Studies at Oyster Bay in Jamaica, West Indies. III. Measurements of Underwater-sunlight Spectra[1]

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ABSTRACT

Spectral distributions of ambient underwater sunlight in Oyster Bay, Falmouth Harbor, Jamaica, West Indies, have been measured during the diurnal rise in the stimulable bioluminescent intensity of the marine dinoflagellate, *Pyrodinium bahamense*. In addition to the changes in light intensity during this period, there are large changes in the relative spectral distributions, as functions of both time and depth in the Bay. The blue-to-red intensity ratios vary by factors of 10 to 100.

Introduction. In this issue, Seliger and McElroy (1968) and Carpenter and Seliger (1968) have described the nocturnal rhythm of stimulable bioluminescence in the photosynthetic dinoflagellate, *Pyrodinium bahamense*. The observations were made at Oyster Bay, Falmouth Harbor, Jamaica, W.I., from April 1966 through May 1967. They showed that (i) the rise in stimulable bioluminescence per organism is initiated approximately one hour before sunset while the sun is still bright; (ii) the intensity of stimulable bioluminescence reaches a maximum within an hour subsequent to sunset and then remains constant until sunrise; (iii) after sunrise, the stimulable bioluminescence per organism drops almost as rapidly as it had risen during sunset; (iv) in the turbid water of the shallow Bay, organisms at lower depths exhibit a rise in stimulable bioluminescence slightly earlier than organisms at the surface, implicating an intensity or a relative spectral-quality dependence of the triggering mechanism.

1. Contribution No. 529 from the McCollum-Pratt Institute and the Department of Biology, The Johns Hopkins University. This work was supported by the U.S. Atomic Energy Commission through contract AT (30-1) 3480 and by the Office of Naval Research through contract Nonr 401016.
Accepted for publication and submitted to press 12 June 1968.
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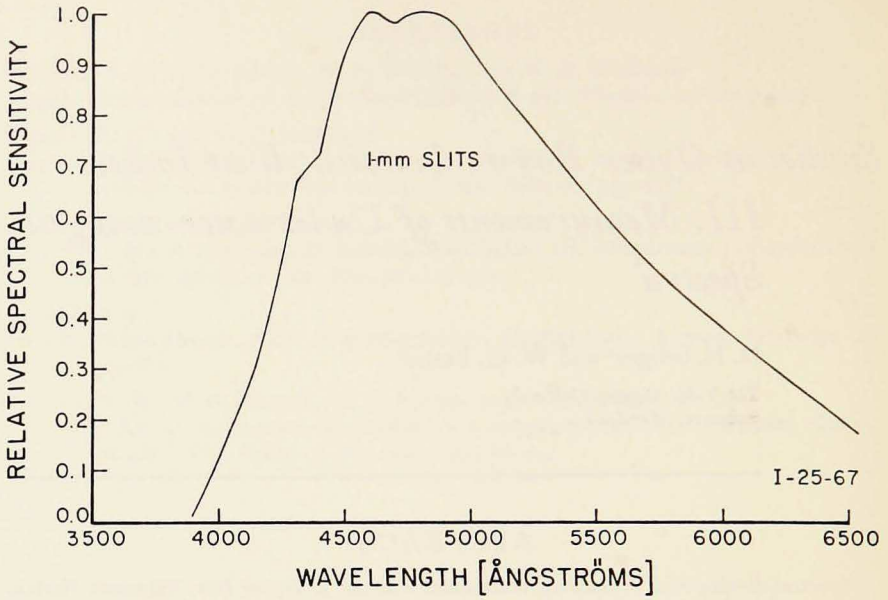


Figure 1. Relative spectral-sensitivity curve for underwater spectrometer-phototube combination.

Prior to laboratory experiments with artificially maintained cultures of *P. bahamense*, we investigated the spectral quality of the ambient sunlight in the Bay and correlated the measurements with the diurnal periodicity in stimulable bioluminescence manifested by *P. bahamense*. This paper presents data obtained at our fixed-station site in the Bay (Seliger and McElroy 1968) using a double-beam underwater spectrometer designed by W. G. Fastie.

Description and Methods. The underwater double-beam photoelectric spectrometer is a modification of the instrument described by Taylor et al. (1966) and used by them for the measurement of the emission spectrum of stimulated bioluminescence in *P. bahamense*. The spectrometer-phototube combination was calibrated for relative photon spectral sensitivity by using a National Bureau of Standards standard lamp of spectral irradiance and a magnesium oxide diffusing surface at 45° to the plane of the entrance slits; the instrument was calibrated for wavelength with a low-pressure mercury-arc lamp.

