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Growth and chemical composition of the toxic dinoflagellate *Gymnodinium galatheanum* in relation to irradiance, temperature and salinity

Marianne V. Nielsen

Trondhjem Biological Station, The Museum, University of Trondheim, Bynesveien 46, N-7018 Trondheim, Norway

ABSTRACT: *Gymnodinium galatheanum* Braarud shows optimum growth (0.57 d^{-1}) at 20 to 24°C and 24‰ S, within a temperature/salinity range of 7 to 24°C and 10 to 34‰ S, respectively. The growth rate is significantly affected by temperature and salinity, but no temperature-salinity interaction is found. No photoinhibition is found below 500 µmol photons m^{-2} s^{-1}. Optimum irradiance for growth is ~120 µmol m^{-2} s^{-1}, while the optimum for the growth-relevant chl *a*-normalized C fixation rate is >500 µmol m^{-2} s^{-1}. This difference in optimum irradiance for the growth and photosynthetic rate is related to a decrease in the cellular chl *a*/carbon ratio with increasing irradiance. Carbon, nitrogen and phosphorus contents per cell are significantly affected by temperature, salinity and irradiance. The high and low P/C and N/P ratios, respectively, for nutrient saturated cells indicate that *G. galatheanum* has a large storage capacity for phosphorus.

KEY WORDS: *Gymnodinium galatheanum* · Toxic dinoflagellate · Growth ecology · Chemical composition

INTRODUCTION

An extensive bloom of *Gymnodinum galatheanum* associated with fish mortality was recorded in Walvis Bay, South Africa, in 1950 (Braarud 1959, Steemann Nielsen & Aabye Jensen 1959). The fish mortalities in Walvis Bay were reported as recurrent events; however, it was not clear whether the fish mortalities were caused by toxic plankton, by anoxic conditions due to hydrogen sulphide release from the bottom sediments, by oxygen depletion due to algal respiration and/or decomposition of the bloom or by a combination of these factors (Copenhagen 1953, Pieterse & Van Der Post 1967). Later studies in Walvis Bay (1964–1967) reported that *G. galatheanum* was one of 4 dinoflagellates that regularly cause red tide blooms in the bay; one of these blooms with high numbers of *G. galatheanum* was associated with fish mortality, whereas other blooms were not (Pieterse & Van Der Post 1967). *G. galatheanum* is also found in northern waters. Blooms have been recorded from the Oslofjord, Norway (Bjørnland & Tangen 1979, K. Tangen pers. comm.) and it has been found along the southern coast of Norway (Dahl & Yndestad 1985). *G. galatheanum* is occasionally found in the North Sea region as an accompanying species in blooms of the toxic dinoflagellate *Gyrodinium aureolum* (Larsen & Moestrup 1989).

Recently *Gymnodinium galatheanum* cultures have been shown to have a negative effect on shell length growth of mussels (Nielsen & Strømgren 1991) and to have lethal effects on juvenile cod (Nielsen 1993). These results and the field observations from Walvis Bay indicate that *G. galatheanum*, at least on some occasions, may produce a toxin.

Physiological indications exist that *Gymnodinium galatheanum* is closely related to the toxic dinoflagellate *Gyrodinium aureolum*. Both lack peridinin, which is found in most other dinoflagellates, and both possess chl c_3, characteristic of several bloom-forming prymnesiophytes (Johnsen & Sakshaug 1993). They also possess the carotenoid 19'hexanoyl-oxy-fucoxanthin (Bjørnland & Tangen 1979, Tangen & Bjørnland 1981), indicating a common origin of their chloroplasts, and

they differ from other studied dinoflagellate species by their almost complete lack of ability to take up NO_3^- in the dark, except when N-deficient (Paasche et al. 1984).

The growth ecology of *Gymnodinium galatheanum* has not previously been investigated (Bjergskov et al. 1990); the present study was undertaken to determine this species' growth and chemical composition at different temperatures, salinities and irradiances.

