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Spectral distribution and species-specific photosynthetic performance of natural populations of *Prorocentrum mariae-lebouriae* (Dinophyceae) in the Chesapeake Bay

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ABSTRACT: *Prorocentrum mariae-lebouriae* is a prominent member of the dinoflagellate flora in the Chesapeake Bay, USA. In late winter to early spring, this species occurs in subpycnocline waters of the estuary where large populations are transported landward in estuarine circulation and seed spring-summer blooms in mesohaline to oligohaline regions. During a weeks-long transport below the seasonally-established density discontinuity, *P. mariae-lebouriae* experiences low-light intensities (≤ 10 $\mu E\ m^{-2}\ s^{-1}$) of a narrow spectral distribution characterized by highest transmission and lowest wavelength-specific light attenuation coefficients, K_λ, in the 565 to 575 nm region of the visible spectrum. We asked the question, 'What is the photosynthetic performance of *P. mariae-lebouriae* in the ambient spectral conditions in Chesapeake Bay?' Photosynthetic action spectra were measured in a series of spring curises in 1986 and 1987 for *P. mariae-lebouriae* cells isolated and concentrated from whole water. Results showed peaks of photosynthetic activity in the blue and red regions of the visible spectrum (chlorophyll absorption), and a smaller shoulder of activity in the green to yellow (peridinin absorption). Low-light adapted cells from below the pycnocline, and surface bloom populations exposed to a downward light-shift, showed enhancement of photosynthetic activity in the 500 to 560 nm region. This feature accompanied photoadaptive increases in per-cell concentrations of chlorophylls *a* and *c*, and of the light harvesting carotenoid, peridinin. Computations of the influence of ambient spectral distribution and wavelength-specific photosynthetic performance of *P. mariae-lebouriae* on rates of primary production showed effects due to light quality that ranged from 31 % underestimates to 57 % overestimates.

INTRODUCTION

The spectral composition of light available to phytoplankton cells changes with depth and is especially influenced by dissolved and suspended (living and non-living) materials in the water column. In the clearest oceanic waters, light in the blue to blue-green (400 to 500 nm) regions of the visible spectrum penetrates deepest with the peak in transmission occurring at 440 to 490 nm. Coastal and inland waters, including estuaries, have greater vertical attenuation of light because of higher densities of phytoplankton and higher concentrations of dissolved organic and suspended particulate materials. Spectral distributions are shifted to longer wavelengths with peaks in transmission often occurring in the green to yellow, 550 to 580 nm. The wavelength distributions of extremely turbid environments can be shifted toward even longer wavelengths in very shallow euphotic zones that have peak transmission in the orange to red, 600 to 700 nm (reviews: Jerlov 1968, 1976, Smith & Baker 1978, Yentsch 1980, Kirk 1983).

As a consequence of the optical properties of turbid environments, phytoplankton cells in estuaries may experience light fields with spectral distributions practically devoid of photic energy in the blue and red wavebands that are effectively absorbed by the chlorophylls. In the upper few meters of the surface mixed layer, there is light energy in these spectral regions (430 to 460 nm and 630 to 680 nm), but wavelength-specific light attenuation coefficients, K_λ, are high and photic energy in these bands does not penetrate to an appreciable depth (Jerlov 1976, Kirk 1983). Phytoplankton from a number of taxonomic

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groups use accessory pigments, such as carotenoids, to absorb available photic energy in other wavebands (see Jeffrey 1980, Yentsch 1980, Prézelin 1981, 1987, Kirk 1983, Larkum & Barrett 1983). Most of these pigments have maximal in vivo absorbance in blue-green to yellow wavebands and are thereby useful in harvesting photic energy in the estuarine light field.

The Chesapeake Bay, USA, is a large estuary with regions of high turbidity and light attenuation coefficients, K_t, for PAR (photosynthetically active radiation; 400 – 700 nm) ranging from ~0.3 to > 3 m^{-1} (Harding et al. 1986). This high turbidity produces photic zones of only 1 to 9 m. The wavelength distribution narrows greatly with depth and an 'orange shift' typical of coastal, estuarine, and inland waters has been reported before (Champ et al. 1980). Chesapeake Bay receives freshwater flow primarily from the Susquehanna R., Potomac R., and several lesser tributaries. The estuary is a stratified, 2-layered system from spring through early fall due to riverine input of freshwater to the surface layer, subpycnocline flow of seawater northward with estuarine circulation, and seasonal increases in insolation and surface temperature (review: Itsweire & Phillips 1987). During the early part of this stratified period in late March and early April, populations of the dinoflagellate *Prorocentrum mariae-lebouriae* that overwinter in the lower estuary undergo a 150 to 200 km transport northward in subpycnocline waters. The transport sequence culminates in advective inoculation of cells to surface waters of the upper estuary where light and nutrient conditions are amenable to the formation of spring-summer blooms that often develop in May and June (Tyler & Seliger 1978, 1981, Harding & Coats 1988).

During the seasonal transport beneath the pycnocline, *Prorocentrum mariae-lebouriae* inhabits a water mass with a light environment that is very low in intensity (≤10 μE m^{-2} s^{-1}) and narrow in spectral distribution (500 to 600 nm). Dense populations of *P. mariae-lebouriae* cells commonly occur beneath the pycnocline at 8 to 10 m where cell concentrations of ≥ 20 000 cells ml^{-1} may be found in nearly unialgal lenses. Upon inoculation of *P. mariae-lebouriae* into the surface mixed layer, light availability remains low because of high turbidity in the oligohaline and mesohaline parts of the Bay. In previous studies focused on light intensity-driven responses (Harding et al. 1983, Coats & Harding 1988, Harding 1988, Harding & Coats 1988), it has been shown using a combination of photophysiological and ultrastructural evidence that this species of dinoflagellate responds to low-light exposure by several adaptive 'strategies'. These responses include increases in both the photosynthetic unit (PSU) 'size' and 'number' (reviews: Falkowski 1980, Prézelin 1981, 1987, Richardson et al. 1983), and produce increased photosynthetic performance in low-light, i. e. an increase in photosynthesis per cell in the ambient photic regime. These adaptations contribute to the survival and proliferation of *P. mariae-lebouriae* in the low-light estuarine environment of the Chesapeake Bay where it is an important floral component.

