Reports

Light to Hide by: Ventral Luminescence to Camouflage the Silhouette

Abstract. *The so-called pony fish of the tropical and subtropical Indo-Pacific region can emit light from a broad area of its ventral surface. An experimental analysis of this luminescent system supports the hypothesis that it functions by emitting light during the daytime, which matches the background light and thereby obscures the silhouette of the animal.*

Many animals conceal their location by matching the color and intensity of the background (*1*). This is straightforward in reflected light, but when the background is the light source itself, as in the case of a fish in the ocean seen from below, the solution to the problem is different. The silhouette can be effectively concealed only if the organism itself emits light.

In the majority of bioluminescent fish, the light is emitted from the ventral surface (*2*, *3*). Some years ago it was hypothesized that one of the functions of bioluminescence in such forms is to provide a special type of countershading—to obscure the silhouette by matching the light intensity of the background (*4*).

In an organism in which the function of ventral bioluminescence is to match background light, the luminescence should have several features. (i) It should be emitted as a continuous, diffuse glow—not in flashes—and be capable of persistence for many hours. Moreover, the control should have a continuous and fine intensity adjustment so as to truly match background (*5*). (ii) Light emission should occur by day, not by night (*6*). Since observations on bioluminescence in the field are commonly made at night, and in the laboratory almost always in a darkened room, it is not surprising that the possibility of bioluminescence by day has escaped interest and attention. On the basis of this hypothesis, the intensity level of bioluminescence should be directly related to the ambient light, and the control should be mediated by the eyes or a photoreceptor. Light emission should not be especially sensitive to mechanical disturbance.

The bioluminescent "pony" fish (family Leiognathidae) studied during the *Alpha Helix* expedition to New Guinea in 1969 appear to possess these features. Their luminescence, emitted as a diffuse light over much of the ventral surface, is due to symbiotic luminous bacteria (*7*) cultured within a special internal organ, which surrounds and communicates with the esophagus at a point where it makes a loop into the edge of the swim bladder (Fig. 1). The bacteria emit continuously, day and night, but the light emanating from the organ is controlled by an eyelid-like shutter (*8*) and is directed into the swim bladder, which is vested internally with silvery reflecting guanine crystals. Ventrally the swim bladder is only "half-silvered," and the light escapes by way of translucent (fiber optic–like) muscle fibers leading to the ventral surface. The light from the organ is thus diffused so as to result in an even glow over much of the ventral surface (*9*).

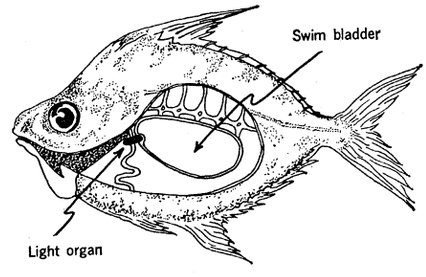

Fig. 1. *Leiognathus equulus* [redrawn after Haneda (*7*) (1940)]. Light from the organ enters the swim bladder which is internally reflecting. The eyelid-like shutter over the organ is not shown. Muscle fibers attaching to the ventral part of the swim bladder permit the light to be diffusely emitted over a broad portion of the ventral part of the body.

The intensity control and optical arrangements are admirably suited to provide a continuous but readily variable ventral glow to match the background light. The "integrating sphere" property of the swim bladder is such that, when the flap covers a fraction of the aperture of the light organ, the intensity is reduced uniformly over the entire emitting area by the same fraction. In addition, the blue luminescence (maximum wavelength, approximately 490 nm) matches well the color of the light that penetrates the ocean to depths of 20 m or below (*10*).

Bioluminescence was very difficult to evoke in these fish by mechanical or electrical stimulation. Upon collection (*11*), the fish were removed from the trawling net and placed in a holding tank, where many of them floated on the surface, apparently stunned. In the collections at night it was noted that these fish, in contrast to the active ones, were emitting bioluminescence, and, further, that upon recovery from the stunned condition their bioluminescence was promptly extinguished. The light could be turned off quite rapidly, and in some cases fish were observed to "blink" their light a few times during this recovery process.

