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EFFECTS OF SMALL-SCALE TURBULENCE ON PHOTOSYNTHESIS, PIGMENTATION, CELL DIVISION, AND CELL SIZE IN THE MARINE DINOFLAGELLATE *GONYAULAX POLYEDRA* (DINOPHYCEAE)[1]

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ABSTRACT

Several experiments were conducted to understand better the physiological mechanisms underlying growth inhibition of the dinoflagellate Gonyaulax polyedra *Stein due to small-scale turbulence shear. To measure photosynthetic ^{14}C uptake, a "phytoplankton wheel" device for rotating cultures in closed bottles was used. Turbulence was quantified biologically in the bottles by comparing growth inhibition with that in cultures with constant shear between a fixed cylinder and an outer concentric rotating cylinder (a stable Couette flow). At saturating irradiances, particulate photosynthesis (P_{sat}) or photosynthesis per unit chlorophyll (P^B_{sat}) were not inhibited completely at the highest turbulence level (26.6 rad·s^{-1}), and photosynthesis was less sensitive than growth. Photosynthesis per cell (P^C_{sat}) was increased by turbulence. In three experiments on the effects of turbulence on photosynthesis versus irradiance curves, the slope of the curve, α, for particulate photosynthesis at limiting irradiances did not change. Photosynthesis per unit chlorophyll per unit irradiance (α^B) decreased at high (but not intermediate) turbulence levels. Photosynthesis per cell per unit irradiance, α^C, increased with turbulence, suggesting an increase in photosynthetic efficiency in turbulent cultures. In two of the three experiments, respiration rates increased with turbulence, and in one experiment excretion of photosynthetically fixed ^{14}C was not affected by motion. Ratios of accessory pigments to chlorophyll a did not change with turbulence, but pigments per cell and per dry weight increased with turbulence. These findings suggest little or no disruption of the photosynthetic apparatus. When turbulence was applied for 1 week, β-carotene increased while peridinin and diadi-*

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noxanthin decreased, suggesting inhibition of synthesis of these latter pigments by prolonged turbulence. Since cell numbers did not increase or decreased during turbulent 72-h incubations, cell division was inhibited and also the cells were very much enlarged. Increases in α^C per cell suggest that, in the sea, photosynthetic metabolism can persist efficiently without cell division during turbulent episodes. After turbulence ceases or reaches low levels again, cells can then divide and blooms may form. Thus, blooms can come or go fairly rapidly in the ocean depending on the degree of wave- and wind-induced turbulence.

Key index words: cell size; Gonyaulax polyedra; *photosynthesis; phytoplankton; pigmentation; Pyrrophyta; red tide; turbulence*

In terms of its effects on phytoplankton in the sea, turbulence can be separated into large- and small-scale processes. Large-scale turbulence processes acting at scales from 1 to 1000 m or more diffuse nutrients to regions of phytoplankton concentration and distribute phytoplankton into the thermocline, nutricline, or various light regimes. Many workers (Platt 1972, Holligan et al. 1980, Denman and Gargett 1983, Legrendre and Demers 1984) have related microalgal distributions to large-scale turbulence and have described some of the effects of these processes.

Despite the importance of large-scale turbulence to phytoplankton in the sea, we are only concerned herein with effects of small-scale turbulence processes that act physiologically at the cellular level on an interesting red tide dinoflagellate.

Cellular activities in phytoplankton can only be directly affected by the turbulence shear (rate of strain) on millimeter scales. Viscous stresses, dissipation rates, and rates of strain are constant on length scales smaller than the Kolmogorov length scale $L_K = (\nu^3/\epsilon)^{1/4}$, where ν is the kinematic viscosity and ϵ is the viscous dissipation rate of turbulent kinetic energy. According to the 1941 Kolmogorov universal similarity theory of turbulence, kinetic energy cascades at rate ϵ between large-scale sources and the viscous scale sink at L_K, so that all scales of turbulence between depend only on ϵ. Motions on scales smaller than L_K (those experienced by phytoplankton) depend also on the viscosity ν.

Small-scale flows resulting from turbulence have profound effects on phytoplankton growth. For instance, dinoflagellate cultures often grow poorly, if at all, when shaken on reciprocal or rotary shakers operated at speeds of around 100 rpm (Tuttle and Loeblich 1975, Galleron 1976, White 1976, Pollingher and Zemel 1981, Berdalet 1992). Such inhibition may partly explain why dinoflagellate red tide blooms off the Scripps Institution of Oceanography in La Jolla Bay have long been known to be associated with protracted periods of calm seas (Allen 1938, 1946). More recent work (Tynan 1993) showed that large abundances of dinoflagellates in 1990 and 1991 at the Scripps Pier were negatively correlated with "significant wave height" (and diatom growth was positively correlated). In a review of the general effects of small-scale turbulence on phytoplankton (Thomas and Gibson 1990a), we present evidence that dinoflagellates are usually more sensitive to turbulence than diatoms. Gibson and Thomas (1995) show that intermittency in laboratory turbulence enhances inhibition of dinoflagellate growth (consistent with the 1990 and 1991 Scripps Pier observations of negative correlation with waves, Tynan 1993).

Most laboratory observations on dinoflagellate cultures have reported the degrees of agitation as speeds of reciprocal or rotational shaking, but recently we quantified inhibitory motion in fluid dynamic terms (Thomas and Gibson 1990a, b, 1992). We showed that growth inhibitory levels of ϵ, the dissipation rate of kinetic energy; of γ, the rate of strain or shear; and of τ, the viscous stress on the cells, were about 0.18 $cm^2 \cdot s^{-3}$, 4.4 $rad \cdot s^{-1}$, and 0.02 $dyne \cdot cm^{-2}$, respectively, when cultures of *Gonyaulax polyedra* Stein were sheared in a cylindrical Couette device. The turbulence parameters ϵ, γ, and τ are constant on length scales much larger than the sizes of the cells, and all are assumed to be equivalent measures of the strength of turbulence that inhibits growth.

