25 Temperature Dependence of Photosynthetic Recovery from Solar Damage in Antarctic Phytoplankton

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ABSTRACT

We investigated the temperature dependence of photosynthesis by phytoplankton from two depths in ice-covered Lake Vanda (Dry Valleys) and from four locations (small ponds) on the undulating ice of the McMurdo Ice Shelf, near Bratina Island. Our aim was to evaluate the influence of temperature on solar damage and recovery processes, and specifically to address the hypothesis that inhibition of the photosynthetic apparatus is unaffected by temperature while biosynthetic repair is temperature dependent. Although this hypothesis has been considered in laboratory cultures, little information is available for natural planktonic communities. Our results showed that the optimum temperature for maximum photosynthesis (P_{max}) was up to 10°C above ambient temperature at the time of sampling. Damage induced by exposure to high solar irradiance and subsequent recovery of photosynthesis under conditions of low irradiance were examined with the use of the protein synthesis inhibitor streptomycin (STR). The kinetics of inhibition were similar in both +STR and -STR treatments across the temperature range, suggesting that repair mechanisms did not operate efficiently during the damage phase. Recovery of photosynthesis took place after transfer to low irradiance and was strongly inhibited in the presence of STR. However, recovery in the -STR treatments was delayed by up to 80 min. This recovery was generally greatest at temperatures corresponding to the optimal temperature for P_{max}. Our results indicate that temperature plays an important role in the regulation of photosynthesis and the balance of damage/repair processes in these Antarctic phytoplankton assemblages.

Key Words: Algae, photoinhibition, photosynthesis, polar, phytoplankton, solar radiation.

INTRODUCTION

Although light is essential for photosynthesis, high levels of visible (photosynthetically available irradiance, PAR; 400-700 nm) and ultraviolet irradiance (UV; 280-400 nm) can damage components of the photosynthetic apparatus and lead to photoinhibition (Barber and Andersson 1992; Vassiliev *et al.* 1994). For example, several studies have shown that the D1 protein in the photosystem II complex is rendered non-functional by excess excitation energy (Krause 1994; Baroli and Melis 1996). This damage, however, can be repaired by *de novo* synthesis of D1, its re-insertion into the thylakoid membrane, and the subsequent reassembly of PS II (Andersson *et al.* 1992). The photoinhibition effect therefore reflects the net balance between photochemical damage and biosynthetic repair (e.g., Lesser *et al.* 1994).

Temperature plays a role in the recovery of cells from photoinhibition because of the implication of enzymes in the repair process. Photochemical damage, on the other hand, is a function of radiation flux rather than temperature (Greer *et al.* 1986; Greer 1988; Wünschmann and Brand 1992). Thus, temperature could regulate the damage-repair balance, with greater net damage in cold environments. This hypothesis has been supported for UV inhibition of growth, but not photosynthesis, by a filamentous Antarctic cyanobacterium in culture (Roos and Vincent 1998). Combined UV and PAR inhibition of photosynthesis in a natural phytoplankton community from a lake in northern Quebec, Canada has also been shown to be more severe at lower temperatures (Rae and Vincent 1998b), but little is known about Antarctic phytoplankton in this regard.

One approach towards understanding the effects of temperature on high irradiance damage and subsequent recovery is by way of antibiotics, such as streptomycin, which inhibit protein synthesis, and which thereby inactivate the normal repair processes (e.g., Wünschmann and Brand 1992; Lesser *et al.* 1994). In this way, it is possible to measure gross as well as net photoinhibition, and consequently obtain an indication of the extent of biological repair to damaged components of the cellular machinery. To date, the focus of these studies has been on higher plants and single species laboratory cultures, and little is known about the damage/repair balance in natural algal communities.

During the austral summer, phytoplankton in lakes and ponds of Antarctica are exposed simultaneously to low temperatures and continuous irradiance, and may therefore be particularly susceptible to photoinhibition. In the present study we investigated the effect of temperature on photosynthesis-irradiance properties, and the role of temperature in the damage/repair balance of natural phytoplankton communities from two depths in Lake Vanda (located in the Wright Valley, adjacent to McMurdo Sound) and from four pond environments on the McMurdo Ice Shelf, close to Bratina Island.

