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Effects of solar radiation on dissolved organic matter cycling in a subtropical seagrass meadow

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Abstract

The influence of sunlight on bacterioplankton production was investigated over a 12-month period in Laguna Madre, a shallow, subtropical, seagrass-dominated lagoon in south Texas. Two types of experiments were conducted every 6 to 8 weeks from June 1996 through June 1997 to assess the effect of photochemical transformations of dissolved organic matter (DOM) on bacterial production and the net effect of sunlight exposure on bacterioplankton and phytoplankton production in surface waters. Photobleaching of DOM was observed; however, estimates of the photomineralization of DOM in May and July were very low and indicated that this process could represent at most 3% of water column respiration. Photochemical transformations of DOM did not have any significant effect on bacterioplankton activity. However, bacterial production measured during exposure of water samples to natural sunlight in the summer months, with and without ultraviolet light, was enhanced relative to dark controls. Phytoplankton release of bioavailable substrates appeared to be responsible for light-mediated increases in bacterioplankton production. Bacterio- and phytoplankton were not photoinhibited by exposure to ultraviolet radiation in surface waters. Overall, we observed no indication of photoinhibition of microbial processes in Laguna Madre, and photochemical transformations appeared to play a minor role in the cycling of DOM. The low photoreactivity of DOM in combination with its relatively high bioreactivity appeared responsible for the minor role of photochemical transformations in the cycling of DOM in Laguna Madre.

Dissolved organic matter (DOM), the largest reservoir of organic matter in most aquatic ecosystems, is the primary substrate fueling bacterioplankton activity (Pomeroy 1974; Azam et al. 1983; Wetzel 1992). DOM is also responsible for the absorption of most of the ultraviolet radiation (UVR) in natural waters (Armstrong and Boalch 1961; Zika 1981). Solar UVR has been found to inhibit both phytoplankton and bacterioplankton activity (Lorenzen 1979; Herndl et al. 1993; Holm-Hansen et al. 1993) and therefore has important

ecological as well as biogeochemical implications. The observation of stratospheric ozone depletion (Kerr and McElroy 1993) has fueled increased interest in the effects of UVR on biological and chemical processes. However, the roles of UVR in the cycling of biologically important elements within various ecosystems remain poorly understood.

UVR is also responsible for photochemical transformations of DOM. Photochemical transformations of DOM can produce many different products including: low molecular weight compounds (Kieber and Mopper 1987; Kieber et al. 1989), CO₂, dissolved inorganic carbon (Wilson et al. 1970; Valentine and Zepp 1993; Miller and Zepp 1995), and inorganic nutrients (Franko and Heath 1982; Bushaw et al. 1996). Phototransformations of DOM have been demonstrated to enhance bacterial activity in a variety of aquatic environments (Geller 1986; Kieber et al. 1989; Lindell et al. 1995; Benner and Biddanda 1998). In fact, the combination of photochemical and microbial processes has been shown to increase the degradation of DOM up to threefold in seawater from a salt marsh (Miller and Moran 1997).

Study of the influence of UVR on the microbial utilization of DOM has primarily focused on environments with high concentrations of humic substances which are known to be very photoreactive (Zepp et al. 1981). The majority of these studies have found exposure of DOM to UVR enhances its

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utilization by bacterioplankton, often measured as an increase in bacterial growth or production. Enhancement of bacterial growth, due to photochemical transformations of DOM, has been found to be as much as 200% in humic rich environments (review by Moran and Zepp 1997). However, there is good evidence to suggest that photochemical transformations can also produce biorefractory compounds (Benner and Biddanda 1998; Tranvik and Kokalj 1998; Benner and Ziegler in press). The availability of UVR and chemical composition of DOM will ultimately determine the relative importance of biological and photochemical processes to the cycling of DOM in an ecosystem.

High levels of UVR and the photoreactivity of seagrass-derived organic matter in Laguna Madre, Texas, suggest that photoprocesses could have a dramatic impact on biological processes in this ecosystem. Laguna Madre is a shallow, seagrass-dominated, subtropical lagoon receiving a large flux of UVR due to its location and semiarid climate. Seagrasses are the primary source of organic matter in this highly productive ecosystem. Stable carbon isotopic signatures of many animals in Laguna Madre, including top carnivores such as redfish and seatrout, have indicated the importance of seagrass-derived C in higher trophic levels (Fry and Parker 1979). Direct utilization of seagrasses is relatively minor, and bacteria in Laguna Madre are considered an important link between seagrass C and N and higher trophic levels (Chin-Leo and Benner 1991). The major sources of DOM in this system include seagrass exudation and leaching, and utilization of this DOM in the water column represents a significant fraction of the benthic primary production in Laguna Madre (Ziegler and Benner 1998; Ziegler and Benner 1999a).

Evidence suggests that UVR may be responsible for the transformation of seagrass-derived organic matter in Laguna Madre. Photobleached seagrass blades on the shoreline of Laguna Madre were found to be devoid of lignin phenols, indicating that much of the aromatic component of the tissues had been photodegraded (Opsahl and Benner 1993). Phenolic compounds are difficult to degrade biologically, and their removal from seagrass tissues results in a relative enrichment in the carbohydrate content. Therefore, the selective removal of phenolic compounds from seagrass tissues and DOM by photochemical processes could result in enhanced microbial activity in the water column.

Bacterioplankton production in Laguna Madre varies diurnally with peaks occurring during the early afternoon indicating that light-mediated processes increase bacterial activity in the water column (Chin-Leo and Benner 1991). The main focus of this study was to determine if solar radiation, through photochemical and photobiological processes, is responsible for enhancing bacterioplankton activity in Laguna Madre. Two types of experiments were conducted over the course of a year investigating the effect of photochemical alteration of DOM on bacterial production and the net effect (enhancement and inhibition) of sunlight exposure on bacterioplankton and phytoplankton production in surface waters.

