Distribution of bioluminescence and plankton in a deep Norwegian fjord measured using an ISIT camera and the Digital Underwater Video Profiler

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ABSTRACT

Bioluminescence and plankton profiles were obtained using a downward-looking ISIT low-light camera and the Underwater Video Profiler system in Sognefjord, Norway. The profiling systems were lowered by CTD wire and recorded continuously from the surface to a depth of 1000 m. The former system delivered the vertical distribution of mechanically stimulated bioluminescent signals while the second provided the vertical distribution of undisturbed marine snow and zooplankton. The number of recorded bioluminescent events showed a maximum of 36.3 mean counts for 50 m depth range between 300 and 750 m depths and was positively correlated with the vertical distribution of copepods and negatively with density of marine snow particles (<0.5 mm). The most likely cause of the bioluminescence was the presence of bioluminescent metridiid copepods.

KEYWORDS: Plankton, Bioluminescence, Marine technology, Mesopelagic zone, fjords

INTRODUCTION

Light permits vision, which in turn allows an enormous diversity of inter- and intra-specific interactions from predation to courting display. In the ocean the intensity of downwelling light decreases rapidly with increasing depth, until 1000 m where no biologically-relevant sunlight remains (Herring 2002). As a result, much of the Earth's surface is continuously dark. Bioluminescent light is often used by animals in temporarily and permanently dark environments to attract and locate prey and mates (Carlson & Copeland 1985, Ruxton & Bailey in press), and to deter predators (Buskey & Swift 1983). As with downwelling light (James & Heck 1994), the intensity and presence of bioluminescent light affects the behaviour of animals and the occurrence and results of predator attacks (Abrahams & Townsend 1993, Fleisher & Case 1995).

The importance of light to meso- and bathypelagic organisms is clearly demonstrated by the large number of taxa that produce bioluminescence (Widder 2002), and the great diversity of both eyes and camouflage methods that have evolved in response (Warrant & Locket 2004). In the mesopelagic zone (200-1000 m depth) the light from the sun, stars, and moon (space light) fades, and so the visual scene changes from a broadly illuminated environment to one where the only light is in the form of short, point source, flashes (Warrant & Locket 2004). This is an ecosystem where there is no terrain, and little water turbidity to provide concealment, and so the effectiveness of even a weak light can be very great.

Surveys of the abundance and spatial distribution of bioluminescence have been undertaken worldwide (Tokarev et al. 1999, Widder & Johnsen 2000, Herren et al. 2004), to depths of over 4000 m (Bradner et al. 1987, Battle et al. 2002). However, although bioluminescence appears to be increasingly important as the intensity of downwelling light decreases, such studies are rare at depths of greater than 200 m. Studies linking quantitative measurements of the abundance of bioluminescent organisms, with similar assessments of the abundances of pelagic organisms are also unusual.

During the present study profiles of bioluminescent events, particles and planktonic organisms were obtained using low-light and strobe-lit video cameras in a deep Norwegian fjord. This site provided access to water of up to 1000 m depth without exposure to adverse surface conditions, and is the first study to present bioluminescence profiles through the entire mesopelagic in conjunction with detailed oceanographic and particle profile data.

METHODS

Ship operations

Three vertical profiles were completed the 19 November 2002 in Sognefjord, Norway (61o 08.40 N and 5o 50.10 E) during an Underwater Video Profiler (UVP) transect in the fjord (Fig. 1). Sognefjord is the deepest and longest fjord system in the world (204 km), reaching depths of up to 1300 m. The sill depth at the mouth of the fjord is 240 m and isolates the fjord from the nearest waters of similar depth, approximately 120 nautical miles N.W. in the Norwegian Sea.

The UVP was deployed at 08:46 hrs and replicate bioluminescence profiles were obtained using an Intensified Silicon Intensifier Target (ISIT) video camera (OE1325, Kongsberg-Simrad, Norway)

immediately before and after the deployment of the UVP. The ship drift was negligible between the 3 profiles.

