Assessment of Marine Bioluminescence

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Introduction

Seafarers are unavoidably aware of bioluminescence. Often beautiful, as when porpoises at a ship's bow streak through luminescent dinoflagellates, outlining their bodies in light and leaving behind persistent glowing tracks, bioluminescence is nearly always noticeable in bow waves, wakes and in breaking waves. Thus, it has implications for many types of naval operations.

The expression of bioluminescence in the sea is a function of processes and events from populational to molecular levels. This biological property is, in turn, modulated by the physical and chemical states of the ocean. Consequently, bioluminescence ranks among the most complex of oceanic phenomena.

Bioluminescence occurs in all marine environments, frequently to a phenomenal extent, and is found as well in a variety of terrestrial and to a vanishingly small degree in freshwater environments. It is far more prevalent in the ocean than on land, occurring in a remarkable variety of organisms representing the majority of marine phyla, from bacteria to fish[1]; see Alberte Table I). It has been demonstrated to play many biological roles ranging from predator-prey interactions, through camouflage, to reproductive and social interactions[2]. One speculates that this list, although extensive, is far from inclusive for so pervasive an oceanic phenomenon.

As investigation of marine bioluminescence has progressed there has been a valuable interplay of pure and applied studies, much of which has been supported by the Navy. Indeed, initiation of the modern phase of mapping oceanic bioluminescence unexpectedly resulted from a study by George L. Clarke[3] of light transmission to depth using an early bathyphotometer equipped with a photomultiplier (PMT) light detector (Fig. 1A). When lowered to the limit of detectable solar light, Clarke's instrument continued to register brief pulses of light. These were soon attributed to luminescent organisms stimulated by motion of the detector.

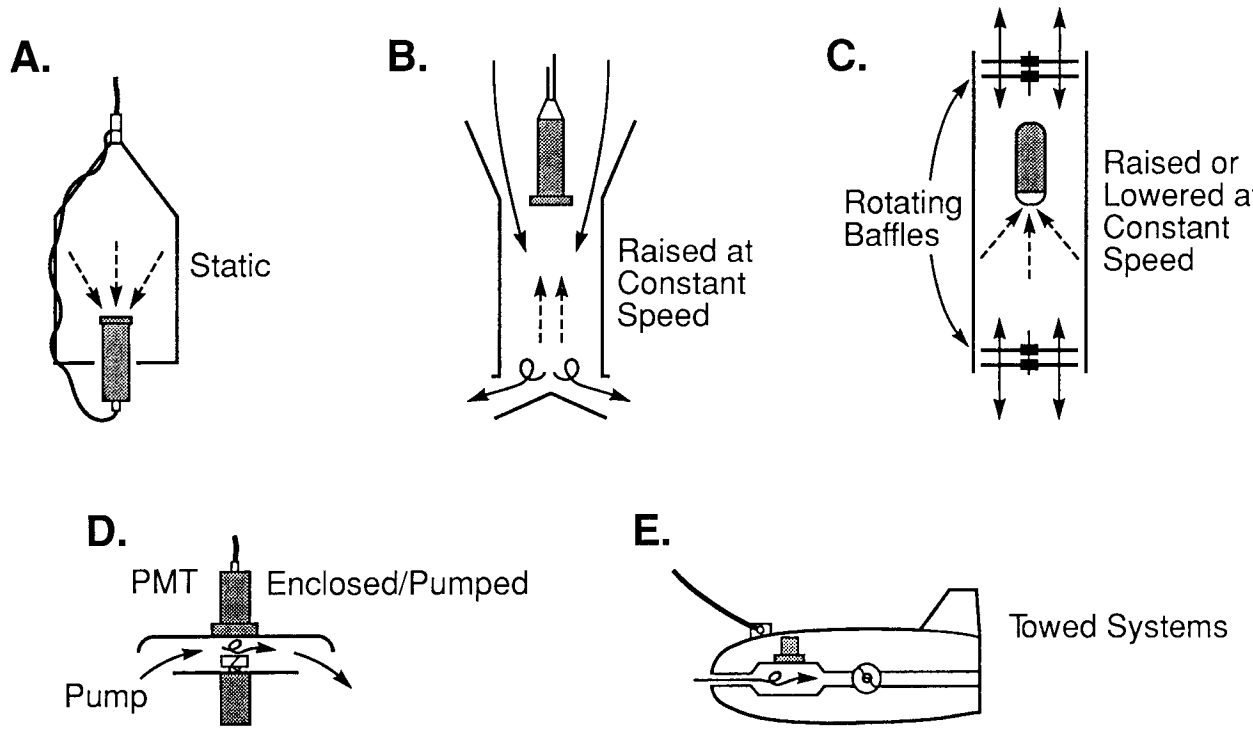
Evolution of Bioluminescence Assessment Methods

As quantitative devices, instruments such as Clarke's suffered from sensitivity to ship-induced motion through the suspending cable and, having an unrestricted field of view, their light measurements lacked volumetric reference. The most valuable further developments of bioluminescence bathyphotometers have emphasized instruments that deliver hydro-mechanical excitation in a repeatable fashion to a known volume of water. These have the greatest potential for rapidly sampling the vertical distribution of bioluminescence in the sea, or, as towed instruments, mapping bioluminescence on large spatial scales. An excellent and extensively used suite of instruments of this type is described by Ondercin[4, 28]. In such instruments, luminescence is triggered by turbulence created by steady movement of the bathyphotometer (Fig. 1 B,C) or by a pump impeller (Fig. 1 D,E).

