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Luminescent properties of deep sea fish

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Abstract: Bioluminescence flash kinetics and quantum emission of specimens of 15 species of Hawaiian deep sea fish of the families Astronesthidae, Gonostomatidae; Malacosteidae, Melanostomiidae, Myctophidae and Sternoptychidae were determined. Peak flash intensities ranged from 5.1×10^{09} to 8.7×10^{11} photons $\cdot s^{-1}$ and average flash durations varied from 160 to 4000 ms. Light emission from ventral photophores of myctophids and hatchetfish was sufficient to match downwelling environmental light. Photophore area and maximum light output increased with standard length. Caudal and body photophores of smaller, vertically migrating myctophids made significantly briefer flashes than orbital photophores of larger stomiatiods, indicating predation pressure may favor brief flash durations. Flash kinetics of *Malacosteus niger* Ayres further supported this theory because its red emitting suborbital photophores produced significantly longer flashes than the conspicuous postorbital blue emitting organs. The distinct flash patterns of two species of *Lampanyctus* may permit recognition between individuals with similar photophore arrays and overlapping habitats. Flashes in intact hatchetfish were observed for the first time.

Key words: Animal behavior; Bioluminescence; Marine biology; Teleost

Introduction

Deep sea teleosts have evolved many adaptations to their unique environment. One that is prevalent in many families is bioluminescence (Herring, 1987). Fish luminescent organs vary widely in structure and function. Some harbor luminous bacteria while others utilize intrinsic luminous tissues (Herring & Morin, 1978; Herring, 1982). Emission spectra are primarily centered in the blue (Herring, 1983) because it attenuates least in water (Lythgoe, 1972; Jerlov, 1976). Many theories of the adaptive significance of bioluminescence in the deep sea have been proposed, including prey attraction and predator avoidance (Nicol, 1967, 1969; Buck, 1978; Herring, 1982).

A major obstacle to the study of deep sea fish luminescence is the difficulty in obtaining viable specimens. The mechanical and physiological stresses of trawling are severe, and opportunities for collection from submersibles are rare. Moreover, diurnal, surface migrators, hand netted at night, fail to survive for any appreciable period (Robison, 1973). Early work was thus restricted to visual observations and gross morphology of the light organs (Beebe & Vander Pyl, 1944; Harvey, 1952; Nicol, 1967).

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These initial studies provided little information on the adaptive significance of the luminescence. To proceed towards this goal, it is imperative to quantify spectral emissions, flash kinetics and intensities.

Early analyses of emission spectra were often limited to subjective color estimates because most flashes were too rapid for spectral analysis by instruments then available. Although Nicol (1960) was able to determine the spectral emission of a myctophid using color filters and a photomultiplier tube, only in the last decade has the application of fast spectrometer systems allowed the emission spectra of a greater variety of fish to be routinely documented with high resolution (Widder et al., 1983). These instruments were vital in documenting the red luminescence of certain deep sea fish, an unexpected discovery considering the marked attenuation of long wavelengths in sea water (Denton et al., 1970; O'Day & Fernandez, 1974; Smith & Baker, 1981; Widder et al., 1984; Denton et al., 1985).

There are a number of studies of deep sea fish luminescence kinetics, principally on myctophids. Flash durations from caudal and body photophores ranged from 60 to 3000 ms (Nicol, 1958; Barnes & Case, 1974; Baguet, 1975; Baguet & Marechal, 1976; Edwards & Herring, 1977; Baguet et al., 1980; Herring, 1982).

Essential to consideration of adaptive significance of bioluminescence is emission intensity as related to visual sensitivity of conspecifics and of potential prey and predators. The eyes of deep sea animals generally seem to have evolved morphological characteristics and visual pigments to maximize light absorption in the dim, predominantly blue downwelling light field (Locket, 1977; Partridge et al., 1988). Only a few studies have quantified luminescence in deep sea fish (Baguet, 1975; Case et al., 1977; Edwards & Herring, 1977). Most theories of the role of bioluminescence that incorporate quantum emissions cite the value of 5×10^{-8} $\mu W \cdot cm^{-2}$ (1.5×10^{10} photons $\cdot s^{-1}$), obtained from a single myctophid (Nicol, 1958, 1978).

The purpose of this study is to lay the groundwork for understanding the roles of deep sea teleost luminescence by presenting kinetic and quantum emission data from a wide assortment of teleosts.

Materials and Methods

Specimens were obtained in the summer of 1987, off the southern coast of Oahu. Fish were captured in an opening/closing 3.1-m Tucker trawl equipped with a thermally insulated cod end that allowed recovery of specimens in good physiological condition (Childress et al., 1977). After net recovery, fish were immediately placed in 4 °C filtered seawater. Even under these conditions, early physiological deterioration necessitated that all experiments be conducted within 1 h of net retrieval.

