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Small-scale turbulence affects the division rate and morphology of two red-tide dinoflagellates

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Abstract

The effects of small-scale turbulence on two species of dinoflagellates were examined in cultures where the turbulent forces came randomly from all directions and were intermittent both spatially and temporally; much like small-scale turbulence in the ocean. With *Lingulodinium polyedrum* (Stein) Dodge (syn. *Gonyaulax polyedra*), division rate increased linearly (from ~0.35 to 0.5 per day) and the mean cross-sectional area (CSA) decreased linearly (from ~1100 to 750 μm^2) as a function of the logarithmic increase in turbulence energy dissipation rate (ε). These effects were noted when ε values increased between $\sim 10^{-8}$ and $10^{-4}\ m^2\ s^{-3}$. However, when ε increased to $\sim 10^{-3}\ m^2\ s^{-3}$, division rate sharply decreased and mean CSA increased. Over the same range of ε, *Alexandrium catenella* (Wheedon and Kofoid) Balech had its division rate decrease linearly (from ~0.6 to 0.45 per day) and its CSA increase linearly (from ~560 to 650 μm^2) as a function of the logarithmic increase in ε. Even at the highest ε examined ($\sim 10^{-3}\ m^2\ s^{-3}$), which may be unrealistically high for their ambits, both *L. polyedra* and *A. catenella* still had fairly high division rates, ~0.2 and 0.45 per day, respectively. Turbulence strongly affected chain formation in *A. catenella*. In non-turbulent cultures, the mode was single cells (80–90% of the population), but at ε of $\sim 10^{-5}$ to $10^{-4}\ m^2\ s^{-3}$, the mode was 8 cells per chain. At the highest ε ($\sim 10^{-3}\ m^2\ s^{-3}$), the mode decreased to 4 cells per chain. The vertical distributions of *A. catenella* populations in relation to hydrographic flow fields were studied in the summers of 1997 and 1998 in East Sound, Washington, USA (latitude 48°39′N, 122°53′W). In both summers, high concentrations of *A. catenella* were found as a subsurface bloom in a narrow depth interval (~2 m), where both current shear and turbulence intensity were at a minimum. Other researchers have shown that *A. catenella* orients its swimming in shear flows, and that swimming speed increases with chain length. These responses, when combined with our observations, support a hypothesis that *A. catenella* actively concentrates at depths with low turbulence and shear.

Keywords: *Alexandrium catenella*; *Lingulodinium polyedra*; Toxic dinoflagellates; Division rate; Catenate colony formation; Vertical distributions; Small-scale turbulence; HAB

1. Introduction

Is small-scale turbulence important to the population dynamics of dinoflagellates in the ocean? Phytoplankton ecologists (Smayda, 2000; Smayda and Reynolds, 2000) have argued that in terms of competition with diatoms, small-scale turbulence is probably not the most important factor determining which taxon dominates the ecosystem. However, there is growing evidence that turbulence does directly affect dinoflagellate physiology. Although small-scale turbulence has been reported to increase nutrient diffusion

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to large (>60 μm) phytoplankton (Lazier and Mann, 1989; Karp-Boss et al., 1996), most previous laboratory experiments that have examined the relationship between turbulence and growth in dinoflagellates reported that division rate in cultures was inhibited or severely reduced under some condition of mechanical mixing, and that cell size, morphology, motility and other aspects of cell biology could be affected (White, 1976; Pollingher and Zernel, 1981; Thomas and Gibson, 1990a,b; Berdalet, 1992; Berdalet and Estrada, 1993; Thomas et al., 1995; Juhl et al., 2000; Zirbel et al., 2000; Juhl and Latz, 2002). In contrast, we will demonstrate both beneficial and inimical effects of small-scale turbulence on two species of dinoflagellates.

The hypothesis that turbulence is particularly damaging to dinoflagellates has had conceptual support from Margalef's Mandela which at one extreme associates diatoms with vigorous large-scale turbulent eddies (meters to tens of meters in scale) and attendant high nutrient concentrations, and at the other extreme, associates dinoflagellates with weak, large-scale turbulence and attendant low-nutrient concentrations (for review, see Margalef, 1978, 1997; Smayda and Reynolds, 2000). Large-scale turbulence is associated with many environmental factors that affect phytoplankton (e.g. Harris, 1986; Smayda, 1997). However, the direct effects of turbulence itself on phytoplankton are thought to act at small scales (mm). The kinetic energy in large-scale eddies that are forced by winds and waves is passed down to smaller and smaller eddies, until at low Reynolds numbers, viscous forces dampen out and convert the energy to heat. The balance between the rate of energy input and the rate of energy dissipation by viscous forces sets a limit on the size of the smallest eddies. In the ocean, that size is generally agreed to be on the scale of a few millimeters (Kolmogorov, 1941). The two dinoflagellate species investigated in this study are both ∼30 μm in diameter and for them, small-scale turbulence is presumed to act as a shear-stress force between the small-scale eddies interacting with each other (Lazier and Mann, 1989; Thomas and Gibson, 1990a).

Early reports of the effects of small-scale turbulence on dinoflagellates did not express the intensity of turbulence in defined hydrodynamic terms, thus comparisons of those results to turbulence intensities measured in natural waters are not possible (White, 1976; Berdalet, 1992; Berdalet and Estrada, 1993, but see Zirbel et al., 2000). More recently, an apparatus which produces a nearly constant, unidirectional shear (Couette flow), has been used to observe the responses of dinoflagellates to shear-stress (Thomas and Gibson, 1990b, 1992; Thomas et al., 1995; Juhl et al., 2000, 2001; Juhl and Latz, 2002). An advantage of Couette flow is that the shear acting on the dinoflagellates can be calculated in hydrodynamic terms, and can be mathematically related to a turbulence energy dissipation rate, ε. However, direct comparison of ε from Couette flow and natural waters is problematic (Kamykowski, 1995; Peters and Redondo, 1997). In natural waters, shear forces are neither unidirectional, nor constant. They come randomly from any direction and are intermittent in time and space. To observe the responses of dinoflagellates to small-scale turbulent shear, we have used an apparatus that produces small-scale turbulence shear flow similar in many aspects to that found in natural waters.

The dinoflagellates used in this study produce blooms, or "red-tides". *Lingulodinium polyedrum* is nominally non-toxic, and may form recurrent annual blooms lasting months (Holmes et al., 1967; Marasovic et al., 1995). *Alexandrium catenella* is responsible for episodic outbreaks of paralytic shellfish poisoning (PSP) (Horner et al., 1997).

2. Methods and materials

Cultures of *Lingulodinium polyedrum* (CCMP 1738) and *Alexandrium catenella* (CCMP 1493) were obtained from the Provasoli-Guillard Center for Culture of Marine Phytoplankton (West Boothbay Harbor, ME). The current CCMP catalogue has now assigned the clone number 1493 to an *A. tamarense* culture. Non-axenic stock and experimental cultures were maintained in sterile-filtered seawater (Gelman 0.2 μm aperture maxi-capsule filter) with nutrients at f/2 levels without silicon (Guillard, 1975), but with L-1 trace metals (Guillard and Hargraves, 1993) replacing the original f/2 trace metal formulation (Guillard and Ryther, 1962). Experimental and stock cultures were grown in light, and temperature, controlled incubators at 20 °C and on a 12:12 LD cycle at a photon irradiance of ∼200 μmol photons

$m^{-2}\,s^{-1}$ in the PAR spectral band ($\lambda = 400$–700 nm) with light produced by cool-white fluorescent lamps. The scalar photon irradiance was measured in flasks and experimental tank cultures using a calibrated Biospherical Instruments (San Diego, CA) QSL-100 scalar irradiance meter.

