperatures (10–14 °C) (Fig. 6A), more similar to carbon fixation than thymidine in-

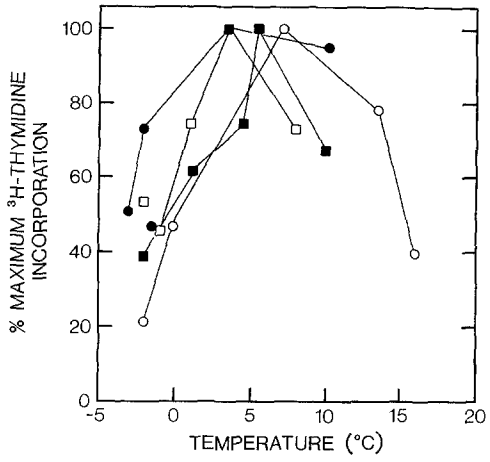

Fig. 5. Temperature dependence of incorporation of thymidine by SIMCO, expressed as percent of maximum incorporation. Legend: SIMCO obtained from congelation ice sampled from the following locations in McMurdo Sound, ○ = HP Dec. 16, 1983; ● = CA Dec. 27, 1983; □ = DI Dec. 29, 1983; and ■ = DI Jan. 5, 1984

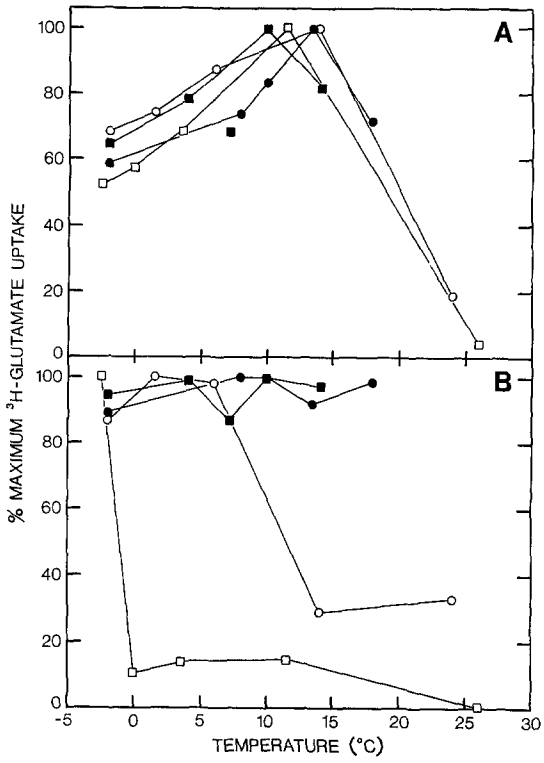

Fig. 6. Temperature dependence of uptake of glutamate by SIMCO (**A**) in the light and (**B**) in the dark, expressed as percent of maximum uptake. Legend: SIMCO obtained from congelation ice sampled from the following locations in McMurdo Sound, ○ = IE Nov. 18, 1983; □ = HP Nov. 29, 1983; ● = DI Dec. 29, 1983; and ■ = DI Jan. 5, 1984