The objective of the present investigation was to study some of the physiological mechanisms behind inhibition of *Gonyaulax polyedra* growth. We hypothesized that growth inhibition would result from inhibition of photosynthesis. However, we show herein that photosynthesis, while inhibited at high turbulence levels (less than those probably found in the near-surface euphotic zone), is less sensitive than growth. Additional work on pigment ratio changes suggested little disruption of the photosynthetic apparatus by water motion. We also show that cell division is inhibited by turbulence and that inhibited cells are larger than those in control cultures.

MATERIALS AND METHODS

Gonyaulax polyedra Stein cultures were kindly supplied by Dr. Mark Huntley of Scripps; their origin is unknown, but the alga is probably from local waters. It was maintained in GPM-enriched seawater medium (Loeblich 1975) at room temperature (~23° C), and at an irradiance (photosynthetically available radiation, PAR) of 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ supplied by Powergroove cool-white fluorescent lights. PAR was measured with a LiCor cosine-corrected quantum sensor with either a LiCor Model 1000 data logger or a LiCor Model 190 readout meter.

Experimental conditions. Cultures for experiments were grown under the same physical conditions but in full-strength seawater (f/2-Si medium, Guillard 1983). This change in culture medium allowed better estimation of total dissolved inorganic carbon for photosynthesis calculations.

Previously we used a concentric cylinder Couette device to apply quantified turbulence to *Gonyaulax polyedra* cultures (Thomas and Gibson 1990a, b). This apparatus was described by Couette (1890), and the historical development of flow studies in such devices has been discussed by Donnelly (1991). Our device (Fig.

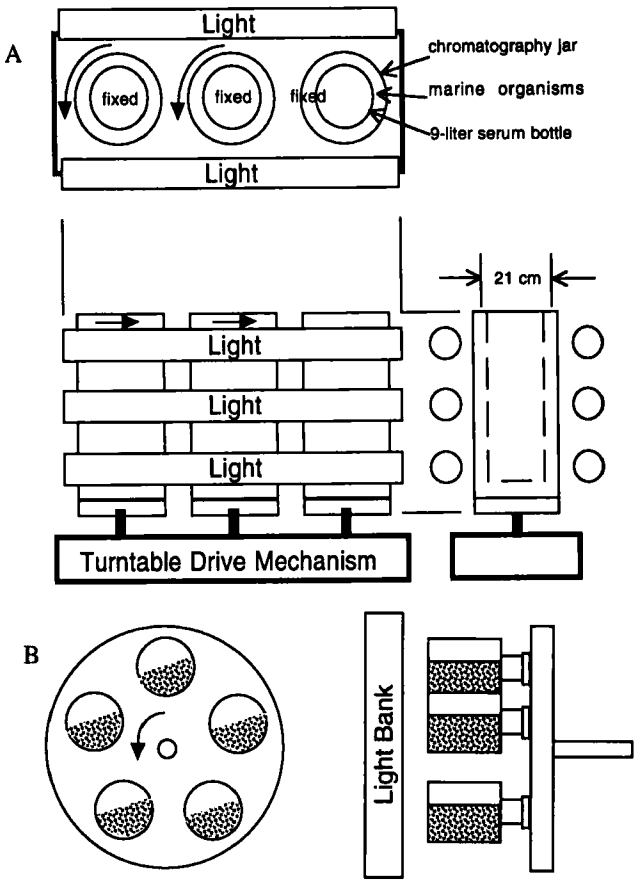

FIG. 1. Apparatus for producing small-scale turbulence shear. A) Couette device. B) Phytoplankton wheel: 125-mL bottles containing 50-mL cultures were mounted on a vertical circular plate that was rotated about its center, as shown on the left. Lighting is shown by the side view on the right.

1A) consists of a 22-cm-diameter Pyrex chromatography cylindrical jar into which a 9-L Pyrex serum bottle was inserted. The outer cylinder was rotated at given constant speeds, and the culture was contained within the 0.5-cm gap between the two glass cylinders. From the rotation speeds, the gap width, and the inner diameter of the outer cylinder, the rates of strain (γ), the kinetic energy dissipation rates (ϵ), and stresses (τ) on the cells could be derived. Growth rates in two rotating Couette devices were compared to those in a fixed control (Fig. 1A). For details, see our previous papers (references earlier).

The Couette device, however, was an open system and, for measuring photosynthetic rates using $H^{14}CO_3^{-1}$ uptake, closed bottles were needed. Pyrex 125-mL bottles were mounted horizontally by their necks and positioned in front of the Powergroove light bank so that they could be illuminated through their bottoms. Light was attenuated with a plastic filter to give uniform irradiances at all bottle positions. These irradiances varied by no more than ±6% from bottle to bottle. The highest irradiance and that used for most experiments was 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Five bottles per turbulence treatment were clamped by their necks to wheels that could be rotated at different speeds (Fig. 1B). Each bottle contained 50 mL of culture, and this liquid was sheared by the wall motion within the bottles as the wheels rotated. There were two sets of five experimental bottles and an additional set of five still control bottles that were positioned in front of the light bank to give irradiances that were identical to those in treated bottles.