Experiments were conducted in six turbulence tank treatments: five intensities of forced turbulence and a quiescent (unmixed) control. The setup and turbulence calibration of the tanks have been described in detail elsewhere (Sullivan and Swift, 2003), and will be briefly reviewed below. The rectangular polycarbonate turbulence tanks had inside length–width–height dimensions of 24 cm × 10 cm × 100 cm, respectively, and were filled with seawater to a height of 80 cm (∼20 l). Turbulence in each water column was generated by vertically oscillating a pair of 2.5 cm diameter rods. The rods were 18 cm in length and the distance between each rod was 36 cm. The stroke length of the rods in each tank was ∼28 cm. As the rods moved through the water, they shed turbulent vortices that interacted and decayed. Changing the vertical velocity of the rods provided different intensities of small-scale turbulence.

The turbulence intensity in each tank was quantified using a Sontek (San Diego, CA) acoustic doppler velocimeter (ADV). The ADV determined velocity in three components, two horizontal vectors separated by 90° (u and v) and a vertical component (w). The ADV had a sampling rate of 25 Hz and a sampling volume of ∼1 cm^3. A special tank was constructed for turbulence calibration measurements that had the same dimensions as the experimental tanks, but also had five sampling ports in the front face of the tank. The port locations were centered at 4, 20, 40, 60, and 76 cm above the bottom of the tank. This allowed the ADV to be placed flush against the inside wall of the tank in any one of the port locations for measurements of turbulence within the tank. Velocity time series (30 min long) were collected at each port location and each motor speed of the oscillating rods, and then analyzed to determine the spatial distribution of ε throughout the tank. The value of ε was estimated using the dimensional approximation: $\varepsilon \sim u'^3/L$, where u' is the root mean square of the variation in the velocity time series and L is the integral length scale (Tennekes and Lumley, 1972). The integral length scale, L, is equivalent to the largest eddy size in the system and was set to the diameter of the stir bar (2.5 cm). The highest turbulence intensities occurred in the volume of the tank swept by the oscillating rods. The rods did not pass through the top and bottom 8 cm of the tanks and the dissipation rates in these parts of the tanks were somewhat lower (Fig. 1). There were no accumulations of non-motile dinoflagellates or other particles (in the tank corners), indicating the entire volume was well mixed. For each motor speed, the average value from the five dissipation measurements in the tank was calculated and used as the representative turbulence intensity for that treatment.

Light for each chamber was provided by vertically mounted banks of cool-white fluorescent lamps that spanned the entire height of each tank. Inoculation of the six tanks with dinoflagellates was from a single, exponentially growing culture. The volume of the inoculum was adjusted to give each tank an initial cell concentration of ∼50 cells ml^{-1}. After a 1-day acclimation period, turbulent mixing began and continued (except when sampling) for the duration of the experiment. Dinoflagellate concentrations were determined through periodic sampling (approximately every other day) near the midpoint of photophase. Each tank was gently mixed before sampling to ensure an even distribution of cells. This short period (∼30 s) of gentle mixing prior to sampling did not significantly affect growth (Sullivan, unpublished). In the tanks that were undergoing turbulent mixing, the stirring motor was turned off for a few minutes while the tank was sampled. Duplicate 10 ml samples were taken from each tank with sterile pipettes and preserved with 5% acid-Lugols solution. One milliliter aliquots were later enumerated using a Zeiss microscope (model RA) and Sedgwick-Rafter counting chambers. Population division rate was calculated from the slope of a least-squares regression of the log of dinoflagellate concentrations as a function of time for each turbulence treatment (Guillard, 1973). This presumed that there was negligible mortality in the dividing population.

Samples to measure cross-sectional area (CSA) and other changes in morphology were taken at the end of each experiment (∼400 cells per treatment). Dinoflagellate CSA was quantified via image analysis of digitized images using the program NIH Image (National Institutes of Health, Bethesda, MD). The

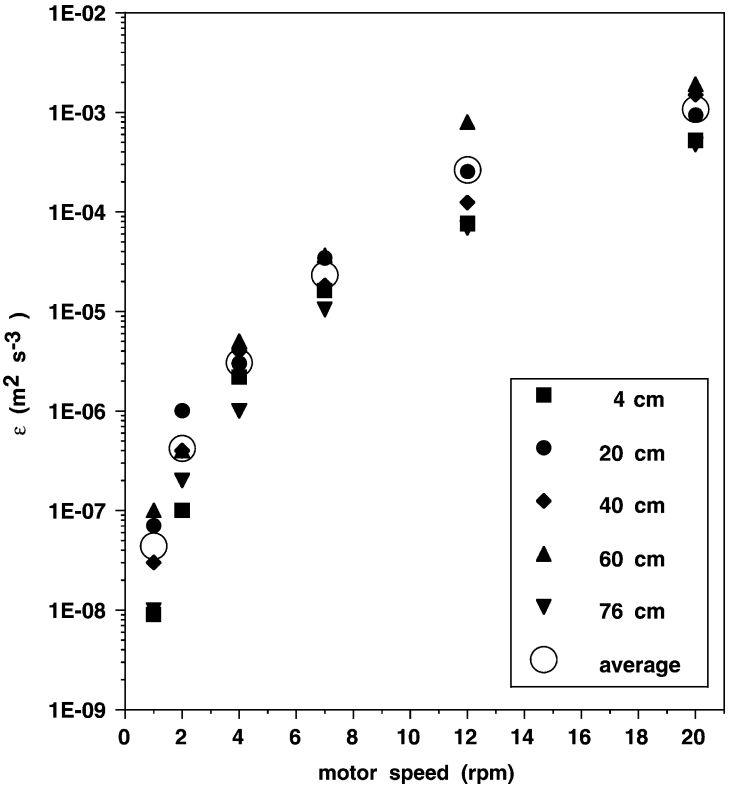

Fig. 1. Turbulence dissipation rate (ε) as a function of stirring motor speed (rpm) at five positions (cm) above the bottom in the 80 cm height turbulence chamber.

number of cells per chain in *A. catenella* was quantified by examining video images of random populations of chains taken from each tank treatment (minimum of 1000 cells per treatment).

2.1. Field studies

During two successive summers (1997 and 1998), the vertical distribution of field populations of *A. catenella* along with measurements of flow field characteristics and hydrographic parameters were examined in East Sound, Washington, USA, a small fjord of Orcas Island (48°39′N, 122°53′W). Vertical profiles of dinoflagellate abundance were obtained by sampling discrete depths using gentle suction on tubing attached to a high depth resolution CTD profiling system described by Donaghay et al. (1992). The water samples (~250 ml in volume) were collected and preserved with 5% formaldehyde for later enumeration. Hydrographic measurements (temperature, pressure, salinity) and calculated density were made using either a Seabird (Bellevue, WA) 911+ or SBE-25 CTD. Current velocity profile measurements were made using a shipboard 1200 kHz acoustic doppler current profiler (RDI Systems, San Diego, CA). Turbulence was quantified using three-dimensional velocity measurements from the same Sontek ADV used in laboratory turbulence tank calibrations. The ADV was mounted on a moored SBE-25 CTD. The combined instrument package was attached to an underwater, bottom-mounted winch system capable of moving the instruments vertically throughout the water column and positioning it at desired depths (Sullivan et al., 1999, 2002).

