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Spectral properties and photosynthetic action in red-tide populations of *Prorocentrum micans* and *Gonyaulax polyedra*

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Abstract

Spectral attenuance and photosynthetic performance over the range 300 to 700 nm were examined in red-tide populations of *Prorocentrum micans* and *Gonyaulax polyedra* collected off La Jolla, California, USA, in May 1969 and May–June 1985; and in spring 1969, November 1981 and April–May 1982, respectively. In the near ultraviolet (UV), high attenuance and diminished photosynthetic effectiveness were observed in both dinoflagellates. This decline in relative quantum yield is ascribed to masking absorption by unidentified and spectrally different UV-absorbing compounds which were soluble in methanol. In the visible region, photosynthetic action spectra displayed the characteristic shapes expected from efficient Photosystem II light harvesting by peridinin, chlorophylls *a* and c_2, in conformity with previous studies on cultured dinoflagellates. In the case of *P. micans*, a high content of diadinoxanthin was found and the possible role of this yellow xanthophyll as a photoprotective pigment is discussed. However, photosynthetic enhancement spectra suggest that some portion of the diadinoxanthin pool functions as a Photosystem I antenna in this species. Our data on *P. micans* and *G. polyedra* support the hypothesis that UV-absorbing compounds and diadinoxanthin play protective roles in screening harmful radiation in red-tide dinoflagellates exposed to high-light conditions in nature.

Introduction

Knowledge of spectral attenuance, photosynthetic spectral performance, and pigment composition of group-representative algal species in culture have played a useful role in predicting the interactions between solar radiation, phytoplankton populations, and primary production. There is increasing recognition, however, of the need to extend such studies to natural populations (Balch and Haxo 1984, Neori et al. 1984, Lewis et al. 1985), where a complex array of environmental factors control cell attenuation, photosynthesis and growth. For such studies, monotypic blooms permit attribution of observed features to single species and comparisons between natural populations and those grown under controlled conditions. The recurrence of near-shore blooms of *Prorocentrum micans* and *Gonyaulax polyedra* off the Southern California coast provided the opportunity to collect and examine spectral features of these two free-living dinoflagellate species. Particular attention was given to the little studied near-ultraviolet portion of the spectrum which may have particular ecological and evolutionary implications for this group of algae (Yentsch and Yentsch 1982).

Both species are common constituents of coastal phytoplankton (Reid et al. 1985) and may form extensive, non-toxic blooms over the continental shelf in the near-shore waters off Southern and Baja California (Sweeney 1975) and elsewhere (Cassie 1981, Avaría 1982, Hata et al. 1982, Pybus 1984). A strong phototactic response is a feature these species share with many other dinoflagellates, which are consequently exposed to a wide range in the intensity and quality of solar radiation. For example, *Prorocentrum micans* has been observed to accumulate in upper layers of the water column (Hattori et al. 1983) and in surface waters (Harvey 1966) and comparable migrations have been noted for *Gonyaulax polyedra*, including the ability to migrate through the thermocline on a diel basis (Eppley and Harrison 1975). In the case of *G. polyedra*, photoadaptive aspects of photosynthesis and growth have been extensively studied under controlled conditions in the laboratory (cf. Prézelin 1987). Whether the shorter wavelengths of the visible and UV solar light play any significant role in photoadaptive responses of such species remains a subject of continuing interest.

Previous studies of free-living and endosymbiotic species have documented a common chloroplast-pigment pattern

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for most photosynthetic dinoflagellates: chlorophylls *a* and c_2, peridinin as the major carotenoid (53 to 86%), and a mixture of minor carotenoids, notably diadinoxanthin (3 to 33%), diatoxanthin (~7%), dinoxanthin (0.5 to 8%), and β-carotene (0.4 to 4%) (Johansen et al. 1974, Jeffrey et al. 1975). Earlier action spectra have shown that the chlorophylls and peridinin are effective Photosystem II antenna pigments (Haxo 1960, Prézelin et al. 1976, Neori et al. 1986). Overall, minor carotenoids appear to be less efficient in Photosystem II photosynthesis, but they may serve a role in photoadaptation to high-light environments (cf. Prézelin 1987).

In this paper, we report spectral absorbance and photosynthetic response features of *Prorocentrum micans* and *Gonyaulax polyedra* populations collected from blooms that developed in nearshore waters off southern California, USA. High cell concentrations, the almost monotypic nature of the blooms, and the proximity to our laboratory offered the opportunity for a range of spectral characterizations not usually possible on natural populations.