Fish (*12*) kept in the dark in an aquarium and monitored photometrically with a sensitive photomultiplier (*13*), with the use of continuous recording, did not emit light over 24-hour periods of observation (*14*). Short of a stunning blow, mechanical stimulation of fish in the aquarium caused no luminescence response. Electrical stimulation via electrodes placed in the tank evoked a prompt and often violent swimming action, accompanied by clear but weak luminescent flashes, which were recorded (duration, approximately 0.2 second). But in a given specimen only a few (two or three) flashes could be evoked, and it seemed clear that we were not evoking "normal" bioluminescent emission.

However, pony fish did emit bioluminescence upon exposure to light. A flashlight (at about 50 cm) was used

to stimulate the fish, and bioluminescence was observed to persist for about 1 second after the flashlight was turned off. The possibility that this emission was the result of phosphorescence or some other such phenomenon was considered and tested, without receiving any support. The luminescence in response to light appears to derive from the emission of the luminous organ. The response was reliable—neither fatigue nor failures were noted, and it was independent of the duration of the exposure, up to 2 minutes.

The observation of light-induced bioluminescence strongly supports the hypothesis that luminescence is used to match the background light intensity. However, experimental studies of the effect of intensity of irradiation upon the intensity of emission will be needed in the evaluation of the proposed hypothesis. Another important but also unresolved question is posed by the fact that the fish are apparently bottom dwellers, where the silhouette-concealing mechanism would seem to be of limited value (*15*). If the proposed hypothesis is correct, it would be expected that in deeper water these fish spend some part of their life off the bottom. Knowledge concerning the natural history, ecology, and especially the behavior of these fish is needed to evaluate this question.

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References and Notes

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2. E. N. Harvey, *Bioluminescence* (Academic Press, New York, 1952); in *Physiology of Fishes*, M. E. Brown, Ed. (Academic Press, New York, 1957), vol. 2, pp. 345–366.
3. D. E. McAllister, *J. Fish. Res. Bd. Can.* **24**, 537 (1967). Ventral bioluminescence is also common in certain other luminous animals, especially crustacea and squid.
4. J. Fraser, *Nature Adrift* (G. T. Foulis and Co., London, 1962); W. D. Clarke, *Nature* **198**, 1244 (1963); A. Jerzmanska, *Przegl. Zool.* **4**, 112 (1960) (in Polish).
5. Alternatively, but not so ideal in practice, the organism might match its emission to that of the background by vertical migration.
6. The converse situation, in which bioluminescence is restricted to or favored during the nighttime, is known to hold for certain other luminous organisms, such as dinoflagellates [J. W. Hastings and B. M. Sweeney, *Biol. Bull.* **115**, 440 (1958), and Harvey (*2*)].
7. J. W. Harms, *Spec. Z. Wiss. Zool.* **131**, 157 (1928); Y. Haneda, *Palao Trop. Biol. Sta. Stud.* **2**(1), 29 (1940); *Pacific Sci.* **4**, 214 (1950); J. W. Hastings and G. Mitchell, *Biol. Bull.*, in press.
8. Harvey [(*2*), p. 528] states that "Control appears to be by chromatophores, as it is necessary to handle the fish or remove it from the water before the luminescence is displayed." Harvey's failure to mention the shutter mechanism, which was clearly described by Haneda (along with the possible involvement of chromatophores) was presumably an oversight.
9. Much but presumably not all of the ventral surface emits light. It is likely that the anterior and posterior extremities may still be visible. Nevertheless, the silhouette would be substantially interrupted. Another matter of concern relates to intensity as a function of viewing angle. E. J. Denton [*Phil. Trans. Roy. Soc. London Ser. B* **258**, 285 (1970)] has recently shown that the even more complicated optical arrangements associated with the photophores in hatchet fish have ingenious features that would enable the fish to match their background regardless of the angle of view. See also, E. Denton, *Sci. Amer.* **224**, 64 (Jan. 1971).
10. J. E. Tyler and R. C. Smith, *Measurements of Spectral Irradiance Underwater* (Gordon and Breach, New York, 1970).
11. The fish used in these experiments were collected within Sek Harbor, near Madang, New Guinea, at the head of Bostrem Bay, by trawling on the bottom at depths of 3 to 10 m. Collections by Drs. Haneda and Paxton were also made off the coast at the mouth of the Ramu River at depths up to 50 m.
12. A number of different species of *Leiognathus*, but principally *L. equulus* and *L. splendens*, were employed in these studies. The experiment was carried out both with a single fish and with several (up to 12) fish in the tank.
13. G. W. Mitchell and J. W. Hastings, *Anal. Biochem.* **39**, 243 (1971).
14. Similar observations were made in the field by Drs. John Paxton and J. M. Bassot. Captured fish were released within a fenced area in shallow water and observed visually during the night. No light emission was noted.
15. The fact that the fish occur on the bottom during the day in shallow water is not necessarily inconsistent with the proposed hypothesis. At an ambient light intensity higher than that which can be matched by the bioluminescence, the fish would presumably be driven to the bottom, attempting to move to greater depths.
16. Supported in part by a grant from NSF to the University of California, Scripps Institution of Oceanography, and in part by a contract with the Office of Naval Research, N00014-67-A-0001. I am deeply indebted to Dr. John B. Buck, chief scientist of Program C, *Alpha Helix*, 1969, for his assistance during the expedition in ways too numerous to mention. I am grateful to Drs. John Paxton and George Mitchell for assistance with the experiments, and to Dr. Y. Haneda for identifying the fish. My thanks to Howard Davis and Baxter O'Brien for help in the collection of the fish.

