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Growth rates of Antarctic marine phytoplankton in the Weddell Sea*

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ABSTRACT: Natural microplankton from summer surface waters of the Weddell Sea was incubated in 10 l Nalgene® flasks at −1 °C and irradiance 45 µEinst m^{-2} s^{-1}. Ambient nutrient concentrations were high enough to support rapid biomass accumulation. Maximum growth rates and generation times of the dominant diatom assemblages were determined by successive cell counts. Growth rates ranged from 0.38 to 1.33 divisions d^{-1} and generation times varied from 18.0 to 63.2 h $division^{-1}$. Thus, rapid growth at low temperatures is possible; growth rates of Weddell Sea phytoplankton are comparable to those of temperate latitudes.

INTRODUCTION

After several decades of biological research in the Southern Ocean, we still lack conclusive data to support the traditional view of the biological richness of the waters (Hart 1934). On the contrary, extensive biomass studies and productivity measurements in the 60's and 70's produced values which were more comparable to those of oligotrophic seas (e.g. Walsh 1969, El-Sayed & Turner 1977). A variety of factors have been considered as rate-limiting for Antarctic phytoplankton growth e.g. light, turbulence, temperature, silicate (e.g. El-Sayed & Mandelli 1965, Neori & Holm-Hansen 1982, Jacques 1983). Very little is known about the metabolic activities of Antarctic phytoplankton, and whether or not they are well adapted to their environment is still a matter of controversy (El-Sayed 1984). Based on the results of their physiological experiments, Tilzer & Dubinsky (1987) conclude that under the nutrient-saturated conditions of the Southern Ocean the temperature dependence of both photosynthesis and algal respiration is a key factor in controlling phytoplankton productivity. On the other hand, the apparent high productivity of the krill population is strongly suggestive of a productive phytoplankton (Priddle et al. 1986). A wide range of cell division rates have been recorded (e.g. Holm-Hansen et al. 1977, El-Sayed & Taguchi 1981, Miller et al. 1985); most of these data are estimates of growth rates based on radiotracer studies and phytoplankton biomass measurements. The highest recorded growth rates together with reports of extensive blooms (El-Sayed 1970, Smith & Nelson 1985) suggest that rapid growth is possible at *in situ* temperatures.

The objective of this study was to determine whether phytoplankton cells from the Weddell Sea are adapted to their cold environment, so that growth rates are high in spite of low temperatures. For this purpose, the natural microplankton from surface waters was incubated in experimental containers on board the RV *Polarstern*. The approach allows accurate estimates of growth rates of individual phytoplankton groups or species under approximate field conditions of temperature, salinity and nutrient concentrations.

MATERIAL AND METHODS

All sampling and growth experiments were conducted during Cruise ANT III/3 on RV *Polarstern* in the austral summer (4 to 27 Feb) of 1985. Station locations are shown in Fig. 1; the experiments are indexed by 'CON' (container) plus the station number. Seawater was collected from the sea surface (bucket) and immediately dispensed into acid-rinsed Nalgene® polycarbonate flasks (10 l volume); the water was not

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prescreened for zooplankton, nor received any additives. Replicate experiments were run at all stations (except 348). The flasks were incubated at −1 °C in a controlled-environment laboratory container on board. An irradiance of 45 µEinst m^{-2} s^{-1} was provided by daylight fluorescent tubes. All experiments were performed under continuous light. The flasks were sampled at regular intervals (1 to 3 d) for pigments, inorganic nutrients, and species analysis. The experiments were terminated when autotrophic biomass reached a maximum and nitrate concentrations were exhausted. Pigment and nutrient samples were analysed within hours.

Pigment extraction followed the procedure given by Evans & O'Reilly (1982). Chlorophyll *a* and phaeophytin *a* were determined fluorometrically with a calibrated (chlorophyll standard) Turner Designs fluorometer. Samples for nutrients (nitrate and nitrite, ammonium, phosphate and silicate) were determined as described by Grasshoff (1976). For species analysis of phytoplankton, 50 to 100 ml seawater samples were preserved with Lugol's solution. Quantitative counting and identification was done ashore according to the Utermöhl (1958) method. The relative abundance of species in a sample is based on quantitative counts or was calculated after counting at least 400 cells in 4 subsamples. Quantitative counts of phytoplankton surface samples in the field were performed by Qingbo Sui (Institut für Meereskunde, Universität Kiel, FRG). The growth constant (k) of the dominant diatoms was determined from successive counts during the exponential growth phase of the batch cultures; the value of k was estimated graphically from a semi-log plot and computated by using the formula of Guillard (1973)

