

Marine Research in Indonesia, No. 19, 1977 : 137 - 146

THE LEIOGNATHIDAE (TELEOSTS): AN HYPOTHESIS RELATING THEIR MEAN DEPTH OCCURRENCE TO THE INTENSITY OF THEIR COUNTERSHADING BIOLUMINESCENCE

by

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ABSTRACT

All species belonging to the Family Leiognathidae (genera *Leiognathus*, *Secutor* & *Gazza*) are bioluminescent. They emit during daytime a downward, diffuse light which tends to disrupt their silhouette, making them less discernible from beneath to potential predators. It is here assumed that the intensity of light emitted should correspond to the intensity of incident light at the depth at which each species generally occurs. Using published information on the relative intensity of emitted light in different species and quantitative data on the mean depth occurrence of the species, it is shown that there is a good correspondence in the ranking order of both light intensity and depth occurrence in five species (e.g. *Secutor ruconius* emits a strong light and occurs in shallow water; *Leiognathus elongatus* emits a weak light and occurs at greater depth). Species not fitting into this pattern (e.g. *Leiognathus splendens* emits a weak light but occurs in very shallow water) tend to occur in murky water, where less light is required for counterillumination.

INTRODUCTION

Bioluminescence in fishes

Light organ in fishes were first discovered by COCCO in 1838 in Mediterranean deep-water fishes (BERTIN 1958). In fact, most of the bioluminescent fishes recorded are from the meso/bathypelagial. In these zones bioluminescence may fulfill a variety of inter- and intraspecific functions, such as luring and illuminating prey, confusing potential predators, attracting sexual partners, other members of the same species or assisting in schooling (BERTIN 1958; BURKENROAD 1943; MCALLISTER 1967; MORIN *et al.* 1975).

The light organs may be located on or in widely different parts of the body such as for example around the mouth, along the flanks, on the back, abdomen and protruding organs (for a review on the occurrence, position and possible function of bioluminescent organs in fishes see MCALLISTER 1967). MCALLISTER (1967) pointed out that many luminescent fishes display ventral bioluminescence and stressed that "fishes possess photophores for a

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number of reasons but they are placed ventrally because this results in reduced predations. This applies to bathypelagic fishes whose predominantly ventral light cannot be seen from predator species swimming above them as well as for close inshore species where the ventral position of the light organ may result, during day time in a "counter-" or "disruptive" illumination which may decrease predation from below.

Thus, the best explanation for the function of light emission in a great number of shallow water bioluminescent fishes appears to be that of counter-illumination, an hypothesis first put forward by JERZMANSKA (1960, vide McALLISTER 1967). McALLISTER (1967), referring to this hypothesis, suggested that it may well apply to those acanthopterigian displaying internal light organs and transparent venter, such as the Trachidae, or the Leioznathidae.

Bioluminescence in Leioznathidae

The Leioznathidae, consisting of the genera *Leioznathus* LACÉPÈDE 1805, *Secutor* GISTEL 1848 and *Gazza* RÜPPEL 1835 are commonly known as slipmouths (official FAO - name), pony-fishes, silver-bellies, pouters, slimies, and are widely spread over the Indo-Pacific with about 30 species. Most of these have already been reported to be bioluminescent and bioluminescence is highly probable for the rest. The bioluminescence of these small fishes was first discovered by HARMS (1928) who described the light organ of *Equula* sp. (*Leioznathus splendens* according to AHRENS 1965). BLEGVAD (1944) erroneously attributed the light emission by *Leioznathus* sp. to the food consumed by these fishes which he believed to consist exclusively of luminescent plankton organisms. HANEDA (1940), working without knowledge of HARMS' publication, rediscovered leioznathid bioluminescence in *Gazza minuta*. Other papers on the structure of the light organs of leioznathids followed (HANEDA 1950, AHRENS 1965, BASSOT 1966, HANEDA & TSUJI 1972). BOISVERT *et al.* (1967) and HASTINGS & MITCHELL (1971) described extensively the symbiotic bacteria which cause the glandular light organ of the slipmouth to glow (Figure 1).

