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Spectral composition of bioluminescence of epipelagic organisms from the Sargasso Sea

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Abstract

The spectral characteristics of single identified epipelagic sources of bioluminescence from the western Sargasso Sea were measured with an optical multichannel analyzer (OMA) system during the April, 1985, Biowatt cruise. The emission spectra of specimens representing 45 species from 8 phyla were measured. Peak bioluminescence emissions typically occurred between 440 and 500 nm, in the blue region of the visible spectrum. Three exceptions involved emission in the green, yellow, and red spectral regions. Intraspecific variability in spectra was noted in several species. One shrimp species exhibited two modes of light emission, each with different emission spectra. Other cases involved dynamic color shifts of 10 to 14 nm; the source of the spectral variability is unknown, but may involve optical filtering or differences in the color of luminescence from multiple sites of light emission. Measurements from independent samples of unsorted plankton revealed different spectral distributions. This suggests that the spectral emissions of bioluminescence in the upper water column will vary, based on species assemblage.

Introduction

The presence of bioluminescent organisms in the oceans is readily detected by bathyphotometers that measure stimulated bioluminescence (e.g. Swift et al. 1983, Lapota and Losee 1984, Ondercin and Fuechsel 1986). Bathyphotometers measure the temporal and quantal characteristics of bioluminescence but, except for a few instances (Kampa and Boden 1956, Losee and Lapota 1981), do not measure the spectral properties of stimulated light. In order to measure emission spectra in detail, it is necessary to collect organisms by conventional methods and make shipboard measurements. Although these measurements have successfully been made on several hundred species of organisms from numerous locations (Herring 1983, Widder et al. 1983, Widder, Latz, Frank and Case unpublished data), very few measurements have been made on organisms from the Sargasso Sea (Swift et al. 1977, Biggley et al. 1981). The present survey of the emission spectra of organisms from this region includes measurements on zooplankton known to be important contributors to epipelagic bioluminescence (Swift et al. 1983), as well as organisms such as gelatinous plankton whose contribution to bioluminescence measurements have not previously been accurately assessed.

Measurements of the spectral properties of bioluminescence were performed with an optical multichannel analyzer (OMA) system (Widder et al. 1983), as part of the Biowatt I study of the optical properties of the upper water column of the western Sargasso Sea (Marra et al. in preparation). The ultimate goal was to assess the effect of biological sources of light on the spectral properties of the ambient light field. The results of this study confirm previous studies that spectral peaks of bioluminescence are generally restricted to the blue region of the visible spectrum, and suggest that the spectral properties of stimulated bioluminescence measured in situ will vary within this range, according to species composition.

Materials and methods

Plankton collections were made in the region 25–35°N, 40°W, in the Sargasso Sea during the April, 1985, Biowatt cruise. Gelatinous plankton and the smaller crustaceans were obtained by night-time net tows of 15 min duration at depths of 0 to 125 m, using 1.0 and 0.5 m diam nets with 333 μm mesh. Larger animals were collected with a Tucker trawl (2 m^2 mouth opening) operated at depths of 50 to

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Table 1. Spectral characteristics of bioluminescence measured during 1985 Biowatt cruise. Spectral emissions characterized by wavelength of maximum emission (max.) full bandwidth at half maximum intensity (FWHM), and signal to noise ratio (S:N). Values represent averaged spectrum for all measurements of a given species with same calibration curve

