EFFECT OF PHOTOPERIODS ON THE BEHAVIOUR PATTERNS OF JUVENILE ATLANTIC SALMON (*Salmo salar* L.)

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BY

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ABSTRACT

The behaviour patterns of juvenile Atlantic salmon exposed to photoperiods (light-exposed fish) and of those exposed to control conditions (control fish) were compared. A negative phototaxis was exhibited by both control and light-exposed fish. The intensity of the light stimulus had very little effect on the intensity of the phototaxis in the light-exposed fish, while the control fish showed an increase in the intensity of the phototaxis with an increase in the intensity of the light stimulus. The control fish showed an increase in the reaction to the light stimulus the longer the stimulus was applied at the higher levels of stimulation, while the light-exposed fish exhibited this behaviour at the lower levels of stimulation. Both the control and light-exposed fish preferred currents to still water, but the preference of the light-exposed fish was stronger than that of the control fish. The control fish tended to avoid the faster flowing water to a greater extent than the light-exposed fish, while the latter were more sensitive to changes in current intensity. In a vertical light gradient, the light-exposed fish were very active, moving rapidly up and down the water column, while the control fish were relatively quiescent and settled to the bottom at low light intensities. In a horizontal light gradient, the control and light-exposed fish remained in the areas of low light intensities. Both groups showed a stronger avoidance of the light sources of higher intensities, but tended to move into the brighter areas with low light sources. The control fish exhibited a stronger reaction to the less intense light gradients than the light-exposed fish, whereas the latter showed the stronger

avoidance reaction to the more intense light sources. These differences in behaviour are attributed to the increased activity and sensitivity of the light-exposed fish, resulting from their exposure to photoperiods. It is shown that the control fish behaved similarly to the salmon parr, while the light-exposed fish behaved similarly to the migrating salmon smolts. The significance of the behaviour patterns studied is discussed in relation to the downstream migration of Atlantic salmon.

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I. INTRODUCTION

It has been demonstrated that light and temperature play a very important role in the maturing and metamorphosis of fish (Hoover, 1937; Hoover and Hubbard, 1937; Bullough, 1939). The theory is that these environmental factors stimulate the pituitary gland, an endocrine organ situated in the cranial region, and it in turn activates the other endocrine organs, chief among which are the gonads. By this sequence of events the various changes associated with maturity are brought about.

Relatively little experimental work has been done on this hypothesis and many of the results are in themselves conflicting. For example, Allison (1951) found that supplementary light delayed spawning in the brook trout (Salvelinus fontinalis), whereas Hazard and Eddy (1951) found that exposing the same species to increased amounts of light accelerated spawning by one month. Furthermore, light was sometimes found to be the most important factor (Harrington, 1950) and at other times temperature seemed to be the dominating factor (Burger, 1939). These relationships were found to vary from species to species and even between males and females in the same species. In all of these experiments, an examination of the gonads or some other histological structure was used as an index of maturation.

In view of the physiological, biochemical and physical changes which the Atlantic salmon (Salmo salar L.) undergoes prior to its migration from the rivers and streams to the sea, this species seems to be admirably suited for research in this field from a new point of view. Although this change is

manifested in radical alterations in the external structure of the fish and the internal mechanisms of the various systems, a less obvious change occurs in the ethology of the fish. Ethology is the study of the various behaviour patterns of a particular species and an ethological change is a change in these behaviour patterns, whereby at one stage of its life history a species behaves in a certain way under a given set of environmental conditions and at another stage it behaves differently under an identical set of conditions.

Although an ethological change has not been clearly demonstrated in the Atlantic salmon, it is not unreasonable to assume that it does occur since it has been worked out in great detail for four species of Pacific salmon, belonging to the same family, Salmonidae (Hoar, 1958). Prior to their seaward migration, coho salmon (Oncorhynchus kisutch) and sockeye salmon (Oncorhynchus nerka) show numerous black marks along the right and left sides of the body which characterize them as being in the parr stage of development. Associated with this stage are distinctive behaviour patterns, which are stereotyped within a given species, but which may vary from species to species. With the onset of seaward migration, the parr marks in these two species disappear and the fish take on a silvery sheen. This is the smolt stage of the downstream migrating fish. With this change in external appearance comes a change in the activity of the endocrine glands and an associated change in the behaviour patterns, some of which may even reverse (e.g. reaction to light, reaction to water currents). The remaining two Pacific salmon, the chum (Oncorhynchus keta) and the pink (Oncorhynchus gorbuscha),

migrate to sea shortly after hatching and in these the ethological change is not as marked.

As a result of these observations on Pacific salmon and assuming that an ethological change does take place in Atlantic salmon at the time of seaward migration, a working hypothesis was set up in experimenting with the effect of light on the development of these juvenile Atlantic salmon. If, as suggested above, light is an important factor in the development of fish, then exposing juvenile salmon parr to photoperiods, and controlling the temperature at a relatively constant level, should cause a change in their rate of development. Therefore, being chronologically of the same age, the fish exposed to light should show behaviour patterns different from control fish, subjected to more normal conditions of light. Some evidence may also be present of the disappearance of parr marks in these light-exposed fish.

II. LITERATURE

A. The Effect of Light on the Maturation of Fish

Seebohm (1888) is usually credited with the original suggestion that natural daylight is a very important environmental factor in the maturing of animals, but before the work of Rowan (1924,1925) practically no experimental evidence had been put forth in connection with this theory and most of it was speculative in nature. Rowan showed that when the junco (Junco hyenalis) was subjected to daily increases of light in

the winter months at low temperatures, the gonads matured and the birds started to sing. Their normal breeding season was in the spring.

Rowan's work stimulated research in this field and many groups of animals were studied.

The results of some of the experiments carried out in this study indicated that altering the given amount of light had the effect of accelerating the rate of maturation of the fish studied, causing them to spawn several months before their normal spawning season. Hoover (1937), Hoover and Hubbard (1937), Hazard and Eddy (1951) and Corson (1955) showed that by subjecting the brook trout (Salvelinus fontinalis) to increasing amounts of light per day followed by decreasing amounts, the fish spawned two months before normal spawning season. However, Hazard and Eddy (1951) found that the same result could be obtained by subjecting the fish to decreasing amounts of light only, but that now the fish spawned only one month before normal spawning season. These experiments were performed six to nine months before the spawning season. Similar results were found by Merriman and Schedl (1941) with the four-spined stickleback (Apeltes quadracus), by Scrimshaw (1944) with the guppy (Lebistes reticulatus), by Harrington (1950) with the bridled-shiner (Notropis bifrenatus) and the sunfish (Enneacanthus obesus), by Medlen (1951) with the poeciliid fish (Gambusia affinis), and by Kawamura and Otsuka (1950) with the goldfish (Carassius auratus). The results from these experiments showed that by exposing the various species of fish to either increased amounts of light or continuous light before the normal spawning season, the rate of

maturation was significantly accelerated and the fish became mature or spawned before the normal breeding season.

From a few of the experiments, it was concluded that varying the amount of light delivered to the fish decelerated their rate of maturation. Allison (1951) gave Salvelinus fontinalis supplementary light each day and found that spawning was delayed about six weeks. Hazard and Eddy (1951) found an identical result with the same species by increasing the amount of light per day over natural daylight. However, the experimental period in this case overlapped the normal spawning season and this may account for the apparent conflict with results of the other workers.

Some experimental work has been done on another aspect of this same problem; viz., the effect of darkness and small amounts of light on the maturation of fish, and it was concluded that in this case maturity and spawning were greatly depressed. Rasquin (1949) and Rasquin and Rosenbloom (1954) state that when the characin (Astyanax mexicanus) was kept in darkness, the immature cyanophil-fuchsinophil ratio was retained or inverted in the pituitary gland and the gonads were reduced in size. However, it was indicated that the light activates the pituitary directly or by organs other than the eyes, since fish, blinded and kept in natural daylight, still showed a normal pituitary ratio. Also, when the fish held in darkness were placed in natural daylight, the cyanophil-fuchsinophil ratio returned to normal. Similarly, Bullough (1940) found that minnows (Phoxinus laevis) showed a delay in the rate of gametogenesis when they were kept in darkness or under reduced light conditions.

Contrary to any of the foregoing results, some workers concluded that light had no effect on the maturation of fish. Burger (1939) subjected the male killifish (Fundulus heteroclitus) to a decrease in the amount of light per day followed by an increase at the same rate and found no significant difference in the rate of spermatogenesis as judged by the microscopic appearance of the testes. The same result was obtained by subjection to an increase in light followed by darkness. Matthews (1939) found an identical result when the same species was subjected to either continuous light or darkness. Finally, Merriman and Schedl (1941) showed that the four-spined stickleback (Apeltes quadracus) exhibited no difference in the rate of gametogenesis, whether they were held under conditions of increased light, constant light of 11.75 hours per day, or several minutes of light each day.

A few experiments on the effect of light indicated that in some instances temperature is more important than light in controlling the rate of maturation of fish. Burger (1939) states this for Fundulus heteroclitus when he found that, under identical light conditions, one group of fish held at 6-10°C showed immature testes while another group held at 14-20°C showed active spermatogenesis. Bullough (1939) similarly found that Phoxinus phoxinus, under conditions of increased light followed by constant illumination, showed a significant increase in gonadal weight at higher temperatures while this increase was absent at lower temperatures.

In summary, the results from the experiments performed on

the effect of light on the maturation of fish have shown that light sometimes accelerates the rate of maturation, it sometimes decelerates this rate, and at other times it has no effect on the rate of maturation. The actual case may be that the effect of light is not the same for all species of fish and in one species it may aid the developmental processes of the gonads and associated structures, whereas in another species it may retard the same processes. Also, temperature may predominate over the effect of light in some species. Another factor important in the effect of light seems to be the period of the year in relation to the normal spawning season that the experiments are performed.

B. Biological Changes Associated with the Seaward Migration of Salmon and Related Species

The biological changes which occur in the various species of salmon at the time of their seaward migration fall into three categories: physical, biochemical, and behavioural (ethological).

(a) Physical changes

In the process of transforming from the parr to the smolt stage, radical alterations occur in the physical appearance of salmonid fishes. In addition to minor changes in the external structure of the fish, the most obvious are the disappearance of the characteristic parr marks and the change in colour from the dark, olive-coloured skin of the parr to the silvery sheen of the smolt. In this connection, Robertson (1948) states that the stripped skin of the parr of the rainbow trout (Salmo gairdneri)

showed intense pigmentation, whereas that of the smolt was silvery with very little pigment being present. The latter was attributed to increased guanine deposition and the disintegration of melanophores in certain areas in the skin of the smolt. The numerous pigments in the skin of the parr being concentrated in particular areas were responsible for the parr marks. This explanation of the physical change from parr to smolt seems to hold true for other species of the Family Salmonidae also.

(b) Biochemical changes

A general review of the physiological and biochemical aspects of the migration of anadromous and catadromous fishes is given by Greene (1926), in which the early theories and conclusions on this subject are considered.

One of the changes deomonstrated in salmonid fishes at the time of seaward migration is the ability to adapt to changing salinities. Rutter (1904) was able to raise the salinity of the blood of Pacific salmon, as these fish grew, while Sumner (1905, 1906) changed young chinook salmon (Oncorhynchus tschawytscha) from freshwater to 1.013 density salt water with no ensuing harm to the fish. Similarly, Scott (1916) concluded that anadromous fish can adapt themselves to great external osmotic changes by a change in the osmotic pressure of the blood. These early results indicated that, at the time of migration, salmonid fish can readily adapt to the change from the freshwater to the marine medium.

In later experiments on salinity adaption, Huntsman and Hoar (1939) found that the survival time of Atlantic salmon in

concentrated saline solutions increased with increased length of the fish, but this would be expected on the basis of the change in surface to volume ratio. Therefore, they concluded that the great resistance to sea water at the time of parr-smolt transformation must come about fairly rapidly. Similarly, Black (1951) found that when the Pacific species of chum and coho salmon fry were transferred from fresh water to sea water, the density of the fish and the body chloride increased above normal in the first few hours, but the body chloride of the chum decreased to normal shortly thereafter. The coho salmon died in the concentrated saline solutions. However, when these fish were returned to fresh water after 12 hours in sea water, the density and body chloride decreased to normal. After acclimation to dilute sea water before transfer to stronger sea water, the chloride decreased with increased acclimation time. The coho salmon adapted less readily to sea water than the chum and this was attributed to the early downstream migration of chum salmon. These later results showed that the adaption of salmon to varying salinities seems to be effected by changes in the density and chloride content of the fish and this ability to adapt develops rather quickly.

Concerning the internal mechanisms associated with downstream migration, the thyroid gland seems to be most closely linked with the biochemical changes related to osmoregulation. Hoar (1939) found that the seaward migrants of the Atlantic salmon showed heightened thyroid activity and the same was found for rainbow trout (Robertson, 1948). Hoar and Bell (1950) demonstrated that the migrating chum and pink salmon fry, and the non-migrant sockeye, coho, and spring salmon fry, of the genus Oncorhynchus, had quiescent

thyroid glands, while the corresponding migrants had varying degrees of activity. In addition, when the migrant fish were held in freshwater over their migration period they developed very hyperplastic thyroids. Hoar (1952) states that the thyroid gland of juvenile underyearling migrant alewives (Pomolobus pseudoharengus) was quiescent, while the gland for sexually mature fish was mildly active. The land-locked forms from Lake Ontario had extremely hyperplastic thyroids. Similar results were found for juvenile underyearling and yearling smelts (Osmerus mordax), where the thyroids were slightly active, while the migrating spawning stage fish had very active glands. The post-spawning fish again had quiescent thyroids.

More generally, these biochemical changes are summarized by Fontaine (1948,1951), who states that, at the time of migration, internal physiological changes, governed by the neuro-endocrine complex, produces a metabolic stress which forces the fish to move into waters of different salinities. Similarly, Hoar (1953) emphasizes that the biochemical changes, at the time of smolt transformation, are in a direction which makes the fish more like a marine species.

In summary, the results from studies on salmonid fishes have pointed to the fact that at the time of migration significant changes occur in the biochemistry of these fish.