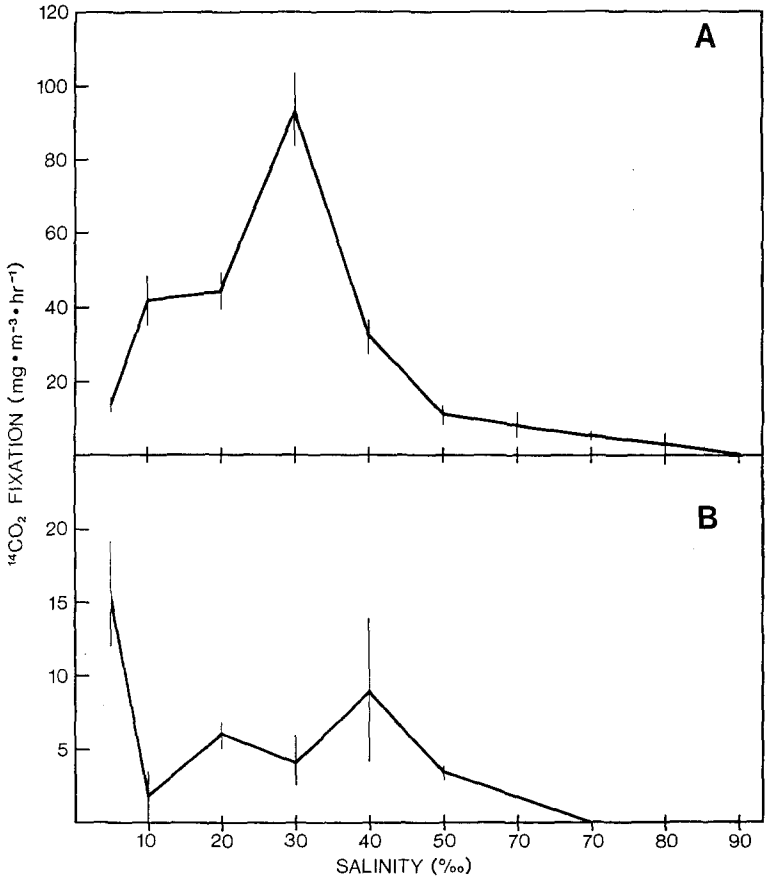

Fig. 7. Salinity dependence of carbon fixation by SIMCO obtained from congelation ice sampled at (**A**) Granite Harbor on Nov. 19, 1984 and (**B**) Hut Point on Dec. 18, 1984. *Vertical bars* represent the range of duplicate assays

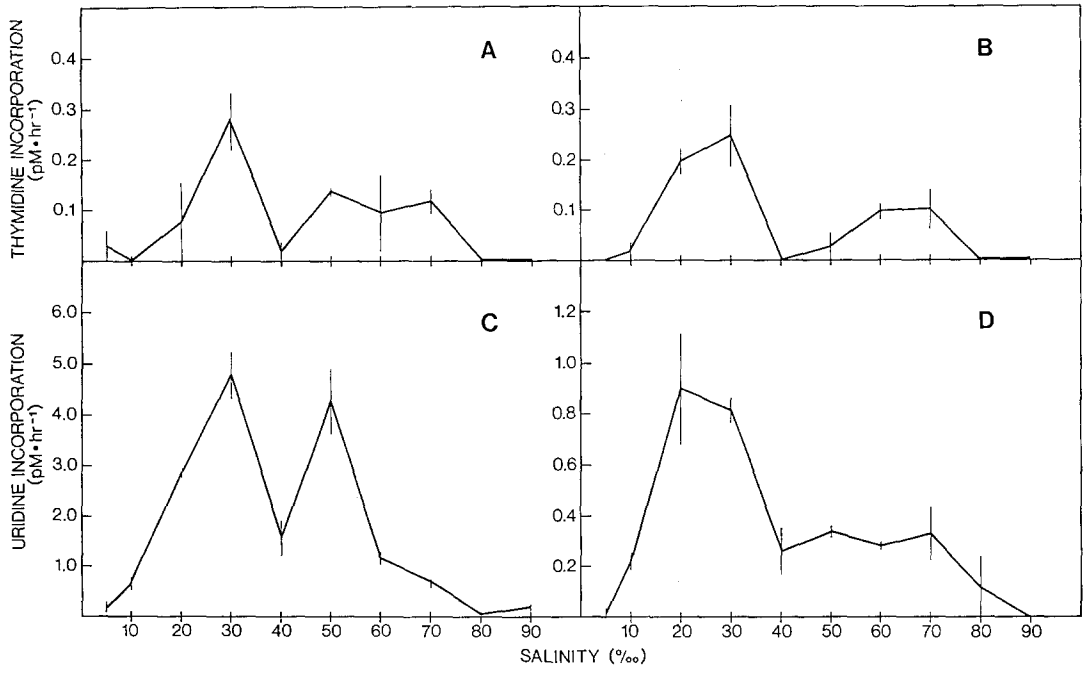

Fig. 8. Salinity dependence of incorporation of thymidine and uridine by SIMCO obtained from congelation ice sampled at **(A, C)** Granite Harbor and **(B, D)** Hut Point on Nov. 19, 1984 and Dec. 18, 1984, respectively. *Vertical bars* represent the range of duplicate assays

corporation. There was, however, only a two-fold increase in uptake of glutamate at the maximum temperature. Uptake of glutamate in the dark showed little difference with increased temperature (Fig. 6B).

