

Bioluminescence and luminescent fish in the Strait of Messina from the mesoscaph “Forel”

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Abstract

Light irradiance was measured at 430, 470 and 500 nm aboard the mesoscaph “Forel” in the Strait of Messina from the surface to 550 m depth in May 1979. The underwater light regime is partly due to the downwelling residual sunlight and partly to bioluminescence. An intense bioluminescence is localized at about 450 m at midday and moves upwards in the evening to reach an area extending from 100 m depth to the surface late in the evening. Two types of luminescence were observed: one associated with luminescent organisms and another diffuse, probably due to bacteria. Three types of luminescent fish were recognized, namely *Argyrops leucostictus*, myctophids and *Cyclothone braueri*, and their time and space distribution were studied. While myctophids were encountered from the surface (21:00 hrs) to 550 m depth (16:00 hrs), *A. leucostictus* were only observed between 180 m (19:45 hrs) and 500 m (12:15 hrs), and *C. braueri* between 330 m (16:00 hrs) and 500 m (19:00 hrs). The results do not show a significant relation between the absolute ambient light intensity and the time or the depth where the fish were observed.

Introduction

Little is known of the behavior of mesopelagic luminescent fish: few such fishes, which nocturnally ascend into surface waters and are dip-netted carefully, live at the most only a few hours in shipboard aquaria. Stressed and confined, their behavior is hardly typical.

The present work presents the first observations of bioluminescence of luminescent fish from the depths of the Strait of Messina (Sicily), made aboard an autonomous submersible, the mesoscaph “Forel” (Jacques Piccard). The observations were conducted in May 1979.

The three following types of measurements were performed on board of the mesoscaph:

- transmission of the violet (430 nm), blue (470 nm) and green (500 nm) components of daylight in the waters of the Strait from the surface to 550 m depth in order to determine the level of light in the biotope frequented by luminescent fish.
- determination of the depth at which luminescent fishes are present at different times of the day.
- qualitative observations of light emission from luminescent fish.

Material and methods

The mesoscaph F. A.-“Forel”

The mesoscaph F. A.-“Forel” created by Jacques Piccard, son of Auguste Piccard, is smaller and lighter than the bathyscaph “Trieste”. It is also more manoeuvrable and offers a much larger visibility. Capable of stabilizing itself in mid water, it allows 3 observers to dive and work in perfect conditions down to 550 m. The vertical stability of the F. A.-“Forel” was one of the key factors on which depended the success of the 21 dives achieved in the Strait of Messina (Fig. 1). Three took place in the Tyrrhenian part, the others in the Ionian part of the Strait. The surface temperature was 21°–22 °C in the Tyrrhenian sea and 14°–15 °C in the Ionian sea.

Light measurements

(a) The photomultiplier

Light was measured with a photomultiplier PM 270 D (International Light) enclosed in a metallic box with a circular aperture upon the photocathode. The light was diffused by a flashed-opal glass screen screwed in a circular aperture above the photocathode (Fig. 2a). A circular black metallic piece with a circular hole, 0.7 mm in diameter in the middle, was sealed to the upper surface

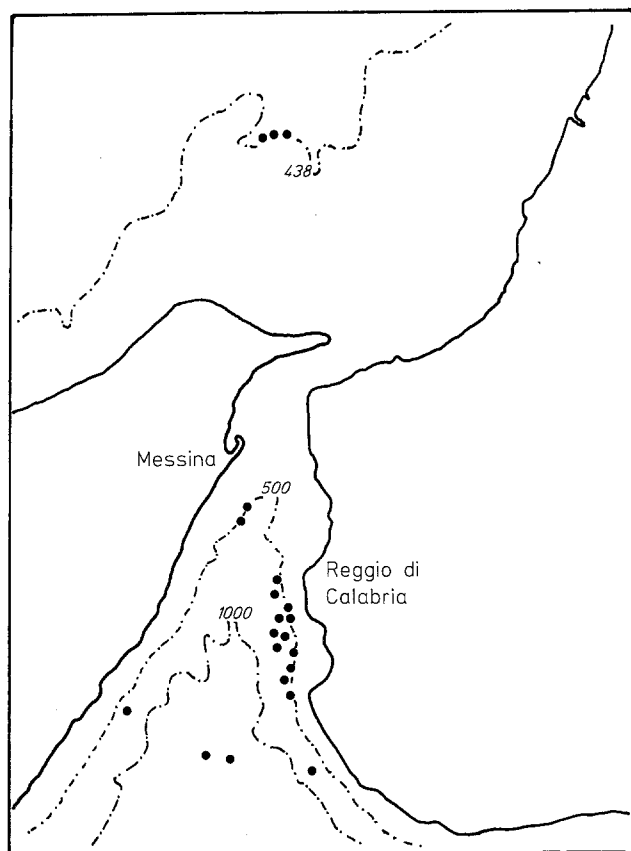


Fig. 1. Location of the 3 dives made in the Tyrrhenian sea and the 18 dives made in the Ionian sea

of the opal diffusing disk. A turret was attached on an axis laterally to the metallic box. Three 1" (2.6 cm) diameter interference filters with peak transmission at 430, 470 and 500 nm (International Light; $\frac{1}{2}$ bandwidth, 10 nm; 45% transmission) were screwed in the turret. By rotating the turret, each filter can be positioned successively over the aperture. The apparatus is fixed laterally under the Plexiglas dome in such a way that the axis of the photomultiplier is perpendicular to the surface of the water with its window pointing upward (Fig. 2b). Measurements of the downward transmitted light at different depths were obtained using each of the three filters. Eighteen simultaneous observations of the intensity of the light incident upon the surface of the sea at the three wavelengths were made with a similar photomultiplier on the deck-house roof of the surface support vessel.

(b) Experimental procedures

All the observations reported in the present work were made under ideal conditions: there were no clouds in the sky and the surface of the sea was nearly smooth.