(c) Behavioural (ethological) changes

One of the most important changes associated with the migration of salmonid fishes, and one that can best explain the mechanisms of their migration, is the change in their behaviour

under various environmental conditions. These behaviour patterns were recognized very early in the study of fish. For example, Lyon (1904,1909) stated that the rheotactic responses of fish were caused by the stimulation of the optic and tactile senses due to the movement of the fish in the water since he found that blinded fish could not orient themselves until they came in contact with a part of their environment. It was concluded that in turbulent streams the difference in velocity serves to orient the fish and in quieter waters the sight of, or contact with, the environment serves the same purpose. In a similar study on the rheotactic behaviour of speckled trout (Salvelinus fontinalis), Elson (1939) found that these fish were randomly distributed in still water, but were oriented against the current in moving water. When they were transferred from still water to moving water, orientation against the current was noted first, then orientation alternated with random distribution, and finally uniform distribution resulted. In this connection, it was found that the shorter the adaption time to still water, the shorter was the duration of the reaction to the transfer to current. When transferred from current to still water, these fish exhibited a high degree of random wandering. Elson also stated that a preference for weaker current and a positive reaction to an increase in current was evident.

Considerable research has been conducted in an attempt to discover the factor or factors responsible for initiating and maintaining the migrations of fish. Roule (1914) contended that salmon migrate toward water of low O_2 supply and, consequently, not into heavily polluted waters. Shelford (1918 a,b) stated

that hydrogen-ion and hydroxide-ion concentration are very important in fish migration, whereas Foerster (1929) concluded that sockeye salmon showed no discrimination of oxygen concentration, but choose waters with a low pH. Foerster further states that the impulse to migrate originates in the reproductive organs. He found that at one time a species may choose warm water in preference to cold water in a tributary or stream and at another time cold water may be preferred. Therefore, he concludes that temperature does not have a clear-cut effect on the upstream migration of salmon. Foerster (1939) found that no correlation existed between the mean annual temperature and the time of the downstream migration of sockeye salmon. However, the colder the water in the period of several months before migration, the longer the migration was delayed. Foerster concluded that an increase in temperature was the initiating factor for migration in these sockeye salmon, while the cessation of migration was brought about by a temperature blanket in the upper layers of the lake, through which the salmon could not penetrate. Wisby and Hasler (1954) observed that coho salmon, with the olfactory mechanism destroyed, failed to choose their parent stream as well as control fish with the olfactory mechanism intact.

In regard to the mechanics of the downstream migration of salmon and the relation of the various behaviour patterns to this migration, Huntsman (1948), in a general way, states that the downstream migration of salmon smolts is because of a failure of the positive rheotactic responses, coupled with random wandering due to increased activity. Again, Clemens (1951) contends that the

downstream displacement of young sockeye salmon is a result of their inability to hold position in the current. In their second spring, the salmon move into the warmer surface waters of the lakes, and, because of increased activity and failure of rheotactic responses, they move into the outlet of the lake and down into the streams. From the streams, most displacement occurs at night when rheotactic responses are at a minimum. Once into the Strait of Georgia, their preference for less saline waters takes the fish into the upper out-going currents. Hoar (1953) states generally that coho salmon, Atlantic salmon and steelhead trout defend territory in the daylight and become inactive at night. This accounts for their prolonged stay in the streams as parr. The prolonged stay of sockeye salmon in lakes is associated with their preference for deeper water, their negative phototaxis and their tendency to form inactive schools. In the parr-smolt transformation of these salmonid fishes, the chief factor seems to be the effect of a photoperiod on the pituitary gland.

Hoar, in a series of papers based on experimental research over a period of years, gives a detailed analysis of the behaviour patterns of four species of Pacific salmon and the changes in these patterns as the fish pass from one stage to another. These results are very pertinent to the experiments described in the present paper, and a detailed consideration of them seems necessary.

In regard to schooling activity, chum and pink fry and coho smolts, in quiet water, school and mill very intensely, whereas the coho fry never show true schooling and milling (Hoar, 1951). Sockeye fry are also schooling fish, but the schools are less

active and more irregularly oriented than in the other species (Hoar, 1954). Schooling behaviour is evident in the sockeye smolts at the time of migration, but it is less intense than in the coho smolts (Hoar, 1954). Nipping and defence of territory in these salmon seems to be inversely related to schooling, in that the more tendency a species has to school, the less tendency it has to nip and to defend territory.

In relation to the internal influences controlling the degree of activity of these salmon, the thyroid gland and the gonads, via their particular hormones, seem to be the most important. Hoar, MacKinnon and Redlich (1952) showed that chum migrants, treated with the thyroid hormone, thyroxine, or the gonadal hormone, testosterone, exhibited less intense grouping than control fish or fish treated with the antithyroid drug, thiourea. The latter, in fact, increased the tendency to aggregate. Also, the thyroxine and testosterone treated groups displayed more activity and swam closer to the surface than the thiourea treated groups and this increased activity accounted for their lesser tendency to aggregate. It was further found that thyroxine and testosterone increased the swimming speed of chum fry while thiourea decreased this speed.

In a series of studies on the rheotactic responses of the Pacific salmon, it was found that chum fry show positive rheotaxis with only occasional displacement by the current (Hoar, 1951), and a marked preference for current over still water (MacKinnon and Hoar, 1953). Pink fry, although showing the same reactions to current as chum fry, are displaced more often by the current (Hoar, 1951). Coho fry also show positive rheotaxis, but they have

only a slight preference for flowing water, and move into lesser flows at high current intensities. They become adapted to current much more rapidly than the chum fry, while the chum fry show greater success in swimming against a current than coho fry (MacKinnon and Hoar, 1953). Sockeye fry show no evidence of adaption to moderate currents. Sockeye smolts show a strong preference for fast water, while coho smolts show an avoidance of fast water. Sockeye are also more successful than coho in swimming against a current (Hoar, 1954). These positive rheotactic responses were found to change to negative responses at high temperatures (Hoar, 1951, and Keenleyside and Hoar, 1954). It will be shown later how these various rheotactic responses are related to the mechanics of the downstream migration of the different species.

It has been shown that the reaction of the Pacific salmon to light varies from species to species. Coho fry and coho smolts show a definite cover reaction but the stronger avoidance of light is demonstrated by the coho smolts (Hoar, 1951). Sockeye fry and sockeye smolts also show a definite cover reaction to light, with the cover reaction of the smolts again being more intense. The negative reaction of sockeye fry is more intense than that for chum or pink fry (Hoar, 1954). Hoar, Keenleyside and Goodall (1957) showed that pink and chum fry were uniformly photopositive under low light intensities, whereas coho fry, coho smolts, sockeye fry and sockeye smolts were photonegative under all light intensities studied. Chum and sockeye fry and sockeye smolts showed a marked tendency to retreat under strong light and to emerge at low light intensities, whereas the reverse picture was found with the pink and coho fry and coho smolts.

These reactions seem to be affected by certain hormones since Hoar, MacKinnon and Redlich (1952) state that treatment with thyroxine and testosterone caused a slight displacement of the coho fry to the lightest area of the experimental tank and the chum fry to the dark area of the tank.

In addition to the eye, at least one other organ seems to be important in these reactions to light; the pineal complex. Hoar (1955) found that blinded sockeye smolts showed no avoidance reaction to movements on the part of the observer in the daytime but were still negatively phototactic. They were also startled by a flashlight at night. When the pineal organ was also probed, no negative phototaxis was apparent, nor were they startled by a flashlight at night. With the pineal organ alone probed, the fish showed an avoidance normal for sockeye both day and night.

Another important behaviour pattern evident in these Pacific salmon is their activity at very low light intensities. Hoar (1951) remarks that as the light intensity decreases to a very low level in the night, the pink and chum fry rise to the surface of the water and their activity increases. The coho fry, on the other hand, are very quiet at night and in shallow water rest on the bottom. The coho smolts are very active both day and night, but they too show increased activity in the night (Hoar, 1951). Hoar, Keenleyside and Goodall (1957) found that recently emerged pink fry rose to the surface at low light intensities and even swam into the surface film, but this behaviour disappeared as the fish grew older. The chum fry showed no marked response to the changing light intensity in the vertical gradient, although a slight tendency of the older migrants to remain nearer the

surface was evident. The coho fry and coho smolts showed no response to the light gradient, although the fry were closer to the surface than the smolts. Both fry and smolts were inactive at low light intensities. The sockeye smolts were indifferent to the light intensity in the vertical light gradient and moved very rapidly straight up and down the water column, causing near random distribution. The reactions of the sockeye fry changed from a photonegative to a photopositive reaction in the period under consideration.

Hoar (1954) observes that the various species of Pacific salmon differ in their preference for depths in a vertical column of water. Sockeye fry showed more depth preference than any other species, while chum and coho fry were more evenly distributed. Sockeye smolts showed random distribution in the vertical water column, due to increased activity, while coho smolts were deeper in the water column than coho fry.

All of the foregoing results have been derived from experiments performed under laboratory conditions. However, Neave (1955) found that some of these results were at variance with the observations of the fish in their natural habitat. He found that, in contrast to Hoar (1951), the pink and chum fry in the streams very often showed negative phototaxis and negative rheotaxis. In explanation of this contrast in observations, Hoar (1956) found that pink salmon fry, which have never schooled, are negatively phototactic and do not emerge into bright light. Schooled fish, on the other hand, show a strong cover reaction only when the increase in light is very abrupt. Since fish held in the laboratory would have a greater chance to develop the

schooling behaviour, this is a possible explanation of the difference between laboratory and field observations.

In summary, let us consider how Hoar (1958) relates the various behaviour patterns of these Pacific salmon to their downstream migration. The chum and pink fry migrate downstream almost immediately after emergence from the gravel. According to Hoar (1958) this can be explained by the following reasoning. In daylight, chum and pink fry are positively phototactic in the laboratory (probably negatively phototactic in the field - Neave, 1955) and positively rheotactic. Therefore, they will not be displaced by the current even though they may wander into exposed fast-running water. However, at night, these fish become more active and rise to the surface of the water. They then lose visual and tactile contact with the bottom, and, consequently, their positive rheotactic behaviour is decreased. The ability to keep up with the current is lost and downstream displacement results.

When the sockeye fry are displaced downstream and reach the deep water of the lake, their negative phototaxis and preference for deep water will result in their prolonged stay in the lake. However, at the time of smolt transformation, their increased activity will cause downstream displacement in the night when visual and tactile contacts with the environment are lost.

The coho fry on the other hand show positive rheotaxis in daylight and decreased activity at night, when they become inactive and settle to the bottom. Consequently, in the daytime,

these fish can keep up with the current and at night they are on the bottom out of the influence of the surface current. Downstream migration of the fry is thus prevented. When these coho fry transform to smolts, however, they become much more active both day and night and will be displaced downstream during the night when positive rheotaxis fails due to loss of contact with the bottom.

Additional evidence to support the above explanation of the downstream migration of juvenile Pacific salmon was put forth by Ali (1959). On the basis of research on the ocular structure, retinomotor and photo-behavioural responses of Pacific salmon, he suggested that the downstream migration occurs as a result of the eyes of the salmon being in a semi-dark-adapted state for a short period at dusk. This is caused by rapid decrease in incident light intensity and the relatively slower rate of dark-adaption of the retina at this time. Consequently, the fish lose their reference points in the stream and swim with the current or are displaced downstream.

III. MATERIALS AND METHODS

A. The Holding Apparatus

The apparatus for holding the juvenile salmon, while the experiments were being performed, consisted essentially of six wooden holding tanks, 91 cm long, 45 cm wide, and 30 cm high, connected to a reservoir tank, 183 cm long, 90 cm wide, and 120 cm high (Figure 1 and Figure 2). Water was delivered from the

reservoir tank to each of the six holding tanks by a rotary pump, operated by an electric motor, and drained back by gravity to the reservoir tank through overflow pipes located in one end of each holding tank. A nylon net was placed in the overflow end of each tank to prevent the fish from entering the water systems. Plastic pipes were used throughout the circulating water system since these were found to be the least toxic to the fish. The water was aerated, and mixed to eliminate serious temperature gradients, by air stones located in each tank, through which air was slowly bubbled from a nearby pressure controlled compressor. Preliminary oxygen determinations of the water were made by the Winkler method and the flow of air was regulated by a valve to give adequate oxygen concentration in each holding tank. The temperature of the water was controlled by means of two refrigeration plates, located in the reservoir tank and connected to a refrigeration unit by black iron pipes. This unit could be adjusted to any desired temperature level, and this level could be maintained within $\pm$ 0.5°C for a considerable period of time.

Mounted above each holding tank was a wooden frame, in which were located three 20 watt fluorescent light bulbs. When the three of these were on, a light intensity of 25 ft-c was maintained at the surface of the water in each tank.

The above water system, however, was not an entirely closed one as the description might imply. It was found that a small flow of water had to be maintained into the reservoir tank, because the mortality in the holding tanks would be high without it. The reason for this was not investigated, but it may have been some

"unknown" substance which the fish were depleting from the water or some substance which was becoming concentrated in the recirculating water, since the temperature was kept reasonably constant and the food supply and oxygen concentration were adequate. It may have been associated with CO_2 concentration but no tests were run to determine if the CO_2 changed significantly while the water was not running into the reservoir.

B. The Experimental Material

The experiments to study the effect of photoperiods on the behaviour of juvenile Atlantic salmon were carried out in the Biology Department of the Memorial University of Newfoundland. The fish were obtained from Margaree Hatcheries, Frizzleton, Nova Scotia, and were all in the yearling stage, having been hatched in the spring of 1958. In this stage young Atlantic salmon have the distinct black marks along the right and left sides of the body and are known as parr. They ranged in length from approximately 2 to 4 cm at the beginning of the experimental period to 6 to 8 cm at the end of the experimental period. The acclimation temperature of the holding tanks was maintained at $15 \pm .5^{\circ}C$ during the experiments carried out in the summer months and dropped down to approximately $10^{\circ}C$ in the fall and $5^{\circ}C$ during the winter months. The experiments were started in May, 1959, and continued until January, 1960 (Figure 3).

