Growth rates of ten diatom species from the Barents Sea at different irradiances and day lengths*

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ABSTRACT: Nutrient-sufficient cultures of 10 arctic diatom species were grown at a combination of 9 irradiances and 4 day lengths at $-0.5\,°C$. The growth rate was calculated on the basis of in vivo fluorescence measurements. Maximum recorded growth rates ranged from $0.41\ d^{-1}$ (*Amphiprora* sp.) to $0.60\ d^{-1}$ (*Thalassiosira antarctica* and *T. bulbosa*). Growth rates generally increased with irradiance up to 50 or 70 μmol $m^{-2}s^{-1}$, above which they depended mainly on day length. The day length response of light-saturated cultures was satisfactorily described by a rectangular hyperbola.

INTRODUCTION

Seasonal variations in irradiance and day length are the largest and most predictable environmental fluctuations that arctic phytoplankton experience. These variations are enhanced by ice cover. This, in combination with generally low temperatures, forms an extreme environment. One might therefore expect phytoplankton to have evolved particular adaptations to varying irradiance, day length, and low temperature.

Numerous papers have documented the effect of light, nutrient supply, salinity, and temperature upon phytoplankton growth at high latitudes (Grant & Horner 1976, Neori & Holm-Hansen 1982, Harrison & Platt 1986, Spies 1987). Some authors have focussed on the effects of the light regime on the growth of polar phytoplankton (Palmisano & Sullivan 1985, Sakshaug & Holm-Hansen 1986, Hegseth 1989). Recorded growth rates for natural phytoplankton communities at low temperatures are $< 0.92\ d^{-1}$ (Durbin 1974, Palmisano & Sullivan 1982, Jacques 1983, Spies 1987).

We present here growth rates for nutrient-saturated phytoplankton cultures grown at combinations of different irradiances and day lengths at $-0.5\,°C$. Ten diatom species were selected, comprising 4 arctic-boreal species, 3 obligate arctic species, and 3 epontic species. Such data are useful for calibration of empirical models for prediction of the light-dependent growth rate.

MATERIAL AND METHODS

The 10 diatom species were collected in the Barents Sea in the summers of 1984 and 1985, and were isolated by Professor Eystein Paasche (no. 1) and Dr Erik Syvertsen (nos. 2 to 10) (Table 1).

Species 1 to 7 may be divided into an arctic-boreal group (Nos. 1 to 4) and a group of obligate arctic species (nos. 5 to 7; Syvertsen pers. comm.). Nos. 8 to 10 are epontic.

Stock and experimental cultures were grown at $-0.5 \pm 0.2\,°C$ in filtered seawater collected at 30 m depth off the Trondhjem Biological Station, Norway (salinity =ca 33 ppt). The water was enriched with the 'f' medium of Guillard & Ryther (1962) at half strength. Stock cultures were grown at a scalar irradiance (PAR) of 120 μmol

Table 1. Diatoms investigated

Species	Clone
1. *Thalassiosira antarctica* Comber var. *borealis*	PMTa1
2. *Thalassiosira nordenskioeldii* Cleve	PMTn3
3. *Porosira glacialis* (Grunow) Cleve	PMPg1
4. *Nitzschia delicatissima* Cleve	PMNd1
5. *Thalassiosira bulbosa* Syvertsen	PMTbu3
6. *Thalassiosira bioculata* (Grunow) Ostenfeld	PMTbi2
7. *Chaetoceros furcellatus* Bailey	PMCf1
8. *Amphiprora* sp.	PMis1
9. *Nitzschia vanhoeffenii* Gran	PMis2
10. *Nitzschia grunowii* Hasle	PMis4

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m^{-2} s^{-1} at the same day length as the experimental cultures.