Each series of measurements aboard the mesoscaph was conducted according to the following schedule. After boarding, a series of 4 measurements of light (total light, 430, 470 and 500 nm) was taken with the dome in open and in closed positions, the photomultiplier being at the

level of the sea surface. The presence of the Plexiglas dome only reduced the total light by about 10%, but for the light transmitted by the filters, in the shorter wavelength part of the spectrum, the reduction was 19% at 430 nm and 16% at 470 and 500 nm. The same series of measurements was repeated at 100-m intervals from the surface; after the mesoscaph was stabilized, all the lights were turned off and the readings began. The time required for the series of 4 measurements was about 60 s. The pilot

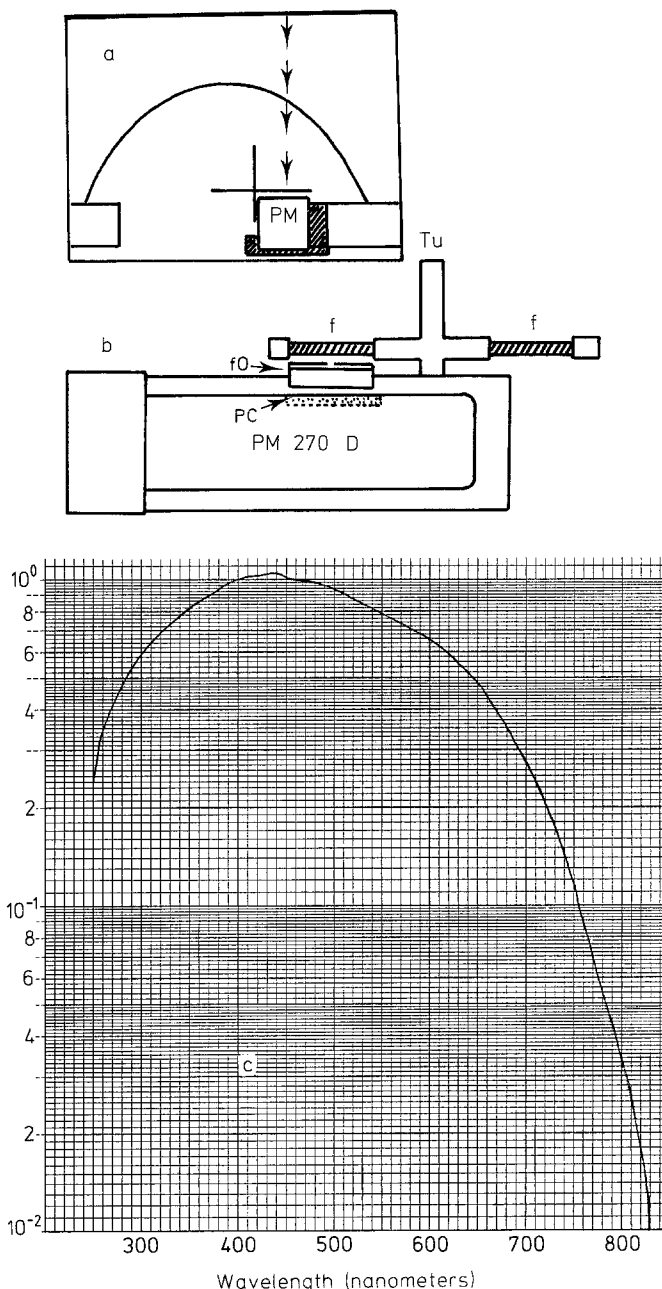


Fig. 2. (a) Schematic drawing showing the lateral position of the photomultiplier (PM) under the Plexiglas dome. The arrows correspond to the direction of the light recorded. (b) The photomultiplier (PM 270 D) and the Turret (T) with the screwed on interference filters (f). A flashed-opal glass screen (f. O.) is fixed above the photocathode (PC). (c) Spectral sensitivity of the photomultiplier

turned the turret and positioned the successive filters while the observer noted the readings on the radiometer. The same sequence was repeated every 100 or 50 m up to the maximum depth attained in the dive (550 m). The readings were conducted in the same way during the ascent of the mesoscaph. Visual estimates of the number of *Argyropelecus hemigymnus*, *Myctophum punctatum* and *Cyclothone braueri* were made from the mesoscaph by one of the two observers during each series of exploratory dives. For each fish encountered, the observer noted the time, the depth, the light level and temperature.

(c) Light recording

The distance between the photocathode and the light source corresponding to the pinhole (0.7 mm diameter) covering the diffusing glass was 20 mm. Since this distance is more than 20 times the diameter of the light source, it can be considered as a point source and the radiance power of the source is correlated with the irradiance power on the photocathode with less than 0.2% error (Tyler, 1973). The readings of the electrical signals were made on an illuminated screen in units calibrated by International Light. The photomultiplier, screened from all instrument lights by a piece of black tissue, was calibrated with the different filters used in preliminary experiments in Ganzirri Laboratory.

The measurements of light at different depths are expressed either in absolute values ($\mu\text{W cm}^{-2}$) or in relative units, corresponding to the ratio of the absolute value measured at the depth to the absolute value measured at the same time at the surface.

(d) Determination of extinction coefficient

The extinction coefficients (k) for the three wavelengths at 430, 470 and 500 nm were calculated between 0 and 100 m depth. k is given as:

$$k = \frac{\log I_0 - I_{100}}{100}$$

where I_0 is the intensity at the surface and I_{100} the intensity at 100 m; k is expressed in m^{-1} (Strickland, 1958).

Results

Luminescence in the Strait of Messina

(a) Midday dives

In Tables 1 and 2 we summarize the data of the relative light intensity measured in a series of 4 dives, 2 in the Tyrrhenian (nos. 13 and 14) and 2 in the Ionian sea (nos. 7 and 8), carried out between 11:30 and 15:00 hrs GMT. Comparison of the data shows that transmission of the 3 wavelengths down to 200 m depth was higher in the Tyr-

renian than in the Ionian sea. The extinction coefficient calculated from the mean value of light recorded at the surface and 100 m depth are respectively 0.021, 0.022 and 0.021 m^{-1} for the Tyrrhenian and 0.031, 0.033 and 0.031 m^{-1} for the Ionian sea. At 300 m depth the light intensity was not different in both waters.