HASTINGS (1971) discussing the function of ventral luminescence in leioznathids referred to the countershading hypothesis, from which he derived a set of features required from light emitted by pony-fish, which should possibly:

- be emitted in a continuous glow.
- occur at day,
- be regulated as to always truly match the background.

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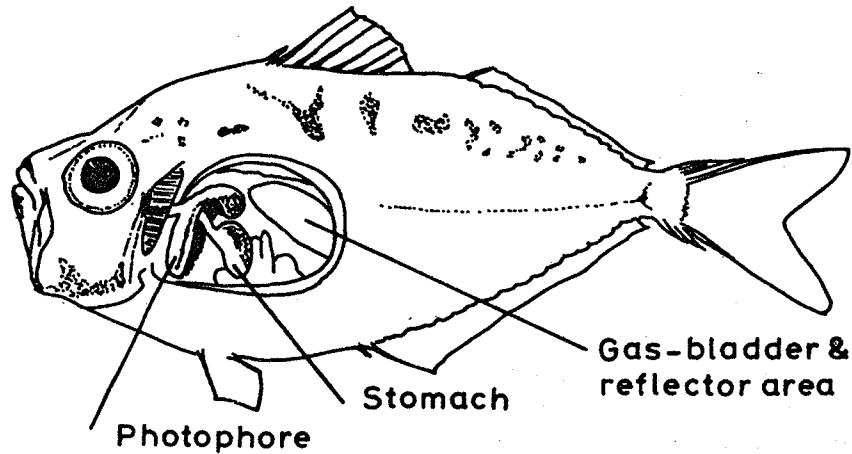


Figure 1. Light organs of *Leiognathus hatai* (redrawn after HANEDA & TSUJI 1972).

Noting that the leiognathids possess all these features, HASTINGS (1971) went on to mention some assumed drawbacks of the hypothesis:

- there is no data on the effect of incident irradiation on the
- intensity of bioluminescent emission.
- there is a general lack of ecological data on these fishes, and finally
- they are bottom-dwellers, where the silhouette-concealing
- mechanism would seem to be of little value.

The latter point does not seem to be a serious drawback to the counter-illumination hypothesis since the leiognathids, like most other reportedly bottom-dwelling fishes generally swim several decimeters or even meters above the bottom, thus exposing themselves to potential predators swimming beneath. The present work presents a preliminary attempt to verify the counter-illumination hypothesis on the basis of ecological data, namely the mean depth occurrence and the habitat of seven species of leiognathid fishes.

The hypothesis

The counterillumination hypothesis implies that, in order to be effective, the light produced by the fish should match the intensity of incident light in water depth at which the fish generally occurs.

Basically, the hypothesis can be tested in two ways:

- in an experiment, by recording the light emission of one or several individuals in relation to an incident light whose intensity can be varied experimentally, as proposed by HASTINGS (1971).

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— with field data, and along evolutionary lines, by relating the light intensity of leiognathid species to their mean depth occurrence, over a series of species.

Thus, the first approach would consist of investigating the possibility to regulate an existing capability (light emission) in a given species, while the second approach would determine the existence of different inherent levels of capability in different species.

The second approach suggested itself to the author during the course of an exploratory bottom trawling survey in the Jawa and South China Seas, where the species composition of Leiognathidae was found to be different at different depths. In deep water the *Secutor* species, known to emit a strong light, and *Leiognathus splendens* and *L. equulus* were gradually replaced by *L. bindus* and *L. elongatus*, the latter of which is known to emit a feeble light only (HANEDA, 1950).

MATERIAL AND METHODS

Mean depth occurrence of leiognathid species

As the number of trawl catches sorted to species level during the cruises mentioned above was too low, data are used here which were gathered by WEBER (pers. comm.) in a similar cruise in the waters off North Borneo in 1972, where 112 of the bottom trawl hauls made yielded leiognathids. The depth distribution of these positive hauls is shown in Table I. The trawl was an unmodified "Thailand-Trawl".

TABLE I. Depth distribution of hauls where leiognathids were caught (after WEBER, pers. comm.)

| depth in m | < 20* | 20-24 | 25-24 | 30-34 | 35-39 | 40-44 | 45-49 | 50-54 | ≥ 55* |
|-----------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| number of hauls | 4 | 13 | 24 | 19 | 15 | 16 | 10 | 7 | 4 |

* Note: For averaging, < 20 m was uniformly considered to correspond to 15-19 m and ≥ 55 m to 55 - 59 m.