Table 1. *Prorocentrum micans*. Spectral characteristics of carotenoids isolated by cellulose column chromatography. Absorption spectra of pigments were taken in a Beckman Acta MVI recording spectrophotometer immediately after elution from column. ~ denotes midpoint of curve inflection. %III/II refers to ratio of Peak 3 to Peak 2, and $E^{1\%}_{cm}$ at λ_{max} denotes weight-specific absorption coefficient used to calculate pigment concentration at peak of maximum absorption, as defined by Davies (1976)

Pigment	Absorption max. (nm)	Solvent	%III/II	$E^{1\%}_{cm}$
Peridinin	~432, 456, 485	1% isopropanol in hexane	ND	1 470[a]
Diadinoxanthin	~424, 446, 475.5	0.5% isopropanol in hexane	0.63[b]	2 250[c]
β-carotene	~425, 449, 476	hexane	ND	2 592[c]

[a] Jeffrey and Haxo (1968), in hexane
[b] Loeblich and Smith (1968): ratio of 0.64, calculated from their Fig. 5
[c] Withers et al. (1977), in hexane

Materials and methods

Cells of *Prorocentrum micans* were collected at high tide with a 35 μm-mesh phytoplankton net off the end of Scripps Pier, La Jolla, California, in May 1969 and in May–June 1985. The samples were filtered through a 100 μm-mesh to eliminate any large debris or zooplankton. Cells were concentrated overnight by phototaxis in a 1-liter graduated cylinder, thus selecting only viable cells for study. Aliquots were taken from such concentrated samples for cell counts, chlorophyll and carotenoid determinations, absorption spectrum analyses, oxygen evolution action spectra, and excitation spectra for chlorophyll *a* fluorescence.

Blooms of *Gonyaulax polyedra* (>90%) occurred in spring of 1969, November 1981 and April–May 1982 (see Balch and Haxo 1984), providing the material for determination of cell absorption, total pigment and photosynthetic action spectra. An isolate of *G. polyedra* from Scripps Pier, initiated on 2 November 1981 by L. Vakassian and maintained in culture for 11 mo at 18 °C in constant light at 25 μE m^{-2} s^{-1}, was used in the determination of the excitation spectrum of chlorophyll *a* fluorescence in vivo.

Cells were counted with a hemacytometer (Spencer, Bright-Line) immediately after immobilization with Lugol. Chlorophyll (chl) *a* and c_2 concentrations were estimated using equations of Jeffrey and Humphrey (1975) following gentle concentration of cells by low-speed centrifugation and extraction of pigments in acetone : water (90 : 10, v/v) for 24 h in the dark at 4 °C.

Carotenoids were separated by cellulose column chromatography (Microcrystalline, E. Merck). A known number of cells was concentrated by centrifugation and extracted in acetone : water (90 : 10, v/v) overnight at 4 °C. Pigments were transferred to fresh diethyl ether in a graduated cylinder by the addition of a cold 10% NaCl solution (Jeffrey 1968) and the hypophase reextracted several times to ensure complete recovery of pigments. Combined ether extracts were dried with solid NaCl, clarified by centrifugation, evaporated to dryness with nitrogen gas, and redissolved completely in hexane, following addition of a few drops of diethyl ether. The extract was introduced at the top of the cellulose column and the adsorbed pigments eluted progressively using hexane and 0.75, 1, and 2% isopropanol in hexane (v/v). Pigments resolved by this system were, in order of elution, β-carotene, chl *a*, diadinoxanthin, peridinin, and chl c_2. Individual pigments were identified by their characteristic absorption spectra and quantified by their weight-specific extinction coefficients (Table 1). The possibility that the diadinoxanthin fraction contained small amounts of diatoxanthin and/or dinoxanthin (Johansen et al. 1974) cannot be completely excluded. However, high purity of this "diadinoxanthin" fraction is suggested by the close correspondence in spectral features to the preparation of diadinoxanthin reported by Loeblich and Smith (1968) (present Table 1).

