J. Exp. Biol. (1968), **48**, 39–53
With 9 text-figures
Printed in Great Britain

VISUAL THRESHOLDS AND SPECTRAL SENSITIVITY OF HERRING LARVAE

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(*Received* 17 *July* 1967)

INTRODUCTION

Although there is little published information on the visual capabilities of marine fish larvae, their behaviour in response to light has received some attention. According to Ali (1959) they are generally photopositive, while demersal freshwater larvae are photonegative. A number of species of marine teleost have a pure-cone retina in the larval stage (unpublished results of the author) while the adult has a duplex retina. In addition, these larvae lack the retinal pigment migrations which are a feature of dark-adaptation and light-adaptation in adult teleosts. Such differences between the larval and adult stage have recently been described in detail in a study of the development of the eye in herring, *Clupea harengus* L. (Blaxter & Jones, 1967).

The free-living larval stage of the herring lasts for 4–6 months depending on temperature and food supply. The larvae on hatching from their demersal eggs are 6–8 mm. in length and have well-developed eyes. The yolk is resorbed after 6–10 days and at the end of the yolk-sac stage the larvae, now 8–11 mm. in length, start to prey on small zooplankton organisms. That light is required for this, and that the time available per day for feeding varies greatly with season and latitude, has been demonstrated by Blaxter (1966). It is only after metamorphosis, at a length of 30–35 mm., that rods develop in the retina and that the retinal pigment starts to show its characteristic responses to changes in light intensity. Thus for a period of some months the larva feeds, avoids predators, and performs limited vertical migrations without the full adult visual equipment. Indeed, the larva also lacks a functional *area temporalis* which is a specialized part of the adult retina. Here very small cones are packed into a ventro-posterior position to give high acuity; this also differentiates fully only after metamorphosis. The larva thus permits a physiological study of an eye, not only at an early stage of development, but also where the retina still consists entirely of cones, and where retinal pigment migration is absent.

The visual capabilities of the larvae were tested by using two light-dependent types of behaviour. By a study of the reduction of phototaxis and feeding at various light intensities and wavelengths it was possible to obtain threshold values and spectral sensitivity curves for these responses.

METHODS

Herring larvae were hatched from eggs artificially fertilized in the laboratory after transport of the ripe gametes from the Clyde herring spawning grounds. Methods of transport, incubation and subsequent rearing are described by Blaxter (1962, 1968).

The experiments were carried out initially in 1965, modified in 1966 and partially repeated in 1967. In every case a temperature-controlled room without windows was used, the temperature varying between 9° and 11° C.

Phototaxis experiments; thresholds

The principle was to determine the threshold light intensity at which phototactic behaviour ceased. This was first done with white light and subsequently with lights of different colour to determine spectral sensitivity. The larvae were used at hatching, at the end of the yolk-sac stage, and 2–3 weeks after hatching when they were well established. To obviate errors due to changes in visual characteristics with age the experiments were carried out within the shortest time possible, usually within 2 days. The need for this curtailed the possibility of very extended series or frequent repetition of experiments.

Batches of 20, and in some cases 30, larvae were placed in a series of clear Perspex troughs measuring 18 × 10 × 4·5 cm. deep and then dark-adapted in light-proof containers for 1 hr. or more. Each trough was placed in turn for 5 min. in the apparatus shown in Fig. 1 A. It consisted of a long horizontal light-proof box, painted inside with matt black paint, and with a hatch at the top for inserting and removing the troughs. The box, which measured 60 × 25 × 25 cm., had an aperture about 5 cm. square in the centre of either end for positioning a light source. This was a 12 V, 36W car headlamp bulb which was run from the mains by means of transformers at a constant voltage. In some later experiments, to get higher intensities, a 12 V, 55 W Philips quartz-iodine lamp was used. The lights were contained in a cubical light-proof box with an aperture coinciding with that in the experimental box. At the aperture a series of slots allowed various combinations of Ilford neutral density filters (5 × 5 cm.) and colour filters to be interposed. A diffusing screen was always used.

In each experiment the intensity of white light was first adjusted to a particular value; the trough was then removed from its container, placed in the experimental box (the room being in darkness) and the hatch was replaced. After 5 min. the hatch was removed in darkness and two Perspex partitions were dropped into special grooves about 4 cm. from either end of the trough. These separated the larvae into three compartments and the numbers could be counted by switching on lights of low intensity positioned below the trough. On the assumption that the larvae were randomly distributed about the trough at the beginning of the experiment the numbers in the three compartments gave a measure of the attractive or repulsive effects of the light intensity used. The response was measured by the difference in numbers of larvae in the two end compartments. For instance, if ten larvae were in the end nearer the light and only two at the other the response score was +8.

In a series of experiments the light was reduced or increased by steps, the smallest of which was equivalent to a reduction to half or increase to double the previous intensity, the minimum optical density of any filter being 0·3. A threshold was established where the response score was within the random range (determined from a number of control experiments in the dark) of ±4. The light intensity was monitored at the end of the trough nearest the light by an EEL 'Microphotometer'. This was calibrated for intensity in metre-candles (m.c.) against a N.P.L. standard and for wavelength by using a series of interference filters in conjunction with a projection lamp under-run at

2600Å to give coloured light of known energy. The drop in light intensity along the the trough was considerably less than the minimum change in intensity from one experiment to another.

No larvae were used again until they had been left for 1 hr. in the dark. Occasional larvae trapped and killed by the descent of the partitions were replaced.