From the ADV measurements, in situ ε was estimated using the methods of Terray et al. (1996). Briefly, ε was calculated from an examination of ADV velocities in the inertial sub range of the frequency

spectrum using the formula:

$$\varepsilon = C \times 2\pi \times \frac{1}{(U^{2/3})^{3/2}} \times [S(f) f^{-5/3}]^{3/2}$$

where C is a constant (1.9 or 2.9 depending on the orientation of the flow to the measurement plane), U the mean velocity, and $[S(f)f^{-5/3}]$ is the portion of the frequency spectra that exhibits a $-5/3$ slope. The value of C is known and the value of U was computed from the ADV data. The w component of velocity was used in these calculations due to the lower doppler noise in that component (Lohrmann et al., 1995).

3. Results

3.1. Laboratory experiments with Lingulodinium polyedrum

The results from three replicate experiments were similar: as turbulence intensity increased from $\varepsilon \sim 10^{-8}$ to $10^{-4}\,m^2\,s^{-3}$, *L. polyedrum*'s division rate increased up to ~25% above that of the controls, but at the highest turbulence intensity ($\varepsilon \sim 10^{-3}\,m^2\,s^{-3}$), it decreased to 25–50% below that of the controls (results for all experiments summarized in Table 1 and one experiment is graphically presented in Fig. 2). The CSA of *L. polyedrum* decreased by 30–40% as the turbulence intensity and division rate increased, but at the highest turbulence intensity where division rate had decreased sharply, the mean CSA of *L. polyedrum* increased to nearly to that of the controls. Histograms of CSA from cultures at the highest turbulence intensity revealed a bimodal distribution with a population of small and large cells (Fig. 2).

Division rate and cell size determinations for the experiments described above were combined with data from two earlier turbulence experiments that only examined two turbulence intensities (Sullivan and Swift, 2003). Analysis of these five combined replicate experiments indicated that division rate increased linearly as turbulence intensities increased exponentially from $\varepsilon \sim 10^{-8}$ to $10^{-4}\,m^2\,s^{-3}$, but division rate then sharply decreased when the turbulence intensity reached $\varepsilon \sim 10^{-3}\,m^2\,s^{-3}$ (Fig. 3). Average *L. polyedrum* CSA decreased linearly along with the exponentially increasing turbulence intensities, but then CSA increased back to that of the

Table 1
Division rate and cell size of *L. polyedrum* at six turbulence intensities ($m^2\,s^{-3}$) and a non-turbulent control

Turbulence intensity (ε)	0 (control)	4E-08	4E-07	3E-06	2E-05	3E-04	1E-03
Experiment 1							
Division rate (per day)	0.36 (±0.04)		0.31 (±0.04)	0.44 (±0.04)	0.45 (±0.05)	0.45 (±0.05)	0.17 (±0.04)
Cell size (μm^2)	1120 (±150)		1000 (±200)	920 (±220)	870 (±190)	780 (±170)	1110 (±370)
Experiment 2							
Division rate (per day)	0.37 (±0.03)		0.38 (±0.02)	0.40 (±0.02)	0.49 (±0.03)	0.48 (±0.03)	0.23 (±0.04)
Cell size (μm^2)	1110 (±140)		1050 (±170)	900 (±180)	760 (±170)	650 (±100)	820 (±290)
Experiment 3							
Division rate (per day)	0.38 (±0.03)		0.38 (±0.04)	0.45 (±0.03)	0.47 (±0.02)	0.46 (±0.03)	0.30 (±0.03)
Cell size (μm^2)	1250 (±220)		1190 (±220)	1060 (±190)	910 (±190)	900 (±190)	1180 (±320)
Experiment A							
Division rate (per day)	0.33 (±0.04)	0.39 (±0.05)				0.53 (±0.05)	
Cell size (μm^2)	1040 (±150)	990 (±130)				680 (±140)	
Experiment B							
Division rate (per day)	0.33 (±0.05)	0.27 (±0.03)				0.49 (±0.04)	
Cell size (μm^2)	1040 (±160)	940 (±130)				740 (±140)	
Average division rate	0.35 (±0.04)	0.32 (±0.04)	0.38 (±0.03)	0.43 (±0.03)	0.47 (±0.03)	0.48 (±0.04)	0.23 (±0.04)
Average cell size	1110 (±170)	980 (±150)	1120 (±200)	960 (±200)	850 (±180)	750 (±150)	1040 (±330)

Division rates are per day (±95% confidence interval of the estimate). Cell size is mean cross-sectional area (μm^2) (±1 S.D.) rounded to the nearest 10. Experiments A and B are from earlier experiments that only examined two turbulence intensities (see text).

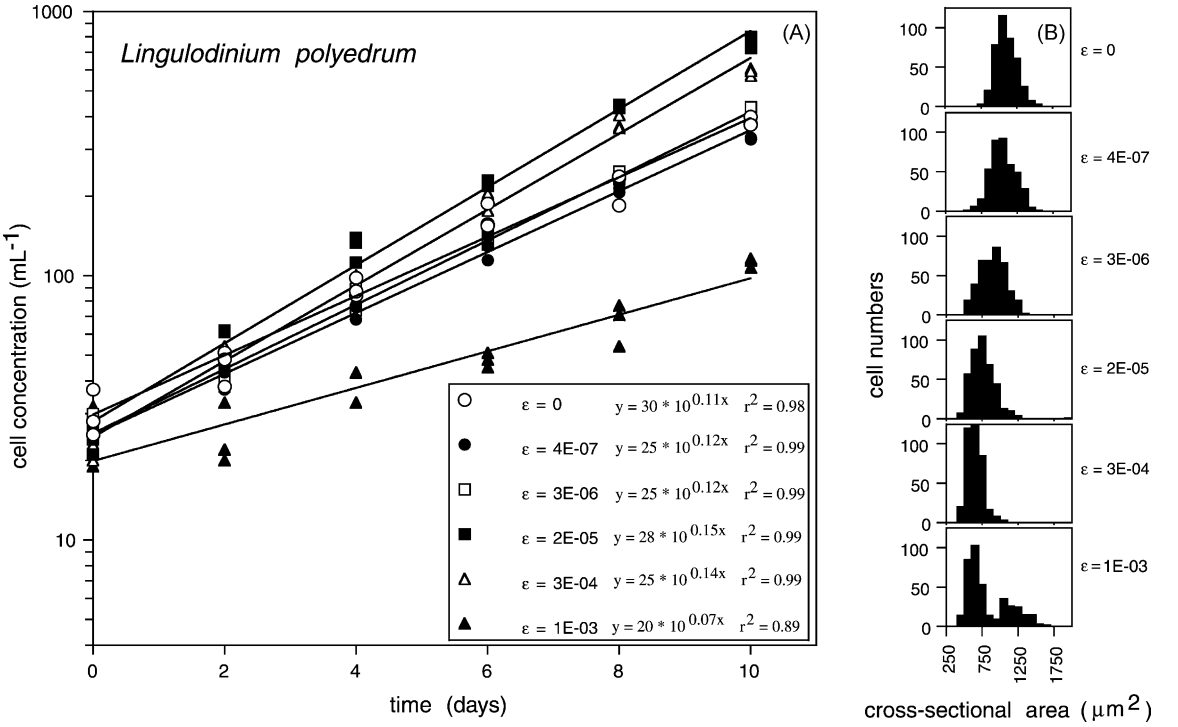

Fig. 2. (A) Cell concentration (ml^{-1}) of *L. polyedrum* as a function of time (days) at six intensities of turbulence. Three replicate cell counts from each turbulence treatment are plotted. Lines are a semi-log curve fit through the data points with formula and r^2 values plotted next to the turbulence dissipation rate of that treatment. (B) Cross-sectional area (μm^2) of *L. polyedrum* for six intensities of turbulence at the end of the experiment. Histograms are the number of cells in a size interval (100 μm^2 interval width). Turbulence dissipation rates (ε) are in units of $m^2\,s^{-3}$.

unmixed control tank when the turbulence intensity reached $\varepsilon \sim 10^{-3}\,m^2\,s^{-3}$ (Fig. 3). Regression analysis of division rate and CSA as a function of the log of turbulence intensity yielded lines with slopes significantly different from zero ($P = 0.05$).