In vivo absorption spectra for cells collected from the 1981 and 1985 blooms were determined on very thin layers of cells collected by gentle filtration onto a glass-fiber filter and measured against a moistened blank filter, employing a Beckman Acta MVI recording spectrophotometer (Balch and Haxo 1984, Neori et al. 1986). For the 1969 *P. micans* bloom, Millipore filters and a Shimadzu MP50 spectrophotometer were employed. In both cases, measured extinctions at 675 nm did not exceed 0.2 OD units. For in vitro spectra, cells were pelleted and extracted overnight in methanol at 4 °C in darkness and the extracts clarified by centrifugation.

Action spectra for photosynthesis were based upon steady-state oxygen evolution rates measured at equivalent energy fluxes across the spectrum, and were quantum-corrected. These measurements were made on immobile monolayers of cells that had settled uniformly on the surface of a recessed Pt electrode as described in previous studies from this laboratory (Haxo and Fork 1959, Prézelin et al. 1976,

Loeblich 1982, Haxo 1985). Except as noted below, oxygen evolution rates were determined in sequence at fixed wavelengths, without background illumination, and with the electrode system operating in the direct current mode. Prior to mounting on the electrode, the cells were suspended in filtered seawater enriched with 0.05 *M* $NaHCO_3$. Actinic light at a bandpass of 10 nm was isolated from either a 250 or a 500 mm Bausch and Lomb grating monochromator using appropriate blocking filters (a Corning filter No. 754 was used in the near-UV region, 280 to 390 nm). Action spectra for *P. micans* were also determined by the modulated oxygen electrode method of Joliot (1972) as modified by Neori et al. (1986). In this case, the background illumination was provided by a 50 W tungsten lamp, focused through a Calflex-C (IR reflecting) filter and a cutoff Hoya filter No. R-70.

An enhancement spectrum, proportional to the ratio of Photosystem I (PS I) excitation to Photosystem II (PS II) excitation, was estimated for *Prorocentrum micans* as detailed by Neori (1986). In this procedure, the algal sample was illuminated by three light beams: (1) the measuring beam – a broad green band (525 nm maximum, as defined by a Corning No. 4010 glass filter), modulated (at 11 Hz) and having an average intensity of 0.25 $\mu E\ m^{-2}\ s^{-1}$; (2) the background beam – a continuous beam, spectrally identical to the first beam, with an intensity of 1 $\mu E\ m^{-2}\ s^{-1}$; (3) the scanning beam – a monochromatic beam, defined by a monochromator, which scanned the UV and visible regions of the spectrum at a constant quantum flux, the intensity of which was low enough to maintain the same quantum yield for modulated oxygen evolution when its spectrum was centered at 525 nm. At this wavelength, predominant absorption for both *P. micans* and *Gonyaulax polyedra* was by peridinin, as peridinin-chlorophyll *a*-protein (Prézelin and Haxo 1976, Hata et al. 1982). Increases in the modulated signal, resulting from pairing of other wavelengths in the scanning beam, were interpreted as enhancement (of PS II quantum yield) on the assumption that they could only arise from an increase in the ratio of PS I excitation to PS II excitation.

In vivo fluorescence excitation spectra of chlorophyll *a* for both species were measured with a Perkin Elmer MPF-44A spectrofluorometer as described by Neori et al. (1986), and are quantum-corrected. For these measurements, very dilute cell suspensions pre-treated with 3-(3,4-dichlorophenyl)-1,1-dimethylurea, DCMU (ethanolic solution) were used.

Results and discussion

Prorocentrum micans

Spectral photosynthetic studies of red-tide organisms have been few; little is known about the relationship between environmental conditions and such features in nature. Here we present the specific conditions associated with the development of the 1985 *Prorocentrum micans* bloom, the source of the population we studied. Chlorophyll *a* values showed that the bloom started around 20 April and lasted until 5 July 1985, with an average concentration of 8 μg chl $a\ l^{-1}$ and maximum values of up to 30 μg chl $a\ l^{-1}$ between 15 and 30 May (G. Hemingway personal communication). Over the same period, surface temperature increased steadily from 16.0° to 18.3 °C. Nitrate concentration was estimated at 0.41 μM (W. M. Balch personal communication). Microplankton cell concentration on 22 May 1985 was 9.4×10^6 cells l^{-1}, *P. micans* comprising 99% of the species present, with some contamination by *Dinophysis* sp. (W. M. Balch personal communication). Similar cell concentrations were observed by Pinckard et al. (1953) for another *P. micans* red tide which occurred locally in July 1953 (4.5×10^6 cells l^{-1} and 99% purity).

