J. mar. biol. Ass. U.K. (1957) 36, 629–642
Printed in Great Britain

SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

By J. A. C. Nicol
The Plymouth Laboratory

(Text-figs. 1–13)

The light of *Chaetopterus* has a bluish hue. From visual examination Lankester (1868) judged that the emission spectrum extended from about 440 to 550 mμ (wavelengths estimated by Harvey, 1952). Other polychaetes said to produce bluish luminescence are found in the families Alciopidae, Syllidae and Terebellidae. The light of Tomopteridae and Cirratulidae is described as yellow or yellow-green (Harvey, 1955). The spectral composition of the light of polynoids has now been measured. It is yellow-green in colour, with maximal emission at about 515 mμ (Nicol, 1957).

The spectral composition of the light of *Chaetopterus variopedatus* is here described. Various physiological aspects of the response, some of them pertinent to the present investigation, have already been dealt with (Nicol, 1952*a–c*). The light is produced by a luminescent secretion discharged into the surrounding sea water. When the glands on segment XII discharge, the light rises to maximal intensity in about 14 sec, and the whole response lasts some 5 min.

MATERIALS AND METHODS

Chaetopterus was removed from its tube, and the anterior region (head) was cut off. The head was pinned out in a black dish, and light was evoked by electrical stimulation of the luminescent glands lying at the bases of the aliform notopodia (segment XII) (Nicol, 1952*a*, *b*).

To analyse the spectral composition of the light, a multiplier phototube and a series of coloured filters were used. The photomultiplier was connected to a cathode-ray oscilloscope, and photographic records were made of the deflexion of the oscilloscope trace on moving paper.

The filters used were Ilford spectrum filters nos. 601–608, covering the visible range (about 400–700 mμ), Chance's purple (OV 1), and an ultra-violet filter transmitting from about 300–400 mμ. A set of filters was mounted in an opaque disc which could be rotated beneath the cathode of a photomultiplier tube. Apertures were cut at regular intervals about the margin of the disc, and a filter was placed over each aperture. The disc was arranged so that the filter-covered apertures passed across the face of the photocathode (arrangement shown in Fig. 1). The dish containing the animal was placed under the disc, close to the filters.

Since the light varies in intensity, it was necessary to have some method of registering changes in light intensity, while records of intensity of filtered light in different spectral regions were obtained. This was accomplished by using a series of identical filters (hereafter called reference filters), one of which was placed between each of the other spectral filters. By this means it was possible to gauge the relative light intensity at the beginning and end of each measurement made with a given spectral filter. For reference filters I employed either Ilford blue-green 603, or Ilford green 604. From the intensity of the light passed by the reference filters, it was possible to correct the records obtained with other spectral filters, so that all the data referred to light of the same initial energy-content before filtration.

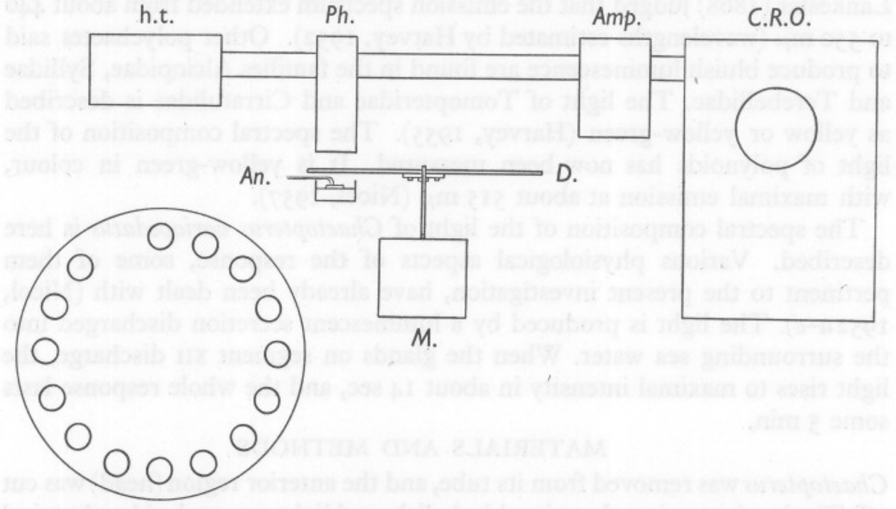

Fig. 1. Diagram of apparatus. *Amp.*, amplifier; *An.*, animal; *D.*, disc; *C.R.O.*, cathode-ray oscilloscope; *h.t.*, high tension supply; *M.*, variable speed motor. The disc is shown in surface view at the lower left.

In order to reduce the disparity in magnitude of responses given with the various filters, neutral filters were used in conjunction with Ilford spectrum filters nos. 601–604. They were either Chance's neutral glass or Ilford neutral density filters. Four combinations of filters that were used are shown in Table 1. The filters are given in the order in which they passed across the face of the multiplier phototube. A blank opaque space was left between each pair of contiguous filters to separate the records clearly. At one point on the disc there was a double blank space as a position-marker, to show when the disc had made one complete rotation, and to provide a means of relating the seriated responses to the filters in their order of rotation. Thus, in disc I, when the filters were rotated in order from red to violet, the photographic trace would show: nil deflexion, long duration (= double space); deflexion (= blue-green filter); nil deflexion, short duration (= single space); deflexion (= red filter);

nil deflexion, short duration (= single space); deflexion (= blue-green filter); etc. Some records, described later, are shown in Figs. 2 and 3.

