Light-Temperature Interactions on the Growth of Antarctic Diatoms

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Summary. The combined effect of various temperatures and light intensities on the growth of seven species of antarctic diatoms in culture has been studied. With the exception of *Chaetoceros deflandrei* whose thermal tolerance is fairly good, these obligatory psychrophils cannot survive in temperatures above 6° to 9°C. Their mean growth rate is relatively low, between 0.24 div d^{-1} for *Corethron criophilum* and 0.63 div d^{-1} for *C. deflandrei*. Regardless of light intensity, growth rate increased with the temperature to reach a maximum between 3° and 5°C. The highest rates were obtained between 115 and 220 μmol m^{-2}s^{-1} with 0.38 div d^{-1} for *C. criophilum*, 0.56 div d^{-1} for *Synedra* sp. and between 0.71 and 0.88 div d^{-1} for the other 5 species. A reduction in light intensity from 220 to 46 μmol m^{-2}s^{-1} slowed growth by nearly 50%. These results suggest that the combined effect of temperature and light is one of the factors involved in the limitation of antarctic phytoplankton growth. The low temperatures of the environment do not permit rapid growth, which, even under optimal light conditions remains low. In addition, in the euphotic layer, the overall light energy available for algae is considerably reduced due to turbulence, a factor which exacerbates the reduced growth rate.

Introduction

Research carried out in the last twenty years has greatly enlarged our knowledge of the characteristics of the antarctic pelagic environment. These characteristics are original and render this ocean unique as a model. It covers an area of 38 million km², and, due to the rarity of immersed land is protected from anthropogenic influences. The temperature of the water is always low with summer values between −1.8°C near the Antarctic continent to +4.5°C near the polar front. For a major part of the year the southern region is covered in ice. The light/dark cycle is very variable depending on the latitude and the season but in the summer the intensity of incident light is equivalent to that found in the tropics (Jacques 1983).

Apart from continental coast where considerable blooms have been noted (von Bodungen et al. 1981; El-Sayed and Weber 1982), the antarctic waters are amongst the most poor in the world. Biomass is between 0.2 and 0.5 mg Chl*a* m^{-3} and production between 0.1 and 0.5 g C m^{-2}d^{-1} (Holm-Hansen et al. 1977; Jacques and Minas 1981). Unlike other oligotrophic seas such as the Mediterranean, nutrients cannot be responsible for this limitation as they have present in abundance (Le Corre and Minas 1983; Le Jehan and Treguer 1983; Simon 1986). Numerous hypothesis have been put forward to explain this paucity (see reviews by Sakshaug and Holm-Hansen 1984, Priddle et al. 1986 and Jacques 1989). If nutritional factors do not seem to be primordial, the role played by trace metals remains to be explicited. Martin and Gordon (1988) have suggested that iron is the limiting factor in arctic and antarctic waters. Their hypothesis tested experimentally in subarctic water (Martin and Fitzwater 1988) is based on the similar situations of the two regions ie. low production, considerable nutrient reserves, very low input of atmospheric dust. This hypothesis is not supported by experimental results which show that biomass and production do not increase when the natural waters are enriched with iron (Hayes et al. 1984; Jacques et al. 1984).

In fact, little is known of the factors which regulate the growth of antarctic phytoplankton but most authors agree that temperature and light play an important role. Temperature has a direct effect on photosynthetic carbon fixation (Neori and Holm-Hansen 1982; Tilzer et al. 1985, 1986; Jacques 1983). Maximum uptake occurs at temperature above those of the environment in which the algae live. In the Antarctic Ocean, the effect of light is more complex. The light intensity received by the algae depends on season, latitude, variations in cloud cover and also on mixing in the upper water layer. Results obtained with cultured species and in natural environment have shown that antarctic phytoplankton present shade adaptation characteristics (Hoepffner 1984; Tilzer et al. 1985; Sakshaug and Holm-Hansen 1986; Tilzer and Dubinsky 1987).