During the experimental period the fish were fed on fresh beef liver. An equal amount of food was delivered to each tank twice daily at $5^{\circ}C$ and $10^{\circ}C$ and three times daily at the higher acclimation temperature of $15^{\circ}C$.

Upon their arrival the 300 juvenile salmon were divided into two groups of 150 fish each. One group, designated as the "light-exposed fish", was held in the three tanks which had the fluorescent lights above them turned on for 16 hours per day (6:00 a.m. - 10:00 p.m.) and off for the remaining 8 hours (10:00 p.m. - 6:00 a.m.). This was accomplished by means of a time switch operating in the circuit.

The three tanks in which the remaining fish (150) were held, had no lights over them. These fish are designated as "control". The only illumination received by them came from the lights over the experimental tanks, plus the illumination from the ceiling lights, when these were on, giving a total of less than 1 ft-c at the surface of the water for 16 hours per day and darkness for the remaining 8 hours. The duration of exposure of the particular fish used in the experiments is given in connection with the individual experiments.

It is realized that under these conditions the "control fish" were not subjected to normal light conditions as found in nature, but rather to reduced light. However, it is felt that these fish exhibited behaviour patterns which were typical of Atlantic salmon parr in nature and this will be verified to some extent in the discussion of results.

C. Experimental Apparatus

Four basic behaviour patterns were studied in these experiments. They were:

(a) Positive-Negative Phototaxis (response to a light stimulus).

(b) Rheotaxis (preference for water currents of various intensities).

(c) Surfacing at low light intensities (vertical distribution in a vertical light gradient).

(d) Behaviour with respect to a horizontal light gradient (horizontal distribution in a horizontal light gradient).

(a) Phototaxis apparatus and methods of observation

The phototaxis experiments on juvenile Atlantic salmon are divided into two groups, referred to as Series I and Series II. The methods of observation in these two series were essentially the same but in Series I experiments the size of the apparatus was much smaller than in Series II experiments. Also, 5 fish were used at one time in Series I experiments and the temperature of the water was 15.0°C, whereas in Series II experiments, 10 fish were used at one time and the water temperature dropped from 10.0°C to 5.0°C throughout the experimental period. Series II experiments were performed at a later date than Series I experiments.

In the phototaxis experiments, Series I, a glass aquarium 51 cm long, 30 cm wide, and 29 cm deep was used (Figure 4). A centre board divided the aquarium into two equal compartments, while a space was left below the board so that the fish could move freely from one compartment to the other. A light of desired intensity was located directly above the centre of each compartment and heavy black curtain extended above the centre of the tank between the two light bulbs, so that each compartment could be illuminated independently of the other. That is to say, one compartment could be kept relatively dark while the opposite

compartment was being illuminated. The entire apparatus was surrounded by black curtain to ensure that no external light rays entered the experimental tank. The light intensity at the surface of the water could be varied by. adjusting an iris diaphragm, interposed between the light bulb and the water surface, by varying the distance between the light bulb and the surface of the water, or by using different wattages of light bulbs. Observation of the fish was made through a peek-hole in the curtain.

The usual procedure of observation in Series I experiments was to place 5 fish in the aquarium, cover it with a light-proof cover, and leave the fish undisturbed with the room darkened for 30 minutes. At the end of this time a light of desired intensity was switched on over the centre of one compartment. Consequently, one compartment of the experimental aquarium was illuminated and the other was darkened. After 10 seconds, the number of fish in the "illuminated" and "darkened" compartments was counted. Another 20 seconds were allowed to elapse and the number of fish in each compartment was again counted. This was 30 seconds after the light had been switched on. Finally, another 30 seconds were allowed to pass and a third count of the number of fish was made. This was 60 seconds after the light had been turned on. At the end of this count, the lights were immediately reversed, the one over the "illuminated" compartment being switched off and the one over the "darkened" compartment being switched on. The former "illuminated" compartment now became "darkened" and the former "darkened" compartment became "illuminated". The above procedure was then repeated for 60 seconds, as before. In this way the lights were reversed four times, giving a total of 5 counts of

the number of fish in the "illuminated" and "darkened" compartments at 10 seconds after the light stimulus was applied, 5 counts at 30 seconds after the stimulus was applied, and 5 counts at 60 seconds after the stimulus was applied. This was considered to be a complete experiment. The fish were then removed and a new group of 5 fish was placed in the tank. A duplicate experiment was then run identical to that outlined above. From 5 to 10 of these experiments were run at each light intensity, giving a total of 25 to 50 counts at each of the 10 seconds, 30 seconds, and 60 seconds periods. These periods after the light was turned on will hereafter be referred to as the 10 second level, the 30 second level, and the 60 second level respectively. Both control and light-exposed fish were tested at 0.1, 0.2, 2.0, 20.0 and 200.0 ft-c.

Since it was felt that the small number of fish and the small size of the apparatus used may have had some effect on the results, another series of experiments using a larger number of fish and larger tank was conducted (Series II).

The apparatus used in the phototaxis experiments, Series II, was similar in principle to that used in Series I. It consisted of a wooden tank, 244 cm long, 30 cm wide, and 30 cm deep (Figure 5). Three or four light bulbs instead of one were used above each compartment and a ground glass plate was interposed between the lights and the surface of the water, to give a uniform light distribution along the bottom of each compartment. In these experiments observation was made through a glass end in the tank and a net was placed 16 cm from the glass to keep the fish away from it. This was necessary because the fish had a tendency to

be attracted by their reflection in the glass. A similar net was placed in the opposite end to make conditions uniform on either side. In the end opposite the glass, an overflow pipe was situated, so that water flowed continually in at the glass end and out through the overflow pipe at the other end. In this way fresh water was kept circulating in the tank, and the temperature remained fairly constant during an experiment.

The observations for the Series II experiments were of two types. The usual procedure in one case was similar to Series I. Ten fish were placed in the tank and left in the light for 60 minutes. This was to ensure that the eyes of the control and light-exposed fish would be in the same state of light-adaption at the beginning of the experiment. It was assumed that the fact that they were living under different light conditions in the holding tanks might have some effect on their true reactions to the light stimulus, because of different degrees of light- or dark-adaption (see Ali, 1960). After this period in the light, the fish were further subjected to 30 minutes of darkness. At the end of this time, a light of known intensity was switched on over one compartment and the observations were made identical to those in Series I experiments. Ten reversals of the lights were made in these experiments, giving a total of 10 counts of the numbers of fish in the "illuminated" and "darkened" compartments at each of the 10 second, 30 second, and 60 second levels. This was considered to be one complete experiment. The lights were then switched off and the same fish were left in the tank in darkness for 30 minutes. The experiment was then repeated. Ten of these experiments were performed on the same group of 10 fish,

giving a total of 100 counts at each of the 10 second, 30 second and 60 second levels. A different group of 10 fish was then placed in the tank and 10 experiments were run identical to that above. This was considered a duplicate group of experiments. Therefore, in all, if the duplicate experiments are combined, a total of 200 counts at each of the 10 second, 30 second, and 60 second levels on 20 fish was made. Experiments were run at 20.0 ft-c and 200.0 ft-c.

While the above experiments tested the reactions of the fish to an intermittent light stimulus, the second type of observations studied the reactions of control and light-exposed fish to continuous light. Ten fish were again placed in the wooden tank and left with the lights on for 60 minutes. At the end of this time, instead of leaving the fish in darkness, the light was turned off over one compartment. The fish were left an additional 30 minutes and observations began. The numbers of fish in the "illuminated" and "darkened" compartments were then counted at 30 second intervals for 15 minutes, giving a total of 30 counts per experiment. The lights were then reversed and the former "illuminated" compartment became "darkened" and the "darkened" compartment became "illuminated". The fish were left 30 minutes under these conditions and a second experiment was run identical to the first. A total of 7 experiments were run in this way on the same group of fish, giving a total of 210 observations. A duplicate group of experiments was performed with a procedure identical to the first group and this gave, in all, a total of 420 counts on 20 fish.

In addition to the usual counts, observations were made on

the reaction times of these fish to the light stimulus. In the procedure outlined above for the reaction to continuous light, immediately following the reversal of the lights, the fish were observed for 10 minutes and the time recorded when each fish entered the shaded compartment. This gave some measure of the time it took for the fish to react to the light stimulus.

(b) Rheotaxis apparatus and method of observation

The apparatus for this set of experiments consisted of a wooden trough 244 cm long, 30 cm wide and 28 cm deep (Figure 6). A longitudinal partition, 30 cm wide and 122 cm long, divided the trough into two equal channels for half its length. At a distance of 13 cm from the end of the longitudinal partition, a screen was placed dividing the trough into experimental and non-experimental chambers. In the non-experimental chamber an overflow pipe was placed, so that the water could be adjusted to any desired level. At the upper end of each channel in the experimental chambers a reservoir was constructed, and this sloped by means of a ramp 18 cm long from a height of 13 cm to the floor of the trough. A white line, drawn from the end of the longitudinal partition to the screen, divided the common chamber into two parts. One part was considered to belong to one channel and the other part to the other channel. Water flowing into one of the reservoirs at the upper end of the trough overflowed the ramp, causing a current in one channel of the trough but no current in the opposite channel. In the common chamber the current flowed through the net and only at high flows (current velocities), was an appreciable current created in the no-current channel. Water for the experiments was drawn from a reservoir, which was controlled

at the desired temperature level by a refrigeration unit. Flows of 2000, 4000, 8000, 16,000, and 32,000 ml/min flowing into the reservoir were obtained by adjusting clamps on two lengths of rubber tubing, which siphoned the water from the reservoir to the experimental trough. The light intensity in all of these experiments was 1-2 ft-c at the surface of the water.

During an experiment, 10 fish were placed in the common chamber of the trough, where a net prevented them from entering either channel. The flow was adjusted to the desired rate and the fish left for 20 minutes to adapt to the trough. At the end of this time the retaining net was removed and the fish left 10 minutes to take position in the flow or no flow channel. At the end of 10 minutes, the number of fish in each channel was counted at one minute intervals for 16 minutes, giving a total of 17 counts per experiment. The fish were then changed and the experiment repeated. Five experiments were run at each flow, giving a total of 85 counts. Channels were alternated as to flow and no flow sides to prevent bias in one or the other of the channels. The maximum temperature difference between channels was 0.3°C.

(c) Surfacing apparatus and method of observation

The apparatus used for the surfacing reactions consisted of a cylindrical tank, 86 cm high and 56 cm in diameter, painted gray on the inside (Figure 7). A cylindrical shield consisting of wire netting, wrapped in the shape of a cylinder and surrounded by black curtain, was placed over the top of the tank and fitted neatly around the top rim on the tank. At the top of the shield,

a cardboard cover was placed and the fish were observed from above through a peek-hole in the cover. The particular light being used was also suspended through this cover.

At the beginning of an experiment 10 fish were placed in the tank, the light turned on, and the fish left undisturbed for 30 minutes. At the end of this time, the number of fish in the upper one-third portion of the tank was counted at one-minute intervals for a period of 10 minutes, giving a total of 10 counts. Another group of 10 fish was then placed in the tank and the experiment was repeated identically. Five of these duplicate experiments were performed at light intensities of 0, 0.04, 0.2, 1.0, and 5.0 ft-c, giving a total of 50 counts on 50 fish at each light intensity.

(d) Light-gradient apparatus and methods of observation

The apparatus for these experiments consisted of a rectangular trough, identical in dimensions to that used in the rheotaxis experiments (Figure 7). At 30 cm intervals along the tank, black lines were painted transversely, dividing it into seven different compartments. These compartments were numbered I-VII. At one end of the tank a glass end was installed and a light reflector and light were attached. This gave a horizontal gradient of light intensities, decreasing from high intensity at the glass end of the tank to low intensity at the opposite end, the absolute intensities depending on the wattage of light being used. Three different lights were used; viz. 7.5 watt, 100 watt and 300 watt, giving three different light gradients. A curtain was hung near the centre of the tank in the first set of experiments, and the fish

were observed through a peek-hole in this curtain. Since this cast some doubt on the results because it was believed that the fish saw the movements of the observer, a second set of experiments was run to determine if this was so. A mirror was mounted above the tank so that the fish could be observed from below the tank. In this way the fish were not disturbed.

The experiments in the light gradient study were divided into two groups. As in the phototaxis experiments, they are referred to as Series I experiments and Series II experiments. The apparatus was the same for both Series I and Series II experiments and the only difference was in the number of fish used and the procedure of observation. The Series II experiments were performed at a later date than Series I experiments.

In the light-gradient experiments, Series I, the trough was filled with water at the desired temperature, 10 fish were placed in the tank, and the light was turned on at the end of the tank. The fish were then allowed to remain 30 minutes to take position in the light gradient. The number in each compartment was then counted at one minute intervals for a period of 10 minutes, giving a total of 10 counts per experiment. Five experiments were performed with each light bulb used, giving a total of 50 counts per light bulb. During an experiment no water flowed into the trough but the temperature remained fairly constant ($\pm$ 0.5°C).

In the second group of experiments, light gradient experiments, Series II, the procedure was somewhat different from that outlined above for Series I. In this case 14 fish were placed in the tank in the evening and left overnight with the light turned on at the end of the tank and the room in darkness. Observations

began at 9:00 a.m. the following morning. The positions of the fish with respect to the compartments I-VII were recorded at 30 second intervals for a period of 20 minutes, giving a total of 40 counts. This was repeated at 12:00 noon, at 3:00 p.m., and at 6:00 p.m. The fish were then left overnight and the observations were repeated the following day. Thus, in all, a total of 280 to 320 counts were made on 14 fish in one experiment. The fish were then removed from the tank and a new group of 14 fish was used. The experiment was then run identical to that above. This was considered a duplicate experiment. Therefore, if the duplicate experiments are combined, a total of 560 to 640 counts were made on 28 fish.

IV. RESULTS

A. General Behaviour of Fish

(a) Series I experiments

Acclimation Temperature = 15.^{o}C

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

Group 1 - 4240-5200 hours (265-325 days)
Fish used in phototaxis experiments, Series I

Group 2 - 1200-2128 hours (75-133 days)
Fish used in rheotaxis experiments, surfacing experiments, and horizontal light gradient experiments, Series I.

