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SOME ASPECTS OF THE VISUAL PHYSIOLOGY OF THE SALMON (*SALMO SALAR*)

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THE study of salmon, particularly its habits and vision, is of considerable interest. Its vision, which is the subject of this article, is of importance from several points of view. First, as every fisherman (sport or commercial) knows, the salmon is an active, fast-swimming fish with large and well-developed eyes and hence a very high sensitivity and acuteness of vision. It is natural therefore that its vision counts for a great deal in all the normal activities of its life like feeding, migration, etc. . . To be aware of this and know how the salmon's vision functions helps the commercial fisherman and the sport fisherman, who seek it eagerly, to understand its life history and habits and therefore enables them to exploit better the salmon population in our rivers, lakes and seas.

The salmon belongs to the economically important fish family known as Salmonidae. The trouts and chars also belong to this family. Our Salmon, scientifically known as *Salmo salar*, which occurs on the northern Atlantic coasts of North America and Europe should not be confused with the Pacific salmon of the genus *Oncorhynchus* which occurs on the northern Pacific coasts of North America and northern Asia (Japan and U.S.S.R.). The latter genus comprises six species of which five occur in North America. Although these species also belong to the same fish family (Salmonidae) as our salmon, there are a number of differences between these fish and our salmon.

My interest in the study of fish eyes started in 1954 when I started working in the University of British Columbia. For five years I studied the vision of the five species of Pacific salmon which were available there. The results of these investigations have been published (Ali, 1959 ; 1960 b ; 1961 a ; Ali and Hear, 1959). In this work I studied the structure of the retina of the fish, the changes brought about in the retina by light and darkness, the course of these changes and the influence of variation in light intensities and temperatures on the course, the differences in the retina between night and day, and so on. These studies enabled me to show a correlation between the migration, feeding and schooling of these fishes and their visual physiology.

After coming east in 1958 to accept a teaching position at McGill University I decided to continue my work with the vision of fishes using our salmon. One of the reasons that I decided to do so was that this fish also belonged to the same family and I thought that it would be of interest to compare the results obtained with this fish with those obtained with the Pacific salmon.

In a study of this sort it is important to being with an understanding of the structure of the eye in general and the retina in particular. To the eye the retina is what the film is to the camera. From a photograpgh of the eye (Fig. 1) which shows the structure of the eye of the salmon, it will be clear that the principle

FIG. 1. Vertical section of an eye of a salmon. *C*—cornea ; *L*—lens ; *I*—iris ; *N*—optic nerve ; *R*—retina.

underlying the structure and functions of the eye is similar to that of a camera. When the light entering through the cornea and the lens strikes the retina, the light-sensitive pigment in the photoreceptor cells (rods and cones) absorbs the light energy and is affected in a way analogous to the chemical in a photographic film. This photochemical process brings about certain mechanical changes in the rods and cones and further, starts an electrical impulse in the nerve fibres which is transmitted through the optic nerve to the brain where it is felt as the visual sensation. Depending on the number and location of photoreceptor cells that are thus affected an image is formed due to the mediation of the brain.

In the case of the salmon, I first studied the structure of the retina and the relation of its thickness and of the various layers composing it to certain features of the fish such as the length, weight, head width and eye diameter. This was followed by a study of the retinal state under various environmental conditions such as different light intensities, wavelengths (colours), temperatures, etc. After this the course of light- and dark-adaptation and the influence of different light intensities and temperatures on the course of adaptation were investigated. The responses of the retina in the enucleated eyes (i.e. eyes removed from the animal) were also studied. Finally, the electrical response of the retina (electroretinogram) and the frequency of a flickering light at which the electroretinogram (ERG) became indistinguishable from that of continuous light were investigated. In this article I propose to give a brief outline of the results and conclusion of these studies conducted since 1958.

Most of salmon used in this research were kindly provided by Mr. A. J. Baxter of the Canada Department of Fisheries; some were obtained from the Eastern Townships Hatchery of the Province of Quebec. Financial support for this work was provided by the National Research Council of Canada. Unless otherwise mentioned the fish used were yearlings measuring about 9-12 centimetres in length. They were kept in the laboratory in running tap water and fed with pork liver, pablum or trout pellets purchased from G. R. Clark & Co., Salt Lake City, Utah, U.S.A.

In this research mainly two techniques were used and it is perhaps desirable to describe them briefly. The first is the histological technique and the second, the electrophysiological technique. Some of the instruments used in these techniques are shown in Figs. 2 and 3.

The aim of the histological techniques is to preserve the tissue in as lifelike a state as possible and to cut very thin slices of it, usually 3 to 8 microns thick, and stain them to make the parts directly visible for microscopic examination. (A micron is 1/25400 inch or 1/1000 millimetre). It is necessary to preserve the organs or tissues, because as we know, the brain and sense organs like all tissues of dead animals, tend to decompose. In order to arrest this decomposition and retain the tissues or organ in a state that resembles as much as possible its living state it is necessary to use either chemical means (pickling) or physical means (freezing). Since the eye decomposes very quickly extreme care has to be taken to ensure its preservation (fixation). This is accomplished either by quickly removing the eye from a living, anaesthetised fish or a decapitated fish or by dropping a living fish into the fixative (pickling solution). I used a fixative called Bouin's fluid. It consists of 75 parts of saturated picric acid, 25 parts of formaldehyde and 5 parts of acetic acid. This solution fixes the eyes very well and was found to be very satisfactory. The eyes were left in this solution for two days after which they were dehydrated in alcohols of increasing concentrations (70%

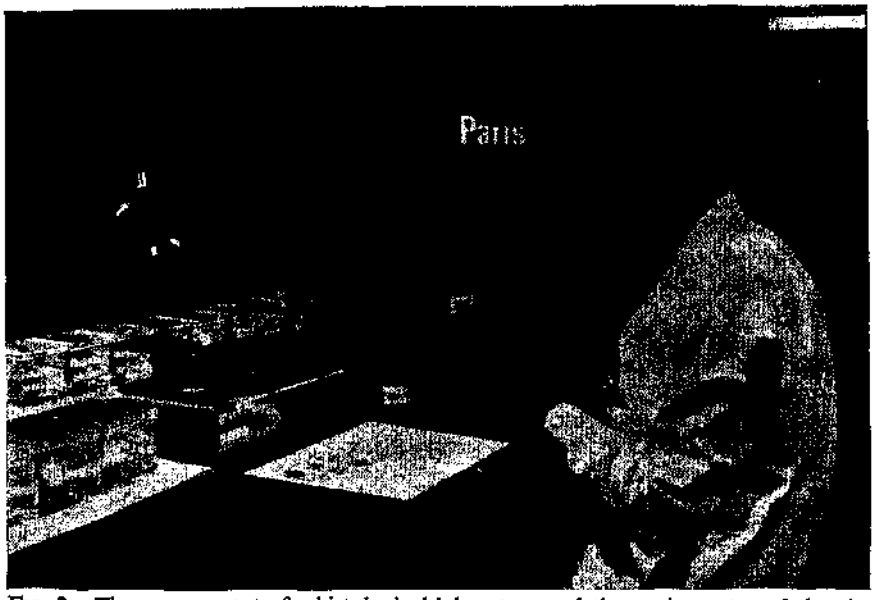

FIG. 2. The arrangement of a histological laboratory and the equipment used therein. *B*—paraffin block; *M*—microtome; *S*—slide warming table (to stretch the paraffin ribbons); *R*—paraffin ribbon (when the paraffin block is cut, each section adheres to the one before and the one after it thus forming a ribbon).

FIG. 3. Arrangement of apparatus for electrophysiological work (see the text for explanation). *C*—constant temperature tank; *O*—oscilloscope; *P*—preamplifier; *F*—fish (rolled in gauze and attached to the paraffin coated bottom of the square plastic dish); *T*—thermistor telethermometer.

90% and 100%). The purpose of this is to remove all water from the eyes. They were then placed in xylene for 45 minutes, transferred to a mixture of xylene and paraffin in the oven. After 30 minutes they were placed in paraffin for an hour. This gradual transfer from alcohol to paraffin enables the paraffin to impregnate the interiors of all the tissues. The material is then blocked in paraffin and is ready to be sliced. For cutting this block into very thin slices (section, as usually called) a microtome is used (Fig. 2). The sections come attached in sequence in the form of a ribbon, pieces of the ribbon are placed on slides and dried, then the paraffin is removed with xylene and the sections of the retina are stained. A few drops of Canada balsam is placed on each slide and a cover slip is placed on top in order to seal the slices. When dried, these slides are ready for microscopic examination.

The aim of the electrophysiological method is to detect and register electrical impulses originating in the retina. These signals are about a few hundred microvolts so they have to be amplified a hundred or thousand times with a preamplifier (Fig. 3). The signals thus amplified are fed into an oscilloscope to make them visible. A camera attached to the oscilloscope photographs these signals so that they can be measured and studied later. To pick up the electrical response from the retina an electrode made of a thin silver strip about a millimetre in width coated with silverchloride is inserted into the eye through a small puncture made in the cornea. A similar electrode known as the reference electrode is placed outside the eye but quite close to it. Both these electrodes are connected by very thin wires to the preamplifier. The difference in potential between these two electrodes is the response as we see it on the face of the oscilloscope.

Structure of the Retina

The retina of our salmon is very similar to that of the Pacific salmon and in general pattern resembles the retina of any bony fish. The accompanying photomicrograph (Fig. 4) of a tranverse section of the salmon retina shows the various layers which compose the retina. There are eight layers and two membranes:

Epithelial pigment layer.
Visual cell layer composed of rods and cones.
External limiting membrane.
External nuclear layer.
External plexiform (reticular or granular) layer.
Internal nuclear layer.
Internal plexiform layer.
Ganglion cell layer.
Internal limiting membrane. (Ali *et al.* 1961b)

For a detailed description of the retina of our salmon and the Pacific salmon reference may be made to Rochon-Duvigneaud's books (1943; 1958, and my papers; Ali, 1959; Brett and Ali, 1958). Note that the pigment layer is quite extensive in the salmon. The visual cell layer is composed of rods and cones which are the actual photoreceptors. The salmon's retina contains a large number of rods as well as cones. Most of the work to be discussed in the following sections will deal with the pigment layer and the cones. It will be seen that the rods are slenderer then the cones and more of them are connected to a ganglion cell than are cones. This is because the rods function when the light intensity is very low and so have

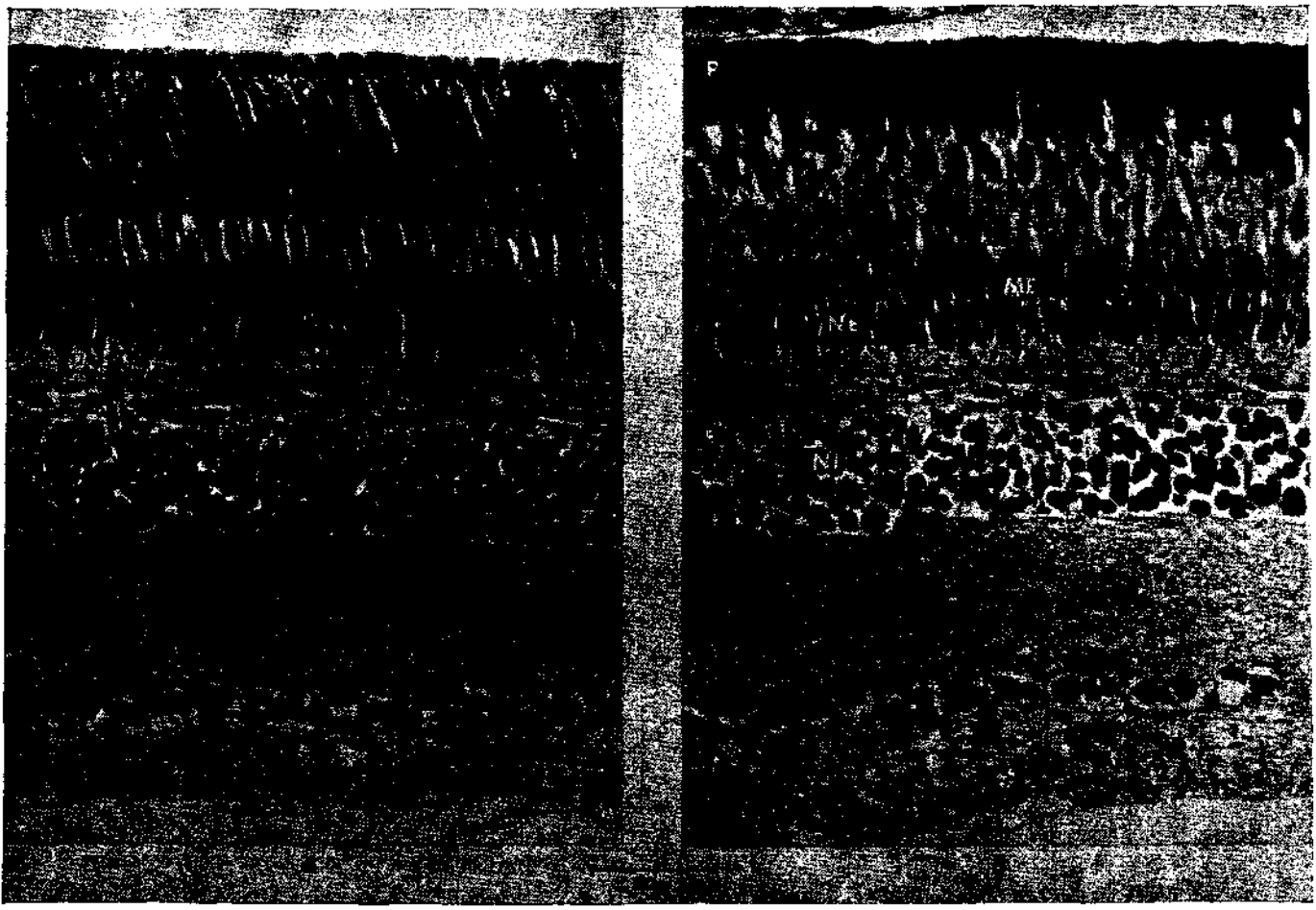

FIG. 4. Histological section of a light-adapted retina. FIG. 5. Histological section of a dark-adapted retina. *P*—retinal epithelial pigment; *C*—cone; *R*—rod; *ME*—external limiting membrane; *NE*—external nuclear layer; *PE*—external plexiform layer; *NI*—internal nuclear layer; *PI*—internal plexiform layer; *GC*—ganglion cell layer; *NF*—nerve fibres (which form the optic nerve); *MI*—internal limiting membrane.

to be more sensitive while the cones are less sensitive but have greater acuity and function in bright light. In other words, the rods are scotopic elements which are able to detect the shapes and outlines of objects in dim light while the cones which are the photopic elements are capable of seeing the details of objects and their colour, etc. Since the rods are very difficult to see and to measure while the cones can be observed without much difficulty the latter were measured in most of the investigations the results of which are discussed in this paper.