The metabolism of phytoplankton organisms is not well understood and their environmental adaptation remains a controversial subject (Mortain-Bertrand 1988; Neori and Holm-Hansen 1982; Priddle et al. 1986; Spies 1987). The effects of environmental factors on the growth are also poorly understood. The small amount of work undertaken to date has been fragmentary and mainly concerned with the role played by light and its fluctuations (Mortain-Bertrand 1989) or that of temperature (Jacques 1983). Because of the importance of these two factors in the natural environment it was of interest to examine their concomitant effect on growth.

In this present work we have studied the combined effect of different light intensities and temperatures on the growth rate of algae in culture. The experiments were carried out in an incubator where seven species of antarctic diatoms isolated from their natural environment, were exposed to various combinations of temperature and light intensity.

Materials and Methods

Seven species, Nitzschia cylindrus (Grun) Hasle, Nitzschia kerguelensis (O'Meaera) Hasle, Corethron criophilum Castracane, Stellarima microtrias Ehrenb., Nitzschia turgiduloides Hasle, Chaetoceros deflandrei and Synedra sp. were isolated from samples collected in the Indian sector of the Southern Ocean between the polar front and the Antarctic continent during the Antiprod II (Jacques 1982) and Antiprod III (Fontugne and Fiala 1987) cruises. All are typical of the antarctic waters and some of frozen seawater. N. kerguelensis, C. criophilum and N. cylindrus are those most often found (Theriot and Fryxell 1985). Of these only C. criophilum and N. cylindrus are also present in arctic waters (Hasle 1976; Clemons and Miller 1984).

The growth of each alga was monitored under controlled conditions of temperature and light in a plant incubator. The cultures were tested between 0° and 6°C to 15°±1°C depending on the species under continuous light ("warm-white" fluorescent tubes).

A range of four light intensities was obtained by covering the bottles with perforated nickel screens to give: $220 \, \mu mol \, m^{-2} s^{-1}$ (100%), $155 \, \mu mol \, m^{-2} s^{-1}$ (70%), $72 \, \mu mol \, m^{-2} s^{-1}$ (30%), $46 \, \mu mol \, m^{-2} s^{-1}$ (20%). The light intensity was measured within the culture flasks using a QSL-100 quantum irradiance meter (Biospherical Instruments). At each temperature, two culture flasks containing 100 ml of medium f (Guillard and Ryther 1962) with a salinity of 34‰ were incubated for each light intensity.

Cells were counted periodically using the following hemacytometers: Malassez, Thoma, Agasse-Lafont and Fuchs-Rosenthal,

depending on cell density. Numerations were carried out on at least six subsamples each containing at least 100 cells. The growth rate (k) was calculated from successive counts undertaken during the exponential growth phase according to the following equation developed by Guillard (1973):

$$k_{(div\,d^{-1})} = (\ln N_2 - \ln N_1) \, (T_2 - T_2)$$

where N_1 and N_2 are the cell concentrations at times T_1 and T_2. Growth rates reported in this paper refer to the mean value of the two subsamples tested.

Results

Mean Growth Rate of Antarctic Diatoms

In culture, antarctic diatoms present variable cellular densities depending on their size. The maximum was 10^6 to $3.3 \, 10^6$ cell ml^{-1} for the smallest species and only $20 \, 10^3$ cell ml^{-1} for the largest (Table 1).

Their growth was relatively low compared with temperate species. The mean growth rate (mean calculated from all experiments performed under different conditions of temperature and light) was always less than $0.7 \, div \, d^{-1}$. For six of the seven species it was between 0.4 and $0.6 \, div \, d^{-1}$ (Table 1); only C. criophilum demonstrated very slow growth ($0.24 \, div \, d^{-1}$). These value are in the same range as those noted elsewhere in culture (Hoepffner 1984; Ribier et al. 1988; Mortain-Bertrand 1989; Sommer 1989) and in natural seawater (Spies 1987).