Exploration of solar light transmission at greater depths in the Ionian sea gave unexpected results.

Fig. 3 shows the attenuation of solar irradiance measured from the surface at 10:40 hrs to 490 m at 13:00 hrs GMT (Lat. 38°N 1.7 km, Long. $15^\circ30'\text{E}$ 3.2 km). The echo-sounder indicated a depth of 1 000 m. Irradiance decreased progressively with depth and at 440 m was reduced to 20×10^{-7} of surface irradiance at 430 nm,

Table 1. Transmission of light: % of surface radiation

No. 7 (Lat. $37^\circ50'\text{N}$, 9.9 km; Long. $15^\circ40'\text{E}$, 1.5 km) Ionian sea				
Wavelength (nm)	430	470	500	Hour (GMT)
Depth (m)				
0	100	100	100	13:45
100	$2.0 \cdot 10^{-2}$	$4.5 \cdot 10^{-2}$	$6.4 \cdot 10^{-2}$	
200	$4.2 \cdot 10^{-4}$	$8.0 \cdot 10^{-4}$	$1.0 \cdot 10^{-3}$	
300	$9.0 \cdot 10^{-5}$	$4.0 \cdot 10^{-5}$	$2.0 \cdot 10^{-4}$	
400	$5.0 \cdot 10^{-6}$	$4.8 \cdot 10^{-6}$	$2.0 \cdot 10^{-6}$	15:00

No. 8 (Lat. 38°N , 7.4 km; Long. $15^\circ30'\text{E}$, 9.4 km) Ionian sea				
Wavelength (nm)	430	470	500	Hour (GMT)
Depth (m)				
0	100	100	100	11:30
100	$1.1 \cdot 10^{-1}$	$6.0 \cdot 10^{-2}$	$8.0 \cdot 10^{-2}$	
200	$8.4 \cdot 10^{-4}$	$7.0 \cdot 10^{-4}$	$8.0 \cdot 10^{-4}$	
300	$3.5 \cdot 10^{-4}$	$5.0 \cdot 10^{-5}$	$5.8 \cdot 10^{-5}$	
400	$5.5 \cdot 10^{-4}$	$6.5 \cdot 10^{-5}$	$6.6 \cdot 10^{-5}$	13:00

Table 2. Transmission of light: % of surface irradiance

No. 13 (Lat. $38^\circ20'\text{N}$, 1.1 km; Long. $15^\circ41'\text{E}$, 1.1 km) Tyrrhenian sea				
Wavelength (nm)	430	470	500	Hour (GMT)
Depth (m)				
0	100	100	100	13:00
100	$6.5 \cdot 10^{-1}$	$5.9 \cdot 10^{-1}$	$7.6 \cdot 10^{-1}$	
200	$1.1 \cdot 10^{-2}$	$1.4 \cdot 10^{-2}$	$1.7 \cdot 10^{-2}$	
300	$1.0 \cdot 10^{-4}$	$2.0 \cdot 10^{-4}$	$1.8 \cdot 10^{-4}$	
400	$9.4 \cdot 10^{-5}$	$1.0 \cdot 10^{-4}$	$1.8 \cdot 10^{-4}$	
450	$2.5 \cdot 10^{-5}$	$4.8 \cdot 10^{-5}$	$5.1 \cdot 10^{-5}$	15:00

No. 14 (Lat. $38^\circ20'\text{N}$, 1.1 km; Long. $15^\circ41'\text{E}$, 1.1 km) Tyrrhenian sea				
Wavelength (nm)	430	470	500	Hour (GMT)
Depth (m)				
0	100	100	100	11:30
100	$6.3 \cdot 10^{-1}$	$6.4 \cdot 10^{-1}$	$7.6 \cdot 10^{-1}$	
200	$8.0 \cdot 10^{-3}$	$8.9 \cdot 10^{-3}$	$1.2 \cdot 10^{-2}$	
300	$2.0 \cdot 10^{-4}$	$4.6 \cdot 10^{-4}$	$3.3 \cdot 10^{-4}$	
400	$2.5 \cdot 10^{-5}$	$4.6 \cdot 10^{-5}$	$4.8 \cdot 10^{-5}$	
450	$1.6 \cdot 10^{-5}$	$3.2 \cdot 10^{-5}$	$3.3 \cdot 10^{-5}$	12:15

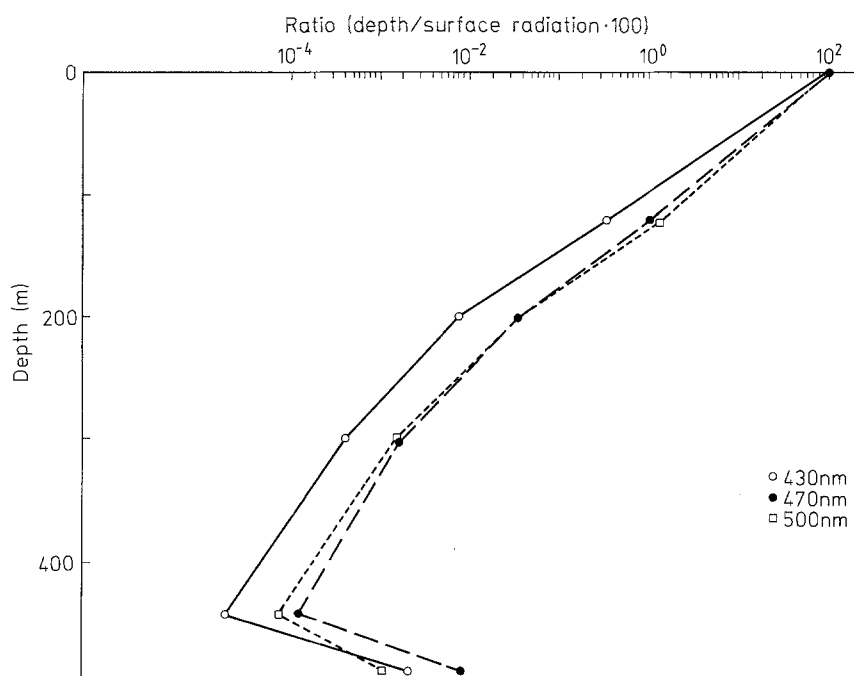


Fig. 3. Typical relation between depth and irradiance at three wavelengths expressed as percentage of irradiance values at the surface, during the descent of the mesoscaph at the midday time in the Strait of Messina (Lat. 38 °N, 1.7 km; Long. 15° 30'E, 3.2 km)