Identification	max. (nm)	FWHM (nm)	S:N
Unsorted plankton			
Mixed plankton (333 μm)[a]	459	66	50
(25 μm)	474	40	66
(25 μm)	478	56	18
(25 μm)	484, 472[b]	62	24
Protozoa			
Rhaphidozoum acuferum	458±4 (2)[c]	87±3	28±11
Acrosphaera murrayana	443	80	36
Siphonosphaera tenera	450	78	34
Myxosphaera coerulea	453±2 (2)[c]	84±5	37±1
Collosphaera huxleyi	456	79	31
Collosphaera sp.[d]	452	77	35
Collosphaera sp.[d]	445	87	71
Collosphaera sp.[e]	443	75	63
Coelenterata			
Chrysaora hysosceles	478	95	67
Bougainvillia carolinensis	452	74	38
Pelagia noctiluca	469	94	32
Aeginea citrea	459	73	149
Pegantha clara	460±2 (2)[c]	71±2	103±23
Pandea sp. nov.	466	80	94
Hippopodius hippopus	447	80	112
Agalma okeni	444	70	94
Amphicaryon ernesti	487	47	144
Amphicaryon acaula	487	65	78
Diphyes dispar	464	92	25
Rosacea larva	488±1 (2)[c]	55±1	90±10
Ctenophora			
Cestum veneris	490	84	72
Tinerfe lactae	486	85	57
Beroe cucumis	479, 496[b]	94	52
Beroe ovata	478	86	51
Bolinopsis sp.	488	80	28
Mollusca			
Phyllirrhoe sp.	475	89	44
Leachia lemur	500, 473[b]	84	55
	514, 489[b]	68	65
Leachia lemur	458, 485[b]	74	58
Leachia lemur	449, 459[b]	86	40
Pyroteuthis margaritifera	477	54	24
Pyroteuthis margaritifera	475	62	81
	485, 470[b]	42	12
Annelida			
Tomopteris nisseni	565	55	92
Crustacea			
Conchoecia imbricata	474	94	47
Conchoecia secernenda	481	95	24
Scina sp.	444	89	38
Pleuromamma xiphias	492, 472[b]	77	117
Pleuromamma abdominalis	486, 465[b]	77	78
Gaussia princeps	479, 489[b]	73	38
Nematoscelis microps	463	43	77
Nematobrachion flexipes	453	32	32
Euphausia brevis	462	43	64
Euphausia gibboides	467	53	42
Oplophorus spinosus	457[f]	69	133
Systellaspis debilis	460[f]	65	73
	467[g]	48	38
Tunicata			
Pyrosoma atlanticum	493, 471[b]	101	39
Pisces			
Ultrastomias mirabilis	477	73	325
Hygophum hygomi	448	76	58
Stomias brevibarbatus	689	–[h]	105

[a] Mesh size of plankton net used for collection
[b] Bimodal spectrum; values correspond to main and second peaks, respectively
[c] Mean ± standard deviation of mean, with number of measurements in parentheses, for emission spectra with different calibration curves
[d] Toroid colony morphology
[e] Spherical colony morphology
[f] Luminescent secretion
[g] Photophore emission
[h] Spectrum extended beyond OMA range

300 m. On several occasions, a 2 m diam net with 333 μm mesh was used concurrently with the trawl. Organisms were immediately sorted, and maintained in darkness at 25 °C until use within 6 h after collection. Specimens were individually preserved in 4% formalin for later identification.

Bioluminescence spectra were measured with an EG&G Princeton Applied Research Model 1215 optical multichannel analyzer (OMA) utilizing a linear array detector consisting of 700 intensified silicon photodiodes. Characterized by high sensitivity and resolution, and capable of essentially instantaneous light collection across a 350 nm spectral window, this system is able to accurately register spectra from transient as well as weak sources. Details of OMA operation and calibration have previously been described (Widder et al. 1983). All spectra from a given species with the same calibration curve were combined into a single averaged spectrum.

Specimens were either placed in filtered seawater in quartz glassware and mechanically stimulated, or were supported between a pair of tungsten electrodes and stimulated with trains of 10 V, 5 ms electrical pulses delivered at 20 Hz by a Grass stimulator. Bioluminescence was focused onto a 1 or 2 mm entrance slit of the polychromator by quartz collection-optics (Widder et al. 1983). In some cases, bioluminescence was induced or enhanced by the addition of 10^{-4} *M* 5-hydroxytryptamine (serotonin) or 4% hydrogen peroxide.