Materials and methods

Study site—Laguna Madre is the southernmost estuary located on the Texas coast, and it is separated from the Gulf of Mexico by Padre Island. This study was conducted in a *Thalassia testudinum*-dominated seagrass meadow in the southern portion of lower Laguna Madre. The study site was located east of the Gulf Intracoastal Waterway at about 26°10' latitude and 97°12' longitude (for map, see Herzka and Dunton 1996). A total of ten 5-d trips were made to lower Laguna Madre approximately every 6 to 8 weeks from February 1996 to June 1997. Experiments assessing the influences of solar radiation on bacterial activity were conducted at the UT PanAm Coastal Studies Laboratory located on South Padre Island about 10 km from the study site.

DOM photomineralization experiments—To estimate rates of DOM photomineralization, water samples were collected in early May and July during periods of high solar radiation. Samples were collected at dawn to reduce photochemical transformations prior to the experiments which were designed to look at these processes on a daily time scale. After collection, samples were immediately filtered through 0.2- μm pore size Nuclepore polycarbonate filter cartridges and stored in the dark at 4°C for 2–6 d until used in the incubations. Water samples were filtered through 0.2- μm pore size Nuclepore polycarbonate filter cartridges a second time immediately before dispensing the water into nine light and nine dark quartz bottles (90 ml). Bottles were incubated submerged (1 cm) under full sunlight and wrapped in aluminum foil (dark controls) in the same incubator used in the other two experiments with flowing Laguna Madre water for about 35 h (~24 h sunlight) at ambient water temperature (24–30°C). Dissolved organic carbon (DOC) concentrations and absorbances at wavelengths from 280–400 nm were measured in all initial and final samples.

Effect of DOM phototransformation on bacterioplankton production—Experiments conducted during each trip were designed to determine the effect of photochemical transformations of DOM on bacterial production. Water samples were collected in the early morning immediately prior to the initiation of the experiments. Samples were filtered through 0.2- μm pore size Nuclepore polycarbonate filter cartridges and dispensed into six light and three dark (wrapped in aluminum foil) quartz bottles (90 ml). These bottles were incubated under natural sunlight in an incubator with flowing Laguna Madre water. Part of the incubator was covered with a sheet of Acrylite OP-2 (Cryo Industries, Orange, Connecticut) to block all ultraviolet (UV) radiation (T50% = 410 nm). A set of bottles were incubated under this shield to determine the effects of photosynthetically active radiation (PAR) in the absence of UVR. Following 6–8 h exposure to sunlight, a natural microbial inoculum in the form of a freshly collected, unfiltered water sample from Laguna Madre was added to these samples in a 1:10 dilution. Bacterial carbon production was measured (³H-leucine incorporation) in the dark in a water bath maintained within ~1°C of ambient water temperature. Samples were collected for bacterial abundance before and after filtration, and following

the incubation in all three treatments to monitor the abundance and growth of bacteria.

Net effect of solar radiation on bacterio- and phytoplankton production—Additional experiments were designed to determine the net effect of solar radiation on bacterial production. Immediately after collection, unfiltered water (20 ml) was dispensed into six light and three dark (wrapped in aluminum foil) quartz tubes (25 ml) with ^3H -leucine at a final concentration of 20 nM. The quartz tubes were placed in the incubator described above, with three of the light tubes placed under the Acrylite OP-2 shield and three exposed to full sunlight. Incubations were terminated after 1 h by placing samples on ice and immediately filtering them for bacterial production measurements in the laboratory (*see below*). Three 1-h incubations were conducted around noon (± 3 h) on 1 d during each trip except in January, when only two incubations were conducted.

Primary production was measured in unfiltered water collected in the early morning in June, July, and September. Six light and three dark (wrapped in aluminum foil) quartz bottles (90 ml) of whole water were incubated with $\text{NaH}^{14}\text{CO}_3$ for 7–8 h in the incubator described above. Three of the light bottles were incubated under the Acrylite OP-2 shield and three under full sunlight to assess the potential photoinhibition of photosynthesis caused by UV radiation.

Measurements—Water samples for bacterial abundance (5 ml) were preserved with 0.2- μm filtered formaldehyde (2% final concentration) and stored at 4°C. All samples were counted within 1 month of their collection. Bacterial abundance was determined by epifluorescence microscopy of DAPI-stained samples collected on 0.2- μm black Nuclepore filters (Porter and Feig 1980). Over 20 fields of view were examined and over 500 cells counted for every filter.

Bacterial production was estimated from rates of protein synthesis using ^3H -leucine (Kirchman et al. 1985). Leucine concentrations and incubation times were determined from substrate saturation curve and time course experiments conducted on 12 June 1996. Leucine incorporation was maximal at 20 nM and incorporation remained linear for 80 min. All samples were incubated either in the light or dark, with a 20 nM final concentration of ^3H -leucine for 1 h. One formaldehyde (4% final concentration)-killed control was incubated with triplicate live samples to determine abiotic sorption of the ^3H -leucine. Incubations were terminated by filtration through 0.2- μm pore size Nuclepore membrane filters. Filters were immediately extracted with ice-cold 5% trichloroacetic acid for 5 min, followed by a 5-ml rinse with ice cold 5% trichloroacetic acid and an additional rinse with 5 ml distilled water. The filters were stored in scintillation vials and refrigerated until measurement of radioactivity within 7 d of collection. Prior to scintillation counting, samples were extracted at 50°C for 1 h using the tissue solubilizer solvable (Dupont, New England Nuclear Inc.; Amon and Benner 1998).

Primary production was measured in water samples (80 ml) incubated in the quartz bottles with 20 μCi $\text{NaH}^{14}\text{CO}_3$ for 7–8 h. The incubations were terminated by placing all bottles in the dark and immediately filtering them through

0.45- μm Millipore membrane filters. Filters were placed in scintillation vials and frozen until count for radioactivity. Prior to scintillation counting, the filters were acid fumed to remove unincorporated label. Initial water samples were collected for dissolved inorganic carbon content in 3.7-ml glass vials fixed with 10 μl of 50 mM HgCl_2 and tightly capped without headspace. Dissolved inorganic carbon (DIC) was determined using a Shimadzu TOC 5000 analyzer with standards of sodium bicarbonate and sodium carbonate. Average coefficient of variance for replicate injections for DIC analysis was 0.28%.