Correlation of Retinal and Body Measurements

The purpose of this study was to ascertain the relationship among retinal measurements such as the thicknesses of the retina, pigment layer and cone layer and body measurements such as length, weight, head width and eye diameter. It is known, for instance, that there is a definite correlation between length and weight in fish (Hoar, 1939). However, in previous investigations with the Pacific salmon it was not clear whether the pigment and cone layer thicknesses should be considered directly or as percentages of the total retinal thickness. In the first investigation (Brett and Ali, 1958) the thicknesses of these layers were expressed as percentages of the total retinal thickness. Later, in a more extensive investigation (Ali, 1959), about 9,000 eyes of Pacific salmon were examined. It appeared then, that the various layers composing the retina did not vary in any proportion to the total retinal thickness but did so at random (in fish belonging to the same age group). In view of this, thicknesses of the layers to be studied were plotted directly. In a subsequent investigation with the chameleon retina (Ali, 1960a), graphs were drawn wherein both the actual thicknesses and thicknesses as percentages of total retinal thicknesses were given. There was no apparent difference between the two graphs.

As a first step I wished to examine whether in a group of fish of the same age there is or there is not a correlation among the various retinal and body measurements. For instance, does the thickness of the retina vary with the weight or length or does the thickness of the pigmented layer vary in any proportion to the thickness of the retina? These questions are interesting in themselves but in addition any available correlation will give a basis for the proper consideration and presentation of results in an extensive investigation such as the one I was carrying out.

Fifty yearlings were sampled under identical light and temperature conditions (25 ft-c; 8°C). Their lengths, weights, head widths and eye diameters were measured. The eyes were then sectioned and the thicknesses of the retinae, pigment and cone layers were measured. A statistical analysis of the data gave the following information:

Between any pair of morphological measurements (length, weight, head width and eye diameter) there was very good correlation. For example, a longer fish was heavier, had a larger head and larger eyes than a shorter fish. However, there appeared to be no good correlation between a set of retinal measurements (thicknesses of retina, pigment and cone layers) nor between a set of retinal and morphological measurements. That is, a longer and therefore a heavier fish with a larger head and eye did not necessarily have a thicker retina or pigment layer or cone layer. Similarly, if a fish had a thicker retina than another it did not necessarily have a thicker pigment or cone layer. It appeared that in a group of fish belonging to the same age group there was no useful correlation between the body and retinal measurements nor between the retinal measurements themselves (Ali *et al.* 1961a). This led to the question whether the relationship among the various measurements would

be the same in fish belonging to various age groups. Experience had indicated that a smaller fish such as an alevin had a retina which was thinner than that of an older fish such as a yearling. In order to study this question in detail the following investigation was undertaken (Ali, 1963).

One hundred and ten salmon belonging to seven age groups, *viz.*, embryos prior to hatching, alevins, fry, fingerlings, one and a half year old and, two year old parr were sampled at a light intensity of 25 ft-c. The lengths, weights, head widths and eye diameters were measured and the eyes were sectioned. The thicknesses of the retinae, pigment and cone layers were measured. These measurements were also statistically analysed.

In this group of fish also, as in the case of the yearlings a very good correlation exists between each set of morphological measurements. Further, unlike in the yearlings, a good correlation exists between the retinal measurements and also between retinal and body measurements. A thicker retina has, in general, a thicker pigment layer and cone layer. Similarly, within certain limits, a longer and heavier fish with a larger eye has a thicker retina, pigment and cone layer than a shorter and lighter fish with a smaller eye. However, it was interesting to see that the thicknesses of the retina, pigment and cone layers did not keep increasing in direct proportion to the increase of the body characteristics throughout the age of the fish. Their thicknesses increased in direct proportion to the body measurements such as length, eye diameter, etc., until the fish reached the age of about a year and a half after which they either remained the same or decreased somewhat. A careful examination of the sections with a microscope suggested the possibility that the retina grew in thickness up to a certain stage at a rate commensurate with the general growth of the fish. This growth of the retina was brought about by the addition of cells. Since nervous elements do not increase indefinitely the growth of the retina does not continue throughout the age of the fish. When the fish reaches a certain age (one and a half years) the growth of the retina ceases. With further increases in the length of the fish or the size of its eye the existing cells in the retina of the fish become slightly spread around in order to cover the entire interior of the eye. If some growth continues in the peripheral regions the thickness of the retina does not decrease. On the other hand, if this growth is slower or non-existent then the retina becomes thinner due to stretching. If this were true, it should be possible to establish a relationship between the length of the fish or the diameter of its eye and the number of ganglion cells or cones per a given length of a transverse section of its retina. In order to ascertain if this were so, about 150 fish of various ages were sampled and their lengths and eye diameters were measured. After sectioning their eyes, the number of ganglion cells and cones per unit length of the section were counted. When these data were analysed it was very clear that, as the fish grew longer or its eye grew larger, the number of these cells per unit length (or their density) decreased. When the number of ganglion cells per unit length in an embryo or alevin is compared with that in a two year old fish it is seen that for every seven ganglion cells per unit length in the small fish there is only one cell in the two year old. The decrease in the number of cones per unit length is not so pronounced. For every two cones in the young fish there is one per unit length in the two year old. It appears that the number of cones does not decrease as greatly because they are formed for a much longer period during the life of the fish while the ganglion cells may all be formed at a very early age and with growth of the eye are simply distributed resulting in a reduction in their density. Examination of the sections shows that in the sections of the embryo's eye there are a large number of well developed ganglion cells while the cones are few and poorly developed (Ali, 1964a)

PHOTOMECHANICAL CHANGES IN THE RETINA

The retinal epithelial pigment layer, cones and rods assume different positions in various light conditions. Their positions are also affected by other environmental factors besides light, such as temperature. In Fig. 4 a photomicrograph of a retina adapted to light of about 100 ft-c is given. It is seen that the pigment and rods are expanded while the cones are contracted. When this situation is compared with that in Fig. 5, the changes occurring in the retina due to its adapta-

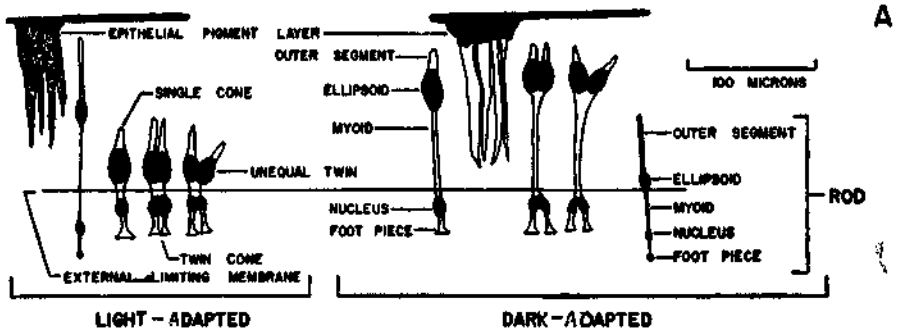

FIG. 6. Schematic repesentations of the positions of the retinal epithelial pigment, cones and rods in the light- and dark-adapted retinae.

tion to darkness are apparent. When the retina is dark-adapted, the pigment and rods are contracted and the cones are expanded. What is the significance of these changes? We can easily understand these changes if we consider how our eyes adapt themselves to light and darkness. When the light in your bedroom is suddenly turned on you blink for a while and are unable to see well. This is because your eyes had hitherto been adapted to darkness and a sudden turning on of the light brought in too much light into your eyes and bleached the visual pigment in the rods and cones. Your eyes become light-adapted in a few minutes when your pupil contracts and controls the amount of light entering the eye, thus controlling the bleaching of the visual pigment. Similarly, when you walk into a dark room from a well lit room you are not able to see well for a little while. In a few minutes you are able to see better. In this case your eye had been adapted to light with its pupil contracted. This made it difficult for the small quantity of light in a darkened room to enter your eye and stimulate the rods and cones. After you have been in the dark room for a few minutes your pupil dilates and permits the full utilisation of the available light and you are able to see better. In the case of the salmon the pupil is not contractile and adaptation to light and darkness is brought about by a different mechanism which is more primitive and slower. As mentioned earlier the cones are the elements responsible for vision in a bright environment while the rods function when the light intensity is very low. When the intensity of light is above a certain threshold changes occur in the retina so as to control the amount of light diffusing into the optic cup, mask the rods which do not function efficiently in bright light and, to place the cones as close as possible to the incoming light quanta. The pigment, by its expansion, not only masks the rods (which have elongated) but also reduces somewhat, the diffusion of light inside the eye. The cones by their contraction come to lie very close to the external limiting membrane, therefore, as close as possible to the light quanta entering the eye. In the dark, just the opposite happens. This is accomplished by the

pigment contracting and assuming the form of a narrow strip thus permitting the maximum diffusion of light; the rods contracting and thereby occupying the position previously occupied by the cones and, the cones expanding and lying close to the pigment. Looking at it teleologically it would appear as if the cones expanded in order to vacate their places for the rods. These changes in the retina, as a result of light and darkness, are referred to as photomechanical changes and Fig. 6 gives a diagrammatic view of pigment, cones and rods in the light- and dark-adapted conditions. They occur not only in the salmon but also in most bony fishes, amphibians and quite a few birds. In general pupillary movement is absent in animals whose retinae light- and dark-adapt by undergoing photomechanical changes. The exception are some flatfishes and the birds which have both pupillary as well as photomechanical adaptation. These photomechanical changes in the salmon's retina have been of considerable interest to me and during the past several years I have studied the course of these changes, the influence of some environmental factors on these changes and the response on the retina to various conditions such as light intensities, wavelengths, time of day and temperatures. I shall outline the results of these investigations in the following pages.

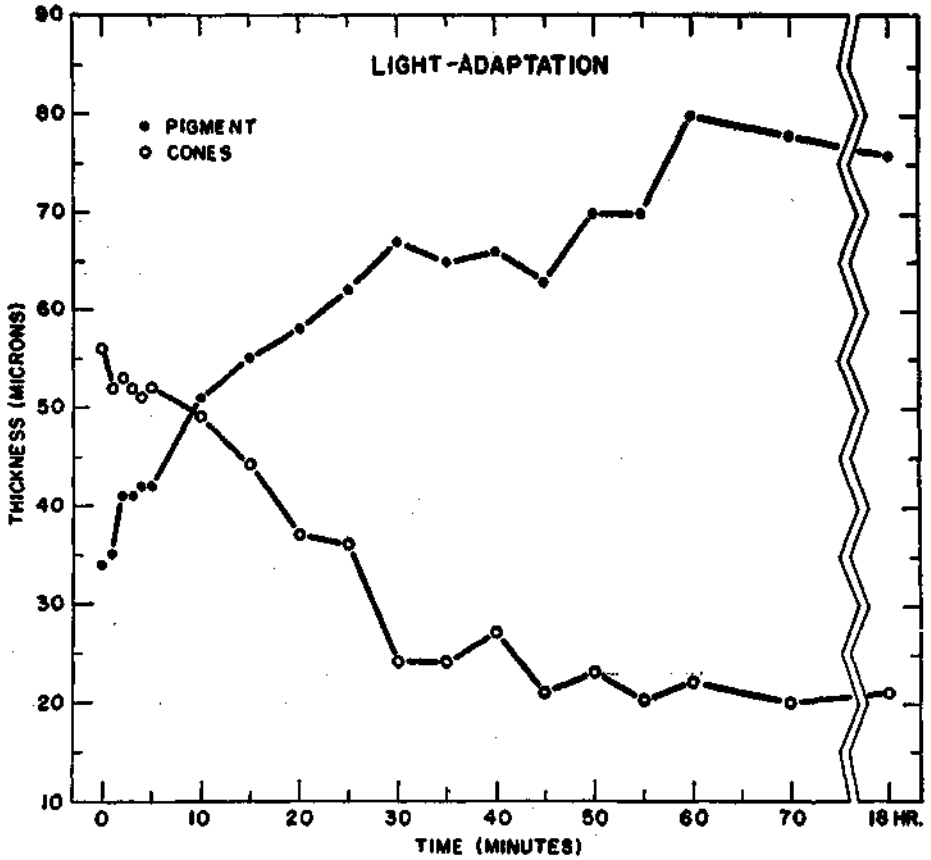

FIG. 7. Graph showing the expansion of the pigment and the contraction of the cones when dark-adapted eyes are exposed to light and sampled at different intervals.

1. *The course of the changes.*

The first thing that interested me was the course of these changes. In order to study this aspect we kept about a hundred fish in the dark for a few hours and

then turned the lights on and sampled five fish each at the following intervals : 0, 1, 2, 3, 4, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, and 70 minutes. Similarly, about a hundred fish were kept in light for a few hours and then the lights were turned off and five fish each sampled at the same intervals as those mentioned above. The eyes were removed, imbedded, sectioned and stained. In the case of each eye the thicknesses of the pigment layer and the cone layer were measured. The thickness of the pigment was taken to be the measurement from the base of the epithelial cells to the farthermost expansion of the pigment in the epithelial cell processes, while the distance between the external limiting membrane and the tips of the outer segments of the cones was considered the thickness of the cone layer. The results of the first experiment indicated the course of light-adaptation while those of the second experiment showed the course of dark-adaptation. The results are presented in graphic

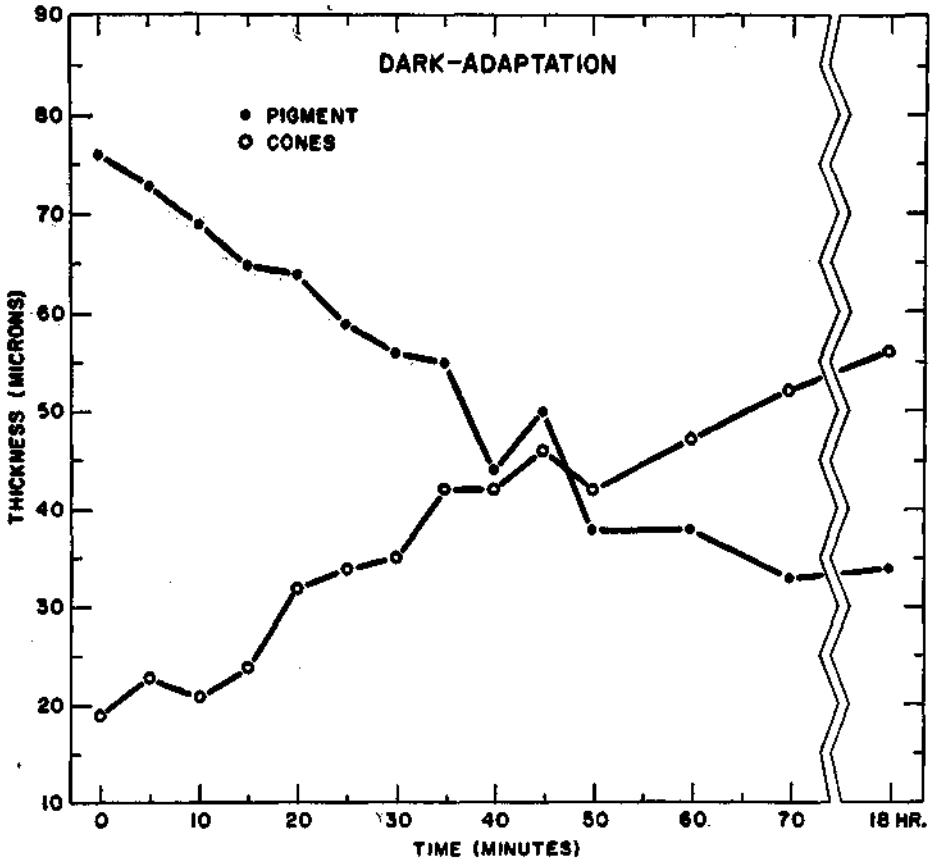

FIG. 8. Graph showing the contraction of the pigment and the expansion of the cones when light-adapted fish are exposed to darkness and sampled at different intervals.

form in Figs. 7 and 8. It is seen that the retinal epithelial pigment commences to expand immediately on exposure to light. It gradually expands and attains a fully light-adapted state in about 60 minutes in light. The reaction of the cones to light also starts instantaneously and they assume a contracted, light-adapted state in 45 minutes in the light. In the case of dark-adaptation (light-adapted fish exposed to dark) neither the pigment nor the cones possess a latent period (time before they

start moving) prior to the commencement of their contraction and expansion, respectively, in the dark (Ali *et al.* 1961b).