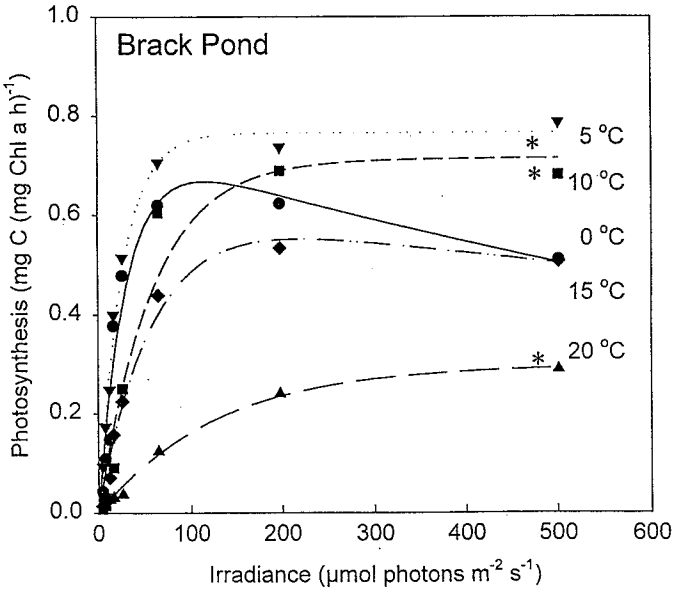

Fig 1.: An illustrative series of photosynthesis-irradiance curves under different temperatures. Data were obtained during 2-4 h incubations of phytoplankton from Brack Pond on the McMurdo Ice Shelf. For those marked with an asterix, the curves were fitted using the Webb *et al.* (1974) equation; all other curves were fitted with the Platt *et al.* (1980) equation.

METHODS

Study sites

Lake Vanda is permanently ice-covered, although ice at the edge melts most summers to form a moat of open water. The lake has a deep chlorophyll maximum (DCM) of close to 1.0 µg l^{-1}, dominated by several species of the cyanobacterium *Phormidium*, and chlorophyll *a* concentrations at other depths as low as 0.05 µg l^{-1} (Vincent and Vincent 1982). The concentration of chromophoric dissolved organic matter (CDOM) in this lake is very low, to the extent that UVB wavelengths have been recorded to depths of 30 m below the 3.5 m ice cover (Vincent *et al.* 1998). Lake Vanda has an inverse temperature profile with warmer temperatures at greater depth, due to solar heating (see Spigel and Priscu 1998). Ambient temperatures in the photic zone vary from 4.9 °C under the ice to 17.6°C in the DCM.

The undulating ice of the McMurdo Ice Shelf has a different type of aquatic environment with ponds of varying size, depth and salinity that are mostly ice-free during summer (Howard-Williams *et al.* 1990). Many of these ponds have thick microbial mat communities, consisting of filamentous cyanobacteria and diatoms (Howard-Williams *et al.* 1990; Hawes *et al.* 1993), but also contain phytoplankton. A recent study of 20 ponds in this area recorded planktonic Chl *a* concentrations ranging from 1.1 to 78.2 µg l^{-1} (James *et al.* 1995). This study enumerated various cyanobacteria and flagellated algae, often dominated by *Ochromonas* and *Chroomonas*, among the plankton, as well as several ciliated protozoans (James *et al.* 1995). Ambient pond temperatures during midsummer are highly variable, with a range from 0.5 °C in freshwater oligotrophic ponds with ice cover to ca. 8 °C in the brackish non-ice covered ponds (Hawes *et al.* 1993).

Water collection

Experiments at Lake Vanda took place from January 8-13, 1996. A hole was drilled with an auger through the 3.5 m thick ice cap over the deepest part of the lake (ca. 75 m). Water samples were obtained from discrete depths (5 m and in the DCM at 63 m) with a Niskin water sampler, and experiments were started immediately upon collection of the water. All sample manipulations were conducted within a tent on the lake ice to eliminate exposure of organisms to sunlight prior to and following experimentation.