Samples (10 ml) for DOC analysis were collected in muffled 20-ml glass vials acidified with 100 μl 20% high-performance liquid chromatography-grade H_3PO_4 , sealed with Teflon-lined caps, and stored upright at 4°C until analysis. DOC was determined by high-temperature oxidation using a Shimadzu TOC-5000 analyzer (Benner and Strom 1993). Average coefficient of variance for replicate injections for DOC analysis was 1.2%.

Absorbance of water samples for wavelengths of light from 280–400 nm was measured using a Shimadzu UV160U spectrophotometer. Absorbance was determined using a 1-cm quartz cell and analyzed against an identical cell with MilliQ-UV water.

Light was measured with an IL 1700 radiometer (International Light Inc., Newburyport, Massachusetts) and three different submersible, broad-band, photodiode sensors. The range of wavelengths detected were UVB, 275–310 nm; UVA, 315–390 nm; and PAR, 400–700 nm. Peak responses for the UVA and UVB sensors are at 290 and 360 nm, respectively. Light attenuation was determined at the field site close to noon during at least 1 d each trip. Light measurements were made every 10 cm from the surface to the bottom, and the attenuation coefficient was calculated from the least-squares fit of the ln-transformed irradiance values versus depth. Irradiance for each of the three wavelength bands was measured at the level of the bottles (~1-cm depth) in the incubator 5–10 times throughout the day while experiments were being conducted.

Results and discussion

Study site conditions—Average daily water temperatures at the study site varied from 11.6 to 30.7°C between June 1996 and June 1997. Bacterial abundance in the water column ranged from 0.9 to 2.8×10^6 cells ml^{-1} , and bacterial production ranged between 1.8 and 9.1 $\text{mmol C m}^{-2} \text{d}^{-1}$ (0.06 and 0.32 $\mu\text{M h}^{-1}$). Both bacterial abundance and production were generally highest in the spring and summer months (Table 1). The highest bacterial production rates were measured in March during a phytoplankton bloom (Table 1). Growth rates estimated from bacterial abundance and production ranged from 0.5 d^{-1} in November to 3.4 d^{-1} in September, and the average over the year was 1.9 d^{-1} .

Instantaneous irradiance, measured just below the water surface close to solar noon, ranged from 10 to 47 $\mu\text{W cm}^{-2}$, 2.4 to 3.8 mW cm^{-2} , and 20 to 42 mW cm^{-2} for UVB, UVA, and PAR, respectively (Table 2). Highest irradiance for all wavelengths occurred in July 1996 and June 1997 and the

Table 1. Average water temperature, depth, bacterioplankton production, abundance, water column community respiration, and water column gross primary production. Error is reported as mean \pm 1 SD for replicate samples ($N \geq 3$).

Trip	Water temperature* (°C)	Depth* (m)	DOC* (μM)	Bacterial production ($\text{mmol C m}^{-2} \text{d}^{-1}$)	Bacterial abundance ($10^6 \text{ cells ml}^{-1}$)	Community respiration* ($\text{mmol C m}^{-2} \text{d}^{-1}$)	Gross primary production* ($\text{mmol C m}^{-2} \text{d}^{-1}$)
Jun 96	30.2 \pm 0.6	1.11	190 \pm 8	6.1 \pm 0.7	1.9 \pm 0.07	27 \pm 2	3 \pm 2
Jul	30.7 \pm 0.1	1.02	175 \pm 16	4.7 \pm 0.4	1.2 \pm 0.13	14 \pm 6	0.4 \pm 4
Sep	30.6 \pm 0.1	1.10	202 \pm 11	5.8 \pm 1.9	0.9 \pm 0.02	10 \pm 1	3 \pm 1
Nov	23.9 \pm 4.9	1.24	167 \pm 11	1.8 \pm 1.0	1.7 \pm 0.10	7 \pm 2	1 \pm 0.7
Jan 97	11.6 \pm 5.7	0.90	414 \pm 47	3.2 \pm 0.2	2.8 \pm 0.04	11 \pm 5	36 \pm 5
Mar	21.5 \pm 1.5	1.18	234 \pm 27	9.1 \pm 1.6	2.1 \pm 0.06	17 \pm 7	9 \pm 3
Jun	27.3 \pm 1.5	1.08	142 \pm 8	5.9 \pm 2.2	ND	15 \pm 3	6 \pm 2

* Data from Ziegler and Benner (1999); ND, not determined.

lowest irradiances were measured in February and April 1996 (Fig. 1). The attenuation coefficients ranged from 3.7 to 7.7 m^{-1} for UVB, 1.7 to 2.8 m^{-1} for UVA, and 0.67 to 1.13 m^{-1} for PAR. The highest attenuation coefficients were measured in January due to the higher concentrations of DOC and phytoplankton caused by a brown tide (Table 2). We calculated that 1% of surface UVB, UVA, and PAR irradiance was found at depths ranging 0.60–1.24 m, 1.65–2.71 m, and 4.80–6.87 m, respectively. These depths indicated that light in all three spectral regions often reached the benthos.