These results differ from those obtained with the Pacific salmon. Of course, the life histories of the two groups are different. Bearing this in mind, it is interesting to compare the results. In general, the Atlantic salmon yearling takes a longer time to adapt itseft to light and darkness. While the pigment of the various species and stages of the Pacific salmon show a latent period before beginning to dark-adapt, the Atlantic salmon does not. Among the species of the Pacific salmon, Coho (*Oncorhynchus kisutch*) is supposed to be phylogenetically closest to the Atlantic salmon but the results of these experiments show no similarities between the two species.

In addition to the reason that these fish were slightly different and their life histories also differed, another possible reason for the difference between the results with the Atlantic salmon and those with the Pacific salmon appeared to be the use of light of a lower intensity in the experiments with the former. In the experiments with the Pacific salmon, a much higher light intensity (400 ft-c) was used. Subjection to a much higher light intensity probably resulted in a more rapid rate of light-adaptation and conversely, fish that had been under a very bright light might have, on subjection to darkness, commenced dark-adapting only after an initial latent period because of the effects of a brighter light lasting longer. Light is an active stimulus and the stronger it is the greater will be its effect. The shorter duration taken by most of the Pacific salmon species to dark-adapt after the latent period may perhaps be due to the magnitude of the contrast between light of 400 ft-c intensity and darkness being considerable. In the experiments with the Atlantic salmon a lower light intensity (25 ft-c, was used and the contrast between it and darkness is far less. This appeared to explain why in the Atlantic salmon the rate of dark-adaptation is gradual, uniform and slower. Further investigations were undertaken to ascertain the influence of different light Intensities and temperatures on the courses of light and dark-adaptation. In the first place, experiments were designed to ascertain the influence of light intensities on the course of light- and dark-adaptation (Ali, 1962 b). Two sets of dark-adapted fish were exposed to light of 1.0 ft-c and 900 ft-c respectively and sampled at the intervals mentioned earlier. The retinal epithelial pigment of dark-adapted fish exposed to light of 1.0 ft-c commenced to expand about two minutes after exposure to light and attained the light-adapted state 35 minutes after exposed to light (Fig. 9). The cones of these fish started contracting about 15 minutes after exposure to light and assumed the light-adapted (contracted) state after 55 minutes. The corresponding figures for the fish exposed to light of 900 ft-c were five minutes and 40 minutes for the pigment and 15 minutes and 45 minutes for the cones. It is of interest that when the light of 900 ft-c was turned on, the fish appeared to be alarmed and excited. Several fish jumped out of the experimental tank. This behaviour ceased 10 minutes after the lights were turned on. Similar observations had been made in the case of the Pacific salmon (Ali, 1959 : Hoar, *et al.* 1957).

In order to study the effect of light intensity on dark-adaptation about a hundred fish were light-adapted at an intensity of 1.0 ft-c and another hundred at 900 ft-c. The light was then turned off and sampling done in a manner similar to that described above. Examination of their retinae gave the following information. The retinal epithelial pigment of the fish that had been exposed to 1.0 ft-c commenced to contract about 5 minutes after the lights were turned off and attained the completely dark-adapted (contracted) state in 45 minutes. The cones started to expand

five minutes after darkening and became maximally elongated 25 minutes after subjection to darkness. In the case of the fish that had been exposed to light of

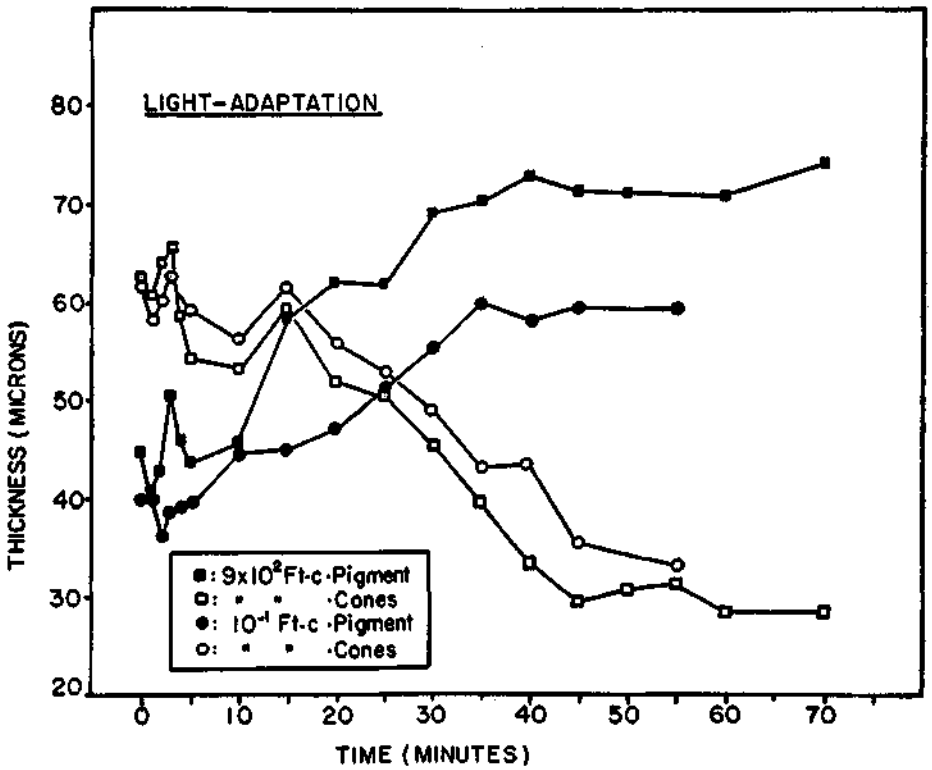

FIG. 9. Graph showing the influence of light intensity on the speed and extent of light-adaptation (see text for explanation). The black circles and squares represent the pigment, the open circles and squares represent the cones. The squares correspond to illumination by 900 foot-candles, the circles to 1.00 foot-candle.

900 ft-c before being subjected to darkness, the retinal epithelial pigment did not commence contracting for about 50 minutes after the lights had been turned off and even in the eyes of fish sampled 70 minutes after the lights had been turned off it was in an expanded (light-adapted) state. The cones too, like the pigment, did not commence expanding even 70 minutes after darkening and were in a fully light-adapted state (Fig. 10).

From the results presented above it is clear that light intensity does influence the course and state of adaptation. In the case of light-adaptation it is seen that the retinal epithelial pigment of dark-adapted fish exposed to 1.0 ft-c attains the maximum thickness (in its case) 35 minutes after exposure to light whereas the pigment of the fish exposed to 900 ft-c takes only about 17 minutes to reach the same thickness. Similarly the cones of fish exposed to 900 ft-c attain the minimum length in 40 minutes whereas the cones of fish exposed to 1.0 ft-c takes 55 minutes. It appears safe therefore to assume that, in the eyes of fish exposed to a higher light intensity, the pigment and cones light-adapt at a faster rate than those in the eyes of fish exposed to a lower light intensity.

It is also evident from these results that the final state of light-adaptation of the retinae of fish exposed to 900 ft-c is in a more pronounced state than that of fish

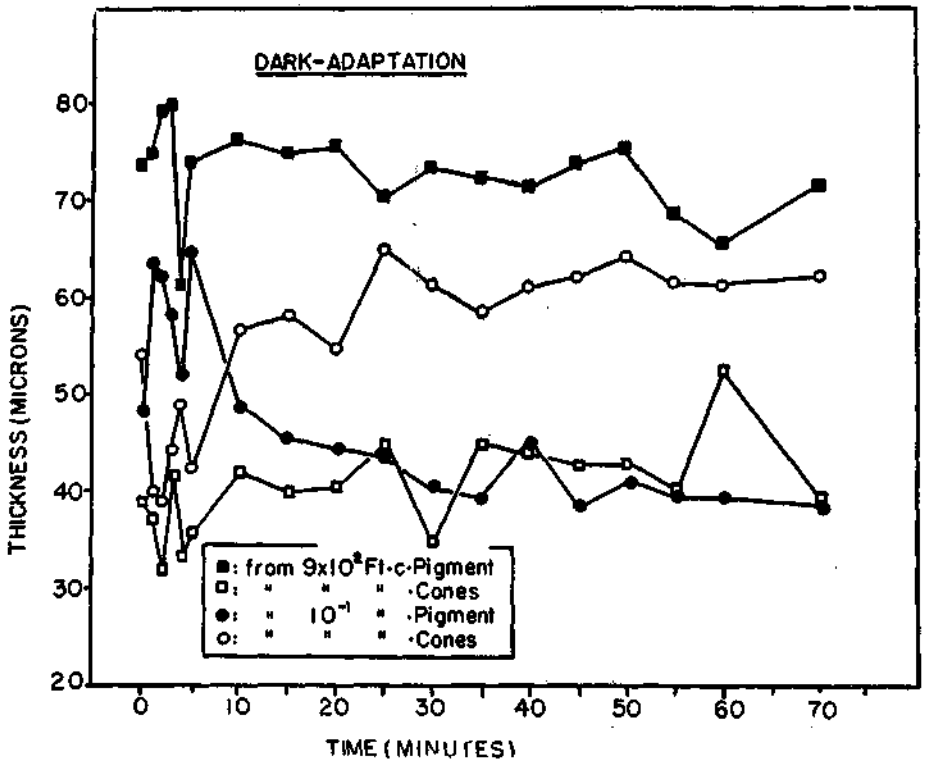

FIG. 10. Graph showing the influence of light intensity on the speed and extent of dark-adaptation (see the text for explanation). The black squares and circles represent the pigment and the open squares and circles represent the cones. The squares correspond to previous adaptation to light of 900 foot-candles and the circles, previous adaptation to 1.0 foot-candles.

exposed to 1.0 ft-c. The pigment is more expanded, the cones more contracted at the state of maximum adaptation in the former group. In other words, within certain limits, the higher the light intensity, the more pronounced the state of adaptation of the retina.

The fact that the difference between the thicknesses of the pigment layers of the two groups is more pronounced than the difference between the thicknesses of the cone layers may be used in support of the suggestion that the function of the pigment layer is to control the amount of light impinging on the cones. In the higher light intensity it is almost completely dispersed in order to reduce this amount, while in the much lower light intensity it is somewhat contracted in order to permit the full utilisation of the available light by the cones. The cones, on the other hand, are receptors which function in light intensities that are at or above their thresholds. Therefore, their function, *viz.* to perceive, remains the same regardless of the light intensity, as long as it is above their threshold. When it decreases below their threshold they elongate, thus permitting the rods to contract and take up the positions previously occupied by them, near the external limiting

membrane and closest to the incoming light quanta. The difference between the thicknesses of the cone layers of the two groups of fish, one adapted to 900 ft-c and the other to 1.0 ft-c, is negligible because it is a little less than the difference between the cone layers of fish sampled 55 and 60 minutes after exposure to 900 ft-c.

These results also indicate adequately the influence of light intensities on the course of dark-adaptation. The retinae of fish subjected to darkness after adaptation to 900 ft-c are in a light-adapted state even after 70 minutes while those of fish subjected to darkness after adaptation to 1.0 ft-c become dark-adapted within this period. The pigment layer of the fish exposed to 900 ft-c has a latent period of at least 55 minutes before it shows even a tendency to commence dark-adapting as opposed to the 5 minutes latent period of fish exposed to 1.0 ft-c. It is abundantly clear from these results that the retinae of fish adapted to a higher light intensity are influenced for a longer period than are those of fish adapted to a much lower light intensity.

Unfortunately, from these results it is not possible to conclude whether or not fish exposed to a higher light intensity would, after an initial latent period, dark-adapt at a very rapid rate while those from a lower light intensity would commence dark-adapting slowly and at an even pace immediately after subjection to dark. Another feature of these results warrants mention here. In the experiments using 1.0 ft-c the cone layers take a longer time to light-adapt than to dark-adapt. The retinal pigment, however, light-adapts faster than it dark-adapts. This is the first time that I have encountered a situation wherein the cones have taken a longer time to light-adapt than to dark-adapt. This may be due to the possibility that a low light intensity invokes only a slow response because its stimulating effect is low. This makes the process of light-adaptation a longer one. On subjection to dark, these retinae dark-adapt quite rapidly because (i) the difference between the low intensity and darkness is comparatively smaller, and (ii) they are not in as great a state of adaptation as are the retinae exposed to a much higher light intensity.

With the information available at present, it is not possible to speculate on the significance of these results to the activities of young salmon. The photobehavioural responses of young salmon will have to be studied in order to understand the significance of the results of histophysiological studies to their life history and activities.

As a next step, it seemed that it would be of interest to ascertain the effect of temperature on the course of light- and dark-adaptation of the cones and pigment. In order to do this about 200 salmon were acclimated to 5°C and another 200 to 20°C. Using the same procedure as that outlined above, they were sampled, at the temperatures to which they had been acclimated, at various intervals after exposure to light or to darkness. The intensity of light used for light-adaptation was maintained constant. The eyes of these fish were sectioned, stained and examined. The results are presented quantitatively in Figs. 11 and 12.

Careful examination of the sections and analyses of the measurements indicated that full adaptation of the pigment (i.e. expansion) occurred in 50 minutes of exposure to light at 5°C while it was completed in 15-20 minutes at 20°C. The cones show a similar difference in response, adaptation to light being completed in 55 minutes at 5°C and in 35 minutes at 20°C.