MATERIALS AND METHODS

Gymnodinium galatheanum Braarud strain KT76E, used in the present study, was isolated in 1976 from the Oslofjord by Karl Tangen. Batch cultures were grown in 200 ml glass bottles in K-medium (Keller et al. 1987), with NaH_2PO_4 (36.2 µM) as the phosphorus source. Filtered seawater (Trondheimsfjord, 120 m depth, off the Biological Station), when necessary diluted with distilled, deionized water to adjust the salinity, was pasteurized for 3 h at 80°C before enrichment. Light was supplied by banks of fluorescent tubes (Phillips TL 20W/55 de luxe and TL 40W/55 de luxe).

Growth and chemical composition of *Gymnodinium galatheanum* were studied (1) as an effect of irradiance (20 to 480 µmol m^{-2} s^{-1}) at constant temperature and salinity (15°C, 34‰ S) and (2) as an effect of temperature and salinity in a factorial design with 30 different combinations of temperature (7, 10, 15, 20, 24°C) and salinity (10, 14, 19, 24, 29, 34‰ S) at constant irradiance (255 µmol m^{-2} s^{-1}). Irradiance was measured inside water-filled flasks with a QSL-100 photometer (Spherical sensor, Biospherical Instruments, Inc.). The different irradiances (20, 25, 50, 66, 80, 100, 116, 121, 183, 232, 249, 315, 481 µmol m^{-2} s^{-1}) were obtained by means of neutral nylon screens. Daylength was 18 h. Temperatures were kept within 0.5°C. Salinity was measured in a CSIRO inductively coupled salinometer. Transfers to the highest and lowest temperatures and salinities were gradual.

Before the experiments were begun, the algae were acclimated to the experimental conditions for at least 3 generations. The algae were kept in the exponential growth phase at concentrations ranging from ~1 to 60 cells $µl^{-1}$ (≤ 27 µg chl *a* l^{-1}). The fastest-growing cultures were regularly diluted with K-medium. In the irradiance experiment, 1 culture was grown at each irradiance, and the experiment repeated from new inocula. In the temperature-salinity experiment cultures were grown in duplicate. *In vivo* fluorescence was measured (Turner Designs) 2 or 3 times per week, and growth curves were generated based on a minimum of 5 measurements.

When the cultures approached the upper concentration limit within the exponential phase, duplicate samples were harvested (pressure > −200 mb) on 2.5 cm pre-ignited GF/C filters for analysis of algal carbon, nitrogen, phosphorus and, in the irradiance experiment, also algal chl *a*. Cell density was determined with a Nageotte slide. Algal carbon and nitrogen were analyzed on a Carlo Erba NA 1500 elemental analyzer. Total phosphorus was determined as orthophosphate after digestion with acid persulphate (Koroleff 1976, as modified by Olsen & Østgaard 1985).

Based on the specific growth rate, μ (d^{-1}), the growth-relevant chl *a*-normalized C fixation rate, ${}^{\mu}P^{B}$ (mg C mg^{-1} chl *a* h^{-1}), was calculated by multiplying the growth rate by the corresponding value of cellular carbon divided by cellular chl *a* and light hours:

$$ {}^{\mu}P^{B} = \mu \cdot \frac{C}{\text{chl } a} \cdot \frac{1}{D} \quad (1) $$

In analogy with the photosynthesis-irradiance equation (see Platt et al. 1980), the relation of μ and ${}^{\mu}P^{B}$ to irradiance is described by the equation:

$$ P = P_m[1 - \exp(-\alpha E_o/P_m)] \quad (2) $$

where P is μ or ${}^{\mu}P^{B}$, respectively; P_m is maximum rate; E_o is irradiance; and α is the initial slope. ${}^{\mu}P^{B}$ differs from the chl *a*-normalized photosynthetic rate (P^B) of P vs E curves in that ${}^{\mu}P^{B}$ here represents the net production of light-adapted algae.