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The occurrence of eight leiognathid species in the positive stations was recorded and expressed as percentage occurrence in the positive stations in each depth range. These percentage values were then averaged to obtain the weighted mean depth occurrence.

Relative intensity of bioluminescence

There are no quantitative data on the light emission of leiognathids which could be used to establish a ranked list of relative light intensity. Here, subjective accounts on the relative light intensity of the species investigated have been used.

From HANEDA (1940) the following information were extracted:

"The luminescence is more intensive in *Gazza minuta* than in *L. equulus*, but the latter is also lightning distinctly".

"The luminescence of *Secutor insidiator* and *S. ruconius* is the strongest, while that of . . . *L. splendens* . . . is mild".

From HANEDA (1950).

"*Gazza minuta* occurs in clear water in Palao at the depth about 30 m, and *L. equulus* lives in turbid water in the vicinity of mangrove trees at the depth of 1 - 2 m".

"*L. elongatus* is an offshore species . . . and . . . possesses a very small luminous organ. In consequence, its luminosity is feeble".

"*Secutor insidiator* and *S. ruconius* are luminous leiognathids . . . possessing relatively larger luminous organs than does *G. minuta*".

In addition, the present author considers that in *S. ruconius* the light and associated organs have evolved further than in *S. insidiator*.

RESULTS

The ranked list of species arranged according to the intensity of their bioluminescence is as follow:

L. splendens

A) *S. ruconius* < *S. insidiator* < *G. minuta* < *L. equulus* < *L. elongatus*

L. bindus

L. splendens and *L. equulus*, however, should be considered differently as they are known to occur mainly in turbid inshore water (HANEDA 1940 and 1950; CHABANNE & PLANTE 1969; PAULY 1976 and see below) where the downwelling light intensity does not decrease with the same factor as in clear water.

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This leaves the following lists of species, which are attributed ordinal numbers:

B) *S. ruconius* (1), *S. insidiator* (2), *G. minuta* (3), *L. bindus* (4), *L. elongatus* (5).

Figure 2 shows the depth distribution and mean depth occurrence of eight species of leiognathids from which *L. splendens*, *L. equulus*, and *L. leuciscus* should be removed to allow for comparison. The ranked list is thus:

C) *S. ruconius* (1), *G. minuta* (3), *S. insidiator* (2), *L. elongatus* (5), *L. bindus* (4) (in list C, the number in brackets are the ordinal numbers of list B).

Lists B and C (Table II) have a coefficient of rank correlation of 0.6 which is significant at the 5% level (SOKAL & ROHLF 1973).

TABLE II. Ranked order of relative light intensity against mean depth of occurrence

| | | | | | | | |
|---|--------------------------|---|---|---|---|---|---------|
| B | relative light intensity | 1 | 2 | 3 | 4 | 5 | r = 0.6 |
| C | mean depth occurrence | 1 | 3 | 2 | 5 | 4 | |

DISCUSSION

The probable existence of an inverse relationship between the intensity of bioluminescence and the mean depth occurrence in some leiognathid species argues for the validity of HASTINGS' (1971) hypothesis that the light emitted by pony-fish has the effect of disrupting their silhouette, hence to reduce predation from below.

The elimination of *L. splendens* and *L. equulus* from list A seem to be justified by the fact that these two species do show a special adaptation to a life in turbid water, namely a profuse slime production (these two species are by far the "slimiest" of the seven species considered).

NIKOLSKI (1963) explains that such an intensive slime production is often found as an adaptation to a life in turbid water, the slime surrounding the fish causing the suspended matter to flocculate, thus enlarging the fish's field of vision. This effect, together with a diagrammatic representation of the main idea expressed in the present paper, is shown in Figure 3.