In the case of dark-adaptation, at 5°C neither the cones nor the pigment responded even after two hours in the dark. However, adaptation seemed to have

commenced as the retinae of fish sampled after 70 minutes appeared to be in a partly adapted state. Surprisingly, even in the fish sampled at two hours the retina was

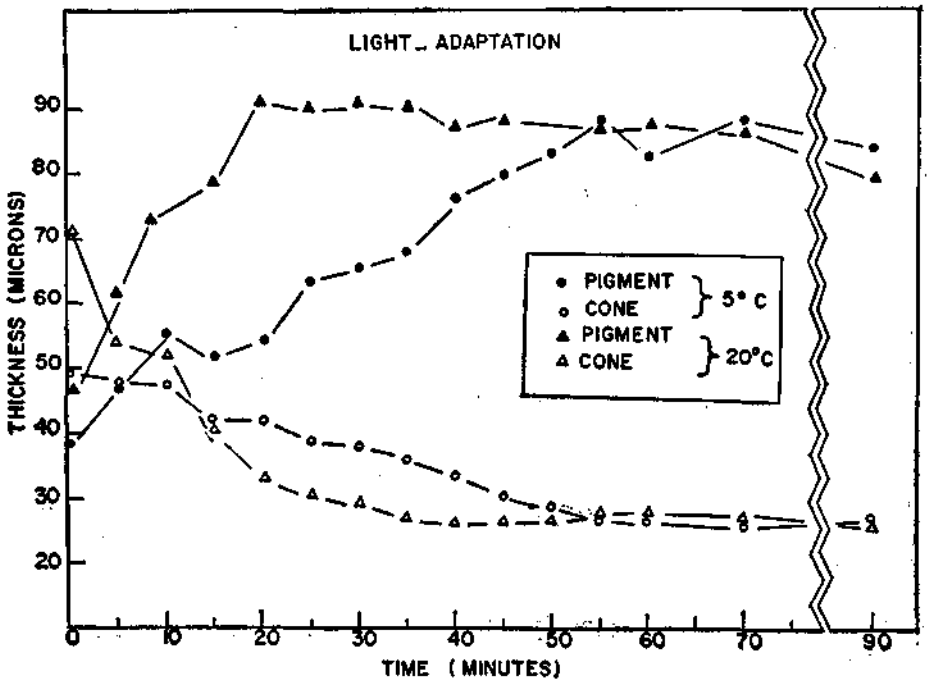

FIG. 11. Graph showing the effect of temperature on the speed and extent of light-adaptation (expansion of pigment, contraction of cones).

in a partially adapted state. Although the pigment and cones were more contracted and expanded, respectively, in the fish sampled after 14 hours in darkness, they were not in typically dark-adapted state (i.e. the pigment and cones were not maximally contracted and expanded, respectively).

Both the cones and the pigment of fish at 20°C commenced responding soon after the lights were turned off (Fig. 12). The cones were almost dark-adapted in about 60 minutes while the pigment did so in 45 minutes (Ali, 1964b).

These results clearly demonstrate the influence of temperature on the speed of retinal photomechanical responses of salmon. From the results it is evident that at the higher temperature the rates of light- and dark-adaptation are faster.

STATE OF THE RETINA UNDER VARIOUS ENVIRONMENTAL CONDITIONS (Ali, 1961b)

1. *At various light intensities*

Five fish each were subjected to 100, 10, 1.0, 0.1, 0.01, 0.001, 0.0001 and 0.00001 ft-c for two hours and then sampled. These experiments were always conducted in the forenoon. The eyes of these fish were sectioned, stained and examined. Thicknesses of the pigment and cone layer were measured.

The pigment was in a light-adapted state in the eyes of fish exposed to 100, 10, 1.0, 0.1, 0.01, and 0.001 ft-c. It was in a dark-adapted state in fish exposed to 0.0001 and 0.00001 ft-c.

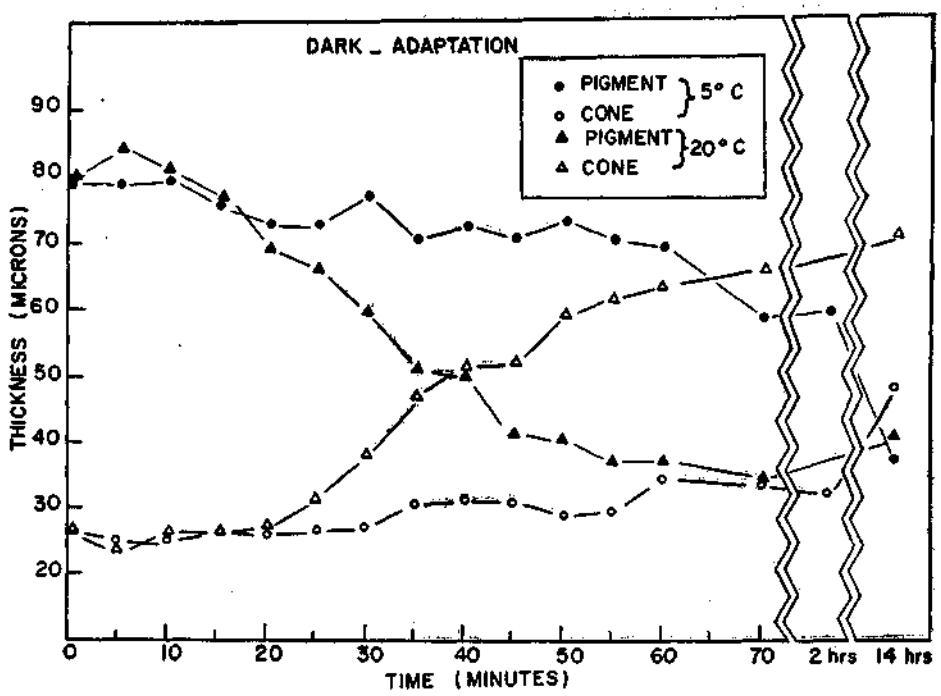

FIG. 12. Graph showing the effect of temperature on the speed and extent of dark-adaptation (contraction of the pigment and expansion of the cones).

The cones were in a light-adapted (contracted) state in the retinae of fish exposed to 100, 10, 1.0, 0.1 and 0.01 ft-c, in a partially adapted state for 0.001 ft-c, and in a dark-adapted state for 0.0001 and 0.00001 ft-c (Fig. 13).

These responses of the pigment and the cones to various light intensities are interesting in themselves because they show the morphological changes occurring within the retina. Evidently, experiments wherein electrophysiological and behavioural methods are employed will have to be carried out in order to ascertain whether there is any correlation between the results obtained by these various methods. In the case of the late fry stages of the pink salmon (*Oncorhynchus gorbuscha*) and the chum salmon (*Oncorhynchus keta*) and the late fry and smolt stages of the sockeye salmon (*Oncorhynchus nerka*) and the coho salmon (*Oncorhynchus kisutch*) the state of the cone layer has been correlated with their feeding response. Further, in the case of the late fry of the pink salmon, the association between its downstream migration and the state of adaptation of the retina has been shown. It is conceivable that similar correlations could also be obtained for the Atlantic salmon in future investigations.

It is also interesting to compare these results with those obtained with the various species and stages of the Pacific salmon mentioned in the previous paragraph. Results of the experiments with the Atlantic salmon (Fig. 13) indicate that the

retina of this salmon has a much lower threshold than the retina of any species or stage of the Pacific salmon. The pigment of the Pacific salmon species commen-

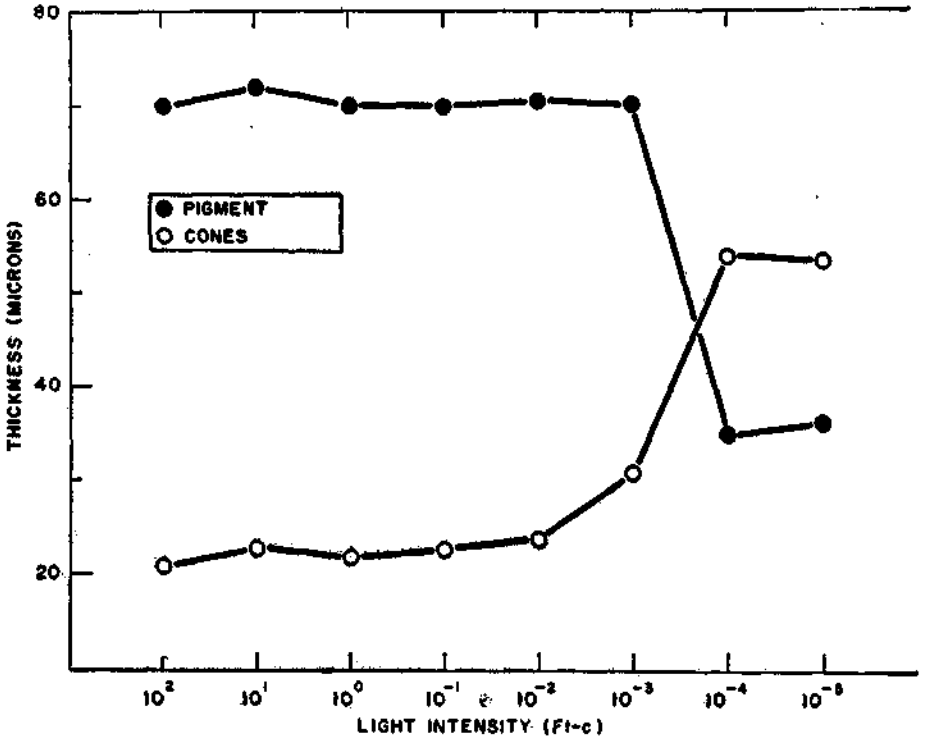

FIG. 13. Thickness of the pigment and cone layers in the retinae of fish adapted for two hours to light of various intensities.

ced dark-adapting at a much higher intensity : 1.0 ft-c in the chum, pink and coho late fry and the coho smolt, and 10 ft-c in the sockeye late fry and smolt. It is also interesting to note that except in the case of the chum late fry, the pigment of all the other species and stages studied was in a partially adapted state under some light intensities (0.1, 0.01 ft-c). This has not happened in the case of the Atlantic salmon. The pigment was in a light-adapted state under 0.001 ft-c and in the next condition studied (0.0001 ft-c) was in a dark-adapted state.

The cones of the four species of the Pacific salmon were also much less sensitive to light. The late fry of the coho and the smolts of the sockeye and coho possessed cones which were more sensitive and commenced dark-adaptation when the intensity decreased below 0.1 ft-c. The cones of the other species and stages remained light-adapted only as long as the light intensity was 1.0 ft-c or above.

It is also necessary to recall that only in the case of the sockeye late fry did the cones assume a partially adapted state (0.1 ft-c) while in all the others they were either light-adapted or dark-adapted. As has been mentioned earlier, the cones of the Atlantic salmon were in a partially adapted state at 0.001 ft-c.

It is interesting that the cones of the coho salmon were more sensitive because based on migratory behaviour it has been suggested that, of the five species of

Oncorhynchus occurring on the Pacific coast of Canada, it is the closest to the trout-like, parental type. Also, coho have a freshwater life history more similar to that of the Atlantic salmon than to any other species of the Pacific salmon.

In their yearling stage, the Atlantic salmon usually inhabit shallow streams and do not migrate downstream at dusk. Yearling salmon in the Little Codroy river in Newfoundland feed on small organisms and are themselves preyed upon by eels. They migrate during the day within the estuary. It may be argued that because of their sensitive eyes they are not subject to downstream displacement at dusk. A more acute vision would, of course, be an asset in capturing small organisms over a greater part of the day. Apart from these suggestions, it is not possible, with the available information, to give any definite reason as to why the Atlantic salmon should have a more sensitive retina.

2. *At various wavelengths*

The principal aim of these experiments was of course, to ascertain the retinal responses to various wavelengths. An additional objective was to obtain from these results, an idea of the visible spectrum of the Atlantic salmon. It is obvious that if the retina of fish exposed to a particular wavelength is light-adapted then the light of that wavelength is visible to the fish ; on the other hand, if it is dark-adapted then it is safe to assume that the fish cannot see in that light. It was thought that, if the visible spectrum could be obtained using this principle, it could later be verified with the aid of electrophysiological methods or using feeding or pseudo-rheotropic responses as indices.

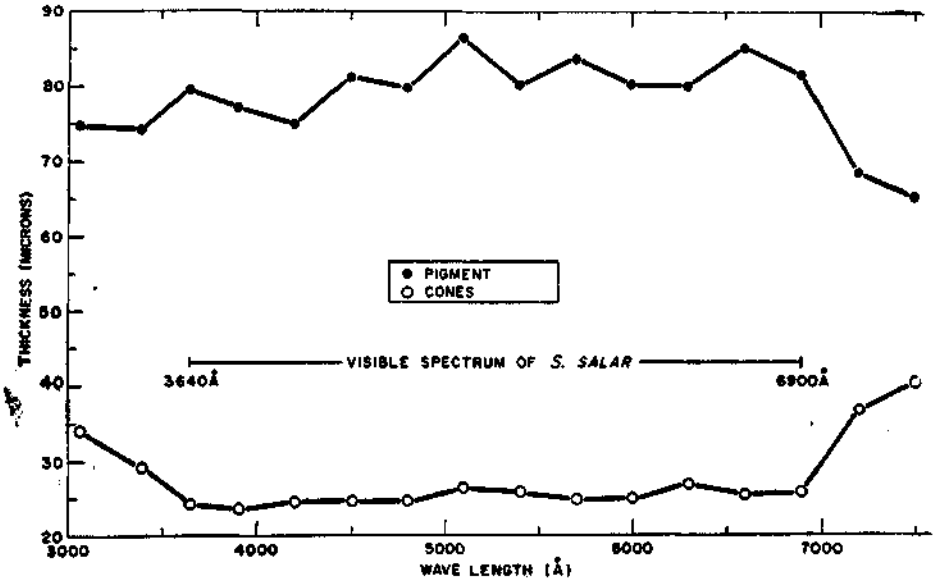

FIG. 14. Thickness of the pigment and cone layers in the retinae of fish adapted for two hours to light of various wavelengths (colours).

These experiments were also conducted only during the forenoons. Lights of sixteen different wavelengths were created using monochromatic interference filters

manufactured by Messrs Barr and Stroud of Glasgow, Scotland. Each filter was placed in a Leitz slide projector in order to create light of its particular wavelength. Light intensity was kept constant at 60 ft-c. This was accomplished by altering the distance between the light source and the aquarium (30×24×24 cm.) in the light proof experimental room and by using apertures of various diameters. The fish were exposed in groups of five to each of the wavelengths for two hours and then the eyes were fixed in Bouin's solution.