While field studies of low-light adaptation in this species were conducted in situ and thereby included spectral effects in measurements, few data are available on the organism's photosynthetic responses in controlled spectral conditions. Spectral 'quality' is known to affect growth, pigmentation, and biochemical composition in phytoplankton, including *Prorocentrum mariae-lebouriae* (Faust et al. 1982, Meeson & Faust 1985), and other algal species and endosymbiotic zooxanthellae (Wallen & Geen 1971a, b, Qasim et al. 1972, Jeffrey & Vesk 1977, Vesk & Jeffrey 1977, Jeffrey 1980, Kinzie et al. 1984, Kinzie & Hunter 1987). The importance of spectral distribution is further supported by recent findings that primary production in natural light regimes may be erroneously estimated using photosynthesis measurements made in broad waveband spectral conditions (Lewis et al. 1985a, b).

In this paper, we address the influence of spectral distribution on species-specific rates of photosynthesis in the dinoflagellate *Prorocentrum mariae-lebouriae* from natural populations. We report the spectral distribution of light available in Chesapeake Bay and wavelength-specific photosynthetic rates of *P. mariae-lebouriae*. Our goals were to: (1) characterize the wavelength distribution of light this dinoflagellate species encounters in Chesapeake Bay, (2) measure photosynthetic action spectra of natural *P. mariae-lebouriae* populations, and (3) determine the influence of spectral quality on in situ primary production of this species.

MATERIALS AND METHODS

Survey. The experiments described in this paper were conducted aboard the RV 'Ridgely' Warfield during 4 cruises (ProPhot series) on the Chesapeake Bay from February to May 1986, thus encompassing the transport and bloom season of *Prorocentrum mariae-lebouriae*, and during 1 cruise in May 1987 when a bloom of *P. mariae-lebouriae* occurred in the vicinity of our laboratory on the West R. On the first day of each cruise, we typically conducted a transect of the entire 314 km length of the estuary along the main channel to characterize the density structure and to locate the center of the *P. mariae-lebouriae* distribution. Vertical profiles of conductivity, temperature, depth, chloropyhll (chl) *a* fluorescence, oxygen, pH and cell numbers were determined with a CTD-rosette sampler or submersible pump and linked instrument array,

including: Plessey-Grundy CTD/General Oceanics Rosette/10 l Niskin bottles, Chesapeake Bay Inst. ICTI, Turner Designs nephelometer, Winkler titrations, Yellow Springs Instruments O_2 meter, Orion pH meter, cell counts on a Sedgwick-Rafter counting chamber.

Photosynthesis measurements. Based on the distribution of *Prorocentrum mariae-lebouriae* in the Bay, we selected 2 stations on each cruise and occupied each for 24 h (Table 1). At these stations, water samples were collected using 10 l Niskin bottles on the rosette. Collection and concentration procedures commenced at 03:30 h and were conducted in darkness at ambient water temperature. Water (50 to 200 l) was prescreened through 20 µm Nitex mesh to remove large zooplankton and netplankton. The sample was then processed using a temperature-regulated cell concentrator. The procedure involved differential gravity filtration with 10 µm and 20 µm Nitex screens. *P. mariae-lebouriae* cells readily passed the 20 µm mesh but were retained on the 10 µm Nitex. A concentrated and relatively unialgal (≥90%) suspension of *P. mariae-lebouriae* was obtained from the concentrator within 1 to 2 h of collection of the whole water. After processing the whole water, the concentrate was diluted to 20 l using station water that had been filtered through Gelman A/E glass fiber filters. This suspension was used in subsequent experiments and measurements. For further details see Harding & Coats (1988).

The *Prorocentrum mariae-lebouriae* suspension was dispensed to a set of acid and distilled water rinsed liquid scintillation (LS) vials (7 ml, glass). Approximately 2 to 4 µCi of ^{14}C-sodium bicarbonate were added to each vial in a 50 to 100 µl injection. Vials with sample were incubated in light of 14 to 16 wavebands (4 irradiances in each waveband), encompassing the 400 to 700 nm region of the visible spectrum. We used a 'photosynthetron' modeled after that described by Lewis & Smith (1983) with a custom set of 10 and 25 nm bandpass filters (Corion Corp.) and nickel screens (Perforated Products, Inc.) to modulate the light supply. The light source was a 208 V quartz-iodine lamp (Sylvania 1500 208 T3) on shipboard, and a 240 V lamp (Philips 1500 T30/CL 240V AB/4) in the laboratory. These samples were not illuminated with background actinic illumination. An additional set of 20 vials was incubated in light without the bandpass filters, using nickel screens to regulate intensity only. Photon flux densities (PPFD, µmol photons m^{-2} s^{-1}) were measured with a factory-calibrated Li-Cor Model 1800 UW spectroradiometer equipped with a 1800-10/11 quartz fiber optic probe and remote cosine collector. The spectroradiometer was recalibrated with a Li-Cor 1800-02 calibrator after the experiments; <0.2 % drift had occurred.

All experiments were conducted at the temperature of collection, as controlled by a circulating water bath (Forma, Inc.). A radiator and heat sink were used to dissipate heat from the light source. Incubations were ca 1 h in duration and were terminated by filtering samples onto 25 mm Gelman A/E glass fiber filters at low vacuum (≤150 mm Hg). Filters were rinsed with 'cold', filtered sample, gently acidified with 0.01*N* HCl to remove residual inorganic label, and placed in scintillation minivials in ACS cocktail (Packard, Inc.). Acitivities (dpm) were measured on a Packard Instruments Model 4530 LS counter and ^{14}C assimilation was corrected for dark uptake. Photosynthesis data in the body of the paper are shown as the mean (± SE) of carbon fixed per µmol photons m^{-2} s^{-1} on per-cell (P^C/I) and/or per-chl (P^B/I) bases for the 4 samples incubated in each waveband.

In a light shift experiment conducted during development of a dense, unialgal bloom of *Prorocentrum mariae-lebouriae* in mid-May 1987, surface sam-

Table 1 Sampling dates, depths, and locations of stations in Chesapeake Bay

Cruise	Date	Depth (m)	Station	Dist. from head of Bay (km)	Coordinates N Latitude	W Longitude
15	27 Feb 86	14.5	804B	177	30° 04′ 01″	76° 12′ 11″
15	28 Feb 86	8	845F	95	38° 45′ 26″	76° 26′ 37″
16	13 Mar 86	Surf	804C	177	38° 03′ 52″	76° 12′ 10″
16	14 Mar 86	Surf	818P	149	38° 18′ 19″	76° 17′ 29″
17	16 Apr 86	12	835	112	38° 35′ 10″	76° 25′ 23″
17	17 Apr 86	5	858C	71	38° 57′ 27″	76° 22′ 43″
18	7 May 86	16	849D	88	38° 49′ 29″	76° 24′ 04″
18	8 May 86	15	858C	71	38° 57′ 52″	76° 22′ 34″
PC1	2 May 87	Surf	Parish Cr	83	38° 52′ 00″	76° 30′ 00″
PC1	6 May 87	Surf	Parish Cr [a]	83	38° 52′ 00″	76° 30′ 00″
24	14 May 87	Surf	West R.	83	38° 52′ 00″	76° 30′ 00″

[a] Same population as 2 May 87, Parish Cr., following 4 d reduced light (20 µE m^{-2} s^{-1}, LD 12 : 12)

ples were collected from a dock near the laboratory at Parish Creek on the West R. *P. mariae-lebouriae* was isolated and concentrated using the procedures outlined above. Pigment concentrations and a photosynthetic action spectrum were determined on the day of collection. After a 4 d incubation in low-light (20 µE m^{-2} s^{-1}, LD 12:12) supplied by HO cool white fluroescent lamps attenuated with neutral density screens at 15 °C (= ambient T), pigment concentrations and an action spectrum were measured again.

