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Effect of large marine diatoms growing at low light on episodic new production

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Abstract

Mesoscale eddies have been shown to be a common feature of open ocean regions such as the Sargasso Sea. By lifting nutrients up to the lower portions of the euphotic zone, these eddies can cause episodic phytoplankton blooms that can lead to substantial new production. In the Sargasso Sea, it has been estimated that such blooms can account for 35%–50% of annual new production. In the present study, it was shown that a common large diatom *Stephanopyxis palmeriana* is capable of growing in a low-light environment typical of the bottom 50 m of the euphotic zone at rates sufficiently high to sustain the contemporary estimates of new production that have been attributed to mesoscale eddies. The diatom was grown in laboratory batch experiments at irradiance levels from 11 to 79 μmol photons m^{-2} s^{-1}, equivalent to irradiance levels occurring in the Sargasso Sea during the summer at depths from ~100 m (the 1% light level) up to 50 m. Resulting growth rates were compared with growth rates from the literature for similar large diatoms, and a simple model of new production was developed to show the dependency of new production on specific growth rate. Included in the model were other important parameters such as the depth of nutrient incursion resulting from lifting of the thermocline when an eddy passes, the duration of the bloom, and the size of the prebloom diatom population. Using realistic ranges for these parameters, it was evident from the model that there is no physiological constraint on these large diatoms from growing fast enough at very low light levels to meet the new production estimates resulting from eddies.

There is growing recognition among oceanographers that mesoscale eddies occur frequently in oligotrophic regions and that, through the introduction of colder, nutrient-rich water into the lower layers of the euphotic zone, they can lead to greatly enhanced new production (Jenkins and Goldman 1985; Woods 1988; McGillicuddy et al. 1998; Oschlies and Garcon 1998; McNeil et al. 1999; Siegel et al. 1999; Mahadevan and Archer 2000; Levy et al. 2001). This form of new production, which, because of its episodic nature and because it occurs deep in the euphotic zone, frequently goes unnoticed. In the Sargasso Sea, for example, episodic eddies have been estimated to account for ~35%–50% of total new production, which is estimated to be ~0.5 mol N m^{-2} yr^{-1} or 3.3 mol C m^{-2} yr^{-1}, under the assumption of a Redfield C:N ratio of 6.6 by atoms in phytoplankton (Jenkins and Goldman 1985; McGillicuddy et al. 1998; Siegel et al. 1999). Important questions then arise as to whether marine phytoplankton are capable of growing in a low-light environment at rates that would support the contemporary new production values.

One of us has shown previously that a small seed population of large marine diatoms residing at the base of the euphotic zone could account for this new production by responding with relatively rapid growth rates once nutrients levels are elevated (Goldman 1988, 1993; Goldman et al. 1992). In the present study we expand on the large diatom–episodic event concept more fully by showing how a large oceanic diatom responds to a simulated nutrient injection at low light intensities characterizing the bottom 50 m of the euphotic zone in a locale such as the Sargasso Sea. We then use the resulting growth-rate data along with additional data from the literature in a simple model depicting episodic new production in this region of the water column. On the basis of these results, the potential large diatoms have for contributing significantly to new production through episodic growth deep in the water column is confirmed.

The experimental portion of the present study was similar to that carried out earlier (Goldman 1993). The large diatom *Stephanopyxis palmeriana* (Greville) Grunow was obtained by net tow at ~100 m depth in the Sargasso Sea in June 1990, maintained in culture at low, blue-filtered light (~60 μmol photons m^{-2} s^{-1}) through repeated transfers (Goldman 1993), and used in a series of batch growth experiments at varying low light levels. Experiments were performed during 1995–1996 at the Woods Hole Oceanographic Institution. The enrichment medium MET 44 (Schöne and Schöne 1982) (the same used for species isolation and maintenance) contained 40 μmol L^{-1} $NaNO_3$, 2.58 μmol L^{-1} $NaPO_4$, 35.7 μmol L^{-1} Na_2SiO_3, 2.16 μmol L^{-1} Na_2 ethylene diaminetetraacetic acid, 0.215 μmol L^{-1} $FeSO_4$, 0.073 μmol L^{-1} $MnCl_2$, and 0.5 μg L^{-1} each of vitamin B_{12}, biotin, and thiamine added to Sargasso Seawater that previously had been filtered through glass-fiber filters (Whatman GF/F). Once

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prepared, the medium was pasteurized at 90°C for 2 h and cooled before use.