With light of wavelengths ranging from 3060 Å to 6900 Å, the retinal epithelial pigment was in a light-adapted state. It was in a dark-adapted state with light of 7200 Å and 7500 Å (Fig. 14). The cones were in a light-adapted state in the retinae of fish exposed to light of wavelengths ranging from 3640 Å to 6900 Å (Fig. 14). In light of wavelength 3640 Å they were in a partially adapted state. At wavelengths of 3060, 7200, and 7500 Å they were in a dark-adapted state.

As has been pointed out earlier, in the case of the Pacific salmon there is a good correlation between the state of adaptation of their cones and their feeding and migratory responses. Although experimental evidence is not yet available, it appears reasonable to assume that such a correlation can exist in the case of the Atlantic salmon also. Since the cones are in a light-adapted state in the eyes of fish exposed to light of wavelengths ranging from 3640 to 6900 Å it may be suggested that the visible spectrum of the yearling Atlantic salmon ranges from 3640 to 6900 Å. The suggestion that the visible spectrum of the salmon is between these wavelengths implies that these fish are able to perceive light whose wavelength falls within this range. It does not imply that they are capable of discriminating among these wavelengths. They may very well possess this capacity but it is not within the scope of this investigation to suggest this.

3. *At various temperatures*

It is known that temperature influences almost all types of physiological activities. In the case of certain fishes and amphibians it has already been shown that temperature has diverse effects on the retinae in light and in darkness. For example, higher temperatures bring about an expansion of the retinal epithelial pigment in darkness in the eyes of the sockeye salmon fry. Lower temperatures had no effect and in light, neither low nor high temperatures had any influence on the retinal elements. It was felt that it would be necessary to ascertain the influence of temperature on the retina of the Atlantic salmon yearling so that the results of our experiments may be properly understood. In these experiments, temperature is often a variable due to unavoidable reasons.

These experiments were also conducted only in the forenoon. Five fish each were subjected to various temperatures ranging from 0°C to 22°C in light for two hours. Similarly, groups of five fish were kept at each of the temperatures for two hours in darkness. All were fixed and their eyes sectioned, stained and examined. The results are given in Fig. 15.

(a) *In light.*—The retinae of fish kept at 2.0°, 5.7°, 11.5°, and 14.3°C demonstrate that the higher the temperature the more contracted the pigment is. On the other hand, temperatures of 18.0° and 21.5° C bring about an expansion of the pigment.

The measurements of cone layer thicknesses indicate that the cones do not respond to temperatures in light. In the fish kept at 11.5°C a slightly thicker cone

layer was observed. This could however be due to several eyes having thicker cone layers as can occur in any sample of the Atlantic salmon yearlings.

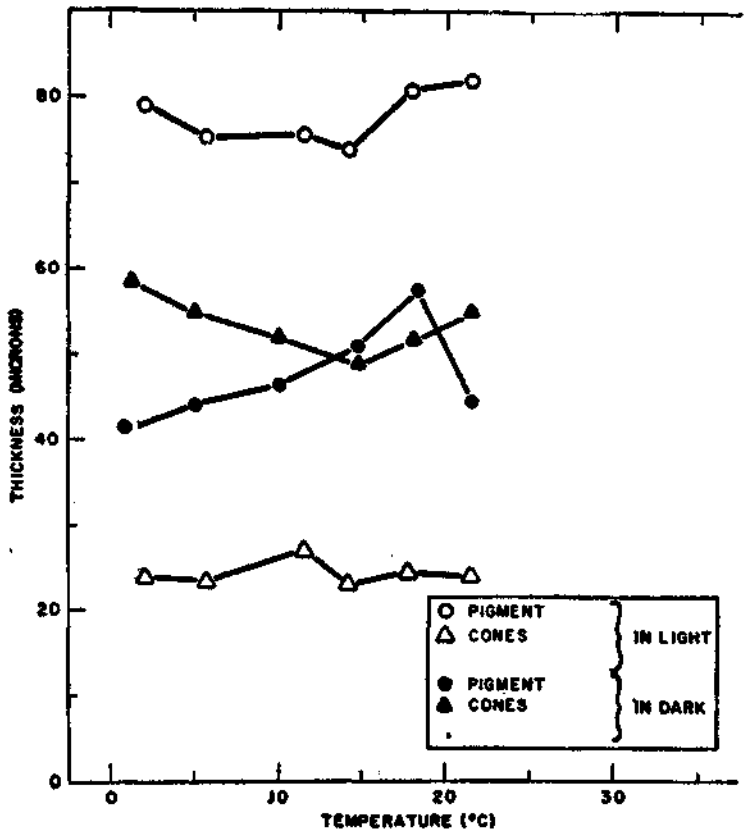

FIG. 15. Thickness of the pigment and cone layers in the retinae of fish adapted to light and to dark at various temperatures.

(b) *In darkness.*—The thickness of the retinal epithelial pigment increased with higher temperatures, but when the temperature exceeded 18.3°C the effect was reversed and in the retinae of fish kept at 21.5°C a marked contraction was observed. The cones contracted with increase in temperature up to 14.8°C, above which the effect was opposite.

The comparatively lesser effect of temperature on the pigment in light and the total lack of response of cones are interesting. It may be taken to indicate that, in the presence of light, which is the primary stimulus in so far as the retina is concerned, secondary factors, such as temperature, have no influence or at best have only a small influence. Another postulation that may be made, based on these and other results is that the difference in the response of the pigment and the cones to temperature in the presence of light may be due to the fact that the former is non-nervous while the latter is nervous. While the pigment may be controlled by hormones alone, the cones, being part of the sensory retina, may, to a large extent if not totally, be under neural influence. It will be worthwhile studying this aspect

for, although some studies along these lines have been made knowledge concerning these factors is scarce.

It is also necessary to discuss the results of some of the experiments described above in the light of those obtained in the temperature experiments. The influence of temperature on the retinal states at various light intensities may be ruled out since during that experiment the temperature was 15±1°C and within this range the influence on the pigment and cone positions would not be sufficient to affect the results significantly. In the experiments with different wavelengths (Fig. 14), however, it appears probable that temperature may have played some part in altering the results. These experiments were conducted during a hot spell when water temperatures ranged between 18°-20°C. It has been pointed out earlier (Fig. 15) that temperatures within this range can affect the retinal epithelial pigment (in light and in dark) and the cones (in dark only). For the sake of comparison, the range 3640 Å to 6900 Å (visible spectrum of salmon) must be assumed to be equivalent to the light condition and wavelengths shorter than 3640 Å and longer than 6900 Å must be considered dark, in terms of the experiment with different temperatures. Notable effects may have been obtained for the pigment at wavelengths shorter than 3640 Å and longer than 6900 Å but not within the range of the visible spectrum because the pigment in the eyes of fish kept at 18°C and 21.5°C in light does not show much difference between the two groups (Fig. 15). The cones would not have been influenced by temperatures ranging from 18°C and 21°C within the visible spectrum, but beyond it, may have been affected. Fig. 15 shows that cones undergo slight contraction at temperatures higher than 18.3°C, in dark. It may be postulated that the reason for the cones being in a partially adapted state in the eyes of fish exposed to wavelengths shorter than 3640 Å may be due to the fact that the temperature of water on the days these experiments were conducted was 21°C. This suggested strongly that strict temperature control would be a valuable precaution in future experiments.

During the experiments with continuous light and continuous darkness, the results of which are described in the following section (Fig. 16), the temperature of the water remained constant at 15°C and so the possibility of temperature having altered the results could be discounted.

4. *In continuous light or darkness.*

These experiments were undertaken in order to determine whether under constant light or darkness, the pigment and/or the cones remain in the same state of adaptation at all time of the day and on all days of the experiment. For instance, if they were to possess a diurnal rhythm in constant light they would be fully light-adapted during the day but during the night not fully light-adapted. On the other hand, in constant darkness these retinal elements will be in a partially dark-adapted state, instead of in a fully dark-adapted state during the day.

When retinal elements possess a diurnal rhythm, the period of its persistence varies. In some cases the rhythm disappears in a day or even less in continuous light or continuous darkness. Generally, it persists longer in continuous darkness and may last as long as a week or longer in some animals.

Experiments of this nature are valuable because they aid considerably the interpretation of results obtained in a extensive investigation of this nature. In the Pacific salmon, for example, it was possible to conclude, from the results of

experiments such as this, that, since the retinal elements did not possess a diurnal rhythm, the downstream migration of the fish was influenced or controlled solely by the light conditions obtained in the environment.

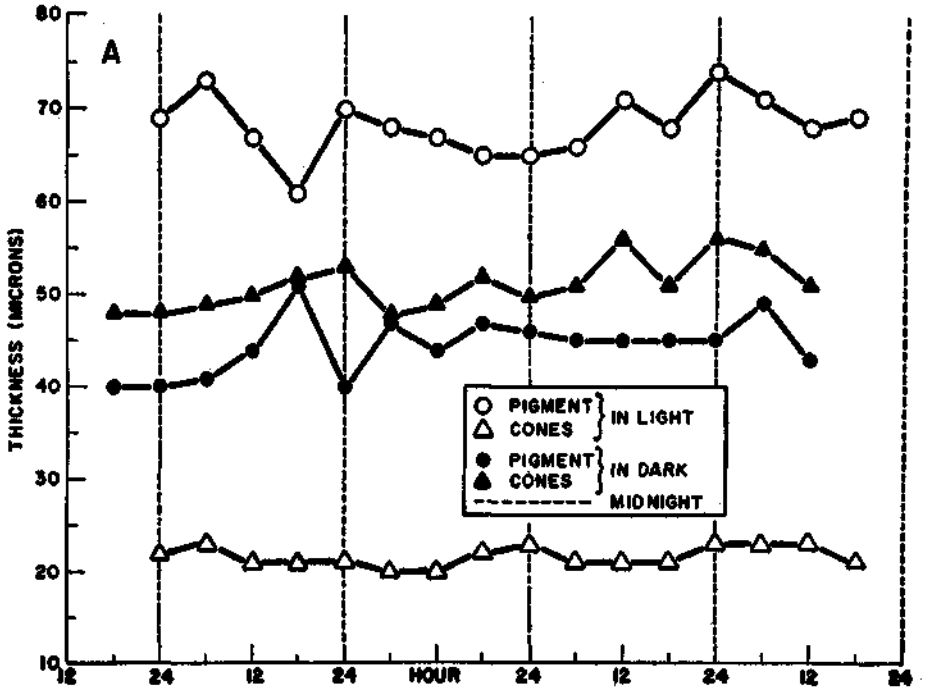

FIG. 16. Thickness of the pigment and cone layers in the retinae of fish kept in continuous light or in continuous darkness for four days and sampled every six hours.

In the present experiment, a group of fish was retained in continous light and another group in continuous darkness. Five fish from each group were sampled every six hours (midnight, 6 a.m., noon, 6 p.m.) for 96 hours (4 days). Their eyes were then sectioned, stained and examined. The results (Fig. 16) showed that in continuous light, neither the cones nor the pigment displayed any diurnal rhythm in their positions although the pigment did show a considerable degree of variation in its thickness. This may perhaps be attributed to the fact that constant light is a stress and may upset the hormonal balance in the fish. The retinal epithelial pigment is known to be influenced by intermedin and it is conceivable that under constant light the intermedin mechanism of the fish is affected. As has been pointed out earlier, light is an active stimulus (to the eye) and the influence of secondary factors such as temperature and time of day appear to be masked by it.

In continuous darkness also the pigment and cones show variation in their thicknesses but that shown by the cones is considerably smaller. Both the measurements and the histological examination indicated that the cones do not possess a diurnal rhythm. The pigment, on the other hand, seems to possess a diurnal rhythm which persists only for a day. After the first day this rhythm becomes irregular and then disappears.

None of the species or stages of the Pacific salmon studied in a previous investigation showed any rhythm in the positions of the retinal epithelial pigment or cones. It was suggested that the absence of a diurnal rhythm in the positions of the retinal elements made it possible for the downstream migration to be related to the light intensity and not to the time of day. That the retinal pigment of the Atlantic salmon has a rhythm in continuous dark is not very significant from the point of view of its behaviour or visual response. The fact that the cones do not exhibit a rhythm is, however, significant because they are the receptors, the visual cells. This would indicate that the Atlantic salmon, like its fellow salmonid, the Pacific salmon, will respond to light conditions regardless of the time of day.

Experiments with Enucleated Eyes

Although in a majority of investigations in the field of visual physiology, eyes of intact living animals have been used, quite a few investigators have resorted to enucleated eyes for the prosecution of histophysiological and electrophysiological studies. It was felt that it would be interesting to ascertain to what extent the enucleated eyes differed, in their histophysiological responses from the intact eyes.

Further, during my investigations of the histophysiology of the Pacific and Atlantic salmon retinae, one question has intrigued me as it has others. What are the factors that initiate and/or control the photomechanical responses of the visual cells (rods and cones) and the retinal epithelial pigment? This question in turn raises others. Are these photomechanical responses brought about directly as a result of the presence or absence of light? Or, are they governed or influenced by the nervous system or the endocrines? As a first step in answering these questions, it was felt that it would be desirable to find out whether the retinae in freshly enucleated eyes (lacking blood and nerve supply) would undergo photomechanical changes as well as those in the intact eyes do.

Experiments with the enucleated eyes were divided into two parts. In the first part, eyes of five anaesthetised, light-adapted fish were enucleated in light. The right eyes were left in light (100 ft-c) in fresh-water teleost saline (FWTS) and the left eyes were left in the dark, also in FWTS. After 60 minutes these eyes were fixed in Bouin's fixative. In the second part of the investigation, eyes of five dark-adapted, anaesthetised fish were enucleated in deep red light of negligible intensity. The light eyes were left in darkness and the left eyes were left in light (100 ft-c), all of them in FWTS. After 60 minutes these eyes were also fixed. The temperature of FWTS in which the enucleated eyes were retained was kept as far as possible constant and at the same temperature as that of the water in which the fish had been living.

Five intact, living fish exposed to light for an hour and five kept in darkness for an hour were sampled. The retinae of these fish were considered to represent the control light-adapted and control dark-adapted states. A comparison of these eyes with those of the experimental ones would indicate the extent of changes that occurred in the enucleated eyes.