Relatively little consideration was given to how effectively early instruments sampled the variety of luminescent species present, to the duration of the luminescent signal relative to the time organisms occupied the detector chamber, and, finally, to the relationship between hydro-mechanical stimulus properties and light output. These design limitations originated, in part, from the early assumption that the dominant component of luminescence in the photic zone was from dinoflagellates, single celled, poorly or nonmotile auto- or heterotrophic phytoplankton (See Hastings). However, zooplankton, or animal, luminescence, primarily from crustaceans and gelatinous forms such as coelenterates and ctenophores (see cover), may be orders of magnitude brighter and of far longer duration than dinoflagellate luminescence. Moreover, the locomotor and sensory abilities of zooplankton raise the possibility of evasion of capture by slowly pumped bathyphotometers. Zooplankton are also generally rarer than dinoflagellates and, thus, are more difficult to sample rigorously with instruments that process small volumes of water.

Figure 1.

Various bioluminescence bathyphotometers. (A) Clarke's,[3] (B) An early sounding bathyphotometer used by Gitelson. Raised at constant speed, water is entrained by upper funnel and luminescence is primarily triggered by turbulent flow at exit baffle. (C) A recent modification of the Gitelsen apparatus equipped with entry and exit baffles which also provide excitation as water is entrained by raising or lowering[30]. (D). Generic sketch of a low volume enclosed and pumped bathyphotometer in which excitation is provided by pump impeller, detector chamber volume about 50 ml with indeterminant flow path. (E) Generic towed system with excitation provided by entry baffle and flow provided either by forward motion or pump downstream from detector chamber[31, 32]



Consequently many types of pumped bathyphotometers do not fully characterize bioluminescence potential in certain environments. In particular, they may underestimate the contribution of zooplankton[5].

HIDEX Bioluminescence Bathyphotometers

Uncertainty about the ability of traditional bathyphotometers to provide comprehensive data on the variety of bioluminescent sources and signals in the sea led, at the request of the Oceanographer of the Navy, to the convening in 1981 of a panel of University and Navy researchers to recommend improvements in marine bioluminescence research and, especially, bathyphotometry. To implement one element of these recommendations the Bioluminescence Group at The University of California at Santa Barbara (UCSB) undertook development of a new type of bioluminescence bathyphotometer.

Design studies were conducted with cultured dinoflagellates of known bioluminescence potential in a full-scale transparent plastic prototype. Laser velocimetry was used to evaluate hydrodynamic excitation stress and low light level imaging (ISIT, intensified silicon intensified target, video) and photomultiplier tube (PMT) measurements were used to assess luminescence induction as a function of excitation. The first prototype instrument was successfully tested at sea in early 1987[6]. The U.S. Naval Oceanographic Office representatives contributed important recommendations for design changes to facilitate operation in heavy seas. These were implemented along with improvements in detector systems and data handling. The first operational instrument incorporating these changes was accepted by Navy on a cruise in June 1990. A similar instrument was provided to Naval Oceanographic and Atmospheric Research Laboratory in December 1990. A third instrument at UCSB is currently being employed in ongoing

Figure 2.

Schematic of HIDEX detector assembly. The detector chamber is 130 x 12 cm diameter. Within the entry, 100 microsecond pulsed infrared strobes provide stop-motion back or side lighting for video camera. The freely rotating baffle blocks ambient light with minimum premature excitation. The excitation grid marks entry to detector chamber. The event counter detects luminescent organisms at up to 100 s^{-1} and shares light with the bioluminescence spectrometer. In the white detector chamber 8 zone array pairs conduct light to eight R647 Hammamatsu PMTs. Total light is detected by 78 fiber optics leading to a single R268 Hammamatsu PMT. At the end of the detector chamber water is extracted past the flowmeter by the pump and exhausted to the outside through a radial diffuser which also serves as a light baffle.