Flash kinetics and photon emission were quantified with an integrating sphere quantum counting photometer (Latz et al., 1987). Specimens were placed between two silver electrodes in clear Plexiglas chambers filled with 4 °C filtered sea water, and

enclosed in a 0.25-m diameter integrating sphere. Light emission was measured by a RCA 8850 photomultiplier tube operating at – 1700 V with a calibrated discriminator setting of – 0.315 V. The resulting frequency signal was counted with an Ortec No. 776 counter/timer and displayed on a Norland No. 5400 multichannel analyzer (MCA). The MCA trace was subsequently stored on disc. Radiometric calibration of the detection system included determination of the combined spectral responsitivity of the integrating sphere/photon counting apparatus using an Optronic Laboratory Model 310 calibration source referenced to an NBS standard. When the emission spectrum of the species was unavailable, calibration was performed with the spectrum of the closest related genus as found in Swift et al. (1977), Herring (1983), and Widder et al. (1983, 1984). Electrical stimuli were applied as monophasic pulses from a Grass stimulator through silver electrodes directly to the integument of the fish. Intermittent stimuli were initiated at 1 V and gradually increased until light was generated. Stimulation frequency ranged from 0.2 to 100 Hz, and pulse duration from 5 to 500 ms. Mechanical stimulation was induced by prodding with a glass rod or by gentle handling. No bioluminescence was detected from electrical or mechanical stimulation of the filtered seawater in which specimens were tested.

Maximum intensities were obtained soon after initial stimulation and output gradually dimmed and shortened with continuous stimulation. To minimize morbidity effects, only flashes that were at least 50% of maximum intensity were used to calculate flash lengths and quantum emissions. Rise time was calculated from flash onset to 90% of maximum emission. Flash length was determined from onset until emission decreased to 10% of maximum intensity. All kinetics data is based on single, discrete flashes.

Flashes were observed directly and with a low light level DAGE ISIT camera. Use of the integrating sphere prevented video recording with simultaneous measurement of flash intensities and kinetics. Flash images were stored on video tape and evaluated using a Megavision 1024xM image analysis system.

RESULTS

Flash kinetics and quantum emission for intact specimens of 15 species are summarized in Table I. The organs noted in that table were observed to provide the majority of the light upon stimulation. Paired, bilateral orbital photophores of *Astronesthes indicus* Brauer, *Echiostomata barbatum* Lowe, *Melanostomias melanops* Brauer, *Photostomias guerni* Collett, were always observed to flash simultaneously. *Malacosteus niger* Ayres, exhibited independent control over its dual orbital photophores although simultaneous flashes were also observed. The displays from *Lampanyctus* sp. Bonaparte and *Taaningichthys minimus* (Tåning) were confined to caudal organs. *Bolinichthys longipes* (Brauer) and *Ceratoscopelus warmingii* (Lütken) produced light from the caudal organs, ventral patches and body photophores with the largest fraction of light originating from the infracaudal region. Displays from *Diaphus* sp. Eigenmann & Eigenmann originated

TABLE I

Figures in parentheses after species names represent sample number. Light organs noted were observed to contribute the majority of light. With exception of maximum intensity, all numbers represent the mean ± 1 SD.