RESULTS

Effect of irradiance

For *Gymnodinium galatheanum* the maximum specific growth rate (0.28 d^{-1}) at 15°C and 34‰ S was found at an irradiance (E_o) of about 120 µmol m^{-2} s^{-1}, the initial slope (α) was 0.008 (µmol m^{-2} s^{-1}) d^{-1} and the index of light saturation ($I_k = \mu_m/\alpha$) was 37 µmol m^{-2} s^{-1} (Fig. 1A). The C fixation rate at light saturation, ${}^{\mu}P^{B}_{m}$, was 3.1 mg C (mg chl *a*)$^{-1}$ h^{-1}, the initial slope (${}^{\mu}\alpha^{B}$) was 0.019 mg C (mg chl *a*)$^{-1}$ (µmol m^{-2} s^{-1})$^{-1}$ h^{-1} and the index of light saturation (${}^{\mu}I_k$) was 163 µmol m^{-2} s^{-1} (Fig. 1B). ${}^{\mu}P^{B}_{m}$ was found at an irradiance of >500 µmol m^{-2} s^{-1}. No photoinhibition was found below 500 µmol m^{-2} s^{-1} (Fig. 1A, B). *G. galatheanum* was observed to survive for several months in the stationary phase.

Cellular chl *a* and the chl *a*/C ratio decreased significantly with increasing irradiance, and cellular carbon and nitrogen decreased significantly with increasing irradiance below the optimum irradiance for growth (120 µmol m^{-2} s^{-1}), while cellular carbon, nitrogen and phosphorus increased significantly with increasing irradiance above 120 µmol m^{-2} s^{-1} (Fig. 2,

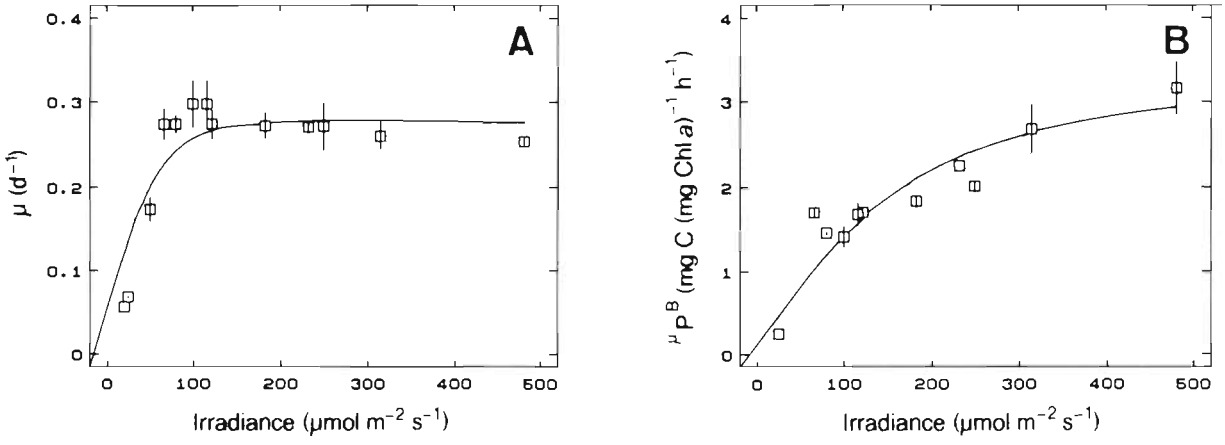

Fig. 1. *Gymnodinium galatheanum*. (A) Specific growth rate and (B) $^{\mu}P^{B}$ related to irradiance. Means ± SE