In the Series I experiments, control fish manifested very little "spontaneous activity". This term is used in the present

paper to mean activity which comes about because of the inherent behaviour patterns of the species such as schooling or roaming to and fro in quiet water. This is opposed to the type of activity manifested when an orienting factor such as a light stimulus is acting upon the fish. Whenever control fish were placed in an experimental tank, exploratory wandering was observed in the first 30-40 minutes. After this initial period, the fish became relatively quiescent, with only occasional drifting to and fro of individuals. Unless the light intensity was fairly high, any movements on the part of the observer disturbed the fish very little.

The light-exposed fish, however, were in marked contrast to the control fish. Instead of becoming quiescent after the initial exploratory period, these fish continued to show marked activity at both high and low light intensities. At all light intensities, they reacted very strongly to movements of the observer and an alarm reaction, resulting in a quick turn and a darting movement to some cover, was very apparent. This continuous and vigorous activity made the observation of the light-exposed fish very difficult at times.

(b) Series II experiments

Acclimation Temperature = 10°C at the beginning of the experiments and 5.0°C at the end of the experiments

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

2080-4000 hours (130-250 days)
Fish used in phototaxis experiments, Series II, and horizontal light gradient experiments, Series II.

In the Series II experiments, both the control and light-exposed fish were less reactive to stimuli in the form of movements of the observer or stimuli from other sources in the experiments. Less spontaneous activity was exhibited by these fish in quiet water but, relatively speaking, the light-exposed fish were still more reactive to stimuli than the controls.

This lower level of activity in the Series II experiments was attributed to the lower temperature of acclimation (10°C-5°C).

Although schooling, and nipping and defence of territory were not studied in detail quantitatively, one observation on what was believed to be schooling behaviour seems worthy of mention. In one of the light gradient experiments described below, a group of light-exposed fish remained "schooled" in the darkest end of the tank, all oriented away from the source of light, for almost two days (see Figure 18d).

B. Behaviour with Respect to a Light Stimulus (Positive-Negative Phototaxis)

(a) Series I experiments

Acclimation Temperature = 15°C

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

4240-5200 hours (265-325 days)

In the statistical analyses of the results, $P = 0.01$ was chosen as the level of significance.

(1) Control fish

In studying the control fish of the Series I experiments in the glass aquarium of the phototaxis apparatus, it was found that the reaction to sudden illumination after dark-adaption was very slight when lights of low intensity were used as stimuli. However, as the intensity of the stimuli increased by the use of higher light intensities, the magnitude of the reaction increased until almost a total response occured at the highest light intensity (200 ft-c). The fish did not respond at low intensities of stimulation until 2 or 3 stimuli had been applied, by flashing the light on over one compartment and off over the other at one minute intervals. The fish was then seen to sway its body right and left and swim slowly into the opposite compartment or around the same compartment once or twice. At the highest light intensities, the fish darted into the dark compartment immediately after the light was turned on and, as a rule, remained there. Occasionally, a fish would move from the dark to the light, but only to dart back again after a little while.

The variations in the reactions of the control fish to the light stimuli were found to be fairly large (Table 1). This is not surprising since these fish did not exhibit an "all-or-none" type of reaction but were usually moving from one compartment to the other. This variation is particularly large at the lower light intensities and is attributed to the small number of fish used, and the possibility of light diffusion between light and dark compartments in the small apparatus. This would cause the dark compartment to be more shaded than dark.

At 0.1 ft-c all of the averages of the per cent of fish in the light compartment are above the 50% level and the t-test shows that the per cent of control fish in the light is significantly greater than the per cent in the dark at the 30 second

level (Figure 9 and Table 2). At 0.2 ft-c there is a significantly greater per cent of fish in the dark compartment as compared to the light compartment at the 60 second level. When 2.0 ft-c was used, a significantly greater per cent of fish was found in the dark compartment both at 30 and 60 seconds after the light was turned on, and this was also the case for 20.0 ft-c. At 200.0 ft-c the reaction to the light is very marked and at the 10 second, 30 second, and 60 second levels there is a significantly greater per cent of fish in the dark (Figure 9 and Table 2). Thus, from these experiments, the conclusion is that the control fish are negatively phototactic to the light stimulus and this negative reaction increases as the light intensity increases.

In the range of light intensities, 0.1 to 20.0 ft-c, there is very little difference among the percentages of fish in the light compartment (Table 3 and Figure 9). A slight tendency toward a greater response at the higher light intensities seems apparent but is by no means pronounced. In comparing the per cent of fish in the light compartment at successive light intensities (i.e. 0.1 ft-c with 0.2 ft-c, 0.2 ft-c with 2.0 ft-c), no significant difference is found. However, when the lowest light intensity (0.1 ft-c) is compared with the highest in this range (20.0 ft-c), a significant difference is found at the 30 and 60 second levels (Table 3). This seems to indicate that the orienting effect of the light in this range is very similar at the various levels of intensity studied but that this effect slowly increases as the light intensity is increased. There may be a tendency for these fish to seek the light at very low light intensity since, if 0.2 ft-c is compared with 20.0 ft-c, no significant difference results.

Outside of this 0.1 to 20.0 ft-c range, there is a very significant difference in the response at 200.0 ft-c (Table 3). Here the response is almost a total one, with only 8% of the fish remaining in the light at 60 seconds after the light was turned on. This seems to be a light intensity which the control fish avoid and they seek cover as soon as possible.

In comparing the per cent of fish in the light at each of the three time levels after the light was turned on, it was found that there was no significant difference at 0.1 ft-c, 0.2 ft-c, or 2.0 ft-c (Table 4 and Figure 9). At 20.0 ft-c, t-test shows that the per cent of fish in the light at the 60 second level may or may not be significantly different from the per cent at 10 seconds. When 200.0 ft-c was studied, the per cent of fish in the light at 30 seconds after the light was turned on was not significantly different from the per cent at 10 seconds, but the per cent at 60 seconds was significantly less than the per cent at either 10 seconds or 30 seconds. The conclusion to be drawn from this is that the reaction to the light at the higher light intensities is more rapid than at the lower intensities.

By a rather indirect treatment of the results of Series I experiments, some measure of the change in the intensities of the reactions of control fish can be derived as the light intensity varied. It is unfortunate that the total numbers of movements of the fish from the dark to the light, or vice versa, at each light intensity were not recorded in Series I experiments, but an approximate measure of their activity and intensity of reaction can be obtained by the following procedure. First, the number of fish in the light at 10 seconds after the light was turned on is

compared with the number in the light at 30 seconds. Then the number in the light at 30 seconds is compared with the number in the light at 60 seconds. These two comparisons would be done between counts in the first observation period after the experiment began. The second observation period begins 10 seconds after the the lights are reversed. It can be seen that the number of fish in the dark compartment at the end of the first observation period becomes the number in the light at the beginning of the second observation period after the lights are reversed. Therefore, by comparing the number of fish in the dark compartment, at the end of the first observation period, with the number of fish in the light compartment at 10 seconds after the reversal of the lights, in the second observation period, a measure of the number of reactions in the first 10 seconds can be obtained. By repeating this procedure for each observation period in each experiment, summing the total number of reactions for all of the experiments, and dividing this total by the number of counts made, an average number of reactions can be obtained for the first 10 seconds, the next 20 seconds and the final 30 seconds after the stimulus was applied. Of course, this procedure does not account for the movement of an individual fish into the light and back again, or vice versa, within the interval between two successive counts. Also, it does not account for the reactions of two different fish, one which moves into the dark or light and one which moves into the light or dark. However, it is felt that this does give some measure of the variations in the reactions with changes in the intensity of stimulation.

In the analysis of the reactions, it seemed best to separate them into positive, negative and zero reactions. Positive

reactions are movements of fish toward the light. Negative reactions are movements of fish away from the light. Zero reactions are instances of no movement on the part of the fish. In Figure 10, the average per cent of reactions to the light in the first 10 second interval after the light was turned on, the average per cent in the first 30 second interval, and the average per cent in the total 60 second interval are plotted against the light intensity of stimulation. This method serves to eliminate many of the irregularities in the graphs.

The positive reactions remained fairly constant throughout the whole range of intensities studied (0.1 - 200,0 ft-c), although there is a slight decrease from 20-50% at 20.0 ft-c to 0.0 - 12.0% at 200.0 ft-c. The per cent of negative reactions increased significantly from 15 - 47% at 0.1 ft-c to 95 - 147% at 200.0 ft-c. To offset this increase, the per cent of zero reactions decreased from 57 - 172% at 0.1 ft-c to 5 - 101% at 200.0 ft-c. This indicates that at lower intensities of stimulation fewer fish are reacting than at higher intensities (Figure 10).

(2) Light-exposed fish

When light-exposed fish were studied in the glass aquarium of the phototaxis apparatus, they behaved very differently from the control fish. Whereas the control fish remained very quiet except at high light intensities, and nearly always remained on the bottom of the aquarium, the light-exposed fish were very active at all light intensities studied, moving freely from one compartment to the other with apparent disregard for the absolute light intensity to which they were subjected. In addition to horizontal movements into and out of the light and dark

compartments, these fish also made vertical movements from the bottom of the tank to the surface of the water, and some ventured to jump over the top of the tank. Fish that rose to the surface and remained quiet there, oriented themselves at a 45 degree angle with the horizon.

As for control fish, the variations of the reactions of light-exposed fish to the light stimulus were found to be fairly large (Table 5). This also is attributed to the small number of fish per experiment and the small size of the apparatus used.

At 0.1 and 0.2 ft-c, there is a greater per cent of fish in the light compartment at 10 seconds after the light was turned on, although this difference is not significant (Figure 11 and Table 6). This may be because of the sluggishness of these fish in reacting at these low light intensities. At 30 seconds and 60 seconds after the light was turned on under these light intensities, there is a negative reaction to the light with the significantly greater per cent of fish being found in the dark compartment. At 2.0 ft-c there is a significant negative response at the 10, 30 and 60 second levels, but at 20.0 ft-c there is a significant response only at the 60 second level. This latter difference seems to be an anomaly, but it may be because of the increased activity of these fish at the higher light intensities, causing a more random distribution in the first 30 seconds after the stimulus is applied. The response at 200.0 ft-c is negative, with the significantly greater per cent of fish being in the dark compartment at the 30 and 60 second levels. The response at this high light intensity is not nearly as intense as that of the control fish, and this is a result of the much greater activity of

the light-exposed fish.

In the whole range of light intensities studied, there is no significant difference in the per cent of fish in the light compartment of the aquarium when successive light intensities are compared, or when the lowest light intensity in the range is compared with the highest (Figure 11 and Table 7). This resulted from the increased activity of these light-exposed fish, causing them to be constantly on the move at all light intensities except the very lowest. There seems to be a slight tendency to move into the dark compartment at the higher light intensities, but a t-test does not show a significant change in response. The increase in negative reaction with increase in light intensity is not nearly as clear-cut as in the control fish, so much so that the light-exposed fish can be said to show no difference in the intensity of their reactions in this range of light intensities.

In comparing the reactions of the light-exposed fish at the three time levels of 10 seconds, 30 seconds, and 60 seconds after the light was switched on, there is a significant increase in negative response between the 10 second and 30 second levels at 0.1 and 0.2 ft-c, but none between the 30 and 60 second levels. The increase in negative response is also significant between the 10 and 60 second levels (Figure 11 and Table 8). This would indicate that the negative response increases as the interval after the stimulus is applied increases, but that the greatest response occurs in the first 30 seconds. At 2.0, 20.0, and 200.0 ft-c, there is no significant difference in the negative response to the light between the 10 and 30 second, the 30 and 60 second, or the 10 and 60 second levels. Since there is a significant

negative response at these intensities, this would indicate that the most of the reaction occured within the first 10 seconds after the light was turned on (Figure 11 and Table 8).

The positive, negative and zero reactions of these light-exposed fish remained almost constant throughout the whole range of light intensities studied, but the positive reactions were very few while the negative and zero reactions were more numerous. The per cent of negative reactions increased from 35-135% at 0.1 ft-c to 80-162% at 2.0 ft-c and then decreased to 55-127% at 200.0 ft-c. The per cent of zero reactions decreased from 47.5-125.5% at 0.1 ft-c to 20-88% at 2.0 ft-c and then increased to 40-120% at 200.0 ft-c. This indicated that the reactions of these light-exposed fish remained fairly constant throughout the range of light intensities studied, (Figure 12).

(3) Comparison of the reactions of control and light-exposed fish

At 0.1 ft-c, there was a significantly greater per cent of control fish in the light compartment at 30 and 60 seconds after the light was turned on, thus indicating that the light-exposed fish reacted more intensely to this light intensity than did the control fish (Table 9). At 0.2 ft-c, 2.0 ft-c, and 20 .0 ft-c, there is no significant difference in the per cent of control and light-exposed fish in the light. Since there is a significant negative response at these light intensities, this must indicate that the intensity of the reaction is the same for both control and light-exposed fish in this range of light intensities. At 200.0 ft-c, the reaction of the control fish is much more intense than that of the light-exposed fish.

(b) Series II experiments

Acclimation Temperature = 10.0°C - 5.0°C

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

2176-4000 hours (136-250 days)

The only major general difference in the behaviour of the fish used in Series II experiments was in the intensity of their reaction. The Series II fish were much more sluggish than the Series I fish and the rate of their reaction was much slower. In fact, very little spontaneous activity was manifested by either the controls or light-exposed fish.

(1) Control fish

The variations in the responses of the individual groups of fish in the different observation periods and in the duplicate experiments were smaller per number of fish than in the Series I experiments (Table 1). This is probably because of the larger apparatus, in the Series II experiments, allowing less light diffusion and the lower temperature causing less activity on the part of the fish.

Only 20.0 ft-c and 200.0 ft-c were studied in these experiments, since heavy mortality occurred at the end of this time and resulted in the loss of all the fish. The experiments were then discontinued.

The statistical analyses show that at 20.0 ft-c there is a significantly greater per cent of fish in the dark compartment of the rectangular tank at 60 seconds after the light was turned on (Table 2 and Figure 9). At 200.0 ft-c the per cent of fish in the dark compartment is significantly greater at both the 30 and 60 second levels. This would point to the fact that the fish are negatively phototactic at these light intensities and this is the same result found in Series I experiments, although the reaction there was more intense.