Growth experiments were conducted in 12-liter glass carboys holding 8 liters of medium. The carboys were maintained in a water bath (20°C) on a 12 h light : dark cycle at irradiance levels of 11, 23, 41, and 79 μmol photons m^{-2} s^{-1}, established with neutral density window screening wrapped around each carboy. Cool white fluorescent bulbs that were filtered with blue acetate sheeting were the light source. Irradiance measurements were made with a Biospherical Instruments QSL-100 4π sensor. Inocula for each experiment were a few cells ml^{-1} taken from exponentially growing stock cultures. Stock cultures were not preconditioned at the experimental irradiance levels. Samples for cell counts and NO_3^- were taken daily for the first 10–15 d of the experiments which lasted up to 55 d and then less frequently. Specific growth rates (μ in d^{-1}) were calculated by regression analysis as the slope of the linear portion of the curve of ln cell number versus time. Cell counts were made with a stereo microscope on 25-ml samples preserved in Lugol's solution. Sampling for particulate organic carbon (POC) was started several days or more after visible growth was observed. POC was measured with a Perkin Elmer 2400 Elemental Analyzer on 25–100-ml samples retained on glass-fiber filters (Whatman GF/F) that were precombusted at 550°C. A few drops of 10% HCL were placed on the filtered material to remove any inorganic carbon before drying at 60°C overnight. NO_3^- and NO_2^- (Wood et al. 1967) were measured on the filtrate.

The exponential portions of each growth curve used in the regression analyses are designated in Fig. 1A. There was no lag phase in growth at the two highest irradiance levels, whereas 5-d lags occurred at the two lower levels. Specific growth rates μ varied from 0.13 ± 0.014 (2 SD) d^{-1} to 0.66 ± 0.082 (2 SD) d^{-1} as a function of increasing irradiance (Figs. 1A, 2). The correlation coefficient for each growth curve was ≥0.98. The response appeared as a typical light saturation curve: μ was linearly correlated with irradiance up to 41 μmol photons m^{-2} s^{-1} and then increased at a reduced rate up to 79 μmol photons m^{-2} s^{-1} (Fig. 2). Growth at the two highest irradiance levels, including a short transitional phase, ended when NO_3^- was exhausted (Fig. 1A,B). In contrast, exponential growth at the two lower irradiance levels was followed by a longer transition phase that continued until the experiments were terminated after 55 days and NO_3^- was still in abundance (Fig. 1A,B). These growth rates were lower than occurred several years previously in similar experiments with the same clone of *S. palmeriana* (Goldman et al. 1992; Goldman 1993) (Fig. 2) and were consistent with observed changes in cell size and cell quota Q_c. For example, Q_c during exponential growth was reduced from 0.42 nmol C $cell^{-1}$ in the earlier study (Goldman et al. 1992) to 0.25 nmol C $cell^{-1}$ in the present study (Fig. 1A,C). Such changes in diatom size and growth rates during long-term maintenance in culture are not uncommon.

To gain some perspective on the range of growth rates possible in large diatoms as a function of irradiance, we compared the values of μ versus irradiance from the current study with those for similar large diatoms grown in culture at varying low irradiance. This data pool included results