The transmission of all filters was measured in a spectrophotometer (Unicam, S.P. 500).

The photomultiplier was an E.M.I. no. 6685, having high sensitivity in the violet and very low sensitivity in the red. The spectral sensitivity of the

TABLE 1. FOUR COMBINATIONS OF FILTERS, LISTED IN ORDER OF ROTATION

Disc I

Double space

1. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
2. Ilford red 608
3. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
4. Ilford orange 607
5. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
6. Ilford yellow 606
7. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
8. Ilford yellow-green 605
9. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
10. Ilford green 604 + Ilford neutral density (D. 0·5)
11. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
12. Ilford blue 602 + Ilford neutral density (D. 0·5)
13. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
14. Ilford violet 601
15. Ilford blue-green 603 + Ilford neutral density (D. 0·5)

Disc II

Double space

1. Ilford green 604
2. Ilford orange 607
3. Ilford green 604
4. Ilford yellow 606
5. Ilford green 604
6. Ilford yellow-green 605
7. Ilford green 604
8. Ilford blue-green 603 + Chance neutral ON 31
9. Ilford green 604
10. Ilford blue 602 + Chance neutral ON 32
11. Ilford green 604
12. Ilford violet 601 + Chance neutral ON 33
13. Ilford green 604

Disc III

Double space

1. Ilford green 604
2. Ultra-violet
3. Ilford green 604
4. Ilford yellow 606
5. Ilford green 604
6. Ilford yellow-green 605
7. Ilford green 604
8. Ilford blue-green 603 + Chance neutral ON 31
9. Ilford green 604
10. Ilford blue 602 + Chance neutral ON 32
11. Ilford green 604
12. Ilford violet 601 + Chance neutrals ON 32 + ON 33
13. Ilford green 604
14. Chance OV 1
15. Ilford green 604

Disc IV

Double space

1. Ilford red 608
2. Ilford green 604
3. Ilford orange 607
4. Ilford green 604
5. Ilford yellow 606
6. Ilford green 604
7. Ilford yellow-green 605
8. Ilford green 604
9. Ilford blue-green 603 + Chance neutral ON 31
10. Ilford green 604
11. Ilford blue 602 + Chance neutral ON 32
12. Ilford green 604
13. Ilford violet 601 + Chance neutral ON 33
14. Ilford green 604
15. Chance OV 1
16. Ilford green 604

photocathode of this tube was determined by the National Physical Laboratory. Voltage for the photomultiplier was supplied by a stabilized power pack. The mains voltage for oscilloscope and power pack was held steady by a voltage stabilizer.

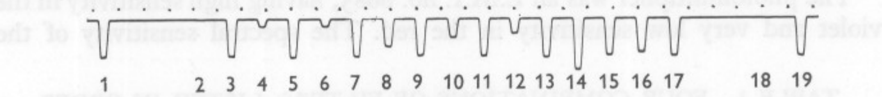

Fig. 2

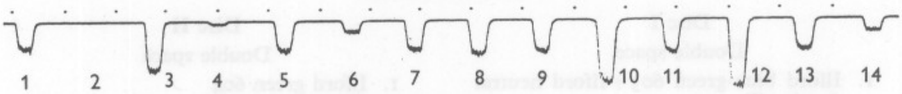

Fig. 3

Fig. 2. Photographic record of oscillograph deflexions given by artificial light source (lamp 2360° K + Chance blue-green OB 2), interrupted by rotation of disc IV. Responses as follows: 1, green 604; double space; 2, red 608; 3, green 604; 4, orange 607; 5, green 604; 6, yellow 606; 7, green 604; 8, yellow-green 605; 9, green 604; 10, blue-green 603; 11, green 604; 12, blue 602; 13, green 604; 14, violet 601; 15, green 604; 16, purple OV 1; 17, green 604; double space; 18, red 608; 19, green 604.

Fig. 3. Similar record for the light of *Chaetopterus*, interrupted by disc III. Responses as follows: 1, green 604; 2, ultra-violet; 3, green 604; 4, yellow 606; 5, green 604; 6, yellow-green 605; 7, green 604; 8, blue-green 603; 9, green 604; 10, blue 602; 11, green 604; 12, violet 601; 13, green 604; 14, deep purple OV 1. Time, both records, $\frac{1}{5}$ sec.

In order to calculate the relative spectral energy of a light source by the method here adopted, it is necessary to know the combined effect of spectral sensitivity of the photomultiplier (S_λ) and spectral transmission of each filter (T_λ). Let R_x be the response for a given filter x, and E_λ the relative spectral energy of emitted light. Then

$$R_x \propto E_\lambda \int S_\lambda T_\lambda \, d\lambda,$$

$$\therefore E_\lambda \propto \frac{R_x}{\int S_\lambda T_\lambda \, d\lambda}.$$

Plots of $S_\lambda T_\lambda$ against λ are given in Figs. 4 and 5. The areas under curves $S_\lambda T_\lambda$ were used to represent the integrals for each filter

$$\eta_x = \int S_\lambda T_\lambda \, d\lambda.$$

The mean wavelength (mean λ) for each filter was taken from the centre of gravity of the areas under the curves. Values for η_x and mean λ are given in Table 2.

