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Thin layers of bioluminescent copepods found at density discontinuities in the water column

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Abstract To learn how organisms apportion space in the open ocean, biological oceanographers have sought to improve temporal and spatial resolution of ocean sampling systems. Their objectives are to simultaneously measure physical, chemical and biological structure in the water column in order to find significant correlations that may reveal underlying processes. Here we report one such correlation between intense peaks of bioluminescence and density discontinuities in the water column. Intensified video recordings made in these bioluminescent "hot spots" were analyzed with a computer image-recognition program that identifies organisms based on the temporal and spatial characteristics of their luminescent displays. Based on this analysis, the source of the "hot spots" was found to be very thin layers (0.5 m) of the bioluminescent copepod *Metridia lucens* present at from 5 to 100 times average background concentrations. Given the recent discovery that the vertical distribution of marine snow is also strongly correlated with density discontinuities in the water column, we suggest that this finding may provide a possible explanation for the disparity between estimated energy requirements of marine copepods and measurements of average in situ food concentrations. The energy costs associated with locating food-rich micro-patches is greatly reduced if those patches are spread out into very thin layers, because the search strategy can be reduced from three dimensions to one.

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Introduction

Bioluminescent organisms are ubiquitous in the marine environment, and it has often been suggested that their light emission could serve as a highly specific bio-optical assay (Broenkow et al. 1983; Losee et al. 1985; Nealson et al. 1986; Gitel'zon and Levin 1989). Just as fluorescence measurements provide valuable data on fine-scale distribution patterns of primary producers, bioluminescence measurements can furnish similar data for significant secondary producers such as dinoflagellates, ostracods, copepods, euphausiids and gelatinous zooplankton. By enabling continuous measurements at sampling frequencies that are compatible with other standard oceanographic instruments, bioluminescence measurements hold enormous potential for revealing factors that govern organism distribution patterns. A variety of different bathyphotometers have been developed that can map the distribution of stimulated bioluminescence relative to environmental variables such as depth, temperature, salinity, and fluorescence (e.g. Aiken and Kelly 1983; Losee et al. 1985; Swift et al. 1985). However, three basic problems have limited the utility of these systems: (1) low pumping rates (0.25 to 1.5 l s^{-1}) have resulted in poor sampling statistics and a strong sampling bias for weak swimmers such as dinoflagellates; (2) undefined and often variable stimulus regimes and residence times have made measurements instrument-specific and therefore not truly quantitative; (3) bioluminescence measurements have little meaning unless the taxonomic composition of the light-emitting assemblages is known. The first two of these limitations have been addressed with the development of the "high-intake defined-excitation bathyphotometer" (HIDEX-BP) (Case et al. 1993; Widder et al. 1993; Neilson et al. 1995). The high pumping rate of this bathyphotometer

captures fast-swimming zooplankton that may evade slower pumping systems, and provides a calibrated and statistically significant measure of the fine-scale structure of stimulated bioluminescence in the water column. The problem of determining which organisms are responsible for the measured luminescence is then the same as that which faces any investigator trying to collect discrete samples within small-scale structures. One approach is to make collections using real-time sensor feedback to verify that the sample is collected within the feature of interest (Donaghay et al. 1992). Here we describe a variation on this technique that uses a radiometer and a submersible platform to collect pumped samples during horizontal video-transects within bioluminescent "hot-spots" revealed by HIDEX-BP profiles.

The purpose of this investigation was to develop a means of assessing the taxonomic composition of light-emitting assemblages without the labor-intensive and time-consuming analysis of individual samples, which is the bottleneck of so much research in biological oceanography. To accomplish this we have been developing an in situ video-transect technique that uses the unique temporal and spatial characteristics of bioluminescent displays to identify sources. With an intensified video camera mounted on a midwater submersible, it is possible to record bioluminescent displays that are mechanically triggered during horizontal transects (Widder et al. 1989). Using this technique, we have been developing a database of identified bioluminescent signatures in the Gulf of Maine (Widder et al. 1992b; Widder 1997). Until recently the analysis of this bioluminescence video data was prohibitively labor intensive. However, we now have a computer image-recognition program that identifies organisms based on the temporal and spatial characteristics of their luminescent displays and maps their coordinates in three-dimensional space (Widder and Johnsen 1998; Widder and Johnsen in preparation).