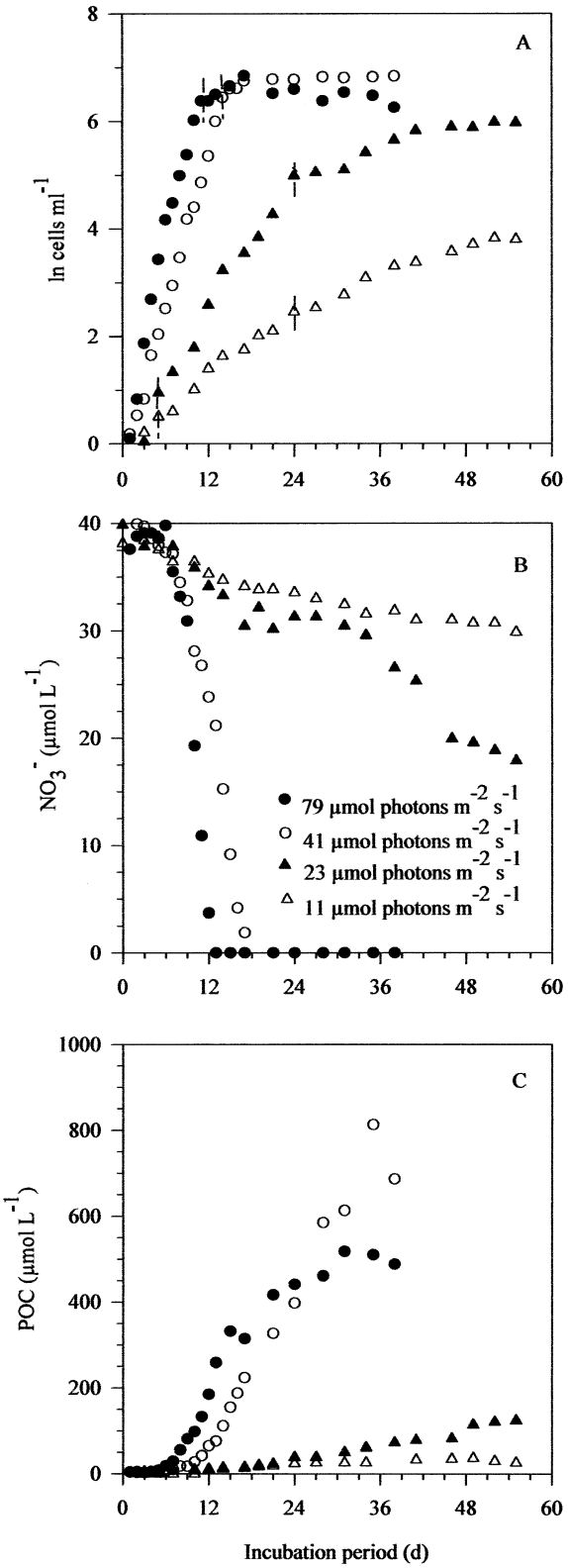

Fig. 1. Changes in biological and chemical parameters during batch growth experiments with *S. palmeriana* at varying irradiance levels: (A) ln cell number, (B) NO_3^-, and (C) POC. Symbols are the same for all panels. Vertical bars on curves represent exponential portion on which linear regression analyses were based.

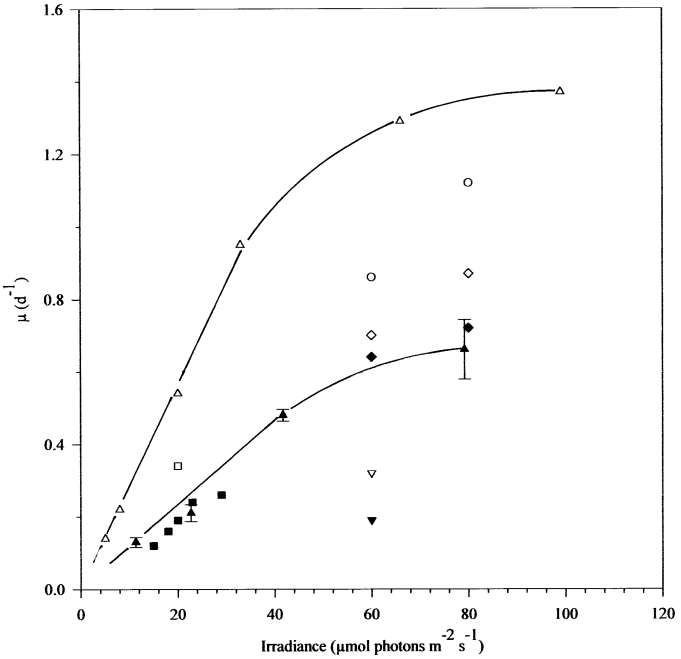

Fig. 2. Effect of irradiance on specific growth rate μ for large diatoms: *S. palmeriana* from current study (filled triangles) (error bars represent ±2 SD); *S. palmeriana* from Goldman et al. (1992) and Goldman (1993) (open circles); *S. palmeriana* from Schöne (1982) (open triangles)—light source, combination of daylight and white fluorescent bulbs; *Planktonella* sp. from Goldman (1993) (inverted open triangle); *Thalassiosira* sp. from Goldman (1993) (inverted filled triangle); *Pseudoquinardia recta* von Stosch from Goldman et al. (1992) and Goldman (1993) (open diamond); *Navicula* sp. from Goldman et al. (1992) and Goldman (1993) (filled diamond); *R. formosa* from Moore and Villereal (1996) (filled squares)—light source, cool white fluorescent bulbs shaded with blue plastic screening; and *S. turris* from Jeffrey and Vesk (1977) (open square)—light source, cool white fluorescent bulbs shaded with blue Belgian signal glass.