Table 2. *Prorocentrum micans*. Pigment content of field population collected in May 1985. Concentrations are average ± standard deviations of two replicates.

Pigment	Conc pg cell^{-1}	Pigment conc relative to chl *a* (w/w)	% carotenoid (w/w)
Chlorophyll *a*	20.23 ± 2.21	1.000	–
Chlorophyll c_2	7.51 ± 0.24	0.371	–
β-carotene	0.52 ± 0.13	0.025	3.54
Diadinoxanthin	5.09 ± 2.73	0.250	34.66
Peridinin	9.08 ± 1.46	0.449	61.79

Pigment identifications and concentrations for the *Prorocentrum micans* bloom of May 1985 (Table 2) were in agreement with high-performance liquid chromatography determinations of Nelson (1986) for the same population. Chl c_2 was similar to values of a red tide in Japan studied by Hata et al. (1982) (chl *a*: $c_2 = 2.5:1$). Peridinin was the most abundant carotenoid (62% of total carotenoids, w/w), in agreement with previous studies of this species (Pinckard et al. 1953, Riley and Wilson 1967). Diadinoxanthin (34% w/w) was in general more abundant in the natural population of *P. micans* than in other species of dinoflagellates cultured at medium light levels (Johansen et al. 1974). Such high levels of diadinoxanthin are consistent with a possible role of this pigment in photoprotection during conditions of high illumination (Krinsky 1971). Diadinoxanthin (5,6-epoxydiatoxanthin) is also part of the xanthophyll cycle involving two pigments, diadinoxanthin and diatoxanthin. The function of this cycle is still unknown (Goodwin 1980), but studies on its mechanism indicate that net de-epoxidation (synthesis of diatoxanthin) occurs under high irradiances. The relationship, if any, between these two processes involving diadinoxanthin is not known.

Prorocentrum micans displayed in vivo absorption maxima in the visible region at 435, 465, 495, 620, and 675 nm, with a broad shoulder between 500 and 570 nm (Fig. 1 A). In the near-UV range of the spectrum (300 to 390 nm), maxima in absorption were observed at 320 and 335 nm and a shoulder at 380 nm. The prominence of absorption and position of the maxima in the UV region are consistent features for

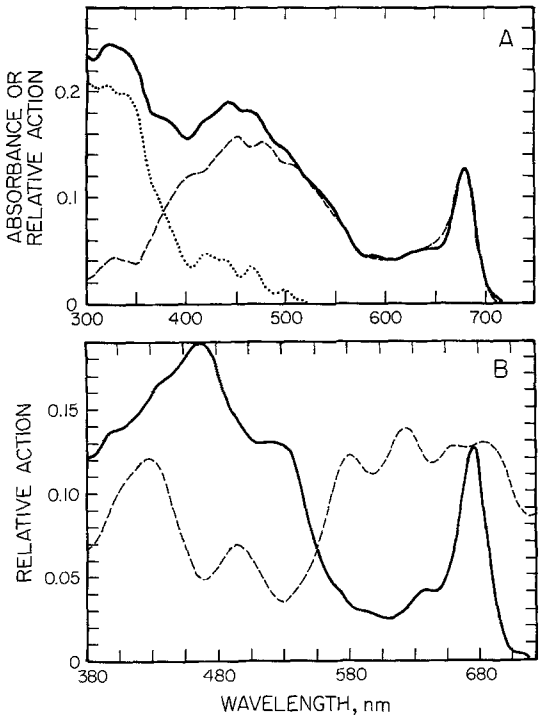

Fig. 1. *Prorocentrum micans.* Ultraviolet-visible action and absorption spectra for organisms collected from a red tide that developed off Scripps Pier during May-June 1985. (A) in vivo absorption (continuous curve), O_2-evolution action-spectrum (without background illumination) (dashed curve) and inactive absorption, i.e., difference between the two curves (dotted curve); (B) spectra for modulated oxygen production (with continuous far-red background illumination) (continuous curve) and for photosynthetic enhancement (PS I : PS II) (dashed curve). (See "Materials and methods" for experimental details)