$$k \text{ (division } d^{-1}) = \log (N_1/N_0) \, (3.322/t) \qquad (1)$$

where N_1 and N_0 = cell concentrations at the end and beginning of a time interval (t).
Knowing k, the generation time (T_d) is:

$$T_d \text{ (h division}^{-1}) = \frac{24}{k} \qquad (2)$$

The growth constant represents the maximal growth rate for that diatom population determined under that one set of conditions of light and temperature, nutrients and species composition.

Hydrographic and environmental data were collected with a Neil Brown CTD-Rosette sampler by a group of physical oceanographers from the Alfred-Wegener-Institut, the Scripps Institution of Oceanography, La Jolla, and the Institut für Umweltphysik der Universität Heidelberg. H. Hellmer kindly provided hydrographic profiles for the stations from which the depth of mixing (z_m) was estimated.

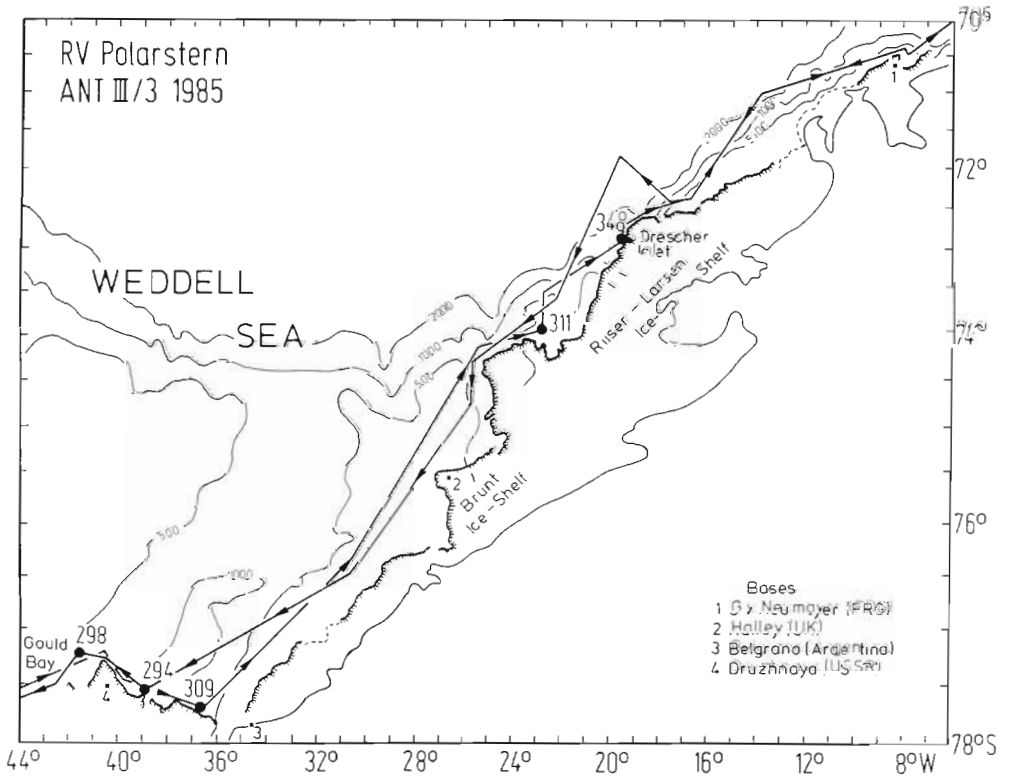

Fig. 1. Location of experimental stations in the southern and southeastern Weddell Sea during the RV *Polarstern* cruise ANT III/3, 1985

RESULTS

The growth experiments were performed in different areas of the Weddell Sea. Regional differences in hydrographical, biological, and chemical conditions are listed in Table 1. During the expedition, pack ice cover in the Weddell Sea varied between 1/10 and 9/10; the recorded lower surface salinities originated from melting pack ice. In general, biomass concentrations were low (except Stn 348) and nutrient concentrations were high at all stations. While the latter values differed regionally, nutrient ratios, especially Si:N and N:P ratios, showed little variation. N:P ratios were close to the Redfield Ratio indicating ideal growth conditions as far as macro-nutrients were concerned.