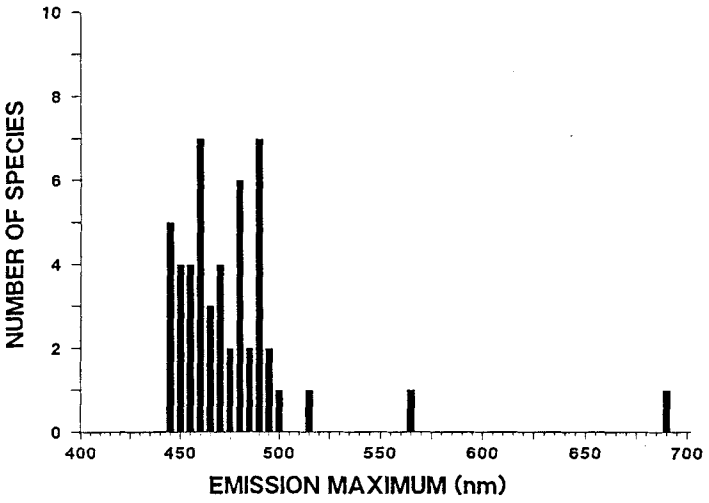

Fig. 1. Spectral distribution of bioluminescence for all species measured; peak wavelength of emission for each species is displayed in 5 nm increments. With a few exceptions, peak bioluminescence emission is in blue region of visible spectrum

Results

The emission spectra of a total of 45 species representing protists, zooplankton, and fishes were measured (Table 1). With few exceptions, emission maxima ranged between 440 and 500 nm, in the blue region of the spectrum (Fig. 1). Selected spectra are displayed in Fig. 2B.

Measurements of emission spectra from independent samples of unsorted plankton collections gave different results (Table 1, Fig. 2A). Peak emissions ranged from 459 to 484 nm, most likely due to different species compositions of the samples. For example, the plankton sample with an emission maximum at 474 nm and FWHM of 40 nm had spectral characteristics similar to those that are unique to dinoflagellates (Herring 1983, Widder et al. 1983). All subsequent measurements were performed on individual identified organisms.

Bioluminescence from the coelenterates was observed to be among the brightest luminescence of all pelagic organisms and was readily elicited by mechanical stimulation (S:N ratios in Table 1). Of the coelenterates examined, the hydrozoans, including the siphonophores, emitted at the shortest wavelengths, with emission maxima between 444 and 466 nm (Table 1, Fig. 2C). The siphonophore *Amphicaryon* species had peak emissions at longer wavelengths (maximum at 487 nm; Fig. 2C). Scyphozoan medusae had peak emissions at wavelengths between 450 and 480 nm. The longest wavelength emissions for gelatinous plankton were from the ctenophores, with emission maxima between 480 and 490 nm (Table 1, Fig. 2B). Three specimens of an undescribed species of the anthomedusan genus *Pandea* were collected (Alvariño in press). Light emission for this new species originated from 4 to 5 sources around the margin of the bell. For all coelenterates examined, light emission was intracellular, except for the scyphomedusa *Chrysaora hysosceles* which produced a luminescent slime.

Other short wavelength emitters, besides the siphonophores, were colonial radiolarians, common members of the near-surface gelatinous plankton (Swanberg 1983, Latz et al. 1987). Their broad spectral distributions had emission maxima ranging from 440 to 460 nm (Table 1; Fig. 2B). Euphausiid spectra were of narrow bandwidth (Table 1), as is characteristic of these organisms (Herring 1983, Widder et al. 1983). For the four species measured, the mean emission maximum was 461 nm, with shoulders at approximately 485 and 505 nm.

Secreted bioluminescence by copepods and ostracods was characterized by emission maxima ranging from 470 to 490 nm (Table 1, Fig. 2D). Even though ostracods comprise approximately 7% of the zooplankton of the Sargasso Sea (Deevey 1971), these are the first reported measurements of emission spectra for any oceanic species. Not all crustaceans which produced a luminescent secretion had emissions which peaked in this range, since the shrimp