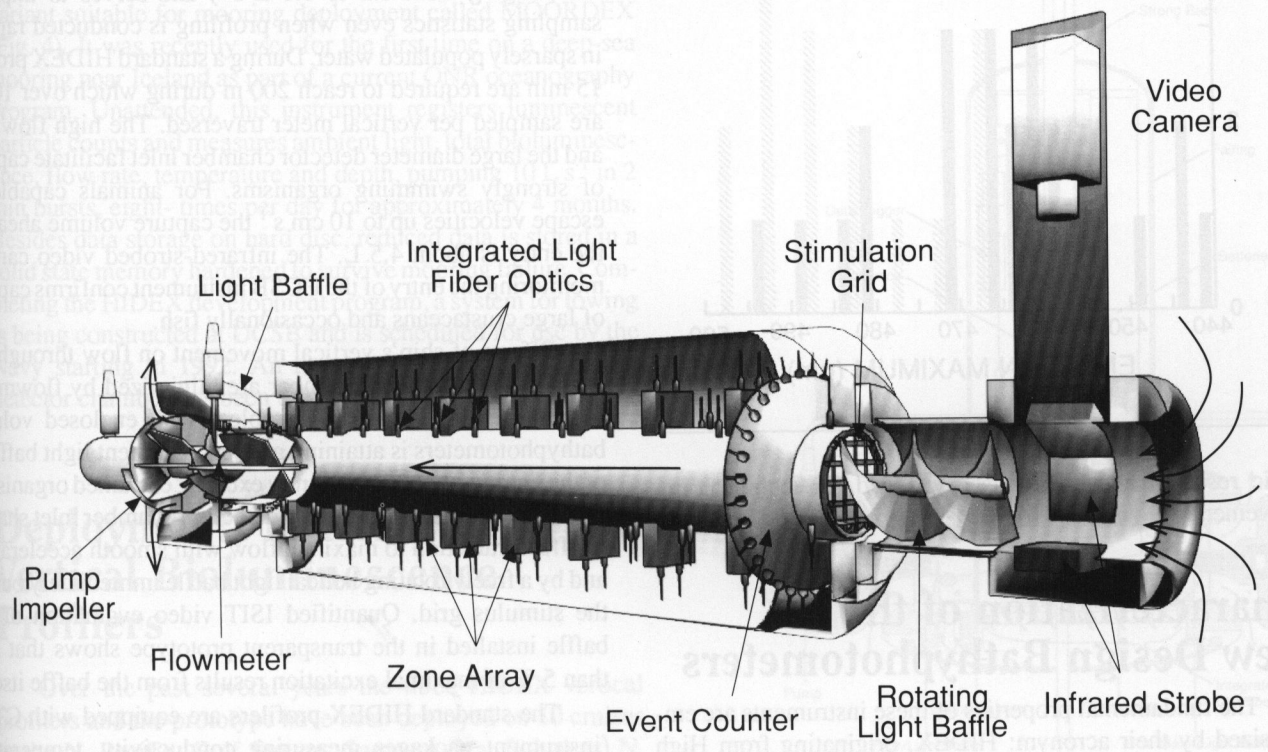
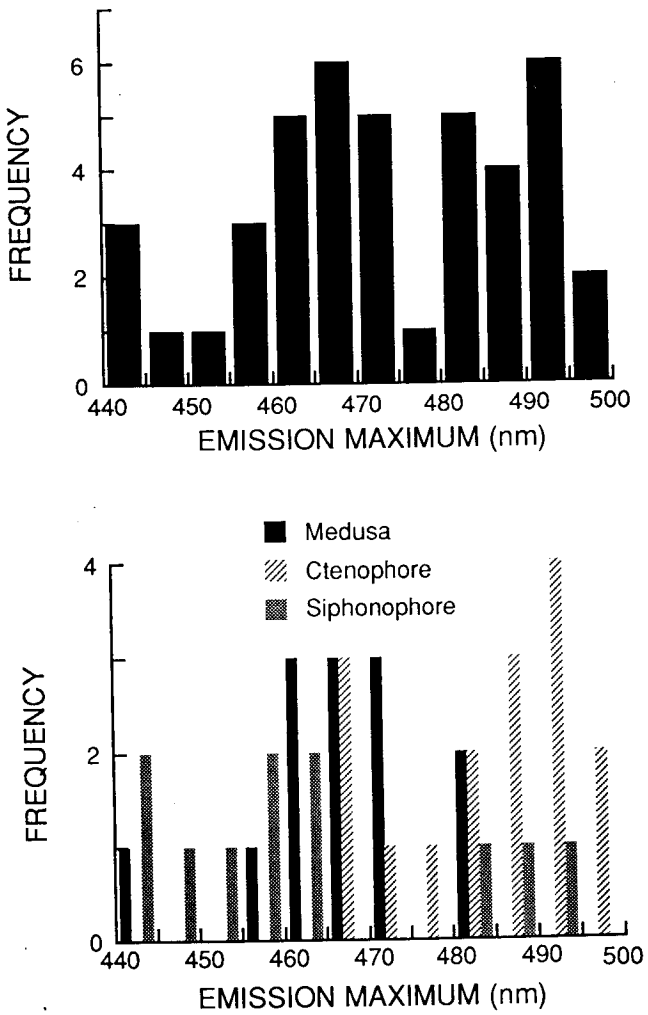


Figure 3.

Examples of variation of color of bioluminescence among marine species. Upper plot shows frequency of emission peaks as distributed among all species tested. Lower plot shows how emission maxima are distributed among three major groups of gelatinous zooplankton. From unpublished data collected in the Bahamas in 1989 by M. I. Latz and S.H.D. Haddock.



basic research and serves as a test bed for technical improvements.[7]

Characterization of the New Design Bathyphotometers

The fundamental properties of these instruments are emphasized by their acronym: HIDEX, originating from High Intake Defined Excitation (Fig. 2). Luminescence is excited by a hydrodynamically and bioassay characterized coarse grid at the chamber entry. Further excitation is minimal during flow through the chamber. Therefore, the total light response can be related to the magnitude of the grid induced turbulence. Bioluminescence is measured during flow through a 130 x 12 cm tube which is long enough to sample most of the bioluminescence triggered by the grid at typical flow velocities.

Light is sampled in several ways to derive maximal information. Total light emitted during passage through the white-surfaced detector tube is sampled by a single PMT receiving light from an array of fiber optics viewing the interior of the entire 16 L volume detector tube. A short distance downstream from the excitation grid, luminescent particles are counted and their instantaneous individual radiances are measured by another photomultiplier viewing a narrow cross section of the chamber through a circumferential light guide. Finally, a set of eight equally spaced PMTs viewing narrow cross-sections along the length of the detector tube assess the kinetics of the populational flash. Information on flash kinetics guides computer controlled adjustment of flow through the chamber so as to capture the populational flash appropriately within its volume. This ensures that the total light signal accurately represents as much of the entire flash as is practical. Flash kinetics also help to identify the general types of organisms emitting light[8,9].