In February 1985, the microplankton in the Weddell Sea surface waters was composed of small and large flagellates (mainly dinoflagellates and *Distephanus speculum*), heterotrophic protozoa, and a diatom assemblage of great diversity. The majority (Cup to >90 %) of the flagellates belonged to the nanoplankton size fraction; cells measured 3 to 6 µm in diameter. Diatom abundance (by numbers) varied between 1.5 % at Stn 309 and 37.7 % at Stn 294. Due to their relatively large cell size, the diatom contribution to total biomass was much larger than their cell numbers suggested. At the station with the highest chlorophyll *a* concentration (Stn 348) diatoms accounted for 22.6 % of the total cell numbers. In Table 2, the diatom assemblages of the laboratory blooms and in the field are compared; most

Table 1. Initital environmental conditions and nutrient ratios for growth experiments. z_m: depth of mixed layer

Date (1985)	Stn	Location	T (°C)	S (‰)	z_m (m)	Biomass (Chl *a*; mg m^{-3})	Nutrients (mg-at m^{-3})				Nutrient ratios		
							$NO_3^- + NO_2^-$	NH_4^+	PO_4^{3-}	SiO_4^-	Si:N	Si:P	N:P
		Gould Bay/Weddell Sea											
04 Feb	294	77°34'S 38°52'W	−1.1	33.85	45	1.17	16.88	0.44	1.18	44.12	2.5	37.4	14.7
05 Feb	298	77°14'S 41°32'W	−1.2	34.35	30	1.20	20.11	0.60	1.44	48.82	2.4	33.9	14.4
09 Feb	309	77°44'S 36°26'W	−1.4	33.00	20	0.98	22.02	0.20	1.68	66.60	2.8	40.5	14.5
		SE Weddell Sea											
11 Feb	311	73°55'S 22°48'W	−0.3	34.60	55	0.87	15.52	0.63	1.15	56.10	3.5	48.8	14.0
20 Feb	348	72°56'S 19°10'W	−1.3	33.99	18	3.14	15.76	1.36	0.95	47.02	2.7	49.5	18.0

Table 2. Composition of the diatom assemblages of genera in experimental containers (CON) and in surface waters at the different sampling stations (Stn). Abundances are based on quantitative microplankton cell counts (flagellates included). The experimental data represent percentages at the Chl *a* maximum in the batch cultures; mean values of replicate containers are given ± 1 SD; field data are presented in symbols; each asterisk represents an order of magnitude in real numbers

Diatoms	CON 294	Stn 294	CON 298	Stn 298	CON 309	Stn 309	CON 311	Stn 311	CON 348	Stn 348
Asteromphalus spp. *Thalassiosira* spp. *Coscinodiscus* spp. (Ø > 50 µm)	0.39 ± 0.55	** **	0.55 ± 0.11	** ***			1.16 ± 0.48	* *	0.22	* * *
Thalassiosira spp. (Ø 20–50 µm)	0.29 ± 0.41	**	3.20 ± 2.68	***	+	***	< 0.1	****	2.12 (Ø < 20 µm)	*****
Odontella spp.	+	**	< 0.2	**	< 0.2	**	< 0.1	**	+	**
Eucampia spp.	0.30 ± 0.42	***	0.32 ± 0.44	***	2.50 ± 0.88	**	0.46 ± 0.12	***	< 0.1	***
Dactyliosolen spp.		**				**		****		*****
Chaetoceros spp.	38.64 ± 3.93	****	30.82 ± 9.79	****	21.18 ± 6.05	***	2.28 ± 0.19	****	2.19	****
Corethron sp.	< 0.2	*	< 0.1	**	–	*	+	*	–	
Rhizosolenia spp.	10.46 ± 5.48	**	9.43 ± 7.48	**	< 0.2	***	< 0.2	**	< 0.2	*
Amphiprora spp.	–		+		–		–		+	**
Navicula spp.	–		< 0.1		–		–		–	
Nitzschia (section Fragilariopsis)	11.16 ± 7.78	*****	23.43 ± 2.87	****	9.06 ± 6.93		56.27 ± 1.03	*****	41.76	******
Nitzschia spp.	11.20 ± 1.31		11.14 ± 10.82		2.32 ± 0.56		31.64 ± 0.82		45.10	
Thalassiothrix spp.	–		–		–		–	**	< 0.1	**