Experimental cultures of 20 ml volume were grown in 18 × 150 mm Pyrex test tubes, which were kept in racks in water baths containing polyethylene glycol in a freezer without cover (temperature regulation by thermostats). Light was supplied from above, either by 2 Osram HQI-T 250 W/D halogen dysprosium lamps (50, 70, 200, 350, and 500 μmol m^{-2} s^{-1}) or fluorescent tubes (Sylvania warm white 22 W, F15 W/WW: 3, 10, 18, and 33 μmol m^{-2} s^{-1}). Light was attenuated by means of neutral nylon screens and by varying the distance between the lamps and the cultures. The cultures were grown at 4 day lengths (D): 10 and 24 h (all irradiances), and 4 and 19 h (irradiances of 50 to 500 μmol m^{-2} s^{-1} only).

Scalar irradiance (E_0, PAR) was measured in the tube racks with a QSL-100 quantum sensor (Biospherical Instruments). In vivo fluorescence was measured once per day (about 2 h into the light period) by inserting the test tubes into the flow cuvette of a Turner 111 fluorometer. Measurements were carried out for 7 to 12 d after an adaptation period of at least 4 d. When in vivo fluorescence reached a reading of about 50 (relative units) for the 1 × slit of the fluorometer, cultures were diluted by a factor of 20 with fresh medium. Readings of 30 to 70 relative units at the 10 × slit of the fluorometer corresponded to about 9 to 20 μg chl a l^{-1}. Dilution, when necessary, has been taken into account in the calculation of the growth rate (Sakshaug et al. 1984). On a semi-log plot, growth curves represent exponential growth at the 1 % significance level when the Product-Moment Correlation Coefficient (r) is > 0.88 (n > 7) for regressions of the natural logarithm of in vivo fluorescence vs time (Wardlaw 1985).

RESULTS

The maximum observed specific growth rates for each species varied within a relatively narrow interval, from 0.41 d^{-1} (0.59 doubl. d^{-1}) (*Amphiprora* sp.) to 0.60 d^{-1} (0.87 doubl. d^{-1}) (*Thalassiosira antarctica* and *T. bulbosa*; Table 2).

All species except *Chaetoceros furcellatus* and *Amphiprora* sp. exhibited their highest growth rate in continuous light (Table 2). The latter 2 grew fastest at 10 and 19 h day length, respectively. *Thalassiosira nordenskioeldii*, *Nitzschia delicatissima*, and *T. bioculata* did not grow in a significantly exponential fashion at 4 h day length.

Growth rates were generally low (< 0.36 d^{-1}) at irradiances of 18 μmol m^{-2} s^{-1} and less, and at 3 μmol m^{-2} s^{-1} were only 0 to 0.08 d^{-1} (Table 2). Photoinhibition, albeit little pronounced, was discernible in the 3

Nitzschia species at 500 μmol m^{-2} s^{-1}, particularly in continuous light (Table 2).

Growth rates of all species increased up to 50 or 70 μmol m^{-2} s^{-1}, above which they were relatively constant, but depended on day length (Fig. 1). The average maximum growth rate for all species increased with day length from 0.16 d^{-1} at 4 h to 0.46 d^{-1} for continuous light (Fig. 2).

The relationship between growth rate (μ) and day length (D) was estimated by a nonlinear regression program based on an algorithm developed by Marquardt (1963):

$$\mu = \frac{0.75 \pm 0.13\,D}{(15.9 \pm 0.56) + D} \tag{1}$$

This equation fits remarkably well to the average maximum growth rate of all species for each day length (Fig. 2) (Table 3).

ANOVA shows that the impact of day length upon growth rates was significant ($F_{(3,33)} = 26.5$, $p < 0.0001$). Taking the total variation among species into account, the standard deviation for observed vs predicted growth rates was 0.08 d^{-1}.

ANOVA indicates no significant difference in growth rates (50 to 500 μmol m^{-2} s^{-1}) between the 3 ecological groups at any day length (4 h, $F_{(2,23)} = 0.14$, $p < 0.9$; 10 h, $F_{(2,23)} = 1.05$, $p < 0.4$; 19 h, $F_{(2,46)} = 0.91$, $p < 0.4$; 24 h, $F_{(2,44)} = 1.67$, $p < 0.2$).