Biological calibration of the wheels. We knew the rate of strain or

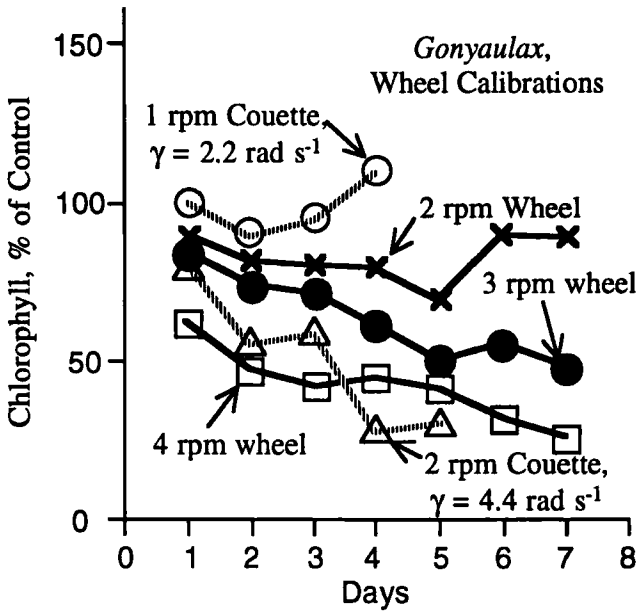

FIG. 2. Comparison of *Gonyaulax polyedra* inhibition in the Couette device with that in wheel bottles.

shear that cells experienced at given Couette rotation speeds and could relate the degree of growth inhibition to cylinder speeds (Thomas and Gibson 1990a, b). To calibrate the wheels, we compared the degree of inhibition in the Couette and associated shear values to the degree of inhibition of growth of wheel bottle cultures at various rotation speeds. We postulated that shear in the wheels would be related to rotation speeds as some coefficient, C', times the angular velocity of the wheel. Therefore, $\gamma = C'(2\pi S/60)$, where γ is the rate of strain in $rad \cdot s^{-1}$ and S is the rpm. The calibration process to determine C' consisted of several experiments in which wheel bottle cultures were rotated at different speeds, and the degrees of growth inhibition in these cultures were compared with those in Couette devices where γ was known from previous experiments (Fig. 2). The Couette devices were large because the cylinders were glass. It would have been desirable to construct them of plexiglass and thus make them smaller, but preliminary experiments showed that this plastic was toxic to *Gonyaulax polyedra*. Because of their size, Couette cultures could not be replicated, and trends over several days had to be followed to show inhibition (Fig. 2). Wheel cultures were replicated (n = 5) at each rpm, and wheel values in Figure 2 had coefficients of variation <10%. Inhibition was followed by *in vivo* chlorophyll fluorescence changes. Previously in Couette cultures, the same amounts of inhibition were found when cell number changes were followed.

Qualitatively, 2 rpm on the wheel gave about the same inhibition of *Gonyaulax polyedra* growth as 1 rpm in the Couette. We calculated previously that γ at 1 rpm in the Couette was 2.2 $rad \cdot s^{-1}$. Taking this value and $S_{wheel} = 2$ rpm, then C' = 10.5. Similarly, 2 rpm in the Couette inhibited growth to the same extent as 4 rpm on the wheel, and again C' = 10.5. More quantitatively, we compared treated/control inhibition ratios in the Couette with similar ratios in the wheel and found a linear relationship between wheel rpm and shear (Fig. 3). From this relationship, C' = 12.7, which is close to 10.5. Thus, we were able to calibrate the wheel biologically.

Photosynthesis measurements. Ten photosynthesis experiments were performed. Turbulence levels and preincubation periods were varied until effects on photosynthesis were observed, and each experiment was designed taking into account the results of previous ones. Eventually we found that 72-h preincubation periods and rotation speeds of 20 rpm were necessary to obtain any

significant inhibition of photosynthesis. Inocula for all experiments were grown at room temperature (~23° C) and 100 μmol·m^{-2}·s^{-1} irradiance in still cultures. For photosynthesis experiments, these late log-phase inocula were diluted 1:5 with fresh f/2-Si medium so that exponential growth could be initiated during preincubations. After dilution, cell numbers ranged from 856 to 2860 cells·mL^{-1} in the various experiments (mean = 1597 ± 574 SD). Such numbers gave exponential growth in still control cultures. Then 50 mL of the dilutions were placed in the 125-mL bottles on the wheels.

During preincubations, turbulence was applied to rotated cultures, but not to still control cultures. Two sets of five bottles were subjected to given shear values by rotating them at given rpms. One set of five bottles was not rotated, and these served as controls. Bottles were incubated at room temperature and, in experiments other than those assessing the effects of turbulence on photosynthesis versus irradiance curves (P vs. I curves), the bottles were incubated at a high constant irradiance (200 μmol·m^{-2}·s^{-1}). Following preincubation, samples from each set of bottles were taken for pigments and cell number determinations. Then, photosynthesis was measured by adding 2–4 μCi (7.4–14.8 × 10^4 Bq) of $NaH^{14}CO_3$ solution (200–400 μL) to all bottles which were incubated for 2 h further at room temperature and at specified irradiances. One bottle in each set (treated and control bottles) was darkened with aluminum foil, and dark uptake of ^{14}C was always subtracted from light uptake.

For determinations of particulate uptake (most measurements), the contents of the bottles were filtered through Whatman GF/C glass-fiber filters after incubation. The filters were fumed over concentrated HCl for 30 min to remove residual inorganic ^{14}C and were placed in vials to which liquid scintillation fluid was then added. To determine the amount of organic ^{14}C excreted back into the medium during incubation, total uptake was determined by placing 5 mL of the labeled cell suspension into 20-mL scintillation vials, acidifying the suspension with 200 μL of concentrated HCl, and letting the vials stand open for 24 h followed by shaking the open vials for 2 h. This removed inorganic ^{14}C completely as determined by adding radioactivity to an initial control cell suspension and taking 5 mL through the whole acidification, standing open, and shaking process. Then, 10 mL of liquid scintillation fluid was added, and the radioactivity was determined by liquid scintillation counting. Excreted organic ^{14}C was determined by subtracting particulate radioactivity from total radioactivity. All radioactivity counts were converted to dpm using an external standard ratio quench curve.

In some experiments, both turbulence and irradiance were varied during incubations. Light was attenuated by placing nickel-perforated screens over the bottles to give attenuations that ranged from 23 to 64% of the ambient 200 μmol·m^{-2}·s^{-1}. Thus, we were able to assess the effects of turbulence on P vs. I curves. In this paper, P_{sat} refers to the absolute amount of photosynthesis in μmol C·L^{-1}·h^{-1} found at the highest irradiance, P^B refers to photosynthesis per chlorophyll *a* (chl *a*), and P^C refers to photosynthesis per cell.