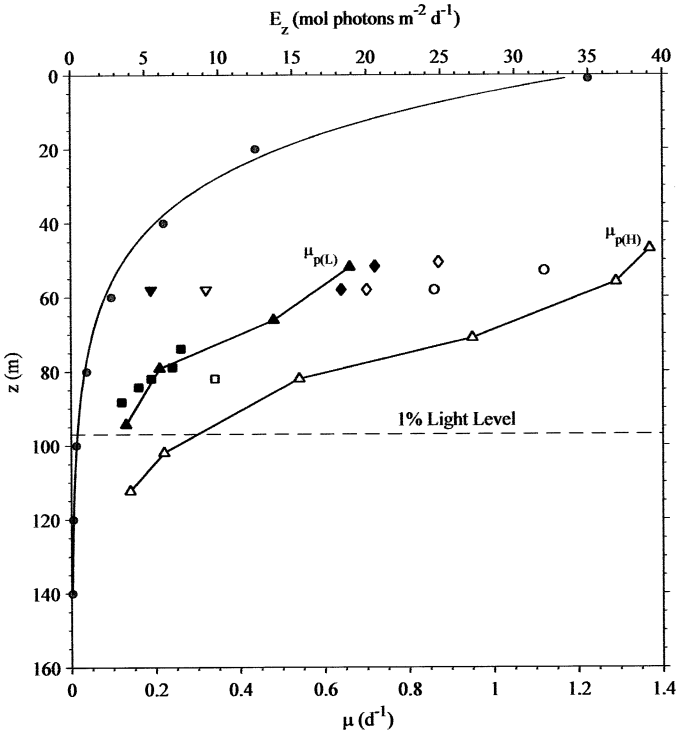

Fig. 3. Attenuation of irradiance E_z with depth z for BATS site in Sargasso Sea during July 1997 (Siegel et al. 2001) (filled circles, fitted with an exponential curve). Also, specific growth rate μ from the data in Fig. 2 for large diatoms as a function of equivalent depth z determined from a regression curve of ln E_z versus z from the attenuation profile and the experimental irradiance levels from Fig. 2 transposed to irradiance levels corresponding to this profile: *S. palmeriana* from current study (filled triangles with a piecewise linear fit); *S. palmeriana* from Goldman et al. (1992) and Goldman (1993) (open circles); *S. palmeriana* from Schöne (1982) (open triangles with a piecewise linear fit); *Planktonella* sp. from Goldman (1993) (inverted open triangle); *Thalassiosira* sp. from Goldman (1993) (inverted filled triangle); *Pseudoquinardia recta* von Stosch from Goldman et al. (1992) and Goldman (1993) (open diamond); *Navicula* sp. from Goldman et al. (1992) and Goldman (1993) (filled diamond); *R. formosa* from Moore and Villereal (1996) (filled squares); and *S. turris* from Jeffrey and Vesk (1977) (open square).

from the earlier studies with *S. palmeriana* and other isolates from the Sargasso Sea (*Planktonella* sp., *Thalassiosira* sp., *Pseudoguinardia recta* von. Stosch, and *Navicula* sp.) (Goldman et al. 1992; Goldman 1993). Also included were results for *S. palmeriana*, isolated off the northwest African coast (Schöne 1982), *Stephanopyxis turris*, a closely related species to *S. palmeriana*, designated MB-31 from the culture collection of the Food Chain Group at Scripps Institution of Oceanography (Jeffrey and Vesk 1977), and *Rhizosolenia formosa*, a very large (6.8–11.8 × 10^6 μm^3) chain-forming diatom isolated from the Sargasso Sea (Moore and Villareal 1996).

An important goal of the current study was to simulate in a laboratory batch experiment a diatom bloom as it might occur deep in the euphotic zone of an oligotrophic locale. To demonstrate that the range of irradiance levels used in the current study was indeed representative of this zone, we first converted the experimental values to mol photons m^{-2} d^{-1} using the experimental 12-h light : dark cycle, to compare them with a typical light profile for the Sargasso Sea in July 1997 obtained from Siegel et al. (2001). This profile represents a period of intense stratification and low productivity in the absence of eddies. Using a regression of lnE_z versus z (E_z is photosynthetically available irradiance in mol photons m^{-2} d^{-1} at depth z in m), we transposed the experimental irradiance levels and corresponding specific growth rates μ for all the data from Fig. 2 to depths corresponding to the Sargasso Sea profile (Fig. 3). With the exception of the very lowest irradiance levels from the study of Schöne (1982), which were at equivalent depths below the 1% light level (equal to 0.43 mol photons m^{-2} d^{-1} in this case), all of the equivalent depths fell within a range from 52 to 94 m (Fig. 3). Given that the 1% irradiance level occurred at 98 m (Fig. 3), which is typical for the Sargasso Sea during stratification (Siegel et al. 1999), the range of experimental irradiances closely represented the bottom half of the euphotic zone.