Significance of photomineralization of DOM in Laguna Madre—Photomineralization of DOM to dissolved inorganic carbon has been measured in natural waters (Salonen and Vahatalo 1994; Miller and Zepp 1995; Graneli et al. 1996), and it appears that photochemical and biological mineralization processes can compete for the same substrate (Benner and Ziegler in press). In the present study, photomineralization of DOM was measured during periods of high sunlight to estimate the maximum rate. Rates estimated from changes in DOC concentration were not significant relative to bacterioplankton respiration. Initial DOC concentrations in the water incubated for the measurement of photomineralization in May 1997 were $310 \pm 7 \mu\text{M}$, and were higher than normal for water in lower Laguna Madre due to a brown tide. Initial DOC concentrations in July 1997 were $156 \pm 5 \mu\text{M}$, more typical of concentrations at the study site throughout the year (Table 1). Surface light levels

around solar noon were much higher in July, especially in the UV region. There was no significant difference ($P > 0.05$; unpaired t -test) in DOC concentrations between either the initial or final dark control as compared with samples exposed to full sunlight in either the May or July experiment (Fig. 2). However, losses in absorbance of ultraviolet light were found relative to both the initial and dark control. For example, loss of absorbance in the exposed samples at 350 nm was 33% and 81% in May and July, respectively.

The approach used to estimate photomineralization of DOC in this study, following changes in DOC after exposure to sunlight, was only sensitive enough to detect photomineralization rates $>0.33 \mu\text{M C h}^{-1}$. Following photoproduction of DIC in samples initially acidified and purged of CO_2 is a much more sensitive approach to measuring photoproduction of DIC. However, this approach involves adding a buffer to the sample to bring it back to the original pH, and we sought to limit manipulation in order to simply determine the significance of this process relative to microbial respiration. Normalized to absorbance at 350 nm, the minimal rates (0.1 and 0.3 $\mu\text{M C m h}^{-1}$, for May and July respectively) detectable were similar to average rates (0.2–0.3 $\mu\text{M C m h}^{-1}$) reported by Miller and Zepp (1995) for riverine and oceanic waters. Although the approach used in this study was not sensitive enough to detect low photomineralization rates, the maximal potential rate based on the limit of detection (0.33 $\mu\text{M C h}^{-1}$) was insignificant relative to biological respiration in the water column. Assuming a constant photomineralization rate throughout the top 0.2 m (depth

Table 2. Surface irradiance of UVB (280–320 nm), UVA (320–400 nm), and PAR (400–700 nm) measured <1 cm below water surface around solar noon, and the corresponding attenuation coefficients (k_d). Error is reported as mean \pm 1 SD for replicate measurements ($N \geq 3$) of attenuation made around solar noon.

Trip	UVB ($\mu\text{W cm}^{-2}$)	UVA (mW cm^{-2})	PAR (mW cm^{-2})	UVB k_d (m^{-1})	UVA k_d (m^{-1})	PAR k_d (m^{-1})
Jun 96	39	3.6	40	3.7 \pm 0.3	2.0 \pm 0.3	0.77 \pm 0.09
Jul	43	3.8	42	4.9 \pm 0.7	2.8 \pm 0.3	0.89 \pm 0.28
Sep	31	3.3	39	5.8 \pm 0.6	2.5 \pm 0.2	0.96 \pm 0.26
Nov	11	2.4	26	4.8 \pm 0.6	1.7 \pm 0.1	0.67 \pm 0.19
Jan	10	2.5	20	7.7 \pm 2.6	3.5 \pm 0.2	1.13 \pm 0.12
Mar	19	2.7	29	ND*	2.0 \pm 0.3	0.91 \pm 0.13
Jun 97	47	3.4	40	3.9 \pm 0.3	1.9 \pm 0.6	0.80 \pm 0.09

* ND, not determined.

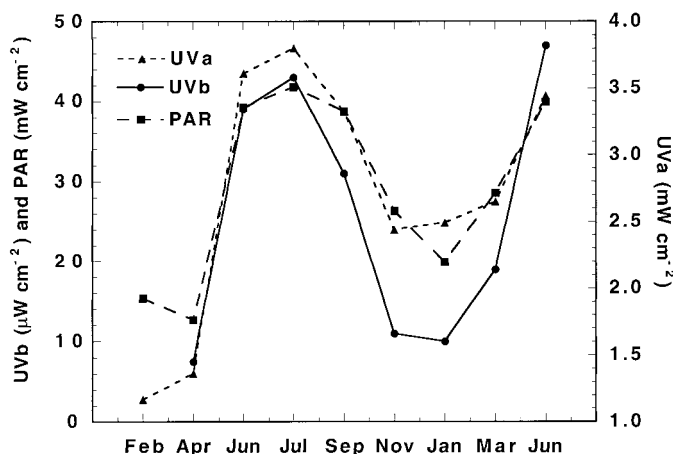


Fig. 1. The surface UVB (275–310 nm), UVA (315–390 nm), and PAR (400–700 nm) irradiance measured at approximately solar noon throughout the year.

where <50% of surface UVB remains), the estimated potential maximum photomineralization rate would have been $<0.8 \text{ mmol C m}^{-2} \text{ d}^{-1}$. This rate represented $\sim 3\%$ of summer water column respiration rates ($\sim 26 \text{ mmol m}^{-2} \text{ d}^{-1}$) and about 0.4% of the average summer community respiration ($\sim 194 \text{ mmol m}^{-2} \text{ d}^{-1}$) (Ziegler and Benner 1998).

The low rates of photomineralization in Laguna Madre relative to rates measured in other riverine, oceanic, and marsh waters (Miller and Zepp 1995) is supported by the low UV-absorbing capacity of Laguna Madre DOM. Absorbance measurements in the UV spectra are useful for the prediction of photochemical reactivity of natural waters (Miller 1994). The absorption coefficient at 350 nm (a_{350}) ranged from 2.2 m^{-1} for the water from the Mississippi River plume to 190 m^{-1} for water from the Suwanee River (Miller and Zepp 1995). The a_{350} value for Laguna Madre water collected in May ($a_{350} = 0.75 \text{ m}^{-1}$) was much lower in comparison to a Gulf of Mexico sample, which had a 45% lower concentration of DOC (Miller and Zepp 1995). In July, when DOC concentrations were similar to those reported for the Gulf of Mexico seawater described above, the a_{350} for Laguna Madre water was much lower ($a_{350} = 0.23 \text{ m}^{-1}$).