Phototaxis; spectral sensitivity

Having established thresholds for white light at the different stages of larval development thresholds for each of eight wavelengths were obtained in the same way. Restricted bands of wavelength were obtained by Balzer B-20 interference filters with peak values at 390, 450, 485, 505, 521, 555, 605, and 645 mμ. The transmission at the peak averaged 20 % and the half-peak band width was about 10 mμ. The filters were placed in such a way that the angle subtended by the troughs at the filter did not exceed 10° which is within the 'acceptance value' for such filters (light leaving the filters on either side of the normal shows a shift in wavelength; at 10° to the normal the shift is about 2 mμ from the peak). It was not possible to use a greater number of filters because of the lack of time for a series of experiments during this rapid phase of growth.

Phototaxis; analysis of response

To test somewhat further the nature of the phototaxis and, in particular, to see whether it could be considered typical of cones, larvae at the end of the yolk-sac stage were light-adapted at about 500 m.c. for at least 1 hr. and the phototactic response to various suprathreshold stimuli was tested immediately and after varying short periods of dark-adaptation.

The possible operation of a dermal light sense was difficult to eliminate, but tests were made of the rapidity of the phototactic response by testing dark-adapted larvae at the end of the yolk-sac stage over very short periods, of the order of seconds, in various experimental situations.

Feeding; thresholds

Older larvae, which were too large for the phototaxis experiments, were used at ages between 5 and 8 weeks (13–17 mm. length) from hatching to test the importance of light in feeding. Each evening batches of 20 larvae which were seen to be feeding well were dark-adapted in black 'Darvic' (an I.C.I. plastic similar to Perspex) tanks measuring 23 × 23 × 15 cm. Because the body wall and gut are transparent at this stage and the gut is straight, it is possible to count the number of food organisms in the gut after picking up the larvae in a pipette. By next morning at the start of experiments digestion was completed and the guts were clear. Each tank was placed in turn, for 1 hr, in the vertical light box shown in Fig. 1 B. This measured 25 × 25 × 54 cm. high. Light of a particular intensity was directed downwards on to the tank from a similar light housing to that of the phototaxis experiments except that the 12 V, 55 W quartz-iodine lamp was used for all feeding trials. Food, either live *Artemia* or *Balanus* nauplii, was pipetted into the tank through a tube in the wall of the box. An attempt was made to keep the density of food similar for each trial. At the end of 1 hr. the tank was removed, an immediate check was made that the food was well distributed at the surface for feeding, and the larvae were removed in turn by pipette under a very bright bench

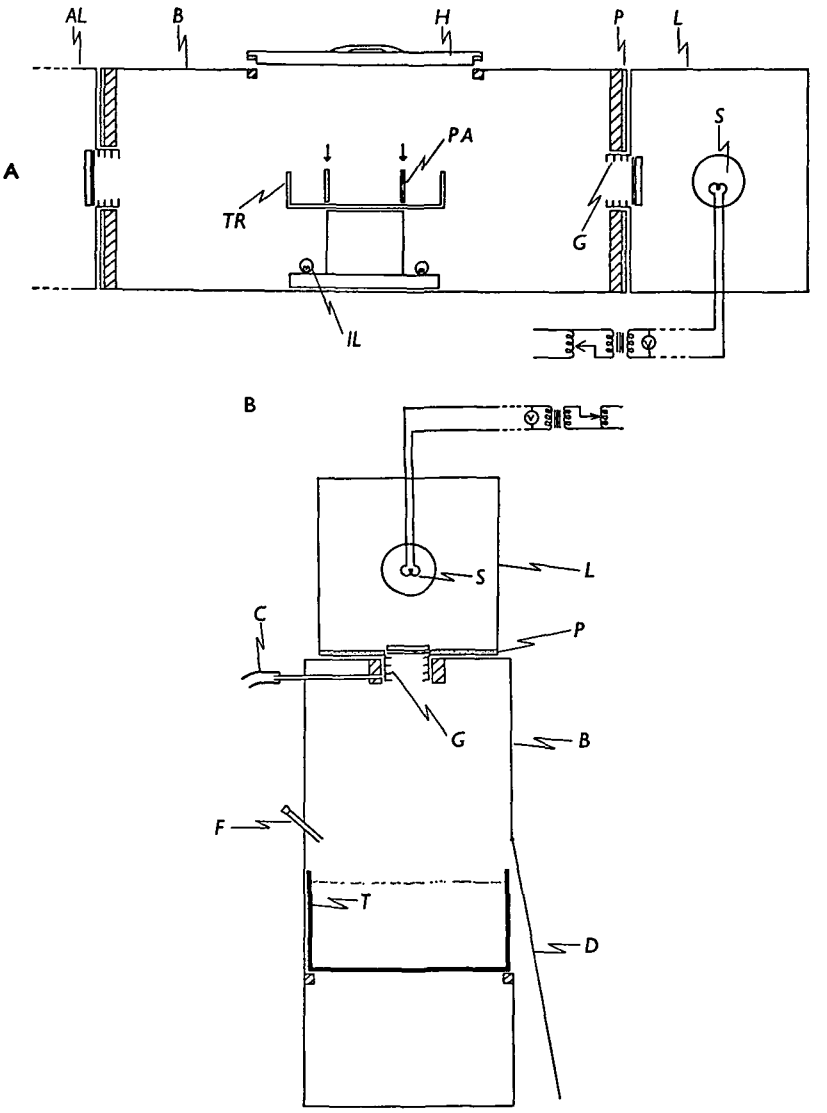

Fig. 1. (A) Phototaxis apparatus in vertical section. (B) Feeding apparatus in vertical section. *AL*, light housing (alternative position); *B* experimental box; *C*, air supply to cool filters; *D*, door, *F*, food tube; *G*, grooves for filters; *H*, hatch; *IL*, illumination used for counting larvae; *L*, light housing; *P*, foam plastic light-proofing material; *PA*, partition; *S*, light source; *T*, tank; *TR*, trough.

lamp. This disturbed them enough to reduce feeding during capture to a minimum. By examination of each larva in the pipette it was possible to count the number of food organisms taken during the experimental period and to detect the occasional larva feeding during the capture process by the anterior position of the food in the gut. In analysing the results the total number of food organisms taken per 20 larvae was plotted against light intensity, a correction being made if the number differed from 20.