+: Present in the experiment, but not at the height of the bloom

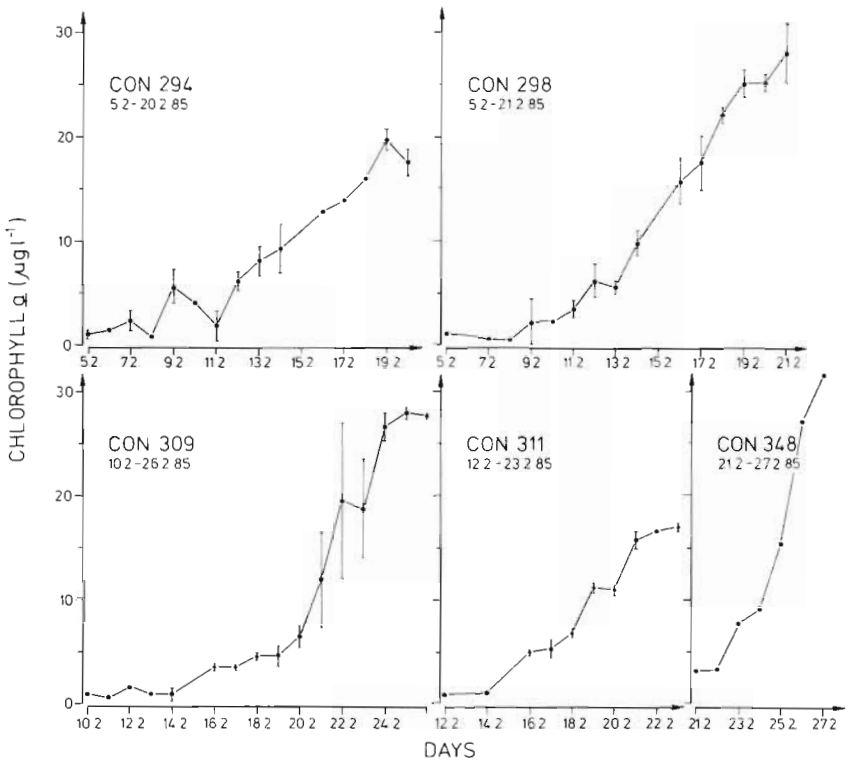

Fig. 2. Chlorophyll *a* concentrations during the growth experiments. Mean values of replicate experiments are shown ± 1 SD, when 1 SD > 0.2 µg l^{-1} (except CON 348)

of the species found in the field were present and grew in the laboratory. In the surface waters of the southern Weddell Sea, centric diatoms were most abundant, whereas at Stns 311 and 348 further to the north in the SE Weddell Sea, pennate diatoms outnumbered the former. The same pattern was found in the laboratory. Very small *Nitzschia cylindrus* (section Fragilariopsis) were present at Stns 311 and 348 and showed weed-like growth in all experimental containers, just before the experiments were terminated; they were not enumerated.

In the experimental containers, growth started after a short lag-phase (Fig. 2). Since initial biomass and nutrient concentrations, as well as the dominant diatom groups, differed between stations, final maximum chlorophyll *a* values were significantly different between treatments. The peak in biomass accumulation coincided with nitrogen (NO_3^- + NO_2^-) exhaustion (Fig. 3); concurrently, phosphate concentrations declined; in Containers 294 and 298 levels were below the detection limit before nitrogen was completely taken up. Silica was never exhausted (Fig. 3).

Growth curves of the dominant diatoms from the Weddell Sea are shown in Fig. 4. The average exponential growth rates and generation times are listed in Table 3. Maximum growth rates of the different diatom groups did not always coincide with the maximum increase in biomass. In the course of the experiments, a diatom succession was observed. Small species reached their maximum in abundance before the general biomass peak, whereas highest growth rates for large diatom species were measured just before or together with nitrogen exhaustion. The dominant groups at the height of the laboratory blooms were those diatom groups which were most abundant in the field and grew fastest in the experimental containers (Tables 2 & 3).