Pigment determinations. Most pigment measurements were conducted in cultures preincubated for photosynthesis estimations. However, in one experiment, a time series of samples for pigment analyses was harvested periodically for 1 week at constant rates of strain (shear) of 5.3 and 8.0 rad·s^{-1} (4 and 6 rpm, respectively).

Chlorophyll *a* was determined by filtering 5-mL portions of each cell suspension through Whatman GF/C glass-fiber filters and extracting the filters overnight in cold 90% acetone. Then, fluorescence was measured in each extract (Parsons et al. 1984). Additional measured portions of cell suspensions were filtered for determinations of other pigments. The filters were stored in liquid nitrogen until extraction and pigment analyses.

Photosynthetic pigments were analyzed by high-performance liquid chromatography (HPLC) on a reverse-phase C-18 column (Alltech Econosphere, 25 cm × 4.5 mm, 5-μm particles) by elution in a high-pressure gradient system consisting of a linear gradient

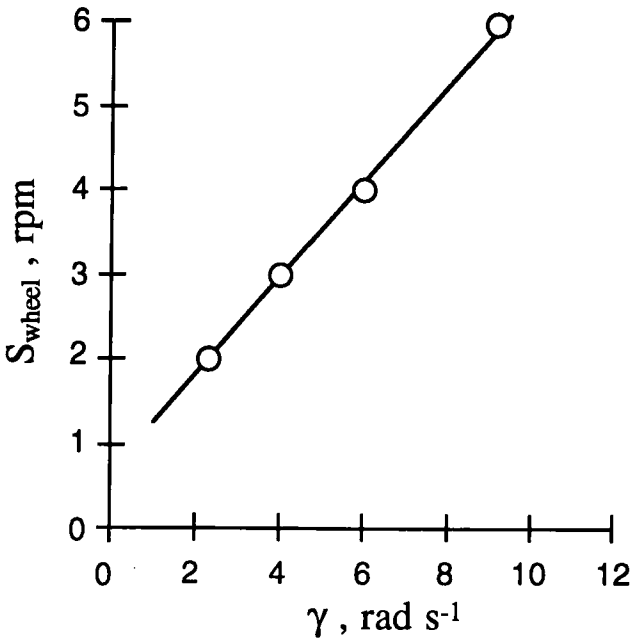

FIG. 3. Relationship between wheel rpm and shear.

from 100% A to 100% B in 12 min and maintaining B for another 13 min. Solvent A (1 L) consisted of 80:20 methanol: water (v:v) where 100 mL of HPLC-grade water was prepared with 1.5 g tetrabutylammonium acetate and 0.96 g of ammonium acetate as an ion pairing agent (Mantoura and Llewellyn 1983). Solvent B consisted of 60:40 methanol: ethylacetate (v:v). Chlorophylls and carotenoids were monitored by absorption at 440 nm and quantified by calibration of the column with pigments isolated with a semipreparatory system (Nelson and Wakeham 1989) from a culture of *Gonyaulax polyedra*. For chlorophylls we used the extinction coefficients of Jeffrey and Humphrey (1975). For carotenoids, extinction coefficients were as follows: peridinin and its derivatives, 160 L·g^{-1}·cm^{-1} at 452 nm; diadinoxanthin, 225 L·g^{-1}·cm^{-1} at 446 nm; diatoxanthin, 250 L·g^{-1}·cm^{-1} at 448 nm; and β-carotene, 262 L·g^{-1}·cm^{-1} at 452 nm (Davies 1976). All samples were extracted overnight in 100% methanol.

Microscopic measurements and observations. Live cells were observed with a phase-inverted light microscope, and additional samples were preserved with Lugol's iodine solution for microscopic cell enumerations using a Palmer-Maloney counting chamber. Size measurements (approximate diameters to the nearest micrometer) were determined in preserved cells with the inverted microscope and an eyepiece micrometer. Cell volumes were calculated from these diameters assuming the cells were spherical. Cellular dry weights were calculated assuming a density of 1.0 and that dry weight = 10% of fresh weight.

RESULTS AND DISCUSSION

Photosynthesis at saturating irradiances. Our experimental apparatus was designed to provide shear to 50-mL bottle cultures. The maximum irradiance incident to the bottoms of these radially mounted bottles was 200 μmol·m^{-2}·s^{-1} supplied over a 2.5 × 1.0-m area, but the light was attenuated along the axes of the bottles so that at the end away from the bottom the irradiance was only 120 μmol·m^{-2}·s^{-1}. This experimental apparatus differed from that used previously (Prézelin et al. 1977) for *Gonyaulax polyedra* photosynthesis measurements. They used still

TABLE 1. *Particulate photosynthesis in sheared* Gonyaulax polyedra *cells at a high irradiance of 200 μmol·m⁻²·s⁻¹.*

Experiment no.	Preincubation time (h)	Speed (rpm)	γ (rad·s⁻¹)	Photosynthesis (μmol C·L⁻¹·h⁻¹)	% of control	Photosynthesis per chlorophyll (μmol C·μmol chl⁻¹·h⁻¹)	% of control	Photosynthesis per cell (10⁻⁶ μmol C·cell⁻¹·h⁻¹)	% of control
1	0	Control	0.0	3.82	100	142.5	100	1.92	100
		2	2.66	3.43	90	128.0	90	1.72	90
		6	7.98	3.71	97	138.4	97	1.86	97
4	0	Control	0.0	14.23	100	287.5	100	12.37	100
		10	13.30	12.54	88	253.6	88	10.90	88
		20	26.60	11.54	81	233.2	81	10.03	81
2	24	Control	0.0	4.89	100	180.6	100	2.82	100
		2	2.66	5.12	105	164.6	91	2.72	96
		6	7.98	4.50	92	150.7	83	3.23	115
5	24	Control	0.0	9.29	100	202.1	100	5.68	100
		10	13.30	8.60	93	200.7	99	4.55	80
		20	26.60	8.65	93	185.4	92	5.13	90
6	24	Control	0.0	9.72	100	318.5	100	6.95	100
		10	13.30	6.83	70	211.2	66	5.74	83
		20	26.60	7.82	80	301.3	95	6.95	100
3	72	Control	0.0	10.46	100	260.5	100	5.48	100
		6	7.98	10.21	98	288.9	111	8.52	155
7	72	Control	0.0	9.87	100	73.8	100	2.56	100
		10	13.30	11.29	114	96.9	131	5.45	213
		20	26.60	7.50	76	82.2	112	5.19	202
8	72	Control	0.0	12.34	100	138.1	100	3.89	100
		20	26.60	7.98	65	8.4	61	5.87	151
9	72	Control	0.0	15.31	100	165.5	100	4.02	100
		10	13.30	14.37	9	214.8	130	5.50	137
10	72	Control	0.0	21.68	100	436.6	100	7.07	100
		20	26.60	12.46	57	264.0	60	7.81	110