Materials and methods

Profiles of stimulated bioluminescence were made with a HIDEX-BP in the Gulf of Maine (Wilkinson Basin 42°N; 69°W) on 12 to 20 August 1992 from the R.V. "Seward Johnson". Bioluminescence was stimulated by hydrodynamically calibrated, pumped flow through a turbulence-generating grid at the entrance to the 16-liter cylindrical detection chamber. Bioluminescence was measured every 10 ms by a photomultiplier tube viewing an array of optical fibers embedded in the walls of the detection chamber. Profiles were made to a maximum depth of 225 m at a pumped volume of 16 liters s^{-1} and an average drop rate of 20 m min^{-1}. Additional sensors measured conductivity, temperature and depth, CTD (InterOcean S4 current meter modified for use as a CTD) and fluorescence (Sea Tech fluorometer). A total of 51 profiles were collected. Statistical analysis of the relationship between the bioluminescent peaks recorded in the profiles and density discontinuities in the water column was made for casts taken immediately before and after nighttime submersible dives. This encompassed the period between 20:45 and 02:45 hrs each night and represented 27 profiles. For the analysis of each profile, seawater density was calculated from the temperature and salinity data using the accepted equation of state (Fofonoff and Millard 1983). The depths of the intense peaks of bioluminescence ($> 2.0 \times 10^{11}$ photons l^{-1}) were compared with the depths of the density discontinuities (defined here as local density maxima). The number of bioluminescence peaks occurring at the same depth as a density discontinuity was compared with the number of expected occurrences using binomial statistics (Sokal and Rohlf 1981). Probabilities from the different casts were combined using Fisher's method (Sokal and Rohlf 1981). Because the HIDEX-BP was tethered to the ship, it was subject to wave motion. Therefore, in heavier seas, the instrument probably disturbed the density gradients. For this reason, only data from casts with an average or less than average wave slope were used. (The wave slope for a given cast was determined by subtracting the average drop rate of the HIDEX-BP from the depth versus time curve, and then calculating the average absolute slope of the resulting sine wave.)

The "Johnson Sea Link" submersible was used to make discrete collections and recordings at depths of interest which were selected based on the HIDEX-BP profiles. The submersible was launched immediately following a HIDEX-BP profile, and video recordings of stimulated bioluminescence were made using an intensified video camera (ISIT 66, Dage-MTI, Michigan City, Indiana), mounted inside the observation sphere of the submersible. A 1 m-diam hoop with 1800 μm-mesh Nitex® nylon stretched across it was mounted in front of the observation sphere and served to stimulate bioluminescence in the plane of focus of the camera. Recordings were made during 4 min horizontal transects run at a forward speed of 0.3 m s^{-1}. A photomultiplier-tube-based auto-calibrating radiometer measured the stimulated photon flux during each transect and was used during daytime dives to measure the diffuse attenuation coefficient at 480 nm (Widder et al. 1992a; Frank and Widder 1997). Also, during each transect a quantitative plankton sample was collected by a suction sampling-pump with in-line flow meter and 64 μm-mesh screen at the outflow of the collection buckets. A minimum of 300 liters was pumped during each transect.

Identification of organisms responsible for bioluminescence in each transect was based on the spatial and temporal properties of the recorded displays. These displays were compared to our existing database of identified displays from this region (Widder et al. 1992b; Widder 1997) and correlated with the abundance of identified bioluminescent organisms in the quantitative plankton samples. The 3-D spatial distributions of identified displays were analyzed using an object-oriented image-analysis routine (MRJ Technology Solutions, Fairfax, Virginia, USA). Video frames were digitized (TCI-SE video capture card, Coreco, Inc., St-Laurent, Quebec, Canada; Eyeview acquisition software, IO Industries, London, Ontario, Canada) and then run through a threshold filter and smoothed to remove camera noise. Bioluminescent displays in each frame were identified as "slices", and frames were stacked to construct 3-D objects from these "slices". Objects were then classified based on length (number of frames where object is visible), volume (number of pixels in object) and maximum area (number of pixels in largest slice of object). The classified objects were then used for 3-D reconstruction of the original transect volume. Graphic reconstructions were made using 3-D reconstruction software (Slicer Version 1.1, Fortner Research, Sterling, Virginia, USA). All software was run on a 200 MHz Pentium personal computer (Dell Computer Corporation, Round Rock, Texas, USA). Because the current version of the object-identification program cannot distinguish dinoflagellates from fragments of the large luminescent clouds released by the ctenophore *Euplokamis* sp., we did not include object counts from below 200 m, where this ctenophore is found, in the correlation analysis.