On the undulating ice near Bratina Island, four ponds were sampled for experiments between January 20-26, 1996: Brack, Fresh, Orange and Tide Ponds. Water was collected from the edge of these ponds, at a depth of 30-40 cm with the use of a 2 m pole with a pre-rinsed Nalgene bottle attached to the end. Pond water was carried in a dark container to the laboratory at Bratina Island where sample manipulations took place inside a hut, within 1 hour of collection.

Photosynthesis-irradiance curves

Photosynthesis-irradiance (P-E) curves were determined with the use of incubation boxes that gave a gradient of 1.0 to 109.2 % of incident irradiance (details in Rae and Vincent 1998a). Aliquots of water sampled from the sites were dispensed into pre-rinsed 20 ml borosilicate glass scintillation vials and were inoculated with ^{14}C-HCO_3^- to a final concentration of 0.5 µCi ml^{-1}. Five controlled-temperature water baths were maintained over the range 0 to 20 °C, at 5 °C intervals. Incubations under ambient solar radiation were conducted for 2 to 4 h. Replicate ^{14}C incubations were also held in the dark for each temperature and dark values were subsequently subtracted from the light values. The samples were filtered through GF75 glass fibre filters (equivalent to GF/F) and the filters stored cold (on ice) until transport to a freezer and subsequent laboratory analysis in New Zealand. The filters were left for 20 h after adding 0.1 ml of 1N HCl to remove unincorporated ^{14}C-HCO_3^-. Seven ml of Wallac Optiphase Hisafe III scintillation cocktail was added and the radioactivity of the samples was then measured with a Wallac LKB 1217 Rackbeta liquid scintillation counter.

	°C	α	β	P_s	P_{max}
Vanda	0	0.18 (0.09)	0.005 (0.004)	0.67 (0.19)	0.60
5 m	5	0.07 (0.01)	0.0005 (0.0009)	0.84 (0.13)	0.80
	10	0.22 (0.05)	0.001 (0.001)	1.21 (0.16)	1.19
	15	0.05 (0.01)	0.003 (0.003)	1.51 (0.45)	1.25
	20	0.03 (0.01)	0.001 (0.001)	0.76 (0.18)	0.69
Vanda	0	0.04 (0.11)	--	0.18 (0.02)	0.18 (0.02)
63 m	5	0.26 (0.04)	--	0.32 (0.02)	0.32 (0.02)
	10	0.08 (0.01)	--	0.42 (0.02)	0.42 (0.02)
	15	0.09 (0.01)	--	0.47 (0.04)	0.47 (0.04)
	20	0.15 (0.02)	--	1.17 (0.10)	1.17 (0.10)
Orange	0	0.004 (0.001)	0.00004 (0.00010)	0.15 (0.03)	0.14
Pond	5	0.004 (0.002)	0.0002 (0.0304)	0.25 (3.34)	0.20
	10	0.003 (0.001)	0.0002 (0.0004)	0.25 (0.11)	0.20
	15	0.002 (0.001)	--	0.15 (0.04)	0.15 (0.04)
	20	0.0001 (0.0001)	0.001 (3.8)	0.7 (1816.0)	0.02
Brack	0	0.024 (0.004)	0.0006 (0.0005)	0.75 (0.12)	0.67
Pond	5	0.030 (0.002)	--	0.77 (0.02)	0.77 (0.02)
	10	0.012 (0.003)	--	0.71 (0.07)	0.71 (0.07)
	15	0.010 (0.001)	0.0003 (0.0003)	0.62 (0.10)	0.55
	20	0.0023 (0.0001)	--	0.30 (0.01)	0.30 (0.01)
Fresh	0	0.045 (0.004)	0.002 (0.001)	2.40 (0.25)	1.94
Pond	5	0.033 (0.003)	--	2.13 (0.08)	2.13 (0.08)
	10	0.04 (0.02)	0.0003 (0.0028)	2.65 (1.48)	2.53
	15	0.04 (0.01)	--	3.00 (0.39)	3.00 (0.39)
	20	0.03 (0.01)	--	2.81 (0.37)	2.81 (0.37)
Tide	0	0.12 (0.01)	0.0016 (0.0004)	3.39 (0.14)	3.16
Pond	5	0.09 (0.01)	0.01 (0.01)	6.85 (4.37)	4.37
	10	0.06 (0.01)	0.004 (0.003)	5.59 (1.19)	4.40
	15	0.04 (0.01)	--	4.11 (0.26)	4.11 (0.26)
	20	0.013 (0.002)	--	1.65 (0.13)	1.65 (0.13)