1.2×10^{-6} at 470 nm and 7.8×10^{-7} at 500 nm. The next measurement taken at 490 m (at 13:00 hrs) showed an increase in the ambient light. From 440 to 490 m depth, i.e. within the next 50 m of depth, the relative magnitude of irradiance increased to 4×10^{-5} of surface irradiance at 430 nanometers, 9.0×10^{-5} at 470 and 1.1×10^{-5} at 500 nanometers. The relative light intensity present at 490 m was equivalent to the residual sunlight intensity transmitted to 200 m depth (Fig. 3).

The values of absolute irradiance at the 3 wavelengths measured at 440 and 490 m are given in Table 3.

The unexpected increase of the surrounding irradiance by about 2 orders of magnitude should indicate the presence of large bioluminescent activity. The observers adapted to nocturnal vision aboard the mesoscaph were unanimous in stating the absence of any visible glowing or flashing organisms. The only visible luminescent animals had been met about 1 h earlier at 337 m (12 luminescent *Argyrolepeus hemigymnus*). The observers had, however, the general impression that darkness was not total but that

the submersible moved in some kind of diffuse mist. The intensity of this ambient light was higher than the diffuse ambient light observed in the range of 430–450. The luminescence was therefore most probably due to organisms not visible to the naked eye.

(b) Afternoon dives

In a series of dives beginning in the afternoon, i.e. between 16:00 and 16:30 hrs GMT, the photometer recorded the presence of a similar diffuse luminescence at about 410 m. Fig. 4a shows the distribution of light for the three wavelengths at different depths during the descent and the ascent periods of a dive beginning at 16:20 hrs (Lat. 38 °N 6.4 km, Long. 15°30'E 9.8 km). Fig. 4b shows the time course of the light intensity (470 nm) at the surface. The ambient irradiance decreases progressively down to 300 m; the measurements taken at 17:40 hrs at that depth show that the light intensity is reduced to 7.5×10^{-6} of surface irradiance at 430 nm, 3.9×10^{-5} at

Table 3. Irradiance ($\mu\text{W}/\text{cm}^{-2}$) measured during midday, afternoon and evening dives

Station		Depth (m)	Time (GMT)	Wavelength (nm)		
				430	470	500
Lat. 38°N	1.7 km	300	11:55	$6.1 \cdot 10^{-5}$	$2.8 \cdot 10^{-4}$	$2.1 \cdot 10^{-4}$
Long. 15°30'E	3.2 km	440	12:30	$3.5 \cdot 10^{-6}$	$1.8 \cdot 10^{-5}$	$1.1 \cdot 10^{-5}$
Midday dive		490	13:00	$4.8 \cdot 10^{-4}$	$1.5 \cdot 10^{-3}$	$1.6 \cdot 10^{-3}$
Lat. 38°N	6.4 km	300	17:40	$1.5 \cdot 10^{-6}$	$7.8 \cdot 10^{-6}$	$7.5 \cdot 10^{-6}$
Long. 15°30'E	9.8 km	430	18:50	$8.0 \cdot 10^{-6}$	$4.0 \cdot 10^{-5}$	$3.6 \cdot 10^{-5}$
Afternoon dive		300	19:15	$3.6 \cdot 10^{-6}$	$2.1 \cdot 10^{-5}$	$2.6 \cdot 10^{-5}$
Lat. 38°N	4.75 km	300	18:40	$3.0 \cdot 10^{-3}$	$1.6 \cdot 10^{-2}$	$1.4 \cdot 10^{-2}$
Long. 15°30'E	10.05 km	500	19:15	$5.2 \cdot 10^{-6}$	$3.2 \cdot 10^{-5}$	$2.7 \cdot 10^{-5}$
Evening dive		400	20:20	$3.1 \cdot 10^{-4}$	$2.2 \cdot 10^{-3}$	$1.9 \cdot 10^{-3}$

470 nm and 3.7×10^{-5} at 500 nm. Only two visible living organisms were observed at 260 m (2 jellyfish, *Solmissus* genus) and at 270 m (1 luminescent *Argyropelecus hemigymnus*). Living organisms, essentially crustaceans, were abundant between 370 and 420 m, whereas *A. hemigymnus* (12) and *Cyclothone braueri* (40–50) were only seen between 345 and 370 m (18:00 hrs GMT). At 430 m, the measurements of ambient light taken at 18:40 hrs revealed an intense luminescence which raised the ambient light intensity to 1.0×10^{-3} of surface irradiance at 430 nm, 5.7×10^{-3} at 470 nm, and 5.1×10^{-3} at 500 nm. Table 3 summarizes the absolute light levels recorded at 300 and 430 m at an interval of 1 h. The increase in the relative ambient luminescence is very close to that observed in the preceding dive between 440 and 490 m; however, the absolute light levels measured at the three wavelengths increased to a lesser extent due to a large

reduction in the sun's altitude between 17:40 and 18:40 hrs (Fig. 4b). Nevertheless, visual observations confirmed once again that this large increase in light was not associated with the presence of visible glowing or flashing organisms. Later in the day, while ascending we encountered numerous luminescent *A. hemigymnus* and myctophids, particularly between 300 and 270 m. While the lights of the submersible were off we observed at 260 m numerous very small luminescent points. We estimated a density of approximately 10 per square cm of dome area. When the lights were turned on, the position of the luminous point was associated with a flocculent material, generally referred to as "snow". The presence of the luminescent points was observed up to about 120 m depth.