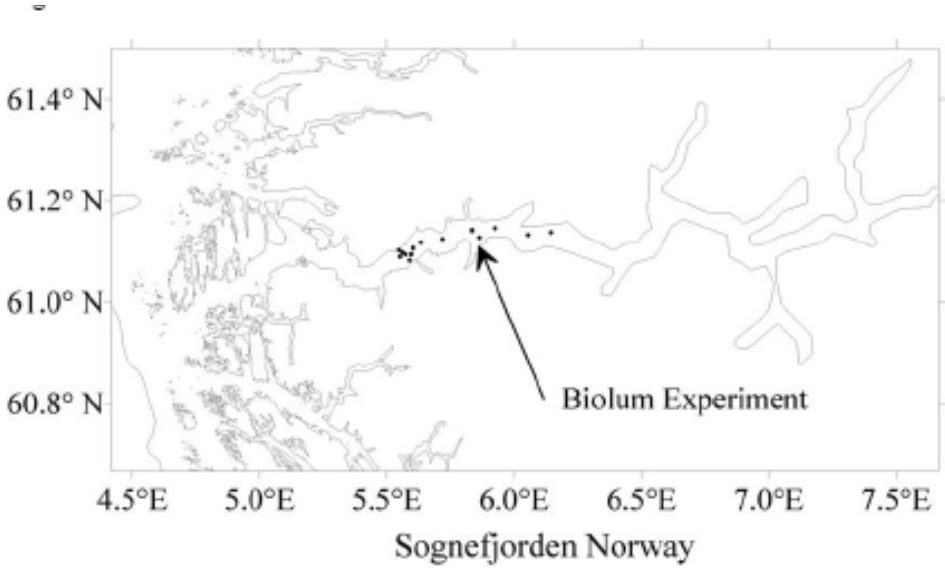

Figure 1. Underwater Video Profiler transect in Sognefjord during the MARECO test cruise held in November 2002. The arrow indicates the ISIT camera deployments.

Profiling equipment

The UVP model IV (Gorsky et al. 2000b) used was a vertically lowered instrument with a structured 8 cm thick light slab. The strobes were synchronized with two full frame 25 and 8 mm C-mount lenses video cameras with IR filters. The illuminated particles in a volume of respectively 1.25 and 10.5 litres were recorded simultaneously. Depth, temperature and conductivity data were acquired using a Seabird Seacat 19 CTD probe (S/N 1539) with fluorometer and nephelometer (both from Chelsea Instruments Ltd.). The system was powered by two 24V batteries and operated by an onboard computer. This computer automatically stored the images from the UVP's structured light beam and performed image processing during the recovery of the system. The images were analysed and treated automatically. The objects in each image were detected, enumerated and the area and 8 parameters of every individual object were measured. Particle parameters were stored and combined with the associated CTD, fluorometer and nephelometer data.

The pixel mm^{-1} relationship was calibrated in a test tank by injection of biological particles (range 40 µm - 20 mm) measured prior to their use with a stereomicroscope (Gorsky et al. 2000a). The results of the calibrations indicated that the tested configuration could detect 60 µm-sized particles and could reliably measure particles larger than 120 µm in diameter.

Particles were sorted into 4 size classes: 120-200 µm, 200-500 µm, 500-1000 µm and >1000 µm (defined as C1-C4) and all particles measuring more than 48 pixels (= 1 mm ESD) have been checked for copepod like objects (Fig. 2a). Consequently, hereafter the word copepod in this paper is used for >1mm ESD objects that shows copepod-like shape: oblong reflective body with antennae.