Results

Fig. 1 shows HIDEX-BP profiles made before and after the nighttime submersible dives on 17 August (Fig. 1A to C) and 18 August (Fig. 1 D to F). The intense discrete

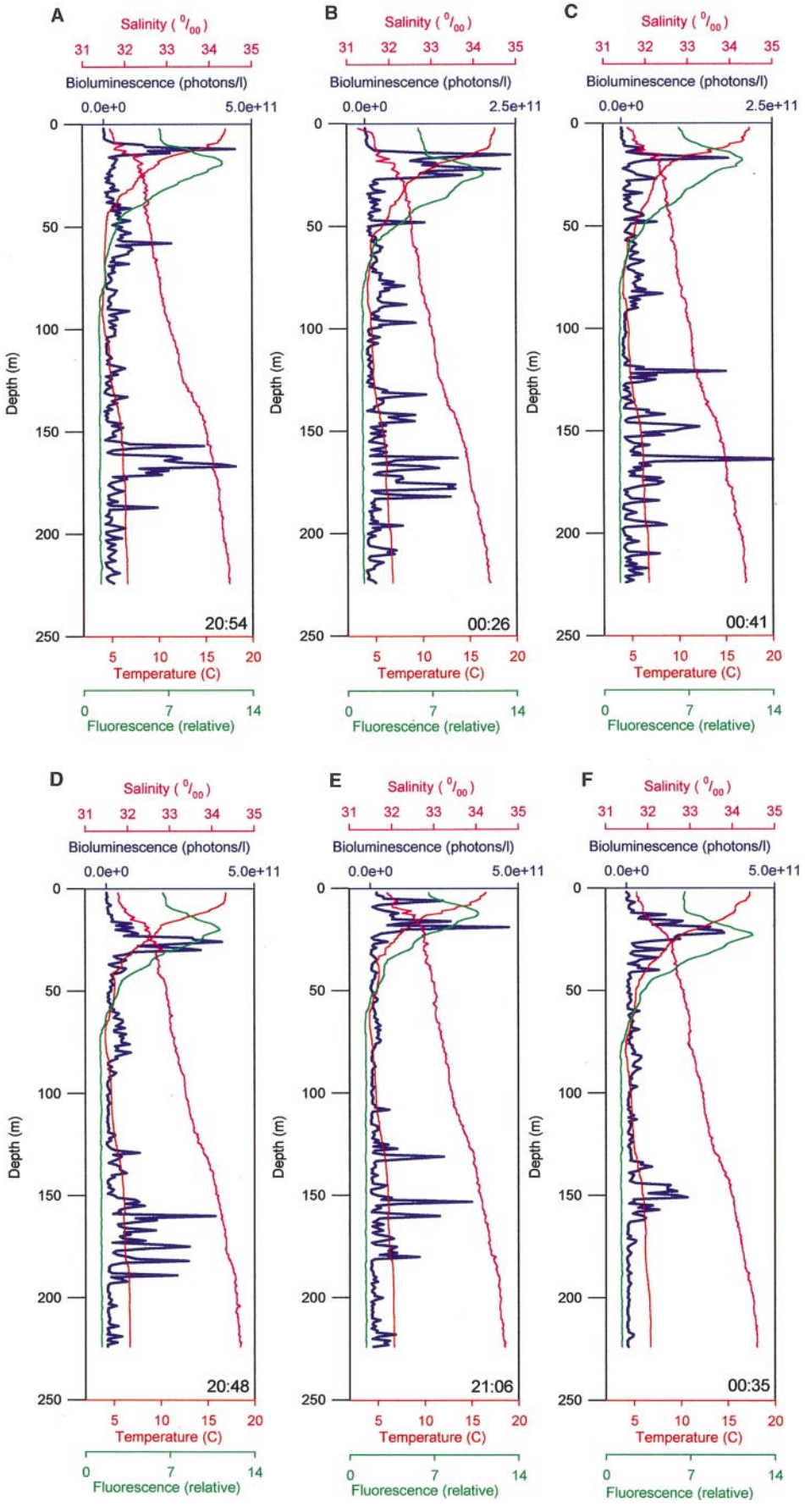
peaks of bioluminescence visible in these profiles were a common feature of profiles collected during the cruise. With an average width at half maximum of 0.5 m ($N = 79$, SD = 0.3 m), these sharply-defined peaks were concentrated in nighttime profiles in the thermocline and at depths below the temperature minimum zone (temperature < 5 °C). In daytime profiles, peaks were generally confined to depths below 150 m. Correlation analysis revealed that bioluminescent peaks were found at density discontinuities significantly more often than would occur by chance ($P < 0.018$, $N = 14$ profiles). Fig. 2 shows a blown-up view of bioluminescence and density (sigma-*t*) from one of these profiles. A similar analysis was performed comparing the depths of the peaks of bioluminescence with the depths of the salinity discontinuities. This revealed that the peaks also occurred at salinity discontinuities significantly more often than would occur by chance, but with a considerably lower *P* value ($P < 0.002$).