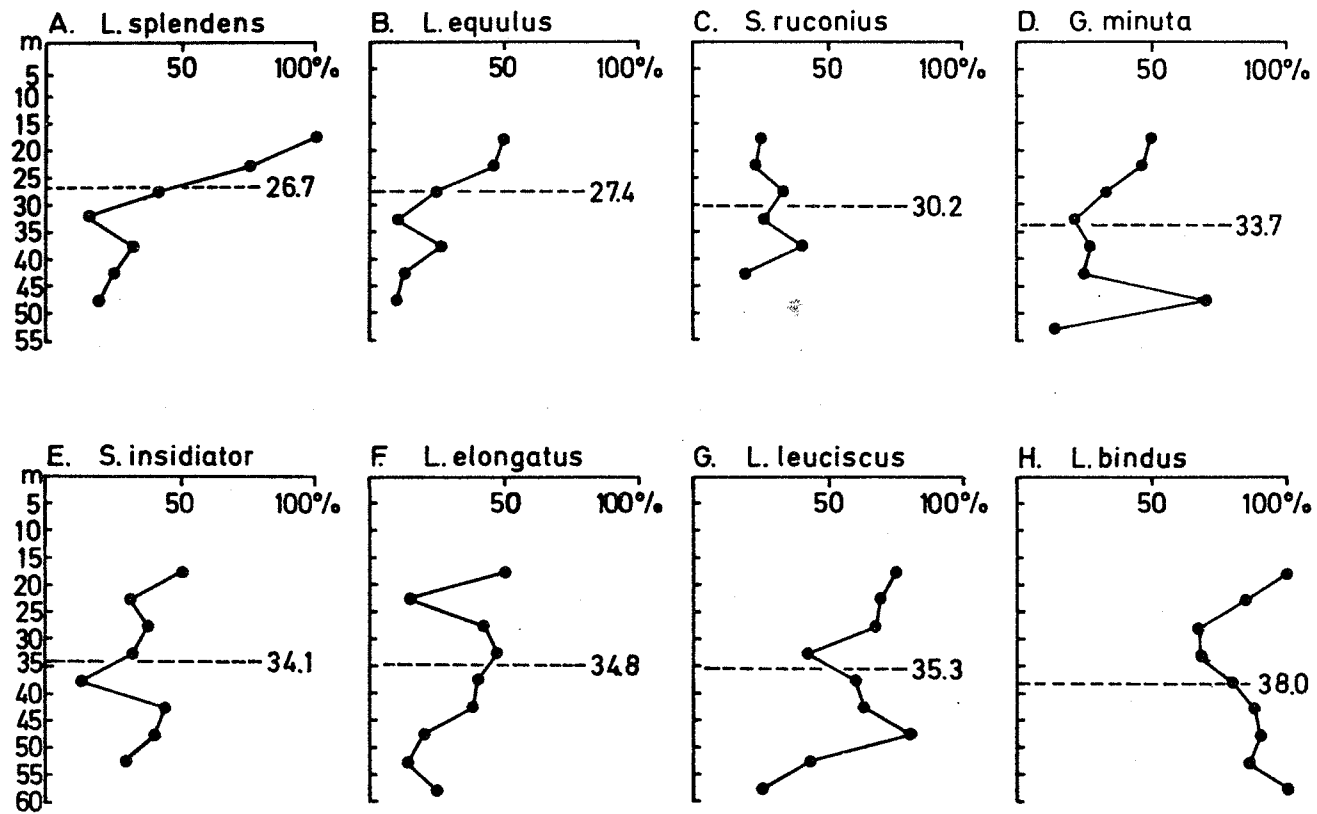


Figure 2. Depth distribution and mean depth occurrence of eight leiognathid species (after data from WEBER, personal communication).