Effect of phototransformation of DOM on bacterioplankton activity—Photochemical transformations of DOM did not appear to significantly influence bacterial utilization of DOM in Laguna Madre. Bacterial production rates measured in the water previously exposed to total solar radiation (UV treatment) for $\sim 6 \text{ h}$ were never significantly different ($P > 0.05$) from rates measured in the water previously held in the dark (Fig. 3). Similarly, bacterial production rates measured in the water previously exposed to sunlight $>400 \text{ nm}$ (PAR treatment) were never significantly different ($P > 0.05$) from the rates measured in the dark control throughout the year (Fig. 3). Prefiltration removed 92–99% of the bacteria in the water samples used in these experiments. From the initial and final bacterial abundances in these filtered water samples we determined that the potential DOC removed by bacteria during the incubation was insignificant (Table 3). Therefore, the lack of significant differences in

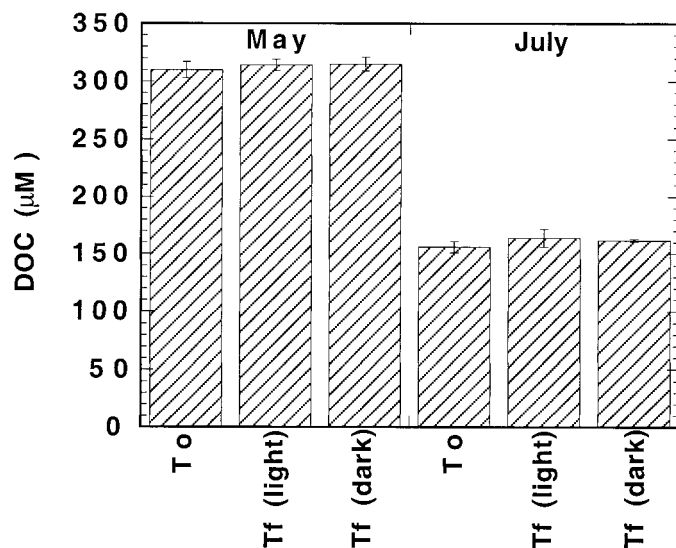


Fig. 2. The DOC concentration of initial samples (To) and samples after 2 d of exposure to surface-level solar radiation (Tf light) or after 2 d held at the surface in dark bottles (Tf dark) for water collected in May and July 1997.

bacterial production in the three treatments was not due to the loss of DOM in the incubations prior to inoculation.

The N or P limitation of bacterial production in the experiments conducted is a possible explanation for the lack of enhanced bacterioplankton production in experimental treatments with previously exposed DOM. However, there is some evidence indicating that nutrient limitation of bacterial production was not likely in Laguna Madre. Throughout the year, a net release of NH_4^+ was measured during both light and dark in situ bottle incubations (Ziegler and Benner 1999b), indicating that bacterioplankton are unlikely to be N limited. Bacterioplankton production in Laguna Madre in-

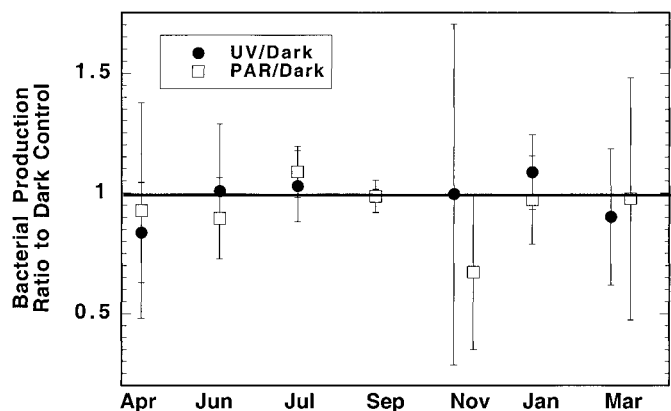


Fig. 3. Results of experiments designed to assess the effect of photochemical transformations of dissolved organic matter on bacterial production, where filtered ($0.2 \mu\text{m}$) water was exposed to total sunlight (UV), light $>400 \text{ nm}$ (PAR), or kept in the dark (control) before inoculation and subsequent measurement of bacterial production. Values are plotted as the ratio of bacterial production measured in the UV or PAR treatments relative to the bacterial production in the dark control. Error bars indicate $\pm 1 \text{ SD}$ of the mean.

Table 3. Initial bacterial abundance in 0.2- μm filtered water used in experiments designed to assess the effects of photochemical transformations of DOM on bacterioplankton production. The increase in bacterial abundance in the 0.2- μm filtered water exposed to total solar radiation (UV), solar radiation >400 nm (PAR), and a dark control. Negative values indicate a decrease in number of cells. The estimated carbon required by the measured increase in bacterial abundance assuming a growth efficiency of 30% and 20 fg C cell $^{-1}$.

	Initial bacterial abundance (10^4 cells ml $^{-1}$)	Increase in bacterial abundance (10^4 cells ml $^{-1}$)			Estimated C utilized (μM C)		
		UV	PAR	Dark	UV	PAR	Dark
Jun	5.2	0.5	2.6	0.5	0.02	0.09	0.02
Jul	9.3	18.7	-3.6	-1.9	0.72	—	—
Sep	0.9	1.3	1.9	2.3	0.05	0.07	0.09
Nov	0.7	3.0	3.2	2.9	0.12	0.12	0.12
Jan	8.5	-3.0	-2.9	-4.3	—	—	—
Mar	16.1	-10.4	-8.8	-9.5	—	—	—

creases during the day as benthic fluxes of DOC increase, resulting primarily from seagrass exudation (Chin-Leo and Benner 1991; Ziegler and Benner 1999a). This release of DOC is accompanied by very little NH_4^+ or PO_4^{2-} (Ziegler and Benner 1999b) and virtually no dissolved organic nitrogen or phosphorus (Benner unpubl. data). This indicates that the benthic release of DOC is primarily responsible for the increases in bacterial production, and it is unlikely that bacterioplankton production in lower Laguna Madre is limited by N or P. Therefore, the lack of enhanced bacterial production in treatments with previously exposed DOM is not likely to have been caused by nutrient limitation but by the lack of additional or transformed substrate relative to the dark controls.