Fig. 3 shows single video frames of bioluminescent displays recorded during the submersible transects on 17 and 18 August. On 17 August, the profile before the dive was completed at 20:54 hrs (Fig. 1A), and the transects were run between 21:45 and 23:10 hrs. On 18 August, the profile was completed at 21:06 hrs (Fig. 1E), and the transects were run between 21:45 and 23:00 hrs. The montage in Fig. 3 is a good visual representation of the different character and abundance of bioluminescent sources seen at different depths. These video recordings also confirmed what the HIDEX-BP measurements showed: that bioluminescent sources were distributed throughout the water column from surface to bottom (bottom depth = 247 to 274 m). Measurements of the average stimulated bioluminescence recorded with the auto-calibrating radiometer during each of these transects is shown in Fig. 4. These values were compared with values measured by the HIDEX-BP as an indication of whether or not the transect was centered in one of the ''hot spots'' visible in the profiles. Also shown in Fig. 4 are the three most abundant luminescent organisms found in the quantitative plankton samples. The distribution of these sources showed a statistically significant correlation with the identified displays recorded in the intensified video transects. The bioluminescent copepod *Metridia lucens* produces a secretory display that is thought to distract or blind a predator (Herring 1988), and appears as a small cloud of light that passes through the transect screen. The 3-D reconstruction of this display is shown in blue in Fig. 5. These displays were visible in all transects, and their abundance correlated with the abundance of *M. lucens* collected in the pumped samples ($r = 0.90$, $P \ll 0.001$). In most transects, these displays were part of a mixed assemblage of luminescent sources. However, in every case where the average photon flux measured during the transect was comparable to that measured in the intense discrete peaks seen in the HIDEX-BP profiles, the displays were essentially monotypic (e.g. the transect run at 16 m on 18 August). Both the pumped plankton samples and the video recordings indicated that these hot spots were due to thin layers of *M. lucens* present at from 5 to 100 times average background concentrations.

In the temperature minimum zone, a different non-secretory display-type predominated and demonstrated a statistically significant correlation with the abundance of the bioluminescent dinoflagellate *Protoperidinium depressum* ($r = 0.99$, $P \ll 0.001$). The 3-D reconstruction of this display is shown in green in Fig. 5. Below 200 m, the most abundant luminescent source in the pumped samples was the ostracod *Conchoecia elegans*. A significant correlation has been demonstrated between the distribution of this ostracod and a display described as a fast repetitive flash, which was quantified by visual inspection of the video-transect data (Widder 1997). Other sources of bioluminescence in the water column that were identified by comparison to our data base of identified displays included the cydippid ctenophore *Euplokamis* sp., which produces a secretory display that passes through the transect screen as a large cloud of luminescent particles (shown in red in Fig. 5C), the siphonphore *Nanomia cara*, which produces a linear display (faintly visible in Fig. 3 at the left of the 71 m frame), and the lobate ctenophore *Bolinopsis infundibulum*, which produces a non-secretory display that looks like a figure of eight (Widder 1997). These gelatinous sources are destroyed in the pumped samples but are easily identified based on their spatially distinct displays. The only other source present in significant abundance was the euphausiid *Meganyctiphanes norvegica*, which produces a persistent non-secretory glow (shown in yellow in Fig. 5B). Although *M. norvegica* evades capture in pumped samples, it has been demonstrated that it does not avoid the transect screen (Greene et al. 1992).