DISCUSSION

The specific growth rate of phytoplankton is an important parameter in evaluating species distribution and in estimating turnover rates of organic matter in aquatic ecosystems (Malone 1982). However, there is no dependable method for estimating phytoplankton growth or division rate in the natural environment (Laws et al. 1984). The conversion of ^{14}C uptake rates into carbon-specific growth is associated with uncertainties in estimating algal biomass as carbon (Banse 1977). In addition, the relationship between short-term variations in photosynthesis and daily growth is poorly understood. For example, photosynthesis is more variable than division rate and varies on time scales shorter than a generation time as a consequence of diel rhythms and environmental effects (Malone 1982). Keeping this in mind, the ongoing controversy as to whether or not Antarctic phytoplankton is well adapted to its environment is rather a matter of experimental

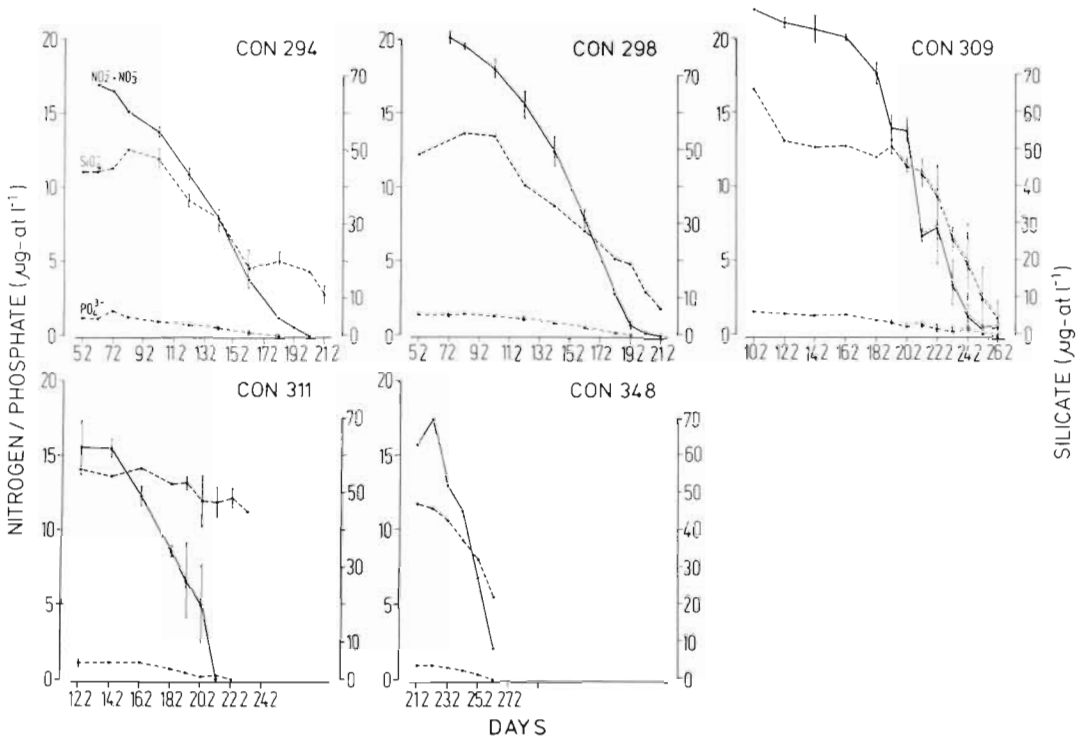

Fig. 3. Nitrogen (nitrate + nitrite), phosphate and silicate concentrations during the growth experiments, shown ± 1 SD, when 1 SD > 0.1 µg l^{-1} (nitrate + nitrite, phosphate), or > 0.5 µg l^{-1} (silicate) (except CON 348)

approach and conditions than a major issue in the context of Antarctic primary production.

All *in vitro* techniques suffer from shortcomings, such as the lack of natural turbulence, wall effects and the artificial light regime. Some of the limitations can be neglected here because of the short duration of the experiments. The experimental approach, however, made it possible to grow natural Antarctic microplankton at *in situ* temperatures, natural nutrient concentrations and a controlled low irradiance light regime. In this study, growth rates of relatively large diatoms from surface waters were determined. Due to their cell size they contribute substantially to the overall biomass in the euphotic zone, and they are known to form extensive blooms (El-Sayed 1971, El-Sayed & Weber 1982). The surface flora was a good representation of the phytoplankton assemblage in the euphotic zone despite considerable variation in the numerical abundance of certain genera (Qingbo Sui, Institut für Meereskunde, Universität Kiel, FRG, pers. comm.).