Influence of Temperature and Light Intensity on Growth Rate

As for most temperate algae (Yolder 1979; Hitchcock 1980; Fawley 1984), the antarctic diatoms' growth rate varied as a function of temperature according to a bell-shaped curve (Fig. 1). At low temperatures (between 0° and 4–5°C), the division rate rose with temperature. However, this increase was considerably more rapid than in temperate species; maximum growth rate was reached with an increase of just a few degrees, except for Corethron criophilum and Nitzschia cylindrus where a lag time was observed in the very first degrees. Taking account of all species studied, the optimum temperature for growth was

Table 1. Characteristics of antarctic diatoms. μ_{mean}: mean growth rate calculated from all the experiments under different conditions of temperature and light (with 95% confidence limit); μ_{max}: maximum growth rate (with 95% confidence limit); T opt: temperature at which maximum growth is observed; T leth: temperature above which the algae cannot survive

| Species	μ_{mean} div day^{-1}	μ_{max} div day^{-1}	max cells n° $\times 10^3$ cell ml^{-1}	T opt.	T leth
Corethron criophilum	0.24 ± 0.04	0.38 ± 0.02	20	4°C	> 6°C
Synedra sp.	0.44 ± 0.05	0.56 ± 0.04	1360	5°C	> 7°C
Nitzschia turgiduloides	0.48 ± 0.06	0.71 ± 0.03	140	3°C	> 8°C
Nitzschia kerguelensis	0.55 ± 0.08	0.78 ± 0.09	220	4°C	> 7°C
Stellarima microtrias	0.60 ± 0.10	0.85 ± 0.04	20	4°C	> 7°C
Nitzschia cylindrus	0.59 ± 0.07	0.86 ± 0.10	3350	5°C	> 9°C
Chaetoceros deflandrei	0.63 ± 0.08	0.88 ± 0.10	1000	5°C	> 15°C
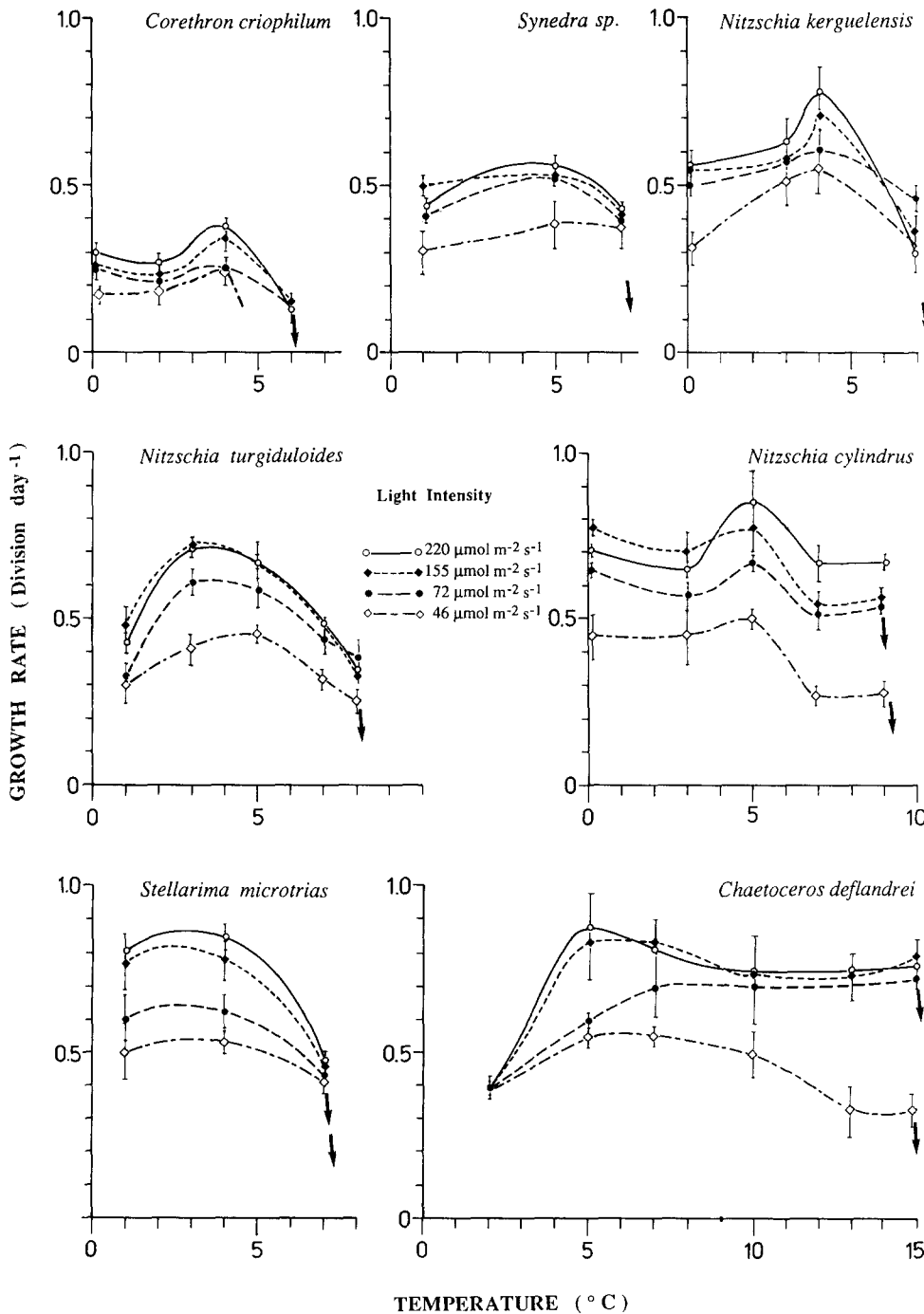
Fig. 1. Variations in the growth rate (div d^{-1}) of antarctic diatoms as a function of temperature and light intensity. *Vertical bars* represent the 95% confidence limit