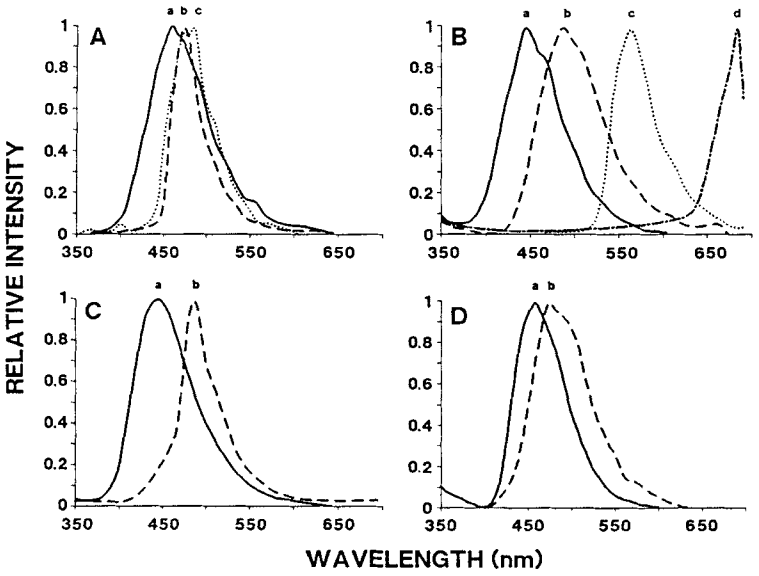

Fig. 2. Emission spectra of selected marine organisms; relative intensity of emission is shown as function of wavelength; two values indicate bimodal spectrum, representing main and secondary peaks, respectively. (**A**) Independent samples of unsorted plankton; a: maximum emission (max.) = 459 nm, full bandwidth at half max. intensity, FWHM = 78 nm, S:N = 36; b: max. = 474 nm, FWHM = 40 nm, S:N = 66; c: max. = 484, 472 nm, FWHM = 62 nm, S:N = 24. (**B**) Range of emissions encountered; a: colonial radiolarian *Collosphaera* sp., max. = 443 nm, FWHM = 75 nm, S:N = 63; b: ctenophore *Tinerfe lactea*, max. = 486 nm, FWHM = 85 nm, S:N = 57; c: polychaete *Tomopteris nisseni*, max. = 565 nm, FWHM = 55 nm, S:N = 92; d: fish *Stomias brevibarbatus*, max. = 689 nm, S:N = 105. (**C**) Siphonophores; a: *Agalma okeni*, max. = 444 nm, FWHM = 70 nm, S:N = 94; b: *Amphicaryon ernesti*, max. = 487 nm, FWHM = 47 nm, S:N = 144. (**D**) Crustaceans; a: spew of shrimp *Oplophorus spinosus*, max. = 457 nm, FWHM = 69 nm, S:N = 133; b: ostracod *Conchoecia imbricata*, max. = 474 nm, FWHM = 94 nm, S:N = 47

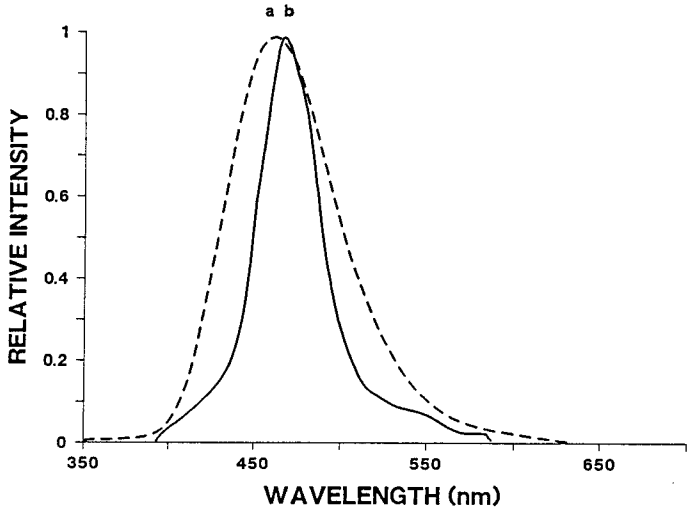

Fig. 3. *Systellaspis debilis.* Two modes of bioluminescence emission. a: broad emission from luminous secretion, max. = 460 nm, FWHM = 76 nm, S:N = 173; b: emission from photophores, max. = 467 nm, FWHM = 48 nm, S:N = 38