To examine the potential response of diatom populations

to eddy-induced upwelling, we formulated a simple model of new production based on the specific growth rate:

$$P_N = Q_c X_0 (e^{\mu t} - 1) \quad (1)$$

where P_N is new carbon production in mol C m^{-3}, Q_c is the carbon cell quota in mol C $cell^{-1}$, X_0 is the initial cell concentration in cells m^{-3}, μ is the specific growth rate in d^{-1}, and t is time in days. To first order, eddy disturbances can be modeled in one dimension as vertical displacements of the background physical and biological profiles (McGillicuddy et al. 1995). Therefore, we can compute a Eulerian representation of the diatom response to an eddy-driven upwelling event (P_{EDDY}) simply by integrating the new production model from the base of the euphotic zone (Z_{EU}) up to the shallowest depth to which water parcels are displaced by the eddy motions ($Z_{EU} + d$) where d is perturbation depth (m):

$$P_{EDDY} = \int_{Z_{EU}}^{Z_{ED}+d} P_N \, dz = \int_{Z_{EU}}^{Z_{EU}+d} Q_c X_0 (e^{\mu t} - 1) \, dz \quad (2)$$

Similarly, the average growth rate within the layer of uplifted water (μ_{EDDY}) can be calculated

$$\mu_{EDDY} = \frac{1}{d} \int_{Z_{EU}}^{Z_{EU}+d} \mu(z) \, dz \quad (3)$$

where the vertical profile of growth rate $\mu(z)$ is specified from the combination of laboratory measurements and the observed light profile. For this purpose, we constructed piecewise linear fits to the Schöne (1982) and the current data; these two fits envelop most of the laboratory data presented in Fig. 3. We refer to these end-member profiles in the growth rates that are possible as $\mu_{p(L)}$ and $\mu_{p(H)}$. Given that half-saturation coefficients for inorganic nitrogen uptake by marine diatoms often are well below 0.1 μmol L^{-1} (Goldman and Glibert 1983), we would suspect that only light would be limiting growth when nutrients are in abundance during an eddy-driven upwelling event.

Our objective herein is to evaluate whether or not the enhanced growth rates due to eddy perturbations are sufficient to meet the contemporary new production estimates. To make this comparison, it was first necessary to make some reasoned assumptions regarding the magnitude of the model parameters. Given uncertainties in the magnitude of d, Q_c, X_0, and t, it seemed prudent to apply ranges for each parameter rather than absolute values. Sensitivity analysis provides a means for quantifying the range in μ_{EDDY} required to achieve a particular level of new production. We refer to the extrema in required growth rates as $\mu_{r(L)}$ and $\mu_{r(H)}$. In effect, any set of conditions for which $\mu_p > \mu_r$ within these ranges would describe a scenario in which it was physiologically possible for this new production to occur.

The physical parameters of the new production model can be estimated from prior studies of eddy-driven upwelling in the Sargasso Sea. From mesoscale biogeochemical surveys (McGillicuddy et al. 1999) and moored observations (McNeil et al. 1999; Dickey et al. 2001), it appears that typical eddy-induced vertical perturbations at the base of the euphotic zone are on the order of 50 m. Hence, we used a range in d from 10 m (a conservative estimate requiring higher growth rates) up to 50 m. Siegel et al. (1999) estimated from their analysis of sea-level anomalies (SLA) during a 3-yr period at the BATS station in the Sargasso Sea that the average time for an eddy to pass this location was 23 d. McGillicuddy et al. (1998) suggested a slightly higher value of 30 d, given that eddies are ~150 km in size and propagate at ~5 km d^{-1}. These estimates are consistent with their observations that NO_3^- and chlorophyll concentrations at 80 and 71 m, respectively, (measured continuously with moored instruments) were elevated substantially for ~20 d (~2 μmol L^{-1} NO_3^- and ~1 μg L^{-1} Chl *a*) during the passage of an eddy in July 1995 at the BATS site (McNeil et al. 1999). From additional pigment data, it was confirmed that a diatom bloom was occurring at this time (McNeil et al. 1999). Thus, we used a range of 20–30 d for t, the lower value representing a more conservative estimate. Note that this is the Eulerian timescale over which an eddy passes by a fixed point; the lifetime of an individual eddy can be considerably longer. As for the biological parameters, we assumed that the initial cell population (X_0) before a bloom ranged from 1 to 10 cells L^{-1}. These values are probably conservative, because the concentration of large diatoms in nonblooming oligotrophic waters, similar in size to the diatoms represented in Fig. 2, typically is on the order of ~50 cells L^{-1}, an ''extremely low number'' according to Guillard and Kilham (1977). Finally, we used a range of Q_c from 0.25 to 0.5 nmol C $cell^{-1}$ (Fig. 1A,C), the lower value coming from the present study and the higher one derived from the cell volume data for *S. palmeriana* found in Goldman et al. (1992) and from the application of the Strathmann equation (Strathmann 1967).