Pigment concentrations. Samples for determining pigment concentrations were collected on Gelman A/E filters at the time photosynthesis incubations were begun. Chl *a* concentrations were measured fluorometrically on 90 % acetone extracts of filter-collected material on a Turner Designs Model 10 fluorometer calibrated with a Beckman DK-2 ratio recording spectrophotometer using pure Chl *a* (Sigma, Inc.). Chl *c* concentrations were measured on spectrophotometric scans of the acetone extracts and calculated by Jeffrey's (1968, 1974) equations. Concentrations of peridinin were measured with high performance liquid chromatography (HPLC) on a Waters Associates system (Millipore, Inc.) by methods described in Harding (1988) and Harding & Coats (1988).

Light intensity and spectral distribution. Ambient light conditions were monitored on transects and continuously at 24 h stations using Li-Cor Model 550 integrating quantum meter equipped with a submersible, spherical 193SB probe. Broad band (400 to 700 nm) light attenuation, K_t, was determined from vertical profiles of intensity measured on a Li-Cor Model 188B quantum meter. The spectral distribution of light was measured at each vertical station on the transects and at 2 h intervals at anchor stations with a Li-Cor Model 1800-UW underwater spectroradiometer linked to a shipboard IBM PC. Data were recorded as binary files, converted to ASCII files, and used to generate K_λ values using a BASIC program to perform least squared linear regressions on log-transformed spectral data as a function of depth.

Spectral effects on primary production. To test the effects of the wavelength distribution on in situ photosynthetic properties of *Prorocentrum mariae-lebouriae*, we first computed I_o/I_k for the 1986 ProPhot cruises from daily insolation, I_o, and daylength, D, using I_k values generated in photosynthetron incubations in 'white' light. The mean (± SE) ratio of I_o/I_k was 3.72 (± 1.04). According to an error analysis made by Lewis et al. (1985a), estimates of the initial, light-limited slope of P-I relations, α^B, are more important to correct estimates of areal production than are those of the light-saturated rate, $P_m{}^B$, for $I_o/I_k < 4.0$. Spectral corrections were applied to the estimation of production in the entire photic zone by Lewis et al. That approach, however, was not directly applicable to the conditions experienced by a *P. mariae-lebouriae* population entrained in a lens beneath the density discontinuity. To address the more specific question of whether production by *P. mariae-lebouriae* in such a lens would be quantitatively influenced by wavelength-specific photosynthetic properties, we combined data for photosynthetic action spectra with those for spectral distribution to compute daily rates of carbon assimilation for an entrained population residing between 8 and 10 m. Occurrence of such a lens is typical of the *P. mariae-lebouriae* distribution during the subpycnocline transport this species undergoes (Harding & Coats 1988).

The computations were made by decomposing I_z into $I_{z,\lambda}$ for 50 nm wavebands, using the wavelength-specific attenuation coefficients averaged over that increment and I_o for each waveband. This produced an array of photon fluxes for 50 nm increments from 400 to 700 nm. These data on the spectral distribution of light with depth were combined with wavelength-specific values for carbon assimilation acquired from the photosynthetic action spectra. 'White' light computations were based on PAR (400 to 700 nm) and photosynthetic rates measured in light unattenuated with spectral filters.

RESULTS

Spectral distribution and turbidity

The maximum light transmission in Chesapeake Bay was at ca 565 to 575 nm from the region of the Potomac R. mouth (38° 04′ N) to the Bay Bridge (39° 00′ N). An example of a light profile from March 1986 is presented in Fig 1A (logarithmic scale); light spectra for depths ≥ 6 m at that station near the Potomac R. are shown in Fig. 1B (linear scale) to demonstrate the narrowing of the wavelength distribution that occurs vertically. This type of data was used to generate K_λ values for the stations we occupied in the 1986 cruises. We found that lowest values of K_λ consistently occurred in the 500 to 600 nm region of the visible spectrum (Fig. 2). K_t was highest in the oligohaline part of the Bay north of the Chesapeake Bay Bridge and declined seaward (Fig. 3), as observed before (Harding et al. 1986). This region of high K_t, values was associated with the turbidity maximum that usually occurs in the area of Station 908N (39° 08′ N; Schubel 1968, Schubel & Biggs 1969). Changes in the seaward penetration of water with $K_t \leq 1.0$ m^{-1} (= photic depth of 4.6 m) detected during the cruise series are known to be related to seasonal variations in streamflow and the loads of suspended particulates in freshwater from the Susquehanna R. (Harding et al. 1986. Fisher et al. 1988). The distributions of average K_λ values for wavelength bands from 500 to

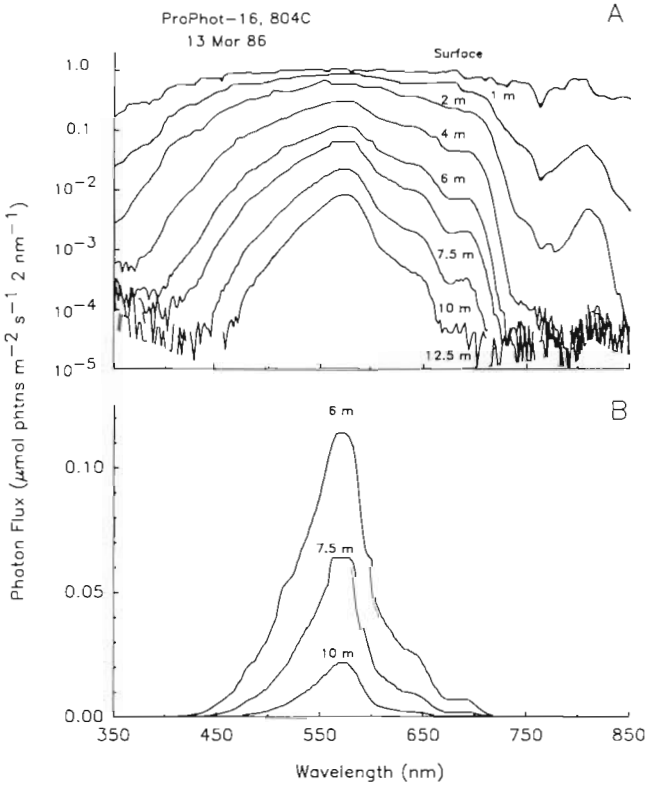

Fig. 1 (A) Example of a depth series of spectroradiometer scans (logarithmic scale) from Stn 804C (Potomac R. mouth); (B) spectroradiometer scans for 3 depths (linear scale), demonstrating the narrowing of spectral transmission in the Chesapeake