17 May 1971; revised 24 June 1971

Lunar Gravity Analysis from Long-Term Effects

Abstract. *The global lunar gravity field was determined from a weighted least-squares analysis of the averaged classical element of the five Lunar Orbiters. The observed-minus-computed residuals have been reduced by a factor of 10 from a previously derived gravity field. The values of the second-degree zonal and sectorial harmonics are compatible with those derived from libration data.*

The results given here represent an extension and refinement of previous work by Lorell (*1*). The second-degree zonal and sectorial harmonics determined here are in agreement with values obtained by libration data given by Jeffreys (*2*) and Koziel (*3*). A comparison is also made between our work and that of Muller and Sjogren (*4*).

The lunar gravity potential Φ is represented by the spherical harmonic expansion

$$\Phi = \frac{\mu}{r}\left\{1 + \sum_{n=2}^{\infty}\sum_{m=0}^{n}\left[\left(\frac{R}{r}\right)^n \times P_n^m(\sin\phi)\,(C_{nm}\cos m\lambda + S_{nm}\sin m\lambda)\right]\right\}$$

where μ is the gravitational constant of the moon, adopted as 4902.78 km^3/sec^2; R is the mean equatorial radius of the moon taken as 1738.09 km; $P_n^m(\sin\phi)$ is the associated legendre polynomial of order m and degree n in sine of lunar latitude ϕ; λ is the lunar longitude; and r is the radial distance of the orbiter from the moon. The harmonic coefficients C_{nm} and S_{nm} have numerical values that are determined from the data.

With the vast quantity of tracking data, a direct reduction of the data becomes a formidable undertaking, even for the high-speed computers of today. Therefore, the radar data were compressed into normal points consisting of five mean orbital parameters, a, e, i, Ω, and ω, averaged over an anomalistic period. A weighting matrix describing the statistics and correlations between the mean elements was associated with each normal point. A complete description of these matrices and data has been given (*5*). Lorell (*1*) was limited to an 8th-degree, 4th-order (8-4) model because of computer limitations. His computer program (*6*) computed the averaged orbital elements and produced the partial derivatives necessary for differential correction by the technique of finite differences. Having access to a third-generation computer, we were able not only to extend the solution to the 15th degree but also to use variational equations to compute the partial derivatives.

Included in the equations of motion were effects of the harmonic coefficients, the point mass perturbations of