5-mL cultures illuminated with a collimated beam from a 500-W incandescent lamp and measured O_2 production polarographically at different incident irradiances, which probably varied very little within their culture vessel. Their saturating irradiance was 4 mW·cm⁻², which is equivalent to 184 μmol·m⁻²·s⁻¹ using a factor of 1 W·m⁻² = 4.6 μmol·m⁻²·s⁻¹ (McCree 1972).

Control values for photosynthesis per chlorophyll and per cell varied greatly from experiment to experiment at an incident irradiance of 200 μmol·m⁻²·s⁻¹ (Table 1). Mean photosynthesis per chlorophyll was 220.6 ± 106.3 (SD) μmol C·μmol chl⁻¹·h⁻¹ at 200 μmol·m⁻²·s⁻¹ irradiance. Assuming a photosynthetic quotient (C/O_2) of 0.8, the previous values P^B_{sat} found by Prézelin and Sweeney (1978) would calculate to 141–245 μmol C·μmol chl⁻¹·h⁻¹. Our mean value is within this range. Previous values for P^C_{sat} in *Gonyaulax polyedra* range from 17.5 to 22.5 × 10⁻⁶ μmol O_2·cell⁻¹·h⁻¹ (Prézelin et al. 1977) for cells grown at a high irradiance. Our mean value for control cultures at 200 μmol·m⁻²·s⁻¹ irradiance was 5.28 ± 3.07 × 10⁻⁶ μmol C·cell⁻¹·h⁻¹. Again assuming a photosynthetic quotient of 0.8, our mean value is about one-half of these previous determinations. This difference may be due to differing experimental conditions, particularly differing irradiance levels.

There was some inhibition of photosynthesis by turbulence after 72 h of preincubation at 26.6 rad·s⁻¹ (20 rpm), but little inhibition with 0 or 24 h of preincubation (Table 1). In contrast to the complete inhibition of growth at low levels of shear (>4.4 rad·s⁻¹) (Thomas and Gibson 1990a, b), photosynthesis was never completely inhibited even at 26.6 rad·s⁻¹. Thus, the photosynthetic rate was not as sensitive to turbulence as the growth rate.

In some experiments, the photosynthetic rate per chl *a* was also inhibited at 26.6 rad·s⁻¹, particularly with a 72-h preincubation period, but again inhibition was not complete as it was for the growth rate (Table 1). With 0- or 24-h preincubations, photosynthesis per chl *a* was only slightly inhibited, if at all. There was little change in photosynthesis per cell due to turbulence with 0- or 24-h preincubation periods. However, after 72-h preincubations, high levels of turbulence greatly increased photosynthesis per cell. This was due to photosynthesis occurring in cells that had not divided (see below).

Photosynthesis versus irradiance. Photosynthesis in experiment 8 was saturated at the highest irradiance used (200 μmol·m⁻²·s⁻¹), and at this intensity P_{sat} was reduced by turbulence (26.6 rad·s⁻¹; 20 rpm) to 65% of that in still control cultures (Fig. 4). Saturation irradiances were 108 μmol·m⁻²·s⁻¹ in rotated cultures compared to 145 μmol·m⁻²·s⁻¹ in still

TABLE 2. *Physiological parameters of* Gonyaulax polyedra *derived from photosynthetic measurements at different irradiances. Comparisons are between still controls and turbulent cultures preincubated for 72 h. Photosynthesis lasted 2 h.*

Parameter	Experiment 8 (26.6 rad·s^{-1})			Experiment 9 (13.3 rad·s^{-1})			Experiment 10 (26.6 rad·s^{-1})		
	Control	20 rpm	% control	Control	10 rpm	% control	Control	20 rpm	% control
P_{sat} (μmol C·L^{-1}·h^{-1})	12.34	7.99	64.7	15.31	14.37	93.9	12.93	7.08	54.8
α·chl^{-1} (μmol C·μmol chl^{-1} (μmol·m^{-2}·s^{-1})$^{-1}$)	1.03	0.87	84.5	0.98	1.28	130.2	1.24	0.85	68.6
α·cell^{-1} (μmol C·cell^{-1} (μmol·m^{-2}·s^{-1})$^{-1}$)	0.029	0.06	210.1	0.024	0.033	137.5	0.02	0.025	125.6
Respiration (μmol C·L^{-1}·h^{-1})	1.29	0.77	59.7	2.47	3.5	141.7	0.86	1.34	155.8
Respiration (as % P_{sat})	10.6	9.7	91.5	16.1	24.4	151.6	6.6	18.9	349.2
% carbon excreted (as % P_{sat})	[a]	[a]	[a]	[a]	[a]	[a]	24.5	24.8	101.2
Cell density, time zero (cells·mL^{-1})	1220	1220		2860	2860		1932	1932	
Cell density, time final (cells·mL^{-1})	3172	1360	42.9	3800	2610	68.7	3067	1595	52.0
Division rate (Doublings d^{-1})	0.459	0.052	11.4	0.137	−0.044	0.0	0.222	−0.092	0.0
Cell volume (10^5 μm^3)	[a]	[a]	[a]	18.82	26.52	140.9	17.32	26.52	153.1

[a] Values not measured.

control cultures. For photosynthesis itself (Fig. 4A), the slopes of the P vs. I curves, α, or photosynthesis per unit irradiance, did not differ in turbulent and control cultures. Algal respiration could be estimated by extrapolating the P vs. I curve to zero irradiance (Table 2). This gave a negative intercept, which may represent respiration. For experiment 8, respiration in turbulent cultures was about 60% of that in control cultures, and in both treatments respiration was about 10% of P_{sat} (Table 2).