between 3° and 5°C. Above this point the growth rate diminished very rapidly until cell death. The lethal temperature varied from 6°C for *C. criophilum* to 9°C for *N. cylindrus* (Table 1). *Chaetoreceros deflandrei* followed a different pattern: having reached a maximum at 5°C, the growth rate decreased slowly and remained practically stable up to 15°C, after which the cell died.

Overall changes in growth rate as a function of temperature were identical regardless of light intensity, only the values reached were dependant on the quantity of light

received. A reduction in the light intensity reduced growth to different degrees according to the species. In the slow-developing diatoms (*C. criophilum* and *Synedra* sp.) the reduction in growth rate between 220 μmol m^{-2} s^{-1} and 46 μmol m^{-2} s^{-1} was slight (around 20%). Conversely, in the other species it can be up to 50%. At the lowest light intensity (46 μmol m^{-2} s^{-1}) growth rate was very low in *C. criophilum* (0.20 div d^{-1}) and between 0.40 and 0.50 div d^{-1} in the other diatoms (Table 2).

Within the range of intensities tested and between 0°C

Table 2. Mean growth rate for antarctic diatoms (calculated from all the experiments at different temperatures) under different intensities of light between 46 and 220 μmol m^{-2}s^{-1}

Species	Light intensity (μmol m^{-2}s^{-1})			
	220	155	72	46
Corethron criophilum	0.27	0.24	0.24	0.21
Synedra sp.	0.48	0.48	0.44	0.36
Nitzschia turgiduloides	0.53	0.54	0.49	0.35
Nitzschia kerguelensis	0.69	0.55	0.54	0.42
Stellarima microtrias	0.71	0.67	0.55	0.48
Nitzschia cylindrus	0.71	0.66	0.59	0.39
Chaetoceros deflandrei	0.73	0.73	0.65	0.41

and the thermal optimum, the relation between growth rate (μ) and light intensity (I) of each species was logarithmic (equation: $\mu = a + b \log I$) characteristic of light shade adaptation (Falkowski 1980). In the antarctic diatoms in culture, light shade adaptation is characterized by changes in the number and the size of the photosynthetic units (Hoepffner 1984).