Table 1.: Parameters (±SE) obtained from P-E curves fitted to data points obtained during incubations of planktonic algal communities from Lake Vanda and McMurdo Ice Shelf ponds. α and β:mg C (mg Chl a h)$^{-1}$ (μmol photons m^{-2} s^{-1})$^{-1}$; P_s and P_{max}:mg C (mg Chl a h)$^{-1}$. In the absence of photoinhibition, $P_s = P_{max}$; when photoinhibition occured, P_{max} was calculated (Platt *et al.* 1980), but SE was not determined (see Smith *et al.* 1994).

Phytoplankton chlorophyll *a* (Chl *a*, μg l^{-1}) for Bratina Island samples was measured spectrophotometrically at 665 and 750 nm (Jasco spectrophotometer) after grinding in 90 % acetone, with correction for phaeopigments by acidification. The Lake Vanda Chl *a* samples were analysed by fluorometry with excitation at 440 nm and emission at 680 nm, and phaeopigment correction by acidification. Dissolved inorganic carbon was determined by use of an infra-red gas analyser, after sparging acidified samples with CO_2-free air. At both field sites, measurements of visible irradiance were taken periodically throughout photosynthesis experiments with the use of a LiCor (LI 1000) 2π cosine-corrected PAR sensor.

Damage-repair experiments

Samples were prepared for determination of photosynthetic uptake rates as above, but one half of the samples was inoculated with 250 μg ml^{-1} (final concentration) of streptomycin (STR) in addition to the ^{14}C-HCO_3. Vials were then placed on racks in the controlled temperature water baths (0 to 20 °C at 5 °C intervals) and exposed to incident irradiance (which in some cases, e.g., 63 m Lake Vanda water, was attenuated by neutral density screens in order to prevent severe irreversible damage). During the first 80 min of each experiment, samples were exposed to potentially photoinhibitory irradiance, at which time a neutral density screen was used to reduce the exposure to low (<15 % initial) irradiance levels for the remainder of the 4 h experiment. Experimental irradiance treatments in μmol photons m^{-2} s^{-1} from high to low were as follows: Orange Pond: 800 to 102; Brack Pond: 858 to 90; Lake Vanda 5 m: 576 to 84; Lake Vanda 63 m: 201 to 19. At nine time intervals during the experiment, one vial was removed from each of the treatment conditions (+STR and -STR at each temperature) and filtered through a GF75 glass fibre filter. Time zero and Time final (dark) vials were also filtered. Chl *a* and DIC were determined as described above.

DATA ANALYSIS

Curves for photosynthesis versus irradiance data were fitted using an iterative non-linear regression (SigmaPlot 3.0) with the equation of Platt *et al.* (1980) when photoinhibition was evident, and with the equation of Webb *et al.* (1974) when photosynthetic values saturated without detection of photoinhibition. All photosynthetic rate values were normalised to Chl *a*.

In some experiments, photosynthesis was low and the subtraction of dark values led to negative uptake rates. In these cases, which include all Orange Pond and shallow (5 m) Lake Vanda experiments (see Table 1; Figs. 2 and 4), values were adjusted such that the lowest negative value for each set of experiments was made to equal zero. Therefore, absolute values of photosynthesis can not be evaluated, but relative changes and trends remain interpretable.

