Correlations of planktonic bioluminescence with other oceanographic parameters from a Norwegian fjord

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ABSTRACT: In August 1985 and 1986, a series of bathyphotometric measurements were made in ice-free waters of Vestfjord, Norway, to quantify stimulative in situ bioluminescence. In 1986, we tested and identified the causative bioluminescent plankton. In all profiles, peak or maximum bioluminescence intensity was always within a zone of 15 to 30 m below sea surface, with marked decreases below 50 m. Maximum bioluminescence intensity from all profiles for both years ranged from 3×10^8 to 2×10^9 photons $s^{-1} cc^{-1}$ of turbulently-flowing seawater. Testing some of the plankton on board ship revealed that the brightest flashes were produced by the copepods *Metridia longa* and *M. lucens* and the ostracod *Conchoecia* sp. Dinoflagellates of the genus *Protoperidinium* emitted light at an intermediate level. The total number of dinoflagellates ranged from 1300 to 3700 cells l^{-1} at water depths of 10 to 30 m, and sharply decreased at 80 to 100 m (2 to 11 cells l^{-1}). It was estimated that dinoflagellates accounted for 96 % of the measured light from the surface to a depth of 100 m. Several species of the luminous dinoflagellate *Ceratium* were found. However, their contribution to the overall light budget never exceeded 25 %. *P. curtipes* contributed at least 50 % of the measured light field at 30 m and above. In general, luminous zooplankton (larval copepods and euphausiids) contributed less than 4 % of the light produced above 100 m. The number of bioluminescent dinoflagellates correlated with bioluminescent intensity at the 0.05 significance level. Correlation analysis of beam attenuation coefficient with bioluminescent intensity yielded high r values resulting in an overall level of significance of less than 0.01, and, therefore, may be a useful indicator for bioluminescence.

INTRODUCTION

An essential element needed to predict the distribution of planktonic bioluminescence in any ocean area is knowing which species are producing the light. However, this, and other, basic information is often lacking. For example, while intensity and distribution of luminescence have been investigated and measured since the 1960's in a variety of oceans, very little has been done at latitudes above the arctic circle in ice-covered and ice-free waters.

In 1985 and 1986, in the ice-free waters of the Vestfjord, Norway, we had the opportunity to measure in situ bioluminescence with submersible bathyphotome-

ters. We were also able to test and identify the plankton responsible for the measured bioluminescence in 1986.

A time series of bathyphotometer profiles (bioluminescence, optical transmission, seawater temperature) was conducted in August 1985 while additional stations were studied in late August 1986. The later studies focused on bioluminescence, optical transmission, seawater temperature, chlorophyll *a* fluorescence, and plankton abundance relationships. These investigations provided us not only with the opportunity to document the variability of the bioluminescence intensity and other parameters in a fjord but also allowed us to determine which plankton were responsible for the bioluminescence.

STUDY AREA

The study area was at the mouth of the Vestfjord on the coast of western Norway above the Arctic Circle between 13° and 15° east longitude (Fig. 1). The Vestfjord is a deep, high-latitude estuary; water depths range from 620 m at the head to 144 m at the sill. The fjord is more than 150 km long and is 70 km wide at the mouth. The characteristics of the Vestfjord hydrography reflect the diversity of contributing water masses. Water from a branch of the Norwegian Coastal Current impinges on outflow from the fjord. In general, coastal waters flow into the fjord along the southeast side, turn westward, and flow seaward with the colder, outflowing fjord water. Winds exert a dominant influence on circulation patterns. Southwest winds set up Ekman transport away from the coast with associated upwelling along the western side of the fjord. Northeasterly winds along the same coast cause net transport out of the fjord (Furnes & Sundby 1981).

Three water masses within the fjord have been described (Furnes & Sundby 1981). The cold, homogeneous surface layer may be as deep as 150 m with a salinity of 33 to 34 parts per thousand (ppt). Below this mixed layer lies a 10 to 50 m thermocline where temperature increases from 4 to 6.5°C. The deep-water layer is of Atlantic origin and has a temperature of 6.5 to 7°C and a salinity of 34.7 to 35 ppt. Warming of surface waters in the summer causes a seasonal thermocline and a shallow mixed layer with temperatures ranging from 10 to 15°C.