Bioluminescence of Hawaiian deep sea fish						
Family Species	Light organ	Standard length (cm)	Flash duration (ms)	Rise time (ms)	Quantum emission	
					Maximum	Average (photons · s^{-1})
Myctophidae						
Bolinichthys	Body and	4.4	408	122	8.7×10^{11}	2.9×10^{10}
longipes (9)	caudal	± 1.4	± 292	± 83		$\pm 5.8 \times 10^{10}$
Ceratoscopelus	Body and	4.8	484	265	1.8×10^{11}	1.1×10^{10}
warmingii (29)	caudal	± 0.9	± 562	± 299		$\pm 5.7 \times 10^{10}$
Diaphus	Head	6.5	346	318	4.5×10^{10}	2.9×10^{10}
sp. (4)		± 0.4	± 230	± 135		$\pm 1.7 \times 10^{10}$
Lampanyctus	Caudal	6.9	332	69	1.2×10^{11}	5.5×10^{10}
niger (3)		± 0.8	± 174	± 19		$\pm 5.3 \times 10^{10}$
Lampanyctus	Caudal	6.7	169	44	4.8×10^{10}	2.0×10^{10}
tenuiformis (5)		± 1.5	± 136	± 19		$\pm 1.9 \times 10^{10}$
Taaningichthys	Caudal	6.0	359	168	3.1×10^{11}	8.9×10^{10}
minimus (12)		± 0.2	± 365	± 179		$\pm 6.8 \times 10^{10}$
Astronesthidae						
Astronesthes	Suborbital	6.5	674	387	5.1×10^{09}	2.6×10^{09}
indicus (1)			± 229	± 176		$\pm 1.4 \times 10^{09}$
Neonesthes	Postorbital	12.2	1672	817	8.2×10^{10}	6.7×10^{10}
capensis (1)			± 1388	± 340		$\pm 1.1 \times 10^{10}$
Gonostomatidae						
Gonostoma	Photophores	13.2	870	356	2.9×10^{10}	1.1×10^{10}
elongatum (2)		± 1.9	± 371	± 123		$\pm 1.3 \times 10^{10}$
Malacosteidae						
Malacosteus	Postorbital	9.6	1502	419	2.8×10^{11}	5.4×10^{10}
niger (23)		± 1.0	± 945	± 215		$\pm 6.5 \times 10^{10}$
	Suborbital		4010	600	2.5×10^{10}	1.0×10^{10}
			± 1200	± 125		$\pm 5.0 \times 10^{09}$
Photostomias	Postorbital	8.3	773	168	2.1×10^{10}	2.0×10^{10}
guerni (2)		± 1.1	± 274	± 61		$\pm 1.0 \times 10^{10}$
Melanostomiidae						
Echiostoma	Postorbital	13.0	557	178	1.7×10^{11}	8.1×10^{10}
barbatum (2)		± 0.7	± 108	± 48		$\pm 5.1 \times 10^{10}$
Melanostomias	Postorbital	9.8	1073	162	5.1×10^{10}	4.2×10^{10}
melanops (3)		± 1.3	± 368	± 107		$\pm 6.9 \times 10^{09}$
Sternoptychidae						
Sternoptyx	Photophores	2.7	346	218	2.5×10^{10}	1.0×10^{10}
diaphana (6)		± 0.6	± 230	± 135		$\pm 7.5 \times 10^{09}$
Sternoptyx	Photophores	5.1	351	278	1.5×10^{11}	7.6×10^{10}
pseudobscura (4)		± 0.7	± 54	± 15		$\pm 4.8 \times 10^{10}$

from the cephalic organs and body photophores with the head region contributing the majority of the light. *Sternoptyx* sp. Hermann and *Gonstoma elongatum* Günther luminescence originated from ventral photophores.

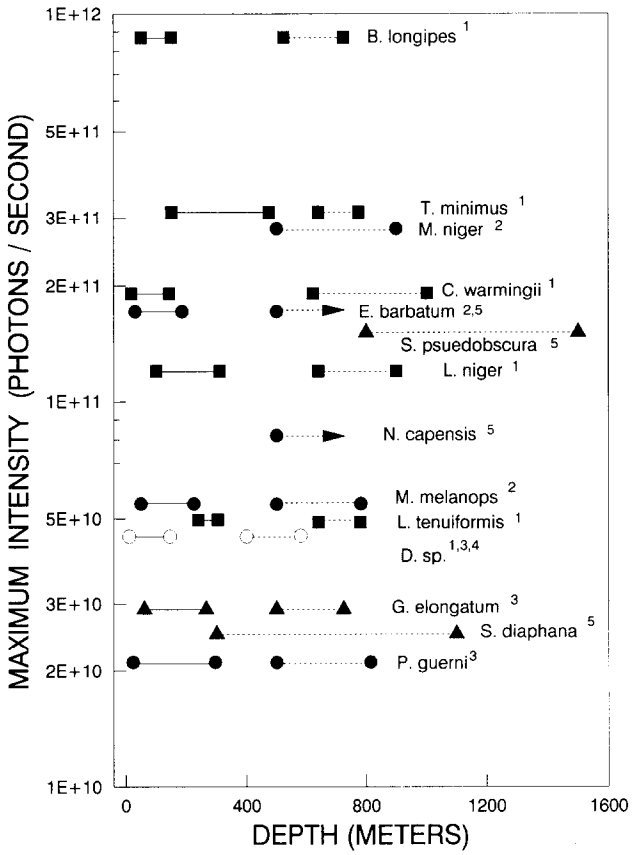

Fig. 1. Light emission correlated with characteristic depth. Maximum intensity is plotted against depth distribution. Lines indicate night (solid) and day (dotted) distribution. Arrows represent indeterminant maximum depth. Light organs are designated by markers: caudal (square), orbital (solid circle), head (open circle) ventral (triangle). Depth distributions were obtained from the following sources: [1]Clarke, 1973; [2]Clarke, 1974; [3]Clarke, 1978; [4]Wisner, 1974; [5]Whitehead et al., 1984.

Most of the species in this study inhabited similar daytime depths. There was no correlation between depth distribution and maximum emission intensity (Fig. 1). Many species migrated to shallower depths during the night.