All ambient light measurements were made on cloudless days at the fixed-station site in Oyster Bay (Seliger and McElroy 1968). This is very nearly the deepest portion of the Bay, varying from 150 to 180 cm in depth, depending on the tide. The spectrometer was lowered manually, and, to measure downwelling light intensities, the diffusing surface was again set at 45° to the plane of the entrance slits.

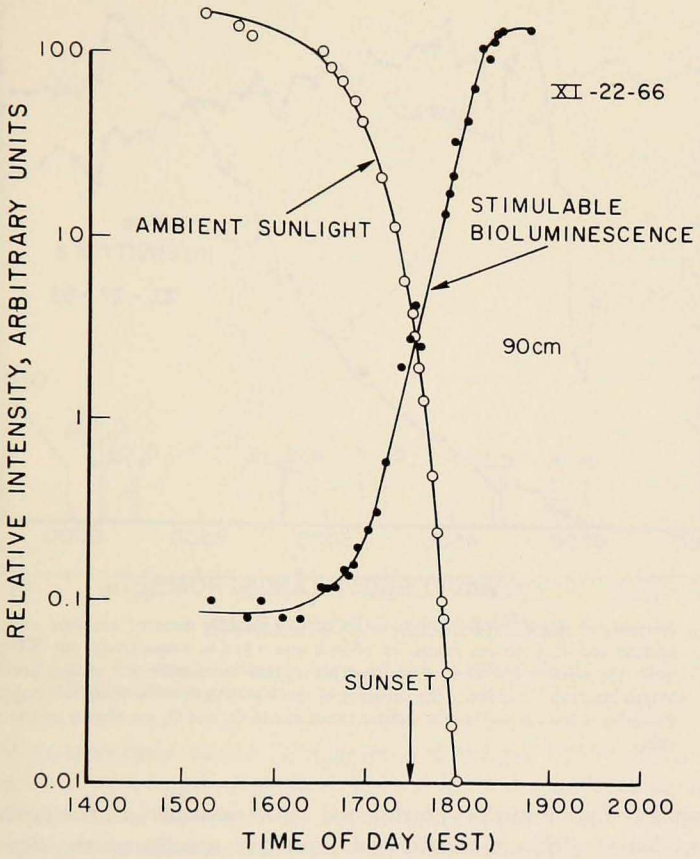


Figure 2. Logarithm of the relative intensity of ambient downwardly directed sunlight (open circles) at a depth of 90 cm throughout the time period when the diurnal stimulable bioluminescent intensity at the same depth increased by a factor of more than 1750.

Concurrent measurements of intensities of stimulable bioluminescence were made manually with the same portable underwater photometer that was used by Seliger and McElroy (1968).

Results. The relative photon spectral sensitivity curve for 1-mm slits is shown in Fig. 1. The nocturnal rise in stimulable bioluminescent intensity at a 90-cm depth is shown in Fig. 2. As shown by Seliger and McElroy (1968), the shapes of the curves for stimulable bioluminescence versus time were the same for all depths. The curve shows a flexion, a straight-line exponential increase for more than three orders of magnitude, and then a leveling off at a maximum value. In this case the time required for the doubling of stimulable bioluminescent intensity was eight minutes, but on other days the doubling