In August 1986, 4 stations were investigated, 2 in the mouth of the Vestfjord (2 and 3) and 2 along the eastern

margin of the fjord north of Landegodefjord (1 and 4). Station work was also conducted near the latter stations in August 1985 and is included for comparison.

MATERIALS AND METHODS

In 1986, bioluminescence, optical transmission, sea-surface water temperature, and chlorophyll *a* fluorescence were measured with a submersible bathyphotometer (Lapota & Losee 1984). In 1985, a similar bathyphotometer was used to measure the same parameters exclusive of chlorophyll fluorescence (Losee et al. 1984). The submersible bathyphotometer system pumped plankton-laden seawater past an RCA 8575 photomultiplier tube (PMT) operating in the single photon-count mode which measured light through a filter wheel with a capacity for carrying 10 optical filters. Neutral density filters of varying attenuation (factors of 10 and 1000) complemented the filter set. All components were contained in an aluminum pressure housing. A 1/3 hp Gould submersible pump (Model 10 EJ) with a flow rate of 0.8 l s⁻¹ was mounted on the exterior of the detector to pull seawater through a viewing chamber fitted with an ultraviolet transmitting window. A light-tight 10 cm i.d. s-shaped plastic black pipe was used to convey seawater into the detector which abruptly narrowed down into an arm of the viewing chamber. The sudden reduction in pipe size introduced turbulence and maintained a constant stimulus for the plankton being viewed.

Signal pulses from the PMT of the stimulated bioluminescence were recorded in several modes. Con-

Fig. 1. Boxed area designates study area and station location in the Vestfjord, Norway.

tinuous 30 s sample blocks were obtained with an Ortec scaler (Model 874) and recorded as an accumulated count on an Otrona microcomputer. High time resolution data of the bioluminescence signal were obtained by bringing the PMT signal pulses into time channels of 10 ms on a Davidson multichannel analyzer (Model 1056). The data were recorded in 1023 channel blocks on the microcomputer.

Optical light transmission (T) was measured using a Sea Tech 0.25 m beam transmissometer with an LED that emitted at 680 nm mounted vertically on the bathyphotometer. Transmission (T) was converted to beam attenuation coefficient ($c = -\ln T/0.25 \text{ m}$). Beam attenuation measures the attenuation of a highly collimated beam of light and is used as a measurement of both absorption and scattering from all particulate matter in the water (dinoflagellates, diatoms, marine snow, other debris). Temperature was measured using a Sea Bird temperature sensor (Model SBE-3) mounted directly on the bathyphotometer. A 2.5 cm i.d. hose from the bathyphotometer's pumping system delivered seawater to the laboratory of the ship for the measurement of *in vivo* chlorophyll *a* fluorescence and the collection of plankton samples. A Turner Designs (Model 10-005R) fluorometer measured fluorescence and the data were reported in relative units. The detector package was deployed down to depths of ca 100 m.

Plankton samples from the bathyphotometer were collected by diverting effluent from the hose to the shipboard plankton collection tank. Plankton samples (each representing 45 l of seawater) were collected in 20 μm collection cups from the bathyphotometer effluent at each station during the ascent from 100, 50, 40, 30, 20, and 10 m depths. A vertical plankton net tow (1/2 m ring, 2 m length, 500 μm net and collection cup) accompanied bathyphotometric measurements from each of the 4 stations from 100 to 0 m (1986 measurements). Plankton samples were washed into sample jars with filtered seawater and preserved in 5% buffered formalin seawater solution. Single phyto- and zooplankters were isolated from plankton tows and individually tested for bioluminescence in the laboratory plankton test chamber (LPTC). To facilitate this testing, isolated organisms were placed into quartz sample holders with 6 ml filtered (0.45 μm) seawater. The lucite base of the sample holders was pre-drilled to accommodate water removal by an applied vacuum. Whatman GF/C filters lined the bottoms of the holders to retain the test organism following water removal. To observe the luminescence, an RCA 8575 photomultiplier tube was mounted onto the test chamber port. The output of the PMT (high time resolution) was displayed as a time sequence of counts (40 ms time channels) from the induced flash. The 'instantaneous' intensity of

the signal is proportional to the number of counts in each channel (Lapota & Losee 1984). Recovery of luminous plankters was accomplished by repeated washings of the sample vial with filtered seawater into a glass dish for later identification.