All measurements of *Chaetopterus* light were made at a room-temperature of 18–19° C.

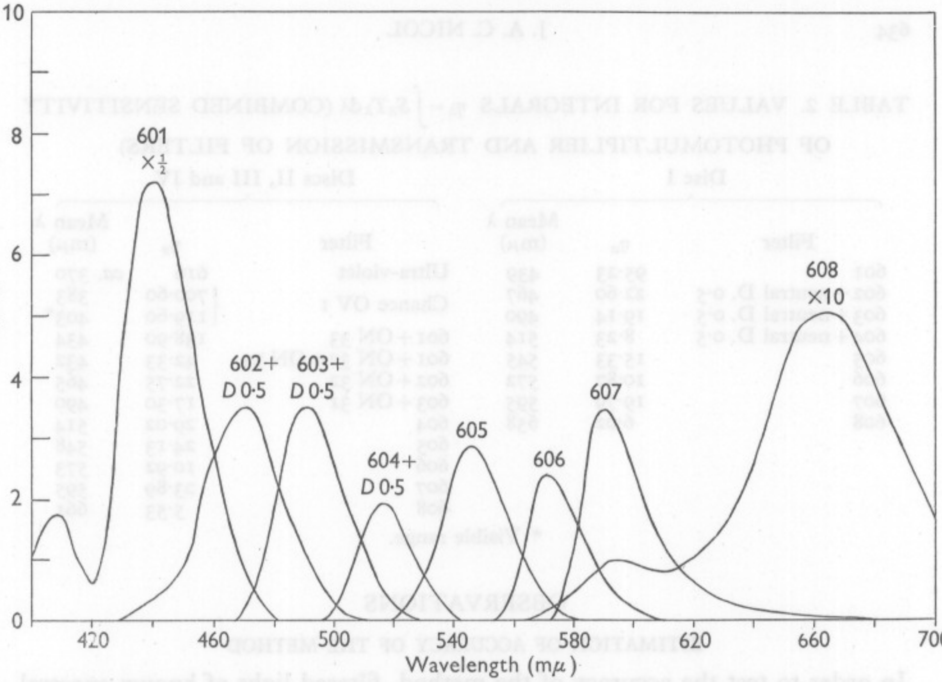

Fig. 4. Plots of $S_\lambda T_\lambda$ against λ for the series of Ilford gelatine filters used in disc I. S_λ = sensitivity of photomultiplier 6685; T_λ = transmission of filters. An Ilford neutral density filter (density D. = 0·5) was used with each of filters 602 to 604. All filters were mounted between two pieces of Perspex.

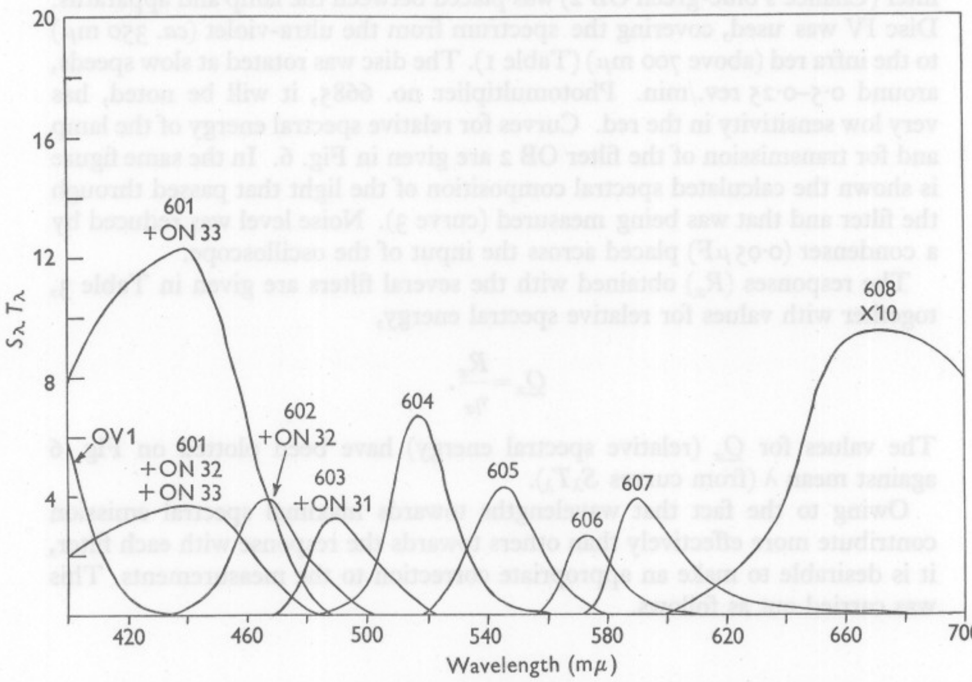

Fig. 5. Plots of $S_\lambda T_\lambda$ for the various filters used in discs II, III and IV. Filters 601 to 608 were gelatine, mounted in glass; the remainder glass.