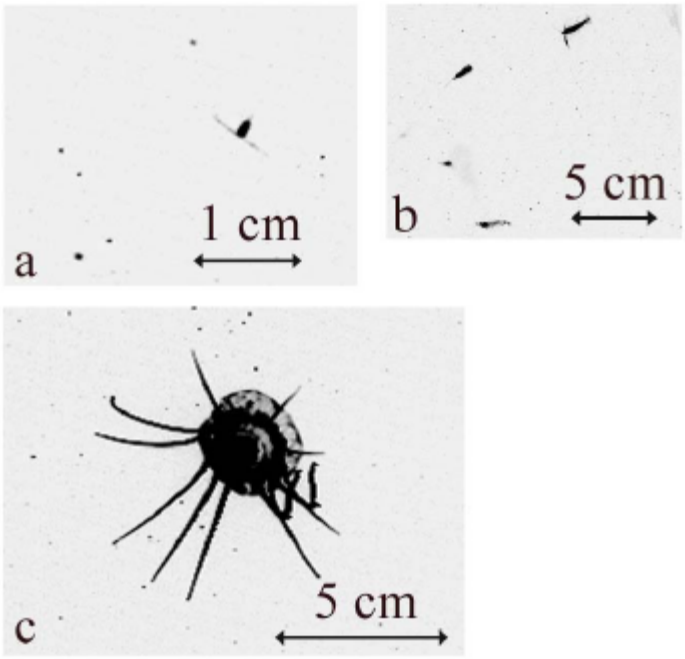

Figure 2. UVP recordings of a copepod (a), euphausiids (b) and of a medusa (c) from Sognefjord, Norway.

Zooplankton vertical distribution was obtained by automatic sorting of images containing the objects of interest. The identification of the objects was manual. As the abundance of large zooplankton was low, except for the copepods, and for one profile of euphausiids, we cumulated the results obtained from the 8 UVP profiles along the previous 31 miles transect in the fjord (Fig. 1). T he Bioluminescence Experiment was carried out in the middle of the transect, and the pattern of zooplankton distribution in the different profiles did not differ significantly. We identified 2 major groups: euphausiids and medusas (Fig. 2b and c). Small numbers of fish and chaetognaths was also present. In contrary to observations made in Sognefjord using the UVP in July 1996 (Gorsky et al. 2000a), the number of larvaceans, siphonophores and other small gelatinous forms in November 2002 was small.

Bioluminescence profiles were obtained by mounting the ISIT camera on a CTD, facing downwards towards a mesh screen (mesh size 0.8 x 1.6 cm) at a range of 50 cm, giving a field of view at the screen of 38 x 50 cm. On deployment the ISIT profiler was lowered on a CTD wire at 50 m min^{-1} while the vessel remained stationary. Recordings were made throughout the descent of the equipment only. Due to the sheltered nature of the station in Sognefjord there was little or no perceptible swell during the deployments.

The bioluminescence video sequences were analysed using the UVP software by replacing the original camera by the ISIT camera digital video recorder. Settings were adjusted to record and count only large bioluminescent flashes (Fig. 3) and avoid internal ISIT camera thermal noise. As the ISIT camera did not record volumetric images, the bioluminescent events were depth integrated (sum of counts for a given depth range). The second profile obtained by the ISIT camera was greatly disturbed by a large medusa fixed on the mesh screen and remaining flashing during the major part of the descent. Thus, we removed this profile from the dataset.

Figure 3. Bioluminescent signals recorded using the ISIT camera in Sognefjord. Large circular shape = medusa flashes, glowing trails = copepod or organic matter bioluminescence, small dots = noise. Only glowing trails were counted.

Statistics

Relationships between the depth distributions of particles and bioluminescent events were explored using Spearman rank correlation. Correlations were also made between the above data and physicochemical parameters such as temperature and salinity.

RESULTS

Bioluminescence profiles

Bioluminescence (sum of counts of glowing trails per 50 m depth) was not measurable (Fig. 3) at depths shallower than 150 m due to the ambient light level. Abundance of luminescent objects increased from 150 m to reach a maximum of 36 counts per 50 m at between 450 and 500 m, falling with increasing depth to an abundance of 15 counts at the end of the experiment at 1000 m (Table 1 and Fig. 4). These maximum and final counts approximated to 3.8 counts m^{-3} and 1.6 counts m^{-3} respectively.