The luminescent 'isolate' data identified which dinoflagellate and crustacean zooplankter species contributed to the measured bioluminescence. All pumped bathyphotometer plankton samples and vertical net tows were analyzed for species composition and numerical abundance. Each sample was completely examined for zooplankton while the dinoflagellate component was enumerated by settling subsamples of seawater and examining with an inverted microscope at 100 $\times$ magnification. A light budget for the luminous plankton collected from the bathyphotometer and from plankton net tows was calculated based on average light output values recorded from individual bioluminescent plankters. This method of analysis has been described for bioluminescent plankton collected from the Arabian Sea (Lapota et al. 1988b).

RESULTS AND DISCUSSION

Bioluminescence intensity and structure in 1986

Two vertical bioluminescence profiles were recorded at each of the 4 stations from 28 to 31 August, 1986. All profile measurements were conducted during the night from 1944 to 2319(Z) h. For a given profile, the lowering rate was held as constant as possible, but among all profiles the lowering rates ranged from 6 m min^{-1} to 10.7 m min^{-1} which corresponds to a vertical spatial sampling resolution of 3.0 to 5.4 m. Bioluminescent structure and intensity were similar at all stations. Peak or maximum bioluminescence intensity was always within a zone of 15 to 30 m depth (Fig. 2). Maximum bioluminescence intensity from all profiles ranged from 3×10^8 to 2×10^9 photons $\text{s}^{-1} \text{cc}^{-1}$, comparable to the high intensities measured in the Arabian Sea (Lapota et al. 1988b). The Arabian Sea is considered to have some of the brightest known bioluminescent displays. Peak bioluminescence intensity at all 4 stations varied by less than a factor of 3. The bioluminescence intensity observed near a depth of 90 to 100 m for all profiles ranged from 3×10^6 to 4×10^7 photons $\text{s}^{-1} \text{cc}^{-1}$ of seawater.

In all profiles, the beam attenuation coefficient increased within the peak bioluminescence layer and decreased below that. In many of the profiles, the thermocline appeared to be associated with all or part of the maximum bioluminescence layer. Chlorophyll *a* fluorescence values were greatest near the bottom of the maximum bioluminescence layer and in some cases appeared to correlate with structure within the lumi-

Fig. 2. Vertical bathyphotometer profiles of bioluminescence intensity, sea water temperature, beam attenuation coefficient, and chlorophyll *a* fluorescence (relative) measured in the Vestfjord in 1986. (a) Station 1, (b) Station 2, (c) Station 3, (d) Station 4

nescent layer. The increase in beam attenuation within portions of the luminescent layer may have been reflective of the increased numbers of dinoflagellates and diatoms.

Bioluminescence intensity and structure in August 1985

Two profiles obtained on 18 August 1985, at depths to 75 m, resembled the 1986 profiles. Maximum

bioluminescence was centered from 17 to 21 m below the sea surface and had an intensity of 1×10^9 photons $s^{-1} cc^{-1}$ (Fig. 3a). Fourteen other vertical profiles (to depths of 50 m) were obtained during 18 to 20 August 1985, from 22:30 to 05:00 h. Of these profiles, only one will be presented to highlight differences (Fig. 3b). The pattern of bioluminescence distribution for these latter profiles was different from those exhibited at the first 2 stations in 1985 and all stations measured in 1986. The peak layer structure was distributed over a greater depth and was not sharply defined as in 1986 profiles.

Fig. 3. Vertical bathyphotometer profiles of bioluminescence intensity, seawater temperature, and beam attenuation coefficient in the Vestfjord in 1985. (a) Measured near Station 1, (b) Station 4

Peak intensity and peak layers were still found within the ranges measured in 1986 (15 to 30 m below the sea surface). The temperature structure in all 1985 profiles was different from that observed the following year. The 1985 profiles indicated a more homogeneous temperature distribution throughout and a slight warming trend in the deep, well-mixed surface layer in contrast to the seasonal thermocline and shallow mixed layer measured at the 1986 stations.