The light measurements at 300 and 120 m depth show that the ambient light was higher than that measured at

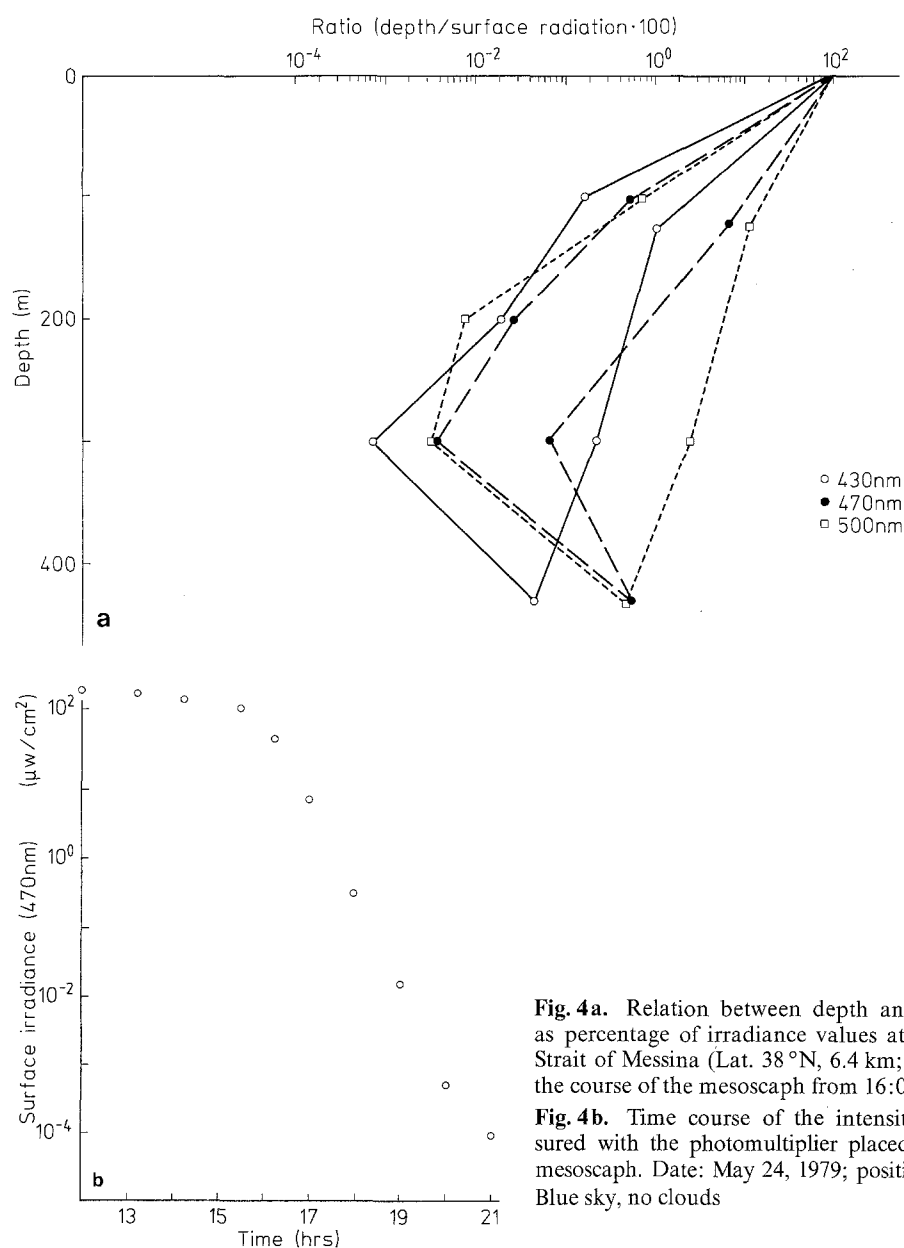


Fig. 4a. Relation between depth and irradiance at three wavelengths expressed as percentage of irradiance values at the surface during an afternoon dive in the Strait of Messina (Lat. 38°N , 6.4 km; Long. $15^{\circ}30'\text{E}$, 0.8 km). The arrows indicate the course of the mesoscaph from 16:00 to 20:00 hrs GMT

Fig. 4b. Time course of the intensity of the sunlight irradiance (470 nm) measured with the photomultiplier placed on the deckhouse of the barge carrying the mesoscaph. Date: May 24, 1979; position: Lat. 37°N , 7.4 km; Long. $15^{\circ}30'\text{E}$, 9.4 km. Blue sky, no clouds

the same depths during the descent about 3 h earlier. The difference is particularly evident at 500 nm, the intensity relative to the surface irradiance being increased by nearly three orders of magnitude, while at 470 nm it is increased by only a factor of 20. It is likely that the high ambient light levels detected by the photomultiplier at 300 m (19:15 hrs) and 120 m (19:40 hrs) were due to some bioluminescent activity, essentially organisms with a continuous luminescence. The spectral shift toward the green 500 nm was confirmed by visual observation of luminescence: the numerous luminescent points looked like green-yellow spots moving quickly in all directions.

(c) Evening dives

During an evening dive we had the opportunity to follow the spreading of bioluminescent activity up to the surface of the sea. Fig. 5 shows the values of the relative light intensity as a function of the depth, measured during a dive beginning at 17:20 hrs and ending at 21:25 hrs. The echo-sounder, when at sea level, recorded a depth of 600 m (Lat. 38°N 4.75 km; Long. 15°E 10.05 km).

As shown in the figure, the ambient irradiance decreased progressively downward to 200 m, where it was reduced to 9.7×10^{-4} of surface irradiance at 430 and 470 nm, and 1.8×10^{-2} at 500 nm. At this time (18:24 hrs) the intensity of ambient light is higher than that recorded at the same depth in afternoon dives, at 16:57 hrs, particularly at 500 nm. The next measurements taken 16 min later at 300 m reveal a tremendous luminescence: irradiance values at the three wavelengths summarized in Table 3, correspond to 3% of the surface irradiance at 430 nm, 5.3% at 470 nm and 1.1% at 500 nm.