DISCUSSION

The present results largely agree with results from field studies at low temperatures (Durbin 1974, Palmisano & Sullivan 1982, Jacques 1983, Sakshaug & Holm-Hansen 1986). Growth rates generally increased with irradiance up to 50 or 70 μmol m^{-2} s^{-1} (Fig. 1) and were quite independent of irradiance above that level. Saturation irradiances were similar to those published by Harris (1978) and Jacques (1983) for phytoplankton growth at low temperatures.

The maximum growth rate among all species was 0.6 d^{-1}, which is close to the rate predicted for −0.5 °C by Eppley's (1972) equation for temperature-dependent growth (0.57 d^{-1}). This may indicate that there are no particular adaptive strategies which allow arctic diatoms to grow faster than temperate species would do at low temperatures.

Phytoplankton respond to variation in the light regime by photoadaptive processes which serve to minimize variations in the growth rate when light is the major factor controlling growth (Sakshaug & Holm-Hansen 1986). The negligible variation in growth rate at irradiances from 50 to 500 μmol m^{-2} s^{-1} indicates that the photoadaptive response in the above sense is flex-

Table 2. Growth rates (d^{-1}) of Barents Sea diatoms at combinations of different scalar irradiances (E_o, $\mu mol\ m^{-2}\ s^{-1}$) and day lengths (D, h)

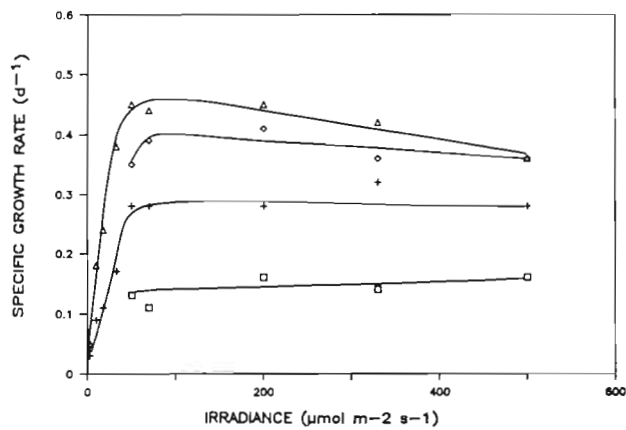|	E_o								
D	3	10	18	33	50	70	200	330	500
T. antarctica									
4	–	–	–	–	0.14[a]	0.16[a]	0.20	0.15	0.16
10	0	0	0	0.07	0.31	0.31	0.33	0.30	0.33
19	–	–	–	–	0.46	0.52	0.53	0.58	0.30
24	0.08	0.01[a]	0.05[a]	0.33	0.60	0.59	0.58	0.48	0.51
T. nordenskioeldii									
4	–	–	–	–	0.11[a]	0.12[a]	0.13[a]	0.20[a]	0.13[a]
10	0.02[a]	0	0.10	0.13	0.31	0.34	0.31	0.30	0.33
19	–	–	–	–	0.29	0.27	0.39	0.44	0.43
24	0[a]	0.13	0.20	0.37	0.56	0.46	0.50	0.58	0.52
P. glacialis									
4	–	–	–	–	0.05[a]	0.07	0.12	0.13	0.15
10	0.04[a]	0	0.08	0.17	0.30	0.29	0.25	0.27	0.26
19	–	–	–	–	0.25	0.31	0.36	0.19	0.25
24	0	0.16	0.10	0.42	0.40	0.24	0.32	0.38	0.35
N. delicatissima									
4	–	–	–	–	0.10[a]	0.05[a]	0.06[a]	0.01[a]	0.11[a]
10	0.02[a]	0.08	0.12	0.19	0.12	0.13	0.11	0.29	0.05
19	–	–	–	–	0.35	0.44	0.42	0.34	0.30
24	0	0.23	0.36	0.41	0.36	0.39	0.50	0.46	0.36
T. bulbosa									
4	–	–	–	–	0.07[a]	0.07	0.20	0	0.12
10	0.02	0.07	0.12	0.20	0.31	0.38	0.34	0.32	0.32
19	–	–	–	–	0.43	0.45	0.46	0.30[a]	0.44
24	0[a]	0.12	0.24	0.42	0.59	0.59	0.60	0.46	0.54
T. bioculata									
4	–	–	–	–	0	0	0	0.12[a]	0.01[a]
10	0	0.05	0.07	0.11	0.16	0.15	0.19	0.23	0.19
19	–	–	–	–	0.29	0.33	0.34	0.30	0.30
24	0.03	0.19	0	0.38	0.42	0.40	0.30	0.43	0.34
C. furcellatus									
4	–	–	–	–	0.15	0.16	0.21	0.14	0.16[a]
10	0.05[a]	0.11	0.14	0.23	0.37	0.37	0.41	0.49	0.30
19	–	–	–	–	0.28	0.33	0.33	0.24	0.46
24	0	0.10	0.15	0.38	0.42	0.43	0.39	0.42	0.31
Amphiprora sp.									
4	–	–	–	–	0.15	0.16	0.12	0.14	0.19[a]
10	0.04	0.11	0.09	0.22	0.12[a]	0.18	0.21	0.25	0.16
19	–	–	–	–	0.41	0.39	0.41	0.39	0.37
24	0	0.22	0.36	0.37	0.30	0.31	0.21[a]	0.35	0
N. grunowii									
4	–	–	–	–	0.10	0.03[a]	0.16	0.15	0.17
10	0.03	0.14	0.17	0.23	0.34	0.31	0.33	0.33	0.34
19	–	–	–	–	0.44	0.43	0.45	0.41	0.28
24	0.25[a]	0.27	0	0.36	0.55	0.55	0.56	0.34	0.14[a]
N. vanhoeffenii									
4	–	–	–	–	0.07[a]	0.09	0.13	0.15	0.19
10	0.04	0.07	0.09	0.15	0.30	0.38	0.34	0.37	0.26
19	–	–	–	–	0.33	0.43	0.42	0.34	0.45
24	0.02[a]	0.20	0.27	0.37	0.28	0.41	0.51	0.29	0.19