Discussion

With each improvement in the temporal and spatial resolution of systems used to sample the ocean, finer scales of patchiness and variability have been found, with the greatest heterogeneity in the vertical plane. Thin layers of both phytoplankton and detritus have been reported, and models have been developed to account for their formation (Franks 1995; MacIntyre et al. 1995; Osborn 1998). Although many studies have shown that vertical distribution patterns of copepods can exhibit sharp peaks in abundance (e.g. Banse 1964; Longhurst 1967; Haury 1976; Herman 1983; Harris 1988) few studies have been able to discriminate a patch from a layer. Haury (1976) addressed this problem by sampling vertical distribution in the California Current with a vertically towed Longhurst–Hardy plankton recorder (LHPR). By comparing the variability of abundance estimates of replicate tows separated by a few hundred meters with random tows separated by 100s to 1000s of meters, he inferred the existence of copepod thin-layers of < 100 m in horizontal extent and < 15 to 20 m in


A
B
C
D
E
F
Salinity (⁰/₀₀)
31 32 33 34 35
Bioluminescence (photons/l)
0.0e+0
5.0e+11
2.5e+11
0 50 100 150 200 250
Depth (m)
20:54
00:26
00:41
20:48
21:06
00:35
5 10 15 20
Temperature (C)
0 7 14
Fluorescence (relative)

◀

Fig. 1 Profiles of stimulated bioluminescence, temperature, salinity, and fluorescence made with the high-intake defined-excitation bathyphotometer (HIDEX-BP) immediately preceding and following nighttime submersible dives on 17 (**A**–**C**) and 18 (**D**–**F**) August 1992. The end time (hrs) for each profile is in bottom right-hand corner of each graph. The two consecutive profiles taken after dive on 17 August (**B**, **C**) and before dive on 18 August (**D**, **E**) demonstrate temporal variability associated with measurements

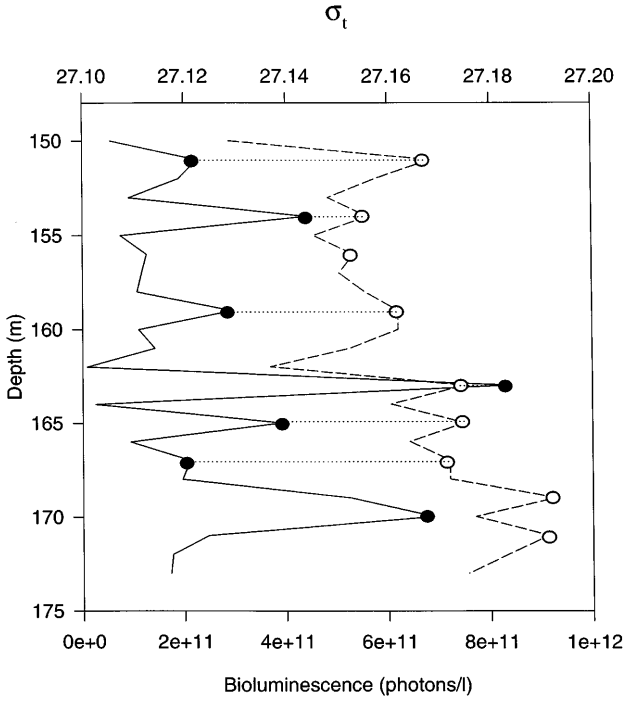
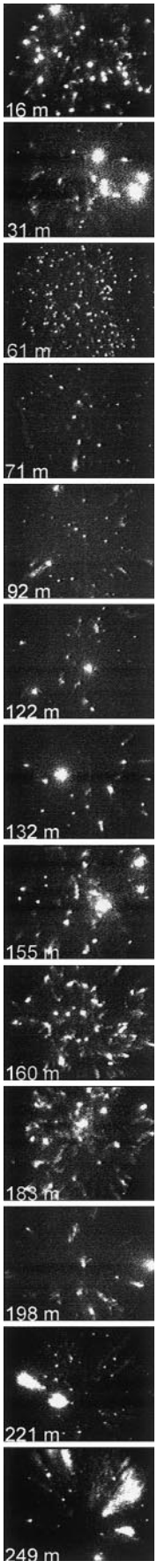