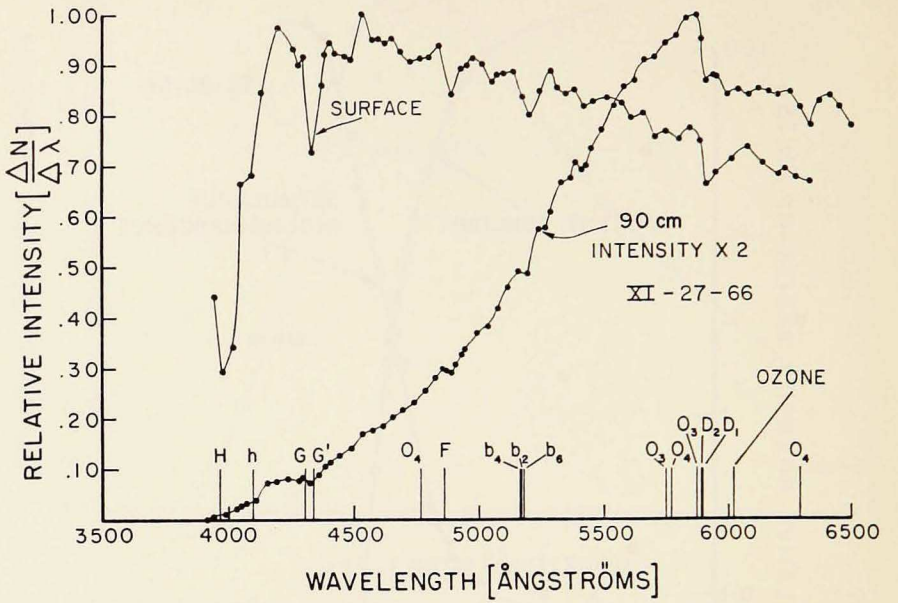


Figure 3. Normalized relative spectral intensities of downwardly directed ambient sunlight at the surface and at a 90-cm depth, at 1600 h and 1612 h, respectively, on XI-27-66. The units are relative numbers of photons per square centimeter per second per unit wavelength interval. To indicate the accuracy of the wavelength calibration, the major terrestrial Fraunhofer lines as well as the diffuse bands due to O_3 and O_4 are shown on the wavelength axis.

was as rapid as four minutes. During the same time period, the spectrometer was suspended at a 90-cm depth, and repetitive spectra of the downwardly directed sunlight were recorded continuously on a strip-chart recorder. The electronic gain was adjusted manually to cover the wide range of light intensities. As a first approximation, the peak intensity reading (5850 Å) for each spectrum was taken to be representative of the incident downwardly directed sunlight intensity; the logarithm of this value, plotted as the same function of time of day, is shown in Fig. 2. In this way, the spectrometer was used as an ambient-light photometer. The intensity is in arbitrary units. The observed time of sunset was 1730 E.S.T.

Because of absorption in the solar and terrestrial atmospheres, the incident solar-intensity spectrum at the surface of the earth is not a smooth function of wavelength. This relative spectral intensity of surface-incident solar radiation, shown in Fig. 3, illustrates the wavelength resolution obtainable with the spectrometer even when relatively large slit openings of 1 mm (30 Å) are employed.

Nearly every afternoon, by 1500 h, the complex water motion produced by the daily easterly wind has completely mixed the water of the inner Bay

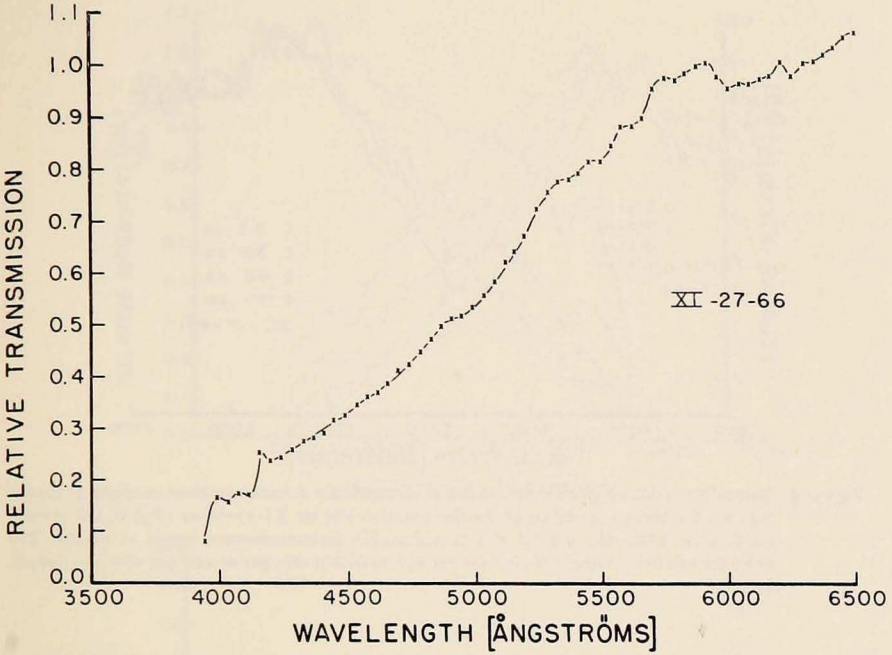


Figure 4. Relative transmission through 60 cm of water between the 30-cm and 90-cm depths at the fixed-station site.

so that it is extremely turbid (Carpenter and Seliger 1968). This turbidity gives rise to a wavelength-dependent scattering of the incident sunlight that markedly attenuates downwardly directed blue light relative to red light. In Fig. 3, the normalized relative spectral intensity of downwardly directed sunlight, measured at the 90-cm depth, has been superimposed upon the solar spectrum at the sea surface. For direct comparison of the 90-cm curve with the surface curve, all 90-cm ordinates must be multiplied by 0.5.