TABLE 2. VALUES FOR INTEGRALS $\eta_\lambda = \int S_\lambda T_\lambda d\lambda$ (COMBINED SENSITIVITY OF PHOTOMULTIPLIER AND TRANSMISSION OF FILTERS)

Disc I			Discs II, III and IV		
Filter	η_x	Mean λ (mμ)	Filter	η_x	Mean λ (mμ)
601	95·23	439	Ultra-violet	616	*ca.* 370
602 + neutral D. 0·5	22·60	467	Chance OV 1	700·60	383
603 + neutral D. 0·5	19·14	490		119·60	403*
604 + neutral D. 0·5	8·23	514	601 + ON 33	138·90	434
605	15·33	545	601 + ON 32 + ON 33	42·33	432
606	10·87	572	602 + ON 32	22·75	465
607	19·79	595	603 + ON 31	17·30	490
608	6·02	658	604	29·02	514
			605	24·13	548
			606	10·92	573
			607	23·89	595
			608	5·53	661

* Visible range.

OBSERVATIONS

ESTIMATION OF ACCURACY OF THE METHOD

In order to test the accuracy of the method, filtered light of known spectral composition was measured by means of a disc of filters, photomultiplier and oscilloscope. Constant light was provided from a substandard lamp of colour temperature 2360° K, obtained from the National Physical Laboratory. A blue filter (Chance's blue-green OB 2) was placed between the lamp and apparatus. Disc IV was used, covering the spectrum from the ultra-violet (*ca.* 350 mμ) to the infra red (above 700 mμ) (Table 1). The disc was rotated at slow speeds, around 0·5–0·25 rev./min. Photomultiplier no. 6685, it will be noted, has very low sensitivity in the red. Curves for relative spectral energy of the lamp and for transmission of the filter OB 2 are given in Fig. 6. In the same figure is shown the calculated spectral composition of the light that passed through the filter and that was being measured (curve 3). Noise level was reduced by a condenser (0·05 μF) placed across the input of the oscilloscope.

The responses (R_x) obtained with the several filters are given in Table 3, together with values for relative spectral energy,

$$Q_x = \frac{R_x}{\eta_x}.$$

The values for Q_x (relative spectral energy) have been plotted on Fig. 6 against mean λ (from curves $S_\lambda T_\lambda$).

Owing to the fact that wavelengths towards maximal spectral emission contribute more effectively than others towards the response with each filter, it is desirable to make an appropriate correction to the measurements. This was carried out as follows.

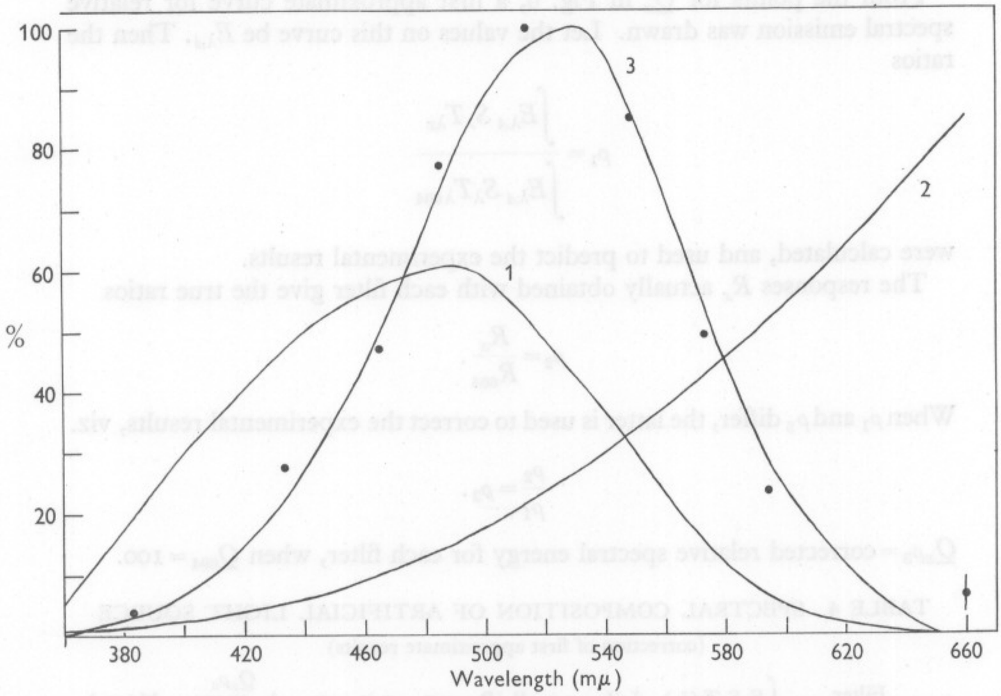

Fig. 6. Curves for (1) transmission (%) of a blue filter, Chance OB 2; (2) spectral emission of a substandard lamp (colour temperature 2360° K), and (3) calculated spectral composition of light passed by filter OB 2 ($T_\lambda \mathcal{J}_\lambda$). Relative $\mathcal{J}_\lambda$ based on $\mathcal{J}=1$ at $\lambda=590$ mμ (from Skogland, 1929). Relative $T_\lambda\, \mathcal{J}_\lambda$ based on $T\mathcal{J}=100$ at $\lambda=530$ mμ. Curve (2), ×50. The points are measured values for spectral composition of light passed by filter OB 2.