When the per cent of fish in the light at 20.0 ft-c is compared with the per cent at 200.0 ft-c, no significant difference is found at either the 10 second, 30 second, or 60 second levels (Table 3 and Figure 9). This is in contrast to the result found in Series I experiments and may be attributed to (a) the larger size of the tank in Series II, allowing more "living-room" and less crowding of the fish, (b) the darker interior (black) of the tank, giving a lower total intensity of light with a given incident light intensity than in Series I, and (c) the lower temperature of Series II experiments.

There is no significant difference in the per cent of fish in the light compartment at increasing times of 10 seconds, 30 seconds, and 60 seconds after the light was turned on, at 20.0 ft-c. However, at 200.0 ft-c, the per cent of fish in the light is significantly less at 60 seconds than at 10 seconds after the stimulus was applied. This indicates, as in Series I, that the longer the stimulus is applied, the greater is the negative response (Table 4 and Figure 9).

The positive reactions of these control fish decrease from 6-33% at 20.0 ft-c to 0.3-6% at 200.0 ft-c. The negative reactions remain about the same, decreasing from 27-85% at 20.0 ft-c to only 24-68% at 200.0 ft-c. The zero reactions increased from 67-181% at 20.0 ft-c to 75-226% at 200.0 ft-c. The zero and negative reactions are in constrast to the results found in Series I experiments, where the negative reactions increased and the zero reactions decreased with increase in light intensity. This may be accounted for by the fact that during these experiments in Series II, the temperature of the water in the experimental tanks dropped steadily from 10°C to 5°C, so that the experiments at 200.0 ft-c were carried out at a lower temperature than those at 20.0 ft-c. Thus the reactions would be slower and the amount of fish reacting would be less at 200.0 ft-c than at 20.0 ft-c. This could cause the observed increase in zero reactions and the resulting slight decrease in negative reactions.

(2) Light-exposed fish

The variations in the responses of the light-exposed fish to the light were much less than in the Series I experiments and this is attributed to the same factors as for control fish (see Page 43) (Table 5).

In general, the behaviour of the light-exposed fish at the two light intensities studied was similar to that of control fish. However, at both 20.0 and 200.0 ft-c, the per cent of fish in the light is not significantly different from the per cent of fish in the dark (Table 6 and Figure 11). This is in contrast to the results found in Series I experiments for light-exposed fish and again may be a result of the larger size of the tank, the lower

temperature, and the lower total light intensity in Series II.

In comparing the number of fish in the light at 20.0 ft-c with the number at 200.0 ft-c, no significant difference is found (Table 7). This is the same result as was found with control fish, and with light-exposed fish in the Series I experiments.

The light-exposed fish in these Series II experiments lacked the tendency for the reaction to be increasingly greater at increasing time after the stimulus was applied. No significant difference between the per cent of fish in the light was found at the 10 second, 30 second, or 60 second levels for either of the light intensities. This result agrees with that for light-exposed fish in Series I, but the explanation is not that the reaction occured immediately but that there was no reaction at all.(Table 8).

The per cent of positive, negative, and zero reactions to the light did not change much between 20.0 and 200.0 ft-c in these light-exposed fish. The positive reactions decreased from 19-59% at 20.0 ft-c to 0.83-9% at 200.0 ft-c. The negative reactions decreased from 11-35% at 20.0 ft-c to 9-21% at 200.0 ft-c. The zero reactions increased from 70-206% at 20.0 ft-c to 90-270% at 200.0 ft-c. The result is the same as that found for control fish in this series and is accounted for in the same way, i.e. temperature effects.(Figure 11).

(3) Comparison of the reactions of control and light-exposed fish

At 20.0 ft-c, there is a significantly greater number of light-exposed fish in the light at the 60 second level, but at 200.0 ft-c, there is no significant difference in the per cent

of control fish and light-exposed fish at either of the 10 second, 30 second, or 60 second levels (Table 9).

(4) Reactions of fish to continuous light

In the second type of observation in the Series II experiments, testing the reaction of fish to continuous light, only two light intensities, 20.0 and 200.0 ft-c, were studied.

(4.1) Control fish

The variations in these experiments using control fish were not too large, considering the greater number of fish used and the larger number of observations made (Table 10). A significantly greater per cent of control fish was found in the dark compartment at both 20.0 and 200.0 ft-c (Table 11 and Figure 15). Also the control fish showed a significantly greater per cent of fish in the dark compartment at 200.0 ft-c than at 20.0 ft-c (Table 12 and Figure 13). This agrees with the Series I experiments and the reactions of dark-adapted Series II experiments where it was found that the control fish reacted more intensely at 200.0 ft-c.

(4.2) Light-exposed fish

The variations in the experiments using light-exposed fish were approximately of the same order as those for control fish (Table 10). Also, like control fish, the light-exposed fish showed a very significantly greater per cent of fish in the dark at both 20.0 and 200.0 ft-c (Table 11 and Figure 13). The intensity of the reaction in the light-exposed fish seemed to be unaffected by the light intensity in this range, since there was no significant difference in the per cent of fish in the light at either

20.0 or 200.0 ft-c (Table 12 and Figure 13). This also agrees with Series I experiments and dark-adapted fish of Series II experiments.

(4.3) Comparison of the reactions of control and light-exposed fish

At both 20.0 and 200.0 ft-c, there is a greater per cent of light-exposed fish in the light. This result is in agreement with the result found in the Series I experiments with dark-adapted fish, where the stimulus was an intermittent light rather than a continuous light.

(5) Comparison of the reaction times of control and light-exposed to a light stimulus

Although there is a considerable spread in the points in Figure 14, a trend toward a greater number of fish in the shade with increasing time is apparent. The stimulus was a light of 200.0 ft-c switched on fish previously kept in the dark. This was verified by the fact that the trend was present in almost every individual experiment. A comparison between the control and light-exposed fish (Figure 14) indicates that the response of the light-exposed fish is more rapid than that of the control fish, and at any given time a greater number of light-exposed fish have entered the dark compartment. This is in line with the greater sensitivity of these fish outlined above. No significance test was run to determine if the difference above is significant or not, but since the difference is fairly large, it probably is.

(c) Summary

In summary, it was found that:

(a) generally, the light-exposed fish were more reactive to stimuli of any form.

(b) Both the control and light-exposed fish were negatively phototactic to a light stimulus at all light intensities studied except the very lowest.

(c) The control fish showed very little difference in the intensity of their reaction to a light stimulus in the range 0.1 - 20.0 ft-c (Series I experiments). At 200.0 ft-c there was a marked difference in their response. The light-exposed fish showed no difference in their reactions among any of the light intensities in the Series I experiments. In the Series II experiments, no difference in the reaction was found between 20.0 and 200.0 ft-c for either control or light-exposed fish.

(d) The control fish showed a significant increase in negative response to the light stimulus the longer the stimulus was applied, at the higher light intensities (200.0 ft-c), whereas the light-exposed fish showed a significant increase in negative response the longer the stimulus was applied, at the lower light intensities (0.1 and 0.2 ft-c). This was found to be true for both Series I and Series II.

(e) The control fish showed an increase in the per cent of negative reactions to the light, a decrease in the per cent of zero reactions, and no significant change in the per cent of positive reactions, with increasing light intensity. The light-exposed fish showed very little change in the positive, negative, or zero reactions, with increasing light intensity. This was modified somewhat in the Series II experiments and this was attributed to temperature effects.

(f) Both control and light-exposed fish showed a significantly greater per cent in the dark at 20.0 and 200.0 ft-c, when they were subjected to continuous light for 30 minutes. At both light intensities there was a greater per cent of light-exposed fish than control fish in the light. There was a significantly greater per cent of control fish in the light at 20.0 ft-c than at 200.0 ft-c, whereas the light-exposed fish showed no difference between the per cent in the light at either light intensity.

(g) The light-exposed fish reacted more rapidly to a light stimulus than the control fish.

C. Rheotaxis (Preference for Water Currents of Various Intensities)

Acclimation Temperature = 15.0°C

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

1200-2128 hours (75-133 days)

These experiments were designed solely to test one phase of rheotactic behaviour; the preference of these salmon for water currents of various intensities. They do not in any way attempt to test the ability or inability of salmon to keep up with or swim against the current of water. To do this, a different type of apparatus would have to be used.

In the various counts made in these experiments, it is not to be expected that the fish would take position in one of the

two channels and remain there. Instead, and as was the case, they would be expected to swim to and fro from one channel to the other, but with the greater per cent of fish spending the longer period in the "current" or "no current" channel, depending on whether current or still water was preferred. This then would give a reasonable measure of their preference for current or the lack of it.

(a) Control fish (Tables 14, 15, and 16 and Figure 15)

The variation in the response to current of the control fish is not too large and rarely exceeds 1.0 - 1.5 fish per series of experiments (Figure 15 and Table 14).

The control fish showed a preference for current in the range of current intensities studied (2000 ml. - 32000 ml. per min.) (Table 15 and Figure 15). The greater per cent of fish was found in the current at 4000 ml/min and this seemed to be the preferred flow for these fish. At the lower and especially higher flows, a lesser per cent of fish was found in the current. The decrease in per cent of fish in the current at the higher flows is believed to indicate a tendency on the part of these fish to avoid fast water. As t-test shows, this preference for current was significant, since at all currents flows there was a significantly greater per cent of fish in the current than in "quiet" water.

These control fish showed a significant difference in the per cent of fish in the current between 4000 and 8000 ml/min in comparing successive current flows. The reaction to the current was of similar intensity at the remaining currents and no significant difference resulted between them. However, the overall

reaction of the fish showed a significant difference between the very lowest flow (2000 ml/min) and the highest flow (32000 ml/min) (Table 16 and Figure 15).

(b) Light-exposed fish (Tables 14, 15, and 16 and Figure 15)

The variation in the response of the light-exposed fish to the current was of the same order as that of the control fish (Table 14 and Figure 15).

The light-exposed fish, like the control fish, showed a preference for current in the range of current intensities studied (2000 ml - 32000 ml/min) (Table 15 and Figure 15). Also, the preferred flow of these light-exposed fish was again found to be 4000 ml/min and a tendency toward avoidance of fast flowing water was again evident.

In comparing successive current flows, the light-exposed fish showed a significant difference in the per cent of fish in the current between all successive currents flows. This is an indication of the greater sensitivity of these light-exposed to the currents, and agrees with qualitative observations, since the light-exposed fish spent much more time in the upper reaches of the current channel where the water was overflowing (Table 16 and Figure 15).

(c) Comparison of control and light-exposed fish (Table 17 and Figure 15)

In comparing control and light-exposed fish in these experiments, it was found that, except at the highest current flows

(32000 ml/min), the light-exposed fish showed a markedly stronger preference for currents. The t-test shows that at every current intensity there was a significant difference between the reactions (per cent of fish in the current) of the control and light-exposed fish. Also, the light-exposed fish showed a much stronger preference for fast water than did the control fish. Whether this came about because of a direct preference for stronger currents or a greater ability to stem the faster currents is not known. However, at the highest current flow studied, both control and light-exposed showed an equal number of fish in the current channel.

There was no consistent selection of either the right or left channels in these experiments (Table 18). This fact was verified in a control experiment in which no water was flowing into either channel. Out of a total of 6 experiments of 17 counts each (102 counts), 52% of the fish were in the one channel and 48% in the other channel.

(d) A source of error

The apparatus and method of observation used in these rheotaxis experiments were not ideal. One-half of the common chamber was considered to belong to the no-flow channel (see page 28), but at high flows some current was created in it. This would mean that the fish in this half of the common chamber, although considered to be in the no-flow channel, would actually be subjected to a slight current. However, since a preference for current was found for both control and light-exposed fish, the error in the apparatus is in favour of the current channel. That is to say, if the apparatus were to be corrected such that the error was

eliminated, the value for the per cent of fish in the current channel would be increased and consequently the preference for current would appear to be increased. Therefore, the general result would not be affected too much. Also, since this was chiefly a relative study, the difference between control and light-exposed fish would still show up.

D. Surfacing at Low Light Intensities (Vertical Distribution in a Vertical Light Gradient)

Acclimation Temperature = 15.0°C

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

1200-2128 hours (75-133 days)

(a) Control fish (Tables 19, 20, and 21 and Figure 16)

During the course of this study, control and light-exposed fish exhibited a marked difference in behaviour. As a rule, control fish showed very little activity at any of the light intensities studied. When they were first placed in the experimental tank, they remained on the bottom for the first 5 to 10 minutes. Then, when they had settled, some of them started to slowly make their way up the sides of the tank. The number acting in this manner was very small, the maximum in the upper one-third of the tank being only 6 fish on one occasion, with the average number being 1 - 2 fish. The movements of these control fish were very slow, and usually it took a fish approximately a minute to traverse the 85 cm column of water. On many occasions,

the fish were seen to remain quiet for minutes at a time, with only slow undulations of the tail and fins serving to offset the opercular breathing movements. At the higher light intensities, more activity was noted than at the lower light intensities.

The variation in the numbers of control fish in the upper one-third of the experimental tank is fairly large in some cases. This is inherent in the apparatus and method of observation, and also because of the fact that, at higher light intensities, the increased activity of the fish would contribute to a fair degree of variation (Tables 19 and 20 and Figure 16).

Peak activity for these control fish occured at 1.0 ft-c, where the per cent of fish in the upper one-third of the tank was significantly greater than at 0.04 or 0.2 ft-c below it or 5.0 ft-c above it (Table 21 and Figure 16). At 0 ft-c (darkness), where observations were made by momentarily flashing on a light of low intensity, only 3.0% on the average were found in the upper one-third of the tank. This tends to indicate that the control fish show very mild activity even at their maximum activity, and, in darkness, they tend to settle to the bottom and become very quiet.