Regression analyses of μ versus log I in the light limited regions of growth predicted compensation growth-irradiance levels (light intensity value at $\mu = 0$) between 10 and 15 μmol m^{-2}s^{-1} for *N. cylindrus* and *N.kerguelensis* and between 2 and 5 μmol m^{-2}s^{-1} for others species. These values correspond to 1% of surface irradiance which usually marks the lower limit of the euphotic zone at a depth of about 80 m in antarctic waters (Panouse 1987). These results are different from those of Holm-Hansen et al. (1977) who reported that antarctic phytoplankton continued to photosynthesize at light levels only 0.1% of downwelling irradiance. By contrast, the compensation light intensity is higher in temperate species than in antarctic species (Falkowski et al. 1985; Falkowski and Owens 1980).

Maximum Growth Rate (μ_{max})

There is little difference between species as regards the optimum growth temperature. μ_{max} were between 3° and 5°C (Table 1), temperatures which are a little higher than those found in the natural environment where the organisms live during summer. Conversely, the optimum for carbon fixation is higher from 7°C (Neori and Holm-Hansen 1982) to 12°C (Jacques 1983).

At 220 μmol m^{-2}s^{-1}, μ_{max} varied according to the species between 0.71 and 0.88 div d^{-1}. Only *C. criophilum* (a large diatom of about 180 μm) with 0.38 div d^{-1} and *Synedra* sp. with 0.56 div d^{-1} demonstrated markedly slower growth (Fig. 2). All these values are lower than those predicted by Eppley (1972). According to the equation described by this author from bibliographic data, maximum values of μ_{max} should be from 1.03 at 3°C and from 1.17 at 5°C.

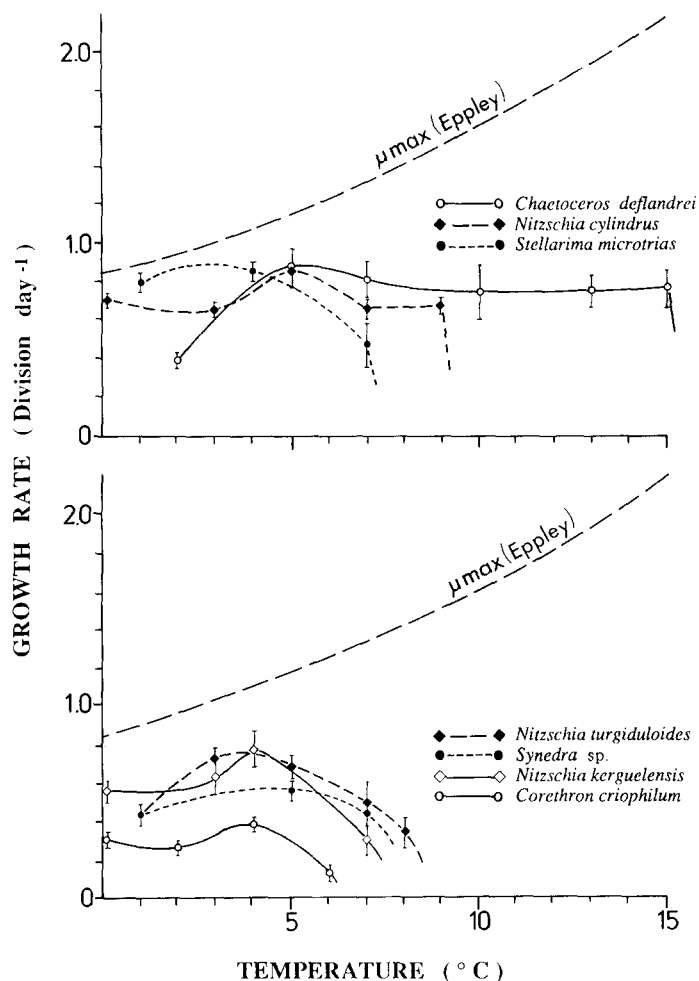Under optimum light conditions (220 μmol m^{-2}s^{-1}), growth increased 1.1 to 2 fold between 0° and 4°C.