Flash kinetics varied widely among the population sampled. Fig. 2 compares the mean flash length of stomiatoid orbital organs and myctophid caudal tissue. Mean flash duration was calculated for each species and mean species flash duration was compared

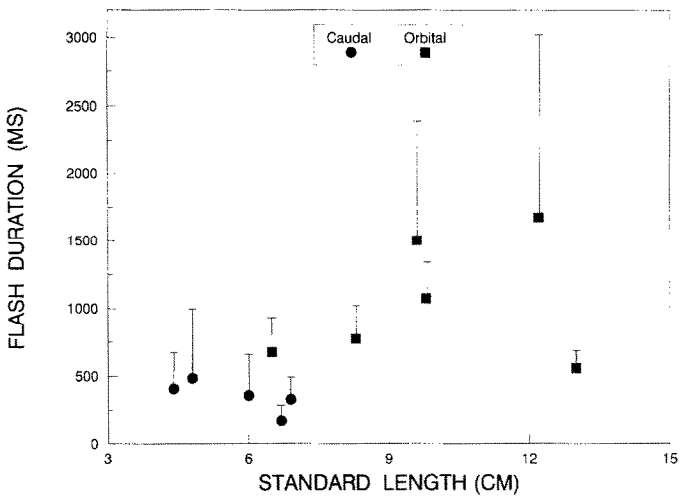

Fig. 2. Mean flash duration of myctophid caudal organs and stomatoid orbital organs. Light organs are represented by markers; caudal (circle) and orbital (square). Each point represents mean flash duration of one species. Errors bars represent 1 SD. Mean flash duration between the two groups is significantly different (two sample t test, $p < 0.01$).

between the two groups. Orbital light organs exhibited significantly longer flashes (two-way t test, $p < 0.01$), averaging longer than one second, while mean duration of the caudal organ display was ≈ 400 ms. Fig. 3 compares the mean flash duration of two species of *Lampanyctus*. Average flash duration (flash number ≥ 5) was calculated for

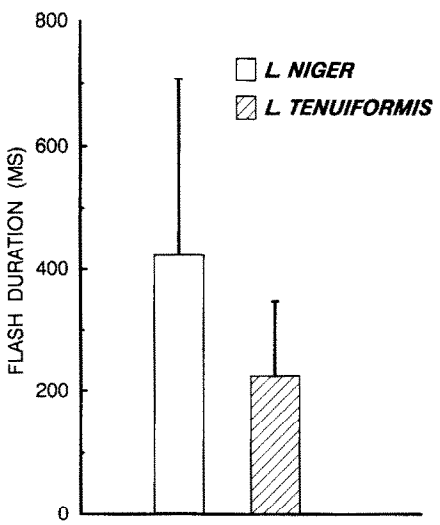

Fig. 3. Mean flash duration of caudal organs of *Lampanyctus niger* and *L. tenuiformis*. Error bars represent 1 SD. Mean flash duration between the species is significantly different (two-sample t test, $p < 0.05$).

each animal and the resulting mean flash durations were compared between species. *L. niger* (Günther) produced significantly longer flashes (two-way *t* test, $p < 0.05$) than *L. tenuiformis* (Brauer).