(b) Light-exposed fish (Tables 19, 20, and 21 and Figure 16)

The light-exposed fish showed a marked difference in the amount of activity manifested, as compared with the control fish. At all light intensities, these fish showed some surfacing behaviour, the absolute amount varying with the light intensity at the surface of the water. The concentration of fish seemed to move up and down the column of water as the light intensity,

was decreased or increased. Sometimes, at low light intensities, one or more fish would swim in the upper layer of water with the dorsal fin protruding and the nose being at intervals pushed above the surface of the water. If startled, the fish would dart for the bottom of the tank, but only to return to the surface shortly thereafter. At the intensity of maximum activity described below, these fish were so active that they would swim up and down the column of water with a large per cent remaining in the upper one-third. This vertical wandering gave some large variation for the light-exposed fish.

The variations in the numbers of light-exposed fish in the upper one-third of the tank is of the same order as that for the control fish. However, the greatest variation now occurs at the lower light intensities, since here is where the most activity was manifested in the light-exposed fish (Table 19 and 20 and Figure 16).

Maximum activity occured in these light-exposed fish at a light intensity of 0.04 ft-c. In darkness (0.0 ft-c), the activity dropped off again with only an average of 7.7% of fish in upper one-third column of water. There was no significant difference between the surfacing reaction at 0.2 ft-c and 1.0 ft-c, but a significant fall off in activity did occur at 5.0 ft-c (Table 21 and Figure 16).

(c) Comparison of control and light-exposed fish (Table 22 and Figure 16)

In comparing the surfacing reaction of control and light-exposed fish, it is found that there was a significantly greater number of light-exposed fish in the upper one-third of the tank

at 0.04 ft-c and at 0.0 ft-c (darkness). At higher light intensities of 0.2, 1.0, and 5.0 ft-c, the control and light-exposed fish showed a similar number of fish in the upper one-third. This is in accordance with their reactions in the phototaxis experiments, where it was found that they reacted with the same intensity at 0.1, 0.2, 2.0, and 20.0 ft-c to a light stimulus.

Thus, at low light intensities, control fish sink to the bottom and remain quiescent, while the light-exposed fish rise into the surface of the water and become very active, causing a near random distribution.

From qualitative observations, it seems that these salmon show positive thigmotaxis, since they rise to the surface usually by the walls of the container. Also, both control and light-exposed fish exhibited nipping and defence of territory in these experiments.

E. Behaviour with Respect to a Horizontal Light Gradient (Horizontal Distribution in a Horizontal Light Gradient)

The relationships between the wattage of light used in these experiments, and the light intensity in ft-c at one foot intervals from the light source are shown in Figure 17.

(a) General Behaviour of control and light-exposed fish

Both control and light-exposed fish showed similar general behaviour in these light gradient experiments. When first placed in the tank, with light on at one end, the fish swam to and fro from one end to the other. Schooling was not studied in detail, but qualitatively, the light-exposed fish seemed to show a closer

aggregation than the control fish in these to and fro movements. Within an hour after transfer to the tank, the fish had become quiescent and had taken position in the different compartments. Some of these compartments were afterwards defended by groups of fish and individuals.

Figure 18 shows the lack of either diurnal variation or change in reaction with respect to time. The variations can be attributed merely to random wanderings, or nipping and defence of territory during the observation period.

(b) Series I experiments

Acclimation Temperature = 15.0° C

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

1200-2128 hours (75-133 days)

Generally, the fish in Series I experiments showed negative phototaxis and avoided the light by staying in the darker end of the tank. This trend is shown in Figures 19 and 20, although the results in the Series I experiments show much variation. The greatest number of fish in each of the three gradients (7.5 watt, 100 watt, and 300 watt - Figure 17) was found in compartment VII, the farthest from the light.

The variations in the reactions of both the control and light-exposed fish is considerable in some cases (Table 23 and 24 and Figure 18). This is not surprising since the fish would not be expected to stay in the same compartments during the

different observation periods or even in the same observation period. However, the trends in these experiments are very obvious and, as will be seen, the statistical analyses usually give a clear-cut picture.

(1) Control fish

The control fish in the light gradient experiments, Series I, showed a significantly greater number in compartment I as compared to II, when the 7.5 watt bulb was used at the end of the tank (Table 25a). Excluding compartment I, a tendency toward increasing numbers of fish in each compartment at increasing distance from the light source is evident (Table 25a and Figure 19). The statistical analyses show that there is no significant difference between the number of fish in compartments II and III, III and IV, IV and V, or V and VI. However, between compartments VI and VII, a significantly greater number was found in VII. Some of this may be because of a tendency to seek corners, but most of it must indicate an avoidance of brighter areas (Table 25a and Figure 19).

Using a 100 watt bulb at the end of the tank, greater variability was found, and there was no significant difference between the number of fish in compartments VI and VII. However, a significantly greater number was found in compartment V than in IV. An anomaly to this trend was found in the significant difference between III and IV, since there was a greater number in III than in IV. This is unexplained. No significant difference was found between compartments I and II or V and VI. However, the trend is still towards an avoidance of brighter areas (Table 25a and Figure 19).

Using a 300 watt bulb at the end of the tank, the picture was essentially the same. There was a significantly greater number of fish in compartment V than in IV, in compartment VI than in V, and in compartment VII than in VI. No significant difference occured between the number of fish in I and II, II and III, or III and IV (Table 25a and Figure 19).

In comparing all the other compartments with compartment VII, a significantly greater number of fish was found in VII when the 7.5 watt and the 300 watt was used. With the 100 watt bulb, the results are more variable (Table 25a).

A significantly greater number of fish was found in compartment I, when the 7.5 watt bulb was used at the end of the tank, than when the 100 watt bulb was used. No significant difference was found in the other compartments when comparing the 7.5 watt bulb with the 100 watt bulb (Table 26).

When the number of fish in each compartment, using the 100 watt bulb, is compared with the number in the corresponding compartments, using the 300 watt bulb, a greater number of fish was found in III, IV, and V in the light gradients created by the 100 watt bulb. (Table 26). However, a greater number of fish was found in VI and VII with the 300 watt bulb, rather than the 100 watt bulb. In other words, these control fish showed a greater avoidance for the 300 watt bulb than the 100 watt bulb.

The same result was found in comparing the 7.5 watt bulb with the 300 bulb, except that now a significantly greater number was also found in compartments I and II when using the 7.5 watt bulb (Table 26).

In summary, it can be said that the control fish showed a strong negative reaction to the light source in a horizontal light gradient and this negative reaction tended to increase as the intensity of the light source increased.

(2) Light-exposed fish

When the 7.5 watt bulb was used at the end of the tank, the light-exposed fish showed the same trends as the controls in their reactions. There was a successively greater number of fish in compartments VI and VII, but no significant differences in the numbers of fish in compartments I, II, III, IV, and V were evident (Table 25b and Figure 20).

With the 100 watt bulb at the end of the tank, the same result was obtained, but now there was also a significantly greater number in III than in II (Table 25b and Figure 20).

With the 300 watt bulb, the avoidance of the lighted areas was also evident, and there was again a significantly greater number of fish in VI than in V, in VII than in VI and in III than in II. No significant difference was found between the numbers in I and II, III and IV, or IV and V (Table 25b and Figure 20).

In comparing the number of fish in the other compartments with the number in compartment VII, a very great significant difference was found when either one of the three light bulbs was used. This shows that the greater number was at all times in compartment VII (Table 25b).

The light-exposed fish showed the same tendency to stay in compartment I nearest the light source as the control fish, but

this is not significant statistically (Table 27). In comparing the reactions of the fish with the 100 watt bulb and the 7.5 watt bulb, a significantly greater number was found in compartment II with the 7.5 watt bulb, but the significantly greater number was in compartments VI and VII with the 100 watt bulb (Table 27).

When the results with the 100 watt bulb and the 300 watt bulb are compared, it can be seen that a greater number was in compartment VII with the 300 watt bulb, but that there is no significant difference in the numbers of fish in any of the other compartments (Table 27).

In comparing the 7.5 watt and the 300 watt bulbs, it can be seen that a significantly greater number of fish was in compartments I, II, and IV with the 7.5 watt bulb, whereas the number in compartments VI and VII was significantly greater with the 300 watt bulb (Table 27).

In summary, the light-exposed fish showed a negative reaction to the light source in the three horizontal light gradients studied, and this negative reaction increased as the intensity of the light source increased.

(3) Comparison of the reactions of control and light-exposed fish

In comparing the behaviour of control and light-exposed fish in a horizontal light gradient, it was found that a significantly greater number of control fish was found in compartment I with the 7.5 watt bulb, and this may be a light seeking tendency of these fish (Table 28). A significant difference also resulted

in compartment VI, with the controls again showing the greater number. However, the reaction of the control and light-exposed fish to the horizontal light gradient created by the 7.5 watt bulb was very similar.

With the 100 watt bulb, there was a significantly greater number of light-exposed fish in compartments VI and VII, but a significantly greater number of control fish in I and II. In other words, the light-exposed fish showed a stronger avoidance of the light source than the controls with the 100 watt bulb (Table 28).

When the 300 watt bulb was used, no significant difference was found between the number of control and light-exposed fish in either of the compartments (Table 28).

Thus it seems that the control and light-exposed fish reacted very similarly to the light gradients created by the 7.5 watt bulb and the 300 watt bulb, but the light-exposed fish showed a greater avoidance of the 100 watt bulb than the control fish.

(c) Series II experiments

Acclimation Temperature = 10.0°C

Exposure Time of "Light-Exposed Fish" to Light of 25 ft-c Intensity and 16 Hours Daily Duration:

2080-3072 hours (130-192 days)

As in the Series I experiments, both the control and light-exposed fish exhibited a negative phototaxis in these Series II

light gradient experiments and avoided the light by congregating in the darkest end of the longitudinal tank. This trend is shown clearly in Figures 19 and 20 and here the results did not show as much variation as in the Series I experiments (Tables 23 and 24). This may be attributed to the larger number of fish used and the fact that the fish were not distributed as much in these experiments as in Series I experiments.

(1) Control fish

The control fish in the light gradient experiments, Series II, showed the same tendency to remain in compartment I as was the case in Series I experiments (Table 23). However, in these experiments, the tendency was present in the gradient created by the 7.5 watt, 100 watt, and 300 watt bulbs and not only in the case of the 7.5 watt bulb as in Series I experiments. This tendency is attributed to the seeking of the ends of the tank.

When the 7.5 watt bulb was used at the end of the tank, the control fish showed a significantly greater number in each successive compartment at increasing distances from the light source, excluding compartments III and IV. In these latter compartments, this trend is reversed and the greater number is found in III rather than in IV (Table 25a and Figure 19).

When the 100 watt and 300 watt bulbs were used, the trend is identical to that found with the 7.5 watt bulb, excluding compartments III and IV, where there is no significant difference in the number of fish (Table 25a and Figure 19).

In comparing the number of fish in the other compartments with the number in compartment VII, a significant difference was

found with all three light bulbs, the greater number at all times being found in compartment VII (Table 25a).

The foregoing results in these Series II experiments are similar to the results found in Series I experiments, in that the fish exhibited a strong negative phototaxis to the light source.

When the numbers of fish in corresponding compartments, using the 7.5 watt and the 100 watt bulb, are compared, a significantly greater number was found in compartment I with the 7.5 watt bulb and this may be a tendency to seek the corners (Table 26). No significant difference was found in the number of fish in II and III with the two bulbs, but the number in compartments IV, V, and VI was greater when using the 100 watt bulb, while the number in compartment VII was greater when using the 7.5 watt bulb (Table 26).

In comparing the 100 watt bulb and the 300 watt bulb, a greater number of control fish was in II, III, and VII with the 300 watt bulb, while a greater number was in I, V and VI with the 100 watt bulb. These differences are significant (Table 26).

A similar comparison between the 7.5 watt bulb and the 300 watt bulb shows that a significantly greater number of control fish was in compartments II, III, IV, and V with the 300 watt bulb, while a greater number was found in I, VI and VII with the 7.5 watt bulb (Table 26).

The results discussed above in the comparisons of the reactions of the fish with the 7.5 watt bulb and the 100 watt bulb, and with the 7.5 watt bulb and the 300 watt bulb are in contrast to those found in the Series I light gradient experiments.

The only possible explanation is that, in Series II, there was increased nipping and defence of territory in the brighter 100 watt and 300 watt bulb gradients. This resulted in more displacement from the end compartments VI and VII of the tank in these higher light gradients.

(2) Light-exposed fish

When the 7.5 watt bulb was used at the end of the tank, there again seems to be a tendency for the light-exposed fish to seek compartment I, since the P is less than the value for significance at the 1% level. All the other compartments show a progressively greater number of fish in each compartment at successively greater distances from the light source (Table 25b and Figure 20).

With the 100 watt bulb, the light-exposed fish still showed the tendency to remain in compartment I and this is again attributed to a preference for corners. The remainder of the compartments, with the exception of III and IV, show the same trend as with the 7.5 watt bulb; a significant increase in the number of fish in each compartment at increasing distance from the light source (Table 25b and Figure 20).

With the 300 watt bulb at the end of the tank, the results were identical to those with the 100 watt bulb (Table 25b and Figure 20).

When the number of fish in compartment VII is compared with the number in each of the other compartments, a very significant difference is found with the three light bulbs, with the greater number being found in compartment VII in each case (Table 25b).

The above results clearly indicate that, as in the Series I experiments, these light-exposed fish are showing a negative reaction to the light source.

In comparing the number of light-exposed fish in corresponding compartments with the 100 watt bulb and the 7.5 watt bulb, a greater number was found in compartments II, III, IV, V, and VI with the 7.5 watt bulb, while a greater number was found in compartment VII with the 100 watt bulb. Thus, a greater avoidance was noted for the 100 watt light source than the 7.5 watt light source (Table 27).

With the 100 watt and 300 watt bulbs at the end of the tank, the number of fish in compartment I was significantly greater with the 100 watt bulb than with the 300 watt bulb. Also, the number was significantly greater in VII with the 100 watt bulb. This indicates that the avoidance for the 100 watt was greater than that for the 300 watt bulb and is the same result as was found above for the control fish in the Series II experiments. Here also it seems to be explained by the increased frequency of nipping in the brighter 300 watt gradient, causing more displacement from compartment VII. (Table 27). The fact that in one experiment with the 100 watt bulb, one group of light-exposed fish remained schooled in compartment VII, would also produce this result.