3.2. Laboratory experiments with Alexandrium catenella

The results from two replicate experiments were similar. The division rate of *A. catenella* was hardly affected by turbulence in the range of $\varepsilon \sim 10^{-8}$ to $10^{-5}\,m^2\,s^{-3}$, but as ε increased above that value there was a 15–20% reduction in division rate (results for all experiments summarized in Table 2 and one experiment is graphically presented in Fig. 4). In the highest turbulence intensity treatment, the CSA of *A. catenella* increased ~20% (Table 2, Fig. 4).

The number of *A. catenella* cells per chain was markedly affected by turbulence (Fig. 5). In the unstirred control treatments, 80–90% of the *A. catenella* population was found as single cells. As the turbulence intensity increased, the number of cells in chains increased (up to 16 cells per chain). Concomitantly, single cells decreased to less than 20% of the total *A. catenella* population. However, in the very highest turbulence intensity treatment, there was a reduction in the percentage of longer cell chains, and 4 cell chains became more common than 8 cell chains.

Division rate and CSA determinations for the two experiments described above were combined with data from two earlier turbulence experiments that only examined two turbulence intensities (Sullivan and Swift, 2003). The combined data indicated that division rate decreased linearly and average CSA increased lin-

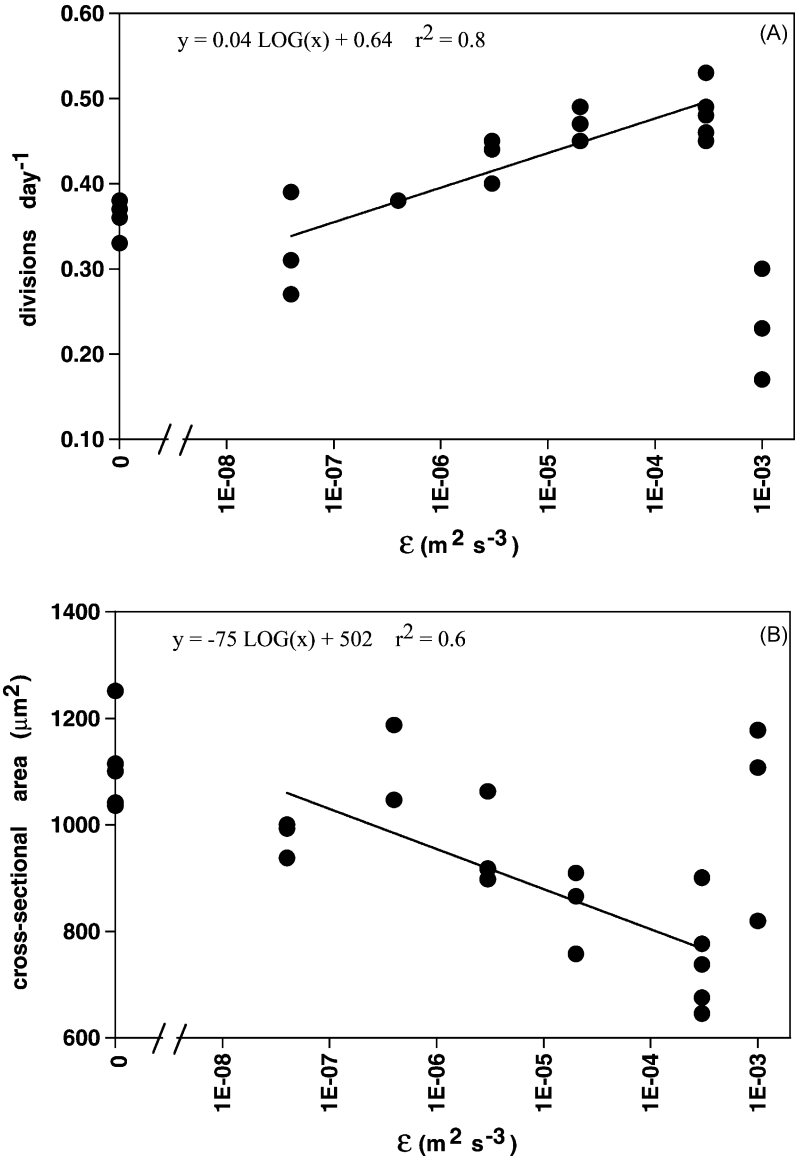

Fig. 3. (A) Division rate (per day) as a function of log of the turbulence dissipation rate (ε) for all experiments with *L. polyedrum*. The line is a semi-log fit to the points in the range of turbulence intensities where division rate increases. (B) Cross-sectional area (μm^2) as a function of log of the turbulence dissipation rate (ε) for all experiments with *L. polyedrum*. The line is a semi-log fit to the points in the range of turbulence intensities where cell size decreases.

early when plotted against the exponential increase in turbulence intensity (Fig. 6). Regression analysis of division rate and CSA as a function of the log of turbulence intensity yielded lines with slopes significantly different from zero ($P = 0.05$ level).

3.3. Field observations

In 1997, *A. catenella* populations in East Sound, WA were present at very high cell concentrations ($\sim$100 ml^{-1}), confined to a narrow depth range

Table 2
Division rate and cell size of *A. catenella* at six turbulence intensities ($m^2\ s^{-3}$) and a non-turbulent control

Turbulence intensity (ε)	0 (control)	4E-08	4E-07	3E-06	2E-05	3E-04	1E-03
Experiment 1							
Division rate (per day)	0.51 (±0.04)		0.55 (±0.03)	0.53 (±0.02)	0.54 (±0.03)	0.48 (±0.03)	0.45 (±0.04)
Cell size (μm^2)	610 (±110)		600 (±90)	610 (±90)	620 (±100)	630 (±100)	670 (±100)
Experiment 2							
Division rate (per day)	0.60 (±0.04)		0.55 (±0.05)	0.60 (±0.06)	0.55 (±0.04)	0.51 (±0.05)	0.48 (±0.05)
Cell size (μm^2)	560 (±120)		590 (±110)	580 (±110)	660 (±110)	600 (±110)	620 (±110)
Experiment A							
Division rate (per day)	0.69 (±0.08)	0.63 (±0.05)				0.69 (±0.03)	
Cell size (μm^2)	480 (±70)	490 (±80)				510 (±70)	
Experiment B							
Division rate (per day)	0.61 (±0.05)	0.63 (±0.06)				0.53 (±0.05)	
Cell size (μm^2)	610 (±110)	570 (±110)				630 (±110)	
Average division rate	0.60 (±0.05)	0.63 (±0.05)	0.55 (±0.04)	0.56 (±0.04)	0.55 (±0.04)	0.55 (±0.04)	0.46 (±0.05)
Average cell size	560 (±100)	530 (±90)	590 (±100)	600 (±100)	640 (±100)	590 (±100)	650 (±110)

Division rates are per day (±95% confidence interval of the estimate). Cell size is mean cross-sectional area (μm^2) (±1 S.D.) rounded to the nearest 10. Experiments A and B are from earlier experiments that only examined two turbulence intensities (see text).

between 4 and 5 m (Fig. 7). The *A. catenella* layer was in a region of minimal current shear, and thus presumably in the depth interval associated with the lowest turbulence intensity in the vertical profile. The highest values of shear in the profile were in the layers above and below it. In this profile, there were marked changes in density, with the *A. catenella* layer in about the middle of the largest density gradient between ~3.5 and 6 m depth.