The profiler is operated, both in descending and ascending mode, at selected flow rates of from 16 to 35 L s^{-1}. This is higher than the rates attained by other pumped vertical profilers (ranging from 0.2 to 1.1 L s^{-1}) and serves to improve sampling statistics even when profiling is conducted rapidly in sparsely populated water. During a standard HIDEX profile, 15 min are required to reach 200 m during which over 100 L are sampled per vertical meter traversed. The high flow rate and the large diameter detector chamber inlet facilitate capture of strongly swimming organisms. For animals capable of escape velocities up to 10 cm s^{-1} the capture volume ahead of the entry is about 4.5 L. The infrared-strobed video camera monitoring the entry of the UCSB instrument confirms capture of large crustaceans and occasionally fish.

Effects of ship's vertical movement on flow through the horizontally deployed chamber are minimized by flowmeter regulated pump control. A problem with enclosed volume bathyphotometers is attaining adequate ambient light baffling of the entry without prematurely exciting entrained organisms. In HIDEX this is managed by a detection chamber inlet shaped to effect transition to maximal flow with smooth acceleration and by a freely rotating helical light baffle immediately before the stimulus grid. Quantified ISIT video evaluation of the baffle installed in the transparent prototype shows that less than 5 % of maximal excitation results from the baffle itself.

The standard HIDEX profilers are equipped with CTDs (instrument packages measuring conductivity, temperature and depth), transmissometers measuring absorption and scat-

tering of light at red and blue wavelengths and fluorometers for quantifying algae such as dinoflagellates by their chlorophyll content. An intensified CCD-based spectrometer was developed for the UCSB instrument by C. Moore (UCSB Free Electron Laser Laboratory). It collects light from the bioluminescent particle counter and can register the populational bioluminescence spectrum as well as the spectra of individual brightly luminescent organisms when flow rate is low[10]. It is expected to contribute to identification of the dominant forms of organisms processed in the bathyphotometer, and also to provide in situ source spectra for radiative transfer calculations. This is desirable since bioluminescent spectra vary among species across a wide spectral range when measured in the laboratory (Fig. 3) and, thus, may be expected to vary in situ according to local species composition[11]. A shipboard 386-based computer communicating with a second computer on the HIDEX is used for system control.

Communication and power is provided by a load-bearing seven-conductor cable and dedicated winch. The shipboard computer manages realtime data display, analysis and archiving during operations. During profiles a plot is maintained of all measured parameters as a function of depth updated every 0.5 s. There is a 100 Hz display of the total light signal and a 500 Hz display of the luminous particle counter signal. A bar graph display tracks the signal from each kinetic array detector. System housekeeping data are continuously displayed. After a profile all data are immediately available for statistical analysis.

The UCSB group has developed a self-contained HIDEX variant suitable for mooring deployment called MOORDEX (Fig. 4). It was recently used for the first time on a deep-sea mooring near Iceland as part of a current ONR oceanography program. Unattended, this instrument registers luminescent particle counts and measures ambient light, total bioluminescence, flow rate, temperature and depth, pumping 10 L s^{-1} in 2 min bursts, eight- times per day for approximately 4 months. Besides data storage on hard disc, reduced data is stored in a solid state memory hardened to survive mooring failure. Completing the HIDEX development program, a system for towing is being constructed at UCSB and is scheduled for use by the Navy starting in 1992. An instrument with a HIDEX-type detector chamber has been used successfully in the arctic[12].

Deployments of HIDEX Vertical Bioluminescence Profilers

Over the past several years the three HIDEX vertical profilers and the prototype have been deployed on 10 cruises in the N. Pacific, Gulf Stream, Sargasso Sea, Bahamas, N. Central Atlantic, Vestfjord (Norway) and the Alboran Sea. The following are examples of work conducted in two characteristic bioluminescence regimes.

Phytoplankton Dominated Bioluminescence

Vestfjord, a large, arctic Norwegian fjord has dense populations of bioluminescent dinoflagellates, both photosynthetic and heterotrophic. In late summer these dominate the luminescent plankton. In August, 1990, contemporaneous shipboard investigations and HIDEX profiles were carried out during dawn and dusk transitions in the daily cycle of luminescence[13]. Shipboard laboratory measurements on fresh samples of the dominant local photosynthetic and heterotrophic dinoflagellates exposed to the local light cycle indicated for both types, that the shift between luminescent and non-luminescent states paralleled in time and intensity those detected by repeated profiles with HIDEX. A dusk HIDEX time series (Fig. 5) of seven profiles at half-hour intervals showed nearly

Figure 4.

MOORDEX, a HIDEX-type bathyphotometer for unattended operation on moorings or drifting buoys, shown in longitudinal section. While the detection scheme is the same as in HIDEX, with luminescent particle counter and total light measurement, power restrictions dictate an impeller excitation mechanism, a 500 msc residence time and 10 L s^{-1} flow rate. Height of the shroud is 1 m.