The similarities and differences in bioluminescence and temperature structure between the 1985 and 1986 data raised the question of the driving mechanism which controlled these relationships. Studies show that vertical structure can vary with wind conditions on relatively short time scales as the thermocline rises and falls with upwelling and downwelling (Furnes & Sundby 1981). In a study of the Masfjord, western Norway, during June and October 1985, advective water flow influenced by wind-forcing strongly affected the vertical biomass structure of phytoplankton and zooplankton (Aksnes et al. 1989). The 1985 Vestfjord profiles were taken during a time of strong winds. If wind serves as a major physical force in determining dinoflagellate distributions in the Vestfjord, then for future studies a bathyphotometer time series taken before, during, and after such events could address the effect that turbulence has on cell layering and the time needed to form these layers. Luminous copepod dis-

tribution, too, may have been layered. In order to define their vertical structure, a series of opening-closing net measurements could be undertaken to more closely approximate their true spatial distribution in the water column and impact on the local light budget.

Observations of plankton in August 1986

The plankton samples from the bathyphotometer effluent were enumerated and sorted. The total number of dinoflagellates among all 4 stations ranged from ca 100 to 3700 cells l^{-1} of seawater at 10 to 30 m and sharply decreased to a range of 2 to 12 cells l^{-1} at 80 to 100 m (Fig. 4). At 20 m, total dinoflagellates (including luminous and non-luminous species) averaged 1600 cells l^{-1} . Below the thermocline, dinoflagellate numbers decreased abruptly.

Although very abundant, dinoflagellates of the genus *Ceratium* are among the dimmest planktonic light producers. However, luminescence was not observed in cells of *C. fusus* and *C. furca* in this study. Bioluminescence has been observed in these species from other studies (Nordli 1957, Sweeney 1963, Gold 1965, Kelly & Katona 1966, Tett 1969, Lapota & Losee 1984). Dinoflagellates of the genus *Protoperdinium* are reported to emit light at an intermediate intensity (Hardy & Kay 1964, Kelly & Katona 1966, Tett 1969,

Fig. 4. Total number of dinoflagellates at the water depths indicated, 1986

1971, Lapota & Losee 1984, Lapota et al. 1988b) (Fig. 5a). The observation of luminescence in *P. curtipes* Jorgensen (1913) in this study is new (Table 1, Fig. 5b), although luminescence has been observed in the closely related species *P. crassipes* Kofoid (Filimonov et al. 1982, M. Kelly pers. comm.).

Non-luminous diatoms were represented by species of *Coscinodiscus*, *Corethron*, and *Rhizosolenia*. Peak distributions of diatoms at 3 of the stations were found in the upper 20 m and ranged from 59 to 1973 cells l^{-1} (Fig. 6). The depth at which the peak number of diatom cells occurred corresponded to peak dinoflagellate cell distributions. Stations 1 and 4 were dominated by *Coscinodiscus* sp. while Station 2 was dominated by *Corethron* sp. Below 30 m, the number of diatoms decreased to a few cells l^{-1} .

Zooplankton assemblages in the bathyphotometer samples were variable in occurrence. Calanoid nauplii were abundant in all samples. The luminescent copepod nauplii *Metridia longa* (Lapota et al. 1988a) were rare, usually less than $1 l^{-1}$, and *M. longa* and *M. lucens* were infrequent (Table 2). This is consistent with the fact that these copepods were never found in numbers exceeding $3 m^{-3}$ seawater from the vertical net hauls at all stations. Analysis of some of the collected plankters revealed that some of the brightest flashes were produced by *M. longa* and *M. lucens*, the ostracod *Conchoecia elegans*, and the euphausiid *Thysanoessa* sp. (Fig. 7). All of these brightly luminescent crustaceans were collected in the net tows but sampled less frequently by the detector (Table 2). The non-luminous copepod *Calanus finmarchicus* was found in all net tows, but was appreciably less abundant at Station 1. The greatest numbers of luminescent crustaceans were found at Station 2.