550 nm and 550–600 nm showed comparable spatial patterns to that of K_t (Fig. 3). Values for $K_{500-550}$ and $K_{550-600}$ in the Potomac R. to Chesapeake Bay Bridge region of the estuary (encompassing much of the transport path of *Prorocentrum mariae-lebouriae*), however, were generally lower than the corresponding K_t values because of an orange shift. Data on light availability averaged over 50 nm intervals for all stations occupied in 1986 are presented in Table 2.

Photosynthetic action spectra

Photosynthetic action spectra for *Prorocentrum mariae-lebouriae* determined in a series of cruises during spring 1986 showed peaks in photosynthetic activity, expressed as P^B/I (see Materials and Methods), in the blue and red regions of the visible spectrum associated with absorption of light by the chlorophylls, and lower activity in the 450 to 650 nm region (Fig. 4). There was also a shoulder of photosynthetic activity in the 500 to 600 nm region of the spectrum. This shoulder in photosynthetic action spectra was observed both in populations of *P. mariae-lebouriae* collected and isolated from below the pycnocline (see examples in Fig. 4, ProPhot-17, Stn 835; ProPhot-18, Stn 849D, 858C), and in populations from the surface mixed layer in early spring (ProPhot-16, Stn 804C, 818). In 1987, we measured photosynthetic action spectra for *P. mariae-lebouriae* during a dense spring bloom that developed during May (ProPhot-24) in surface waters of the West R. near the Chesapeake Bay Institute (Fig. 5). The per-cell photosynthetic action spectrum (P^C/I vs λ) was relatively flat for *P. mariae-lebouriae* from the West R. (open circles). A typical action spectrum for a low-light adapted, subpycnocline sample measured at approximately the same time of year (May 1986; ProPhot-18, Stn 849D) is presented for comparison (closed circles). These data show generally lower rates of carbon fixation per chl in the deep sample than in the surface sample across the visible spectrum. The per-cell action spectrum for the deep sample showed higher carbon fixation in wavebands generally corresponding to light absorption by the chlorophylls and a shoulder of activity in wavebands absorbed by carotenoids, although photosynthetic activity in this latter spectral region was not as high as in the blue or red.

A light-shift experiment on bloom material collected at Parish Creek in May 1987 produced the per-cell and per-chl action spectra shown in Fig. 6. The action spectra determined prior to the light shift (Day 0, open circles) were relatively flat across the visible spectrum. After the shift to low-light (Day 4, closed circles), P^C/I increased at all wavelengths, whereas P^B/I vs λ showed lesser changes. This change in the per-cell spectrum (Fig. 6A) accompanied increases in cellular pigmentation (Table 3). Light saturation intensities (I_k) were virtually unchanged in this short-term downward light shift, indicating that approximately proportional changes in α and P_{max} occurred (see Harding et al. 1983, 1987), and that cells in the surface bloom were low light-adapted to some extent as they had a low I_k value (Harding & Coats 1988).

Spectral effects on primary production

For each of the 1986 data sets, we calculated depth-integrated production (PP) for *Prorocentrum mariae-lebouriae*, assuming a uniform distribution of cells between 8 and 10 m. Results are expressed as the percentage of PP computed from spectrally-corrected data for light and photosynthesis, of PP computed from PAR and white light photosynthesis values [(spectrally-corrected × 100)/PAR]. For 7 of 8 stations, combining photosynthetic action spectra with the ambient wavelength distribution of light gave a *lower* estimate of PP than did using data that did not take into account spectral differences (Fig. 4). The mean (± SE) percent-

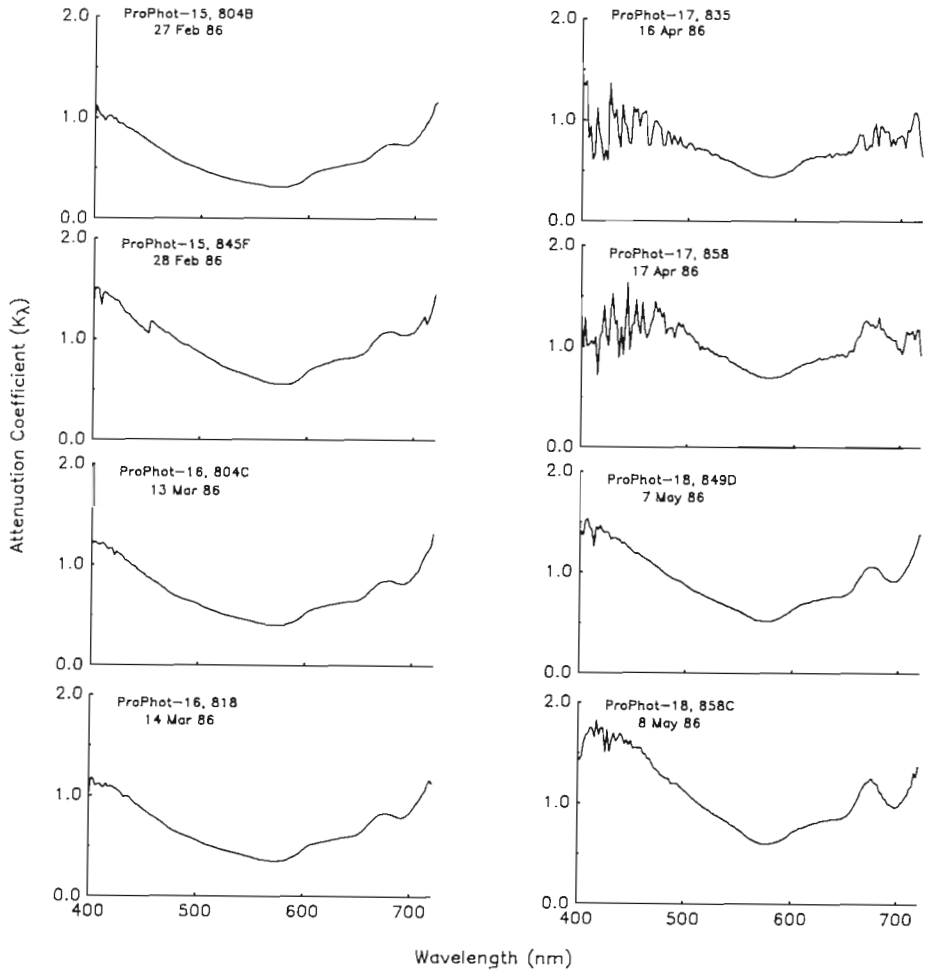

Fig. 2. Wavelength-specific light attenuation coeffients, K_λ for stations occupied in 1986