Rates of carbon fixation versus salinity for SIMCO from Granite Harbor prior to in situ melting of ice and from Hut Point after onset of melting are shown in Figs. 7A, B, respectively. For SIMCO from Granite Harbor, maximum carbon fixation occurred at 30‰, with a secondary peak from 10‰ to 20‰. A marked decline in carbon fixation occurred at salinities above 30‰. For SIMCO from Hut Point, maximum carbon fixation occurred at 5‰, with a secondary peak at 40‰. There was a marked decline in carbon fixation at salinities above 50‰, with no net carbon fixation observed from 70‰ to 90‰.

Rates of incorporation of thymidine and uridine versus salinity for SIMCO from Granite Harbor and Hut Point are shown in Fig. 8A–D. Maximum incorporation of both substrates occurred at salinities from 20‰ to 30‰, with secondary peaks from 50‰ to 70‰. Much lower incorporation rates were found at lower and higher salinities.

Discussion

The ability of SIMCO to grow luxuriantly within the physicochemical gradients found in sea ice indicates that these microorganisms are well adapted not only to the varying quantity and quality of the light regime (Sullivan et al. 1985; Grossi and Sullivan 1985; Palmisano et al. 1985a,, 1987a; Grossi et al. 1987; Kottmeier et al. 1987; SooHoo et al. 1987), but also to the lowest known oceanic temperatures and wide ranging salinities which characterize this unique environment. Due to the moderate duration of acclimation in our experiments, we are confident that the metabolic rates measured reflect the "stabilized state" of SIMCO, and not the short-term "shock reaction" or long-term "acclimated state" (sensu Li et al. 1984). The metabolic rates observed also reflect a microbial community response to variations in temperature and salinity (sensu Williams 1973). Distribution of microalgal and bacterial species in sea ice is due to their growth in situ (Grossi and Sullivan 1984, 1985; Grossi et al. 1984; Kottmeier et al. 1987) and to their accumulation in sea ice by physical processes of ice accretion (Bunt 1968; Ackley et al. 1979; Garrison et al. 1983; Grossi and Sullivan 1985). The results of the present study, coupled with our previous measurements of primary production and bacterial production in sea ice (Kottmeier et al. 1984, 1985, 1987; Kottmeier and Sullivan 1987; Grossi et al. 1987), indicate that these microorganisms are well adapted for growth within various microhabitats of sea ice and in seawater when released from melting ice.

Temperature

Substantial autotrophic (fixation of carbon) and heterotrophic (incorporation of thymidine and uptake of glutamate) metabolism in SIMCO occurs at temperatures close to −1.9 °C found in situ at the ice-seawater interface. However, maximum metabolic rates occur at tem-

peratures considerably above −1.9 °C but below 15 °C. These results confirm our earlier observations that psychrophilic bacteria inhabit congelation ice (Kobori et al. 1984a, b) and the observations of others that psychrophiles represent a significant proportion of the bacterial assemblages in Antarctic waters (Christian and Wiebe 1974; Wiebe and Hendricks 1974; Morita 1975; Morita et al. 1977). The results of the present study indicate that most, if not all, species of microalgae comprising SIMCO of McMurdo Sound are psychrophiles as well. Our results for SIMCO, although showing higher metabolic rates, are consistent with the general metabolic response to temperature reported for Antarctic microplankton (Holm-Hansen et al. 1977; Baross and Morita 1978; Olson 1980; Hodson et al. 1981; Neori and Holm-Hansen 1982; Jacques 1983), which is expected since SIMCO are derived from some fraction of the microplankton (Bunt 1968; Ackley et al. 1979; Garrison et al. 1983; Grossi and Sullivan 1985).

Enhanced metabolic activity by SIMCO up to a maximum temperature not greater than 15 °C is possibly due to the energetic cost of enzyme production and thermodynamics of enzyme catalyzed reactions. Production of high concentrations of enzymes at low temperatures to yield reaction rates comparable to higher temperatures may be energetically very costly for an organism (Herbert and Bhakoo 1979; Berry and Bjorkman 1980; Platt et al. 1982; Li et al. 1984). As a result, temperature-dependent responses are exhibited for enzyme catalyzed reactions up to a maximum temperature, such as those described recently for light-saturated and light-limited photosynthesis by Antarctic phytoplankton (Jacques 1983; Tilzer et al. 1985, 1986) and sea ice microalgae (Palmisano et al. 1987b). At temperatures greater than maximum, however, other processes may occur in a cell leading to declining reaction rate. These processes have been termed rate effects and weak-bond, structural effects, and may include cell structural changes, domination of different reactions, inactivation of enzymes, denaturation of proteins, and changes in membrane fluidity which influence membrane function such as permeability, and ion regulation (Stanley and Morita 1968; Hochachka and Somero 1973; Inniss and Ingraham 1978; Li 1980, 1985; Jones and Morita 1985).