Particle profiles

Abundances of particles (mean P m^{-3} in a 50 m layer) and identifiable individual animals (mean ind $\cdot m^{-3}$ in a 50 m layer) were determined (Table 1 and Fig. 4). Large copepods were infrequent in the 50-150 m layer. The highest concentrations were observed between 300m and 650 (mean of 31 ind $\cdot m^{-3}$) with the maximum of 43 ind m^{-3} in the layer 550-600 m. Medusas were observed at depths greater than 200 m and their average concentration in the water column was 0.11 ind m^{-3} with

maximum of 0.2 ind m^{-3}. Euphausiids were observed in low densities (<0.2 ind m^{-3}), apart from a very dense patch of 1000 ind m^{-3} at 108 m at station 1 (western station).

Particles were sorted by size between C1 and C4. The concentration of small particles (C1) decreased slowly from the surface (130 P L^{-1}) to 300 m (Fig. 4). Below this depth their concentration remained stable, between 50 and 75 P L^{-1}. Medium size particles C2 showed 3 maxima (18, 24 and 23 P L^{-1}) between 0-50, 150-200 and 800-850 m. Minimum concentration was observed at a depth of 500 m. Larger particle (C3) concentrations ranged from 0.2 to 1.4 P L^{-1} and showed an increasing trend from the surface to 1000 m deep, while particles above 1 mm (C4) showed a maximum of 0.5 P L^{-1} between 200 m and 600 m. The proportion of large particles identified as copepods ranged from 0% between 50 and 100 m to 70% between 550 and 600 m (Fig. 4).

Figure 4

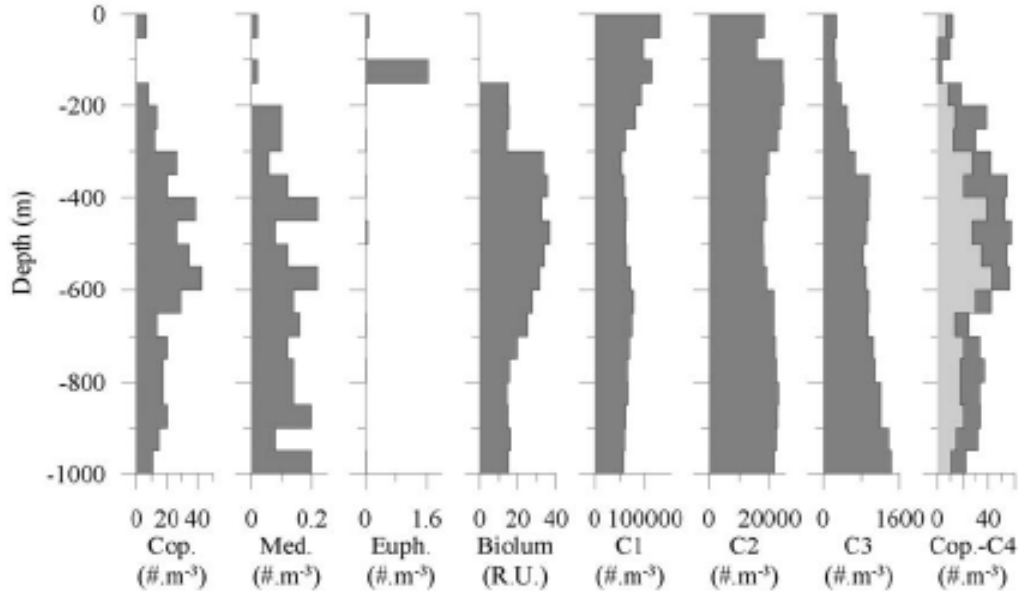

Figure 4. Vertical profiles of biological parameters. The values are averages densities (per m^3) for 50 m depth bins for UVP data, and total numbers of events for a 50 bin for bioluminescence. Cop. = copepod-like organisms, Med. = medusas, Euph. = euphausiids, Biolum. = bioluminescent trails, C1- C4 = different size classes of particulate matter (see text). Cop.-C4 = superimposed distribution of Cop. on the distribution of large particles (C4). Med. and Euph. Values represent the means of all the UVP profiles in Sognefjord. The other vertical profiles' values represent the profile related to the bioluminescence data.