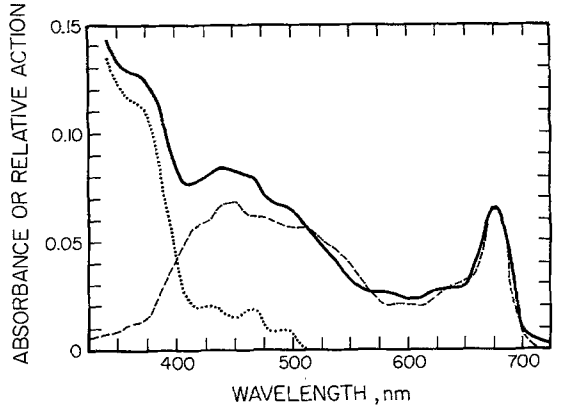

Fig. 2. *Prorocentrum micans.* Oxygen-evolution action-spectrum, without background illumination (dashed curve) and in vivo absorption (continuous curve) of organisms collected from red tide occurring in May 1969 off Scripps Pier. Inactive absorption, i.e., difference between the two curves, is indicated by dotted curve

blooms along the Southern California coast, as demonstrated by the close similarity in absorption and action spectra of the 1969 and 1985 field populations (Figs. 1 A and 2).

Oxygen-evolution action-spectra of *Prorocentrum micans* measured by both methods show maxima or shoulders of activity at 436, 462, 500, 530, 625, and 675 nm (Figs. 1 B and 2). Evidence of a marked decrease in activity at wavelengths below 400 nm was seen in all action spectra. At wavelengths above 420 nm, action spectra of *P. micans* were broadly similar to previously measured dinoflagellate spectra (Prézelin et al. 1976, and references therein, Neori et al. 1986), in that peaks and shoulders coincided with major fractional absorption by chlorophylls *a* (436 and 675 nm) and c_2 (462 and 630 nm) and peridinin (500 to 550 nm).

The drop in photosynthetic effectiveness in *Prorocentrum micans* in the blue-violet end of the spectrum (~420 to 520 nm) coincided with absorption by carotenoids other than peridinin, which in *P. micans* constituted 38% of the total carotenoids (Table 2). Membrane-bound β-carotene in algal cells is considered to be largely associated with PS I and PS II reaction centers (Thornber et al. 1977, Anderson et al. 1978). From the small amount of β-carotene detected in *P. micans*, we infer that the decline in photosynthetic effectiveness can largely be attributed to masking absorption by the more abundant "diadinoxanthin" fraction. The difference spectrum between photosynthetic action and cell absorption (Figs. 1 A and 2) supports this interpretation in that the spectrum is three-peaked and not unlike that expected for in vivo absorbance by diadinoxanthin.

It is of interest that the low photosynthetic effectiveness in the blue-violet region of the spectrum was less marked than in *Glenodinium* sp. grown at high irradiance levels (Prézelin et al. 1976). We believe that this difference may relate to the differing relative concentration of yellow xanthophylls with respect to peridinin and chlorophylls in the two species. The ratio of the yellow xanthophylls to chl *a* was 0.22 in *Prorocentrum micans* in contrast to 0.45 in *Glenodinium* sp. grown under high-light (3 000 μW cm^{-2}) conditions (Prézelin 1976). The increased yellow xanthophyll:chl level in *Glenodinium* sp. could account for the more pronounced drop in effectiveness.

More striking is the marked antiparallelism below 400 nm between action spectra for oxygen production and cell absorption in *Prorocentrum micans*. Low but positive oxygen production was observed down to 300 nm (Figs. 1 A, 2). The precipitous decline in photosynthetic efficiency is clearly relatable to the abundant presence in *P. micans* of a UV-absorbing fraction recoverable in methanol (see Fig. 4 A) and displaying a prominent peak at 323 nm and a shoulder at 370 nm (absorbance 323 nm : absorbance 665 nm = 7.33). The results indicate that the bulk of this UV-absorbing fraction does not function in photosynthetic light-harvesting.