The metabolic responses of SIMCO to variation in temperature, are probably linked to an overall strategy of microbial cell growth and survival, such that the microorganisms are adapted for growth within the range of temperatures normally encountered in situ. Few microorganisms exhibit maximum rates of growth at the temperature of their habitat, whether they live at the lower limits (Morita 1975) or upper limits (Brock et al. 1984) of temperature for life. In the present study, microalgal growth rates (μ) were calculated according to Eq. (2) of Eppley (1972):

$$\mu = \frac{1}{t} \log_2 \left(\frac{(C_o + \Delta C)}{C_o} \right),$$

where C_o = microalgal carbon at the start ratio of the incubation period and was derived from Chl *a* by a C:Chl *a* of 38 (Sullivan et al. 1985), ΔC = increase in microalgal carbon during incubation, and t = fraction of light day. Results were compared in an Arrhenius plot to curves of maximum growth proposed by Eppley (1972) and Goldman and Carpenter (1974) (Fig. 9). At temperatures below 15 °C, growth rates were consistently higher than predicted by the Goldman and Carpenter (1974) Arrhenius model and in over half of the experiments higher than predicted by Eppley's (1972) empirical equation. From direct cell counts of accumulating microalgae in snow-free congelation ice, Grossi and Sullivan (1984) estimated in situ growth rates as high as 0.3 day^{-1}; these are also higher than predicted by the Goldman and Carpenter (1974) Arrhenius model. These results suggest that microalgae of SIMCO are adapted for more rapid growth than predicted by the empirical relationships of Eppley (1972) and Goldman and Carpenter (1974). Alternatively, these empirical relationships may be inaccurate at low temperatures due to a paucity of low temperature data at the time of their studies.

In either case, microalgae of SIMCO seem well adapted for growth at low temperatures, although they are not maximally active at the temperatures found in sea ice. Our results differ from those reported for Antarctic phytoplankton, which do not exhibit higher growth rates than predicted by either model of growth rate versus temperature (Neori and Holm-Hansen 1982; Jacques 1983;

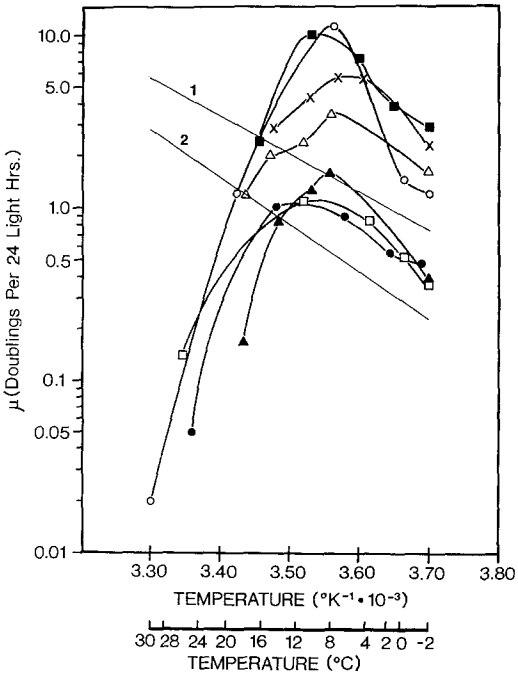

Fig. 9. Temperature dependence of specific growth rates of microalgae in SIMCO, calculated from Eq. (2) of Eppley (1972), compared to relationships predicted by Eppley (1972) (*line 1* $\mu = 0.851\ (1.066)^T$) and Goldman and Carpenter (1974) (*line 2* $\mu = (5.35 \times 10^9)\ e^{-6472/T\ °K}$) derived from empirical data. See text for details. Legend as for Figs. 3 and 4

Sakshaug and Holm-Hansen 1986). Recent work, however, suggests that potential growth rates of Antarctic phytoplankton are not severely affected by prevailing low temperatures of the Southern Ocean under adequate irradiance during long summer days (Tilzer and Dubinsky 1987).