In experiment 8, P^B, P_{sat} per chlorophyll, was reduced in turbulent cultures, and the slope, α^B, was slightly reduced (Fig. 4B, Table 2). According to Prézelin (1987), these changes in dinoflagellate photosynthesis per chlorophyll in P vs. I experiments indicate an increase in the size of the photosynthetic unit (PSU). However, pigment data indicate that PSU numbers were also changed (see later).

Changes due to turbulence in photosynthesis per cell (Fig. 4C, Table 2) were much more pronounced than those in photosynthesis itself or in photosynthesis per chlorophyll. P_{sat} per cell (P^C_{sat}) was increased at a shear of 26.6 rad·s^{-1} (20 rpm rotation) by about 50%, and the slope, α^C, was increased over two-fold. These changes indicate increases in both the sizes of the PSUs and in the numbers of PSUs per cell (see Prézelin 1987), but Prézelin's model is based on constant cell sizes and, in our experiments, cell sizes increased with increasing turbulence. The increase in α per cell indicates an increase in photosynthetic light utilization efficiency under light limitation although with this experimental setup it was not possible to calculate actual quantum efficiencies.

In subsequent P vs. I experiments 9 and 10, light saturation was not achieved at 200 μmol·m^{-2}·s^{-1}. A rate of strain of 13.3 rad·s^{-1} (10 rpm) was used in experiment 9, and 26.6 rad·s^{-1} (20 rpm) was used in experiment 10. In both of these experiments, cell volume increases due to turbulence were estimated, and in experiment 10 excretion of ^{14}C taken up was estimated from differences in total and particulate photosynthesis.

The results from all three P vs. I experiments (Table 2) showed that at 26.6 rad·s^{-1} (20 rpm rotation), P_{sat} (that at 200 μmol·m^{-2}·s^{-1}) was reduced in all experiments, but only slightly at 13.3 rad·s^{-1} (10 rpm). Similar decreases in α per chlorophyll were observed at 26.6 rad·s^{-1}, but this parameter was increased at 13.3 rad·s^{-1} compared to the controls. The α per cell was increased by turbulence in all three experiments. Respiration was increased by turbulence in experiments 9 and 10 as compared to a decrease in experiment 8, and algal respiration ranged from 10 to 24% of P_{sat} depending on the experiment and the treatment. In experiment 10, ^{14}C excretion was about 25% of P_{sat} and did not differ between turbulent and control cultures.

Effects on pigments. Stress due to shear did not affect the ratio of accessory pigments to chl *a* at 13.3 and 26.6 rad·s^{-1} (Table 3). Intracellular pigment concentration, on the other hand, increased with shear, about 20% at 13.3 rad·s^{-1} and 50% at 26.6 rad·s^{-1} (Table 4). Variability was high among experiments and seemed to increase with increasing shear. Intracellular pigment concentrations were measured for two experiments where we measured cell size (Table 5). No change was observed in concentrations per dry weight at 13.3 rad·s^{-1}, but a 50% increase was observed at 26.6 rad·s^{-1}. These results suggest that the changes in cellular pigment concentrations were not due to increased cell volume but to real intracellular increases in accessory pigments.

The lack of changes in pigment ratios and increased cell pigmentation might support the hypothesis of increased number of PSUs as a response to increased stress (Prézelin 1987). Increased PSU number has been invoked as a mechanism to increase light absorption under conditions of light limitation (Steeman Nielsen and Jorgensen 1962, Prézelin 1981). *Gonyaulax polyedra* is also known to