In comparing the 7.5 watt and 300 watt bulbs, the results show the same trend as found in Series I experiments, with light-exposed fish, and Series II experiments above, with control fish. There is a greater number of fish in compartments III, IV, V, and VI with the 7.5 watt bulb, whereas the significantly greater

number was in VII with the 300 watt bulb. There is no significant difference in the number in compartment II, while compartment I shows a greater number using the 300 watt bulb (Table 27).

In summarizing, it was found that, generally, the light-exposed fish showed a stronger avoidance reaction the stronger the source of light.

(3) Comparison of the reactions of control and light-exposed fish

When the behaviour of control and light-exposed fish in the light gradient tank during Series II experiments is compared, it is found that there were more control fish than light-exposed fish in compartments I and VII when the 7.5 watt bulb is used (Table 28). Compartments II and III showed no significant difference in the number of control and light-exposed fish, whereas compartments IV, V, and VI showed more light-exposed than control fish. This indicates that the light-exposed fish showed less avoidance for the 7.5 watt bulb than did the controls, and ventured more into the brighter areas of the tank.

With the 100 watt bulb at the end of the tank, there was no significant difference in compartment I, whereas a significantly greater number of control fish was in compartments II, III, IV, V and VI. Consequently, a greater number of light-exposed fish was found in compartment VII. Therefore, in these Series II experiments, the light-exposed fish showed a stronger avoidance of the brighter areas in the 100 watt light gradient than the controls (Table 28).

When the 300 watt bulb was used, there was a greater number

of control fish in compartments I, II, III, IV, and V, whereas there was a greater number of light-exposed fish in compartment VII. The conclusion is as before, that the light-exposed fish showed a stronger avoidance of the 300 watt bulb than the control fish (Table 28).

(d) Summary

In the horizontal light gradient experiments, the following results were found.

1. Both the control and light-exposed fish showed a negative reaction to the light source when the 7.5 watt, 100 watt, and 300 watt bulbs were used at the end of the tank. This was true for both Series I and Series II experiments.
2. Both the control and light-exposed fish tended to remain in compartment I at the end of the tank nearest the light source. This is attributed to a tendency on the part of these fish to seek corners.
3. In Series I experiments, both the control and light-exposed fish showed a greater avoidance for a stronger light source (300 watt bulb) than for a weaker light source (7.5 watt or 100 watt bulb). In Series II experiments, these relations were not as well defined as in Series I experiments and this difference was attributed to increased nipping and defence of territory in the Series II experiments, with the high light sources.
4. A comparison between the reactions of control and light-exposed fish revealed that, in the Series I

experiments, there was no significant difference in their reactions with the 7.5 watt or the 300 watt bulbs. However, with the 100 watt bulb, the light-exposed fish were found to have a greater negative reaction to the light source than the controls. In Series II experiments, the light-exposed fish were found to have a stronger avoidance reaction than control fish for the 100 and 300 watt bulbs, but a lesser avoidance for the 7.5 watt bulb. This difference in the results of Series I and Series II experiments is believed to be because the fish were disturbed in the Series I experiments, with the 300 watt bulb, by the method of observation.

V. DISCUSSION AND CONCLUSIONS

A. General Behaviour

It has been established that constant amounts of light (15, 16, 34), increasing amounts of light (8, 17, 29, 30, 32), decreasing amounts of light (8, 17, 29, 30), and continuous light are effective in accelerating the rate of development and maturity of widely different species of fish. Concerning the salmon, Hoar (1953) states that the parr-smolt transformation of coho and Atlantic salmon seems to result from the effect of a photoperiod on the pituitary, which in turn affects the other endocrine glands.

Evidence presented in this investigation has shown that the Atlantic salmon fry, which were exposed to photoperiods, were generally

more active and reacted more readily to stimuli than the fish subjected to control conditions. Hoar (1951) showed that Pacific salmon of the genus Oncorhynchus exhibited more activity and a lower threshold of stimulation in the smolt stage than in the parr stage. The difference in the behaviour of control and light-exposed fish must have been because of a direct effect of their exposure to photoperiods, which accelerated the rate of development of the fry, and caused the light-exposed fish to be physiologically more advanced and nearer the smolt stage of development than the control fish.

B. Behaviour with Respect to Light Stimuli

It has been shown in the present study that both control and light-exposed fish showed a negative response to a flashing light stimulus (Figures 9 and 11) and continuous light (Figure 13). This was evident at all intensities except the very lowest. This is obviously a behaviour pattern of great survival value to the species, since a preference for the darker, more shaded areas of a stream or river would decrease the probability of capture by predators. In this connection, Hoar, Keenleyside, and Goodall (1957) found that coho fry, coho smolts, sockeye fry, and sockeye smolts, were also photonegative under a light suddenly flashed on them, or under continuous illumination. This is in agreement with the results found in this study for control and light-exposed fish. The coho and sockeye salmon are the two species of Pacific salmon closely related ecologically to the Atlantic salmon.

Control fish showed a stronger cover reaction (negative phototaxis) at higher than at lower light intensities, whereas the

intensity of the reaction of the light-exposed fish was less affected by the intensity of the light used, although the tendency toward increased response at high light intensity was still present (Figures 9, 11 and 13). This difference was believed to have resulted from the increased activity of the light-exposed fish, causing more random wandering between light and dark compartments. This tended to produce a lesser number of light-exposed fish in the darker compartment than would be warranted by the light intensity alone.

From similar results, Hoar, Keenleyside, and Goodall (1957) remark that chum and sockeye fry and sockeye smolt showed a marked tendency to retreat under high light intensities and to emerge under lower light intensities, whereas the pink and coho fry and coho smolt showed the reverse tendency. Also coho fry, at 10 and 45 ft-c, showed a significantly greater number in the light, whereas at higher intensities they either became indifferent or retreated to the shade.

These results for chum and sockeye fry and sockeye smolts, agree fairly well with the results found for control and light-exposed fish. However, the results, for pink and coho fry and coho smolts, do not agree with the results of the present study, but complete agreement should not be expected, since these Pacific salmon are of a different genus than the Atlantic salmon, and even interspecific differences in the reactions to light were found in the Pacific salmon. Also, the nature of the apparatus and the observations were somewhat different in the two studies. The fact that the light-exposed fish were living under conditions of light, different from the control fish in the present study, may

have had some indirect effect on their behaviour, through its effect on the retina or some other structure of the eye, but this aspect was not investigated further. In any event, the difference in the behaviour of the control and light-exposed fish must have been a result of the exposure to light, since apart from light, they were subjected to the same conditions in the holding tanks, and the same conditions and stimuli in the experimental apparatus.

The control fish showed an increase in the number of fish in the shade, with increase in time after the light was turned on, only at the higher light intensities (Figure 9). The light-exposed fish, however, showed this behaviour only at the lower light intensities (Figure 11). This difference can be explained by several factors. The greater sensitivity of the light-exposed fish caused the greater part of the negative reaction to occur within the first 10 seconds after the light was turned on, at the higher light intensities. Thus, there was no significant increase in the reaction after the first 10 seconds. This greater sensitivity of the light-exposed fish, at the lower intensities, caused their negative reaction to commence more quickly than in the control fish, while the sluggishness of reacting would tend to spread the reaction over a longer period of time, after the light was turned on. This would give the observed increase in the number of fish in the dark with increase in time. At the lower light intensities, the control fish were so sluggish in their reaction that the increase in numbers in the dark compartment, with increase in time, did not show statistically, although the trend was still present.

Hoar, Keenleyside, and Goodall (1957) state that, at all light intensities, sockeye smolts exhibit a stronger negative reaction to the light than the fry, and the same was found to be true

for the coho smolt and fry. It was found in the present study that, at the lower intensities of light (0.1 ft-c), the light-exposed fish showed a stronger negative reaction than the control fish (Table 9), while at the highest light intensity, the control fish showed a marked stronger negative reaction to the light than the light-exposed fish. At 0.2, 2.0, and 20.0 ft-c., there was no significant difference in the reaction of control or light-exposed fish. If it is assumed that the light-exposed fish are physiologically nearer the smolt stage of development than the control fish, then the results of this study at the higher light intensities are somewhat in conflict with some of the literature results. However, the difference in the species of the fish, the exposure to light, and especially the increased activity of the light-exposed fish, may have had some effect in masking their reactions.

The greater sensitivity of the light-exposed fish to the continuous light (Figure 14) is in line with their greater general sensitivity to stimuli and their greater activity, and is believed to be because of a direct effect of the photoperiods on their rate of development.

In one of the experiments with the intermittent light stimulus, Series II, there was a greater number of light-exposed fish than controls in the lighted area of the tank, but this was attributed to the fact that these fish had not been fed during the experiment and therefore sought the lighted area more than usual. This is based on observations by Woodhead (1955), that hungry minnows (Phoxinus phoxinus) spent more time in the lighted areas, when searching for food, than in the darker areas.

Subjecting the fish to continuous light resulted in a

greater negative reaction being exhibited by the control fish. This is the same result as was found generally with the intermittent light stimulus and is attributed to the greater activity of the light-exposed fish. It was noted that these fish were much more active in these particular experiments than the control fish. Whereas the light-exposed fish were frequently found to be on the move from one compartment to the other, the controls were found to move into the dark compartment within the first 10 minutes after the light was turned on and to remain there, with only occasional fish moving into the light. The fact that the light was acting for a longer period of time in these experiments also allowed this difference in the behaviour of the fish to show itself.

Further evidence that the lower temperature in the Series II experiments with the intermittent light stimulus was the factor responsible for the difference in the reaction of the fish from the Series I experiments, is obtained from a comparison of their reactions under an intermittent light stimulus and continuous light (Series II). When using the intermittent stimulus in Series II experiments, the fish showed very little reaction to the light, while using continuous light there was a very significant reaction. With the intermittent stimulus, the fish had been adapted to darkness previous to the experiment and the low temperature coupled with the fact that the fish were subjected to the stimulus for only 60 seconds resulted in very little reaction on their part. That is to say, the fish did not have time to react under the given conditions at such a lower temperature (4.0 - 5.0°C). However, with the continuous light, the "stimulus" was applied for a period (30 minutes) long enough for the reaction to occur, even at the low temperature.

The general conclusion is that the exposure to photoperiods caused the fish to become more active under conditions of the experiments and more sensitive to stimuli of all kinds, but that the reaction to a flashing stimulus is not significantly altered; the difference that did occur in the reactions of control and light-exposed fish was a result of the increased activity and sensitivity of the light-exposed fish. However, the behaviour of the fish under continuous light was very different, with the controls showing the greater negative reaction, and this was attributed to the fact that the fish were subjected to the stimulus for a longer period of time in these experiments.

C. Rheotaxis (Preference for Water Currents of Various Intensities)

In this study, it was found that the light-exposed fish showed more preference for current of all intensities studied than the control fish. This difference is attributed to the increased activity of the light-exposed fish and their greater sensitivity to stimuli, brought about by their exposure to photoperiods. The increased sensitivity to stimuli, especially, would cause the fish to be stimulated more by the moving water than the still water. Consequently, a greater percentage of light-exposed fish than control fish would be found in the current channel. The fact that, for both control and light-exposed fish, the maximum preference for current occured at 4000 ml/min, seems to indicate that this flow represents the optimum strength of current for maximum response in this range. The differences in the per cent of fish in the current channel between successive flows for light-exposed fish, and the lack of it for controls, is in agreement with the increased sensitivity of light-exposed fish (Figure 15 and Table 16).

In a similar study with a similar type of apparatus, MacKinnon and Hoar (1953) state that chum salmon fry showed a preference for greater current flows, whereas coho fry did not. Also, Hoar (1954) states that sockeye smolts showed a preference for fast water, while coho smolts showed an avoidance of fast water. MacKinnon and Hoar (1953) also found that the current strength for maximum response for these salmon was in the vicinity of 4000 ml/min, and this agrees very well with the figure found in this study.

If it is assumed again that the light-exposed fish are nearer the smolt stage than the controls, and remembering that the chum and pink fry, and the sockeye and coho smolts are in the migrating stage, it can be seen that these results and the results of our experiments with current agree very well.

The general conclusion is that the exposure to light resulted in increased activity of the Atlantic salmon fry and increased sensitivity to stimuli. This in turn caused the light-exposed fish to show greater stimulation by the moving water and a greater preference for current. The increased activity would bring the light-exposed fish in contact with the current more often per unit time and result in a greater chance for reaction to the current.

D. Surfacing (Vertical Distribution in a Vertical Light Gradient)

Results from these experiments indicated that the control fish settled to the bottom of the water column and became very quiescent, whereas the light-exposed fish rose in the water column and became very active, causing a near random vertical

distribution at low light intensities. Also, the peak activity for the control fish occured at 5.0 ft-c, whereas that for light-exposed fish was found to be at 0.04 ft-c. This increase in behaviour of the light-exposed fish was believed to be because of their increased activity, resulting from their prolonged exposure to photoperiods. This increased activity was apparent at all light intensities, but was especially accentuated at the lower light intensities.

In this connection, Hoar (1951) states that pink and chum fry rise to the surface of the water at night under low light intensities. Also, coho smolts show a lower threshold of stimulation at night than the coho fry, and are much more active both day and night. Hoar (1953) states that coho and Atlantic salmon fry, and steelhead trout become inactive at night and this accounts for their prolonged stay in the streams. Hoar (1954) found that sockeye fry showed more depth preference than any other species, whereas chum and coho fry were more evenly distributed in the water column. Sockeye smolts showed random distribution in deep water, whereas coho smolts were deeper in the water column. This behaviour of the sockeye smolts is believed to be one of escape rather than a light intensity reaction.

From a comparison of the results of this study and the results of Hoar for Pacific salmon given above, it can be deduced that the behaviour of the light-exposed fish is similar to the behaviour of the migrant species of chum and pink fry and coho and sockeye smolts, in the water column. The control fish behaved much like the stages of coho and sockeye fry, which remain in the rivers and lakes. .

It is concluded from these experiments that the exposure of the Atlantic salmon fry to photoperiods resulted in a general increase in activity over that of control fish, and this caused the light-exposed fish to be randomly distributed in a vertical water column at low light intensities. This behaviour pattern is very characteristic of migrant stages of Pacific salmon.