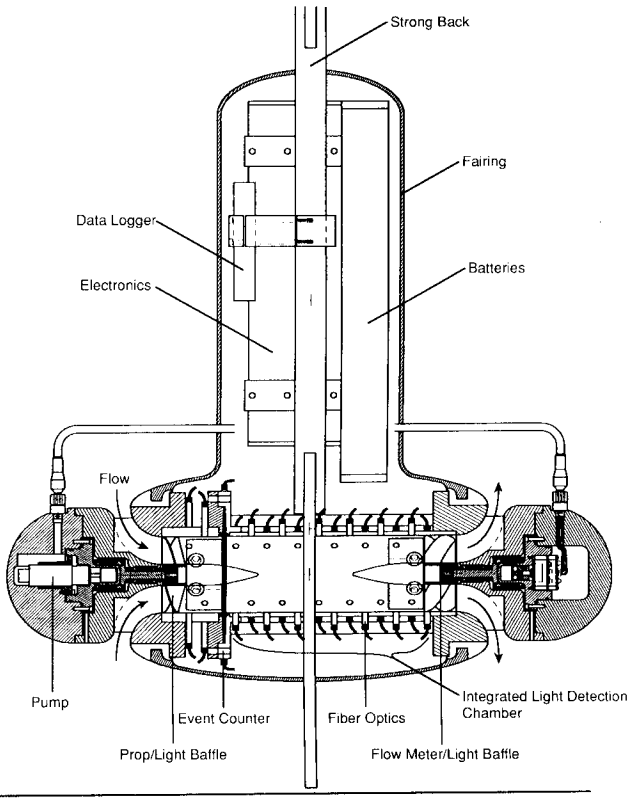
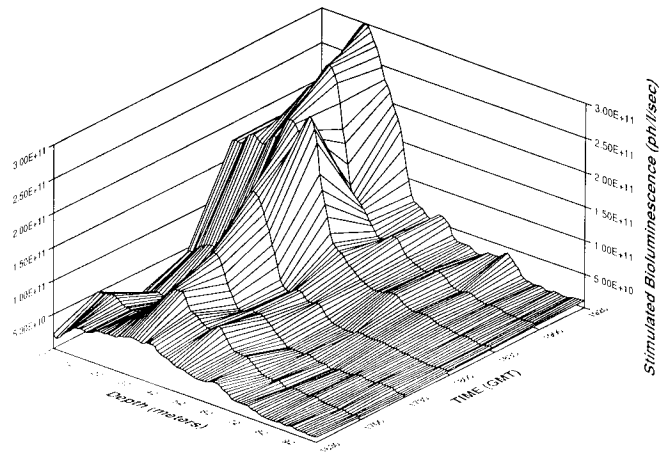


Figure 5.

HIDEX dusk profile series from Vestfjord showing only the total stimulated light signal as a function of depth and time.



an 8-fold increase in stimulable light at about 25 m depth. The profile series in conjunction with net casts also eliminated the alternative hypothesis that vertical migration of luminescent organisms from deeper water, might have produced the 25 m peak, a common occurrence in other situations. Since little increment in bioluminescence was noted deeper than 35 m, the dusk increase in bioluminescence must have occurred in place and could only be explained by daily cycling in bioluminescence potential of a persistent shallow zone of dinoflagellates. Indeed, laboratory studies (see Hastings) have shown that there is circadian regulation of bioluminescence in some species of dinoflagellates and that in these species significant bioluminescence capability exists only during the night period (see also refs. 14 and 15).

Mixed Phytoplankton and Zooplankton Bioluminescence

The Alboran Sea, has been noted for intense luminescence by various observers. Donaldson (1989) made extensive measurements throughout much of the Mediterranean using a laboratory photometer to measure water samples from the condenser flow of the USS John F. Kennedy. The brightest signals in that survey, 10^9 photons L^{-1} s^{-1}, were from the Alboran Sea, while the remainder of the very large Mediterranean sample set was in the range of 10^7 to 10^8 photons L^{-1} s^{-1}. These are substantial intensities considering that the tested samples must have undergone premeasurement excitation in the condenser flow and from other unavoidable manipulations.

In the Spring of 1991 in the Alboran Sea, two HIDEX profilers were used in a two-ship survey with the Johnson-Sea-Link submersible. The bioluminescent environment was complex with unusually high concentrations of brightly luminescent *Noctiluca*, a large heterotrophic dinoflagellate, in the upper few meters. Crustaceans (copepods and euphausids) were in large numbers at deeper levels together with gelatinous zooplankton. Immediately after a HIDEX profile, the submersible conducted short transects at depths of interest revealed by the HIDEX. Luminescence was evaluated on the submersible transects by low light level video of a coarse screen mounted at the front of the submersible, as referenced below.

An example of data collected by the two methods is shown in Figure 6. The HIDEX profile shows intense luminescence very near the surface, so bright that the interior of the submersible was lit enough for reading. Stimulated light then drops rapidly 3 orders-of-magnitude and levels off at around 40 m to intensities that are still high. The ISIT video images at 12 m also show intense luminescence. The video tape reveals short duration flashes almost exclusively. The HIDEX kinetics plot at position 1 in Fig. 6 is confirmatory, showing short duration flashes decaying to half maximum in about 0.3 sec. This value is characteristic of dinoflagellate flashes under laboratory conditions[17]. The increase in flash duration appearing on the kinetics plot from positions 1 through 2 to 3 is matched by a marked change in the 90 m video image. At that depth, screen excited luminescence is dominated by large, amorphous shaped glows produced by long persistent luminescence from copepods and euphausids along with a diminished dinoflagellate signal. This shift from dinoflagellate to crustacean dominated luminescence continues to greater depths where the video image reveals rare, bright luminescences of long persistence almost exclusively from copepods and euphausids and rarer gelatinous zooplankton. Much of the signal is from highly persistent secreted luminescent material discharged when animals strike the screen. The high variability in the kinetics trace from position 3 through 4 and beyond is indicative of bright but increasingly rare luminescent sources. Finally, the HIDEX fluorescence signal confirms the presence of nannoplankton in near surface water.