Fig. 2. Relation between maximum growth rate (μ_{max}) and temperature in antarctic diatoms. The *upper curve* represents μ_{max} determined according to Eppley (1972) from the equation: $\mu_{max} = 0.851 (1.066)^T$. *Vertical bars* as in Fig. 1

Extrapolation over a 10°C interval places Q_{10} between 1.20 for *Stellarima microtrias* and 5.80 for *N. turgiduloides*. Three species, *N. cylindrus*, *C. deflandrei* and *N. turgiduloides* showed a greater dependance on temperature (Table 3). These values are close to those predicted by

Table 3. Temperature dependance of maximum rate (μ_{max}) at 220 μmol m^{-2}s^{-1}. Q_{10} values were calculated by using the linear regression μ_{max} versus temperature

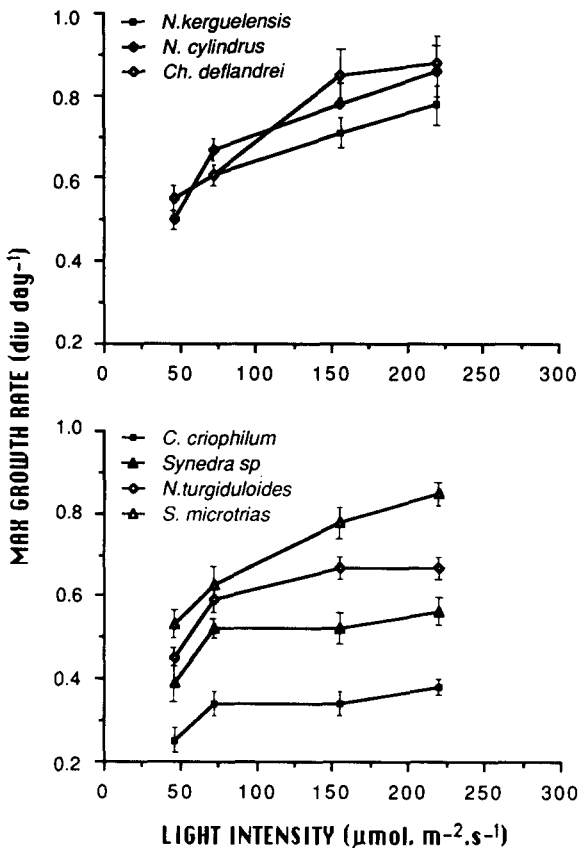| Species	Q_{10}	r^2
Stellarima microtrias	1.16	1.00
Corethron criophilum	1.71	0.70
Synedra sp.	1.73	1.00
Nitzschia kerguelensis	1.87	0.80
Nitzschia cylindrus	2.56	1.00
Chaetoceros deflandrei	4.14	0.86
Nitzschia turgiduloides	5.80	1.00

Fig. 3. Relation between maximum growth rate and light intensity in antarctic diatoms. *Vertical bars* as in Fig. 1

Tilzer and Dubinsky (1987) in natural antarctic phytoplankton incubated between $-2°$ and $+8°C$, but lower than those concerning photosynthetic responses (Tilzer et al. 1986). Temperature dependance of antarctic algae is not fundamentally different from temperate species: Q_{10} values for interval between 5° and 15°C are within the same range for both groups (Eppley 1972; Hobson 1974; Yolder 1979; Hitchcock 1980).

In most of the species studied optimal growth occurred at 220 μmol m^{-2} s^{-1}. Exceptions were *Synedra, N. turgiduloides* and *C. deflandrei* where saturation occurred at 155 μmol m^{-2} s^{-1}. These values are close to those found in

antarctic populations (Holm-Hansen et al. 1977; Sakshaug and Holm-Hansen 1986). For the three species *Corethron crioplilum, N. turgiduloides* and *S. microtrias*, Mortain-Bertrand (1989) found I_{sat} between 100 and 400 μmol m^{-2}s^{-1} according to the light fluctuations.

A reduction in light intensity from 220 to 46 μmol m^{-2} s^{-1} lowers μ_{max} by about one and half times. Under the most unfavourable conditions, *C. Criophilum* presented a μ_{max} of 0.25 div d^{-1}, *Synedra* sp 0.40 div d^{-1} and the five other species about 0.50 div d^{-1} (Fig. 3).