When these eyes were sectioned, stained and examined it was observed that the retinal epithelial pigment in these eyes remained in approximately the same state it was in at the time of enucleation regardless of whether it was subsequently placed in light or in darkness (Fig. 17). Regardless of whether the enucleated

eyes were placed in light or in darkness, the cone myoids of dark-adapted eyes remained expanded while those of light-adaptation eyes became expanded (or relaxed). In other words, the retinal epithelial pigment and the cones of the Atlantic salmon are unable to respond either to light or darkness if the blood and

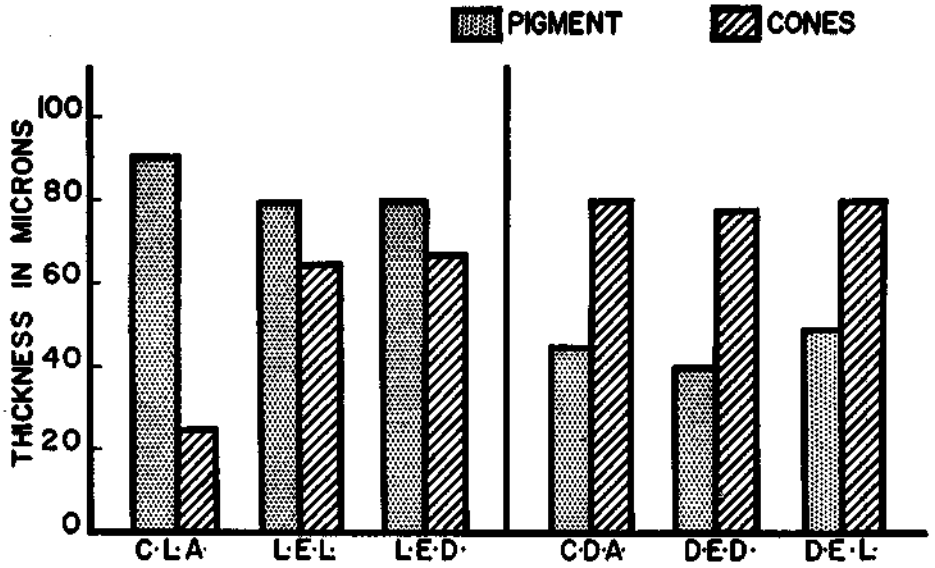

FIG. 17. Histogram showing the thickness of the pigment and cone layers in the retinae of control fish and enucleated eyes. *CLA*—control light-adapted ; *LEL*—eyes enucleated from light-adapted fish and then left in light ; *LED*—eyes enucleated from light-adapted fish and then kept in darkness ; *CDA*—control dark-adapted ; *DED*—eyes enucleated from dark-adapted fish and then kept in darkness ; *DEL*—eyes enucleated from dark-adapted fish and then exposed to light.

nerve supply are interrupted. It is also evident that the retinae, especially the visual cells (rods and cones), die as a result of enucleation and the cones relax as a result of death. It appears that the retinal epithelial cells die within 60 minutes after the enucleation of the eye thereby rendering the pigment incapable of responding to light or darkness (Ali, 1962 a).

The reason for the inability of the cones to respond appears to be simple and straightforward. The salmon is an active fish with well developed eyes and lives in cold (usually running) waters rich in oxygen. It has a highly demanding (circulation wise) retina which is well supplied by a choriocapillaries layer and possibly also by the prominent falciform process (Hanyu, 1962). Due to enucleation the supply of blood is stopped and therefore, the retina cannot obtain enough oxygen and dispose of carbon dioxide. Due to this, it is reasonable to assume that the death of visual cells ensues. The death of a contractile element results in its relaxation. This is precisely why the cone myoids of the enucleated eyes, regardless they were subjected to light or darkness, were in a relaxed state at the time of fixation.

In the case of the retinal epithelial pigment, the results of the present experiments were not expected to indicate whether nervous or hormonal factors controlled its movement. The main purpose was to ascertain whether in the absence of

both the nervous and the blood supply the pigment could respond to changes in light conditions. This question has been sufficiently answered, that is, in the salmon the pigment does not respond to light or to dark when the eye is enucleated. If it had responded, it may have indicated the possibility of light having a direct effect on it. This leads to the question whether the death of the retinal epithelial cells (in which the pigment is situated) could have stopped the pigment from responding directly to light. This does not appear probable since the gelation of the epithelial cell protoplasm could not have occurred instantaneously. It would therefore follow that, had the pigment in the enucleated eye been capable of responding to light and darkness, it would have undergone at least a slight degree of expansion or contraction on exposure to light or darkness, respectively. This has not been so and examination and measurements clearly indicated that the pigment retained about the same thickness it had at the time of enucleation. However, examination of the sections indicates the possibility that the retinal epithelial cells may have died and their protoplasm gelled before the end of the experiment (60 minutes). The pigment in the epithelial cell processes of the eyes enucleated from light-adapted fish and left in light or darkness, while retaining the same expansion shows a vertical clumping in each of the cell processes. Since this is unusual, it may be suggested that this might have been caused by the gelation of the protoplasm due to the death of the epithelial cells.

Electrophysiological Experiments

The aim of these experiments was to study the electroretinogram and its flicker fusion frequency at various intensities of light and temperatures. It is hoped that a correlation of these results with those of the investigations discussed above and the behaviour of the fish would give us a better understanding as to how the eye of the salmon functions and how it is adapted to its environment.

When light strikes the retina it bleaches the visual pigment in the rods and cones. The resulting chemical reaction is converted to an electrical action potential. By means of the electrodes placed just inside the cornea and behind the eye, the electrical changes can be recorded by appropriate instruments. The details of this technique have been described earlier. Such a record is known as the Electroretinogram (ERG) which represents the total electrical activity of the retina. This is similar to the Electrocardiogram used by heart specialists to find out the functional condition of the heart. The ERGs of different animals vary depending on whether the retinae are predominantly composed of cones or of rods or a mixture of the two. The ERGs of light-adapted animals differ from those of dark-adapted ones. ERGs can be recorded by stimulating the eye with a steady light or with flickering light. Usually, when a visual stimulus is presented, there is a ' latent period ' before the sensation develops and the sensation lasts longer than the duration of the stimulus by a ' persistence time ' or the so-called ' after image '. If an identical second stimulus evokes full sensation before the after image of the first has started to fade, the second sensation will merge with the first. Thus, in intermittent stimulation, as the frequency of the flashes increases, individual flashes become indistinguishable or fused to a steadily burning light at a certain point called critical frequency of fusion or flicker fusion frequency. We wanted to study the influence of various light intensities and temperatures on this flicker fusion frequency obtained with electroretinograms and also the influence of these environmental factors on the ERG itself (Hanyu & Ali, 1964).

The fish to be used were acclimated to the temperature at which the experiment was to be conducted for at least 48 hours. This was done in a specially built temperature controlled tank. Three temperatures *viz.* 5°, 15° and 25°C were employed. Light-adapted fish were anaesthetised with 0.3 to 0.6% urethane, the concentration depending upon the temperature. Generally, at lower temperatures higher concentrations of the anaesthetic were used. The fish was then wrapped in gauze which was in turn pinned to the paraffin coated bottom of a square plastic dish. A solution of 0.1 - 0.3% urethane from a constant temperature bath was kept flowing into the fish's mouth through a glass tube (bent eye dropper) attached to the bath with a rubber tube. The temperature of the fish was measured under the operculum with a thermister thermometer and was kept constant by controlling the temperature of the solution in the bath and its rate of flow. Throughout the experiment the temperature did not vary more than ±0.5°C. As mentioned earlier, a small puncture was made in the cornea and an electrode was introduced into the eye. Another electrode (the reference electrode) was placed in the nostril. All fish outlived the experiment, which lasted usually 20-40 minutes. After their recuperation from their experience they appeared normal in their reactions.

A projector with a 500 or 750 watt bulb was used as the source of light for stimulating the eye. Light from this projector was concentrated on a sectored disc with a convex lens which was placed in front of the projector. The beam then was made almost parallel by passing it through another convex lens located next to the disc. The rays thus obtained were reflected on to the fish's eye with a mirror. Filters made of photographic plates subjected to various exposures of light were placed next to the second convex lens in order to reduce the light intensity. Flickering light was obtained by the rotation of the sectored disc with a motor whose speed was controlled with a variable transformer. Single flashes of light were obtained with a shutter which was installed, whenever required, in one of the perforations of the sectored disc. The arrangements of this apparatus is shown in Fig. 18.

FIG. 18. Arrangement of apparatus for creating flickering light (see the text for explanation). *D*—rolling disc; *L*—lenses; *T*—transformer; *TV*—variable transformer; *M*—motor.

1. *Electroretinogram*

A generalised ERG can be described as follows: When light strikes the retina, following a latent period, a negative deflection (' a ' wave) ensues. This is followed by a positive rise called the ' b ' wave which is usually prominent. After the decline of this wave, another positive but much slower deflection (' c ' wave) occurs. When the stimulus is removed a positive or a negative deflection (' d ' wave) develops.

A typical ERG of the salmon obtained at a high light intensity (400 ft-c) at 25°C is shown in Fig. 19A. The stimulus was about 500 msec (half a second) in duration and was sufficient to evoke all the phases of an ERG. A distinct ' a ' wave and a relatively small ' b ' wave and a quite well pronounced ' d ' wave, characteristic of a light-adapted retina, are clearly seen. A small ' c ' wave is distinguishable. A feature to be noted is the occurrence of ripples super-imposed on the ' a ', ' b ' and ' d ' waves following the turning on and off of the light. These are more marked on the ' a ' and ' b ' waves than on the ' d ' wave and are also more prominent at higher light intensities. Their significance is not known yet. Figs. 19A,

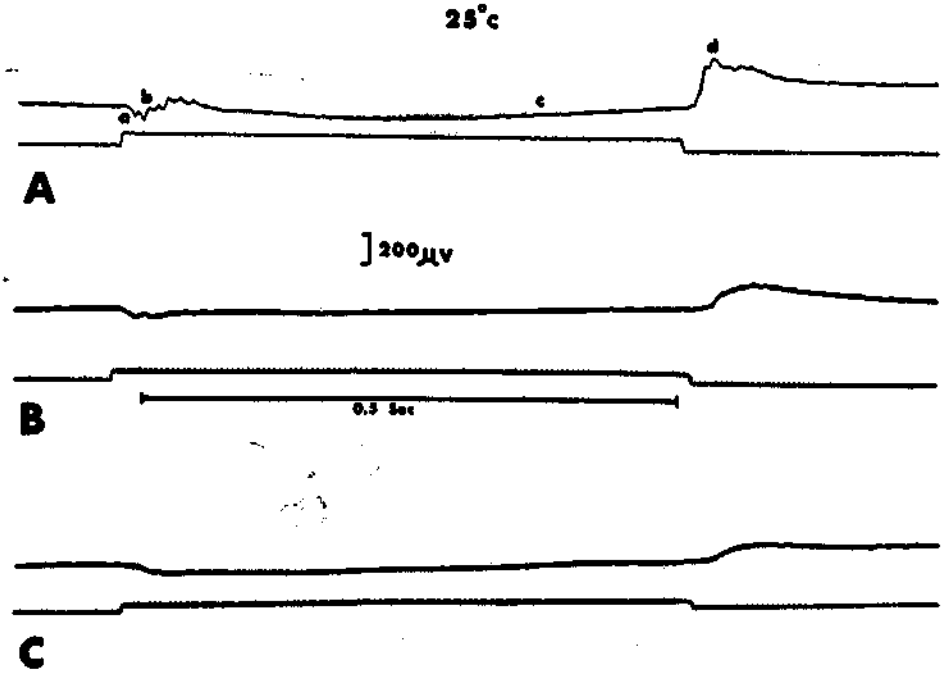

FIG. 19. Electroretinograms of the salmon at 25°C. *A*—at 400 foot-candles (*a*, *b*, *c* and *d* are the waves of the electroretinogram); *B*—at 15 foot-candles; *C*—at 4 foot-candles. In these records the upper trace represents the electroretinogram and the lower one, the duration of the stimulation. Time scale is shown by the thick line in record *B*.

B and C show that as the intensity of light is reduced the electrical response from the retina becomes smaller and slower. Lowering the temperature has also a similar effect. Fig. 20A shows an ERG at 15°C obtained when the eye was stimulated with light of high intensity (480 ft-c). It is seen that this ERG is smaller and slower than that obtained at 25°C. Here also when the light intensity is reduced (Fig. 20B) the response becomes slower and smaller. Finally at 5°C, even at the high light intensity the ERG is small and quite slow (Fig. 20C). It becomes even

slower and smaller when the light intensity is reduced (Fig. 20D). Thus we see that both lower temperatures and lower intensities of light have about the same effect on the retina.

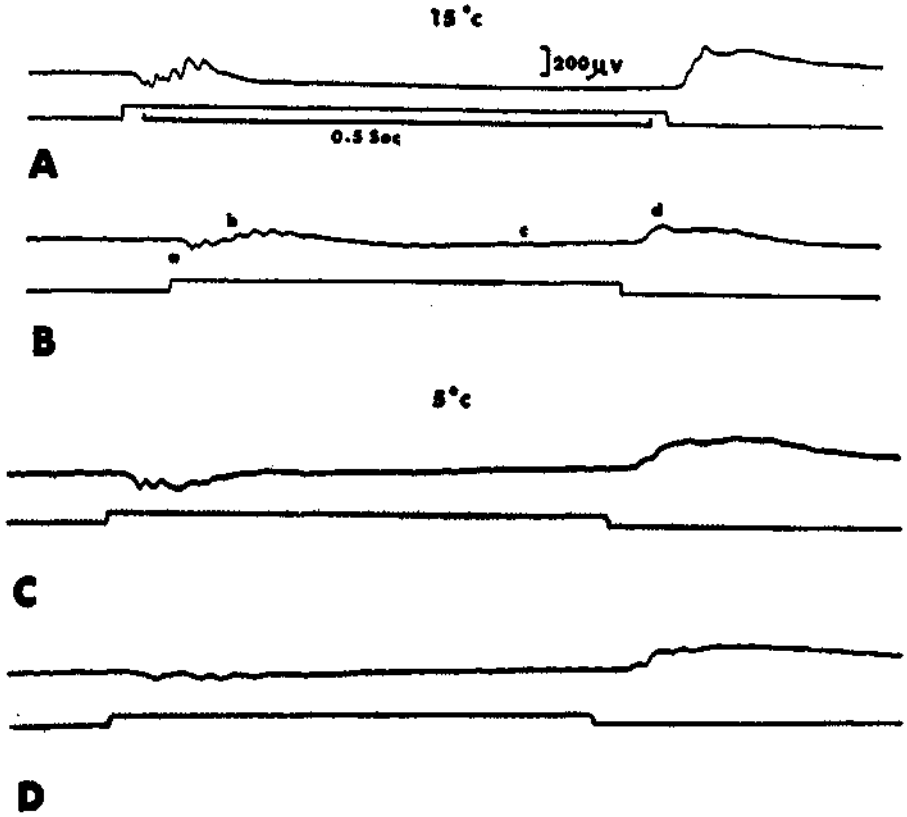

FIG. 20. Electroretinograms of salmon at 15°C (*A* and *B*) and at 5°C (*C* and *D*). *A*—at 420 foot-candles; *B*—at 36 foot-candles; *C*—at 520 foot-candles; *D*—at 42 foot-candles. *a*, *b*, *c* and *d* are the waves of the electroretinogram (see the text for explanation). In these records, the upper trace represents the electroretinogram and the lower trace, the duration of stimulation. Time scale is given by the thick line in record *A*.