Other Methods of Assessing Oceanic Bioluminescence

Tests on Collected Organisms

In parallel with bioluminescence bathyphotometry in the sea, there has been a long-term research effort to identify bioluminescent sources and to assess their luminescent properties. Such information is essential to an understanding of the populational basis of luminescence which, in turn, is essential to developing predictive capability. Organisms may be collected by quantitative net tows, by net capture of organisms in the exhaust of low pumping volume bathyphotometers, or directly by plankton pumps. Enumeration of such material provides information on population structure. These data to-

Figure 6.

Alboran Sea joint HIDEX and Johnson-Sea-Link bioluminescence profile. Width of video field is 1.0 m. (See text).

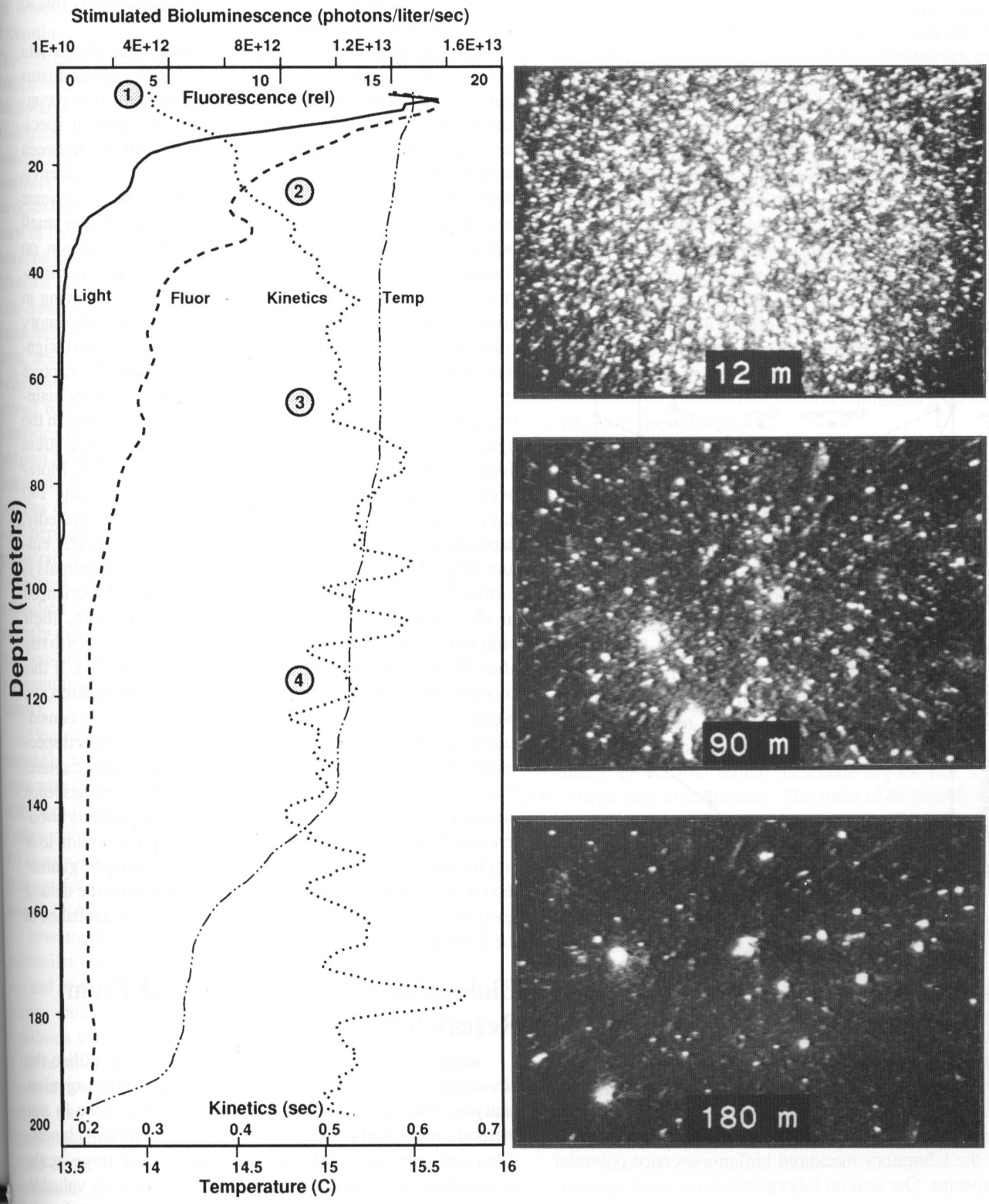
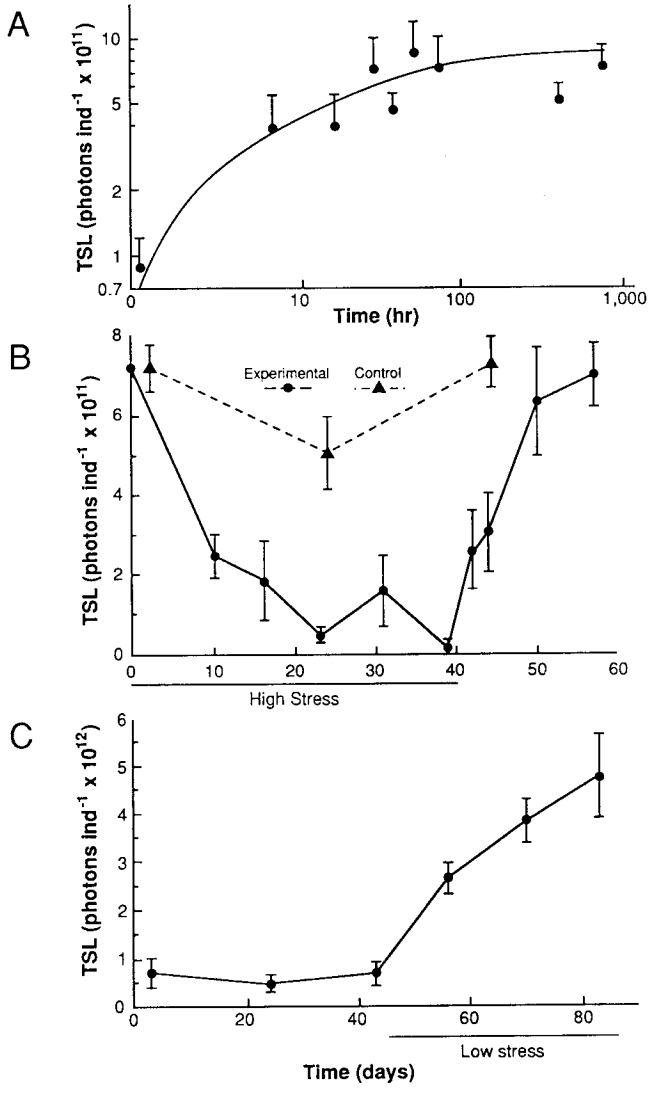