[a] Product-moment correlation not significant at the 1 % level

Fig. 1. Average specific growth rates (d^{-1}) of 10 Barents Sea diatoms vs irradiance (μmol m^{-2} s^{-1}) at different day lengths. Curves drawn arbitrarily by hand. (□) 4 h; (+) 10 h; (◇) 19 h; (△) 24 h
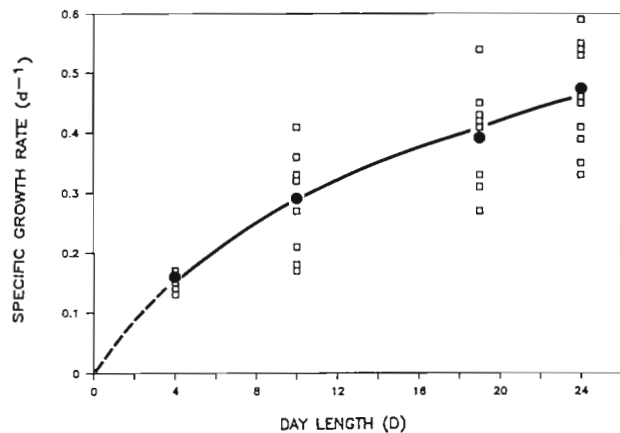

Fig. 2. Maximum specific growth rates (d^{-1}) of 10 Barents Sea diatoms vs day length (D). Curve represents Eg. (1); (●) average maximum growth rate for 10 species at each day length

ible. This flexibility may, for instance, enable arctic diatoms living in a shaded epontic regime to grow well when exposed to strong light in the upper part of the sea during ice edge blooms, and may also explain why they occur in large amounts during spring blooms at the ice edge.