The absorption and enhancement spectra for *Prorocentrum micans* (Fig. 1 B) relate in a non-quantitative way the variations in PS I : PS II excitation ratio across the spectrum, maxima and minima corresponding to spectral regions in which absorbed quanta preferentially excite PS I and PS II, respectively. (Because of overlapping absorption of pigments below 685 nm, only longer wavelengths can be considered as nearly pure PS I excitation, this region coinciding with the "red drop" in photosynthesis where PS II activity declines rapidly.) The observed minima in the *P. micans* enhancement spectrum at 529 nm and 468, 593, and 643 nm

are in agreement with in vivo prominences of absorption by peridinin and chl c_2, respectively, the major PS II light-harvesting antennae of dinoflagellates. Enhancement maxima observed at 428 and 683 nm, and with less certainty those at 580 and 625 nm, can probably be attributed to dominance of chl *a* absorbance in PS I. The enhancement peak at 494 nm reflects the combined absorption by carotenoids other than peridinin, i.e., β-carotene and diadinoxanthin. The magnitude of the 494 nm enhancement peak, although not quantitative, suggests that some portion of the β-carotene and/or diadinoxanthin pools may act as light-harvesting antenna pigments for PS I (Thornber et al. 1977). In the case of chloromonads, Haxo et al. (1984) reported that some portion of the diadinoxanthin fraction may function as a PS II antenna, while studies by Mandelli (1972) on *Amphidinium klebsii*, which showed that the diadinoxanthin: peridinin ratio increases markedly with growth at high irradiance levels, imply a photoprotective role for diadinoxanthin in this species (Prézelin 1987). It is of further interest that in dinoflagellates, the enhancement maxima associated with chl *a* absorption in the blue (428 nm) and in the red (683 nm, mostly PS I chl) were of comparable magnitude, suggesting that in *P. micans* a significant fraction of the total chl *a* is associated with PS I.

Gonyaulax polyedra

The parallelism and divergence features seen in the spectra for absorption and oxygen evolution for the field population of *Gonyaulax polyedra* (Fig. 3A) are in good agreement, through the visible region, with previous findings on laboratory cultures (Haxo 1960), while extending spectral coverage into the near-UV region (300 to 390 nm). In the visible spectrum, activity peaks were located at 675, 630, 590, 470, and 437 nm, reflecting efficient photosynthetic light-harvesting at in vivo peaks or shoulders identifiable with peridinin (500 to 560 nm), chl *a* (675 and 437 nm) and probably chl c_2 (630 and 462 nm). Similar features were seen in the fluorescence excitation spectrum for chl *a* fluorescence (Fig. 3B). The decline in photosynthetic effectiveness from 520 to 400 nm can probably be attributed to absorption by yellow xanthophylls, which account for 11 to 20% of total carotenoids present in this species, depending on the irradiance level during growth (Prézelin and Sweeney 1978). However, as reported earlier for cultures of *G. polyedra*, some depression of photosynthetic activity in the 400 to 420 nm region can probably be attributed to tailing absorption by the strong UV absorbing fraction present (Haxo 1960, and Haxo unpublished observations).

Photosynthetic effectiveness in *Gonyaulax polyedra* also declined below 400 nm, as seen in both the oxygen and fluorescence excitation spectra (Fig. 3), but a positive photosynthetic response was evident down to 300 nm. This decline in photosynthesis coincided with strong attenuance in the near UV region, seen in vivo as broad absorption maxima at 365 to 370 nm and 320 nm, and in methanol extracts at 371 and 324 nm (absorbance 324 nm: absorbance 665 nm = 4.6)

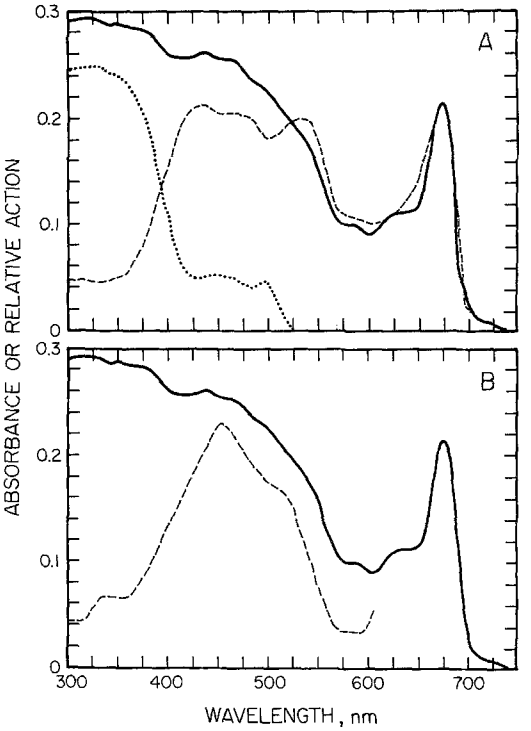

Fig. 3. *Gonyaulax polyedra.* Action and absorption spectra for organisms collected from red tide that developed off Scripps Pier during November 1981. (A) in vivo absorption (continuous curve), oxygen evolution, without background illumination (dashed curve) and inactive absorption, i.e., difference between the two curves (dotted curve); (B) in vivo absorption (continuous curve) and fluorescence excitation of chlorophyll *a* (F_{685}) (dashed curve)