In subsequent experiments the light intensity was changed by neutral density filters in a similar way to the phototaxis technique until a threshold was established,

the light being monitored at the position of the water surface by the EEL 'Microphotometer'. Because of the proximity of the light source there were considerable variations in intensity at different places on the surface. At the periphery of the tank the light was $\frac{1}{4}-\frac{1}{10}$ of the intensity at the centre. However the food organisms tended to collect near the centre and it was here that the light intensity for threshold values was measured. The threshold was established each week between 5 and 8 weeks, comparing where possible the effects of using *Balanus* and *Artemia*, until no more *Balanus* were available.

Feeding; spectral sensitivity

Each week, between 5 and 8 weeks, the spectral sensitivity of the larvae was also determined by finding the threshold for feeding using the Balzer interference filters. With eight hourly experiments per day this required a full week.

RESULTS

Phototaxis

(a) White light thresholds

At high light intensities there was a positive phototaxis which became weaker at reduced intensities, so giving an upper threshold where the positive response was lost. At lower light levels still the phototaxis became strongly negative and was eventually extinguished at very low light intensities, so giving a lower threshold. An example of the relationship between intensity and phototactic response is shown in Fig. 2. The upper and lower thresholds for all experiments are given in Table 1. These were obtained from similar graphs by finding the intercept on the abscissae of the line relating the response to the light intensity. Because of random variations in the response at very low light levels and similar variations in control experiments in the dark low scores between ± 4 were used cautiously when finding the intercepts. In general the positive thresholds were more difficult to determine and were not as satisfactory as the negative ones.

The results show that the lower thresholds are 4 to 5 log. units less than the upper values. For a pure-cone retina the lower thresholds seem very low. In fact, the upper thresholds, around 10^{-1} to 10^{0} m.c. coincide much better with cone thresholds based on behaviour experiments as reported in the literature (e.g. Ali, 1959). Sensitivity seems to increase with age, but is greatest at the end of the yolk-sac stage. Experiments carried out on still older larvae showed a reduction of these responses, presumably due to behavioural factors rather than visual ability.

(b) Spectral sensitivity

Using colour filters similar behaviour was observed; two examples of the relation between phototaxis and light of a restricted wavelength are given in Fig. 3A, B. The action spectra for both loss of the positive and loss of the negative phototaxis were obtained by plotting the reciprocals of the threshold for each colour filter on a logarithmic scale to show sensitivity, see Fig. 4A-C. Not all the action spectra are complete because of the problem of getting a light bright enough for a positive phototaxis at some wavelengths, and because the response at the early feeding stage was in some cases much less marked, see Fig. 3B. Thresholds were only used where a clear

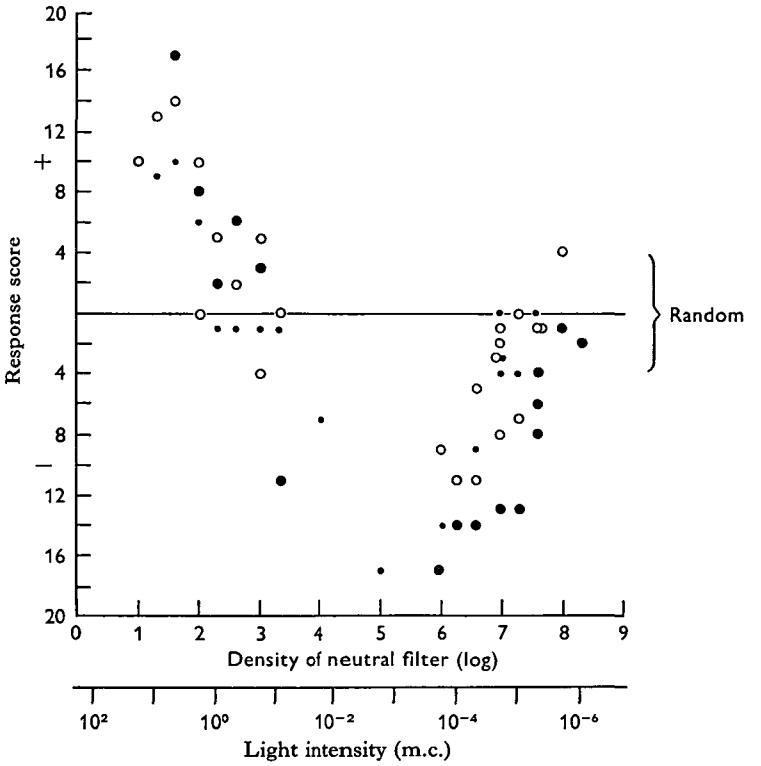

Fig. 2. Changes in phototaxis of herring larvae, shown as positive and negative responses, in relation to intensity of white light (1967 experiment). Light is given both in terms of density of the neutral filters used (e.g. a 3·0 filter reduces the light source (36 W.) by 1000 times) and in metre-candles. The maximum range of random responses in the dark is shown by the bracket. •, Newly hatched; ●, end of yolk-sac stage; ○, established.

Table 1. *Visual thresholds (white light) in m.c. for herring larvae at different stages using a phototaxis technique; experiments in* 1966 *and* 1967

Stage (weeks) after hatching)	Threshold for positive phototaxis (m.c.)		Threshold for negative phototaxis (m.c.)	
	1966	1967	1966	1967
Hatching (0)	$3{\cdot}0 \times 10^{-1}$	$1{\cdot}2 \times 10^{0}$	$2{\cdot}7 \times 10^{-5}$	$1{\cdot}5 \times 10^{-5}$
Yolk resorbed (1)	$2{\cdot}7 \times 10^{-1}$	$1{\cdot}9 \times 10^{-1}$	$7{\cdot}5 \times 10^{-7}$	$3{\cdot}4 \times 10^{-6}$
Established and feeding (2–3)	$7{\cdot}5 \times 10^{-1}$	$3{\cdot}2 \times 10^{-1}$	$9{\cdot}4 \times 10^{-6}$	$8{\cdot}0 \times 10^{-6}$

loss of the response was observed; in general the loss of the positive response was more difficult to determine.