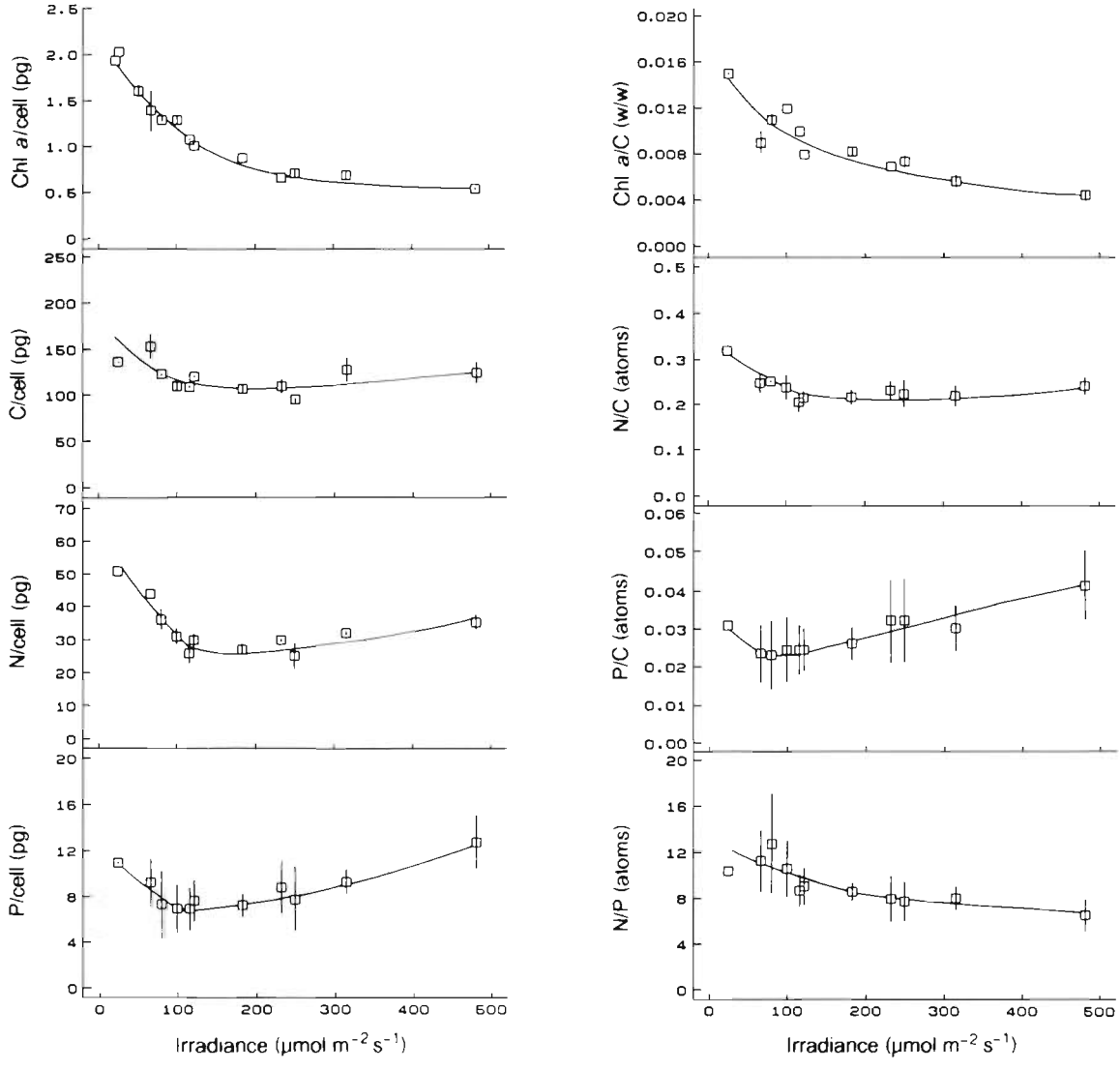

Fig. 2. *Gymnodinium galatheanum*. Cellular chl *a*, C, N, and P, and the chl *a*/C, N/C, P/C and N/P ratios related to irradiance. SE indicated by vertical bars. Curves fitted by eye

Table 1. Significance results of a regression analysis of irradiance (E_o, µmol m^{-2} s^{-1}) effects on: *Gymnodinium galatheanum* growth rate (μ); ${}^{\mu}P^{B}$; chl *a*/C ratio (w/w); cellular chl *a*, C, N and P; and the N/C, P/C, and N/P ratios. The significance results are indicated for regressions using all irradiance data ($20 \le E_o \le 480$ µmol m^{-2} s^{-1}), irradiances ≤120 µmol m^{-2} s^{-1}, and irradiances ≥180 µmol m^{-2} s^{-1}. Significance levels: •••p < 0.001, ••p < 0.01; •p < 0.05; NS: not significant