Fig. 4 is a plot of the relative transmission of a 60-cm water path (between 30 and 90 cm) obtained by dividing, point-by-point, the values for a relative-intensity curve at 90 cm by values for a relative-intensity curve at 30 cm.

Fig. 5 shows the normalized relative spectral-intensity curves of downwardly directed sunlight measured at various depths. The data were collected in two minutes in order to obviate any spectral shifts due to changes in the sun's elevation. Even before correction, the intensities in the red region beyond 5850 Å varied by less than a factor of two between the 7.5-cm and 90-cm depths.

Fig. 6 shows the normalized relative spectral intensities of downwardly directed sunlight at the 90-cm depth.

Discussion and Conclusions. Elucidation of the mechanism of the endogenous, light, and photoperiod-entrained rhythms of stimulable bioluminescence re-

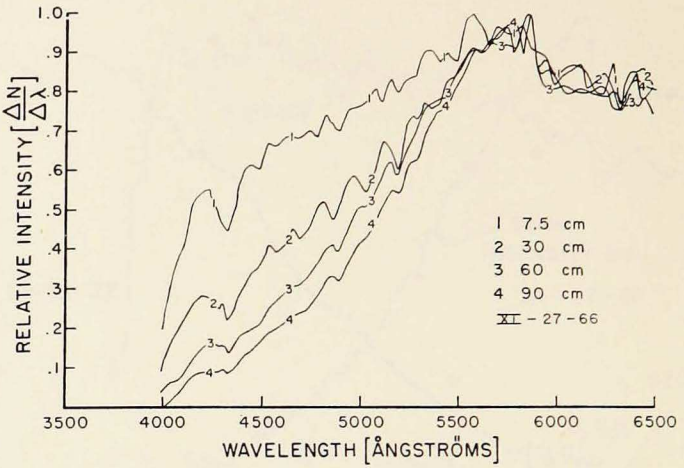
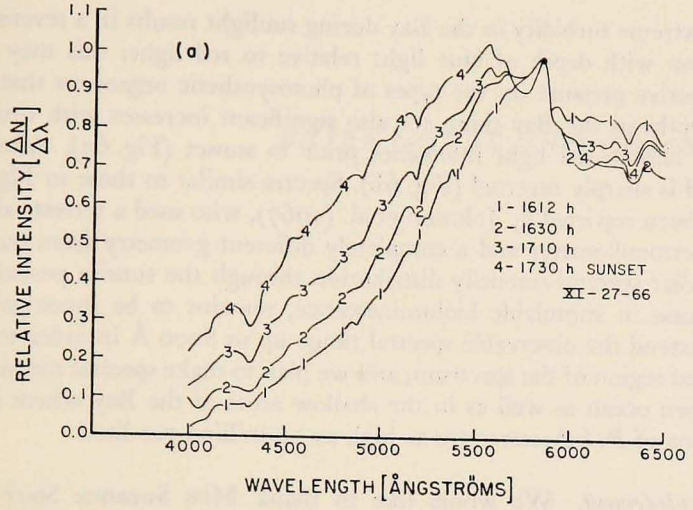
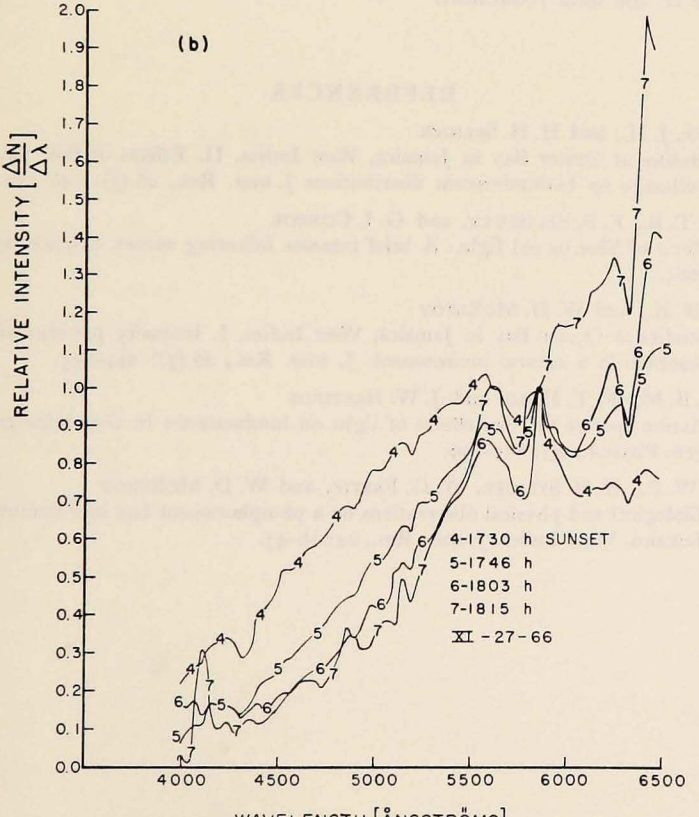