The growth rate increased progressively less with increasing day length. This result is similar to results for *Fragilaria striatula* and *Synedra tabulata* (Castenholz 1964), *Dunaliella tertiolecta* (Eppley & Coatsworth 1966) and *Ditylum brightwellii* and *Nitzschia turgidula* (Paasche 1968). In fact, the average maximum growth rates for each day length can be described by a rectangular hyperbola. Thus arctic diatoms have a less flexible response to variations in day length than to variations in irradiance.

Growth rates and the level of light saturation are within the ranges that would be expected in temperate phytoplankton at low temperatures. Low temperatures apparently imply a decreased level of saturation and photoinhibition irradiance (Talling 1957, Palmisano et al. 1985). The present study does not indicate any particular physiological mechanisms which counteract low light or low temperature in phytoplankton from arctic waters in accordance with Harrison & Platt (1986).

Arctic diatoms may, however, be particularly adapted to tolerate strong light in combination with long day and low temperature. Many temperate species are not able to grow under these circumstances (Sakshaug unpubl.), and other species are not able to grow at all in continuous light (Brand & Guillard 1981). This may explain the absence of many temperate species at high latitudes.

There were no indications that the 3 different ecological groups have different growth strategies. The varia-

Table 3. Average maximum growth rates (d^{-1} ± SD) of Barents Sea diatoms for irradiances between 50 and 500 μmol m^{-2} s^{-1} at different day lengths

Species	4 h	10 h	19 h	24 h
T. antarctica	0.17 ± 0.03	0.32 ± 0.01	0.54 ± 0.03	0.59 ± 0.01
T. nordenskioeldii		0.32 ± 0.02	0.42 ± 0.03	0.53 ± 0.05
P. glacialis	0.13 ± 0.02	0.27 ± 0.02	0.27 ± 0.06	0.35 ± 0.06
N. delicatissima		0.17 ± 0.07	0.39 ± 0.05	0.45 ± 0.06
T. bulbosa	0.16 ± 0.06	0.33 ± 0.03	0.45 ± 0.01	0.54 ± 0.07
T bioculata		0.18 ± 0.03	0.31 ± 0.02	0.39 ± 0.04
C. furcellatus	0.17 ± 0.03	0.41 ± 0.06	0.33 ± 0.08	0.41 ± 0.02
Amphiprora sp.	0.14 ± 0.02	0.21 ± 0.03	0.39 ± 0.02	0.33 ± 0.03
N. grunowii	0.16 ± 0.01	0.33 ± 0.01	0.43 ± 0.02	0.55 ± 0.01
N. vanhoeffenii	0.16 ± 0.03	0.36 ± 0.02	0.41 ± 0.05	0.46 ± 0.07
Average maximum growth rate of all species	0.16 ± 0.02	0.29 ± 0.08	0.39 ± 0.08	0.46 ± 0.08
Estimated growth rates	0.151	0.29	0.408	0.451
Coefficient of variation (%)	4.1	0	3.2	1.4

tions in growth rate are clearly larger within groups than among groups.

The results largely agree with growth rates recorded for cultures of ice algae from Antarctica (up to 0.4 d^{-1} at 46 μmol m^{-2} s^{-1}; Palmisano & Sullivan 1982) and growth rates recorded for cultures of pelagic antarctic diatoms (up to 0.49 d^{-1} at 80 μmol m^{-2} s^{-1}; Sakshaug & Holm-Hansen 1986).

Algae in the Barents Sea do not receive continuous constant irradiance. At 70 °N, day length increases from 9 h on 1 March to continuous light on 13 May. Considering the relatively low ability of algae to compensate for differences in day length, day length should have a strong impact on growth rates and should be important for the timing of the spring bloom.

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