	$20 \le E_o \le 480$	$E_o \le 120$	$E_o \ge 180$
μ	•••		
${}^{\mu}P^{B}$	•••		
Chl *a*/C	•••		
Chl *a*	•••		
C		•	NS
N		•••	••
P		NS	•
N/C	NS	••	NS
P/C	•	NS	NS
N/P	••	NS	NS

Table 1). The N/C ratio decreased significantly with increasing irradiance below 120 µmol m^{-2} s^{-1}, but was approximately constant at higher irradiances; the P/C and the N/P ratios increased and decreased significantly with increasing irradiance, respectively, between 20 and 480 µmol m^{-2} s^{-1} (Fig. 2, Table 1).

Effect of temperature and salinity

A multiple regression of the specific growth rate (μ) on temperature (T) and salinity (S) yielded:

$$\mu = 0.073T + 0.027S - 0.002T^2 - 0.0006S^2 - 0.564$$

The model is highly significant according to ANOVA ($p < 0.001$) and 83% of the variance is explained by the variables. Derivation of the model yields optimum temperature and salinity at 21°C and 23‰ S, respectively, and an optimum specific growth rate of 0.53 d^{-1} (Fig. 3). The measured maximum growth rate (0.57 d^{-1}) was observed at 20 to 24°C and 24‰ S (Table 2).

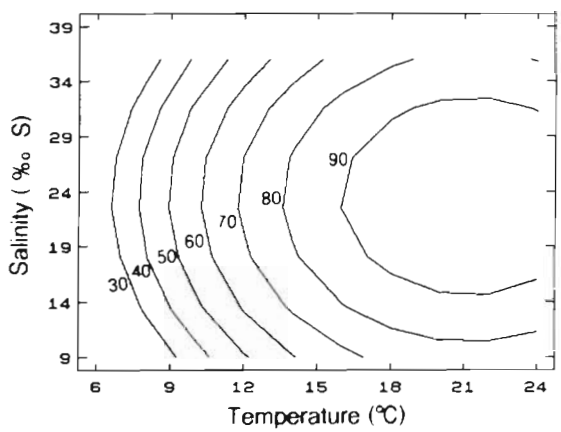

Fig. 3. *Gymnodinium galatheanum*. Response surface contours of the combined effect of temperature and salinity on growth rate (d^{-1}). Numbers on figure indicate percentage of model-predicted optimum

Table 2. *Gymnodinium galatheanum*. Specific growth rate (d^{-1}) under different combinations of temperature and salinity (SE indicated in parentheses)

Salinity (‰)	Temperature (°C): 7	10	15	20	24
10	0.13 (0.007)	0.17 (0.007)	0.28 (0.020)	0.45 (0.029)	– –
14	0.17 (0.002)	0.21 (0.005)	0.41 (0.012)	0.63 (0.005)	0.33 (0.015)
19	0.18 (0.002)	0.27 (0.007)	0.48 (0.002)	0.57 (0.010)	0.45 (0.012)
24	0.17 –	0.25 (.012)	0.45 (0.007)	0.57 (0.005)	0.57 (0.017)
29	0.18 (0.012)	0.22 (0.002)	0.41 (0.007)	0.56 (0.005)	0.51 (0.017)
34	0.19 (0.005)	0.21 (0.010)	0.38 (0.005)	0.47 (0.037)	0.38 (0.010)

The growth rate of *Gymnodinium galatheanum* was significantly affected by temperature ($7 \le T \le 24$°C) and salinity ($10 \le S \le 34$‰ S), according to the 2-factor analysis of variance (Table 3). No temperature-salinity interaction was found for the growth rate. The carbon, nitrogen and phosphorus contents increased significantly at combinations of low temperature (7, 10°C) and low salinity (10‰ S); at higher salinities (14 to 34‰ S) carbon and nitrogen contents were independent of salinity, whereas the phosphorus content decreased significantly with increasing salinity (Fig. 4, Table 3). Carbon, nitrogen and phosphorus contents, however, decreased with increasing temperature; an