Other studies have documented enhanced bacterial production or growth in water samples previously exposed to natural or simulated light (Geller 1986; Lindell et al. 1995; Wetzel et al. 1995; Miller and Moran 1997; Benner and Biddanda 1998). In many of these studies, significant stimulation of bacterial production or growth occurred within 3–6 h of sunlight exposure. Bacterioplankton production in Laguna Madre has been observed to increase during the day, with the highest rates observed in the early afternoon (Chin-Leo and Benner 1991; Ziegler and Benner 1999a). This suggests that mechanisms responsible for stimulating bacterial production operate on time scales of a few hours. Therefore, if photochemical processes were important for influencing

bacterial production, they would have been detected within the 6-h incubation time used in the present study.

In Laguna Madre, photochemical processes may not be ecologically important because of the chemical composition and bioavailability of the DOM. We considered two main reasons photochemical transformations did not affect bacterial utilization of DOM: most of the DOM was not photoreactive, and a large fraction of the DOM was bioreactive; therefore, phototransformations had no significant effect on its utilization. Many of the studies that have demonstrated the enhancement of bacterial activity due to exposure of DOM to UV radiation were conducted with humic-rich waters (Wetzel et al. 1995; Bushaw et al. 1996; Lindell et al. 1996; Miller and Moran 1997; Reitner et al. 1997). In humic-rich waters, the bioavailability of DOM can limit bacterial growth and photochemical transformations appear to be important for enhancing bioavailability (Lindell et al. 1995). In such cases, photochemical processes act as an energy “subsidy” causing the DOM to become more biologically available. Thus, the importance of photochemical transformations of DOM on bacterial activity is probably related to the initial bioavailability of the DOM. Relative bioavailability of DOM in Laguna Madre, expressed as a ratio of bacterial production to concentration of DOC, is much higher than for DOM in the types of aquatic ecosystems or water samples where phototransformations of DOM have been found to increase bacterial activity (Table 4).

Table 4. The relative bioavailability of dissolved organic matter (DOM) calculated as the average bacterial production (BP; μM C h $^{-1}$) divided by the concentration of dissolved organic carbon (DOC; mM) for waters collected from different environments or sources.

Bioavailability of DOM (BP/[DOC]) (μMh^{-1})/(mMC)	Environment or source	Reference
1.01	Laguna Madre	This study
0.35	Gulf of Mexico (0–150 m)	Benner and Biddanda (1998)
0.24	Gulf of Mexico (150–1,000 m)	Benner and Biddanda (1998)
0.20	Rio Negro, blackwater river	Amon and Benner (1996)
0.18	<i>Juncus effusus</i> leachate	Wetzel et al. (1995)
0.09	Ogeechee River, blackwater river	Meyer et al. (1987)
<0.06	“Ruster Poschn,” humic pond	Reitner et al. (1997)