2. *Flicker Fusion Frequency*

As the frequency of the flickering light increases, the response (ERG) becomes smaller and finally reaches a stage where it fails to correspond to the individual light flashes. This is the part which is taken as flicker fusion. The maximum frequency at which the response corresponds to the stimulus is the fusion frequency and it is determined by comparing the response of the eye (upper traces in Fig. 21A) with the lower trace which bears the stimulus (light on or off) and time marks. Since it is virtually impossible to pinpoint the exact spot at which fusion frequency occurs, we averaged several succeeding flicker stimuli in the region of flicker fusion.

Figs. 21A and B show the influence of light intensity on fusion frequency. A more or less complete record of an experiment carried out at 25°C and at an intensity of 390 ft-c is shown in Fig. 21A. Here it is seen that fusion frequency occurs

when the frequency of the flashing light is 94 flashes per second. When this is compared with the record shown in the lower part of the same Fig. 21B the influence

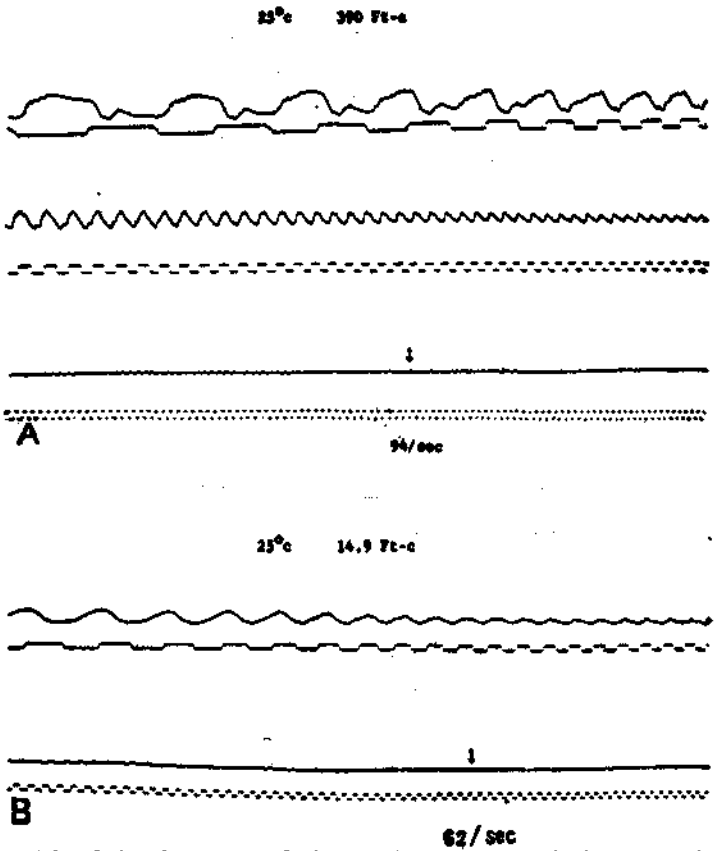

FIG. 21. Flicker fusion frequency of electroretinogram (*R*) obtained at 25°C. *A* shows a record at 390 foot-candles. This is a more or less complete record of the experiment until the fusion point was reached. The lower trace (*S*) shows the frequency of stimulation (flickering light). *B* shows the beginning and the fusion point of the electroretinograms at a light intensity of 14.9 foot-candles. The arrows indicate the region of fusion. The frequency of fusion is indicated below the arrow.

of light intensity becomes clear. In this Figure the complete record is not shown but only the beginning and the end of the experiments are shown. It is clear that the response is smaller and that because it is slower, fusion frequency occurs when the frequency of the intermittent light is only 62 flashes per second. At lower temperature also the fusion frequency decreases. Fig. 22A shows the record of an experiment done at 15°C with light intensity of 510 ft-c. In spite of the use of the high intensity the fusion frequency occurs when the flashes are 73 per second. At this temperature also a decrease in light intensity brings about a reduction in fusion frequency. Fig. 22B shows that fusion frequency at 19.5 ft-c occurs when light flashes at a rate of 43 per second. At the lowest temperature used (5°C) even at a high intensity fusion frequency occurs when light flashes at 50 per second (Fig. 23A). At 14.9 ft-c it is 23 per second (Fig. 23B).

What is the significance of these results ? As mentioned earlier, the ERG gives us an indication of the activity of the retina. Therefore, from the results presented

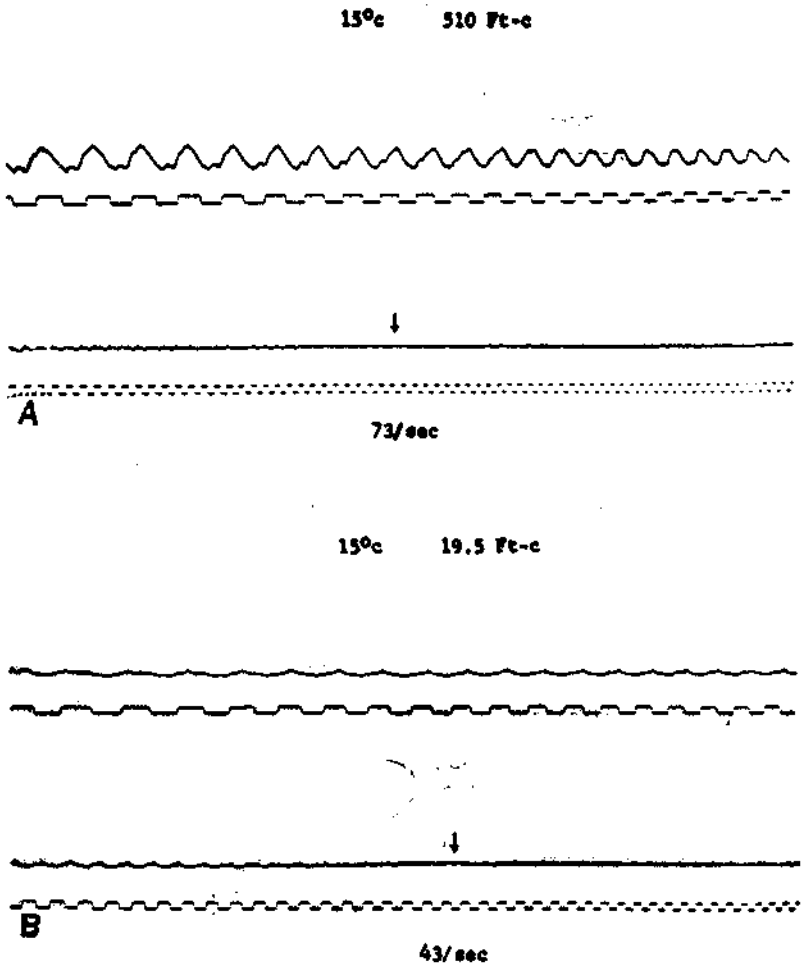

FIG. 22. Flicker fusion frequency of electroretinogram obtained at 15°C. *A* shows a record at 510 foot-candles. *B* shows a record at 19.5 foot-candles. *A* and *B* show the beginning and the fusion point of response at the two light intensities. The arrows indicate the region of fusion. The frequency of fusion is given below the arrow.

above it is evident that the ability of the retina to respond to light stimulation is greatest when the temperature of the environment and the intensity of the light are higher. The flicker fusion frequency data indicate to us the ability of the salmon to perceive moving objects and its capacity to distinguish one small point in its environment from another. Here also we see clearly that at higher temperatures and light intensities the ability of the salmon to follow a moving object is much greater than at a lower temperature and intensity. Its visual process, therefore, would appear to be much more alert when light and temperature are higher.

Perhaps one could conclude that the salmon sees much better during the Summer when the water temperatures are higher and sunlight is plentiful than during the cold and bleak months.

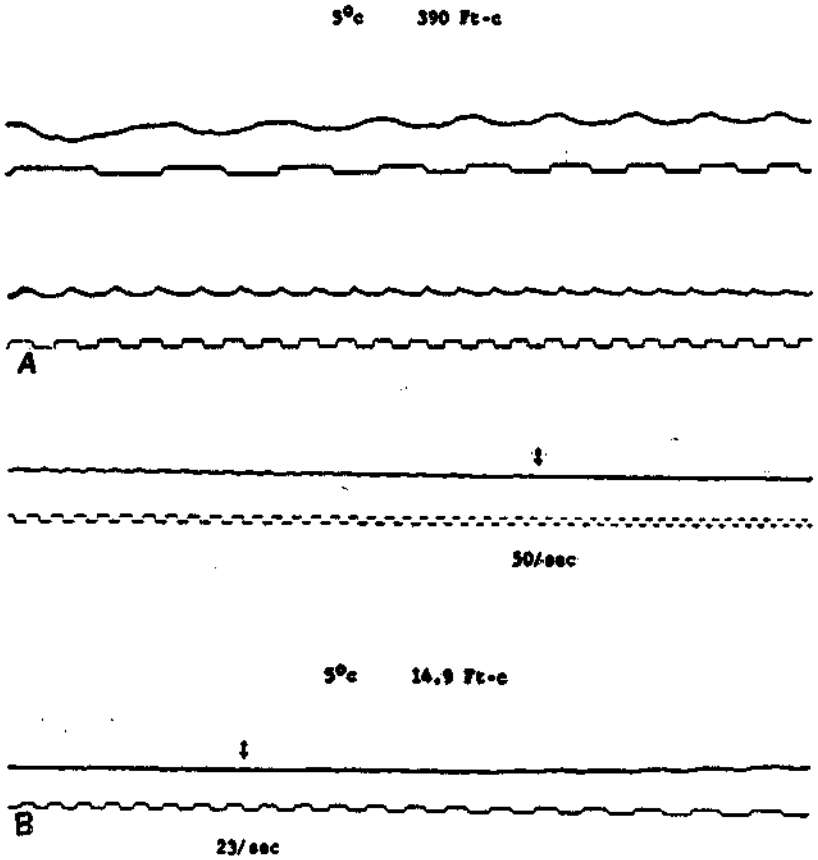

FIG. 23. Flicker fusion frequency of electroretinogram obtained at 5°C. *A* shows a record at 390 foot-candles. The record is an almost complete one ranging from the beginning of the experiment to the point of fusion. *B* shows the region of fusion at an intensity of 14.9 foot-candles. The arrows indicate the region of fusion. Fusion frequencies are indicated below the arrows.

The work of which the results are presented in this article touches only two aspects of the study of the vision of salmon. Much work has to be done with its behaviour and the photochemistry of its vision as well as the electrophysiology of its sense organs before a good understanding of its life-history and habits could be obtained.

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STUDIES ON THE FOOD HABITS OF WHITING, REDFISH, AND POLLOCK IN THE GULF OF MAINE

By RALPH W. DEXTER

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I. INTRODUCTION

THE stomach contents of food-fishes landed at Gloucester, Massachusetts, by commercial trawlers were analyzed in the summers of 1959-61.[1] Periodic visits were made to the wharves at Gloucester Harbour to obtain stomachs from fishes landed by ground fishing vessels operating in the Gulf of Maine.[2] While the fishes were being processed, stomachs were removed and taken to the science laboratory at the Gloucester High School for volumetric analysis. Results are given in Tables 1-6.

The species of fishes and identified invertebrates referred to in the text and tables are as follows :

Osteichthyes (Names follow Bigelow and Schroeder, 1953)
Herring—*Clupea harengus*
Blueback—*Pomolobus aestivalis*
Eel—*Anguilla rostrata*
Conger eel (American Conger)—*Conger oceanica*
Whiting (Silver Hake)—*Merluccius bilinearis*
Cod—*Gadus callarias*
Haddock—*Melanogrammus aeglefinus*
Pollock—*Pollachius virens*
Hake—*Urophycis* spp.
Cusk—*Brosme brosme*
Blackbacked Flounder (Winter Flounder)—*Pseudopleuronectes americanus*
Sand Dab (Sand Flounder)—*Lophopsetta maculata*
Mackerel—*Scomber scombrus*
Butterfish—*Poronotus triancanthus*
Redfish (Rosefish)—*Sebastes marinus*

[1] Acknowledgment is made to the U.S. Atomic Energy Commission for support given to this study through contract AT (11-1)—411. I am also indebted to Arthur N. Smith, Principal of the Gloucester High School, for use of laboratory facilities ; to John B. Auditore of the Marine Biological Suppy at Gloucester, and to Richard S. Short, Supervisor of Conservation Education in the Massachusetts Department of Education, for field and laboratory assistance ; and to Dr. Fenner Chace and his staff in the Department of Marine Invertebrates at the U.S. National Museum for identification of certain invertebrates.

[2] Fish stomachs were obtained from the following processors to whom thanks are given for their co-operation. Cape Ann Sea Foods, Adams and Son, Morning Star Fish Company, Empire Fish Company, Codinha Fishery, Favolora Fish Plant, Progressive Fish Company, and Cape Ann Fisheries.

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Longhorn Sculpin—Myoxocephalus octodecemspinosus
Cunner—Tautogolabrus adspersus
Sand Launce-Ammodytes americanus
Shanny—Leptoclinus maculatus

Crustacea

Euphausids-Meganyctiphanes norvegica
Decapods-Dichelopandalus leptocerus ; Crangon septemspinosus ; Pagurus pubescens ; Pandalus borealis ; P. montagui

Mollusca

Squid-Illex illecibrosus
Octopus-Bathypolypus arcticus

II. Food of the Whiting

Studies on food habits of whiting (*Merluccius bilinearis*) have been published in recent years by Jensen and Fritz (1960) and Schaefer (1960). Both of these, however, are based upon small samples. The present study is based upon stomach analyses of over 13,000 whiting of commercial size (12-24 inches) from four areas in the southern portion of the Gulf of Maine.

In 1959 whiting fed largely on the sand launce (53.3%) with herring as the second most important food (13.8%). See table 1. The small whiting (less than

Table 1

Analysis of Food of Whiting—Summers, 1959 and 1960—Gulf of Maine

	1959				1960			
	No.	Vol. (L.)	% Frequency	% Vol.	No.	Vol. (L.)	% Frequency	% Vol.
Herring ..	22	2.245	7.6	13.8	241	27.620	32.5	44.5
Sand Launce ..	168	8.770	56.2	53.3	9	0.220	1.2	0.3
Whiting ..	14	0.925	4.6	5.7	244	19.630	32.9	31.6
Fish Remains ..	64	1.567	21.4	9.7	213	11.890	28.7	19.1
Squid ..	16	1.540	5.3	9.6	21	1.790	2.8	2.8
Euphausids ..	32	0.918	10.7	5.6	8	0.052	1.0	0.0
Long-horned Sculpin ..	2	0.140	0.6	0.8	—	—	—	—
Haddock ..	2	0.115	0.6	0.7	—	—	—	—
Hake ..	—	—	—	—	7	0.455	0.9	0.7
Sand Dab ..	1	0.040	0.3	0.2	3	0.095	0.4	0.1
Butterfish ..	—	—	—	—	1	0.120	0.1	0.1
American Eel ..	—	—	—	—	2	0.075	0.2	0.1
Brittle Star ..	2	0.005	0.6	0.03	—	—	—	—
Amphipods ..	1	0.002	0.3	0.01	—	—	—	—
Black-backed Flounder ..	—	—	—	—	1	0.060	0.1	0.0
Decapod Shrimp ..	—	—	—	—	1	0.010	0.1	0.0
Mud Star ..	—	—	—	—	1	0.005	0.1	0.0
Total No. of Stomachs—299					Total No. of Stomachs—740			
Total Volume—16.267 L.					Total Volume—62.022 L.			