Undoubtedly, we were in the presence of a strongly luminescent layer; however, after the submarine's lights were turned off none of the observers could detect any

luminescent organisms around the mesoscaph. Nevertheless, after becoming dark-adapted they had the impression of being surrounded by a feeble luminous mist. The absence of spikes or undulations on the light records (full scale signal in 0.1 s) and the visual observations are fair indications of the luminescent conditions at that depth, i.e. diffuse and not associated with visible organisms. On the other hand, several flashing or glowing organisms were encountered later between 350 and 500 m. At 500 m (19:15 hrs) the light level was much lower than it had been at 300 m about 30 min earlier: the intensity of ambient irradiance was about 3 orders of magnitude less (Table 3).

While ascending from 500 to 300 m, the observers were particularly impressed by the absence of any luminescent organisms, even though we met numerous non-luminescent organisms, such as shrimp or chaetognaths. The water seemed to diffuse a feeble luminescence. At 400 and 300 m, the ambient light level was much higher than that recorded at 500 m (Fig. 5).

The most striking luminescence records were obtained at 100 m: at this time, i.e. 21:00 hrs, the irradiance values were $4.8 \times 10^{-4} \mu\text{W}/\text{cm}^2$ at 430 nm, $3.2 \times 10^{-3} \mu\text{W}/\text{cm}^2$ at 470 nm and $2.9 \times 10^{-3} \mu\text{W}/\text{cm}^2$ at 500 nm, corresponding respectively to 436, 533 and 483% of the surface radiation. While ascending from 100 m up to the surface, we examined the medium through the dome and the frontal window after extinguishing the submarine's lights; we had the same sensation as a driver on a road masked by a thick fog. We were moving through a "milky water" studded with myriads of sparks.

Distribution of luminescent fish

The most common luminescent fish encountered in the 21 dives were *Argyrops leuciscus*, *Cyclothone braueri*

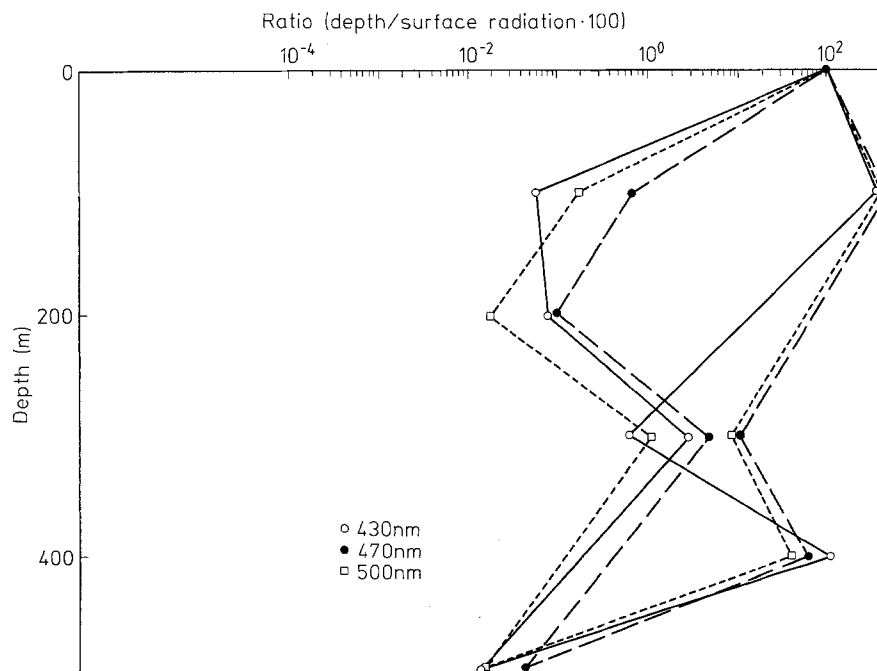


Fig. 5. Relation between depth and irradiance at three wavelengths expressed as percentage of irradiance values at the surface during an evening dive in the Strait of Messina (Lat. 38°N, 4.75 km; Long. 15°30'E, 10.05 km). The arrows indicate the course of the mesoscaph from 17:00 to 21:25 hrs GMT

and myctophids. Exceptionally we observed 3 to 4 *Vinciguerria braueri*. In the Tyrrhenian part of the Strait, we observed about 50 *Maurollicus muelleri* exclusively near or on the bottom at 455 m depth. The pattern of vertical distribution of the three main luminescent fish encountered is shown in Fig. 6.

While myctophids were encountered from the surface to 550 m, *Argyrolepiscus hemigymnus* was observed only between 180 and 500 m, and *Cyclothone braueri* between 330 and 530 m. The sample is limited to a small area extending a few meters around the mesoscaph: consequently visual observation of fish made through the dome or the window at a given depth can only be taken as indicating the presence of fish at that time and depth.

Light emission of luminescent fish

It was readily observed that all the organisms, luminescent or not, that generally stayed at the edges or beyond the limits of the illuminated area in front of the window, were attracted by the small side light near the dome.

In two cases with the lights off, we had the opportunity to record and to observe simultaneously, through the Plexiglas dome, the luminescence produced by one *Argyrolepiscus hemigymnus*; its distance from the dome was estimated to be about 20 to 30 cm. The anterior part of the fish, with the ventral photophores, was more luminescent than the rest of the body (337 m depth, 12:05 hrs). On one occasion we observed the luminescent behaviour of one *A. hemigymnus* caught in the trap mounted on the front of the window (Fig. 7). When the fish entered the trap at 430 m depth (17:00 hrs), it was luminescent and the ambient light level was $3.1 \times 10^{-5} \mu\text{W cm}^{-2}$. A diffuse and continuous luminescence originating from the ventral photophores was visible when the fish was in the upper part of the trap. At 370 m and 6 min later, we saw the fish turning slowly around its antero-posterior axis and orientating its ventral photophores upwards. About 4 min later at 330 m, at a light level of $2 \times 10^{-4} \mu\text{W cm}^{-2}$, it stopped luminescing and turned its body again, orientating the ventral photophores downwards. The fish remained in this position, apparently in good condition, since 18 min later it succeeded in escaping through the aperture of the trap at 38 m depth, and vanished in the depths of the Strait.