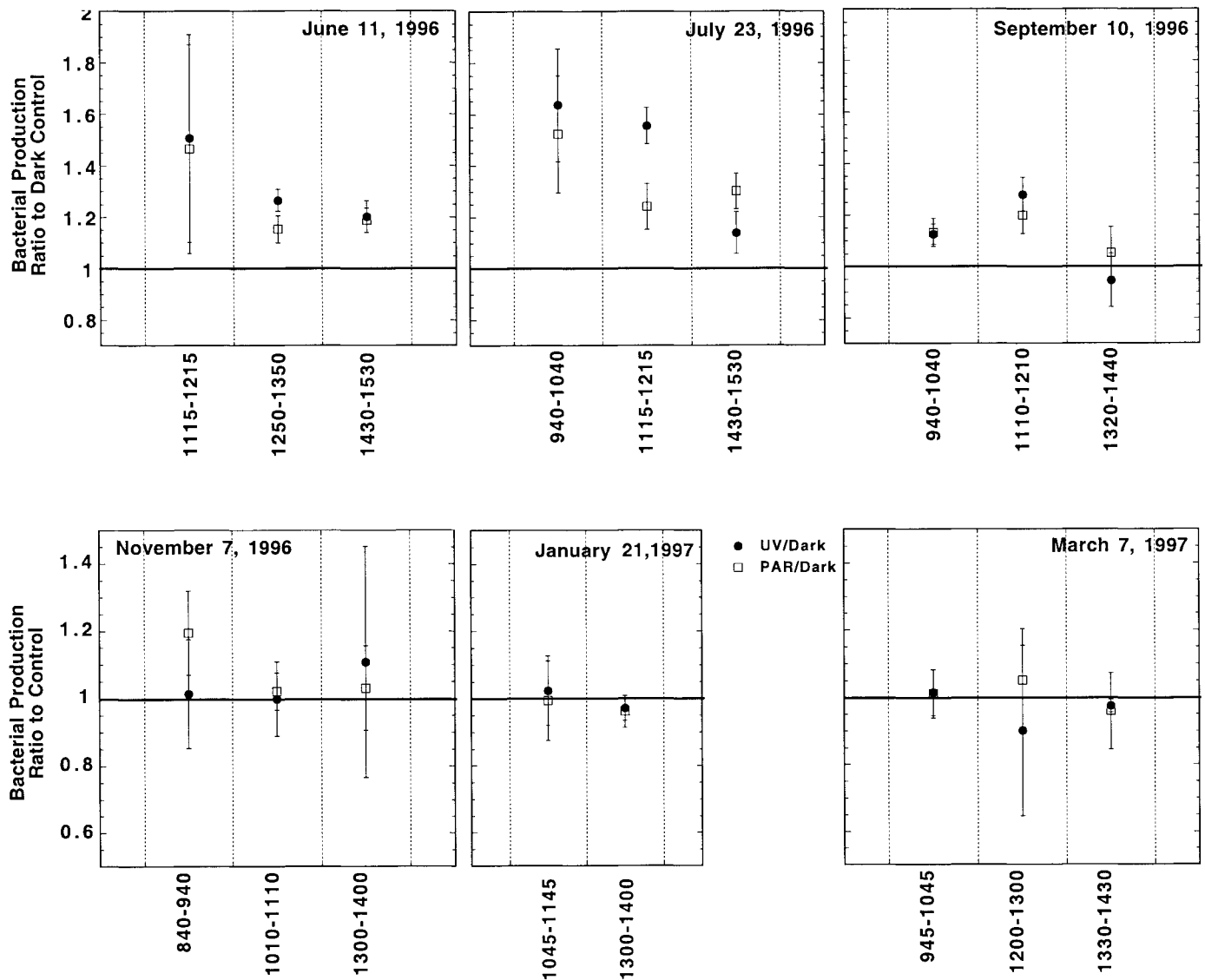


Fig. 4. Results of experiments conducted to assess the net effect of solar radiation on bacterial production, where bacterial production was measured in whole water samples exposed to total sunlight (UV), light >400 nm, or kept in the dark (control). Values are plotted as the ratio of bacterial production measured UV or PAR treatments relative to bacterial production in the dark control. Incubation times are indicated on the x-axis. The error bars indicate ± 1 SD of the mean.

Net effect of sunlight on phyto- and bacterioplankton production—Rates of primary production ranged from 0.05 to $0.15 \mu\text{M C h}^{-1}$, with the highest rate occurring in September. There was no significant difference (*t*-test; $P > 0.05$) between rates of primary production measured in UV or PAR treatments. Bacterial production measured in whole water incubated in both the UV and PAR treatments were significantly greater (*t*-test; $P < 0.05$) than in the dark control during June, July, and September 1996 (Fig. 4). The increases in bacterial production in the UV and PAR treatments relative to the dark control ranged from 13% to 63% and 13% to 52%, respectively, with the greatest increases in July (Table 5). There was no significant difference (*t*-test; $P > 0.05$) in bacterial production measured among the three treatments during November 1996, January 1997, or March 1997 (Fig. 4). Bacterial production was significantly higher (*t*-test;

$P < 0.05$) in the UV as compared with the PAR treatments at midday, when light levels were highest, in June, July, and September (Fig. 4).

The observed enhancement in bacterial production in whole water incubations exposed to light was probably due to the release of DOM by phytoplankton. By design, these experiments included all plankton in order to observe the net effect of the exposure of both the planktonic organisms and the DOM on bacterial activity. The enhancement of bacterial production occurred in both UV and PAR treatments, and primary production was similar and high enough in both of the treatments to support the measured increase in bacterial production. The enhancement of bacterial production due to the presence of phytoplankton was reported in other studies of the effect of UV radiation on bacterial activity (Aas et al. 1996; Sommaruga et al. 1997). Although phytoplankton ex-

Table 5. Data from experiments where a significant increase (t -test; $P < 0.05$) in bacterial production relative to the dark control was observed in unfiltered water samples exposed to total sunlight (UV) and to wavelengths >400 nm (PAR). All values are reported as the mean \pm 1 SD for replicate samples ($n = 3$).

Date	Time	Bacterial production dark control ($\mu\text{M C h}^{-1}$)	Bacterial production (% dark control)		Primary production ($\mu\text{M C d}^{-1}$)	
			UV	PAR	UV	PAR
11 Jun 1996	11:10	0.16 \pm 0.06	151 \pm 1.3	147 \pm 1.4	0.55 \pm 0.3	0.78 \pm 0.1
	12:50	0.17 \pm 0.01	127 \pm 0.3	115 \pm 0.6		
	14:40	0.14 \pm 0.01	120 \pm 0.5	119 \pm 0.4		
23 Jul 1996	9:30	0.13 \pm 0.03	163 \pm 0.6	152 \pm 0.8	0.81 \pm 0.3	0.80 \pm 0.4
	12:30	0.16 \pm 0.01	156 \pm 0.3	124 \pm 0.6		
	15:30	0.18 \pm 0.01	114 \pm 0.9	130 \pm 0.4		
10 Oct 1996	10:30	0.19 \pm 0.01	113 \pm 0.5	113 \pm 0.6	1.45 \pm 1.5	ND*
	11:20	0.14 \pm 0.01	128 \pm 0.4	120 \pm 0.6		

* ND, not determined.

udation caused increased bacterial activity in water column incubations from Laguna Madre, diel variation in bacterioplankton production measured in this ecosystem is primarily fueled by light-mediated release of DOM from the benthos (Ziegler and Benner 1999a).

Photochemical transformation of refractory components of DOM into labile compounds was probably not responsible for the observed enhancement in bacterial production measured during the summer months. The enhancement occurred in samples exposed to and shielded from UV radiation. There is sufficient energy in wavelengths of sunlight >400 nm to promote some photochemical reactions (Zika 1981), and a few studies have demonstrated photochemical processes in lake water exposed to PAR in the absence of UV radiation (Graneli et al. 1996). However, most studies of marine photochemistry have reported the occurrence of photochemical transformations with wavelengths <350 nm (Gjessing and Gjerdahl 1970; Zika 1981; Zafiriou 1983; Kieber et al. 1990; Mopper and Zhou 1990). In Laguna Madre, no effect of the phototransformations of DOM on bacterial production was detected in the experiments where filtered water was exposed to ~ 6 h of sunlight. Therefore, it is unlikely that phototransformations of DOM were responsible for the enhancement of bacterial activity observed in the 1-h incubations where bacterial production was measured during exposure to sunlight.