Fig. 5. High time resolution scans of flashes emitted from *Protoperidinium depressum* and *P. curtipes* collected in net tows from the Vestfjord in 1986; y axis = flash intensity (photons per 10 ms or 40 ms channels). (a) The armored dinoflagellate *P. depressum* emitted ca 3.5×10^8 photons in this flash, Aug 31, 1986; (b) the armored dinoflagellate *P. curtipes*, a dominant dinoflagellate found at all stations, emitted ca 4.6×10^9 photons in this flash, Aug 31, 1986

High time resolution scans of the luminescent plankton viewed by the bathyphotometer indicate significant differences in intensity and frequency of events at various depths at all 4 stations (Fig. 8). Generally, the number of bioluminescent events decreased with depth

Table 1. Luminescence of plankton in the Vestfjord (Norway) in August 1986. Light output values were generated from single flashes in the LPTC and do not necessarily represent the maximum output from a single individual

Species	Photons per flash	
	Mean	Range
<i>Metridia longa</i> (Lubbock)*	2×10^{11}	7×10^{10} – 4×10^{11}
<i>Metridia lucens</i> Boeck*	4×10^{10}	3×10^{10} – 1×10^{11}
<i>Conchoecia elegans</i> *	1×10^{10}	5×10^8 – 5×10^{10}
<i>Thysanoessa furcilia</i> Kroyer* ^a	5×10^9	2×10^8 – 1×10^{10}
<i>Protoperidinium curtipes</i> Jorgensen*	3×10^9	4×10^8 – 8×10^9
<i>Metridia longa</i> nauplii* ^b	2×10^9	1×10^7 – 1×10^{10}
<i>Protoperidinium depressum</i> Bailey* ^a	2×10^9	2×10^8 – 6×10^9
<i>Ceratium fusus</i> (Ehrenberg) ^{+,a,c}	2×10^8	–
<i>Ceratium horridum</i> (Cleve) Gran ^{+,a}	7×10^7	4×10^7 – 1×10^8
<i>Ceratium furca</i> (Ehrenberg) ^{+,a,c}	2×10^7	–

* Observed luminescent in this study
 * Not tested in this study, but observed luminescent in other studies
 + Tested, not observed luminescent in this study, but observed luminescent in other studies
^a Data from individuals collected in the Norwegian Sea, April 1983 (Lapota unpubl.)
^b Lapota et al. 1988a
^c Light output value from a single cell

Fig. 6. Mean number and range of total number of diatoms at the depths indicated; Stations 1, 2 and 4, 1986

and is reflective of the diminishing numbers of luminescent dinoflagellates below the thermocline.

Light budget analysis

The plankton samples collected at all 4 stations were analyzed for dinoflagellates and zooplankters (to species level when possible). From this a 'Light Budget' estimate was constructed. The probable planktonic contributors responsible for the measured bioluminescence (bathypotometer) intensity at depth were enumerated.

The light budget for all depths at all stations is presented as 'dinoflagellate upper limit', 'dinoflagellate lower limit', 'zooplankton upper limit', or 'zooplankton lower limit' for each station by the significant contributing species. The upper limit is defined as the total of species observed luminescent in this study or in past studies. The lower limit is restricted to species observed luminescent in this study. The peak luminescent dinoflagellate layer was always between 10 to 30 m, and ranged from 796 to 486 cells (upper limit) l^{-1} for all 4 stations (Fig. 9) to a lower limit range of 76 to 213 cells l^{-1} . The mean upper and lower limit of bioluminescent dinoflagellates at 20 m was 613 and 102 cells l^{-1} , respectively.

Bioluminescence intensities at all stations at all depths were dominated by dinoflagellate sources (Fig. 10, upper) with one exception (Station 4, 100 m). Dinoflagellates were estimated to account for 96 % of the measured light from surface water to 100 m. At Station 4, however, the presence of *Metridia longa* copepods and nauplii and the paucity of luminous dinoflagellates at 100 m shifts the major contributor in the light budget to the zooplankton at that depth (Fig. 10, lower).

Dinoflagellates of the genus *Protoperidinium* contributed significantly to the bioluminescence field at all 4 stations. At depths to 30 m, *P. curtipes* contributed at least 60 % of the measured bioluminescence. At 3 of these stations, the percent contribution ran as high as 70 to 80 % at the lower limit. As the contribution from *P. curtipes* decreased with increasing depth, other species of *Protoperidinium* increased in importance, including *P. depressum*.