RESULTS

Temperature effects on photosynthesis

The photosynthesis-irradiance curves obtained for each of the six sampling sites showed temperature effects on both the initial slope, α and the maximum photosynthetic rate, P_{max}. In general, the photoinhibitory response which is represented by ß, when present, was not severe but temperature effects could not be evaluated due to the large variability both within and between experiments (e.g., Fig. 1; Table 1). Optimum temperature for P_{max} (T_{opt}; taken to be the temperature of the highest experimental P_{max} value) was generally up to 10 °C above the ambient temperature of the environment (Fig. 2a) and was 15 °C for all communities except that from the DCM at 63 m in Lake Vanda. This latter community showed a 140 % increase in photosynthetic rate between 15 and 20 °C, while for all other experiments, P_{max} increased from 0 °C to T_{opt}, and photosynthetic rates at 20 °C were lower than those at all or most other temperatures (Fig. 2a). There was a trend for α to decline with an increase in temperature (Fig. 2b). This trend was least evident in the Lake Vanda samples.

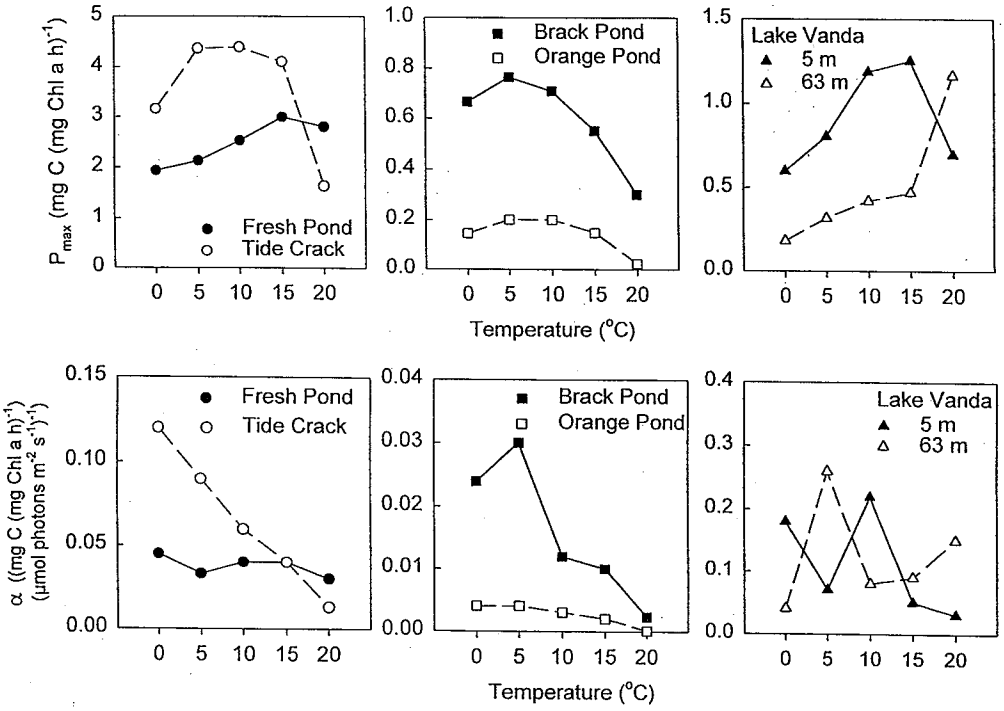

Fig 2.:
Photosynthetic parameters as a function of temperature for phytoplankton sampled from four ponds on the McMurdo Ice Shelf, and from two depths in Lake Vanda, Dry Valleys; a) P_{max}; b) α. Ambient temperatures of the water at the time and depth of sampling were 2.4°C, Tide Pond; 4.5°C, Fresh Pond; 5.4°C, Brack Pond; 7.6°C, Orange Pond; 4.9°C, Lake Vanda, 5m; and 17.6°C, Lake Vanda, 63 m. Data were obtained from 2-4 h incubations.

Photosynthetic recovery from high-irradiance damage

The photosynthetic response during the initial phase of high irradiance was generally one of a rapid decrease to a constant rate (e.g., Fig. 3), except for the Lake Vanda 5 m community which showed a trend of increasing photosynthesis during this period (data not shown). In all four experiments, the response was similar for +STR and -STR treatments and did not vary with temperature.

Following the switch to low irradiance conditions, after 80 min of high irradiance exposure, some -STR treatments immediately showed the expected exponential increase of photosynthetic rates, but in many instances a lag period of 10 to 80 min was observed before photosynthesis in the -STR treatment increased (Table 2). Recovery of photosynthesis during the low irradiance phase did not always occur. In addition, the +STR treatments often showed some increase of photosynthetic rate after the switch to low irradiance, although rates at the end of the experiment (T240 min) were always at or below the -STR rates (Fig. 4).