TABLE 3. MEASUREMENT OF SPECTRAL COMPOSITION OF AN ARTIFICIAL LIGHT SOURCE

Lamp of colour temperature 2360° K + Chance blue-green filter OB 2. Responses and first approximation of relative spectral energy.

Filter	Mean λ (mμ)	Response R_x	$R_x/\eta_x = Q_x$
OV 1	383	10	0·0143
601 + ON 33	434	15	0·1080
602 + ON 32	465	4·2	0·1846
603 + ON 31	490	5·2	0·3006
604	514	11·3	0·3894
605	548	8·0	0·3315
606	573	2·1	0·1923
607	595	2·2	0·0921
608	661	0·15?	0·0271?

From the points for Q_x in Fig. 6, a first approximate curve for relative spectral emission was drawn. Let the values on this curve be $E_{\lambda A}$. Then the ratios

$$\rho_1 = \frac{\int E_{\lambda A} S_\lambda T_{\lambda x}}{\int E_{\lambda A} S_\lambda T_{\lambda 604}}$$

were calculated, and used to predict the experimental results.

The responses R_x actually obtained with each filter give the true ratios

$$\rho_2 = \frac{R_x}{R_{604}}.$$

When ρ_1 and ρ_2 differ, the latter is used to correct the experimental results, viz.

$$\frac{\rho_2}{\rho_1} = \rho_3.$$

$Q_x \rho_3$ = corrected relative spectral energy for each filter, when $Q_{604} = 100$.

TABLE 4. SPECTRAL COMPOSITION OF ARTIFICIAL LIGHT SOURCE

(correction of first approximate results)

Filter	$\int E_\lambda S_\lambda T_\lambda(\zeta_x)$	$\zeta_x/\zeta_{604} = \rho_1$	$R_x/R_{604} = \rho_2$	$\rho_2/\rho_1 = \rho_3$	$Q_x\rho_3$ $\lambda_{530} \equiv 100$	Mean λ
OV 1	201·0	1·16	0·885	0·763	2·79	395
601 + ON 33	227·7	1·32	1·33	1·007	27·83	445
602 + ON 32	66·66	0·385	0·372	0·966	45·63	466
603 + ON 31	79·34	0·459	0·460	1·002	77·08	491
604	173·0	—	—	—	97·56	516
605	108·75	0·629	0·708	1·126	95·51	542
606	26·67	0·154	0·186	1·208	59·45	572
607	31·00	0·179	0·195	1·089	25·65	592
608	2·27	0·013	0·013?	1?	6·93?	622

In Table 4 are given the details of these calculations for filtered blue light from the substandard lamp. The second column lists areas of the curves $E_{\lambda A} S_\lambda T_{\lambda x}$ plotted against $\lambda(\zeta_x)$. Columns 3–5 give values of ρ_1, ρ_2 and ρ_3, for the various filters. The sixth column $Q_x\rho_3$ gives relative spectral energy for each filter, based on $\lambda_{530} \equiv 100$, the estimated region of maximal emission. The last column shows recalculated values for mean λ, based on curves $E_{\lambda A} S_\lambda T_{\lambda x}$.

The final corrected values for relative spectral energy for each filter are plotted on Fig. 7, together with the calculated relative energy curve (based on $\mathcal{J}_\lambda T_\lambda$). The degree of agreement, which can be seen from inspection, seems reasonable enough to trust the method for measurement of animal luminescence.