Using the ranges established above for d, t, Q_c, and X_0, we were able to describe different episodic growth scenarios in which P_{EDDY} was plotted against μ (Fig. 4A). For clarity, only curves for the extreme cases are presented, where d = 10 m, Q_c = 0.25 nmol C $cell^{-1}$, X_0 = 1 cell L^{-1}, and t = 20 d for the highest required growth rates, and d = 50 m, Q_c = 0.5 nmol C $cell^{-1}$, X_0 = 10 cell L^{-1}, and t = 30 d for the lowest required growth rates. The shaded area within the two curves describes all the possible scenarios for the ranges of the different parameters that were considered in the new production model. A common characteristic of the curves in Fig. 4A is the extreme sensitivity of P_{EDDY} to very small changes in μ. For example, using the low estimate curve, only a 0.02 d^{-1} increase in μ from 0.20 to 0.22 d^{-1} leads to a two-fold increase in P_{EDDY} from 0.1 to 0.2 moles C m^{-2} per event. It is important to note that such small differences in μ are extremely difficult to distinguish in controlled laboratory experiments and are virtually impossible to measure in the field. Additionally, the two extreme curves are separated by a difference in μ of only ~0.3–0.4 d^{-1}.

From the prior studies of mesoscale eddies in the Sargasso Sea (McGillicuddy et al. 1998, 1999; McNeil et al. 1999; Siegel et al. 1999), it appears that, on average, a typical eddy can contribute sufficient NO_3^- to the euphotic zone to sustain conservatively $P_{EDDY} \approx 0.2$ mol C m^{-2}, under the assumption of a Redfield C : N ratio in phytoplankton of 6.6 : 1 by atoms. Siegel et al. (1999) estimates that ~6 such events occur annually in this location, so that the yearly contribution from eddies (~1.2 mol C m^{-2} yr^{-1}) is ~35% of total annual new