Fig. 2 Close-up of one HIDEX profile showing sigma-*t* (*dashed line*) (calculated from temperature and salinity) and bioluminescence (*continuous line*) versus depth [○ local density maxima; ● local maxima of intense bioluminescence ($>2.0 \times 10^{11}$ photons l^{-1}); *dotted lines connecting circles* show coincidence of maxima of density and bioluminescence at a given depth]

vertical extent. Here we report on very thin layers of the bioluminescent copepod *Metridia lucens*, with a horizontal extent of >72 m (the distance traveled during a 4 min transect) and with a mean vertical extent of 0.5 m. We also describe a correlation between these thin layers and density discontinuities in the water column. Although a higher significance was found with salinity discontinuities, than with density discontinuities, we at-



▶

Fig. 3 Single video frames illustrating different character and abundance of bioluminescent displays seen throughout water column. Depth of transects is indicated in bottom left-hand corner of each frame. Depths selected on 17 August (31, 61, 92, 122, 160, 198 and 249 m) were based on HIDEX-BP profile made immediately preceding dive (Fig. 1A). Transect depths on 18 August (16, 71, 132, 155, 183, 221 m) were selected based on HIDEX-BP profile in Fig. 1E, which was made immediately prior to that dive. Frames shown were 1 min after start of each transect; field of view = 1 m

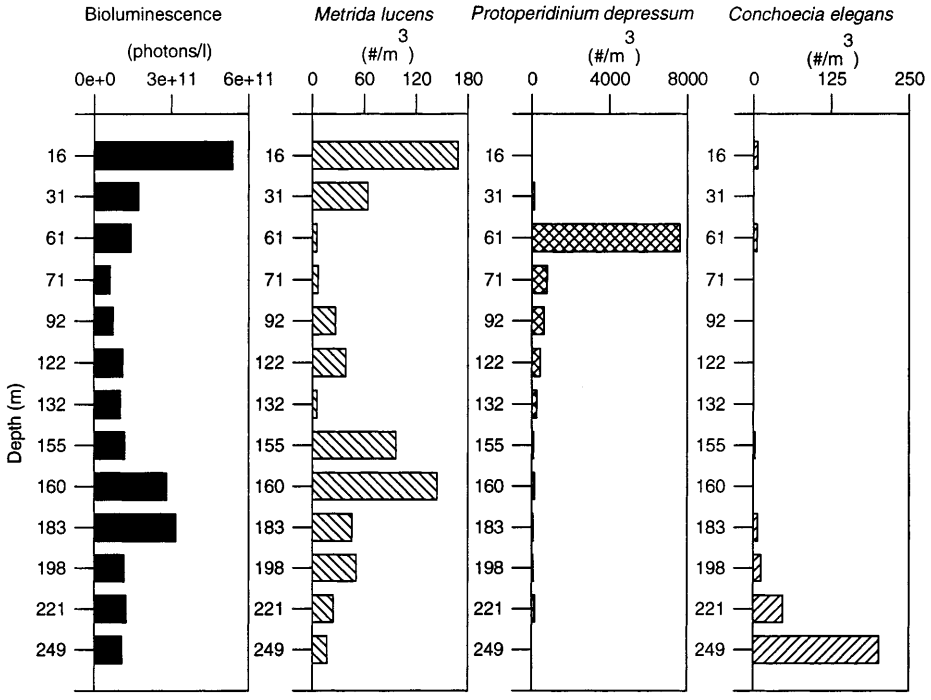


Fig. 4 Average bioluminescence measured during each submersible transect run on 17 and 18 August and abundance of three most abundant bioluminescent organisms collected in pumped samples

tribute this difference to the fact that the salinity calculations are based on salinity alone, while the density calculations introduce error from both temperature and salinity measurements.