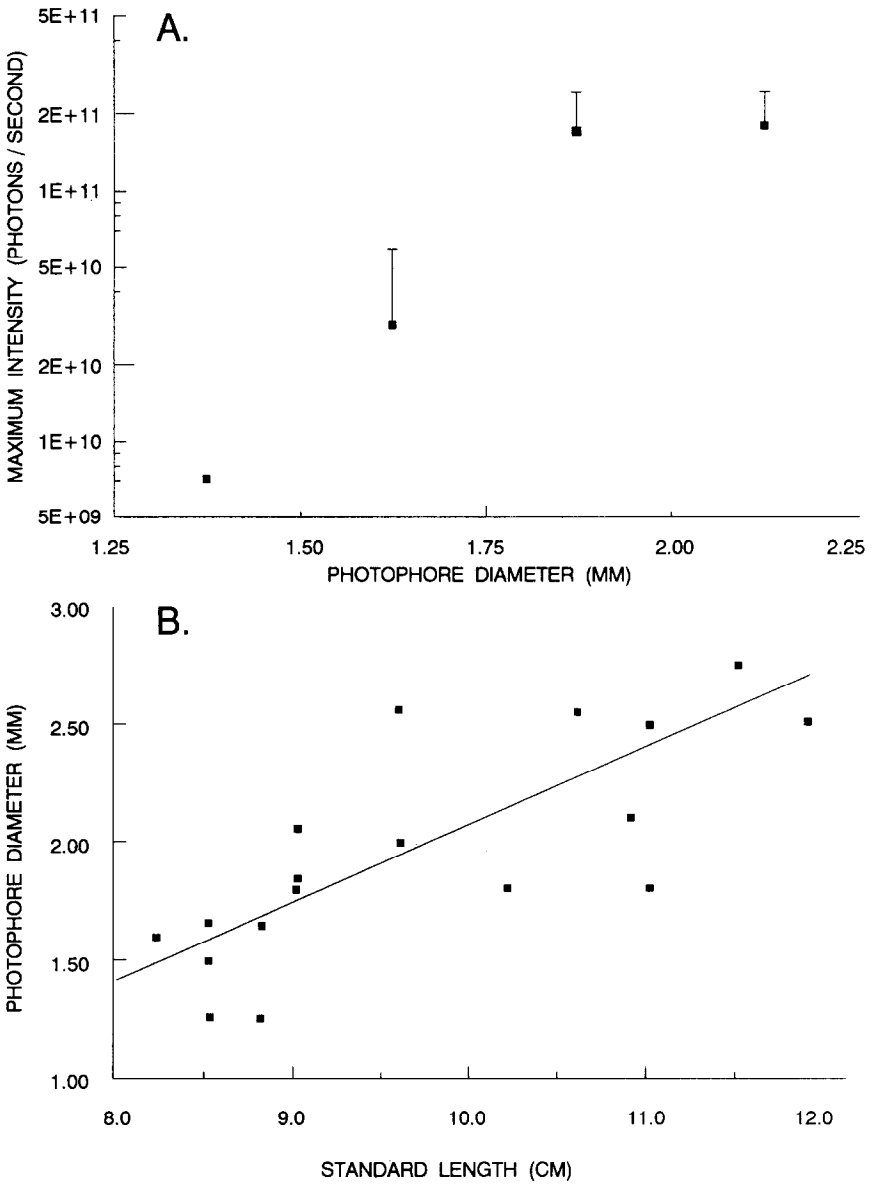

Fig. 4. (A) Maximum intensity (photons $\cdot s^{-1}$) is plotted against the photophore diameter (mm) of the postorbital photophore of *Malacosteus niger*. Error bars equal 1 SD. (B) The photophore diameter (mm) is plotted against the standard length (cm) of the fish. Line represents calculated least-squares linear regression of photophore diameter on standard length, according to equation: $y = -0.77 + 0.28x$, $r^2 = 0.60$.

Photophore area and light output increased with standard length in both *M. niger* (Fig. 4) and *C. warmingii* (Fig. 5).