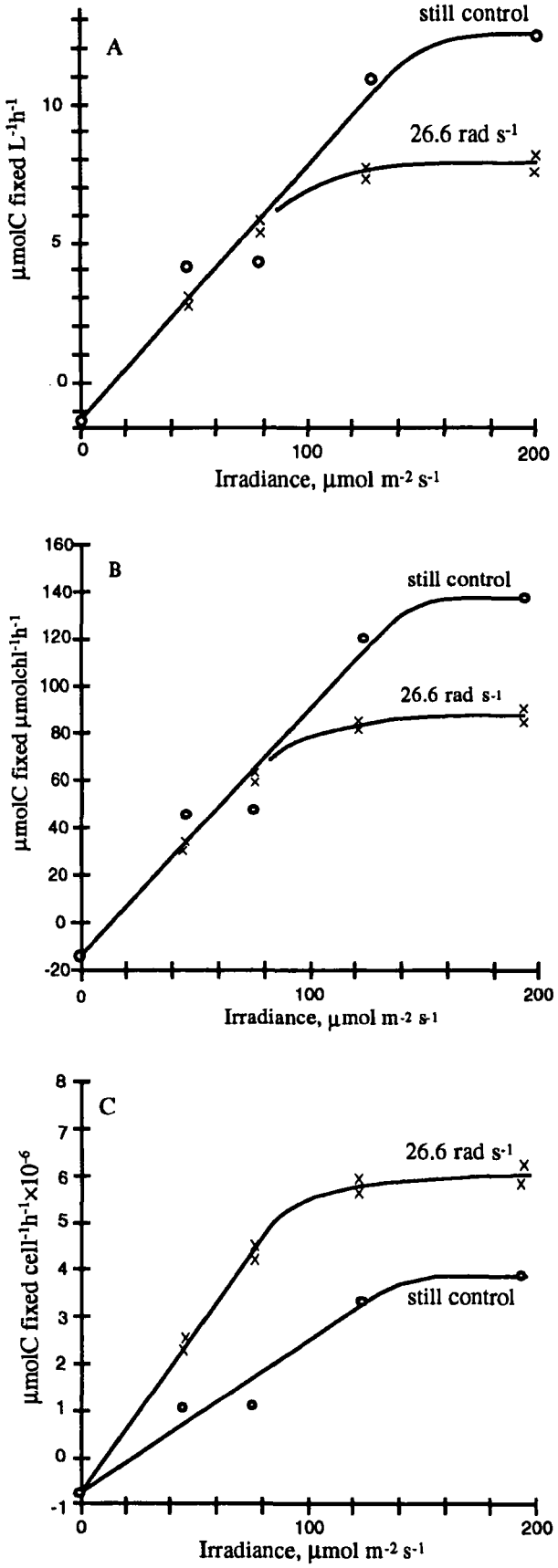

FIG. 4. Particulate photosynthesis at different irradiances (P vs. I curves) at 26.6 rad·s^{-1} (20 rpm) after 72 h preincubation. Experiment 8. A) Particulate photosynthesis in µmol C·L^{-1}·h^{-1}. B) Photosynthesis per unit chl *a*. C) Photosynthesis per cell.

TABLE 3. *Ratios of accessory pigments to chl* a *in sheared* Gonyaulax polyedra *cells with respect to those nonsheared cells (controls). Ratios = (pigment·chl* a^{-1}*) in sheared cells per (pigment·chl* a^{-1}*) in nonsheared cells.*

Speed (rpm)	Experiment no.	γ (rad·s^{-1})	Chl c_2	Peridinin	Diadinoxanthin	Diatoxanthin	β-carotene	Overall
10	5	13.3	1.99	1.28	1.37	1.53	1.48	
10	6	13.3	0.60	0.52	0.59	0.60	0.92	
10	7	13.3	1.04	0.93	0.93	1.07	0.92	
10	9	13.3	0.49	0.68	0.79	0.74	0.95	
Mean			1.03	0.85	0.92	0.98	1.07	0.97
SD			0.59	0.29	0.28	0.36	0.24	0.08
20	5	26.6	0.65	0.67	0.71	0.84	0.78	
20	6	26.6	1.08	0.79	0.68	1.57	1.05	
20	7	26.6	1.16	0.98	0.97	1.27	0.85	
20	8	26.6	0.96	0.88	1.14	1.02	0.98	
Mean			0.96	0.83	0.87	1.17	0.91	0.95
SD			0.19	0.11	0.19	0.27	0.11	0.12

change PSU size as response to light limitation (Prézelin 1976). Our results show that another type of stress (i.e. small-scale turbulence) may trigger a different mechanism to maintain photosynthetic performance: increased PSU numbers.

Changes in chl *a* and β-carotene concentrations were observed in some, but not all, experiments. For example, increases in β-carotene and chlorophyll epimer (chl *a'*) were observed in cultures kept at 8.0 rad·s^{-1} (6 rpm) for 192 h (Table 6). Levels remained high and constant from 72 to 192 h. Other pigments also increased relative to the control but at lower levels. The carotenoid peridinin had a peak concentration at 72 h, which decreased thereafter. Diadinoxanthin showed a similar pattern but a larger decrease at the end of the experiment. We interpret these results as an interruption of the synthesis of these latter pigments after 72 h, following an initial accumulation that occurred between 24 and 72 h. On the other hand, β-carotene, a precursor in carotenoid synthesis, continued accumulating in the cells.

We do not have a simple explanation for the qualitative and quantitative variability in pigmentation observed among the various experiments. It may be due to the previous history of the strain, changes in the seawater used for culture media, or molecular changes occurring in the strain. Variability could also be due to transient responses in pigmentation. Such responses were observed when cultures were transferred from one to another irradiance (Prézelin and Matlick 1980) and can occur at periods of several days to weeks and vary with the direction of the gradient. In our studies, no experiment was extended for more than a week, but transient responses were observed within that time (Table 6).

TABLE 4. *Ratios of pigments per cell in sheared* Gonyaulax polyedra *cells to pigments per cell in nonsheared cells (controls). Ratios = (pigment·chl a^{-1}) in sheared cells per (pigment·chl a^{-1}) in nonsheared cells.*

Speed (rpm)	Experiment no.	γ (rad·s^{-1})	Chl *a*	Chl c_2	Peridinin	Diadinoxanthin	Diatoxanthin	β-carotene	Overall
10	5	13.3	0.65	0.76	0.83	0.88	0.99	0.96	
10	6	13.3	1.97	1.19	1.03	1.17	1.19	1.81	
10	7	13.3	1.31	1.36	1.22	1.22	1.4	1.21	
10	9	13.3	1.67	0.82	1.13	1.32	1.24	1.60	
Mean			1.40	1.03	1.05	1.15	1.2	1.39	1.17
SD			0.50	0.25	0.15	1.16	0.15	0.33	0.07
20	5	26.6	1.67	1.80	1.31	1.13	2.61	1.75	
20	6	26.6	1.35	1.56	1.32	1.31	1.72	1.15	
20	7	26.6	1.26	0.81	0.84	0.89	1.05	0.98	
20	8	26.6	1.98	2.07	2.24	1.74	1.94	2.02	
Mean			1.56	1.56	1.43	1.27	1.83	1.47	1.52
SD			0.28	0.47	0.51	0.31	0.55	0.42	0.17

High variability is also reported in the literature for mechanisms of light adaptation in this species. For example, increases in both PSU size and number have been observed as a response to light limitation in *Gonyaulax polyedra* (Prézelin 1987).