Discussion

Temperature has long been considered (Saijo and Kawashima 1964) one of the major factors which control the productivity of Antarctic waters. Throughout the year the temperature of the open seawater is below 5°C, which directly influences the metabolism of planktonic cells, particularly in the incorporation of CO_2 (Neori and Holm-Hansen 1982; Jacques 1983), the assimilation of lipids (Smith and Morris 1980) and growth rate (Spies 1987). In microorganisms the growth rate is a good indicator of their general metabolic state which is directly influenced by environmental conditions.

The results we have obtained from culture diatoms confirm the hypothesis of El-Sayed and Tagushi (1981) concerning the obligatory psychrophilic nature of antarctic diatoms, i.e. they can only grow at low temperatures. In fact, none of the species tested here can survive above 6° to 9°C with the only exception of *Chaetoceros deflandrei*, an organism demonstrating higher thermal tolerance that do not exceed 15°C.

Low temperatures slow the overall metabolism of phytoplankton and thus reduce their division rate. Growth rate values for antarctic diatoms, always below 0.9 div d^{-1}, are within the range found in the natural environment (Table 4). It should, however, be noted that apart from the experiments carried out on natural populations (Sakshaug and Holm-Hansen 1986; Spies 1987; Fiala and Debas, in preparation), the other values reported are derived from calculations which have necessitated the utilization of different conversion factors for the estimation of carbon, a situation which renders comparisons difficult.

Growth rate varies as a function of temperature: it increases with temperature to reach a maximum between 3° and 5°C. The optimum temperature for both the growth and photosynthesis of algae in culture is a little higher than in their natural environment (Smayda 1969; Li 1980). This being so, it can be considered that the algae in antarctic waters are growing at their maximum rate.

These diatoms therefore present a certain degree of adaptation to the thermal conditions of the Antarctic: their growth is strictly limited to cold waters but as their development is restricted by the slow division rate, large blooms cannot occur even under the most favourable light conditions.

The processes involved in this adaptation to the cold conditions are still largely unknown. Antarctic algae do

Table 4. Growth rate of antarctic marine phytoplankton; [a] growth rates observed in experiments on natural populations (chlorophyll biomass or cells numeration); the other values are the result of calculations from ^{14}C production measurements of seawater samples

Location	Growth rate (Div day^{-1})	Temperature (°C)	Irradiance (μmol m^{-2} s^{-1})	Reference
Natural communities				
Ross Sea	0.10−0.33			Holm-Hansen et al. (1977)
Weddell Sea	0.49−0.88			El-Sayed and Taguchi (1981)
Scotia and Weddell Seas	0.37−0.49[a]	−1° to +4°	37 to 105	Sakshaug and Holm-Hansen (1986)
Weddell Sea	0.38−1.33[a]	−1°	45	Spies (1987)
Indian Ocean Sector	0.16−0.66			Jacques and Minas (1981)
Indian Ocean Sector	0.51−2.10			Miller et al. (1985)
Indian Ocean Sector	0.60−1.10[a]	+3 to 8°	68 to 20	Fiala and Debas (unpublished)
Species cultures				
Corethron criophilum	0.20−0.33	3°	40	Mortain-Bertrand (1989)
Nitzschia turgiduloides	0.53−0.61	3°	40	Mortain-Bertrand (1989)
Stellarima microtrias	0.13−0.22	3°	40	Mortain-Bertrand (1989)
Stellarima microtrias	0.60	3°	120	Ribier et al. (1988)
Nitzschia turgiduloides	0.20−0.43	5°	140	Hoepffner (1984)
Chaetoceros deflandrei	0.25−1.04	5°	140	Hoepffner (1984)
Corethron criophilum	0.40	0°	160	Sommer (1989)
Rhizosolenia alata	0.45	0°	160	Sommer (1989)
Rhizosolenia truncata	0.45	0°	160	Sommer (1989)
Thalassiosira antarctica	0.47	0°	160	Sommer (1989)
Biddulphia weissflogii	0.46	0°	160	Sommer (1989)
Eucampia zodiacus	0.38	0°	160	Sommer (1989)
Rhizosolenia hebetata	0.34	0°	160	Sommer (1989)
Thalassiosira subtilis	0.46	0°	160	Sommer (1989)
Thalassiothrix longissima	0.41	0°	160	Sommer (1989)
Nitzschia kerguelensis	0.56	0°	160	Sommer (1989)
Chaetoceros criophilum	0.32	0°	160	Sommer (1989)
Pyramimonas sp.	0.53	0°	160	Sommer (1989)
Nitzschia seriata	0.55	0°	160	Sommer (1989)
Phaeocystis pouchetii	0.71	0°	160	Sommer (1989)
Nitzschia cylindrus	0.69	0°	160	Sommer (1989)
Corethron criophilum	0.13−0.38	0° to 6°	46 to 220	Present work
Stellarima microtrias	0.42−0.85	1° to 7°	46 to 220	Present work
Chaetoceros deflandrei	0.33−0.88	2° to 15°	46 to 220	Present work
Nitzschia turgiduloides	0.25−0.71	1° to 8°	46 to 220	Present work
Nitzschia cylindrus	0.27−0.86	0° to 9°	46 to 220	Present work
Nitzchia kerguelensis	0.30−0.80	0° to 7°	46 to 220	Present work
Synedra sp.	0.31−0.56	1° to 7°	46 to 220	Present work