Although UVB was probably high enough in the summer to have caused photoinhibition of phytoplankton or bacterioplankton production in the surface waters of Laguna Madre (Lorenzen 1979; Herndl et al. 1993; Holm-Hansen et al. 1993), net inhibition of either process was not detected. The depth at which 10% of surface UVB and UVA irradiance ranged 40–62 cm and 82–135 cm, respectively, throughout most of the year. These depths represented a large fraction of the average depth of the water column. Mixing of this shallow water column also exposes bacteria to surface light levels frequently. It appears bacterioplankton in Laguna Madre have adaptive strategies for withstanding exposure to UVR. There is some evidence of adaptation to UVR in bacteria collected from the surface water as compared with those found in the deep sea (Yayanos 1989). Natural bacterial communities have also been observed to increase pig-

mentation with prolonged exposure to UV radiation (Thomson et al. 1980).

In the experiments designed to determine the net effect of sunlight exposure on bacterial activity, bacterial production was estimated from the incorporation of leucine in water samples during exposure to natural sunlight. It is unlikely that the radiolabeled leucine was photochemically altered during exposure to sunlight because it does not absorb light above 230 nm. It is also possible that the added leucine was utilized by phytoplankton as a nitrogen source; however, phytoplankton only incorporate the amine group and do not incorporate the tritium which is left behind in the α -keto acid (Palenik and Morel 1990, 1991).

Another commonly used approach for determining the net effect of sunlight on bacterial activity is the measurement of bacterial production in an unfiltered water sample after exposure to sunlight (Herndl et al. 1993; Lindell et al. 1996). On 23 July 1996, a comparison was conducted between this approach and the one used in this study, where bacterial production was measured during exposure to sunlight. The results from these two approaches were slightly different. Bacterial production measured in water previously exposed to PAR and measured during exposure to PAR were both significantly higher (t -test; $P < 0.05$) than the corresponding dark controls (Fig. 5). The similarity in the bacterial production measured in the PAR treatments of these two approaches verified that phytoplankton-derived DOM was probably fueling the measured increases in bacterial production in the light. Measurements of bacterial production in the water previously exposed to UV was not significantly different (t -test; $P > 0.05$) from the dark control. However, bacterial production measured in the UV treatment during the incubation was significantly higher (t -test; $P < 0.05$) than the dark control (Fig. 5). The lack of net enhancement in bacterial production measured after 1.3 h exposure to UV may have indicated that some inhibition of bacterial activity occurred after an exposure >1 h, but that inhibition was counteracted by DOM released by phytoplankton during the same period (Fig. 5).

Inhibition of bacterial activity in Laguna Madre is probably minimal considering no net inhibition of bacterial activity could be measured at surface level irradiation. Many

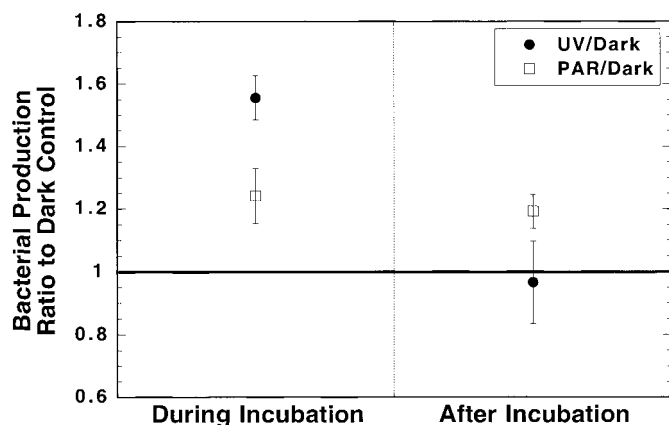


Fig. 5. A comparison of two methods to assess the net effect of sunlight on bacterial production. "During incubation" refers to experiments where whole water was incubated in the light with radiolabeled leucine. "After incubation" refers to experiments where whole water was incubated in the light but the radiolabeled leucine was added after the incubation and bacterial production was measured in the dark. Values are reported as the ratio of bacterial production measured in the samples exposed to total sunlight (UV) or samples exposed to light >400 nm (PAR) relative to bacterial production in the dark control. Error bars indicate ± 1 SD of the mean.

other studies have reported the inhibition of bacterial activity due to exposure to natural levels of UVB and UVA (Bailey et al. 1983; Sieracki and Sieburth 1986; Herndl et al. 1993; Aas et al. 1996; Lindell et al. 1996; Kaiser and Herndl 1997; Reitner et al. 1997; Sommaruga et al. 1997; Pakulski et al. 1998). Most of these studies exposed water samples for 2–12 h before measuring bacterial production in the dark. Aas et al. (1996), as in the present study, incubated water samples with the label, but for up to 11.7 h, and they observed inhibition after 3 h of exposure. The results of the present study represent the net effect of surface solar radiation over the short term, which is probably applicable to Laguna Madre, where the entire water column is thoroughly mixed throughout the day.

Significance of photoprocesses to DOM cycling in Laguna Madre—Photochemical processes had very little affect on the cycling of DOM in Laguna Madre. This is contrary to most other studies of photochemical processes in aquatic systems where photochemical transformations of DOM have been found to significantly influence bacterial utilization of DOM (Geller 1986; Kieber et al. 1989; Lindell et al. 1995; Benner and Biddanda 1998). The UV absorptivity and photomineralization rates of DOM were low indicating the minor role photochemical processes play in the cycling of DOM relative to biological processes in Laguna Madre, where bacterial utilization of DOM represents $>60\%$ of benthic primary production (Ziegler and Benner 1999a). Diel variation in bacterioplankton production is primarily due to the light-mediated release of DOM from seagrasses (Ziegler and Benner 1999a). The DOM released from seagrasses in Laguna Madre is rich in carbohydrates (unpubl. data), which are bioreactive but not photoreactive. The large source of

bioreactive relative to photoreactive DOM in Laguna Madre is responsible for the greater significance of biological versus photochemical processes in this ecosystem. Therefore, the ecological significance of photochemical processes in the aquatic environment is greatly dependent on the relative photo- and bioreactivity of the DOM.

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