(Figs. 3 and 4B). Compared to *Prorocentrum micans*, near-UV attenuance in *G. polyedra* was less prominent, characterized by broader absorption peaks, and had a higher proportion of a component absorbing at 371 nm (Fig. 4).

It is of particular interest that the high near-UV attenuances we report here for both red-tide species are persistent, but diminished and variable features of isolates grown at low to medium irradiance levels in the laboratory (Haxo unpublished observations). Indeed, strong irradiance effects on formation of prominent UV-absorbing substances in isolates of the red-tide dinoflagellate *Alexandrium excavatum* as well as *Prorocentrum micans* have been reported by Carreto and co-workers (personal communication 1987 and Carreto et al. 1988) who have shown that these species have the ability to synthesize UV-absorbing compounds within hours after exposure to high irradiances.

UV-absorbing substances

Molecules that absorb in the UV seem to have a widespread distribution in marine organisms exposed to high-light situations: e.g. Cyanobacteria (Shibata 1969, Haxo et al. 1987), corals (Dunlap et al. 1986), and marine macrophytes (Sivalingam et al. 1974, Wood 1987, 1989). The high UV attenuances seen in cells and extracts of both *Prorocentrum micans* and *Gonyaulax polyedra* suggest the occurrence of

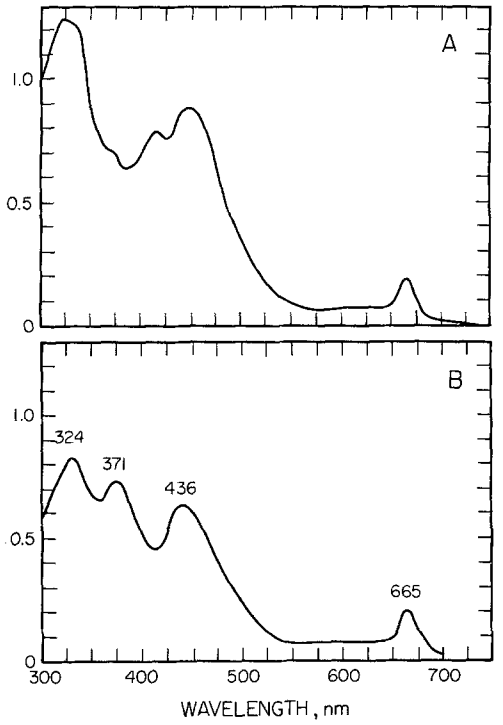

Fig. 4. *Prorocentrum micaus* (A) and *Gonyaulax polyedra* (B). Absorption spectra of total methanol extracts collected from red-tide blooms (B redrawn from Balch and Haxo 1984). High UV to red absorption peak ratios (*P. micans*, absorbance 323 nm:absorbance 665 nm = 7.33; *G. polyedra*, Abs 324 nm:Abs 665 nm = 4.6) indicate prominence of UV-absorbing substances relative to photosynthetic pigments, which contribute little to measured absorbance at 323 to 324 nm. Absorption maxima of *P. micans* spectrum are 324, 368, 406, 435, 665 nm

analogous compounds in these phototactic dinoflagellates. Such UV-absorbing molecules could provide a mechanism by which these red-tide dinoflagellate species screen harmful radiation during accumulation at, or migration to, the sea surface. The same situation could well apply to *G. catenella* (Haxo 1980), *G. tamarensis* var *excavata* (Yentsch and Yentsch 1982) and *Noctiluca miliaris* (Balch and Haxo 1984), which display high attenuances in the near-ultraviolet region. Although the ability to synthesize UV-blocking compounds is not universal among dinoflagellates (*Amphidinium carterae* does not display high attenuance in the UV region, Haxo unpublished data), this capacity may well be a necessary attribute for migratory species capable of forming blooms in high-light, high-UV environments. More experimental studies are needed, however, to establish a causal relationship between UV screening and the ability to withstand high solar irradiances.

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