Metridia lucens is a strong vertical migrator that characteristically demonstrates bimodal nighttime distribution patterns, with adult females located primarily in surface layers and adult males remaining primarily at depth (Bollens et al. 1993; Osgood and Frost 1994). Described as a "voracious feeder", *M. lucens* is an omnivore with a demonstrated selective preference for zooplankton (*Artemia* sp. nauplii) over phytoplankton in laboratory experiments (Haq 1967). Given the recent finding that marine snow abundance is correlated with density discontinuities in the water column (MacIntyre et al. 1995), one interpretation of our findings is that, in nature, *M. lucens* is a marine snow consumer or possibly a predator of marine snow consumers. Marine snow, which consists of aggregates of detritus, inorganic matter and microorganisms, is a rich food source (Alldredge and Silver 1988; Dilling et al. 1998). Its consumption could account for the apparent inadequacy of measured average in situ food concentrations relative to the daily metabolic requirements of marine copepods (Mullin and Brooks 1976; Dagg 1991; Gifford 1993; Batchelder and Williams 1995; Cowles and Fessenden 1995). Although the possibility has been raised that this disparity could be accounted for by the existence of food-rich micropatches (e.g. Batchelder and Williams 1995), this solution depends on how much energy grazers must expend to locate such patches (Haury et al. 1978). Locating food-rich thin layers, especially for a vertical migrator such as *M. lucens*, is less problematic since the search strategy is reduced from three dimensions to one. A copepod moving up or down through the water column has a much higher probability of encountering food-rich micropatches if those patches are spread out into very thin layers.

An alternative hypothesis is that aggregation into thin layers is an avoidance response to current shears or turbulence, causing the copepods to accumulate in homogenous zones between layers (Angel 1968; Haury 1976). To test this alternative, it will be necessary to measure the shear stress and turbulence in and around the layers. Another approach would be to assess the abundance of marine snow or other possible food sources at density discontinuities and look at the strength of the correlation between copepod and food abundance within the layers. With this in mind, it is interesting to note that although we found *Metridia lucens* throughout the water column we did not find aggregations at all density discontinuities in the water column, perhaps because some layers lack marine snow accumulations.

An additional point to consider in assessing possible advantages of this particular aggregation behavior is that of the selective advantage afforded by bioluminescence. Recent laboratory experiments demonstrating increased susceptibility of zooplankton to visual predators in the presence of bioluminescent dinoflagellates suggest that animals maneuvering in the dark must avoid stimulating the bioluminescent plankton that surrounds them or risk revealing themselves to visual predators (Mensinger and Case 1992; Abrahams and Townsend 1993; Fleisher and Case 1995). The risk of encountering a luminescent source will be highest where nearest neighbor distances are small, raising the possibility that organisms may enhance the repellent capacity