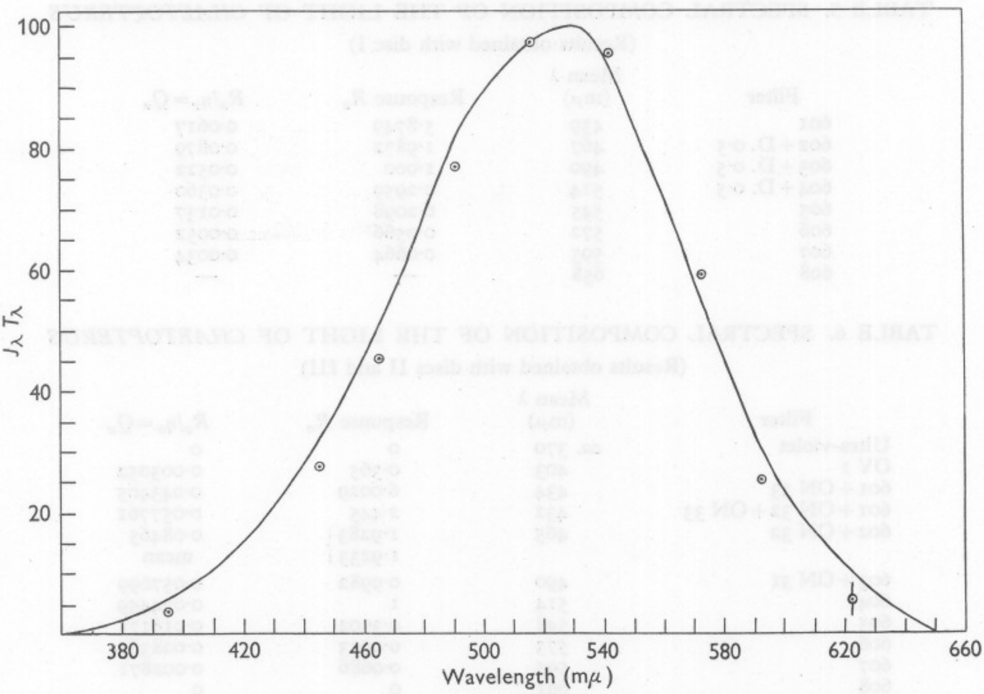

Fig. 7. Curve for relative spectral energy of artificial light (lamp 2360° K + Chance OB 2). The points are corrected measurements made with the various filters, and plotted against mean λ (determined from curves $E_{\lambda A} S_\lambda T_{\lambda x}$).

MEASUREMENTS OF THE LIGHT OF *CHAETOPTERUS*

As a first attempt, the light of *Chaetopterus* was measured by means of disc I, containing Ilford filters 601 to 608. This disc was designed for green light. It was rotated at various speeds, varying from 1 to 3 rev./sec. The data obtained are summarized in Table 5, and first approximate estimations of relative spectral energy are plotted against λ in Fig. 8 (mean λ for each filter based on curves $S_\lambda T_\lambda$).

From these preliminary results it appeared that the light possessed a maximum well into the blue, around 460 mμ, and discs II and III were devised, accordingly, to extend the spectral range of analysis. Discs II and III were spun at low speeds, around 0·5 rev./min, at which rate it was possible to use a condenser (0·05 μF) to filter off most of the noise. The data obtained with discs II and III are shown in Table 6, and values for relative spectral energy are plotted in Fig. 9 against mean λ (derived from curves $S_\lambda T_\lambda$).

In order to correct these values, the same procedure was employed, as described in the previous section. First approximate values for relative

TABLE 5. SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

(Results obtained with disc I)

Filter	Mean λ (mμ)	Response R_x	$R_x/\eta_x = Q_x$
601	439	5·8749	0·0617
602 + D. 0·5	467	1·9872	0·0879
603 + D. 0·5	490	1·000	0·0522
604 + D. 0·5	514	0·2959	0·0360
605	545	0·2098	0·0137
606	572	0·0566	0·0052
607	595	0·0664	0·0034
608	658	—	—

TABLE 6. SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

(Results obtained with discs II and III)

Filter	Mean λ (mμ)	Response R_x	$R_x/\eta_x = Q_x$
Ultra-violet	*ca.* 370	0	0
OV 1	403	0·365	0·003052
601 + ON 33	434	6·0029	0·043405
601 + ON 32 + ON 33	432	2·445	0·057761
602 + ON 32	465	1·9283 } 1·9233 }	0·08465 mean
603 + ON 31	490	0·9982	0·057699
604	514	1	0·034459
605	548	0·3902	0·016171
606	573	0·0913	0·008361
607	595	0·0686	0·002871
608	661	0	0

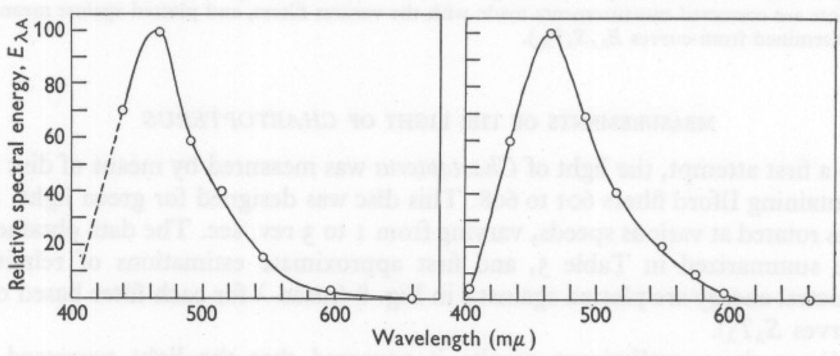

Fig. 8 Fig. 9

Fig. 8. Spectral composition of the light of *Chaetopterus*. Approximate curve based on records obtained with disc I. Mean λ for each filter obtained from curves $S_\lambda T_\lambda$.

Fig. 9. Spectral composition of the light of *Chaetopterus*. Approximate curve based on records obtained with discs II and III. Mean λ for each filter obtained from curves $S_\lambda T_\lambda$.

spectral emission $E_{\lambda A}$ were estimated from a curve resembling that in Fig. 9, and these values were used to draw curves for $E_{\lambda A}S_{\lambda}T_{\lambda x}$ (Fig. 10). Computed values are listed in Table 7, together with subsequent calculations to determine corrected values for spectral emission. Final values are collected in Fig. 11, which depicts a corrected spectral emission curve. Maximal emission occurs at about 465 mμ, well into the blue. There is no emission in the ultra-violet, and emission in the red, above 600 mμ, is negligible.