age for these stations was 64.3 % (± 6.8), indicating that computations using PAR and white light photosynthesis rates overestimated PP. In contrast, spectrally-corrected data from one cruise ProPhot-16, Stn 804C produced a *higher* estimate of PP than did PAR and white light data. Notably, this station was occupied early in the transport sequence, had a pronounced 500 to 550 nm peak in the photosynthetic action spectrum, and coincided with very low light attenuation coefficients ($K_{500-550}$) in this waveband (Figs. 2 and 3).

DISCUSSION

In general, less attention has been afforded to the effects of spectral distribution or light 'quality' than to those of light intensity on pigmentation and photosynthetic properties in algae. Our own previous work with *Prorocentrum mariae-lebouriae* is no exception. We have stressed autecological aspects of low-light adaptation in this important dinoflagellate in the Chesapeake Bay estuary and have reported our findings previously (Harding et al. 1983, Coats & Harding 1988, Harding 1988, Harding & Coats 1988). Summarizing earlier results, a combination of laboratory and field studies showed that *P. mariae-lebouriae* increases per-cell concentrations of photosynthetic pigments in low-light. These pigment changes contribute to enhanced photosynthetic performance by improving light harvesting and driving an increase in the photosynthetic efficiency, α cell^{-1}, the rate of photosynthesis at light-limiting irradiances. The light-saturated rate of photosynthesis, P_{max} cell^{-1}, also changed, but to a lesser extent than did α cell^{-1}, producing a decrease in the saturation point for photosynthesis, I_k ($=P_{max}/\alpha$). These changes in pigmentation and photosynthetic properties appear to be specific to the timescale of change in the light environment (Harding et al. 1987). Supportive evidence for changes at the subcellular level that are coupled to physiological changes was obtained from ultrastructural analyses of chloroplast thylakoid membranes. Data on the number and surface area of thy-

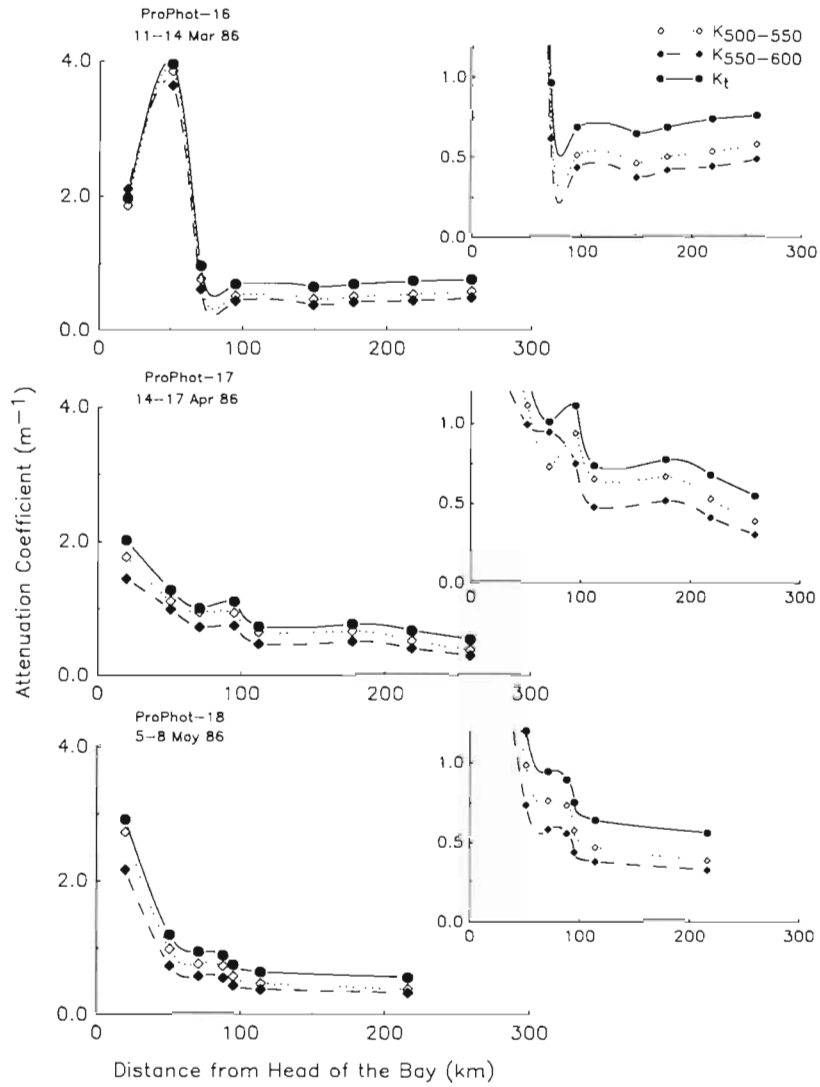

Fig. 3. Distributions of K_t (400 to 700 nm) and K_λ (500 to 550 nm and 550 to 600 nm) along the axis of the Chesapeake in 1986 ProPhot cruises

Table 2. Mean (± SE) of wavelength-specific values for surface irradiance (I_0), light attenuation coefficient (K_λ), and light-limited rates of photosynthesis per chl and cell for 1986 ProPhot Cruises. Units: $\%I_0$, % of daily surface irradiance (E m^{-2} d^{-1}) in each waveband; K_λ, m^{-1}; P^c/I, fg C $cell^{-1}$ h^{-1} (μmol phtns m^{-2} s^{-1})$^{-1}$; P^B/I, pg C pg Chl^{-1} h^{-1} (μmol phtns m^{-2} s^{-1})$^{-1}$

Parameter	Wavelength band (nm)					
	400–450	450–500	500–550	550–600	600–650	650–700
$\%I_0$	8.7 (± 1.0)	14.6 (± 0.52)	17.4 (± 0.43)	18.5 (± 0.60)	18.2 (± 0.40)	16.6 (± 0.54)
K_λ	1.2 (± 0.08)	0.94 (± 0.09)	0.67 (± 0.07)	0.52 (± 0.05)	0.69 (± 0.05)	0.90 (± 0.05)
P^c/I	1.2 (± 0.36)	0.36 (± 0.08)	0.37 (± 0.08)	0.31 (± 0.07)	0.25 (± 0.05)	0.49 (± 0.11)
P^B/I	0.11 (± 0.04)	0.03 (± 0.01)	0.04 (± 0.02)	0.03 (± 0.01)	0.02 (± 0.01)	0.04 (± 0.01)

lakoids are consistent with a photoadaptive strategy that includes changes in both the 'size' and 'number' of photosynthetic units (Coats & Harding 1988).