Table 3. *Gymnodinium galatheanum*. Significance results of an ANOVA of growth rate, cellular C, N and P, and the N/C, P/C and N/P ratios on temperature (7, 10, 15, 20, 24°C) and salinity (10, 14, 19, 24, 29, 34‰ S). Significance levels: •••p < 0.001, ••p < 0.01, •p < 0.05; NS: not significant

Source of variation	μ	C	N	P
Temperature[a]	•••	•••	••	•••
Salinity[a]	•••	•••	•••	•••
Temperature[b]		•••	•	••
Salinity[b]		NS	NS	••

Source of variation	N/C	P/C	N/P
Temperature[a]	••	•••	•••
Salinity[a]	NS	•••	••

[a]All data; [b]Data at 10‰ S excluded

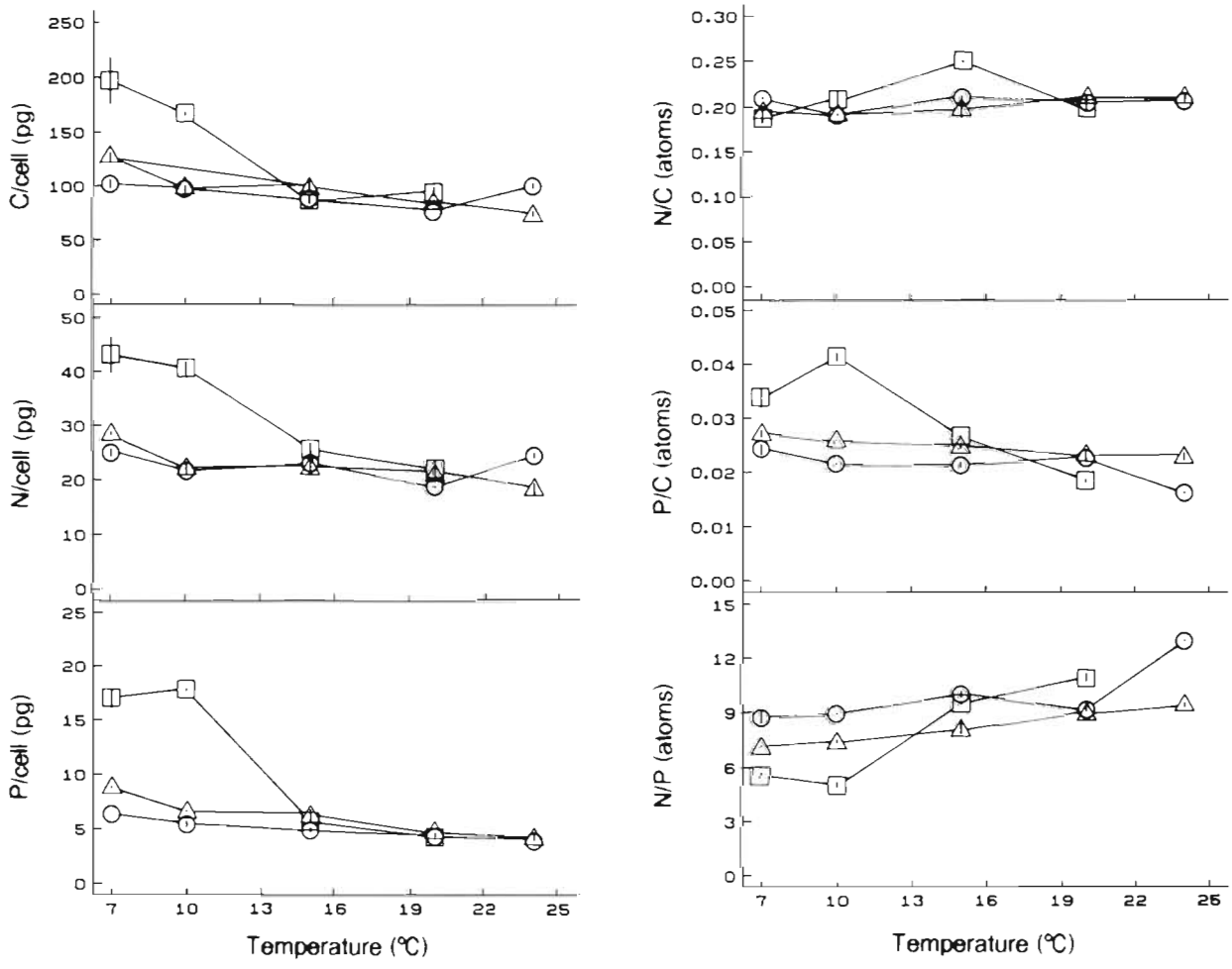

Fig. 4. *Gymnodinium galatheanum*. Effect of temperature and salinity on cellular C, N and P and on N/C, P/C and N/P ratios. Data shown for the lowest and the highest salinity used and for the optimum salinity for growth: (□) 10‰, (△) 24‰, (○) 34‰. SE indicated by vertical bars

ANOVA on the total data set showed significant effects of both temperature and salinity on carbon, nitrogen and phosphorus (Fig. 4, Table 3). The ratios between cellular C, N and P showed significant temperature effects; the P/C and N/P ratios also varied significantly with the salinity, while the N/C ratio was independent (Fig. 4, Table 3).

DISCUSSION

Gymnodinium galatheanum grew at all experimental temperatures (7 to 24°C) and salinities (10 to 34‰ S), with optimum growth at high temperatures and moderate to high salinities, ~17–24°C and 15–32‰ S, respectively (Fig. 3). Differences in growth rate of *G. galatheanum* at identical experimental conditions (15°C, 34‰ S, 255 µmol m^{-2} s^{-1}, 18 h daylength) were