Figure 7.

Stress effect on bioluminescence potential in a copepod crustacean, Gaussia princeps. (A) In this plot zero denotes time of capture by a deep trawl with a thermally protected, closing cod end. The first 100 hr were on shipboard. (B) Under shore laboratory conditions with standardized high and low stress environments.



gether with measurement of total stimulable light of identified specimens measured in shipboard photometers are used to construct bioluminescence light budgets. These are estimates of *in situ* bioluminescence potential derived from the estimated numbers of bioluminescent organisms present multiplied by the laboratory measured bioluminescence potential of each species. Our several laboratories have made substantial improvements in this methodology by using integrating sphere quantum counters in conjunction with fast spectrometers to precisely characterize bioluminescence emissions from many varieties of luminescent organisms. Such data, however, is of uncertain value as a basis for construction of bioluminescence light budgets, even when low values presumably due to capture stress are discarded[18].

This pessimism comes from the view that the *in situ* bioluminescence stress level of many, perhaps most organisms can only be determined by *in situ* measurement. It is recognized that the bioluminescence potential of captured specimens is strongly influenced by recovery conditions between capture and measurement[19, 20]. The recovery time and environment available on shipboard is likely to be inadequate except, perhaps, for dinoflagellates and some other very small organisms. This is illustrated by a recent investigation on Gaussia princeps, a large (5 mm long) and brilliantly luminescent copepod which has the great advantage of surviving in good condition indefinitely under shore marine laboratory conditions[21]. It is, therefore, a model organism for investigation of bioluminescence potential as influenced by capture stress and stress derived from conditions of laboratory maintenance. Figure 7A shows nearly an eight-fold increase in the light response of Guassia to a standard mechanical stress during the first 1000 h (42 days) after net capture[20, 22]. Moreover, shore laboratory tests continued over the ensuing 140 days show that luminescence potential, not unexpectedly, depends on the physical stress levels experienced under culture (Fig. 7B). Remarkably, when stress on control animals is further reduced to an absolute minimum from that experienced in the standard laboratory maintenance regime, their bioluminescence potential rises markedly and continues to rise after 20 days on the minimal stress regime (Fig. 7C). If this copepod species can be considered typical of zooplankton, the bioluminescence potential of organisms *in situ* may be considerably at variance with measurements made on captured specimens irrespective of how they may be treated after capture. This is because it is logical to expect that in situ luminescence potential varies with environmental conditions such as turbulence and predator encounters. Consequently, restoration to *in situ* bioluminescence capacity after capture cannot be guaranteed by any period of recovery before testing since the natural level of excitation, being unknown, cannot be reestablished in the laboratory.

Bioluminescence Measurement From Research Submarsibles

Research submersibles have the capacity to utilize the advantages of both bathyphotometry and single organism analysis, with the considerable advantage that these *in situ* methods avoid the problems of capture stress. While submersibles are not practical for continuous and large scale bioluminescence survey work, they are an extremely valuable means of verification for other methods and provide information that would otherwise be unavailable regarding in situ

excitability and fine scale resolution of local distributions of organisms, as exemplified in the Alboran Sea study.