Among other variables the maximum growth rate of microalgae is correlated with cell size; in general, smaller algae grow faster than larger ones (Geider et al. 1986). Thus, the growth rate estimates of the relatively large diatoms which were present in the field and in the experimental containers were probably less than the growth rates of the pico- and nanoplankton cells (e.g. *Nitzschia cylindrus*). The growth rates of the nanoplankton are difficult to assess in the same experimental design, because the consumers of this size fraction (e.g. tintinnids, heterotrophic flagellates) belong to the microplankton, the same size class as the large diatoms. On the other hand, pico- and nanoplankton represent a considerable fraction of the natural Weddell Sea plankton (von Bröckel 1981, 1985, El-Sayed & Taguchi 1981, this study); further experiments are necessary in order to evaluate their growth dynamics. The experiments presented here confirm earlier suggestions that Antarctic diatoms are very well adapted to the environmental conditions (Priddle et al. 1986). Growth rates, obtained from the container experiments, for Weddell Sea diatoms are comparable to values observed in the Bering Sea (Saino & Hattori 1977) and in the Canadian Arctic (Harrison et al. 1982, Hsiao 1985). They also fall within the range observed in the euphotic zone of waters in temperate and tropical oceans (Parsons et al. 1977, Goldman et al. 1979).

Usually, nutrients are considered unlikely to be a limiting factor for primary production in the Southern Ocean (Hayes et al. 1984). In 2 experiments (CON 294 and CON 298), phosphate concentrations dropped below the detection limit before nitrogen was exhausted. Further experiments will be necessary to test whether phosphate can become limiting under