TABLE 2

Analysis of Food of Whiting—Summer, 1961—Gulf of Maine

Comparison by Time Sequence

Food	7-27/8-4				8-8/8-18				8-22/9-1				Total			
	No.	Vol. (L)	% Frequency	% Vol.	No.	Vol. (L)	% Frequency	% Vol.	No.	Vol. (L)	% Frequency	% Vol.	No.	Vol. (L)	% Frequency	% Vol.
Herring	178	18.122	12.3	26.0	1151	129.858	42.5	60.4	474	46.104	24.8	35.5	1803	194.084	29.8	46.8
Herring Sardines	2	0.006	0.1	0.0	7	1.225	0.2	0.5	424	21.582	22.2	16.6	433	22.813	7.1	5.5
Whiting	507	27.074	35.2	38.8	863	54.001	31.9	25.1	934	45.317	49.0	34.9	2304	126.392	38.0	30.5
Euphausids	906	21.311	62.9	30.5	468	8.468	17.3	3.9	45	0.774	2.3	0.5	1419	30.553	23.4	7.3
Blueback	1	0.004	0.0	0.0	126	9.688	4.6	4.5	10	1.140	0.5	0.8	137	10.832	2.2	2.6
Butterfish	..	..	..	..	25	1.485	0.9	0.6	74	8.775	3.8	6.7	99	10.260	1.6	2.4
Squid	6	0.365	0.4	0.5	31	3.340	1.1	1.5	36	2.783	1.8	2.1	73	6.488	1.2	1.5
Hake	11	0.733	0.7	1.0	28	1.845	1.0	0.8	18	1.090	0.9	0.8	57	3.668	0.9	0.8
Pollock	7	0.860	0.4	1.2	41	2.620	1.5	1.2	..	..	..	..	48	3.480	0.7	0.8
Fish Remains	21	0.506	1.4	0.7	63	1.598	2.3	0.7	10	0.295	0.5	0.2	94	2.399	1.5	0.5
Sand Launce	31	0.353	2.1	0.5	7	0.214	0.2	0.0	24	0.727	1.2	0.5	62	1.294	1.0	0.3
Sand Dab	2	0.035	0.1	0.0	13	0.217	0.4	0.0	21	0.352	1.1	0.2	36	0.604	0.5	0.1
Haddock	1	0.115	0.0	0.1	1	0.060	0.0	0.0	1	0.070	0.0	0.0	3	0.245	0.0	0.0
Mackerel	..	..	..	..	..	..	..	..	4	0.245	0.2	0.1	4	0.245	0.0	0.0
Decapod Shrimp	8	0.051	0.5	0.0	4	0.024	0.1	0.0	26	0.124	1.3	0.0	38	0.199	0.6	0.0
Cusk	..	..	..	..	..	..	..	..	4	0.145	0.2	0.1	4	0.145	0.0	0.0
Conger Eel	..	..	..	..	..	..	..	..	1	0.140	0.0	0.1	1	0.140	0.0	0.0
Sea Cucumber	1	0.040	0.0	0.0	..	..	..	..	2	0.075	0.1	0.0	3	0.115	0.0	0.0
Cod	1	0.020	0.0	0.0	..	..	..	..	3	.060	0.1	0.0	4	0.080	0.0	0.0
Amphipods	11	0.50	0.7	0.0	..	..	..	..	6	0.008	0.3	0.0	17	0.058	0.2	0.0
Shanney	1	0.005	0.0	0.0	1	0.005	0.0	0.0	2	0.006	0.1	0.0	4	0.016	0.0	0.0
Decapod Crabs	..	..	..	..	1	0.002	0.0	0.0	2	0.001	0.1	0.0	3	0.013	0.0	0.0
Isopods	..	..	..	..	1	0.005	0.0	0.0	..	..	..	..	1	0.005	0.0	0.0
Polychaetes	2	0.003	0.1	0.0	..	..	..	..	1	0.001	0.0	0.0	3	0.004	0.0	0.0
	Total No. of Stomachs—1439 Total Vol.—69.653 L.				Total No. of Stomachs—2704 Total Vol. —214.657 L.				Total No. of Stomachs—1908 Total Vol.—129.824 L.				Total No. of Stomachs—6049 Total Vol.—414.134 L.			

TABLE 3

Analysis of Food of Whiting—Summer, 1961—Gulf of Maine

Comparison by Area

Food	Off Maine Coast No.	Vol.	%Frequency	% Vol.	Ipswich Bay No.	Vol.	%Frequency	% Vol.	Off Cape Cod No.	Vol.	%Frequency	% Vol.	Cultivator Shoal No	Vol.	%Frequency	% Vol.
Herring	523	57.529	45.7	63.2	137	15.197	20.4	34.0	520	52.963	27.0	42,1	121	11.565	11.4	21.2
Herring Sardines	6	1.125	0.5	1.2	209	8.425	31.1	18.8	205	12.561	10.6	9.9	..	..	..	..
Whiting	319	20.939	27.8	23.0	148	6.771	22.0	15.1	776	41.614	40.3	33.1	489	28.471	46.3	52.3
Euphausids	274	6.524	23.9	7.1	149	2.085	22.2	4.6	420	9.630	21.8	7.6	416	8.111	39.3	14.9
Blueback	21	1.365	1.8	1.5	25	2.818	3.7	6.3	28	1.685	1.4	1.3	33	2.799	3.1	5.1
Butterfish	..	..	..	..	53	8.103	7.8	18.1	15	0.557	0.7	0.4	2	0.035	0.1	0.0
Squid	9	0.770	0.7	0.8	8	0.354	1.1	0.7	22	1.900	1.1	1.5	8	0.545	0.7	1.0
Hake	14	0.965	1.2	1.0	2	0.070	0.2	0.1	21	1.500	1.0	1.1	9	0.593	0.8	1.0
Pollock	15	0.985	1.3	1.0	1	0.040	0.1	0.0	12	0.810	0.6	0.6	16	1.305	1.5	2.4
Fish remains	22	0.554	1.9	0.6	6	0.175	0.8	0.3	28	0.704	1.4	0.5	26	0.696	2.4	1.2
Sand Launce	7	0.095	0.6	0.1	18	0.273	2.6	0.6	26	0.694	1.3	0.5	5	0.084	0.4	0.1
Sand Dab	2	0.035	0.1	0.0	3	0.085	0.4	0.1	20	0.342	1.0	0.2	1	0.025	0.0	0.0
Haddock	..	..	..	..	..	..	..	..	2	0.175	0.1	0.1	..	..	..	..
Mackerel	..	..	..	..	2	0.175	0.2	0.3	2	0.070	0.1	0.0	..	..	..	..
Decapod Shrimp	2	0.010	0.1	0.0	7.7	0.048	1.0	0.1	21	0.112	1.0	0.0	4	0.012	0.3	0.0
Cusk	..	..	..	..	..	..	..	..	2	0.085	0.1	0.0	..	..	..	..
Conger Eel	..	..	..	..	..	..	..	..	1	0.140	0.0	0.1	..	..	..	..
Sea Cucumber	..	..	..	..	..	..	..	..	..	..	..	..	1	0.040	0.0	0.0
Cod	..	..	..	..	..	..	..	..	3	0.060	0.1	0.0	1	0.020	0.0	0.0
Amphipods	1	0.001	0.0	0.0	1	0.001	0.1	0.0	4	0.009	0.2	0.0	9	0.044	0.8	0.0
Shanney	..	..	..	..	..	..	..	..	2	0.006	0.1	0.0	1	0.005	0.0	0.0
Decapod Crabs	..	..	..	..	..	..	..	..	2	0.003	0.1	0.0	..	..	..	..
Isopods	1	0.005	0.0	0.0	..	..	..	..	..	..	..	..	..	..	..	..
Polychaetes	..	..	..	..	..	..	..	..	1	0.002	0.0	0.0	1	0.001	0.0	0.0
	Total No. of Stomachs—1144 Total Vol. 90.902 L.				Total No. of Stomachs—671 Total Vol.—44.620 L.				Total No. of Stomachs—1922 Total Vol.—125.622 L.				Total of No. Stomachs—1056 Total Vol.—54.353 L.			

1 foot in total length) fed almost exclusively on euphausid shrimps. The larger fish consumed a great many of its own species.

In 1960 herring was the most important food (44.5%), and its own species was second (31.6%). Squid and hake were also important. In 1961 herring (46.8%) and whiting (30.5%) remained the most important food, but with a variety of 26 other species including the blueback, butterfish, hake, and pollock among the fishes, and euphausid shrimp and squid among the invertebrates. See table 2.

In the early summer cannabalism was very high (38.8%) and euphausids and herring ran second and third in volume. By middle summer, however, herring (60.4%) composed the bulk of the diet. Euphausids dropped from about one-third of the diet in early summer to a small amount by middle summer.

In the late summer herring (35.5%) and smaller whiting (34.9%) made up the bulk of the diet and herring sardines were becoming of increasing importance while the euphausids continued to drop in volume except for the small whiting.

Comparing the areas from which whiting were taken, herring was found to be the bulk of food off the Maine Coast, in Ipswich Bay, and off Cape Cod. On Cultivator Shoal the whiting was primarily cannabalistic. In that area herring was second and euphausids were third in importance. Whiting and euphausids were secondary off the Coast of Maine ; sardines and butterfish were secondary in Ipswich Bay ; and whiting and sardines were secondary off Cape Cod. See table 3.

In 1961 whiting under 12 inches fed almost entirely on euphausids with occasional other crustaceans. Whiting from 12-18 inches fed largely (67.6%), but not entirely on euphausids, while whiting 18-24 inches in length fed predominantly on herring. See table 4.

III. Food of the Redfish

Information on food of redfish (*Sebastes marinus*) is available in the publications of Anon (1954), Steele (1957), and Lambert (1960).

Because the vast majority of stomachs of redfish examined in the present study were either empty or everted, having come from considerable depths, little quantitative data could be obtained. Those with food remaining in the stomach fed largely on euphausids, decapod shrimps, hyperiidean amphipods, and the sand launce. See table 5.

IV. Food of Pollock

Kendall (1898) and Steele (1963) give data on food of the Pollock (*Pollachius virens*).

The number analyzed by us was not great. See table 6 for results. Those that were analyzed fed largely on euphausids, herring, squid, and whiting.

TABLE 4

Analysis of Food of Whiting—Summer, 1961—Gulf of Maine
Comparison by Size

	Size 12-18 inches				Size 18-24 inches			
	No.	Vol. (L.)	% Frequency	% Vol.	No.	Vol. (L.)	% Frequency	% Vol.
Euphausids	774	13.906	85.6	67.6	645	16.647	12.5	4.2
Herring	21	1.540	2.3	7.4	1782	192.544	34.6	48.9
Herring Sardines	41	1.051	4.5	5.1	392	21.762	7.6	5.5
Whiting	139	3.649	15.3	17.7	2165	122.743	42.0	31.1
Blueback	1	0.035	0.1	0.1	136	10.897	2.6	2.7
Butterfish	1	0.010	0.1	0.04	98	10.250	1.9	2.6
Squid	—	—	—	—	97	6.488	1.8	1.6
Hake	1	0.050	0.1	0.2	56	3.618	1.0	0.9
Sand Launce	17	0.163	1.8	0.7	44	1.131	0.8	0.2
Fish remains	5	0.086	0.5	0.4	89	2.313	1.7	0.5
Pollock	—	—	—	—	37	3.480	0.7	0.8
Decapod Shrimp	8	0.054	0.8	0.2	30	0.135	0.5	0.0
Amphipods	8	0.022	0.8	0.1	9	0.036	0.1	0.0
Sand Dab	—	—	—	—	34	0.604	0.6	0.1
Polychaetes	2	0.003	0.2	0.01	—	—	—	—
Mackerel	—	—	—	—	4	0.245	0.0	0.0
Haddock	—	—	—	—	3	0.245	0.0	0.0
Cusk	—	—	—	—	1	0.140	0.0	0.0
Conger Eel	—	—	—	—	1	0.140	0.0	0.0
Sea Cucumber	—	—	—	—	3	0.115	0.0	0.0
Cod	—	—	—	—	4	0.080	0.0	0.0
Shanney	—	—	—	—	4	0.016	0.0	0.0
Decapod Crabs	—	—	—	—	3	0.013	0.0	0.0
Isopods	—	—	—	—	1	0.005	0.0	0.0
Total Number of Stomachs	904				5145			
Total Volume	20.569 L.				393.654 L.			

TABLE 5

Analysis of Food of Redfish—Summers, 1959 and 1960—Gulf of Maine

Food	1959				1960			
	No.	Vol. (L.)	% Frequency	% Vol.	No.	Vol. (L.)	% Frequency	% Vol.
Euphausids with copepods	36	0.296	49.3	57.4	385	1.522	99.4	86.5
Decapod shrimp	27	0.145	36.9	28.1	9	0.059	2.3	3.3
Hyperiidean amphipods	29	0.050	39.7	9.6	42	0.141	10.8	8.0
Sand Launce	2	0.015	2.7	2.9	1	0.005	0.2	0.2
Fish fry	1	0.010	1.4	1.9	2	0.020	0.5	1.1
Octopus	—	—	—	—	1	0.010	0.2	0.5
Isopods	—	—	—	—	1	0.001	0.2	0.0
Total No. of Stomachs	73				387			
Total Volume	0.516 L.				1.758 L.			

TABLE 6

Analysis of Food of Pollock—Summers, 1959 and 1960—Gulf of Maine

Food	1959 No.	1959 Vol. (L.)	1959 % Frequency	1959 % Vol.	1960 No.	1960 Vol. (L.)	1960 % Frequency	1960 % Vol.
Euphausids with copepods	291	8.112	98.9	91.1	149	92.90	83.7	78.2
Herring ..	—	—	—	—	24	2.205	13.4	18.5
Squid ..	9	0.565	3.1	6.3	—	—	—	—
Fish remains ..	24	0.146	8.1	1.6	5	0.047	2.8	0.3
Whiting ..	—	—	—	—	5	0.220	2.8	1.8
Hyperiidean amphipods	39	0.046	13.3	0.5	—	—	—	—
Cunner ..	—	—	—	—	1	0.060	0.5	0.5
Sand Launce ..	1	0.030	0.3	0.3	—	—	—	—
Isopods ..	—	—	—	—	1	0.001	0.5	0.0
	Total Number of Stomachs—294				Total Number of Stomachs—178			
	Total Vol.—8.901 L.				Total Vol.—11.868 L.			

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