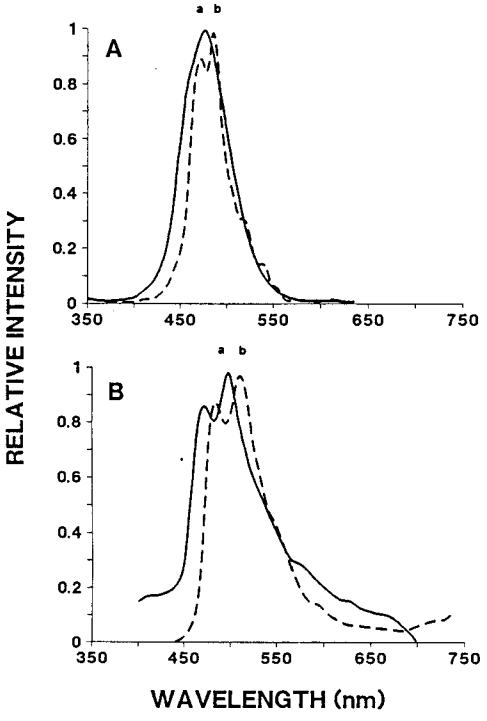

Fig. 4. Shifts in spectral distributions. (**A**) Squid *Pyroteuthis margaritifera;* a: initial two measurements, max. = 475 nm, FWHM = 62 nm, S:N = 81; b: subsequent measurement, max. = 485, 470 nm, FWHM = 42 nm, S:N = 12. (**B**) Squid *Leachia lemur;* a: initial measurement, max. = 500, 473 nm, FWHM = 84 nm, S:N = 55; b: subsequent measurement, max. = 514, 487 nm, FWHM = 68 nm, S:N = 65

Oplophorus spinosus had an emission maximum at only 457 nm (Table 1, Fig. 2D).

Luminescence by the caridean shrimp *Systellaspis debilis* originated from numerous cuticular photophores as well as a luminescent secretion. The secretion occurred during tactile stimulation and was characterized by a fairly broad featureless spectrum with an emission maximum at 460 nm. Emission from the photophores, stimulated by serotonin, was shifted to slightly longer wavelengths and had a narrower bandwidth (Table 1, Fig. 3).

The transparent pelagic polychaete *Tomopteris nisseni* produced yellow light of intracellular origin within the parapodia (Dales 1971), with maximum emission at 565 nm and a half bandwidth of 55 nm (Table 1, Fig. 2B). Both mechanical and electrical stimulation induced luminescence in the one specimen examined.

The bioluminescence from the three fish species measured resulted from different modes of production. Bioluminescence from the myctophid *Hygophum hygomi* originated from epidermal photophores (Herring and Morin 1978), the stomiatoid *Ultrastomias mirabilis* produced a ventral glow from the mucous sheath enveloping its skin (O'Day 1973), and *Stomias brevibarbatus* light-emission originated from suborbital organs (Herring and Morin 1978). *S. brevibarbatus* bioluminescence peaked in the red region of the visible spectrum at 689 nm and extended into the far-red beyond the spectral range of the OMA polychromator at the time of measurement (Table 1, Fig. 2B).

Bioluminescence from two genera of squids was highly variable in spectral distribution. *Pyroteuthis margaritifera* generally produced featureless unimodal spectra with an emission maximum of approximately 476 nm (Table 1). However, one specimen, which initially produced a unimodal spectrum, within 4 min shifted to a bimodal spectrum of reduced intensity with a peak at 485 nm and a subpeak at 470 nm (Fig. 4A). Light originated from two pairs of light organs on the ventral surface of the mantle, numerous subocular organs, and several tentacular light organs (Herring 1977). Bioluminescence spectra from the subocular light organs of two specimens of *Leachia lemur* typically had a bimodal distribution with a 27 nm separation between peaks, even though the emission maxima were different in each measurement (Table 1). A second spectrum obtained from one specimen 5 min after the first, was shifted 14 nm towards the longer wavelengths, although the 27 nm separation was conserved (Fig. 4B).

Discussion and conclusions

The blue bioluminescence of plankton of the upper 100 m of the water column is in the same spectral range as the wavelength of maximum transmission of downwelling illumination in the Sargasso Sea (approximately 480 nm; Marra et al. in preparation). This assures that the energy of light emission will be conserved, since it will be minimally attenuated by seawater, compared to emissions at other wavelengths.

Spectral characteristics related to function

Species-specific emissions are most probably ultimately determined by their adaptive roles as well as biochemical

constraints (discussed by Herring 1983). Narrow bandwidth emissions from the photophores of euphausiids and the shrimp *Systellaspis debilis* are believed to function, in part, to counterilluminate the body with downward-directed bioluminescence to minimize being silhouetted against downwelling illumination (Clarke 1963, Herring 1976, Herring and Locket 1978, Young, 1983). Measurements of their photophore spectral emissions (Swift et al. 1977, Herring 1983, Widder et al. 1983, and present study) indicate that the bioluminescence is well adapted for a camouflage function, since it exhibits emission maxima and narrow bandwidths similar to that of oceanic illumination (Jerlov 1968, Marra et al. in preparation).