found between the irradiance experiment (0.28 d^{-1}) and the temperature/salinity experiment (0.38 d^{-1}), possibly because the experiments were carried out at different times of the year and involved different batches of seawater. In addition, Johnsen & Sakshaug (1993) reported *G. galatheanum* growth rates of 0.25 d^{-1} under conditions of 20°C, 34‰ S, 170 µmol m^{-2} s^{-1}, and 12 h daylength.

$^{\mu}P^{B}_{m}$ for *Gymnodinium galatheanum*, 3.1 mg C (mg chl *a*)$^{-1}$ h^{-1}, is similar to the maximum $^{\mu}P^{B}$ found for *Prorocentrum micans* (Falkowsky et al. 1985; calculated from their Table 1), while $^{\mu}P^{B}_{m}$ for *Gyrodinium aureolum* (0.82; Nielsen 1992) is lower. Variation in $^{\mu}P^{B}$ among the 3 dinoflagellates is thus within a factor of 3.7. This variation is small compared to the variation in P^{B} found between different taxa (a factor of 10; Geider 1993), which supports Geider's conclusion that P_m shows little variation within taxa compared to among taxa. Differences in $^{\mu}P^{B}_{m}$ are due to variations in both growth rate and chl *a*/C ratio, and for the 3 species discussed above, variations in growth rate and chl *a*/C amount to factors of 1.6 and 6.3, respectively.

Most of the variation is thus accounted for by the chl *a*/C ratio.

The saturation irradiance at 15°C and 34‰ S for ${}^{\mu}P^{B}_{m}$ of *Gymnodinium galatheanum* (>500 µmol m^{-2} s^{-1}) is higher than for maximum growth (μ_m; 120 µmol m^{-2} s^{-1}) (Fig. 1). This difference reflects the decrease in the chl *a*/C ratio with increasing irradiance (Fig 2).