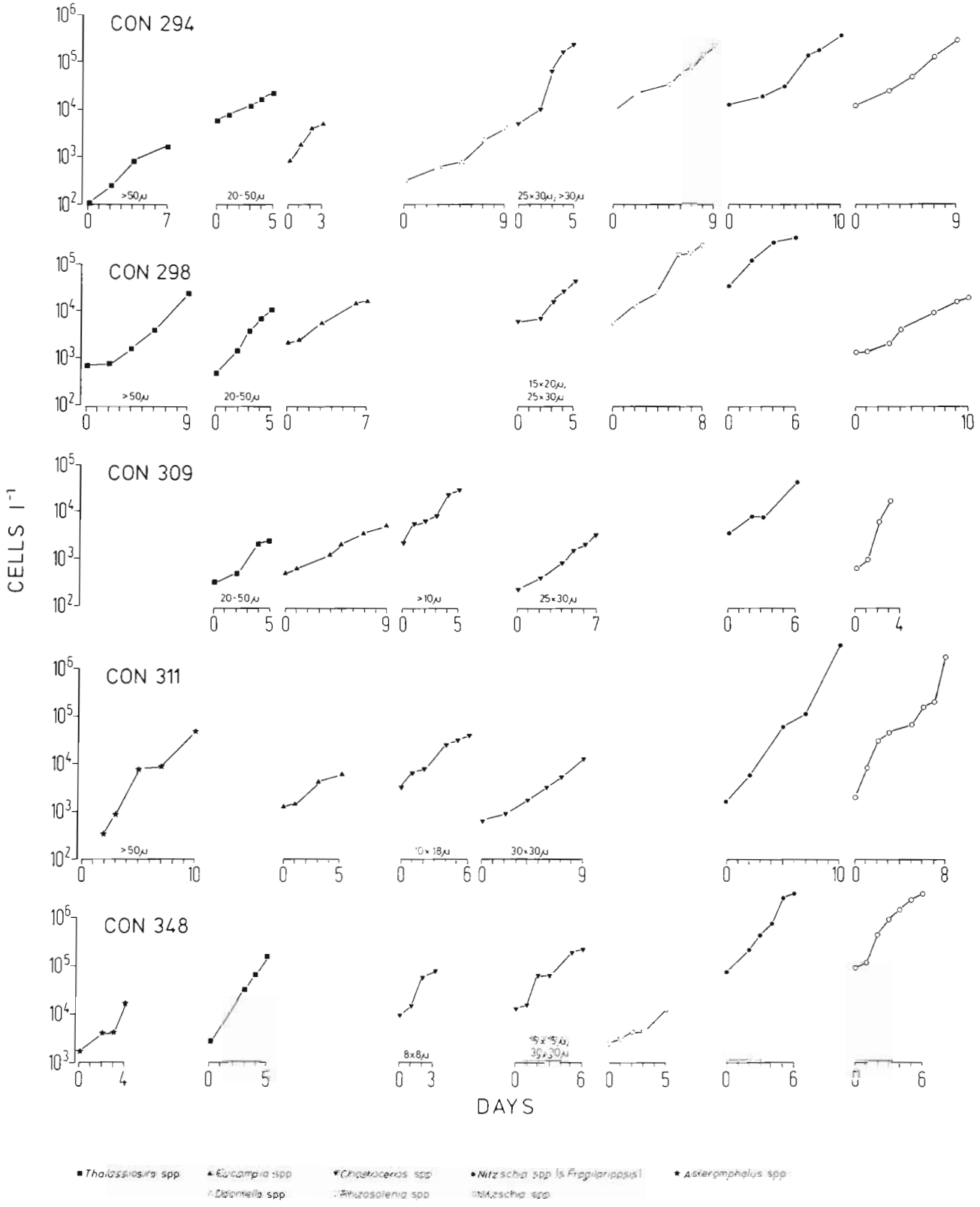

Fig. 4. Growth curves of dominant diatom groups of Antarctic marine phytoplankton in the Weddell Sea. Period of exponential growth and sampling frequency is indicated

Table 3. Average maximum growth rates (k; division d^{-1}) and generation times (T_d; h division^{-1}) of natural Antarctic marine diatoms under approximate field conditions of temperature, salinity and nutrient concentrations in experimental containers

Diatom	CON 294		CON 298		CON 309		CON 311		CON 348	
	k	T_d	k	T_d	k	T_d	k	T_d	k	T_d
Asteromphalus spp. *Thalassiosira* spp. *Coscinodiscus* spp. (Ø > 50 µm)	0.64	37.5	0.71	33.8			0.84	28.6	0.67	35.8
Thalassiosira spp. (Ø 20–50 µm)	0.38	63.2	0.98	24.5	0.72	33.3			1.16 (Ø 12–20 µm)	20.7
Odontella spp.	0.42	57.1								
Eucampia antarctica	1.15	20.9	0.47	51.1	0.39	61.5	0.55	43.6		
Chaetoceros dichaeta (25 × 30 µm)					0.57	42.1				
Chaetoceros spp. Small (< 10 µm)									1.19	20.2
Medium (10–30 µm)	1.33	18.0	0.70	34.3			0.66	36.4	0.76	31.6
Large (> 30 µm)							0.54	44.4		
Rhizosolenia spp.	0.48	50.0	0.70	34.3					0.48	50.0
Nitzschia spp. (section Fragilariopsis)	0.62	38.7	0.77	31.2	0.60	40.0	1.09	22.0	0.90	26.7
Nitzschia spp.	0.57	42.1	0.41	58.5	1.07	22.4	1.23	19.5	1.09	22.0

certain bloom conditions when temperatures are low. In other marine ecosystems, phosphate regeneration is considered to be very fast.

In the short summer season, the near shelf-ice areas of the Weddell Sea are characterized by a stable 20 to 55 m deep surface layer, and only strong storms may erode the pycnocline. Thus, during the main growing season, the depth of vertical mixing is considerably reduced. An apparent seasonal progression of maximum primary production southward was indicated by a larger proportion of diatoms at the most southern stations and in Drescher Inlet, whereas small heterotrophic flagellates, dinoflagellates, silicoflagellates and protozoa were characteristic of stations further to the north.

Growth characteristics, rates and generation times of the Weddell Sea diatoms will vary from month to month and probably from year to year with species composition, mixing depth and other environmental parameters. The present study shows that high growth rates are possible at very low temperatures and relatively low irradiance. This confirms that Antarctic algae are well adapted to their cold environment and that factors other than temperature control Antarctic phytoplankton growth.

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