Despite the fact that most studies of low-light adaptation in algae have concentrated on the responses only to light *intensity*, low-light responses also have spectrally-specific manifestations. Both in vivo absorbance and photosynthetic action spectra (O_2 evolution) in the small dinoflagellate, *Glenodinium* sp., have been known for some time to respond to decreases in illumination that evoke increased cellular pigmentation (Prézelin et al. 1976). An increase in whole cell absorbance in low-light, documented by the low- minus high-light difference spectrum, was principally in the blue-green

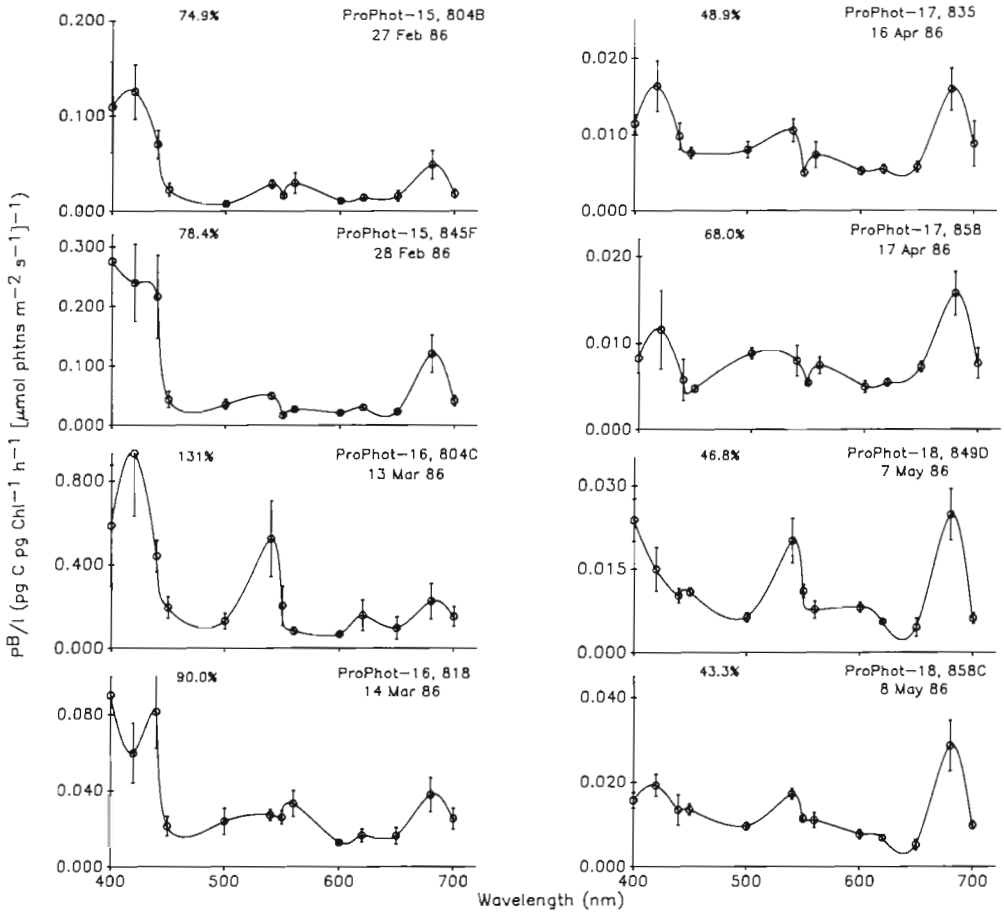

Fig. 4. *Prorocentrum mariae-lebouriae*. Photosynthetic action spectra for cells isolated at 8 stations in the 1986 ProPhot cruise series. Superimposed on each panel is the percentage represented by primary production (PP) computed from data on the in situ spectral distribution and photosynthetic action spectra, relative to PP calculated using PAR and measurements of photosynthesis in white light

and red regions of the visible spectrum. The largest changes were across a broad waveband from 400 to 525 and in a narrower band from 650 to 680 nm. Absorption spectra with comparable shapes have been reported previously for other species of dinoflagellates, including *Ceratium furca, Gonyaulax polyedra*, and coral zooxanthellae (Haxo & Blinks 1950, Blinks 1960, Haxo 1960, 1970, Halldal 1974, Meeson 1981). In dinoflagellates, the main carotenoid in the light harvesting component is a peridinin-chlorophyll *a*-protein (PCP) complex that confers the ability to absorb photic energy in the 470 to 560 nm range (e.g. Prézelin et al. 1976, Jeffrey 1980, Meeson 1981, Prézelin 1981, 1987, Meeson & Faust 1985). PCP is a xanthophyll-based complex that increases significantly in concentration when cells are grown at or shifted to low-light equivalent to a few percent of surface sunlight illumination. Increased concentrations of PCP per cell enhance light absorption and produce improved photosynthetic performance as energy is efficiently transfered from PCP to chlorophyll *a* (Haxo et al. 1976, Prézelin & Haxo 1976, Prézelin et al. 1976).

In previous work with the same strain of dinoflagellate used in the present study, *Prorocentrum minimum (= P. mariae-lebouriae)*, Meeson & Faust (1985) presented a whole cell absorption spectrum that resembles that of *Glenodinium* sp., *Ceratium furca*, and *Gonyaulax polyedra*, including strong absorbance from 400 to 550 nm with a shoulder at ~525 nm. A concurrent study by Vogel & Sager (1985) reported wavelength-specific rates of photosynthesis (CO_2 uptake) for 5 wavebands using the same strain of *Prorocentrum*. The highest slope of the P–I relation, α cell^{-1}, was in broad waveband (~100 nm) blue light centered at 450 nm, whereas α cell^{-1} in green light centered at 520 nm was ca 25 % lower.