Despite variability within communities examined, some patterns of recovery were apparent. Photosynthesis by the Lake Vanda 5 m community stabilised immediately following the switch to low irradiance, and after a lag period of 80 min increased by 100-200 % in the -STR treatments at all temperatures except 20 °C (Table 2). The +STR treatments at all temperatures and the -STR treatment at 20 °C showed smaller increases of up to 40 %. The Lake Vanda 63 m community photosynthetic rates remained depressed for both STR treatments following the high to low irradiance switch. The one exception to this was the -STR treatment at 20 °C which began to increase following a lag period of 40 min (Table 2). This increase was low relative to the rate at T80 min, but relative to the rate at T120 min (time of onset of recovery), it was a 45 % increase.

Orange Pond showed some recovery of photosynthetic rates at all temperatures except at 20 °C. The recovery varied in magnitude among temperatures with the greatest differences for -STR at 10 and 15 °C with 365 and 172 % increases in photosynthesis, respectively, during this time (Table 2). The +STR treatments showed small increases (<38 %) at 0 and 15 °C. Photosynthetic response for the Brack Pond community was similar to Orange Pond, but with a greater response, up to 122 %, by +STR treatments at low (0 and 5 °C) temperatures.

In all four experiments, rate constants for the low irradiance period (determined as the slope of the natural log of photosynthesis as a function of time) show that recovery peaked at a temperature corresponding closely to T_{opt} for photosynthesis (Fig. 5).

DISCUSSION

The optimal temperature (T_{opt}) for P_{max} in the communities examined was up to 10 °C above the ambient water temperature for these organisms. This is consistent with the fact that many of these organisms inhabit environments where seasonal temperature changes occur, and therefore a T_{opt} greater than ambient temperature allows a window for adjustment to changes in environmental temperature. This is less true for the thermally stable conditions of the Lake Vanda water column, but indicates that microorganisms in this environment are nonetheless growing at sub-optimal temperatures.

The increase of P_{max} with temperature is consistent with biochemical processes occurring in carbon fixation (Falkowski and Raven 1997) and has been shown in many experimental studies elsewhere in the polar and subpolar regions (e.g., Smith *et al.* 1994; Rae and Vincent 1998a). The large response to temperature by Vanda 63 m algae is likely due to the higher ambient temperature of this environment in comparison to the others studied, but may also be connected to the species composition in this particular community. The DCM of Lake Vanda is composed mainly of filamentous cyanobacteria (Vincent and Vincent 1982) which have been shown to be strongly stimulated by temperature (Tang *et al.* 1997). The planktonic algal community below the ice layer in Lake Vanda (5 m) and those in the ponds of Bratina Island are dominated by flagellated microorganisms (Vincent and Vincent 1982; James *et al.* 1995).

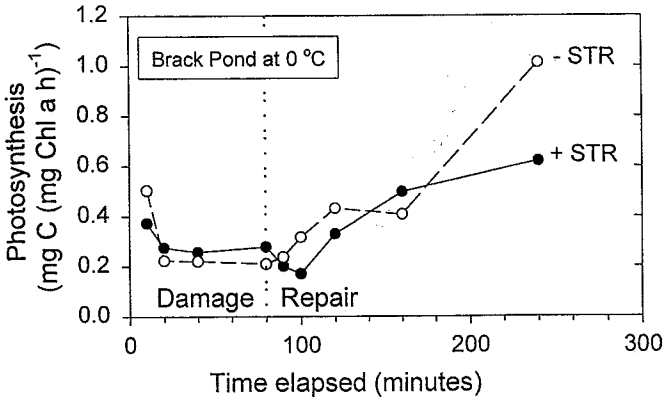

Fig 3.: An illustrative time series for the 4 h incubations of phytoplankton, with and without streptomycin (STR). The curves shown are from Brack Pond incubated at 0°C. The vertical line indicates the time (T80 min) at which irradiance conditions were changed from high (858 µmol photons m^{-2} s^{-1}) to low (90 µmol photons m^{-2} s^{-1}).