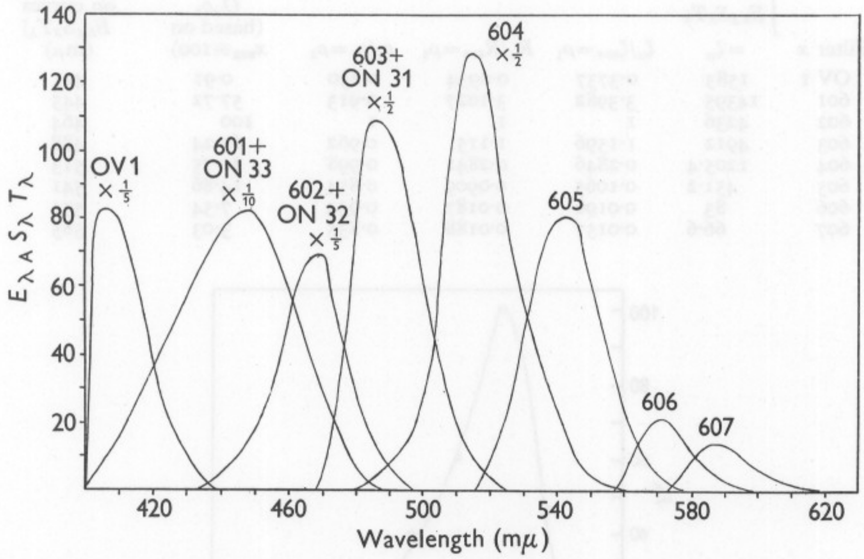

Fig. 10. Curves for $E_{\lambda A}S_{\lambda}T_{\lambda}$ against λ, based on first approximate measurements of relative spectral emission of *Chaetopterus* light.

COMMENT

Most of the light of *Chaetopterus* is concentrated in the blue region of the spectrum, more so than that of any animal hitherto measured. *Cypridina* has a somewhat similar emission spectrum, with a maximum at *ca.* 480 mμ (Coblentz & Hughes, 1926). Polynoid light is greenish, with maximal emission at about 515 mμ (Nicol, 1957).

The biological significance of the light of *Chaetopterus* still awaits an explanation. *Chaetopterus* is light-sensitive, and presumably could detect its own light. However, the spectral sensitivity of *Chaetopterus* in unknown, so it is not possible to relate this to the colour of the luminescence. *Chaetopterus* is preyed upon by various animals, including *Limulus* and coastal fish, which may have occasion to perceive the light.

Absorption curves are available for the eye pigments (rhodopsins) of marine coastal fish, and the curves can be used to represent the spectral sensitivity of these animals (Fig. 12) (Wald, 1946; Kampa, 1953). The spectral sensitivity curve of *Limulus* has been determined (Graham & Hartline, 1935). This has a maximum at 520 mμ (Fig. 12). In Fig. 13 I have drawn curves for 'luminous flux' of *Chaetopterus* light, based on visibility values taken from the curves of

TABLE 7. SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

(Correction of first approximate results)

Filter x	$\int E_{\lambda A} S_\lambda T_\lambda = \zeta_x$	$\zeta_x/\zeta_{602}=\rho_1$	$R_x/R_{602}=\rho_2$	$\rho_2/\rho_1=\rho_3$	$Q_x\rho_3$ (based on $x_{602}\equiv 100$)	Mean λ (based on curves $E_{\lambda A} S_\lambda T_\lambda$) (m$\mu$)
OV 1	1583	0·3737	0·0934	0·250	0·91	411
601	14395	3·3982	3·1027	0·913	57·72	443
602	4236	1	1	1	100	464
603	4912	1·1596	1·115	0·962	61·24	488
604	1205·4	0·2846	0·2841	0·998	40·75	513
605	451·2	0·1065	0·0909	0·854	14·86	541
606	83	0·0196	0·0187	0·954	7·54	571
607	66·6	0·0157	0·0188	0·835	3·03	585

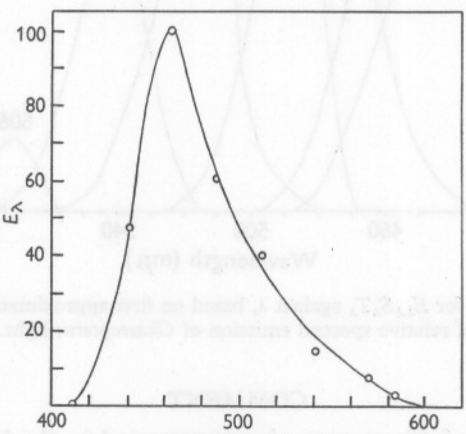

Fig. 11. Corrected values for relative spectral energy of *Chaetopterus* light, and a spectral emission curve based on these values.

Fig. 12, and on human scotopic vision (C.I.E. values). The luminous efficiency of radiation is given by the ratio of total luminous flux to total radiant flux (Harvey, 1940). For human scotopic vision, *Chaetopterus* light is 67% efficient; for fish having visual purples with maxima at 505 mμ, *Chaetopterus* light is 71% efficient; and for the eye of *Limulus*, *Chaetopterus* light is 56% efficient.