The next summer, 1998, *A. catenella* populations were again found in high cell concentrations (~40 ml^{-1}) in a narrow depth range between ~8 and 10 m (Fig. 8). In addition to the measurements made in 1997, profiles of ε were made with the ADV. These confirmed that the *A. catenella* population was located in a layer of low turbulence. Turbulence intensity in the profile was maximal near the surface ($\varepsilon \sim 10^{-5}\ m^2\ s^{-3}$), but decreased to its minimum values (less than $\varepsilon \sim 10^{-7}\ m^2\ s^{-3}$) in the *A. catenella* layer, before rising again toward the bottom. The peak of the *A. catenella* layer was experiencing very low horizontal current velocities (~2 $cm\ s^{-1}$) and hardly detectable current shear (<0.1 $cm\ s^{-1}\ m^{-1}$). The strongest shear in the vertical profile was just above the peak of the *A. catenella* layer, where the current speed decreased from 12 to 2 $cm\ s^{-1}$ over a depth interval of about 1 m. Again, the *A. catenella* were associated with a depth interval where there was a strong density gradient.

4. Discussion

The hypothesis that turbulence negatively affects the physiology of dinoflagellates has become a common paradigm among many phytoplankton ecologists (e.g. Heil et al., 1993; Hallegraeff et al., 1995; Estrada and Berdalet, 1997; Smayda, 1997). However, Smayda (2000, 2002) has recently described the potential positive role that turbulence may play in stimulating dinoflagellate blooms. The key ecological question is, for the ambit that they occupy, does small-scale turbulence help or hinder dinoflagellates in maintaining or increasing their populations? This is a very difficult question to answer from field observations, requiring long term, simultaneous measurements of both in situ growth rate and small-scale turbulence, while tracking a population's water mass in space. Even if these measurements are made, potentially confounding environmental factors that influence growth (e.g. light, nutrients and temperature) would have to be measured and considered. It would also be difficult to draw generalizations about the responses and behaviors of all dinoflagellates because

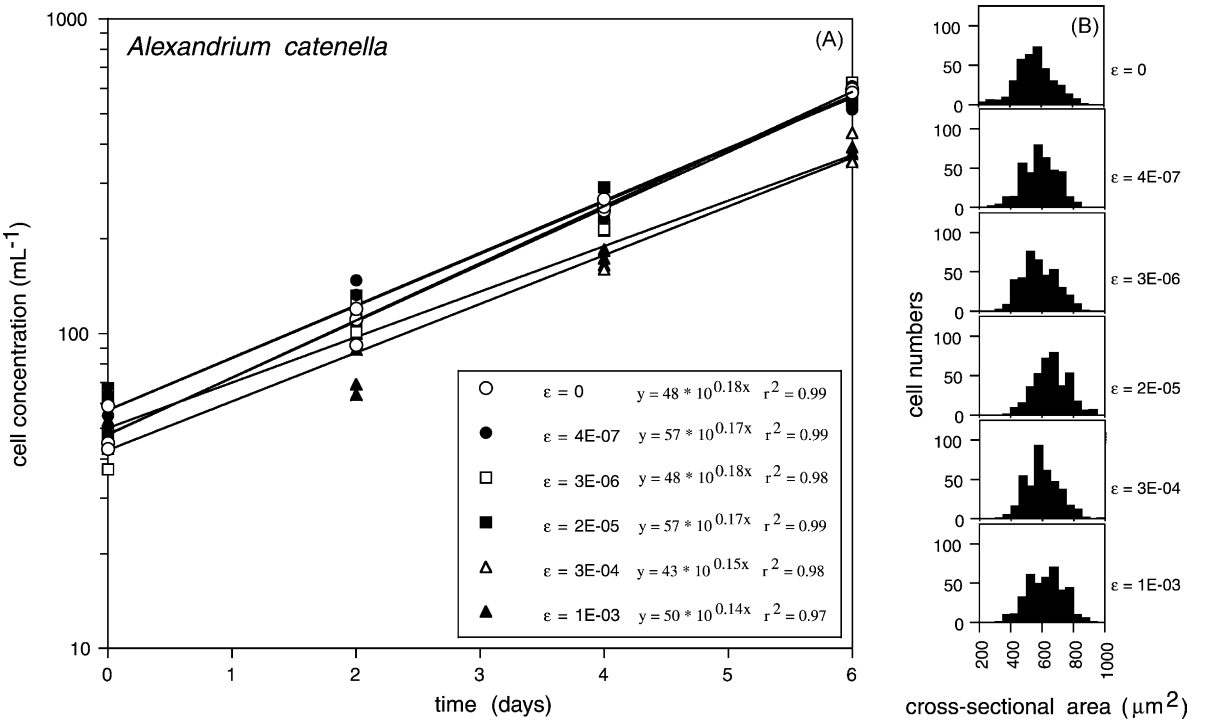

Fig. 4. (A) Cell concentration (ml^{-1}) of *A. catenella* as a function of time (days) at six intensities of turbulence. Three replicate cell counts from each turbulence treatment are plotted. Lines are a semi-log curve fit through the data points with formula and r^2 values plotted next to the turbulence dissipation rate of that treatment. (B) Cross-sectional area (μm^2) of *A. catenella* for six intensities of turbulence at the end of the experiment. Histograms are the number of cells in a size interval (50 μm^2 interval width). Turbulence dissipation rates (ε) are in units of $m^2\ s^{-3}$.

experimental data have shown that sensitivity and responses to turbulence are different among different taxa (e.g. Thomas and Gibson, 1992; Sullivan and Swift, 2003).

Defining functional relationships between small-scale turbulence and dinoflagellate physiology in the laboratory is perceived as a first step toward producing mathematical relationships describing turbulence effects. These quantified relationships could be integrated into existing population dynamics models describing how dinoflagellate growth and motility are affected by other environmental factors. These models might be particularly useful in examining variable physical and environmental forcing on population dynamics (Donaghay and Osborn, 1997). To generate functional relationships between any physiological response and turbulence, we first must consider, what is the appropriate way to generate turbulence for phytoplankton in the laboratory, and more important—how does this laboratory generated turbulence relate to what occurs in natural waters?