The action spectra are rather plateau-like with varying numbers of peaks and varying overall sensitivity. The curves for negative phototaxis at hatching (Fig. 4A) show good agreement in the two experiments with distinct peaks at around 450, 520 and 600 mμ, perhaps corresponding to three cone populations. The positive curves are incomplete with a suggestion of peaks which do not correspond well with those obtained from the negative thresholds.

At the end of the yolk-sac stage (Fig. 4 B) over-all sensitivity increased, as with white light, but the three distinct peaks were lost, with greatest sensitivity now at about 490 mμ with a lesser, broader peak at 520–550 mμ. There is a fair measure of agreement in the action spectra obtained from the negative and positive thresholds. When the larvae were established and feeding (Fig. 4 C) the over-all sensitivity dropped and the peaks found at hatching were, to some extent, restored.

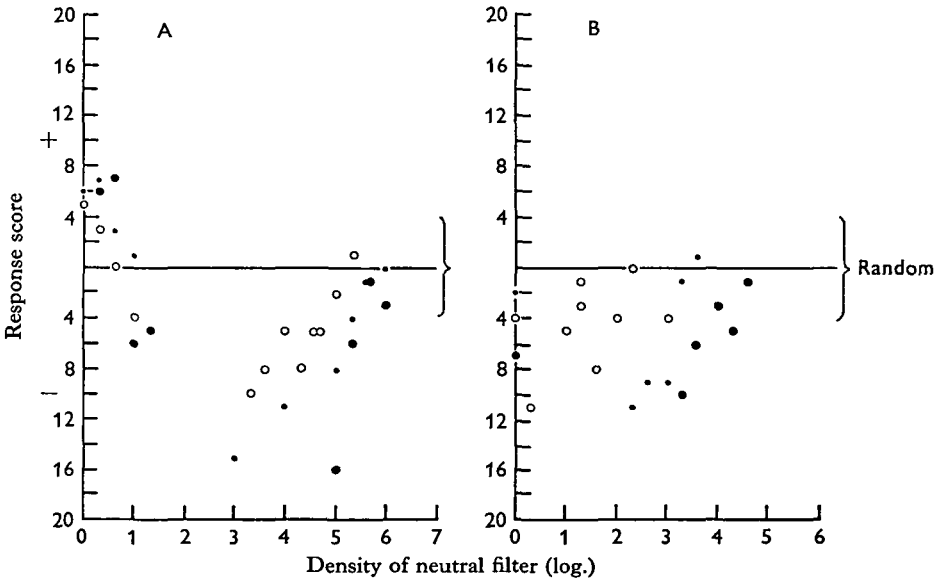

Fig. 3. Examples of changes in phototaxis using coloured light (1967 experiments). Axes same as in Fig. 2. A, 522 mμ; B, 390 mμ. ●, newly-hatched; ●, end of yolk-sac stage; ○, established.

(*c*) *Analysis of the response*

The very low thresholds for phototaxis in white light, 10^{-5} to 10^{-6} m.c., are below the threshold values usually given for cones and suggest a different sensory unit. The effect of light-adaptation is shown in Fig. 5, from which it can be seen that short periods of 5 min. or so in the dark after exposure to light are insufficient to permit the response. To obtain a strong reaction a considerable period of 10–15 min. was required in the dark before the experiment. This must be a feature caused by rate of visual pigment regeneration because the retinal masking pigments are *not* functional in the larva. Low-threshold cones requiring dark-adaptation may be operating or, alternatively, a dermal light sense might be involved which also requires dark-adaptation for full sensitivity (Steven, 1963).

The presence of a dermal light sense is difficult to determine without blinding. However, a rapid response in dark-adapted larvae would be evidence of the eye acting as the receptor, the dermal light sense being characterised by slow-acting photokineses with rather poor orientation effects. The results in Fig. 6 indicate a rapid reaction within 10–15 sec. Considering the agitation of the water due to placing the trough in the experimental box, a response of this speed suggests directional behaviour controlled by the eye.