Bioluminescence has been a constant motif in the history of research submersibles. William Beebe described bioluminescence during his pioneer bathysphere descents as "pyrotechnic fireworks"[23]. His enthusiastic descriptions accompanied by dramatic paintings of luminescent animals in his popular writings undoubtedly marked many "tyro" marine biologists for life. Piccard and Dietz[24], observed from the bathyscaph Trieste "luminescent animalcules in very large numbers". Also working from the Trieste, Rechnitzer (1962) as described by Boden and Kampa[25], observed bioluminescence in terms of "the number of stars that can be seen in the heavens on a clear, dark night". On dives in the Straights of Messina using the mesoscaph Forel, Baguet et al.[26] made the first quantitative bioluminescence measurements from submersibles. They used a PMT to measure downwelling irradiance, and noted a visually diffuse luminescence, which they believed to be bacterial. Similar phenomena have been observed repeatedly since then at many locations but without identification of the causal organisms. Losee et al.[27] used both an open field and a pumped bathyphotometer on the Johnson-Sea-Link and Alvin submersibles to make the first vertical profiles of bioluminescence from a submersible. Widder et al.[28] deployed an ISIT video camera on the single person submersible Deep Rover to record both stimulated and unstimulated bioluminescence in Monterey Canyon and then quantified the video data by computer image analysis. More recently this procedure has been adapted for use on the Johnson-Sea-Link submersible in combination with an open field photomultiplier tube calibrated for irradiance (Widder, unpublished).

Measurements of bioluminescence from research submersibles have two major advantages over measurements made with bathyphotometers lowered from ships. First, undesirable premature stimulation of organisms is reduced because a submersible in neutral buoyancy is largely motionless relative to surrounding water. A submersible is, therefore, an ideal platform for investigations on the extent of background, or natural, bioluminescence in the ocean.

Investigations of bioluminescence in Monterey Canyon[28] and similar investigations in the Gulf of Maine, off the Bahamas and in the Mediterranean Sea have failed to detect spontaneous emission (Widder, unpublished). This supports the hypothesis that the majority of background bioluminescence in the ocean is a consequence of encounters between organisms and, where encounters are rare, natural bioluminescence will be rare, even in regions of high levels of stimulable bioluminescence[12]. Similar results are obtained at much greater depths when open field detectors are uncoupled from ship motion, as demonstrated in test deployments of components of the prototype DUMAND nutrino detector array off Hawaii[29]. Bottom anchored, open-field detectors at about 4500 m detected less luminescence than free-falling or ship tethered instruments.

The second advantage of the research submersible as a measurement platform is the ability to identify organisms responsible for stimulable bioluminescence. In addition, it is possible to make simultaneous, quantified luminescence measurements on individuals and on the populational sample stimulated by the grid pushed ahead of the submersible. This methodology is, indeed, perhaps the only one available for coping with the fragile and often very large (lengths up to several meters) gelatinous organisms which are destroyed by nets and pumps, but which represent some of the brightest sources of light in the ocean[28]. From submersibles it is often possible to identify the dominant light producers by relating an organism to a particular display. More recently it has become possible to measure the intensity and kinetics of identified zooplankton bioluminescence *in situ* using a radiometer mounted on the Johnson-Sea-Link submersible to evaluate luminescence of single organisms in situ after non-stimulatory isolation in a suction stimulatory screen device (Widder, unpublished).

Problems Remaining

Marine scientists typically have considered bioluminescence to be an interesting curiosity with little relevance to the central problems of marine ecosystems. While it has been a matter of endless fascination to molecular biologists, physiologists and behaviorists, investigation of bioluminescence has never become part of the routine of oceanographic research. When it has been studied at sea, it has usually been on those rare instances when bioluminescence has been a research focus of a cruise. This neglect seems unfortunate because the prevalence of oceanic bioluminescence argues that it must play a large role in the oceans. The roles of bioluminescence thus far defined seem almost trivial in view of this fact.

In large part this perceived neglect may be an example of a problem waiting for adequate technology. Marine bioluminescence survey work has been so limited that correlations of bioluminescence with oceanic conditions are insufficient to support any but the most elementary hypotheses concerning its roles in marine life. Indeed, one might as well derive an empirical transfer function between bioluminescence and biomass and be done with it as far as present knowledge is concerned. This solution, however, neglects the possibility that bioluminescence may itself have a role in population dynamics beyond those now understood. It may have a more general role in regulation of marine populations, especially in that dominant fraction of the world's inhabitable volume in which bioluminescence is the only light and, thereby, the only indicator of the state of the local environment outside the limited spatial coverage of the chemoreceptors and mechanoreceptors of the inhabitants.

Perhaps the instrumentation and methods described here point out a new path in marine biology in which new methods and apparatus will permit testing hypotheses in which bioluminescence is seen as playing a regulatory role in population dynamics along with the more traditional driving forces. Technology is now available or conceptually plausible to explore larger questions such as bioluminescence potential as a regulatory signal in optimal exploitation of biological carrying capacity in oceanic communities.

Biography

James F. Case is Professor of Biology and Associate Vice Chancellor for Research at the University of California, Santa Barbara. He received the PhD from Johns Hopkins University. His research interests are in invertebrate sensory physiology and in bioluminescence from the physiological and behavioral points of view, with emphasis at present in assessing the role of bioluminescence in marine population dynamics and in developing instrumentation to facilitate investigations of marine bioluminescence. His research on bioluminescence has been conducted on expeditions to New Guinea, Malaysia and Indonesia and on many research cruises.

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