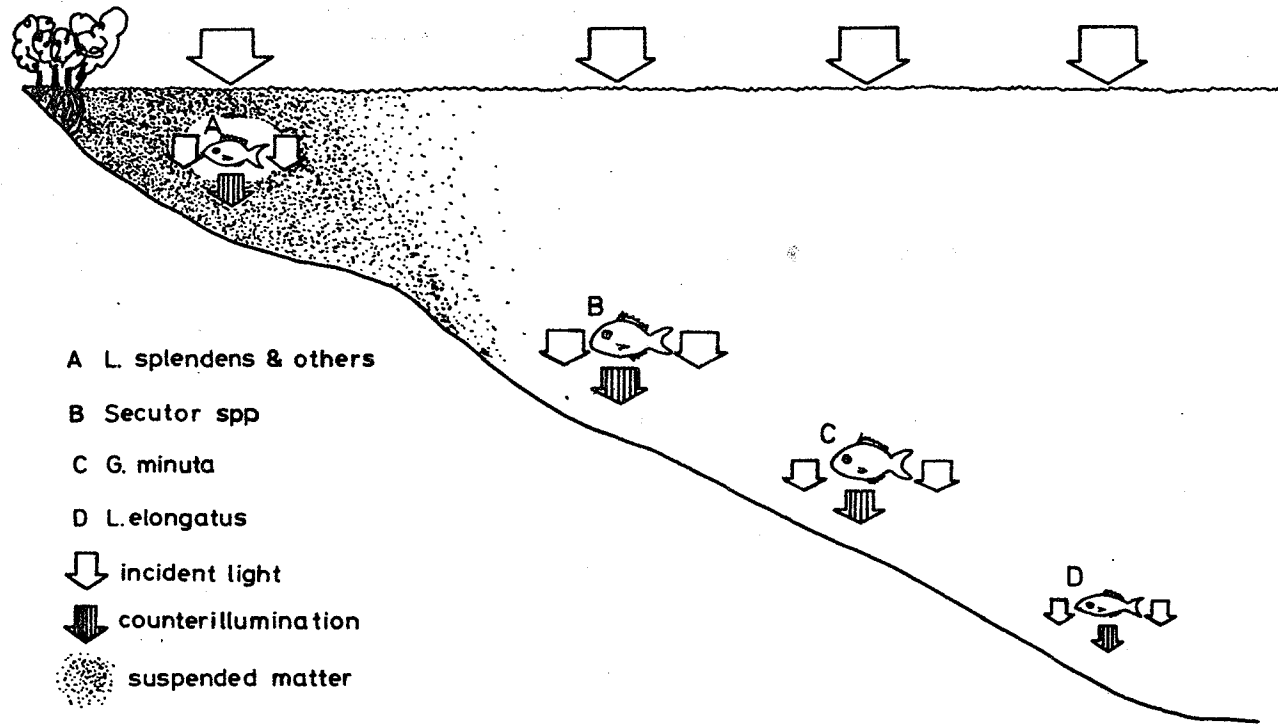


Figure 3. Diagrammatic representation of the depth distribution of leiognathid species and its relationship to incident light and counterillumination.

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The counterillumination hypothesis takes into account the remark by BERTIN (1958) that the position of the light organ and the shape of the reflector suggest the ambient medium is actually illuminated by the pony-fish.

It does not explain, however, why flashes of light are emitted both at night and by day (BALAN 1967; LOSSE pers. comm.), which seem to be produced when the fishes are excited. BASSOT (1966) even suspects that only the light produced after a strong excitation (e.g. by Adrenalin) can be seen through the body wall, but this statement does not hold in the face of the many reports of a continuous emission of glowing light (HARMS 1928; HANEDA 1940, 1950; HASTINGS 1971).

Possibly the leiognathids developed a secondary function for their ability to luminesce, which would explain the relationship between excitation and flashing light. An explanation may be the "burglar-alarm effect" (BURKENROAD 1943) where an organism — here a fish — attacked or threatened by predators reveals the presence of the latter to second order predators.

The present work is of a very preliminary nature, and the "counterillumination hypothesis" still needs confirmation in a series of experiments. *In vitro* or better *in vivo* photometric measurements of the intensity of light emission and their possible regulation in different species would be most adequate, and these measurements should be related to the mean downwelling light intensity in the various leiognathid habitats.

ACKNOWLEDGEMENTS

The author is indebted to DR. W. WEBER, German Federal Board of Fisheries, who contributed his data on depth occurrence of leiognathid species, and to DR. Y. HANEDA for sending copies of even his oldest papers as well as comments on the manuscript. MR. G.F. LOSSE critically read the first draft of this paper and PROF. J.W. HASTINGS kindly helped revising the manuscript and formulating some of the ideas expressed here.

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