Physical and chemical parameters

Salinity increased from 31.4 at the surface to 35.4 PSU at 500 m and remained stable to 1000 m. Three water masses were encountered. Surface fresh water covered the fjord to 25 m depth. Mixed Atlantic warm salty waters were observed from 25 m to 400 m, with deeper cold water originating from the fjord remaining below. Fluorescence was highest at the surface. The turbidity peaked at the surface and at 150 m.

BIOLOGICAL DATA		MIN	MAX	MEAN
Copepodlike (> 1000µm)	(ind · m^{-3})	0.00	42.67	18.60
Medusae	(ind · m^{-3})	0.00	0.22	0.11
Euphausiids	(ind · m^{-3})	0.00	1.64	0.01
Biolum	(per 50 m depth)	13.9	36.3	23.1
LPM tot (> 120 µm)	(P · m^{-3})	73615	146786	94503
LPM C1 (120-200 µm)	(P · m^{-3})	53195	128288	72840
LPM C2 (200-500 µm)	(P · m^{-3})	15570	24404	20797
LPM C3 (500-1000 µm)	(P · m^{-3})	233	1432	831
LPM C4 (> 1000 µm)	(P · m^{-3})	3	57	34
Copepodlike/LPM C4	%	0	76	49

CTD DATA		MIN	MAX	MEAN
Temperature	(°C)	6.94	9.10	7.39
Salinity	(PSU)	32.94	35.35	35.16
Turbidity	(FTU)	0.009	0.031	0.015
Fluorescence	(RU)	0.018	0.181	0.029
Density	(kg · m^{-3})	25.48	27.69	27.49

Table 1. Summary data for biological and physicochemical profiles made of Sognefjord, Norway using the UVP and ISIT camera. The mean value for the euphausiids excludes the Station 1 subsuperficial patch animal density considered as an exceptional event.

Relationships between parameters

Fourteen physical and biological parameters were compared to each other using Spearman correlation. Of the 78 correlations, 24 significant results were obtained, including relationships both between and within physicochemical and biological parameters (not shown here).

There were significant positive correlations between occurrence of bioluminescence and abundance of copepods, C4 particles, and salinity. Significant negative relationships with C2 particles, and euphausiids were also observed.

DISCUSSION

Bioluminescence was observed at all depths at which the ISIT camera recorded, but was most abundant between about 300 and 750 m depth. Several classes of particles or planktonic organisms were discriminated and counted, each with differing depth distributions. Of the particle classes identified the distribution of copepods in the water column matched most closely with the presence of bioluminescence. Various explanations exist for this correlation, of which the simplest is that some of the copepods were themselves bioluminescent.

The most likely candidates in Norwegian fjords are metridiid copepods described by (Falkenhaug et al. 1997). They are bioluminescent (Widder 2002), display behavioral versatility in the emission of luminescent light and are large enough to be seen and identified by the UVP. It was not possible to discriminate between copepod species using the UVP, so the depth distribution of this copepod genus in Sognefjord is not known. In the mesopelagic metridiid copepod *Gaussia princeps* (Bowlby & Case 1991) occurring below 400 m in the waters of southern California, fast-slow flashes are produced by a short emission from several light organs followed by a longer expulsion

of luminous material. Copepods emit a luminous secretion when exposed to mechanical or other stimuli. According to Widder (1992) luminescent material in *Gaussia princeps* is released from the caudal glands on the urosome. This glowing matter provides a long-lived, spatially defined target that may distract the predator away from the escaping copepod. In addition, in the vicinity of this light source the probability that a larger organism will capture the predator is increased.