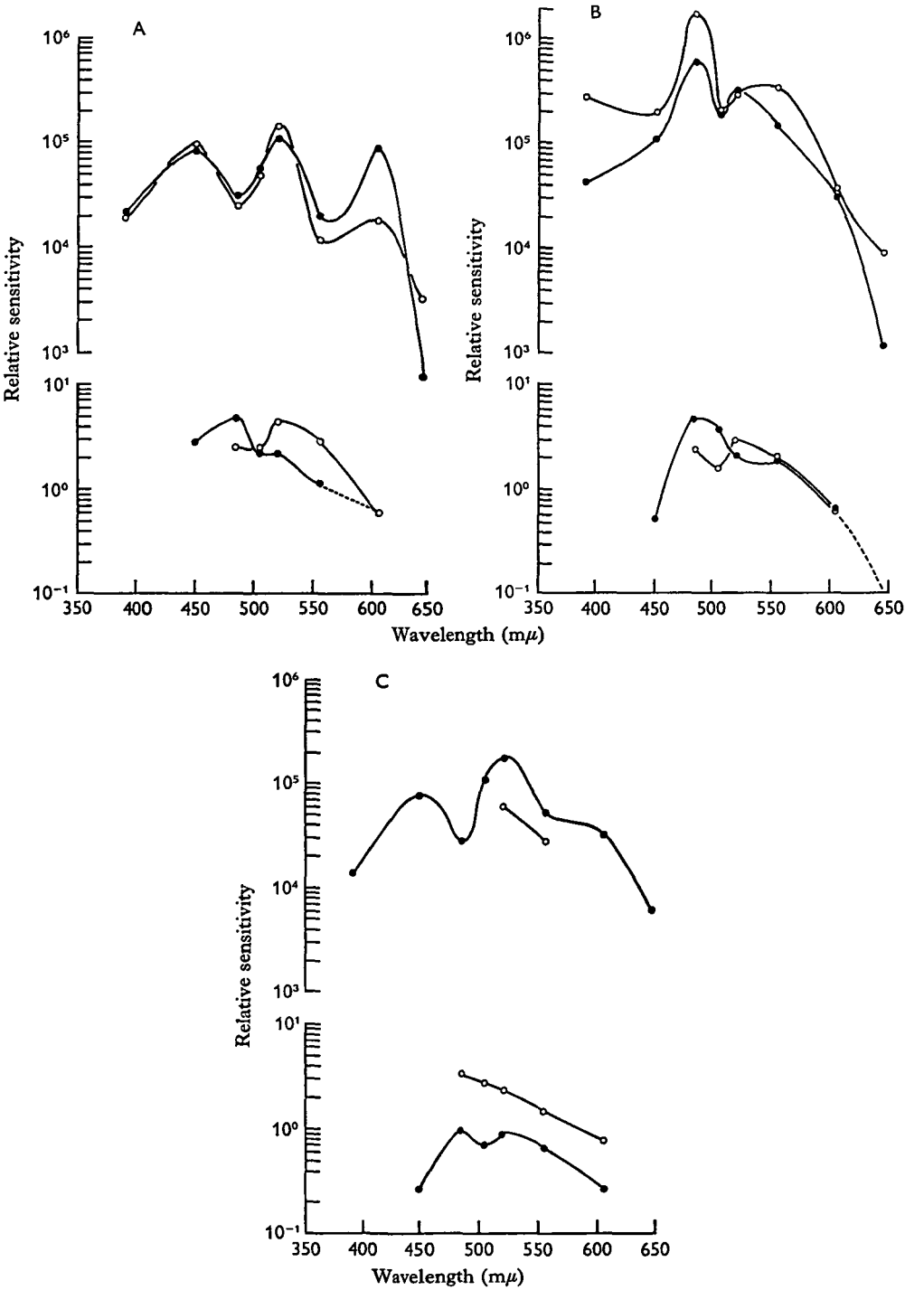

Fig. 4. Action spectra for phototaxis experiments. The upper sets of curves are derived from the thresholds for negative phototaxis, the lower sets for positive phototaxis. Broken line where threshold uncertain. ●, 1966 experiments; ○, 1967 experiments; A, newly-hatched; B, end of yolk-sac stage; C, established.

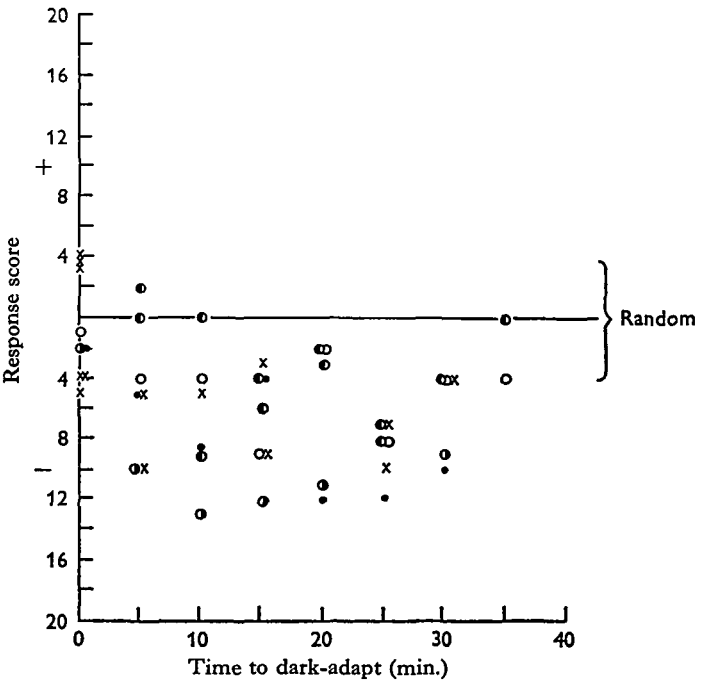

Fig. 5. Photonegative responses to various suprathreshold light stimuli after different periods of time to dark-adapt following exposure to bright light. ●, White light + 6·0 neutral density filter; ×, white light + 5·0 n.d. filter; ○, coloured light, 485 mμ + 3·0 n.d. filter; ◐, coloured light, 505 mμ + 5·0 n.d. filter; ◑, coloured light, 505 mμ + 4·0 n.d. filter.