When generating small-scale turbulence in laboratory cultures, no method can produce a completely realistic simulation of an oceanic turbulence field (Peters and Redondo, 1997). The complexity of the natural forcing of turbulence and the requirement for a large range of turbulent eddy scales makes this nearly impossible. We have attempted to reproduce as natural a turbulence field as possible, incorporating three-dimensional, small-scale spatial and temporal intermittence in the shear-stress and strain forces. In doing so, we have found different responses for one of the same species of dinoflagellates that have been tested in Couette flow at what was reported as a similar value of ε (e.g. Thomas and Gibson, 1990b; Juhl et al., 2000). The discrepancy between Couette

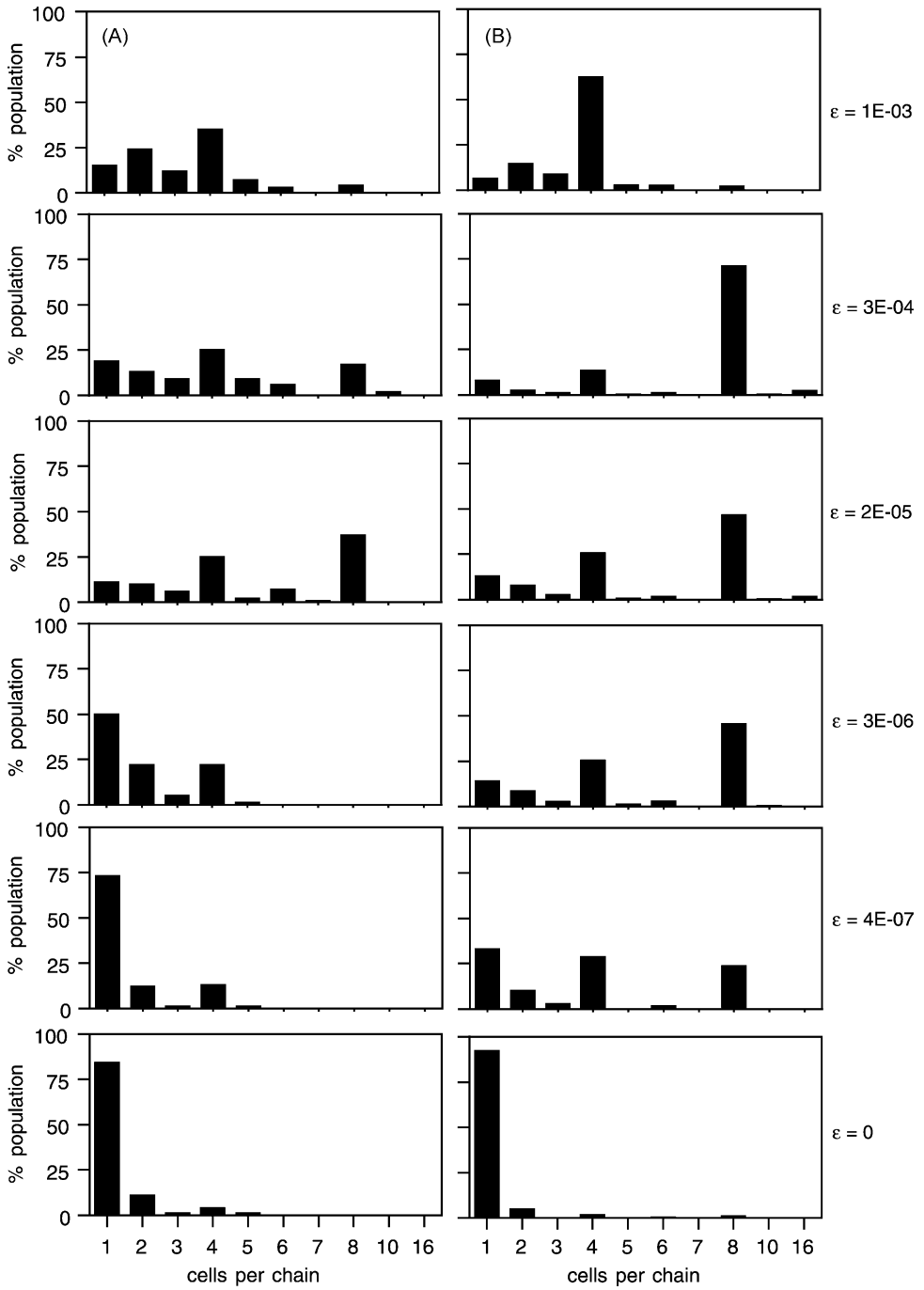

Fig. 5. The number of cells per chain of *A. catenella* as a percent of the population at six turbulence dissipation rates (ε, $m^2\,s^{-3}$) for two replicate experiments (A and B). The minimum population size examined was 1000 cells at each value of ε in each experiment.

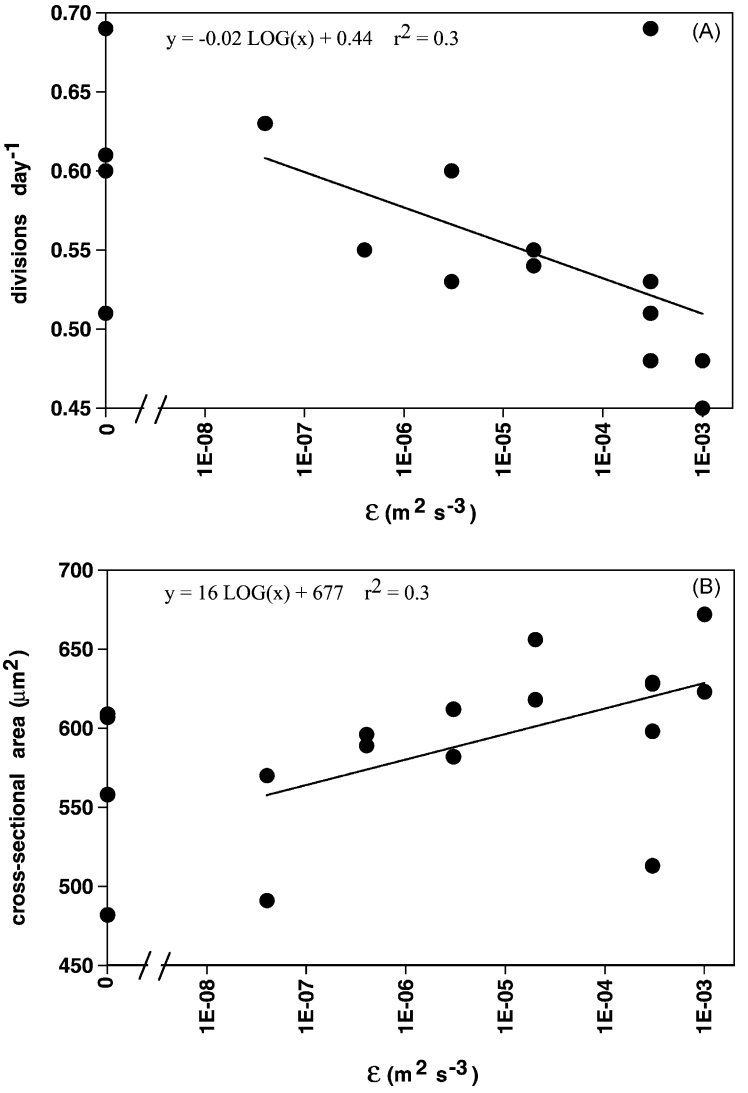

Fig. 6. (A) Division rate (per day) as a function of log of the turbulence dissipation rate (ε) for all experiments with *A. catenella*. (B) Cross-sectional area (μm^2) as a function of log of the turbulence dissipation rate (ε) for all experiments with *A. catenella*. Lines are semi-log fits to the points over the range of turbulence intensities (excluding the non-turbulent treatments).

flow generated and the present results demonstrates some of the challenges of comparing laboratory experiments that use different turbulence generation mechanisms. Hopefully, these differences in results will lead to a clearer understanding of the role of small-scale turbulence in natural waters.