The inclusion of several species of the dinoflagellate

Table 2. Plankton composition (number of individuals) of vertical net tows (500 μ m mesh net and collection cup) 100 to 0 m collected at Stations 1 to 4 in 1986

Zooplankton	Station	Total	Per cubic meter	Zooplankton	Station	Total	Per cubic meter
<i>Calanus finmarchicus</i>	1	675	22	<i>Oithona helgolandica</i>	1	11	< 1
	2	4871	154		2	11	< 1
	3	3416	83		3	7	< 1
	4	3238	67		4	5	< 1
<i>Metridia longa</i> *	1	1	< 1	<i>Thysanoessa</i> sp.*	2	4	< 1
	2	105	3		4	11	< 1
	3	43	1	<i>Nyctiphanes</i> sp.*	2	3	< 1
	4	69	1		4	5	< 1
<i>Sagitta</i> sp.	3	5	< 1	<i>Hyperia</i>	2	4	< 1
	4	36	1		3	3	< 1
<i>Metridia lucens</i> *	1	3	< 1	<i>Evadne</i>	1	4	< 1
	2	31	1	Ophiopluteus	1	3	< 1
	3	3	< 1	Zoea	1	1	< 1
	4	19	< 1	Pteropod	2	1	< 1
<i>Centropages elegans</i>	3	17	< 1	Larvacean	1	1	< 1
	4	4	< 1	<i>Microsetella</i> sp.	4	1	< 1
<i>Conchoecia elegans</i> *	4	13	< 1				

* Observed luminescent in this study

Fig. 7. High time resolution scans of flashes emitted from single zooplankters collected in net tows from the Vestfjord in 1986; y axis = flash intensity (photons per 40 ms channel). (a) Copepod *Metridia longa* emitted ca 2.1×10^{11} photons, Aug 31, 1986; (b) ostracod *Conchoecia elegans* emitted ca 4.5×10^{10} photons in this flash, Aug 31, 1986; (c) furcilia of euphausiid *Thysanoessa inermis* emitted ca 8.5×10^8 photons in the 2 larger peaks, Aug 31, 1986

Fig. 8. High time resolution scans of bioluminescent events at Station 4 at depth recorded with the bathyphotometer (A–D). All scans were of a 10 s duration; y axis = bioluminescence intensity (photons per 10 ms channel). (a) Bioluminescence events at 10 m; (b) bioluminescence events reached a peak in frequency and intensity at 20 m; (c) bioluminescence decreased at 30 m; at 40 m (d), the frequency of events was markedly less

genus *Ceratium* into the light budget (upper limit) did not significantly affect the percentage of light contributed by *Protoperidinium* spp. dinoflagellates. Assuming that the *Ceratium* were luminescent (hundreds of cells l^{-1} at the shallower depths), their contribution to the overall light budget never exceeded 25 %, while *P. curtipes* still contributed at least 50 % of the measured light field at 30 m and above.

The few luminous copepods (*Metridia longa* and *M. lucens*) found from the net tows (100 to 0 m) did not alter the light budget with respect to the plankton collected from the effluent of the bathyphotometer.

Fig. 9. Mean number of total and bioluminescent dinoflagellates at the depths indicated for Stations 1 to 4, 1986

Fig. 10. Light budget breakdown (upper limit) for Stations 2 and 4. Breakdown presented as percent contribution of estimated light output (ELO) per liter of seawater by dinoflagellates of the genera *Protoperidinium* and *Ceratium* and by the copepods *Metridia* spp. Upper: Station 2; lower: Station 4

Correlations among measured parameters

Bioluminescence, chlorophyll *a* fluorescence, beam attenuation, and dinoflagellate cell number data were

Table 3. Correlation analysis for bioluminescence (photons $s^{-1} cc^{-1}$) versus number of dinoflagellate cells per liter seawater at Stations 1 to 4, Vestfjord, 1986. r = correlation coefficient; p = significance level (alpha level)

Station	Total dinoflagellates		Bioluminescent dinoflagellates (upper limit)		Bioluminescent dinoflagellates (lower limit)	
	r	p	r	p	r	p
1	0.860	0.05	0.964	0.01	0.691	>0.10
2	0.925	0.01	0.929	0.01	0.930	0.01
3	0.932	0.01	0.963	0.01	0.953	0.01
4	0.889	0.02	0.961	0.01	0.890	0.02

collected and analyzed for all stations. Scatter plots of the data revealed that possible linear correlations existed and, subsequently, correlation analyses were performed on these parameters. Since plankton samples were taken discretely (10, 20, 30, 40, 50, and 100 m), correlations utilizing cell numbers had an $n = 6$. This assumes depths are replicates of the same linear relationship of the 2 variables being correlated. Sample depths (for cell number analysis) were matched with data from the continuous vertical profiles (bioluminescence, fluorescence, and beam attenuation) at the closest depth (within 2 m or by extrapolating between 2 data points if the data were too widely spaced). Other correlations had various n values due to slight variations in bathyphotometer descent rate.