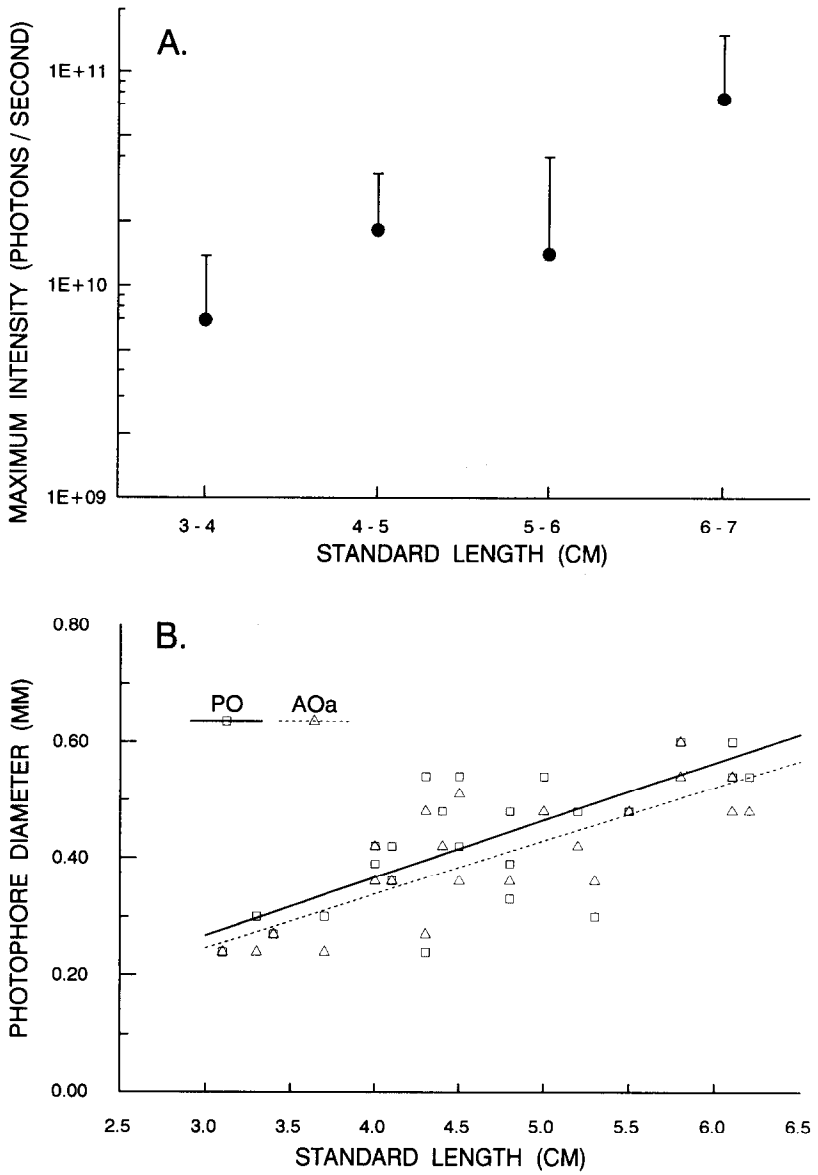

Fig. 5. (A) Maximum intensity (photons $\cdot s^{-1}$) and (B) photophore diameter (mm) of PO_4 (squares) and AOa_2 (triangles) of *Ceratoscopelus warmingii* as a function of selected classes of standard length (cm). Error bars equal 1 SD. Lines represent calculated least-squares linear regression of photophore diameter on standard length, according to equations; PO_4 (solid), $y = -0.10 + 0.12x$, $r^2 = 0.66$; AOa_2 (dashed), $y = -0.05 + 0.09x$, $r^2 = 0.61$.

DISCUSSION

In an attempt to gain a better understanding of the roles of teleost bioluminescence in the deep sea environment, the flash kinetics and quantum emissions of a wide variety of fish were determined (Table I). In interpreting our results, it must be kept in mind that the fish were subjected to physiological stress during recovery. Similar studies with the midshipman fish *Porichthys notatus* Girard demonstrated initial depletion of bioluminescence after trawling from much shallower depths, with at least a week of laboratory maintenance needed to obtain peak intensities (Mensinger and Case, unpubl. data). Although all animals tested exhibited some swimming ability, their physical condition most likely compromised luminescent capacity. Therefore, values should be treated conservatively, with maximum intensities perhaps being more indicative of the normal. There is at present, no less stressful way to obtain such data.

Maximum luminescent intensity ranged from 2×10^{10} to 8.7×10^{11} photons $\cdot s^{-1}$, discounting the single *Astronesthes indicus* specimen (5×10^{9} photons $\cdot s^{-1}$). This variation is not surprising considering the size range of the fish and light organs in addition to the diverse photophore arrays in the sampled group. Arrays of small photophores equaled, if not exceeded, the intensity of large, paired orbital photophores. Larger conspecifics had greater light emission capacity than smaller fish, which was attributed to greater photophore area although an increase in emission capacity per unit area could not be dismissed.

No correlation was exhibited between depth distribution and luminescent capacity. Most fish captured inhabited similar daytime depths. A survey of fish from a wider range of depths might reveal greater light capacity in shallower species to offset the higher ambient light. The one species of myctophid, *B. longipes*, inhabiting shallower daytime depths did, in fact, have the highest flash capacity noted in this investigation for the family.

The fish examined had four main types of light organs: orbital, ventral body, caudal, and barbels. Flashes were not recorded from barbel organs due to damage or insensitivity to stimuli.

Various theories concerning teleost luminescence have been reviewed (Nicol, 1967; Buck, 1978; Herring, 1982) encompassing the remaining three categories of photophores. Orbital photophores have been the focus of several hypotheses. Their large size and position seems ideal to provide a wide beam for prey illumination (Beebe & Vander Pyl, 1944; Harvey, 1952). Other hypotheses include mate or prey attraction (Denton et al., 1985) and blinding or confusing light sensitive predators (Nicol, 1978). Members of the Melanostomiidae and Malacosteidae in the experimental group were characterized by at least one pair of orbital photophores. The approximate intensity of individual photophores was obtained by halving the values in Table I as the bilateral pairs were never observed to flash independently. The intensities ranged from 1×10^{10} to 1×10^{11} photons $\cdot s^{-1}$, relatively high values for single organs. The blue emission and high emission intensity are ideal for maximum penetration of the water column, lending

credence to the signalling and defensive theories. A major obstacle to the prey illumination hypothesis is the black and red body pigmentation of many deep sea animals which absorb rather than reflect blue light (Nicol, 1958). An additional orbital organ evolved in the malacosteids, whose far red emission may offset the effects of red coloration. The far red emission appears optimal to illuminate red prey and can be produced independently of the blue organ. However, the attenuation of red light in water and the intensity limitations imposed by its screening filter, severely curtails its effective range (Denton et al., 1985).