Though the individual was confined in a trap, these visual observations emphasize that *Argyrolepiscus hemigymnus* can tolerate a decompression from 430 to 38 m depth at a mean rate of 8 m s^{-1} , and that it can easily orientate its body, swimming as well with the belly pointed up or down. With regard to myctophids, when observed through the dome, they emitted a sustained luminescence originating from their ventral photophores. Photophores were not separately visible. Owing to the rapid swimming of these fishes we have never been able to record any light emission. We know that, *in vitro*, isolated photophores respond to electrical stimulation by a light emission which

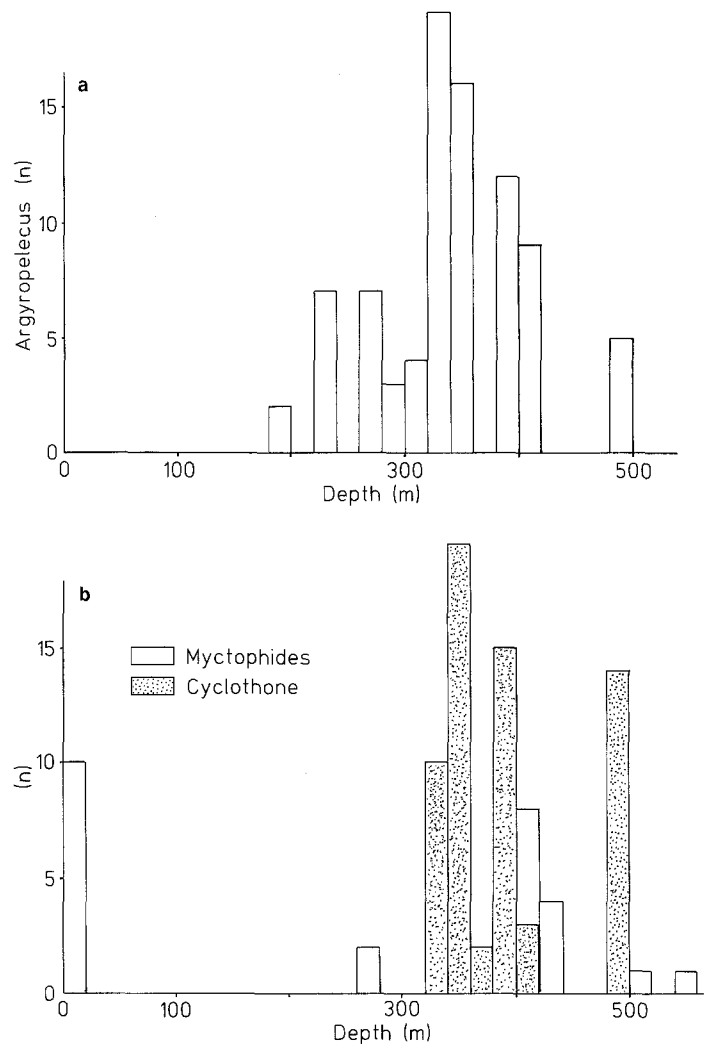


Fig. 6. Vertical distribution of the three main luminescent fish observed in the strait of Messina from the surface to 550 m depth during 21 dives. Ordinates indicate the number of individuals observed at the corresponding depth. (A) *Argyrolepiscus hemigymnus*; (B) *Myctophids* and *Cyclothone braueri*

is somewhat less intense than the response of *A. hemigymnus* photophores.

Concerning *Cyclothone braueri*, we never observed a luminescent specimen; *in vitro*, we never succeeded in recording light produced by electrical stimulation of isolated photophores.

Discussion and conclusions

Distribution of luminescence with depth

Early dives with submersibles (Beebe, 1934; Pérès and Piccard, 1956; Tregouboff, 1958) and immersions of bathyphotometers (Clarke and Backus, 1956; Clarke and Wertheim, 1956; Clarke and Breslau, 1959) disclosed the presence of varying amounts of bioluminescence at depths beyond the penetration of surface light. Although the underwater radiometers gave quantitative measurements of luminescence, these instruments gave no indication of

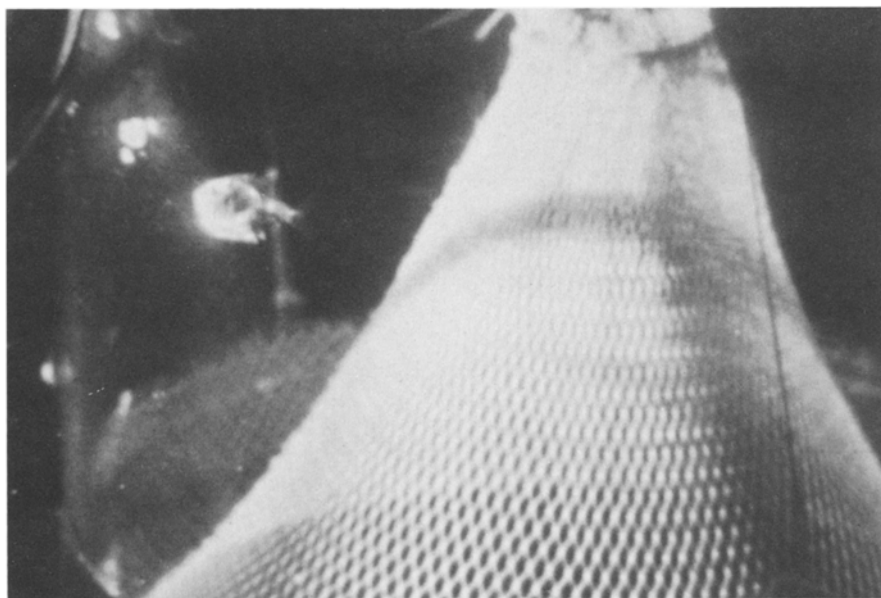


Fig. 7. Living *Argyropelecus hemigymnus* captured in a trap fixed in front of the front porthole of the mesoscaph

the identities of the organisms responsible for the luminescence. The use of a stable mesoscaph, equipped with a large window and a dome, gave us the opportunity to observe, identify, photograph and record light phenomena, with particular attention to luminescent fish.