Acquisition of a large and coherent data set concerning SIMCO metabolism versus temperature provided us with an opportunity to test the hypothesis concerning differential growth of phytoplankton and bacterioplankton at very low temperatures proposed recently by Pomeroy and Deibel (1986). They suggested that the rate of phytoplankton photosynthesis declines more slowly at lower temperatures than bacterial metabolism and growth, leading to an uncoupling of primary production and bacterial production in cold waters. Their hypothesis was formulated largely from results of independent investigators reported in the literature. They compared the growth of clonal cultures of individual Antarctic psychrophilic bacteria in the laboratory (Christian and Wiebe 1974; Morita 1975) to field measurements of primary production of phytoplankton assemblages from coastal water off Newfoundland. Several potential problems exist in this type of comparison. Bacterioplankton and phytoplankton may exhibit different rates of growth due not only to temperature but also to species composition, availability of nutrients, and phase of growth. Such problems can make interpretation of cause and effect very difficult, especially when laboratory data are compared with environmental data.

We tested the hypothesis of Pomeroy and Deibel (1986) directly using rates of fixation of $^{14}CO_2$ by autotrophs and incorporation of ^{3}H-thymidine by heterotrophs to estimate growth rates in similar assemblages of SIMCO derived from the bottom of congelation ice in McMurdo Sound. Rates of $^{14}CO_2$ fixation were used to estimate autotrophic growth by microalgae of SIMCO. Uptake of ^{3}H-glutamate represents potentially heterotrophic metabolism of bacterial, microalgae, and possibly protozoa. Bacteria and microalgae of SIMCO are capable of utilizing reduced organic substrates such as amino acids (Palmisano et al. 1985a; Sullivan et al. 1985), but only bacteria have been shown to incorporate ^{3}H-thymidine at the nanomolar concentrations used (Sullivan et al. 1985). Therefore, rates of incorporation of ^{3}H-thymidine were used to estimate heterotrophic growth by bacteria of SIMCO. In addition, nutrient concentrations were high in the suspensions of SIMCO used in our temperature experiments, ranging from 0.48 to 2.2 µmol for PO_4^{-3}, 34 to 49 µmol for SiO_4, and 10 to 33 µmol for NO_3^- (S. T. Kottmeier and C. W. Sullivan, unpublished observation) and generally not considered to be limiting to microalgal growth in the bottom ice habitat (Bunt and Lee 1970; Grossi and Sullivan 1985). Last, all of our SIMCO suspensions represented microorganisms originating from microalgal blooms at the bottom of congelation ice during austral spring and summer.

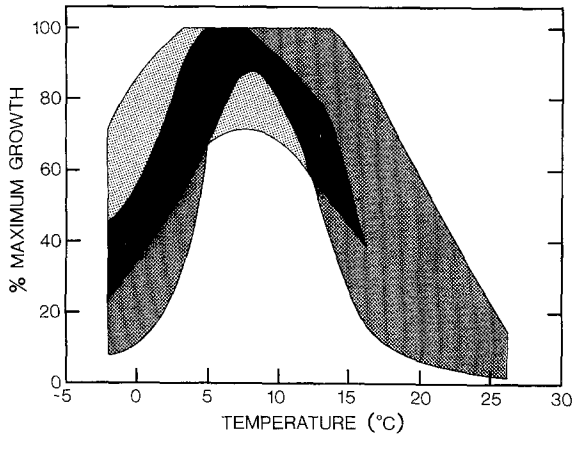

Fig. 10. Comparison of relative growth rates of microalgae (autotrophs) and bacteria (heterotrophs) in SIMCO as a function of temperature. *Stipled areas* represent "envelopes" which describe the relative growth rate versus temperature relationships for autotrophs (*dark stipling*) and heterotrophs (*light stipling*). *Darkened area* represents region of overlap. Growth rate data is based on rates of fixation of $^{14}CO_2$ (autotrophs) and incorporation of ^{3}H-thymidine (heterotrophs) derived from data presented in Figs. 3B and 5, respectively

If we assume that the rates of fixation of $^{14}CO_2$ and incorporation of ^{3}H-thymidine reflect rates of autotrophic and heterotrophic growth respectively in SIMCO, then the range of growth rates found in our experiments can be defined by envelopes as shown in Fig. 10. These envelopes show similar response of autotrophs and heterotrophs to low temperature; the maxima for growth of autotrophs and heterotrophs overlap from 4° to 7°C. This suggests that autotrophs and heterotrophs of SIMCO from the same environment exhibit similar growth responses at low temperatures. Primary production and bacterial production are therefore not uncoupled in SIMCO due to differential growth of microalgae and bacteria at low temperatures. This evidence supports our earlier observation that after a short lag period the rate of bacterial production parallels the rate of primary production during austral spring and summer in annual sea ice of McMurdo Sound (Kottmeier et al. 1987).