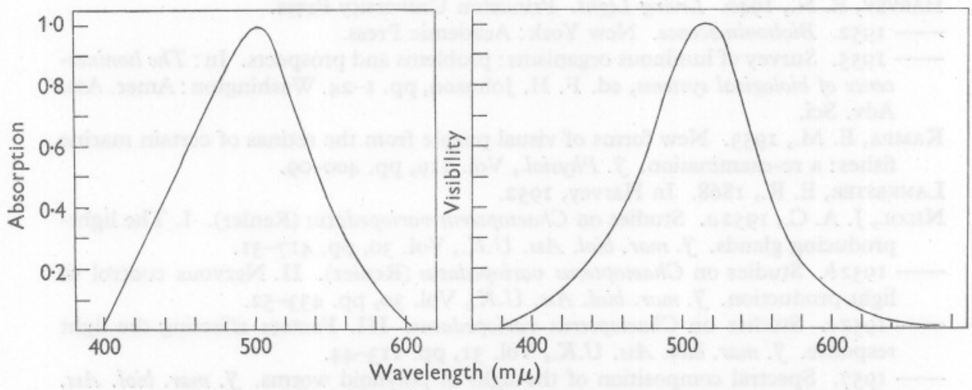

Fig. 12. Left, generalized absorption curve for visual purple of coastal marine fish (based on measurements of Wald, 1946, and Kampa, 1953). Right, visibility curve for *Limulus* (based on measurements of Graham & Hartline, 1935).

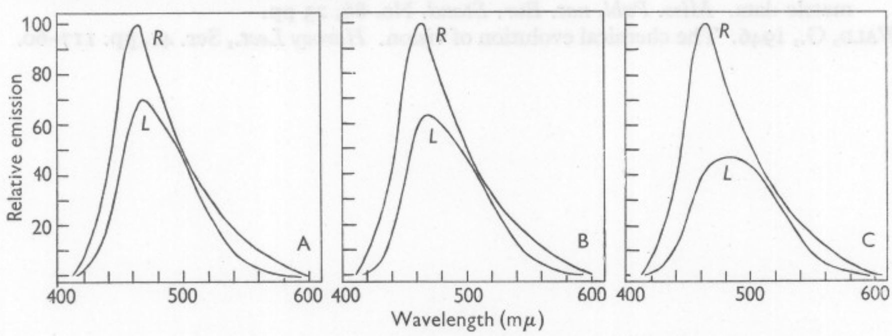

Fig. 13. Relative spectral energy curves (radiant flux) of *Chaetopterus* light, and estimated curves of luminous flux based on fish rhodopsin (A), human scotopic vision (B), and *Limulus* vision (C). *R*, radiant flux; *L*, luminous flux.

SUMMARY

The spectral composition of the light of *Chaetopterus variopedatus* has been measured by means of spectral filters and multiplier phototube. Spectral emission extends from about 405 to 605 mμ, with a maximum at about 465 mμ. The spectral curve of *Chaetopterus* light is compared with a human visibility curve (scotopic vision), a visibility curve for *Limulus*, and an absorption curve for fish visual purple. Luminous efficiencies, based on these curves, are calculated.

REFERENCES

Coblentz, W. W. & Hughes, C. W., 1926. Spectral energy distribution of the light emitted by plants and animals. *Sci. Pap. U.S. Bur. Stand.*, Vol. 21, pp. 521–34 (no. 538).

Graham, C. H. & Hartline, H. K., 1935. The response of single visual cells to lights of different wave lengths. *J. gen. Physiol.*, Vol. 18, pp. 917–31.

HARVEY, E. N., 1940. *Living Light*. Princeton University Press.
—— 1952. *Bioluminescence*. New York: Academic Press.
—— 1955. Survey of luminous organisms: problems and prospects. In: *The luminescence of biological systems*, ed. F. H. Johnson, pp. 1–24. Washington: Amer. Ass. Adv. Sci.
KAMPA, E. M., 1953. New forms of visual purple from the retinas of certain marine fishes: a re-examination. *J. Physiol.*, Vol. 119, pp. 400–09.
LANKESTER, E. R., 1868. In Harvey, 1952.
NICOL, J. A. C., 1952*a*. Studies on *Chaetopterus variopedatus* (Renier). I. The light-producing glands. *J. mar. biol. Ass. U.K.*, Vol. 30, pp. 417–31.
—— 1952*b*. Studies on *Chaetopterus variopedatus* (Renier). II. Nervous control of light production. *J. mar. biol. Ass. U.K.*, Vol. 30, pp. 433–52.
—— 1952*c*. Studies on *Chaetopterus variopedatus*. III. Factors affecting the light response. *J. mar. biol. Ass. U.K.*, Vol. 31, pp. 113–44.
—— 1957. Spectral composition of the light of polynoid worms. *J. mar. biol. Ass. U.K.*, Vol. 36, pp. 529–38.
SKOGLAND, J. F., 1929. Tables of spectral energy distribution and luminosity for use in computing light transmissions and relative brightnesses from spectrophotometric data. *Misc. Publ. nat. Bur. Stand.* No. 86, 23 pp.
WALD, G., 1946. The chemical evolution of vision. *Harvey Lect.*, Ser. 41, pp. 117–60.