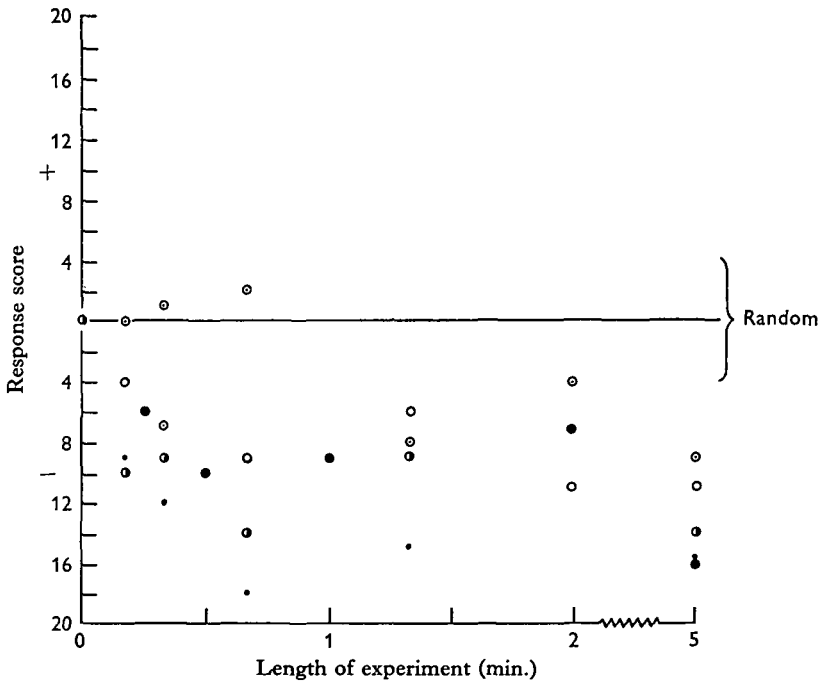

Fig. 6. Photonegative responses of dark-adapted larvae to various suprathreshold stimuli over short periods of time. ●, White light + 6·0 n.d. filter; ○, coloured light, 485 mμ + 3·0 n.d. filter; ⊙, coloured light, 485 mμ + 4·0 n.d. filter; ◑, coloured light, 505 mμ + 4·0 n.d. filter; ●, coloured light, 555 mμ + 5·0 n.d. filter.

Feeding

(*a*) *White light thresholds*

The total number of food organisms, either *Balanus* or *Artemia* nauplii, taken by 20 larvae in 1 hr. is shown for different intensities of light in a number of experiments at different ages in Fig. 7. The reduction in feeding with light intensity is clear in all experiments and thresholds obtained by extrapolation to zero feeding are given in Table 2. In control experiments using *Artemia* and *Balanus* with larvae of the same age the threshold for *Artemia* tended to be lower, presumably due to its greater size and opacity. There was also a slight tendency for increased sensitivity with age. The general level of the thresholds, 10^{-1} to 10^{-2} m.c., is in fair agreement with the threshold performance of the light-adapted eye in fish.

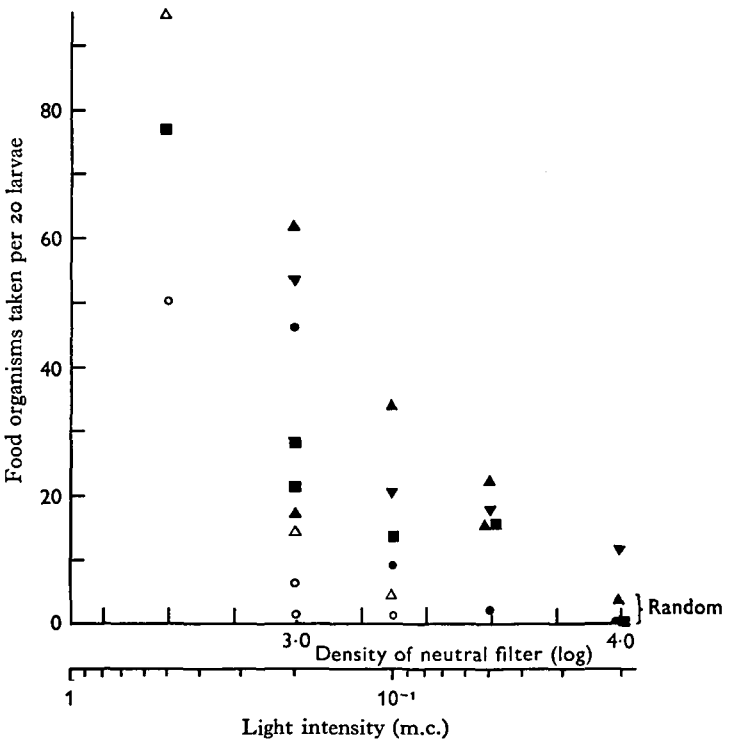

Fig. 7. Total number of food organisms taken by 20 larvae at different intensities of white light. Light is given both in terms of density of neutral filters used to reduce the intensity of the source (55 W) and in metre-candles. The maximum range of feeding during capture is shown by the bracket. Feeding on *Balanus* nauplii: ○, 5th week; △, 6th week. Feeding on *Artemia* nauplii: ●, 5th week; ▲, 6th week; ▼, 7th week; ■, 8th week.

(*b*) *Spectral sensitivity*

An example of feeding at different intensities of blue-green light (522 mμ) is given in Fig. 8, showing the same type of result as for white light. Action spectra, obtained by plotting reciprocals of thresholds for each colour filter on a logarithmic scale, are shown for different ages between 5 and 8 weeks in Fig. 9A, B. The curves are photopic

in nature with a tendency to peak at 560 mμ, though with possible subsidiary peaking at 505 and 450 mμ. There was again a somewhat greater sensitivity using *Artemia* as food.

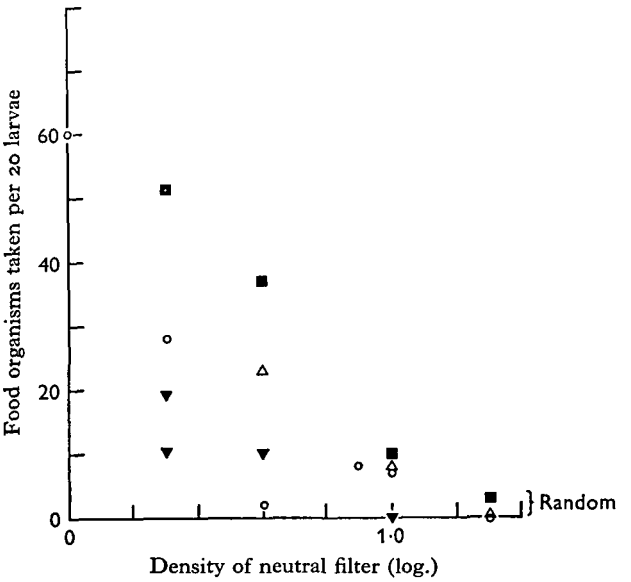

Fig. 8. Example of a feeding experiment in coloured light (522 mμ). Light intensity is shown only as neutral filters used with colour filter. Feeding on *Balanus* nauplii: ○, 5th week; △, 6th week. Feeding on *Artemia* nauplii: ▼, 7th week; ■, 8th week.