The species-specific photosynthetic action spectra we measured for *Prorocentrum mariae-lebouriae* populations in Chesapeake Bay resembled, with some exceptions, results for natural assemblages and other

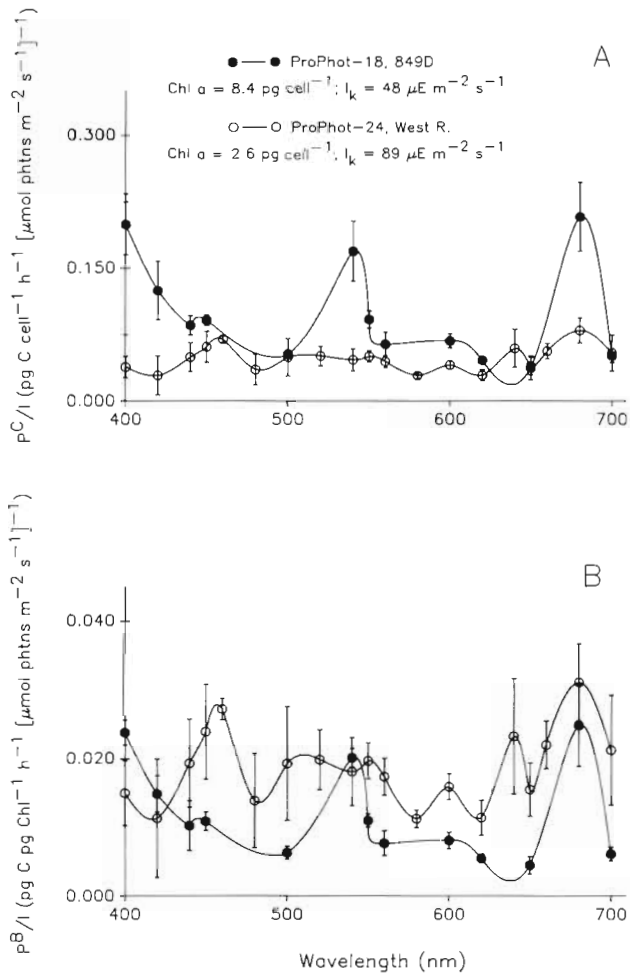

Fig. 5. *Prorocentrum mariae-lebouriae*. Photosynthetic action spectra (A) per cell; (B) per chl for cells collected below the pycnocline at Stn 849D and from a surface bloom in the West R. Superimposed on the upper panel are the chl concentrations and I_k values

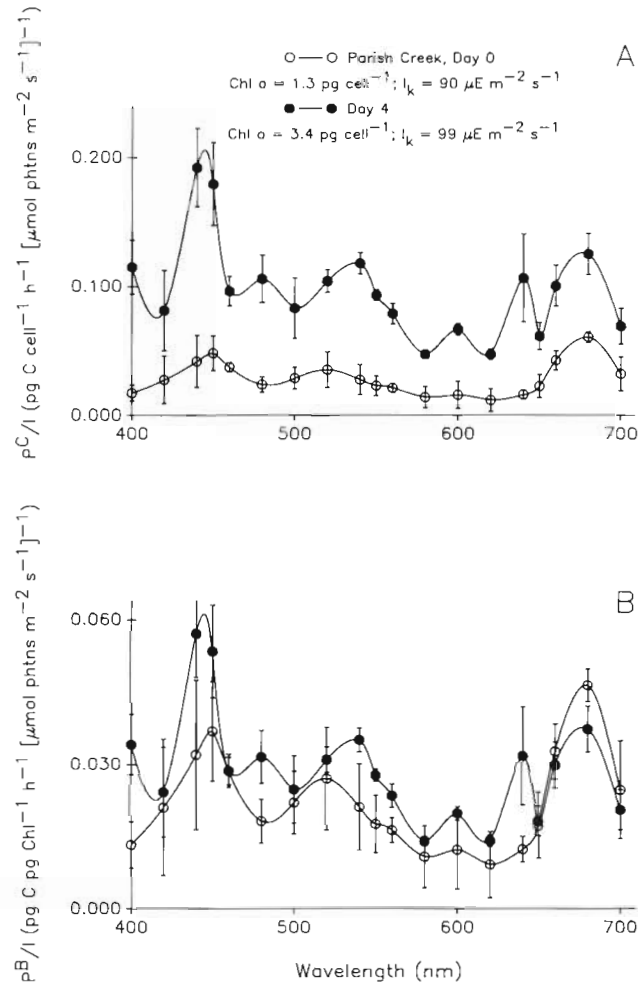

Fig. 6. *Prorocentrum mariae-lebouriae*. Photosynthetic action spectra (A) per cell; (B) per chl for cells collected from Parish Creek adjacent to the Chesapeake Bay Institute during a surface bloom of >20 000 cells ml^{-1}. Measurements were made on the day of collection and after 4 d in low-light. Superimposed on the upper panel are the chl concentrations and I_k values

species in culture that have shown: (1) high photosynthetic activity in regions of the visible spectrum where light is absorbed by chlorophylls (430 to 460 nm and 660 to 680 nm), (2) generally lower activity in the middle of the spectrum (460 to 650 nm), and (3) a shoulder in the green to yellow (500 to 560 nm) region where carotenoids absorb light (Haxo & Blinks 1950, Blinks 1960, Haxo 1960, Prézelin et al. 1976, Lewis et al. 1985a, b). The most apparent difference between action spectra for *P. mariae-lebouriae* and another dinoflagellate is with *Glenodinium* sp. (Prézelin et al. 1976). The shoulder in photosynthetic activity from ca. 480 to 560 nm was much more pronounced in *Glenodinium* sp. than in *P. mariae-lebouriae*. The photosynthetic action spectra we measured for *P. mariae-lebouriae* were similar in shape to α^B action

Table 3. *Prorocentrum mariae-lebouriae*. Pigment concentrations (fmol cell^{-1}; mean ± SE, n = 4) for samples used for measuring action spectra in the light-shift experiment

Sample	Chl *a*	Chl *c*	Peridinin	*a* : *c*	Per : *a*
Day 0	1.46 (± 0.03)	0.91 (± 0.04)	1.66 (± 0.42)	1.60	1.14
Day 4	3.81 (± 0.22)	2.09 (± 0.09)	2.45 (± 0.29)	1.82	0.64

spectra for deep samples of mixed species composition reported by Lewis et al. (1985a).