The present results indicate that luminescent populations of organisms move upwards or downwards according to the time of day. Visual observations prompt us to distinguish two types of luminescence: one associated with visible organisms responsible for glowing or flashing phenomena and the other a diffuse luminescence that is not associated with visible organisms. We never found the presence of this second type of luminescence in the Tyrrhenian part of the Strait. Measurements of light emission from oceanic seawater samples containing natural populations of luminous bacteria indicated that their light emission was undetectable (Ulitzur and Hastings, 1979). If a swab from the surface of a marine fish is streaked onto seawater nutrient agar plates, luminous colonies almost always arise in number exceeding those that might be obtained by plating seawater directly (Nealson and Hastings, 1979). Baguet and Maréchal (1976) reported the constant occurrence of luminous bacteria in the intestinal tract of *Argyropelecus hemigymnus* collected in the Ionian part of the Strait of Messina. In different samples, 40 to 100% of the colony-forming units were luminous and were single species, *Phosphobacterium phosphoreum* (Nealson and Hastings, 1979).

It is possible that the diffuse luminescence detected from the mesoscaph might be from bacteria that have escaped from gut tracts or other sources and still possess plenty of luciferase and other luminescent substrates.

These bacteria might multiply on flocculent materials and other suspended particles present in large amounts at these depths. This striking phenomenon certainly needs further work.

Concerning visible luminescent organisms, we observed fish, shrimp and copepods; a large number of

flashes were due to organisms that we could not identify. A large number of non-luminescent living organisms, with a predominance of shrimp, was observed between 250–350 m during the day and between 100–50 m late after sunset. We did not observe a large number of luminescent organisms in the latter 50-m layer at midday or in the afternoon; in general the amount of natural luminescence observed is considerably less in this layer than in deeper layers. In the Tyrrhenian part of the Strait it was particularly evident that this dense layer was at 250–300 m, while all the luminescent material was located near the bottom, i.e. at 400 m depth. In the limits of our investigations there was in general no relationship between luminescence and the presence of the layer of increased animal density. Since previous observations indicate that maximum luminescence occurs within a deep scattering layer, the layer we observed should not correspond to such a scattering layer.

Light irradiance and vertical distribution of luminescent fish

The vertical as well as the horizontal distribution of luminescent fish have been systematically investigated by day and night catches at various latitudes in the eastern north Atlantic (Badcock and Merrett, 1976) and in the western and the eastern Mediterranean (Goodyear *et al.*, 1972). Depths of occurrence of adult *Argyropelecus hemigymnus* were 100–600 m in the Atlantic and 300–500 m in the Mediterranean. In both cases *A. hemigymnus* appeared to migrate upward at night since most specimens were taken at 200 m or shallower.

During submarine prospecting in the bathyscaph “FNRS III” in the vicinity of Villefranche-sur-mer, Pérès (1958) and Tregouboff (1958), observed numerous *Argyropelecus hemigymnus* located between 110 and 270 m at night, and at a depth of 530 m in the daylight.

Our results show that in the Strait of Messina, the depth of occurrence of *Argyropelecus hemigymnus* is

180–500 m, the fish migrating to the upper layers (180 m) in the evening.

Roe and Harris (1980) using a deep-sea photometer mounted on the back of an opening and closing net used in the northeast Atlantic, showed that most of the *Argyrolepelecus hemigymnus* caught were located at the dimmest light level sampled ($3.2 \times 10^{-5} \mu\text{W cm}^{-2}$). Our simultaneous visual observations and light measurements show that *A. hemigymnus* was present in an ambient irradiance extending from 1.5×10^{-5} to $8.0 \times 10^{-3} \mu\text{W cm}^{-2}$. Though the depth of occurrence varies with the time of day, it seems that the vertical movements of *A. hemigymnus* were not associated with a constant light regime.

The counterlighting hypothesis suggests that a luminescent fish equates its ventral luminescence and ambient light by comparing the intensity from its orbital photophores(s) with the intensity of the ambient light. In this hypothesis, the absolute value of irradiance of the two sources of light is compared and the animal migrates up or down, or modulates its light emission accordingly. Assuming that *Argyrolepelecus hemigymnus* or myctophids use their ventral photophores as camouflage, they must be able to luminesce with an intensity that matches the ambient luminescence, i.e. to produce a maximal luminescence as high as about $5.10^{-3} \mu\text{W cm}^{-2}$. The ability to see a luminescent *A. hemigymnus* from its ventral side through the dome of the mesoscaph raises the question of the effectiveness of the fish luminescence as a concealment from predators. Beebe (1935) was also able to observe luminescing hatchet-fish “*in situ*” and even to distinguish between the genus *Sternoptyx* and *Argyrolepelecus* simply by their luminescent patterns. When there is background light, the ability to distinguish a luminous animal depends upon contrast, which falls off with distance. Consequently the presumed camouflage should become efficient when the predators are far enough from *A. hemigymnus*, i.e. at a distance that we certainly underestimate since the visual sensitivity of deep-sea fishes could have a threshold lower than that of the human eye by a factor of 10 to 100 (Nicol, 1978).

Another explanation could be offered to explain partly our results: *Argyrolepelecus hemigymnus* uses its photophores as a luminescent lure! We observed that *A. hemigymnus* can orientate its body in all the directions: by orientating its ventral luminescent patch, positively phototropic motile organisms might be attracted.

The camouflage and the lure functions of the photophores are not necessarily exclusive: *Argyrolepelecus hemigymnus* may use its ventral light organs as camouflage only when ambient light is still of significance at a depth and at a time that it might meet predators.

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