Figure 5. Normalized relative spectral intensities of downwardly directed ambient sunlight at depths 7.5, 30, 60, and 90 cm taken at the fixed-station site on XI-27-66 at 1630 h, the approximate time when the diurnal rise in stimulable bioluminescence began at 90 cm. The units are relative numbers of photons per square centimeter per second per unit wavelength interval.

quires consideration of an intensive interplay of physiological and biochemical factors. To avoid ruling out other possible factors in light emission, we have consistently referred to the observed light emission as "stimulable" bioluminescence. It may be that only in or on certain structures, and triggered by shearing forces, can luciferin react with the luciferase enzyme and oxygen to produce light. The reactants may otherwise be maintained physically or chemically separate and may possibly be accessible to biochemical extraction. In both darkness (Sweeney et al. 1959) and light (Seliger and McElroy 1968), stimulable bioluminescence can be photoinhibited. Fig. 2 shows that, for at least 30 minutes before the diurnal rise in stimulable bioluminescence was observable, the incident sunlight intensity varied by no more than a factor of 2; the major drop in incident ambient-light intensity occurred subsequent to 1630 h. A future laboratory experiment should reproduce the light intensity and spectral quality decrease to that reported for 1630 h and then maintain the spectral-intensity constant at the 1630 h level in order to ascertain whether the remainder of the nocturnal increase will occur.

Figure 6. Normalized relative spectral intensities of downwardly directed ambient light at a depth of 90 cm at the fixed-station site throughout the period of diurnal rise in the stimulable bioluminescence of *P. bahamense*. The units are relative numbers of photons per square centimeter per second per unit wavelength interval. The data are normalized to unity at 5860Å. (a) Relative spectral changes before sunset, from 1612 h to 1730 h; (b) Relative spectral changes after sunset, from 1730 h to 1815 h.


(a)
RELATIVE INTENSITY [ΔN/Δλ]
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1 - 1612 h
2 - 1630 h
3 - 1710 h
4 - 1730 h SUNSET
XI - 27-66
4000
4500
5000
5500
6000
6500
WAVELENGTH [ÅNGSTRÖMS]


(b)
RELATIVE INTENSITY [ΔN/Δλ]
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
4-1730 h SUNSET
5-1746 h
6-1803 h
7-1815 h
XI - 27-66
4000
4500
5000
5500
6000
6500
WAVELENGTH [ÅNGSTRÖMS]

The extreme turbidity in the Bay during sunlight results in a severe relative attenuation with depth of blue light relative to red light; this may produce some selective pressure on the types of photosynthetic organisms that prevail. At all depths in the Bay there are also significant increases with time in the ratios of blue-to-red light intensities prior to sunset (Fig. 6a). After sunset this trend is sharply reversed (Fig. 6b). Spectra similar to those in Fig. 6 have recently been reported by Johnson et al. (1967), who used a terrestrial wedge-filter spectroradiometer and a completely different geometry from ours.

The solar spectral-intensity distribution through the sunrise period, during the decrease in stimulable bioluminescence, remains to be investigated. We plan to extend the observable spectral range up to 8000 Å in order to include the far-red region of the spectrum, and we plan to make spectral measurements in the open ocean as well as in the shallow areas of the Bay where the concentrations of *P. bahamense* are as high as 10 million per liter.

Acknowledgment. We would like to thank Miss Suzanne Starr for her assistance in the data reduction.

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