The broader spectral distributions characteristic of emissions of gelatinous plankton, ostracods, copepods, and shrimps may serve a defensive role. These luminescent displays, which appear subjectively brighter than the photophore emissions discussed above, may be related as well to the visual sensitivity of potential predators (e.g. Anctil 1974, Nicol 1978). Sudden luminous secretions in crustaceans are often associated with locomotory activity and may serve a diversionary role during an escape response (Dennell 1955, David and Conover 1961, Tsuji et al. 1970, Herring 1976).

The shrimp *Systellaspis debilis* exhibits both modes of luminescence. Light emission from the epidermal photophores had a narrower spectral bandwidth and an emission maximum at a slightly longer wavelength than the secreted luminescence. Herring (1983) has measured a similar relationship for the emissions of the shrimp *Oplophorus spinosus*. The two modes of light emission suggest a diversity of luminescent behaviors for these species; the photophores may function in counterillumination while the secretion may serve as a direct defense against predators.

A few organisms exhibited spectra with longer wavelength emission maxima. Bioluminescence of the squid *Leachia lemur* extended into the green while the emission maximum for the polychaete *Tomopteris nisseni* was in the yellow-green (565 nm). Such bioluminescence may have an intraspecific function, although nothing is known of tomopterid luminescent behavior. The luminescent displays of tomopterids may function during sexual swarming, as in the syllid polychaetes (Harvey 1952, Markert et al. 1961). Wilkens and Wolken (1981) have shown that the spectral sensitivity of the eye of the luminescent syllid *Odontosyllis enoplana* is well matched to its green bioluminescence.

The longest wavelength emission was red luminescence from the suborbital light organs of the stomiatoid fish *Stomias brevibarbatus*. Red-bioluminescence emission-spectra have also been obtained from two other stomiatoid species (Widder et al. 1984). Since red light can be detected by these fishes (O'Day and Fernandez 1974) but not by most marine organisms (e.g. Denton and Warren 1957, reviewed by Young 1981), the red emission of the suborbital organ would serve as a secure channel for intraspecific communication or for detecting prey (see Widder et al. 1984).

Color shifts

Spectral shifts in bioluminescence emission have been documented in several species of marine organisms (Young and Mencher 1980, Herring 1983, Widder et al. 1986). In the present study, two species exhibited the ability actively to alter the color of emission. The squid *Leachia lemur* was capable of emitting at least six colors of bioluminescence, from deep blue to green, as demonstrated by emission peaks at approximately 450, 460, 473, 485, 500, and 514 nm. A shift in peak emission of 15 nm toward longer wavelengths monitored in one specimen suggests active control. The squid *Pyroteuthis margaritifera* also showed a color change, shifting not only the peak emission from 475 to 485 nm but also changing to a bimodal distribution. Changes in spectral emissions could result from the recruitment of different photophores (Young and Mencher 1980) and utilization of interference filters and reflectors associated with the photophore (Young and Mencher 1980; Young and Arnold 1982, Young 1983). Young and Mencher observed that squid bioluminescence utilized for counterillumination had a unimodal emission spectrum during the day and changed to a bimodal spectrum at night to better match the ambient illumination. In the present study, all measurements were made at night.

Spectral properties of ambient bioluminescence field

The spectral properties of the bioluminescence light field at depth should not be constant, but should vary according to species composition and abundance, and to a minor extent, mode of emission. In situ spectral distributions of bioluminescence are known from only a few measurements (Kampa and Boden 1956, Losee and Lapota 1981), that indicate maximum emission generally at 480 nm with a FWHM of approximately 75 nm. The limited resolution of these measurements, performed with 8–16 interference filters, does not allow fine-scale analysis of the in situ spectral distributions for the purpose of identifying subpeaks. In the present study, utilizing high-resolution spectroscopy, the 25 nm range of emission maxima from samples of unsorted plankton suggests spectral variability at depth. The source of this variability is most likely variations in organism assemblage. In special situations where a single species dominates the assemblage, such as during phytoplankton blooms or zooplankton swarming, it may be possible to infer the spectral properties of in situ bioluminescence, even when not directly measured.

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