For *Gymnodinium galatheanum* the cellular contents of C, N and P ranged from 72 to 197, 17 to 51 and 4 to 17 pg $cell^{-1}$, respectively (Figs. 2 & 4). Johnsen & Sakshaug (1993) reported 43 to 62 pg C $cell^{-1}$ Cellular C, N and P reached minimum values around the saturation irradiance for growth (120 µmol m^{-2} s^{-1}). At irradiances below the saturation irradiance for growth, cells became enriched with respect to C, N and P (Fig. 2). A similar trend has been found for *Gyrodinium aureolum* (Nielsen 1992) and *Skeletonema costatum* (Sakshaug & Andresen 1986) and may be explained as an adaptive change to inactive, long-term viable stages. The irradiance relationships of cellular C, N and P were very similar; this is reflected in the ratios between the elements, with no significant differences found below and above the saturation irradiance for growth, except for the N/C ratio where a significant increase was found with decreasing irradiance (Fig. 2, Table 1).

The N/C, P/C and N/P ratios ranged from 0.18–0.32, 0.016–0.041 and 5.0–11.3, respectively. These ratios are similar to those found for *Gyrodinium aureolum*, although the N/C ratio is slightly higher for *Gymnodinium galatheanum*. The N/C ratio found in the present study (~0.19) is slightly higher than that (0.15) reported by Paasche et al. (1984) at 20°C and 24‰ S and that (0.15–0.19) reported by Johnsen & Sakshaug (1993) under conditions of 20°C, 34‰ S, 30 to 170 µmol m^{-2} s^{-1} and 12 h daylength. Compared to the P/C and N/P ratios reported for other dinoflagellates (0.009–0.014 and 8–17, recalculated by converting organic phosphorus to total phosphorus by a conversion factor; see Table II in Sakshaug et al. 1984), the values for *G. galatheanum* indicate a high relative cellular phosphorus content and a large storage capacity for phosphorus.

The blooms of *Gymnodinium galatheanum* in Walvis Bay were associated with high surface temperatures compared with temperatures just outside the bay (Copenhagen 1953, Pieterse & Van Der Post 1967). The blooms of *G. galatheanum* in the Oslofjord also occurred in years with high surface temperatures (K. Tangen pers. comm.). Thus temperature may be a regulating factor for blooms of *G. galatheanum*, as has been found for *Gyrodinium aureolum* (Nielsen & Tønseth 1991).

Gymnodinium galatheanum successfully forms red tide blooms, as does the closely related *Gyrodinium aureolum*. Results from the present study add to the list of similarities between *G. galatheanum* and *G. aureolum*. Saturation irradiances for growth and for ${}^{\mu}P^{B}_{1}$ respectively, are similar for *G. galatheanum* (120 and >500 µmol m^{-2} s^{-1}) and for *G. aureolum* (150 and >400 µmol m^{-2} s^{-1}) (Nielsen 1992), and their saturation irradiances for ${}^{\mu}P^{B}$ are higher than found for many other dinoflagellates (Partensky & Sournia 1986). Both species may survive for long periods (several months) in the stationary phase and both are able to accumulate large amounts of P compared to other dinoflagellates, an ability which may be important in bloom formation (Nielsen & Tønseth 1991). The maximum growth rates are quite similar for the 2 species. Growth of *G. galatheanum*, however, is less sensitive to temperature-salinity changes, and it has a broader temperature-salinity tolerance range than does *G. aureolum*, which did not grow at <10°C and <12‰ S (Nielsen & Tønseth 1991). Growth of *G. galatheanum* is not photoinhibited at irradiances <500 µmol m^{-2} s^{-1} as is *G. aureolum* (Nielsen 1992). There may be a slight difference in the origin of the blooms; while the *G. galatheanum* blooms reported from the eutrophic Walvis Bay seems to arise in the bay, blooms of *G. aureolum* typically evolve offshore in tidal fronts where combinations of high nutrient levels and high temperature occur, and when conditions are suitable they are transported towards coastal areas (Nielsen & Tønseth 1991). Given that these algae are physiologically alike, but that *G. galatheanum* is the hardier of the two, one would expect *G. galatheanum* blooms to be more frequent than *G. aureolum* blooms, assuming that initial stocks are present. Why this is not the case in North European waters is a question which still has to be answered.

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