Lingulodinium polyedrum exhibited a functional relationship between turbulence intensity and division rate similar to those found in other autecological studies that have examined, for example, the relationship between photosynthetic rate and light intensity. Division rate increased linearly with increased turbulence intensity until a threshold was reached, and then sharply decreased. This is somewhat analogous to a generalized photosynthesis–irradiance curve, where photosynthesis increases linearly with an increase in

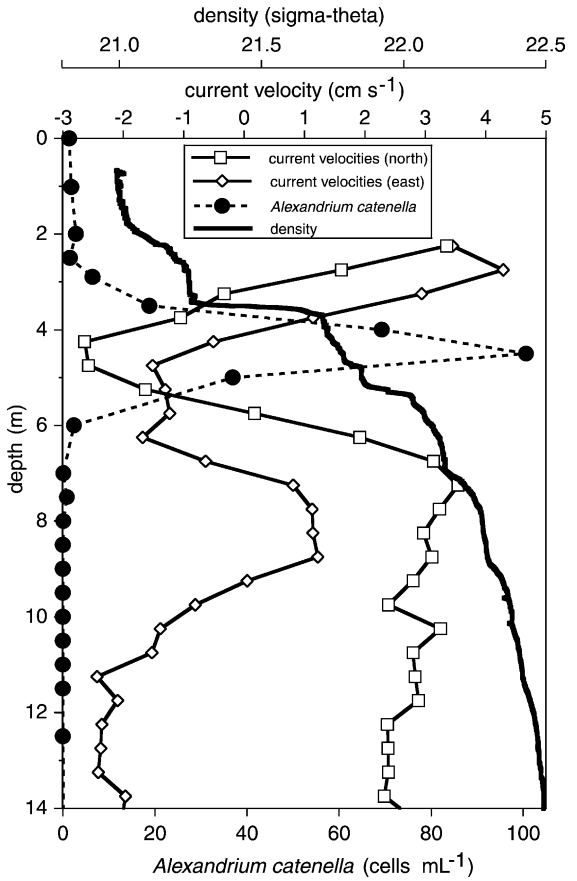

Fig. 7. The vertical distribution of cell numbers of *A. catenella* in relation to the horizontal velocity components (cm s^{-1}) and density structure (sigma–theta) in East Sound, WA, 1997.

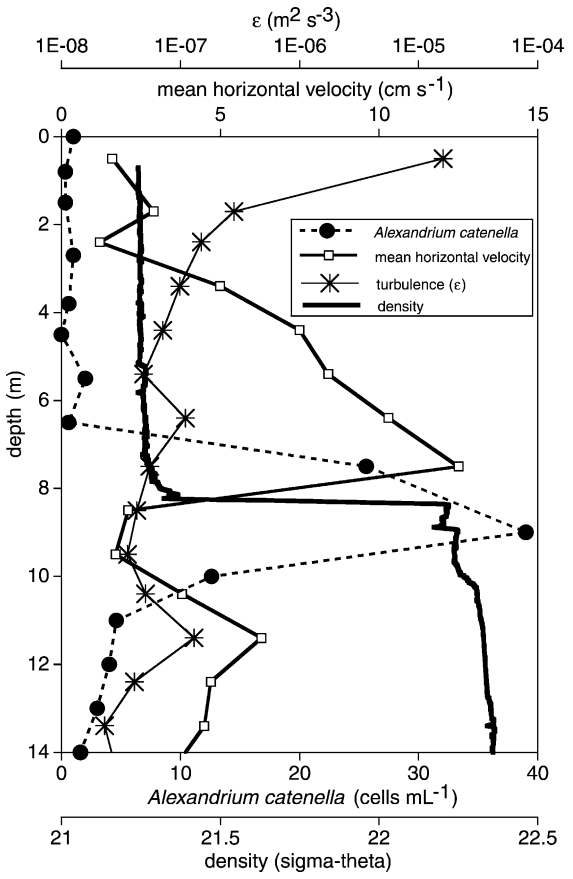

Fig. 8. The vertical distribution of cell numbers of *A. catenella* in relation to the mean horizontal velocity (cm s^{-1}), density structure (sigma–theta), and turbulence dissipation rate (ε) in East Sound, WA, 1998.

light intensity, plateaus, and then decreases at very high light intensities (e.g. Platt et al., 1980).

The division rate in *L. polyedrum* was reduced (relative to controls) only when the turbulence intensity reached $\sim 10^{-3}\,m^2\,s^{-3}$. This is an extremely high value and is close to what is thought to be the upper range of oceanic turbulence intensities, predicted, for example, under breaking waves (Gargett, 1989, 1997). Even at this high turbulence intensity, cell division continued (~0.20 divisions per day) in the population. In previous experiments with *L. polyedrum*, Thomas and Gibson (1990a,b) reported that division was completely inhibited at ε values greater than $\sim 10^{-5}\,m^2\,s^{-3}$. However, as noted previously, these experiments were carried out under conditions of constant, unidirectional shear using Couette flow.

Lingulodinium polyedrum blooms are often associated with calm weather (e.g. Holmes et al., 1967), but there are a number of reasons beside the diminution of turbulence that may explain the association. Smayda (2000) and Smayda and Reynolds (2000) have characterized *L. polyedrum* as their type V dinoflagellate, one that blooms in less turbulent periods when coastal upwelling "relaxes" (reverses). In that case, nutrient-poor surface water moves toward the coast and colder, nutrient rich water may flow away from the coast at depth. *Lingulodinium polyedrum* blooms are commonly reported under these conditions (Marasovic et al., 1994). Blooms during less turbulent periods may be associated with shallow surface thermal stratification, which Eppley and Harrison (1975) reported gave *L.*

polyedrum an advantage (e.g. over diatoms) of using daily vertical migration to assimilate nutrients below the thermocline at night, and obtain light energy above the thermocline in low-nutrient waters during the day. Due to the direction of the two-layer flow during upwelling relaxation, such daily vertical migrations could also tend to move and concentrate the dinoflagellates as an onshore surface bloom (Donaghay and Osborn, 1997).

As a complementary hypothesis to explain the correlation of calm weather and *L. polyedrum* blooms, several authors have extrapolated the results of laboratory studies to suggest that *L. polyedrum* population increase is negatively affected by small-scale turbulence when winds and waves are forcing turbulent energy into the mixed-layer. They suggest that this species may not be able to grow or survive and form blooms when mixed-layer turbulence intensities are at "ecological" intensities (Thomas and Gibson, 1990b; Juhl et al., 2000, 2001).

We report a 25% increase in *L. polyedrum* division rates caused by exposure to moderately high turbulence. This could have a significant effect on its natural population dynamics. If two populations had the same initial cell concentration and one divided 25% faster than the other, after four divisions (about a week with *L. polyedrum*), the faster-dividing one would have more than double the cell concentration of the other population, and after nine divisions (about 2 weeks), more than five times the cell concentration. From the above example, moderately high intensities of turbulence could contribute to the formation of a dinoflagellate bloom rather than inhibit it, as commonly proposed (e.g. Margalef, 1978; Hallegraeff et al., 1995; Smayda, 1997, but see Smayda, 2002).

The fastest division rate reported in the literature for unstirred, nutrient and light-replete "batch" cultures of *L. polyedrum* was ~0.35 per day (Meeson and Sweeney, 1982). In our study, quiescent control cultures of *L. polyedrum* had division rates similar to this value, but those cultures exposed to moderate to high turbulence intensities had division rates near 0.50 per day. This example, of how small-scale turbulence modifies the physiological response of dinoflagellates serves as a reminder that experimental responses studied in quiescent "batch" cultures could differ from the responses in nature where turbulent motions are ubiquitous.