Our data for the malacosteid *M. niger* allows a rough quantitative evaluation of the ecological significance of blue and red bioluminescence. The larger suborbital organ emits light in the far red with a peak emission of 705 nm, while the emission spectrum of the postorbital photophore is centered in the blue-green region of the spectrum with maximum emission at $\approx$475 nm (Widder et al., 1984). Our ISIT observations show that both organs do not directly illuminate the eye, an important feature for a visually sensitive hunter. Red light was predominantly emitted laterally and ventrally while blue emission was more widely distributed due in part to its greater intensity. Quantification of the emission from the dual photophores allows an estimation of the distance over which the fish can utilize its bioluminescence. It should be noted that the optics of the photophore are not defined and its emission may have attributes of both a point source and a collimated beam. Functional limiting distances are based on the more conservative point source estimate. Light from a point source diminishes in intensity inversely with the square of the distance, and also because of absorption and scattering in the light path (Lythgoe, 1972). However, light scattering into the eye is ignored due to the low ambient light intensities and low particle number density in the deep sea. It is estimated that the visual threshold of a deep sea fish is 10×10^{-10} $\mu W \cdot cm^{-2}$ (Nicol, 1978). Using this value and the inverse square law, the distances the fish can detect its own bioluminescence can be estimated. The calculations are based on analogous visual sensitivities for both wavelengths although certain morphological adaptations, such as a red tapetum and yellow lens, may increase sensitivity to red light. The tapetum reflects red light, increasing sensitivity to longer wavelengths, while the lens absorbs light in the blue spectral region, and might thereby increase contrast enhancement of red light (Locket, 1977; Somiya, 1982). The intensity of the blue photophores was reduced in the calculations 50% to account for lens absorption (Somiya, 1982). Although red sensitive visual pigments have not been isolated, the presence of a rhodopsin–porphyropsin system of paired pigments has been reported in *M. niger*, suggesting that the long wavelength sensitive rods are an adaptation enabling the fish to perceive its own red luminescence (Bowmaker et al., 1988).

Two examples illustrate the probable ranges of these organs and their behavioral consequences. The first considers intraspecific signalling and the second prey detection (Fig. 6). During signalling, the fish are assumed parallel to each other with the emitting surface of the first fish and the pupil of the second both being normal to a line joining the two (Denton et al., 1985). The advantage of shorter wavelengths in typical oceanic

water (Type I; Jerlov, 1976) is clearly illustrated as the postorbital organ is visible from a distance four times greater than the red photophore (Fig. 6, 100% reflection indicates intraspecific signalling) allowing long range intraspecific communication to almost 11 m, a significant advantage in the depauperate deep ocean environment. The wavelengths and intensities of the postorbital photophore are optimal to attract mates or prey from relatively long ranges in the sparse environment.

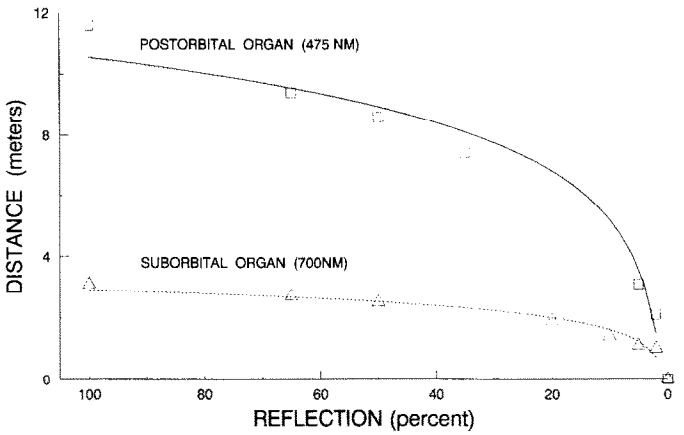

Fig. 6. Estimated distance (meters) that *M. niger* can detect its own bioluminescence reflected from objects of various reflectances. Lines represent calculated least-squares logarithmic regression of distance on reflection, according to equations: postorbital organ (solid), $y = -0.15 + 2.32 \cdot \ln x$, $r^2 = 0.97$; suborbital organ (dotted) $y = 0.33 + 0.56 \cdot \ln x$, $r^2 = 0.95$.

The second example concerns luminescence diffusely reflected from an object back into the signaller's eye (Fig. 6). The advantage of blue light rapidly declines when reflected by black- and red-pigmented surfaces. Although a silvery-sided fish may reflect up to 65% of incident light, a black- or red-bodied animal reflects only 2–5% of blue wavelengths (Nicol, 1958). If the prey absorbs 98% of blue light, it would only be visible at <2 m although the predator's bioluminescence itself may be detected by other predators and prey from a far greater range. The situation improves significantly for the suborbital organ. Nicol (1958) estimated that 20% of red light striking a red carapace is reflected which would allow prey detection at 2 m. Even if only 2% of the light is reflected, *M. niger* could detect a black target over a meter away with its red organ, gaining a tremendous advantage in an environment devoid of most visual cues.