There are several possible explanations for this finding. First, *Prorocentrum mariae-lebouriae* has a significantly lower cellular content of the major dinoflagellate carotenoid, peridinin, than does *Glenodinium* sp. (or *Gonyaulax polyedra*), and molar ratios of peridinin to chl *a* in the latter 2 species can attain greater values than we have measured in *P. mariae-lebouriae* (compare Prézelin & Sweeney 1978, Prézelin & Matlick 1980, Meeson 1981, Coats & Harding 1988, Harding & Coats 1988). This relatively low peridinin content would be expected to limit the ability of *P. mariae-lebouriae* to harvest light in the 480 to 560 nm region as compared to the other dinoflagellates with more peridinin and higher peridinin:chl *a* ratios. Second, we have no data on the cellular concentrations of photosynthetically-inactive carotenoids in *P. mariae-lebouriae* that could absorb light in this spectral region, but that would not produce a shoulder or peak in photosynthetic activity. Such pigments, perhaps operating in a photoprotective capacity, could reduce the light absorbed by photosynthetically active pigments, including PCP. Third, the dinoflagellate action spectrum most often cited (Prézelin et al. 1976) is expressed as relative O_2 production vs wavelength at a constant light energy and with background actinic illumination, rather than as function of PPFD and without a bright background beam. The spectra are, therefore, not directly comparable because different methods of measurement and different units were used. But the shapes of photosynthetic action spectra for the 2 species are probably more similar than they appear at first glance, because plotting the *Glenodinium* sp. action spectrum as a function of photon flux would reduce the peak or shoulder height in the green to yellow by 17 to 28 % compared to the blue peak just by the change from light energy units ($\mu W\ cm^{-2}$) to PPFD ($\mu mol\ photons\ m^{-2}\ s^{-1}$).

In the light-shift experiment, a bloom population of *Prorocentrum mariae-lebouriae* showed a general (i.e. at all wavelengths), increase in per-cell photosynthetic activity (P^C/I) accompanying low light-induced increases in chl *a*, chl *c*, and peridinin. This increase in photosynthetic activity (P^C/I) over a broad spectral region is similar to the results obtained with *Glenodinium* sp. (Prézelin et al. 1976). We did not test for a change in cell pigmentation or in the photosynthetic action spectrum as a response to both low-light and a narrowed spectral distribution in this experiment, and this combination should be used in future studies of this and other species.

The ranges of P^C/I and P^B/I values for *Prorocentrum mariae-lebouriae* samples encompassing the spring transport period from February to May (ProPhot-15 to ProPhot-18) were approximately an order of magnitude (Fig. 4). Largest values were measured in the early part of the season. These findings are consistent with species-specific data for the P-I relationship from in situ photosynthetic measurement on *P. mariae-lebouriae* that show highest α^C and α^B values in the early spring when temperature and irradiance are low, and a progressive decrease in α^C and α^B as the seasonal transport continues and cells arrive in the mesohaline to oligohaline part of the estuary (Harding & Coats 1988).

Primary production (PP) estimates using parameters of the photosynthesis-irradiance (P-I) relation are influenced by spectral quality and wavelength-specific photosynthetic rates in certain conditions. Lewis et al. (1985a, b) reported that values of α^B, the light-limited slope of the chlorophyll-based P-I relation, may vary 2- to 4-fold for light of different spectral distributions. This indicates that wavelength-specificity may be of comparable importance in estimating PP as diel periodicity of photosynthesis that produces variations in α^B of a similar magnitude. In the case of *Prorocentrum mariae-lebouriae*, natural populations that we sampled were exposed to low-light of a relatively narrow spectral distribution in situ, as indicated by spectroradiometer-determined light profiles and wavelength-specific attenuation coefficients, K_λ, derived from them. To assess the importance of in situ spectral quality and wavelength-specific photosynthetic properties in estimating primary production of *P. mariae-lebouriae*, we computed primary production from the combination of broad waveband optical data and photosynthetic rates in white light, and from data and rates for specific wavebands. These computations were made for a population undergoing subpycnocline transport at depths between 8 and 10 m.

The magnitude of discrepancies in estimates of PP varied and, in most instances, using the ambient spectral distribution and wavelength-specific rates of photosynthesis to compute integral production by a *Prorocentrum mariae-lebouriae* population entrained beneath the pycnocline produced a *lower* estimate than did using PAR and photosynthesis rates determined in white light. The exception was for *P. mariae-lebouriae* collected on cruise ProPhot-16 at Stn 804C for which use of spectrally-corrected values produced a *higher* estimate of PP (see 'Results'). The largest discrepancies for PP estimates for a population at 8 to 10 m coincided with the relatively turbid conditions at stations sampled on cruises ProPhot-17 and 18 in April and May (Fig. 4). On Prophot-15 and 16 in February and March, samples were collected further seaward in the estuary (Table 1) where water clarity was greatest (Fig. 3). PP estimates for subpycnocline *P. mariae-lebouriae* for those stations were closer to the estimates derived from PAR and white light measurements of photosynthesis.

The differences between PP estimates claculated using wavelength-specific photosynthesis and light

data, versus broad waveband values based on PAR, ranged from 31 to 57 %. These differences were not as large as would be expected for phytoplankton in clearer waters where wavelength-specific values of photosynthetic efficiency, α^B, that vary 2- to 4-fold would proportionately influence the amount of carbon fixed (Lewis et al. 1985a, b). The less pronounced effect in Chesapeake Bay may be related to turbidity. Clearer waters transmit significant amounts of light in the blue and red regions of the visible spectrum that are effectively absorbed by the chlorophylls and that drive photosynthesis, whereas turbid waters experience an orange shift and transmit very little light in the blue and red wavelengths to appreciable depth (Figs. 1 and 2). The shoulder in photosynthetic action spectra at 500 to 550 nm typical of carotenoid-containing organisms such as *Prorocentrum mariae-lebouriae*, coupled with the relatively greater availability of light of these wavelengths beneath the pycnocline, compensates to some extent for the lack of light availability in the chlorophyll-absorbing range. That is, increased peridinin content leads to greater absorbance and photosynthesis in the green to yellow wavelengths than would occur without photoadaptive pigment synthesis. The overall effect, though, appears to be lower and in the opposite direction from that expected to occur in less turbid waters. The shoulder of photosynthetic activity between 500 and 600 nm for *P. mariae-lebouriae* is not very pronounced and would not be expected to produce a large effect, although it does resemble the shape of photosynthetic action spectra presented by Lewis et al. (1985a) for natural assemblages of phytoplankton from depths of 40 to 100 m in the open ocean. Even the relatively large (> 50 %) discrepancies we computed for estimates of PP may be low in absolute terms because of the low photon flux density below the pycnocline and the low rates of photosynthesis in situ.

It is clear from this limited data set on a single species that empirical measurements on photosynthetic action spectra and spectral distribution, such as we present, need to be expanded in a theoretical teatment such as presented by Lewis et al. (1985a) to encompass estuarine conditions. While such a treatment is outside the scope of the present paper, the effect of spectral distribution and wavelength-specific photosynthesis we report suggests that light-limited rates of photosynthesis may be influenced by wavelength sufficiently to affect estimates of PP in specific circumstances.

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