Cell size differentiation between low to no turbulence treatments and moderate to high turbulence treatments was evident in *L. polyedrum*, where cell size decreased as turbulence intensity increased. However, in the highest turbulence treatment, the size distribution became bimodal, with the appearance of both small and large cells. This phenomenon has been reported in both cultured and natural populations of other dinoflagellate species (Partensky and Vaulot, 1989; Partensky et al., 1991). While cell size differentiation and the production of small swarmers (gametes) is often part of the sexual life cycle of dinoflagellates, we do not believe that the small cells observed in this study were gametes. Previous studies have shown "small" forms of dinoflagellate cells that are able to divide asexually and return to the large form by simple enlargement of the cell body (Partensky and Vaulot, 1989). Further, these authors found that small forms generally divide at a faster rate than large forms, with up to a 40% increase in division rate. The reduced size of these cells may also enhance photon capture and nutrient uptake efficiencies (Raven, 1986; Kirk, 1994). Again, the presence of turbulence may hasten the formation of a bloom by rapidly increasing the concentrations of *L. polyedrum* in the small flagellate stage, and then converting these small forms to the larger forms when the turbulence is less intense.

The functional relationships between small-scale turbulence, division rate and cell size for *A. catenella* contrast with those of *L. polyedrum*. The responses of *A. catenella* to turbulence were similar to most of the previously reported effects of turbulence on dinoflagellate growth and cell size (White, 1976; Pollingher and Zernel, 1981; Thomas and Gibson, 1990a,b; Berdalet, 1992). These investigators reported that division rate was reduced or totally inhibited and cell size was increased by small-scale turbulence. More recently, Juhl et al. (2001) reported that *Alexandrium fundyense* Balech was prevented from increasing its population size by 12 h a day or more of Couette flow with a shear of $0.003\,\mathrm{N\,m^{-2}}$, which the authors reported was "similar to [turbulence intensity] levels expected in near-surface waters on a windy day". We found that as turbulence intensity increased logarithmically, *A. catenella* exhibited a decrease in division rate and an increase in cell size. However, even at very high turbulence intensities, division rate was still

~0.5 divisions per day, and fast swimming chains were forming. While it might benefit populations of *A. catenella* to avoid turbulent environments, the ability to maintain a relatively high division rate during extremely high turbulence events might allow it to exploit environments which would prevent growth and division in other species of dinoflagellates.

Smayda and Reynolds (2000) present data to classify *A. catenella* as their type IV dinoflagellate, one that tends to bloom along frontal zones, and one that may concentrate and bloom at subsurface pycnoclines. *Alexandrium tamarense* (Lebour) Balech var. '*excavata*' is well known for its frontal-zone blooms in Argentina (Carreto et al., 1986; Smayda and Reynolds, 2000). It is apparently well adapted to entrainment in coastal currents, and thus rapid dispersion (for review, see Smayda, 2000; Smayda and Reynolds, 2000). *Alexandrium catenella* also seems to be dispersed by frontal currents and sometimes it or other *Alexandrium* taxa occur in years when *L. polyedrum* fails to bloom (Marasovic et al., 1995). In their study of a fjord in British Columbia, Taylor et al. (1994) observed that *A. catenella* differed from many other phytoplankton species with regular seasonal and spatial distribution patterns, since its occurrence in the late summer was unpredictable.

Alexandrium catenella produces a strong toxin that is responsible for paralytic shellfish poisoning in humans that have consumed contaminated filter-feeding shellfish (e.g. Sommer et al., 1937). Harmful algal blooms of *A. catenella* are common occurrences along the open coastal environments of the Pacific coast of the USA and blooms of *A. catenella* have lead to numerous human fatalities (for review, see Horner et al., 1997). Many inland coastal areas of Washington state including Puget Sound and areas north (e.g. East Sound, WA) have reported HABs of *A. catenella* (Nishitani et al., 1985; Horner et al., 1997). These inland coastal environments are often subjected to large tidal ranges (>3 m during spring tides) that can produce strong tidal currents and turbulence in the channels and fjords of the area (Gargett, 1976; Griffin and LeBlond, 1990).

East Sound is a fjord of Orcas Island, WA which is part of the San Juan Islands located between the Strait of Georgia and the Strait of Juan de Fuca in a hydrographically complex region (Rattray, 1964; Thomson, 1981). During two successive years in East Sound, concentrated populations of *A. catenella* were found only in a subsurface layer ~2 m thick. Compared to the rest of the water column, this layer had little turbulent mixing, small horizontal current velocities and low shear. Nishitani et al. (1985) also reported finding a subsurface bloom of *A. catenella* that remained in a layer between 3 and 5 m in Quartermaster Harbor, WA, however they could not make estimates of the vertical profile of turbulence. The combination of being able to sustain high division rates when exposed to strong turbulence and to maintain a vertical position in a layer of the water column with low turbulence may play an important role in *A. catenella*'s ability to inhabit coastal environments like the Pacific Northwest that have periodic intense turbulent mixing.

Smayda (2000) has suggested that when *A. catenella* makes chains, it can swim faster to depths where conditions are more suitable for its growth. In support of this, Grindley and Sapeika (1969) reported that *A. catenella* formed chains of up to 4 cells during blooms in upwelling systems (which are associated with strong wind forcing). Taylor (1987, p. 40) has reported that *A. catenella* may form chains as long as 64 cells, but that chains of two, four, or eight individuals are much more common. Chain-forming dinoflagellates like *A. catenella* are generally thought to thrive in turbulent environments where solitary cells do not, although the mechanisms that control this biophysical relationship are poorly understood (ECOHAB, 1995). Do they "thrive" or do they just "survive" as chains? Here, increases in turbulence increased chain lengths, but these higher turbulence intensities and longer chain lengths were associated with slower division rates. The strong relationship between chain formation and turbulence in *A. catenella* provides clues as to the adaptive value of this response.

When *A. catenella* was grown in non-turbulent conditions, 80–90% of the population was solitary cells. However, when it was grown in turbulent conditions, both the frequency of chain formation and chain length increased dramatically. Fraga et al. (1989) have shown both phenomena to result in increased swimming speeds over that of single cells (and shorter chains) in the dinoflagellates *Gymnodinium catenatum* Graham and *Alexandrium affine* (Inoue & Fukuto) Balech. These authors speculated that during downwelling, the higher swimming speeds of long chains may allow the cells to remain in the photic zone at surface

convergences and that this may be a mechanism for producing localized high concentrations of cells in layers at fronts. Karp-Boss et al. (2000) have shown that while the dinoflagellate *Glenodinium foliaceum* Ehrenberg maintained a random swimming orientation in the presence of shear-stress, both single cells and chains of *A. catenella* oriented in response to shear. The magnitude of this effect increased with increasing shear-stress rate. The formation and length of chains in *A. catenella* in response to turbulence could be a mechanism that this species uses to avoid turbulent areas of the water column through fast, well-directed swimming away from shear and turbulence.

The effect(s) of small-scale turbulence on dinoflagellate physiology and ecology is a complex problem and thus, the paradigm that turbulence negatively affects dinoflagellates is too simplistic. We suggest a change in this paradigm that is shared in the recent work of Smayda (2002), who states: "tolerance of turbulence, growth within well-mixed watermasses and survival and dispersal while entrained within current systems are well developed capacities among dinoflagellates". While the hypothesis that turbulence negatively affects the physiology of dinoflagellates may have some general validity and support from the results of laboratory experiments, we have shown that the range of intensities of turbulence examined and the way that it is generated in the laboratory is clearly important. *Alexandrium catenella* had slower division rates in high turbulence, a negative effect, or part of an adaptive response that produces longer cell chains that aid in migration to a more suitable habitat? We feel that combining both laboratory experiments and using newly developed sensors and sampling techniques (Sullivan et al., 1999, 2002) to examine the "turbulent environments" that dinoflagellates inhabit may ultimately provide the answers to the role of turbulence in the ecology of dinoflagellates.

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