Table 2. *Visual thresholds (white light) in m.c. for herring larvae at different stages using* Balanus *and* Artemia *nauplii in a feeding technique; all experiments in* 1966

Weeks from hatching	Threshold for feeding (m.c.) *Balanus*	*Artemia*
5	$1{\cdot}8 \times 10^{-1}$	$9{\cdot}0 \times 10^{-2}$
6	$1{\cdot}0 \times 10^{-1}$	$2{\cdot}0 \times 10^{-2}$
7	*	$< 2{\cdot}0 \times 10^{-2}$
8	*	$2{\cdot}5 \times 10^{-2}$

* Not available

DISCUSSION

Thresholds

It must be emphasized that the criteria used here give thresholds based on the most sensitive larvae. The values for feeding and positive phototaxis (10^{0} to 10^{-2} m.c.) in white light suggest that similar visual mechanisms might be in operation, although it was not possible to use both techniques at the same age. The values agree with earlier experiments on feeding of herring larvae at different light intensities where a threshold of 10^{-1} m.c. was found (Blaxter, 1966) and for feeding and positive phototaxis in herring about one-year-old where the threshold was about 10^{-2} m.c. (Blaxter, 1964). They also accord with the light intensity range, 10^{0} to 10^{-2} m.c., when the change from light-adaptation to dark-adaptation takes place in adult herring as judged

by movements of the retinal masking pigments and cone myoids (Blaxter & Jones, 1967) though it must be emphasized that such retinomotor responses are not present in larvae, as used in the present experiments. Ali (1959) suggested that the cone threshold is the light intensity when feeding starts to drop from the level in very bright light, that is at about 10^0 to 10^1 m.c. in the young stages of various species of *Oncorhynchus*, the Pacific salmon. The lowest level for feeding of fry on *Daphnia* nauplii was, however, 10^{-3} to 10^{-4} m.c. in his experiments and 10^{-4} m.c. in those of Brett & Groot (1963) on young coho salmon. *O. kisutch.*

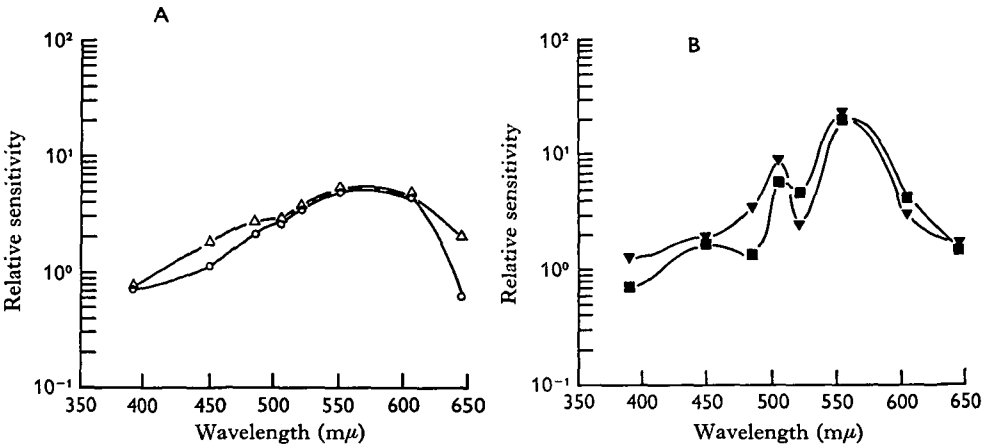

Fig. 9. Action spectra for feeding experiments. Ordinates are the same as in Fig. 4. A, Feeding on *Balanus* nauplii: ○, 5th week; △, 6th week. B, Feeding on *Artemia* nauplii: ▼, 7th week; ■, 8th week.

The activity of young herring larvae was observed at different light intensities down to 0·3 m.c. by Woodhead & Woodhead (1955). They found a basal level of activity, even in the dark, but as the light was vertically directed it was not possible to separate geotactic and phototactic effects easily. Woodhead (1957), using the larvae of *Salmo trutta* and *S. irideus*, found that the general level of activity increased with light intensity above a threshold level of about 5×10^{-3} m.c. Combined with a negative phototaxis this served to retain the larvae within the dark interstices of the spawning redd. Later the photonegative behaviour was lost and activity increased generally at all light levels. According to Hoar (1958) the young of most Pacific salmon except coho become active at night. This is probably a migratory phase when they rise to the surface at dusk and either swim with, or are displaced by, the current. There are clearly both age and species differences in the light reactions of fish larvae making it desirable to perform experiments in the shortest possible time.

The thresholds found for negative phototaxis in the present experiments, 10^{-5} to 10^{-6} m.c., may at first be considered as surprisingly low for a response mediated by cones, for it is clear that no rods are present in the larval retina (Blaxter & Jones, 1967). It should be stressed, however, that these are levels of illumination measured at the cornea. On the retina the level must be increased considerably as the light source is effectively a broad field subtending about 16° at the eye. Two examples of thresholds for phototactic movements may be taken from invertebrates. Strange

(1961), using a rather similar technique to the present experiments, reported a threshold of 10^{-5} m.c. for *Calliphora* maggots, and Marriott (1958) a threshold of 10^{-3} m.c. for *Dendrocoelum lacteum*. In fish, only Grundfest (1932) appears to have measured a threshold for vision behaviourally, finding a value of about 10^{-5} m.c. for the rods of *Lepomis*.