not seem to have developed mechanisms to overcome the constraints imposed by the low temperatures (Tilzer et al. 1986). In antarctic diatoms, enzymes involved in inorganic carbon fixation are identical to those in temperate species (Descolas-Gros and Fontugne 1985) but the affinity coefficient of RuBP carboxylase is at a minimum between 3° and 5°C which indicates their aptitude for fixing carbon at low temperatures (Descolas-Gros and De Billy 1987).

Apart the temperature which is, because of its low level, a primordial factor in the lack of algal development, the role played by light should also be examined. In Antarctic waters because of the turbulence that affects the surface, the quantity of light available for photosynthesis varies rapidly due to the movement of cells in the euphotic zone. The algae must therefore adapt their metabolism to the abrupt changes in energy levels. According to Falkowski and Wirick (1981), these variations have little effect on phytoplankton photosynthesis, whereas, for Marra (1978), they are beneficial. Mortain-Bertrand (1989) has shown that the quantity of carbon incorporated in three antarctic diatoms is greater with a 2h/2h dark/light cycle than with a 12h/12h cycle. According to Barlow (1984) the incorporation of carbon into proteins was more rapid in stable water than under mixing conditions. Since algal growth is linked to protein synthesis, he suggested that the growth of community in stable environment was faster than in turbulent environment. Moreover, the growth rate of antarctic phytoplankton is not controlled by light intensity but rather by total daily irradiance (Mortain-Bertrand 1989). Because of their movement through the euphotic zone, the cells receive a daily quantity of light considerably lower than the maximum tested (220 μmol m^{-2} s^{-1}). Consequently, their growth rate in the natural environment should be less than the maximum

values noted at this intensity. Nevertheless, it should be noted that the adaptational status of algae in culture reflects the experimental light intensity and may be different from that in natural waters, specially in mixed waters.

Although it is always hazardous to transpose results obtained in a laboratory to the natural environment, our results lead us to believe that the combined effect of temperature and light is one of the key factors in explaining the low phytoplankton biomass in the antarctic waters. Of these two physical factors the temperature seems to be the more important for although the algae are capable of reaching their maximum rate of development in cold water this nevertheless remains relatively low even under optimum light conditions. A reduction in the amount of available light energy due to surface turbulence has a negative impact on growth rate which exacerbates that caused primarily by the temperature.

Our results have demonstrated the importance of these two factors in the growth regulation of antarctic diatoms. These factors alone do not however explain everything. The production of antarctic phytoplankton is probably governed by multiple factors of inequal importance; factors amongst others such as trace metal, grazzing, sedimentation. The field of investigation remains open for determination of the real impact of these factors.

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