Cell division and sizes. In all three P vs. I experiments, cell numbers increased very little or decreased in turbulent cultures during the 72-h preincubation period, and cell division rates were small or negative compared to those in control cultures (Table 2). After a 72-h preincubation, *Gonyaulax polyedra* cells were very much enlarged in turbulent cultures (experiments 9 and 10), and the cell volumes were significantly different ($P < 0.001$) from those in control cultures. Berdalet (1992) reported similar results on cell division and enlargement in turbulence-inhibited cultures of the dinoflagellate *Gymnodinium nelsonii*. In this alga, division was inhibited along with an accumulation of nucleic acids, and the cells enlarged to about the same degree as in our *Gonyaulax polyedra* cultures. She used a rotary shaker (100 rpm) and did not quantify the turbulence in fluid dynamic terms, but it was probably much more than our 26.6-rad·s^{-1} (20-rpm) cultures on the wheel.

Relationships to natural marine conditions. The main effect of turbulence on *G. polyedra* was an inhibition of cell division as indicated by cell number values and division rates before and after 72 h incubation and by our previous results (Thomas and Gibson 1990a, b). In those papers, we established that the inhibition threshold was about 4.4 rad·s^{-1}. Here we show that photosynthesis was strongly, but only partially, inhibited at rates of strain of 13.3 or 26.6 rad·s^{-1}. Thus, this process was not as sensitive to turbulence as growth.

It is difficult to compare these rates of strain values to those that are found in the euphotic zone just a few meters below the sea surface because so little is known about near-surface turbulence levels that would affect phytoplankton growth. Measurements

TABLE 5. *Intracellular pigment concentrations in* Gonyaulax polyedra *as affected by small-scale turbulence (percentage of dry weight, based on cellular volume, and assuming 10% of fresh weight = dry weight).*

Speed (rpm)	Experiment no.	γ (rad·s^{-1})	Chl *a*	Chl c_2	Peridinin	Diadinoxanthin	Diatoxanthin	β-carotene	Overall
0	9	0	0.39	0.049	0.46	0.18	0.015	0.013	1.10
10	9	13.3	0.46	0.029	0.37	0.16	0.013	0.014	1.05
0	10	0	[a]	[a]	[a]	[a]	[a]	[a]	[a]
20	10	26.6	0.52	0.14	0.51	0.26	0.023	0.024	1.47

[a] Not available.

from vertically rising turbulence profilers (Soloviev et al. 1988) suggest dissipation rates consistent with a constant-stress turbulent boundary layer driven by surface winds. However, evidence is accumulating that the average dissipation rates may be much larger than those implied by this simple model and that sparse vertical profiling undersamples the rare turbulent events that dominate the average. Agrawal et al. (1992) and Kitaigorodskii et al. (1983) used tower mounted sensors to show that turbulence near the surface is extremely intermittent with large (unresolved) local values, due to breaking surface waves that penetrate to some fraction of a wavelength. Sparse sampling of extremely intermittent dissipation rates may have caused large underestimates of average values in many ocean layers (Gibson 1987), including the euphotic surface layer. Moreover, the effective dissipation rate ϵ_{eff} for growth inhibition may be much larger than the mean ϵ because the inhibition responds to the maximum dissipation encountered for time periods of a few minutes per day rather than to the mean (Gibson and Thomas 1995). Surface wind stress values for 4-knot (2.1-m·s^{-1}) winds will result in a rate of strain of 4.4 rad·s^{-1} (the threshold for cell division inhibition for *Gonyaulax polyedra*), but 15-knot (7.7-m·s^{-1}) winds would be needed to match the strain rates of our 20-rpm wheel (26.6 rad·s^{-1}). However, surface wave-breaking begins for winds of about 4 knots (2.1 m·s^{-1}),

TABLE 6. *Intracellular pigment concentration in* Gonyaulax polyedra *obtained during time series experiments of cultures grown at 4 and 6 rpm (γ = 5.33 and 7.98 rad·s^{-1}, respectively) for a week (in units of pigment per cell, expressed as ratios of treatment: control).*

Speed rpm	Hours	Chl c_2	Peridinin	Diadinoxanthin	Chl *a*	Chl *a'* (epimer)	β-carotene
4	2	1.02	0.54	1.10	1.07	0.0	1.08
4	24	1.56	1.47	1.50	1.50	3.26	1.58
4	72	0.55	0.46	0.63	0.64	3.85	0.80
4	120	0.86	0.45	0.80	0.91	[a]	0.92
4	192	1.80	1.26	1.33	1.88	3.47	1.86
6	2	0.93	0.56	1.20	1.13	0.0	1.04
6	24	0.79	0.60	0.51	0.55	9.9	1.63
6	72	4.71	3.80	5.12	4.87	74.69	16.87
6	120	5.14	3.56	1.18	7.14	[a]	14.59
6	192	5.04	2.21	1.15	4.90	71.65	16.33

[a] Not available.

resulting in instantaneous ϵ values much larger than those due to wind stress. Clearly, more careful measurements of the statistical laws of turbulence near the sea surface (and in the euphotic zone), as a function of winds and waves, are needed to properly model the effects of ocean turbulence on phytoplankton growth.

Efficient photosynthesis under strongly turbulent conditions was indicated by increases in the slope, α, of the P^C vs. I curve for photosynthesis per cell (Fig. 4C). Ecologically, this increased efficiency may be an advantage in that cells, which are not able to divide due to wind-induced turbulence in the sea, can maintain their photosynthetic metabolism at least for a 72-h period and be poised to divide when calm conditions again prevail following a windy period. Berdalet (1992) reported that nondividing *Gymnodinium nelsonii* cells subjected to 10 d of turbulence would start to divide when turbulence was stopped. We previously obtained similar results with *Gonyaulax polyedra* (Thomas and Gibson 1990b). The metabolism seems to be maintained by a lack of disruption of the photosynthetic apparatus within this time frame. Thus, blooms can come and go fairly rapidly in the sea, once blooms are initiated by a lengthy period of calm weather. Such initiation of blooms associated with weeks of calm weather has been known for dinoflagellate blooms for over 50 years (Allen 1938, 1946). The new interpretation that our laboratory results suggest is that dinoflagellates can metabolize efficiently even when cell division is inhibited between periods of calm weather.

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