The monochromatic, dim photic environment has led to the evolution of morphological adaptions to maximize sensitivity to blue wavelengths at the expense of acuity and long wavelength sensitivity (Locket, 1977). The scarcity of red visual pigments in the deep ocean (Partridge et al., 1988) allows use of the suborbital organ for communication with minimal chance of discovery by interlopers and allows detection of prey or predators while remaining unseen.

The caudal organs have been assigned predator avoidance roles (Beebe & Vander Pyl, 1944; Bolin, 1961), which is consistent with the relatively intense (up to 3.1×10^{11} photons $\cdot s^{-1}$) flashes and their posterior location. The bright flash could easily blind or startle light sensitive predators. Despite the moribund condition of the myctophids in this investigation, caudal organ flashes were usually accompanied by a tail flick consistent with a flash and swim strategy. The innervation of the caudal organs by spinal neurons is consistent with this function (Anctil & Case, 1977). The brief caudal organ flashes may meet defensive requirements while minimizing opportunity for visual localization of the source by a predator.

Ventral and lateral body photophores have been associated with two main functions, counter-illumination (Lawry, 1974; Case et al., 1977) and intraspecific communication (Paxton, 1972). The ventral photophores are thought to obscure the body outline from predators when viewed against downwelling light, while the species specific lateral photophore distributions appear useful for species recognition. Light emission measured in this study from the myctophids *B. longipes* and *C. warmingii* included contributions from body photophores and ventral patches in addition to caudal tissue. The principal tail emissions appeared to originate from the infracaudal tissue. Total photophore light output (1×10^{8}–1×10^{11} photons $\cdot s^{-1}$, excluding the caudal tissue, was within the intensity range (3×10^{8}–3×10^{12} photons $\cdot s^{-1}$) that the fish would encounter at their daytime depth of 600–1000 m and during their nightly migration (Clarke & Denton, 1962; Clarke, 1973). Therefore, the physiological capacity to produce sufficient light to counter-illuminate is present.

Hatchetfish ventral photophores appear structurally well suited for counterillumination and the dim glow observed immediately after capture was consistent with earlier observations (Herring, 1977; Denton & Herring, 1978). However, direct electrical stimulation to the integument produced quick, intense flashes never before observed in intact animals. These were up to two orders of magnitude greater than the glow reported by Herring & Morin (1978). As a number of midwater animals have visual adaptations that tend to defeat counter-illumination, we speculate that the capacity to emit bright flashes may serve either to startle or to temporarily blind predators once an attack commences or to have a burglar alarm effect.

Luminescence kinetics provides insight into bioluminescent behavior that is not evident from measurements of peak intensities. For example, the myctophids captured were all relatively small (4–7 cm), vertical migrators that generate quick flashes. On the other hand, representatives of the Stomiatoidei that we studied were larger (≤ 14.5 cm) and exhibited longer flashes than the myctophids. Their dentition reflects their predatory nature and higher trophic level position. The nightly upward trek of myctophids subjects them to epipelagic predators, possibly increasing predation pressure. Longer displays increase exposure time to predators except during counter-illumination. It thus appears plausible that visual predation pressure selected for shorter flashes. This argument is supported in even larger fish as seen for the dual light organs of *M. niger*. The blue postorbital photophore is more conspicuous based on its greater intensity, lower attenu-

ation of its output, and the prevalent visual pigments of deep sea animals. Although its 1.5-s duration is relatively long contrasted to the myctophids, it is still short in comparison to the 4-s emissions of the red suborbital photophore. The lack of red visual pigments in most other animals at these depths allows use of the red photophore with relative impunity.

If bioluminescence in deep sea fish has a role in intraspecific communication, signalling differences must exist between groups. At the generic level, although differences were apparent, either our results were too variable or the samples too small to arrive at significant conclusions. However, there was one instance in which two species were collected from one genus. These two species of *Lampanyctus* have similar photophore distributions and overlapping habitats (Clarke, 1973). *L. tenuiformis* emits much briefer flashes than *L. niger* which potentially allows differentiation between two species when photophore distributions are nearly alike, as in these fish.

The emission intensities reported here for midwater fish are greater than the frequently cited maximum intensities (1.5×10^{10} photons $\cdot s^{-1}$) obtained by Nicol (1958). The values presented here ranged from 5.1×10^{09} to 8.7×10^{11} photons $\cdot s^{-1}$. Our higher values may be explained by the increased accuracy of the integrating sphere method over previous recording devices and possibly to the relatively good physiological state of specimens obtained using the thermally insulated cod end.

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