The threshold in the human eye varies with the technique adopted; for a point source of white light it is about 10^{-7} m.c. for foveal vision or 4×10^{-9} m.c. peripherally (see Pirenne, 1956). For a continuously exposed test field subtending 47° at the eye, Denton & Pirenne (1954) reported an absolute human (presumably rod) threshold of $0{\cdot}85 \times 10^{-6}$ cd/m^2. This is nearer to the experimental situation used for herring larvae. A calculation shows that the threshold range for herring larvae ($1{\cdot}5 \times 10^{-5}$ to $7{\cdot}5 \times 10^{-7}$ m.c.) corresponds to a field brightness of about 9×10^{-5} to $4{\cdot}5 \times 10^{-6}$ cd/m^2, the field being at a distance of 18 cm from the eye and subtending an angle of about 16°. With the variety of experimental conditions and size of eye it is not easy to equate threshold values for vision in widely divergent groups of animals.

There remains the possibility that a dermal or other type of light sense is operating. The circumstantial evidence for this lies, perhaps, in the *change* of response from positive to negative phototaxis. In addition, the central nervous system or pineal is not protected by pigment and there is the possibility that this might respond directly to light as Young (1935) found for the spinal cord of *Lampetra*. Hoar (1955) also reported that the pineal or associated area in young sockeye salmon was involved in photonegative behaviour and in pigment response. However, a dermal light sense has been shown to operate most often in blinded teleosts or cave-dwelling species (see Steven, 1963) and, in general, the response is not clear-cut, being rather slow and requiring relatively high levels of illumination. Threshold values ranging from about 10^{1} m.c. in *Lampetra* to $3{\cdot}4 \times 10^{-3}$ m.c. in blinded *Phoxinus laevis* are quoted by Steven. The fairly rapid response found for herring larvae, and its low threshold, suggests it is more likely to be mediated by the eye, though the need for dark-adaptation beforehand could be either a characteristic of low-threshold cones or of a dermal light sense. Without specific experiments to ablate the eyes, which would be difficult in such delicate subjects as larvae of marine fish, the existence of other light-sensitive tissue cannot be discounted. The alternative is that they possess some cones of high sensitivity which may be operating to produce the photonegative response at low intensities. The photopositive response and feeding might then be a function of the whole cone population and, indeed, this is what one might expect with feeding where image formation and the concerted action of numbers of cones would be required.

Spectral sensitivity

Action spectra obtained by behaviour experiments may be influenced by a number of factors which prevent their response corresponding precisely with the absorption spectrum of the visual pigments concerned. Non-visual pigment in the light path may change the distribution of light which reaches the retina or there may be interactions between cone populations resulting in inhibition effects at certain wavelengths of stimulation.

There was considerable variation in the action spectra at different ages and using different behavioural criteria. Those obtained from thresholds for feeding or positive phototaxis are somewhat similar, rather broad and flat with maxima in the yellow-green and similar to some of the photopic curves obtained by electroretinogram (Kobayashi, 1962; Protasov, 1964). The greatest variability is shown in the action spectra obtained from thresholds for negative phototaxis. The three maxima at 450, 520 and 600 mμ shown at hatching, while possibly representing the peak sensitivities of three types of cone, do not resemble very well the components making up a photopic curve, for they are rather too narrow to correspond with the absorption spectra of three visual pigments. Donner (1953), however, also found components ('modulators') with narrow curves in the pigeon. These modulators, investigated by ERG, were of three types with peaks at 480, 540 and 590–610 mμ. Summed together they would produce a photopic curve. In fish MacNichol (1964) using transmission densitometry, found three types of cone pigment with peaks at 455, 530 and 625 mμ. Trimodal action spectra were obtained by ERG in euphausiids by Boden, Kampa & Abbott (1961). In herring larvae the changes in action spectra with age may be due to alterations of relative sensitivity or of interactions of the cone populations. In older herring (Blaxter, 1964) differences in spectral sensitivity were found by the use of different behaviour techniques, but the main peak, at a stage when rods were well developed, was between 500 and 520 mμ.

It may be argued that behaviour techniques for determining sensory abilities are, in general, suspect unless some form of training is used. However, behaviour criteria do represent the way in which animals respond to their sensory environment and provide, therefore, one valid definition of spectral sensitivity. The ERG may be a more objective technique but it does not indicate whether sensory information is being processed in the brain or responded to. Probably both techniques should be applied, though it is questionable in the present instance whether larvae of marine fish are sufficiently robust to make adequate subjects.

SUMMARY

1. Herring larvae are characterized by eyes with no rods and no retinomotor responses, though both are present in the adult.

2. By observing the extinction of phototactic behaviour and feeding in herring larvae of different ages held at low intensities of white and coloured light, it was possible to obtain a measure of both threshold light intensities and spectral sensitivity for a pure-cone eye.

3. The phototaxis was positive at higher intensities, the threshold being 10^0 to 10^{-1} m.c. Below this threshold a negative phototaxis was observed which disappeared at a much lower threshold, about 10^{-5} to 10^{-6} m.c. The threshold for feeding varied with age and the type of food organism, lying between 10^{-1} and 10^{-2} m.c.

4. The high sensitivity for negative phototaxis was probably a visual response and not one mediated by a dermal light sense.

5. Spectral sensitivity varied depending on age and behavioural criteria. Using feeding and positive phototaxis the action spectrum was broad and plateau-like with a maximum in the yellow-green and would appear to be similar to other photopic curves.

The action spectra for negative phototaxis showed a number of peaks. At hatching three peaks at 450, 520 and 600 mμ might represent three types of cone as postulated by the Young–Helmholtz theory of colour vision.

I am grateful to Professor E. J. Denton for a very helpful discussion.

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