The correlation coefficient (r) values for bioluminescence intensity versus number of dinoflagellates (Table 3) ranged from 0.691 to 0.964. With the exception of Station 1 (total dinoflagellates and lower limit bioluminescent dinoflagellates) these r values reflected a high degree of correlation. For the upper limit bioluminescent dinoflagellates, correlations with bioluminescence intensity at all stations were significant at the 0.05 level. In the total and lower limit tests of Table 3, 3 out of the 4 stations exhibited correlations significant at the 0.05 level. These results were consistent with the light budget analysis.

In general, beam attenuation correlated less than bioluminescence with number of dinoflagellates. The r values at Stations 2 and 3 ($0.893 < r < 0.989$) appeared to be higher than those for Stations 1 and 4 ($0.518 < r < 0.964$). This lowered correlation could be expected since beam attenuation is a measure of all particulate matter in the water column. Maximum beam attenuation occurred in the upper 30 m, coincident with peak intensity of bioluminescence and chlorophyll fluorescence.

Like beam attenuation, chlorophyll *a* fluorescence did not exhibit a high degree of correlation with numbers of dinoflagellates. In fact, the correlation analysis indicated that the overall significance level for each of the three sets of correlations is well above the 0.2 level. A possible explanation for this low observed correlation

is that not all dinoflagellates contain chlorophyll pigments (i.e. *Protoperdinium* spp.). Although not included in the table, the number of diatoms found in the discrete samples also did not correlate with chlorophyll *a* fluorescence. This may be attributed to smaller, chlorophyll-bearing diatoms and micro-flagellates not retained by the 20 μ m mesh collection cups for counting and relative differences in fluorescence among the chlorophyll-bearing cells.

Correlation analysis of beam attenuation coefficient (m^{-1}) with bioluminescence intensity (photons $s^{-1} cc^{-1}$) yielded high r values (Table 4a) resulting in an overall level of significance of less than 0.01 (99 % confidence).

Table 4. Correlation analyses; r = correlation coefficient; p = significance level (alpha level)

(a) Beam attenuation coefficient (m^{-1}) versus bioluminescence intensity (photons $s^{-1} cc^{-1}$)			
Station	r	p	n
1	0.862	0.001	19
2	0.792	0.001	18
3	0.886	0.001	25
4	0.779	0.001	17
(b) Chlorophyll <i>a</i> fluorescence (relative units) versus bioluminescence (photons $s^{-1} cc^{-1}$)			
Station	r	p	n
1	0.670	0.01	14
2	0.717	0.02	10
3	0.843	0.001	19
4	0.624	0.05	13
(c) Chlorophyll <i>a</i> fluorescence (relative units) versus beam attenuation coefficient (m^{-1})			
Station	r	p	n
1	0.740	0.01	14
2	0.379	>0.10	10
3	0.832	0.001	19
4	0.791	0.01	13

In analyses of chlorophyll *a* fluorescence with bioluminescence (Table 4b) and beam attenuation (Table 4c), however, only 3 out of 4 stations showed significance at the 0.05 level. These relationships may be reflective of the increasing numbers of chlorophyll-bearing dinoflagellates (*Ceratium* spp.), diatoms co-occurring at the same depth, and heterotrophic bioluminescent dinoflagellates grazing on diatoms (Jacobson 1987). Other studies have found correlations between chlorophyll *a* fluorescence and bioluminescence on small spatial scales (< 10 km) in the Gulf of California (Lieberman et al. 1987).

Because of the significant correlations between the aforementioned parameters, beam attenuation may be a useful indicator for bioluminescence. However, the relative contribution from all sources of light attenuation would have to be understood for a given water column before any generalization could be drawn on the usefulness of beam attenuation as a predictor of bioluminescence potential.

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