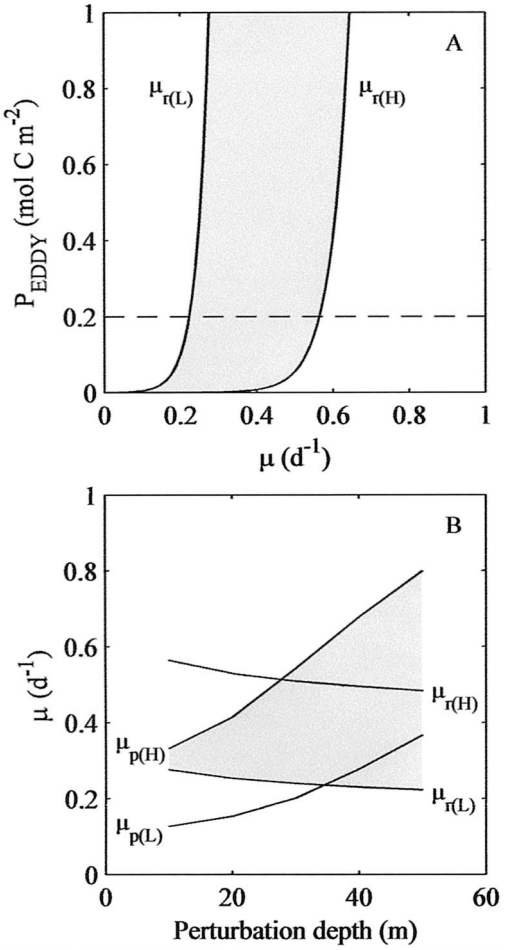

Fig. 4. Impact of specific growth rate μ on extreme high and low new production scenarios in large diatom-mesoscale eddy model. (A) Effect of μ on new production P_{EDDY} for extreme cases involving *S. palmeriana* where $d = 10$ m, $Q_c = 0.25$ nmol C cell^{-1}, $X_0 = 1$ cell L^{-1}, and $t = 20$ d (highest required μ, labeled as $\mu_{r(H)}$) or $d = 50$ m, $Q_c = 0.5$ nmol C cell^{-1}, $X_0 = 10$ cells L^{-1} and $t = 30$ d (lowest required μ, labeled as $\mu_{r(L)}$). (B) Possible specific growth rates ($\mu_{p(L)}$ to $\mu_{p(H)}$) and required growth rates ($\mu_{r(L)}$ to $\mu_{r(H)}$) for extreme high ($Qc = 0.25$ nmol C cell^{-1}, $X_0 = 1$ cell L^{-1}, and $t = 20$ d), or low ($Q_c = 0.5$ nmol C cell^{-1}, $X_0 = 10$ cells L^{-1}, and $t = 30$ d) growth rate scenarios involving *S. palmeriana* plotted against the perturbation depth d required to allow $P_{\text{EDDY}} = 0.2$ mol C m^{-2}. The ordinate in each of the four curves represents the average growth rate over the perturbation depth d: i.e., $\mu = (1/d) \int_{Z_{EU}}^{Z_{EU}+d} \mu(z)\, dz$.

production (~3.3 mol C m^{-2} yr^{-1}) excluding mode-water eddies and ~50% with them included. Winter convection is another major source of NO_3^- (~34%), along with smaller contributions from diapycnal and isopycnal diffusion, large-scale Ekman pumping, and atmospheric input (Siegel et al. 1999). Thus, to address the question of how fast large diatoms must grow to sustain eddy-driven new production in the Sargasso Sea, we solved Eq. (2) for μ given $P_{\text{EDDY}} = 0.2$ mol C m^{-2} per event. Sensitivity analysis was then used to determine the range of required growth rates $\mu_{r(L)}$ to $\mu_{r(H)}$, given the uncertainties in model parameters described above. We evaluate the model by comparing the required growth rates μ_r with the possible growth rates μ_p as a function of the magnitude of the eddy-driven perturbation d (Fig. 4B). The shaded area within the contours represents any of a number of combinations of conditions for which $\mu_p > \mu_{r(L)}$, and the intersection of the curves for $\mu_{r(L)}$ and $\mu_{p(H)}$ sets the lower limit of d for these conditions.

It is evident from the size of the shaded area in Fig. 4B that the large diatom-episodic eddy scenario is robust over an increasing range of possible growth rates as d increases from 10 up to 50 m (the maximum considered). In fact, because P_{EDDY} is so sensitive to small changes in μ, only an approximate 0.1 d^{-1} increase in μ for a given set of conditions can result in P_{EDDY} increasing from 0.2 to 3.3 mol C m^{-2} per event, which is the full yearly new production attributed to mesoscale eddies. Thus, from the standpoint of light limitation alone, growth rates of large diatoms appear to be sufficient to support a full year's production in one event.

Clearly, however, an important constraint on new production per event is the quantity of nutrients that are brought into the euphotic zone as nutrient-rich water is uplifted during eddy formation. The depth-averaged NO_3^- concentration in the perturbed layer required at the start of a bloom to achieve $P_{\text{EDDY}} = 0.2$ mol C m^{-2} would vary from ~0.6 μmol L^{-1} for $d = 50$ m to ~3.0 μmol L^{-1} for $d = 10$ m (under the assumption of a Redfield C : N ratio of 6.6 : 1). Such a range of NO_3^- concentrations in the euphotic zone is realistic—eddy-induced displacements ≥50 m at the base of the euphotic zone have been observed in the vicinity of the BATS station in the Sargasso Sea, leading to NO_3^- concentrations of 2–3 μmol L^{-1} in the lower euphotic zone (McGillicuddy et al. 1999; McNeil et al. 1999). Moreover, these values are conservative, because the observed concentrations reflect the balance between input and uptake. As was stated earlier, light, rather than nitrogen, would be limiting because of the very low half-saturation coefficients of marine diatoms for inorganic nitrogen. In this regard, there is evidence for significant dark uptake of NO_3^- by the large diatom *R. formosa*, a finding consistent with the notion that NO_3^- uptake into storage vacuoles at low to no light can be uncoupled from growth in large diatoms, thereby allowing for nutrient-replete but light-limited growth in this region of the water column (Moore and Villareal 1996). However, an important caveat is that there are virtually no data on nutrient uptake by large diatoms available in the literature for extremely low light environments.