Free-swimming copepods often produce emission of luminous material, resulting in a luminous trail extending several body lengths. Such trails were observed during the vertical profile (Fig. 3) and were clearly distinguishable from the medusa luminous display caught on the ISIT mesh screen. Another metridiid copepod, *Pleuromamma xiphias* (Latz et al. 1987) exhibits flash types similar to those of *Gaussia princeps*. Fast flashes from the smaller thoracic glands may function primarily to temporarily blind a predator.

Other animals might be bioluminescent and associated with copepods. Copepods are deterred by bioluminescence (Buskey & Swift 1983), and made more vulnerable to predators when feeding in the presence of bioluminescent organisms (Mensinger & Case 1992, Abrahams & Townsend 1993, Fleisher & Case 1995). A high level of copepod predation is a potential selective pressure towards the use of bioluminescence as a protective measure in midwater animals. For this later theory to apply the copepods must be able to detect that bioluminescence has been triggered, and a visual predator of copepods must be a significant threat. Note though, that the copepods need not necessarily be able to see the bioluminescence themselves. Of the objects observed by the ISIT camera, the identifiable bioluminescent animals were larvaceans and medusas. The abundance of the former group was low during the cruise, while the distribution and the abundance of the second correlated poorly with the prevalence of bioluminescence, indicating that medusas make up only a small proportion of the bioluminescent fauna. Bioluminescing objects viewed by the ISIT were more than ten times as abundant (per m^3) as the medusa viewed by the UVP.

Ecological consequences

Bioluminescent objects are common in Sognefjord, at depths where downwelling light is limited by attenuation and shadowing from the mountains immediately surrounding the fjord. Bioluminescent light is likely to have a powerful effect on the midwater ecology of the fjord, affecting the ranges at which animals detect detritus and other animals. The potential effects are therefore far-reaching, changing the effective level of energy supply to visual feeders by increasing encounter frequency, altering the relative strengths of different trophic interactions and affecting the selective pressures for swimming performance. The presence of light fundamentally changes the ecology of a system and the rates and routes by which energy flows through it.

Technical considerations

The present study utilized several profiling instruments in a deep fjord to allow the physical and biological characteristics to be recorded, including the distribution of bioluminescent organisms for the first time in this environment. The close temporal and spatial occurrence of the profiles permits a high degree of confidence in the correlations obtained between the widely differing profile parameters. For the first time this allows a wide range of parameters to be compared to the abundance of bioluminescence, to a depth of almost 1000 m.

The particle profiling methods used here are novel. The Underwater Video Profiler is well adapted to count and measure fragile aggregates such as marine snow as well as delicate zooplankton (Gorsky et al. 2000b) as the UVP system does not disturb the recorded particles or organisms

before observation. The approach of the UVP is associated with the flashing of strobes (perpendicularly to the lowering direction). Even if the flash duration is short and the intensity of forward scattered light low, some reaction of copepods to the UVP may occur. However, it was observed on continuous records of large volumes of water (Stemmann et al. 2002) that most the escape reaction occurred near to the focal plan and therefore most of the organisms were recorded by the UVP.

The ISIT system works by disturbing the animals, causing them to produce bioluminescent light. The wire-mode deployment could have caused some vertical smearing of the data due to ship heave. Undertaking the study in a sheltered fjord we were able to take measurements in deep water without the exposure and subsequent swells that might have been experienced on the high seas. The bioluminescence is stimulated by the equipment, and so the true visual field of a pelagic animal is not simulated here. Field observations have shown that unstimulated bioluminescence occurs at very low frequencies in the pelagic environment. The abundant hidden, but potentially bioluminescent, animals have been likened to a three-dimensional minefield (Widder & Johnsen 2000).

The advantages of closely-coordinated multi-instrument studies are clear, and future experiments combining these active and passive cameras with acoustic imaging will likely have a major impact on our understanding of biological process in the water column.

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