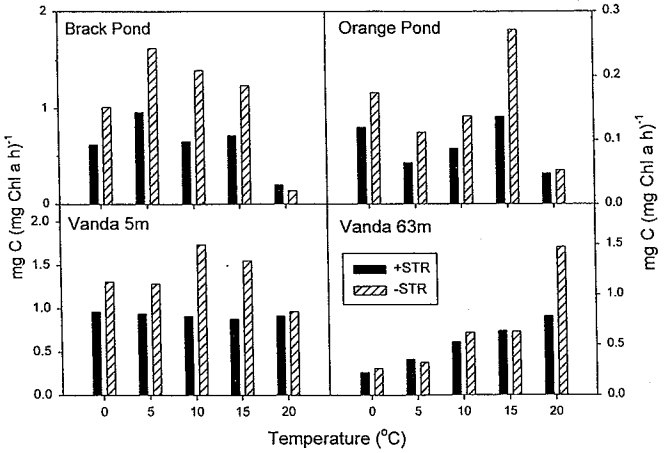

Fig 4.: Photosynthetic rate at the end of each damage-repair experiment (T240 min) for treatments in the presence and absence of streptomycin, at five temperatures.

	Temperature (°C)	Lag-time to onset of recovery in -STR treatment (min)	% change of photosynthesis at T240 relative to T80 min	
			+ STR	- STR
Vanda 5 m	0	80	+34	+109
	5	80	+39	+109
	10	80	+40	+210
	15	80	+23	+119
	20	80	+23	+31
Vanda 63 m	0	--	-33	-36
	5	--	-36	-39
	10	--	-27	-14
	15	--	-49	-51
	20	40	-43	+2
Orange Pond	0	40	+37	+99
	5	20	-67	+2
	10	10	-2	+365
	15	40	+27	+172
	20	--	-20	-34
Brack Pond	0	0	+122	+380
	5	10	+73	+145
	10	10	+5	+158
	15	0	+22	+56
	20	--	-68	-45

Table 2.: Results from four damage/repair experiments, using streptomycin (STR), to show the lag time to onset of recovery in the -STR treatment after a change from high to low radiance, and the % change in photosynthesis from beginning to end of the low irradiance period (i.e. photosynthesis at T240 min relative to that at T80 min). - - no observed recovery.

The decreasing α values with increased temperature cannot be readily explained. The initial slope of the P-E curve, representing photochemical reactions, is generally considered to be independent of temperature, although some components of electron transport have some temperature dependency which could translate into a minor positive temperature response by α (Falkowski and Raven 1997). However, in our Antarctic data set, α consistently decreased with increasing temperature and therefore light harvesting efficiency was lower at high temperature. This might reflect a loss of membrane integrity and function at temperatures above ambient, due to a lipid composition that is optimised for low temperature and is less able to tolerate higher temperatures (Wada *et al.* 1994). At greater temperature, there may also have been an increase of extracellular organic carbon release by the photosynthetic cells (Collins and Boylen 1982; Watanabe 1982), due to more fluid membranes at higher temperatures.

The low, and sometimes lack, of photoinhibition in the algae examined indicates that these planktonic communities can withstand moderately high irradiance on the timescale of a few hours. During the austral summer, microorganisms are exposed to long periods of light and it is therefore probable that the organisms are acclimated to continuous irradiance. However, as evidenced by our damage/repair series of experiments, these organisms can be damaged when exposed to high irradiance, with declines of up to 80 % from initial photosynthetic rates. In this study we did not examine cell responses to visible and ultraviolet radiation separately, but it is probable that both of these components of the solar spectrum contributed to the observed damage.