The results presented herein suggest that diatoms are able to utilize nutrients upwelled into the lower euphotic zone by mesoscale eddies and that eddy-driven blooms can contribute a significant fraction of the annual new production observed in the Sargasso Sea. However, this simple model is not necessarily sufficient to explain the observed seasonal accumulation of oxygen in the upper ocean. If the eddy-driven upwelling process were purely isopycnal, then the oxygen produced by an eddy event would eventually subside during eddy decay as the isopycnals return to their original depth prior to eddy formation. How might the oxygen signal associated with eddy-driven productivity events get ''left behind'' in the upper euphotic zone? The key lies in the interaction between eddy-induced isopycnal upwelling and dia-

pycnal mixing processes in and below the mixed layer. It is evident from satellite data that some connection takes place, because eddies are clearly visible in sea-surface temperature imagery. This surface manifestation arises because isopycnals perturbed by eddy motions outcrop in the mixed layer. However, the detailed linkages between these two regimes remain obscure. We know that surface layer turbulence creates a well-mixed layer in which diffusivity is very large. In contrast, diapycnal diffusivity in the main thermocline is very small (on the order of 10^{-5} m^2 s^{-1}), as evidenced by microstructure measurements and tracer release experiments (Lewis et al. 1986; Gregg 1987; Ledwell et al. 1993, 1998). The nature of the transition from the actively mixed surface layer to the more quiescent waters of the main thermocline is not well constrained by the extant database. Estimates of diapycnal diffusivity in the upper ocean based on surface-layer tracer release experiments range from values close to that of the main thermocline (Law et al. 1998; Iron-Ex I, 2.5×10^{-5} m^2 s^{-1}) to an order or magnitude larger than that (Zhang et al. 2001; GasEx98, 1.0×10^{-4} m^2 s^{-1}; Law et al. 2001; UK Prime, 1.95×10^{-4} m^2 s^{-1}). These measurements can be used to assess the degree to which oxygen would accumulate in the upper ocean as a result of eddy-induced blooms. For example, consider an isopycnal that was lifted from 100 to 50 m. Using the scaling $K \sim L^2/T$ (where K is the diffusivity and L and T are characteristic length and timescales, respectively), the time required for the eddy-induced signal at 50 m to diffuse half-way to the surface (another 25 m upward into the euphotic zone) can be computed. Diffusivities at the high end of the range cited above yield a timescale on the order of 30 days—the same as the Eulerian timescale for an eddy event. Clearly, such conditions would facilitate preservation of the bloom-induced oxygen anomaly in the upper ocean. In contrast, diffusivities at the lower end of the range would preclude significant diapycnal oxygen flux on the timescale for eddy passage. Needless to say, quantitative reconciliation of the oxygen and nutrient budgets in the euphotic zone remains an enigmatic issue that requires further research on mixing processes in the upper ocean and the associated biogeochemical transports.

There are additional caveats that deserve mention. The simple model described herein characterizes a one-dimensional biological response as an eddy passes a given point and assumes that nutrients are well mixed in a given layer d for a fixed time t. In reality, the life of an eddy is a highly dynamic three-dimensional process, involving intensification of primary production as nutrients are injected into the euphotic zone during eddy formation and subsequent decay as the eddy subsides, all while the eddy is traversing great distances. Modeling such a time-variant process was beyond the scope of the present study but needs to be considered.

Another important caveat concerns phosphorus nutrition. The fact that the phosphate cline is deeper than the nitrate cline in this region (Michaels et al. 1994; Wu et al. 2000), suggests that P, rather than N, may limit primary productivity. Possibly, dissolved organic P, which is in far greater abundance than inorganic P (Wu et al. 2000), is available for uptake, thereby allowing complete utilization of available nitrate and keeping the cellular N : P ratio in Redfield proportions. Regardless, the fact that nitrate and oxygen budgets in the Sargasso Sea are consistent with Redfield stoichiometry (Siegel et al. 1999) indicates that the organisms' phosphorus demand is somehow being met. Further research on this important question is needed. Additionally, it is important to note that the present results were based on a few large diatom species grown in the laboratory, and, moreover, some that displayed variable growth characteristics when kept in culture for a long period. In the natural environment there most likely are numerous large diatom species with growth characteristics equal to or even greater than those of the large diatoms depicted in Fig. 2, so the composite growth rate data presented herein may be conservative.

A major consequence of the large diatom-episodic event scenario is that these events are difficult to detect with conventional sampling. It is only recently with the advent of moored arrays for continuous and simultaneous measurements of key parameters such as temperature, NO_3^-, and chlorophyll at strategic locations in the water column (McNeil et al. 1999; Dickey et al. 2001) and satellite altimetry for measuring SLA (Siegel et al. 1999) that the importance of mesoscale eddies to regional new production has been confirmed. Moreover, there seems to be substantial recent evidence that large diatoms play the key role in responding to episodic nutrient injections (Brzezinski et al. 1998; Scharek et al. 1999). Although it remains to be determined just how important eddies are to new production on a global scale, it is unequivocal that the biological response to these episodic events is swift and efficient.

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