Our results suggest therefore that the conclusions of Pomeroy and Deibel (1986) should not be generalized to all polar ocean microorganisms, particularly those comprising SIMCO. Contrary to their hypothesis, heterotrophs of SIMCO may be even better adapted for growth at low temperatures than autotrophs of SIMCO, since heterotrophs exhibited maximum incorporation of ^{3}H-thymidine at a lower range of temperature than autotrophs did for fixation of $^{14}CO_2$. We have proposed that the timing and amount of bacterial production in sea ice are dependent upon the phase of growth of microalgae, quantity and quality of compounds in the DOM pool available for bacterial growth, and rates of bactivory and herbivory (Kottmeier et al. 1987). One or more of these factors may better explain apparent uncoupling of primary production and bacterial production during transient periods of low bacterial growth in polar oceans than low temperatures per se.

Salinity

Autotrophs and heterotrophs of SIMCO exhibited two quite different patterns of metabolic rates in response to variation in salinity, depending upon the recent salinity of the congelation ice from which the microorganisms were collected. Neither response was due to nutrient limitation in suspensions of melted ice as others have hypothesized recently (Vargo et al. 1986), since suspensions of SIMCO at each salinity were amended with nutrients and vitamins at concentrations found in F/2 medium (Guillard and Ryther 1962).

Autotrophs of SIMCO are capable of substantial metabolism at salinities which characterized the ice from which they were collected. Before onset of melting of congelation ice in McMurdo Sound (as early as mid-November through December), maximum rates of carbon fixation occurred close to 34‰, the average salinity of surface seawater in McMurdo Sound (Littlepage 1965). Following onset of melting of congelation ice, maximum rates of carbon fixation by SIMCO occurred at lower salinities, close to those found by Bunt (1964) for platelet ice microalgae of McMurdo Sound collected in late December. Autotrophs of SIMCO may be "preconditioned" by low salinity water infiltrating the ice during melting and fix more carbon at lower salinities. Alternatively, some fraction of cells exposed to hypotonic conditions during melting of the ice may be damaged or killed (Palmisano et al. 1985b, 1987b; Bates and Cota 1986; Garrison and Buck 1986) and only eurytolerant organisms survive and remain metabolically active. The lack of net carbon fixation by SIMCO at high salinities may partially explain why Grant and Horner (1976) found little growth by Arctic ice diatoms at salinities of 60‰ and higher. Further, our results support the conclusion that high salinity brine may be one factor that limits the vertical distribution of microalgae within congelation ice (Meguro et al. 1967; Grant and Horner 1976; Palmisano et al. 1987b).

Heterotrophs of SIMCO exhibited less variation in their metabolic response to salinity than autotrophs of SIMCO, since maximum rates of incorporation of thymidine and uridine occurred from 20‰ to 30‰ before and after onset of ice melt. In addition, heterotrophs may be better adapted for growth at higher salinities than autotrophs of SIMCO as significant incorporation of thymidine and uridine was observed at salinities from 50‰ to 70‰. It is somewhat surprising then that 50% of bacterial number and 90% of bacterial biomass are found in only the bottom 20 cm of congelation ice (Sullivan and Palmisano 1984) and not in higher salinities of brine chambers farther away from the ice-water interface. We propose that other factors, such as very low temperature and scarcity of microalgae to supply exuded carbon for bacterial metabolism and growth, determine bacterial distribution in upper regions of congelation ice.

Adaptations which permit substantial metabolism at low temperatures and variable salinities account partially for the distribution and growth of microalgal and bacterial species within SIMCO. As a result of these adaptations and other factors, SIMCO accumulate a significant biomass in sea ice and provide a rich source of carbon for grazing organisms in food webs associated with sea ice. SIMCO also maintain a potential to increase their metabolic rate in response to warmer temperatures and lower salinities which occur in the water column as the ice melts. When released into seawater from melting ice, inocula of these actively growing microorganisms may contribute to microbial blooms of marginal ice edge zones, which in turn support cryopelagic food webs in these widespread dynamic regions of polar oceans.

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