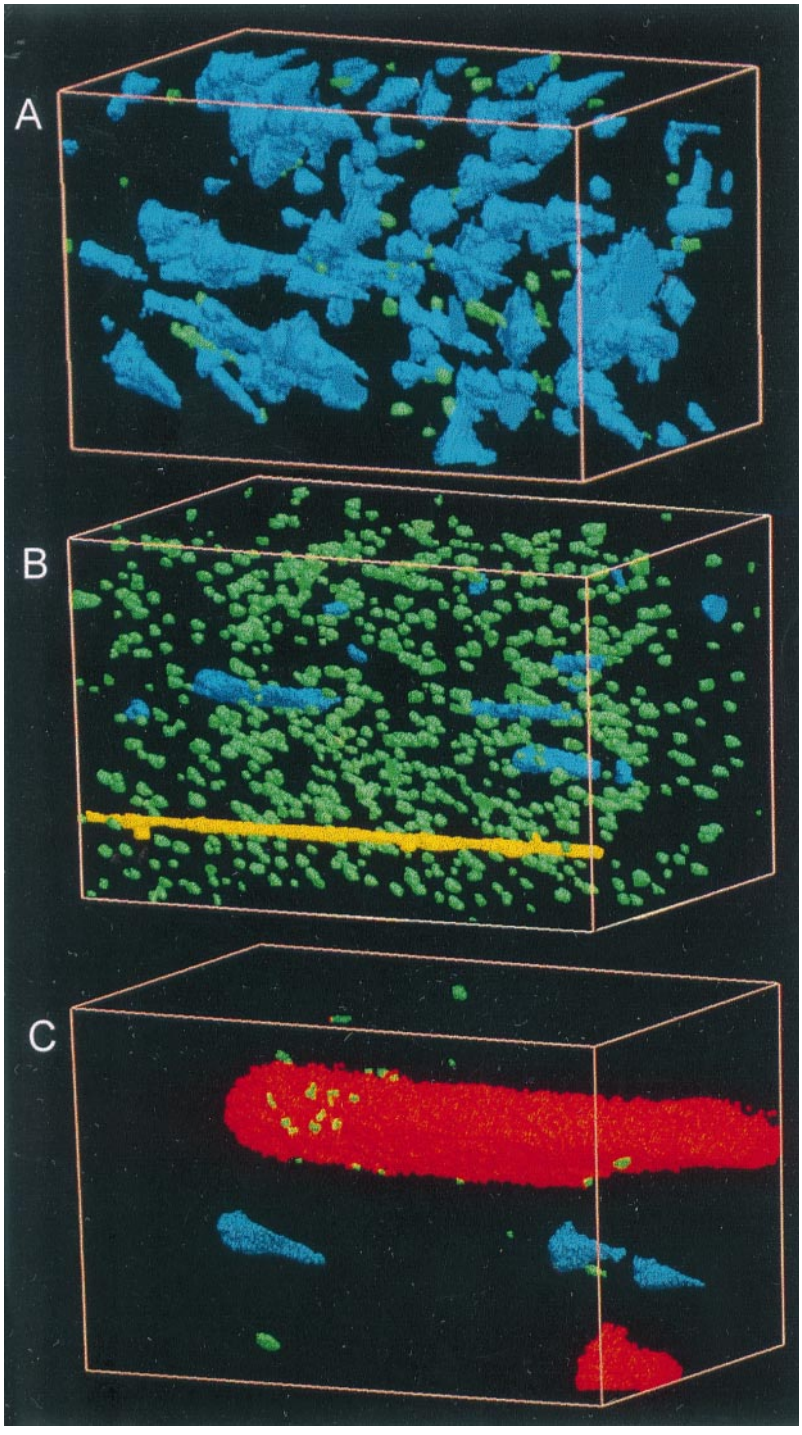


Fig. 5 3-D reconstruction of displays recorded during transects at 16 m (**A**), 61 m (**B**) and 249 m (**C**), showing small clouds of bioluminescence (*blue*) correlated with abundance of bioluminescent copepod *Metridia lucens*, and short-duration, intrinsic displays (*green*) correlated with abundance of bioluminescent dinoflagellate *Protoperidinium depressum*. Persistent glow (*yellow*) is characteristic of euphausiid *Meganyctiphanes norvegica*, and large clouds of bioluminescence (*red*) are characteristic of cydippid ctenophore *Euplokamis* sp. (green displays in **C** are actually fragments of the large luminescent cloud released by *Euplokamis* sp.: for details of object-identification software see "Materials and methods"). Dimensions indicated by white frames are $0.35 \times 0.35 \times 4.0$ m. In order to show bioluminescent signatures more clearly, time dimension is compressed and therefore not to scale

of their bioluminescence by forming aggregations. However, if this were the only advantage for *Metridia lucens*, a patch would be more efficient than a thin layer for this purpose. Additionally, if the aggregation was purely behavioral, one would expect the nearest-neighbor distances to be less than the median of $\simeq$10 cm found in the thin layers (Widder and Johnsen in preparation) and closer to the maximum perceptive distance of a copepod ($\leq$13 mm: Haury and Yamazaki 1995). Whatever the mechanism for the formation of these thin layers, their existence adds additional complexity to the submarine light field. Given the many predator avoidance strategies in the open ocean involving both morphological (e.g. transparency and counterillumination) and behavioral (e.g. vertical migration) adaptations to avoid detection by visual predators, it seems likely that thin layers of intense bioluminescence may have a significant impact on the distribution and behavior of visual predators and their prey.

The critical importance of determining the extent and nature of microscale patchiness in the oceans is well established (Fasham 1978; Steele 1978; Mackas et al. 1985; Marine Zooplankton Colloquium 1989; Owen 1989; Davis et al. 1991), and has lead to many new developments in underwater optical-imaging systems (e.g. Davis et al. 1996 and references therein). The use of bioluminescence described here for both fine-scale and micro-scale measurements provides yet another rapid means of assessing plankton distribution-patterns relative to the physical and chemical variables in the environment, and another view of the spatial complexity of the open-ocean environment.

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