Temperature did not appear to have an effect on the initial inhibition in our damage/repair experiments. This is contrary to two studies that conducted similar experiments on higher plants and found a temperature-dependence of the initial photoinhibitory damage (Greer *et al.* 1986; Greer 1988), but supports our hypothesis of temperature-independence of initial damage. Temperature affects net photoinhibition in algal cultures through the dependence of repair and recovery processes on temperature (e.g., Wünschmann and Brand 1992; Jensen and Knutsen 1993). Our experiments were performed on natural phytoplankton communities under conditions of ambient irradiance and the variability in our results may have masked any subtle temperature effect on the kinetics of inhibition. However, there is no evidence from our results that repair processes occur simultaneously with damage, as has been suggested previously (Greer *et al.* 1986; Jensen and Knutsen 1993; Sass *et al.* 1997). In our experiments, the initial change in the +STR and -STR treatments was very similar, suggesting that photochemical damage was taking place but that repair mechanisms were not operating in either treatment. Experiments with UV damage have suggested that the protein repair machinery itself is susceptible to damage, since a decreasing extent of recovery was observed with increasingly longer UV exposures (Sass *et al.* 1997). Also, in many instances in the present study, a lag phase was observed between the switch to low irradiance conditions and the onset of recovery. This further indicates that repair mechanisms were not

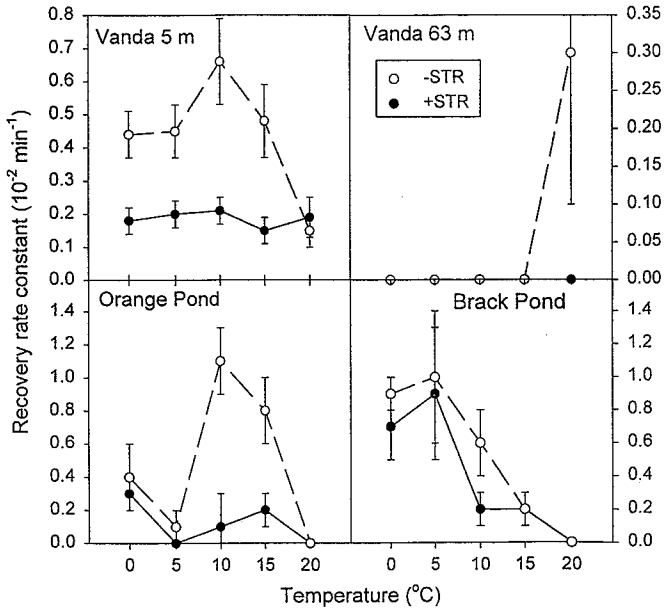

Fig 5.: The effect of temperature on the rate constants for recovery (T80 to T240 min) in four Antarctic lake and pond environments. Error bars are ± SE from the slope of the ln(rate) versus time curve.

operating at the time of high to low irradiance transition, and that up to 80 min time at low irradiance was required before recovery processes got underway to the point that they were detectable by carbon uptake measurements.

When recovery in -STR treatments was observed, it was generally greatest at temperatures close to T_{opt} for P_{max}. This was consistent among the four experiments, and implies that recovery from solar damage is repressed by the low ambient temperatures present in the environments of the communities examined. Similar results have been reported for Southern Ocean phytoplankton, in which negligible rates of recovery were observed over time periods of 0.5-4 hours, (Neale *et al.* 1998a; 1998b), although protein synthesis inhibitors were not used in these experiments to partition damage and recovery. The +STR treatments did at times show some recovery, although it was generally not as substantial as the recovery in the absence of streptomycin. Nonetheless, the +STR recovery suggests that chloroplast protein synthesis by organisms in the community was not completely inhibited by streptomycin and/or certain cells were unaffected by the antibiotic. Since +STR photosynthetic rates were always lower than -STR rates, streptomycin evidently succeeded in stopping or slowing protein synthesis in a portion of the organisms. No other studies have reported a partial inhibition such as this, but also have not examined whole microbial communities, and species-specific responses may prevent a clear-cut effect being evident.

In conclusion, our results imply that phytoplankton in Antarctic lakes and ponds are growing at suboptimal temperatures for both maximum photosynthetic rates and recovery from solar damage. While irradiance levels that are damaging to the photosynthetic apparatus persist, it appears that repair mechanisms do not operate efficiently and are unable to keep pace with damage. Under lower irradiances, repair mechanisms are repressed by the cold ambient temperatures and full recovery may be delayed or even unable to be achieved before the next exposure to photoinhibiting light conditions.

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