E. Behaviour with Respect to a Horizontal Light Gradient (Horizontal Distribution in a Horizontal Light Gradient)

The results found in this study were very variable, but this is not surprising when one considers the type of apparatus and the methods of observations used. The same trend was however present in both Series I and Series II, and the differences were apparent only in the detailed analyses of the results.

In all of the experiments in this study, the fish were found to be photonegative, whether the intensity of the source of light was high (300 watt bulb) or low (7.5 watt bulb). This is in agreement with the results found in the positive-negative phototaxis experiments, in which the light source was suspended directly above the water level and the stimulus was intermittent of one minute duration in one case, and a continuous light in another case. This seems to indicate, therefore, that the direction of the reaction to light of the control and light-exposed Salmo salar parr is not greatly affected by (a) the direction of the incident light or (b) the duration of the light "stimulus", provided that this duration is longer than some definite latent period not determined in this study.

Woodhead (1955) found that minnows (Phoxinus phoxinus) show negative phototaxis in a horizontal light gradient, with an

experimental apparatus similar to the one used in this study. Jones (1955) also found that Phoxinus phoxinus were negatively phototactic in an experimental apparatus similar to the one used in the positive-negative phototaxis experiments of this study. These experiments agree very well with the results found by the writer for Atlantic salmon.

The results of this study showed that, generally, both the control and light-exposed fish exhibited a stronger avoidance reaction (negative phototaxis) the stronger the source of light. This was very apparent in the Series I experiments but was modified somewhat in the Series II experiments. This modification was attributed to the fact that in the Series II experiments the fish were in the tank for a longer period of time during any experiment, and thus were allowed a greater opportunity for nipping and defence of territory than in Series I experiments. This was verified by the fact that, qualitatively, more nipping was noted in Series II than in Series I experiments. Since nipping and defence of territory have been shown to increase with increasing light intensity (Stringer and Hoar, 1955), the increase in the number of fish in the brighter areas with the 300 watt bulb, giving the impression of a greater avoidance of the 100 watt bulb, was caused by the greater aggressive behaviour of these fish. This resulted in more displacement from the darker areas with the 300 watt bulb.

Woodhead (1955) found a similar result with Phoxinus phoxinus. They showed a greater avoidance of higher light sources in a horizontal light gradient.

The results of these experiments indicate that the light-exposed fish showed a greater avoidance of the brighter areas

at least in the higher light gradients, while in the lower light gradients the light-exposed fish may have more of a tendency to seek the brighter areas than the controls.

F. Significance of the Behaviour Patterns Studied

If we assume that the above theory is correct, and that the light-exposed fish are actually nearer the smolt stage of development than the control fish, we can attempt some partial understanding of the role of these behaviour patterns in the downstream migration of Atlantic salmon. This theory is probably feasible since Hoar (1953) states that the parr-smolt transformation is most likely connected with the effect of a photoperiod on the pituitary gland. The salmon parr (control fish) in seeking cover at high light intensities, would avoid open, exposed areas, and this, as can be readily imagined, is of great survival value to the species. Their lower preference for current would tend to keep these fish out of the stronger currents. Since it has been shown for Pacific salmon (Hoar, 1958) that rheotaxis is lost when the light intensity falls below a certain level, and if we assume this for the Atlantic salmon, then the decrease in activity and the lack of "surfacing" shown by the control fish could be considered as a factor preventing premature downstream migration in the parr stage. These fish would retreat to some quiet water and have less chance of being swept downstream.

The smolts (light-exposed fish), on the other hand, would become very active as the light intensity decreased in the evening, and swim to and fro vertically in the waters of the lake or stream. Thus they would lose visual contact with their environment and their positive rheotaxis would be lost. Then, since their

preference for faster currents would take them into the faster water, they would be displaced downstream.

This attempt at explaining the downstream migration of the Atlantic salmon is only an attempt, and until further knowledge has been gained and less assumptions made, it can only be accepted as a working hypothesis for future research.

VI. SUMMARY

1. The effect of photoperiods on the parr-smolt transformation of Atlantic salmon (Salmo salar L) was studied, using changes in behaviour patterns as criteria.

2. Negative phototaxis was exhibited by control fish in the vicinity of 2.0 to 200.0 ft-c, while the light-exposed fish showed this behaviour at all intensities studied. The size of the experimental tank and the temperature were credited with having some effect on the intensity of this reaction to light.

3. Both the control and light-exposed fish showed a gradual increase in the response to the light at successively higher light intensities, although there was only a significant difference between 20.0 and 200.0 ft-c for the control fish, and no significant difference between any successive light intensities for the light-exposed fish. However, the difference was significant when comparing the lowest with the highest light intensity.

4. The control fish showed a greater number in the shade at increasing time after the light was turned on, at 200.0 ft-c, while the light-exposed fish showed this behaviour at 0.1 and 0.2 ft-c.

5. The control fish showed an increase in the per cent of negative reactions to the light, a decrease in the per cent of zero reactions, and no significant change in the per cent of positive reactions, with increasing light intensity. The light-exposed fish showed no significant change in the per cent of negative, zero, or positive reactions, with increasing light intensity. The intensity of these reactions are modified by temperature.

6. The reaction to continuous light was negative for both control and light-exposed fish at 20.0 and 200.0 ft-c.

7. The reaction to continuous light was more rapid for the light-exposed fish than the control fish.

8. Both control and light-exposed fish showed a preference for current in the range studied, but the preference of the light-exposed fish was greater than that of the control fish. The light-exposed fish also showed more preference for fast water, since they were found in the faster flows more often than the control fish.

9. The light-exposed fish exhibited increased activity and random distribution in a vertical column of water at low light intensities, while the control fish showed decreased activity and settled to the lower reaches of the water column at low light intensities.

10. Both the control and light-exposed fish showed a negative phototactic response in a horizontal light gradient.

11. A tendency to remain in the end compartments of the horizontal light gradient tank was apparent in both control and

12. Both the control and light-exposed fish showed a stronger avoidance of the brighter areas in a horizontal light gradient the stronger the source of light, in Series I experiments, but this was not as clear-cut in Series II experiments. This was attributed to the fact that, in Series II experiments, the fish were in the tank for a longer period of time, and were thus given more opportunity for nipping and defence of territory. This caused more displacement into the brighter areas in the strongest light gradient, with the 300 watt bulb.

13. In Series I experiments with the horizontal light gradient, the light-exposed fish showed a stronger avoidance of the brighter areas than the control fish. In Series II experiments, the light-exposed fish showed a greater avoidance reaction when the 100 and 300 watt bulbs were used at the end of thettank, while the control fish showed a stronger avoidance of the brighter areas with the 7.5 watt bulb. This indicates a tendency for the light-exposed fish to seek the brighter areas at the lower light intensities, in the Series II experiments at least.

14. The general conclusion from all the experiments is that the exposure to photoperiods resulted in the light-exposed fish being physiologically nearer the smolt stage of development than the control fish. Consequently, the light-exposed fish exhibited behaviour patterns essentially similar to those of the smolt.

15. The significance of the behaviour patterns studied is discussed in realtion to the downstream migration of Atlantic salmon.

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APPENDIX (TABLES AND FIGURES)

are per cent of fish in the light compartment at 10, 30 and 60 seconds after the stimulus was applied. The stimulus was a light of given intensity switched on fish previously kept in darkness. See text for definition of Series I and II).

Exp. No.	0.1 ft.-c.			0.2 ft.-c.			2.0 ft.-c.			20.0 ft.-c.						200.0 ft.-c.					
										Series I			Series II			Series I			Series II		
	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"
1	40	40	40	32	36	32	32	28	20	40	28	16				16	12	4			
2	44	40	44	36	44	32	40	32	28	48	40	32				24	12	8			
3	48	48	44	44	44	36	48	36	36	48	40	32				24	20	8			
4	48	56	48	48	44	40	52	48	48	56	40	40				40	24	8			
5	52	56	52	52	48	44	52	56	48	56	48	40				44	32	12			
6	52	56	56	52	48	44															
7	52	60	56	56	48	44															
8	56	64	60	64	52	48							45 - 54	45 - 59	35 - 51				46 - 56	42 - 52	39 - 51
9	60	68	68	68	56	52															
10	60	88	72	68	56	60															
Range in per cent	20	48	32	36	20	28	20	28	28	16	20	24	9	14	16	28	20	8	10	10	12
Range in actual fish	1.0	2.4	1.6	1.8	1.0	1.4	1.0	1.4	1.4	0.8	1.0	1.2	0.9	1.4	1.0	1.4	1.0	0.4	1.0	1.0	1.2
No. of averages	10	10	10	10	10	10	5	5	5	5	5	5	20	20	20	5	5	5	40	40	40

after stimulus was applied).

No. of fish in light	0.1 ft.-c.			0.2 ft.-c.			2.0 ft.-c.			20.0 ft.-c. Series I			20.0 ft.-c. Series II			200.0 ft.-c. Series I			200.0 ft.-c. Series II		
	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"
0	2	2	3	4	1	3	1	1	1	2	3	5	1	4	5	4	7	15	11	2	5
1	4	3	3	7	13	15	4	6	8	2	6	8	10	5	8	10	14	10	16	16	19
2	18	13	16	9	11	11	11	11	11	6	7	6	22	26	27	8	3	0	28	41	44
3	19	18	17	15	17	14	6	6	5	13	7	4	24	28	37	2	0	0	45	45	63
4	4	9	6	15	7	6	3	1	0	1	2	2	26	28	22	0	0	0	77	73	69
5	3	5	5	0	1	1	0	0	0	1	0	0	31	24	30	1	1	0	52	56	58
6													22	26	23				76	74	68
7													28	31	24				54	46	39
8													29	21	19				37	31	24
9													5	4	4				12	11	11
10													2	3	1				2	0	0
Total (N)	50	50	50	50	50	50	25	25	25	25	25	25	200	200	200	25	25	25	400	400	400
Average	2.56	2.88	2.70	2.60	2.38	2.16	2.24	2.00	1.80	2.48	1.96	1.60	5.05	4.90	4.57	1.48	1.00	0.40	508	484	458
%	51.2	57.6	54.0	52.0	47.6	43.2	44.8	40.0	36.0	49.6	39.2	32.0	50.5	49.0	45.7	29.6	20.0	8.0	508	484	458
t	0.55	3.15	1.60	0.78	1.04	2.79	1.86	3.88	6.09	0.12	3.25	5.19	0.41	0.88	3.77	6.42	10.3	29.6	011	219	576
P	0.6	.001	.10	.45	.30	<.01	.05	<.001	<001	.99	.001	<001	.70	.40	<001	<.001	<.001	<001	.99	.02	<001

Table [illegible]. Comparisons and statistical analyses of the responses of Salmo salar [illegible] (Control fish) to a light stimulus of the different light intensities. (Values are average number of fish in the light compartment at 10", 30" and 60" after stimulus).

Light intensities compared ft.-c.	10 Seconds						30 Seconds						60 Seconds					
	Series I			Series II			Series I			Series II			Series I			Series II		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
0.1 0.2	2.56 2.60	0.2	.85	-- --	-- --	-- --	2.88 2.38	2.1	.03	-- --	-- --	-- --	2.70 2.16	2.2	.03	-- --	-- --	-- --
0.2 2.0	2.60 2.24	1.2	.25	-- --	-- --	-- --	2.38 2.00	1.5	.10	-- --	-- --	-- --	2.16 1.80	1.3	.20	-- --	-- --	-- --
2.0 20.0	2.24 2.48	0.8	.40	-- --	-- --	-- --	2.00 1.96	0.1	.999	-- --	-- --	-- --	1.80 1.60	0.7	.50	-- --	-- --	-- --
20.0 200.0	2.48 1.48	3.1	.001	5.05 5.08	0.2	.85	1.96 1.00	3.1	.001	4.96 4.85	0.3	.75	1.60 0.40	4.5	$<.001$	4.58 4.59	.05	.99
2.0 200.0	2.24 1.48	2.5	.01	-- --	-- --	-- --	2.00 1.00	3.6	$<.001$	-- --	-- --	-- --	1.80 0.40	7.4	$<.001$	-- --	-- --	-- --
0.1 20.0	2.56 2.48	0.3	.75	-- --	-- --	-- --	2.88 1.96	3.1	$<.01$	-- --	-- --	-- --	2.70 1.60	3.0	$<.01$	-- --	-- --	-- --
0.2 20.0	2.60 2.48	0.4	.70	-- --	-- --	-- --	2.38 1.96	1.3	.20	-- --	-- --	-- --	2.16 1.60	1.9	.06	-- --	-- --	-- --

Table 4. Comparisons and statistical analyses of the responses of *Salmo salar* L. to a light stimulus at the three different time levels (10, 30 and 60 seconds) (Control fish).

Time Levels Compar.	0.1 ft.-c.			0.2 ft.-c.			2.0 ft.-c.			20.0 ft.-c. Series I			20.0 ft.-c. Series II			200.0 ft.-c. Series I			200.0 ft.-c. Series II		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
10 Sec.	2.56	1.4	.15	2.60	0.9	.35	2.24	0.9	.35	2.48	1.6	.11	5.05	0.7	.51	1.48	1.6	.11	5.08	1.7	.08
30 Sec.	2.88			2.38			2.00			1.96			4.90			1.00			4.84		
30 Sec.	2.88	0.7	.45	2.38	0.9	.35	2.00	0.8	.38	1.96	1.1	.30	4.90	1.4	.25	1.00	2.6	<.01	4.84	1.8	.06
60 Sec.	2.70			2.16			1.80			1.60			4.58			0.40			4.58		
10 Sec.	2.56	0.6	.55	2.60	1.8	.06	2.24	1.7	.08	2.48	2.7	<.01	5.05	2.1	.03	1.48	4.0	<.001	5.08	3.5	<.001
60 Sec.	2.70			2.16			1.80			1.60			4.58			0.40			4.58		

Table 5. [illegible] (Values are per cent of fish in which [illegible] was a light of given intensity switched on fish previously kept in dark. See text for definition of Series I and II).

Exp. No.	0.1 ft.-c.			0.2 ft.-c.			2.0 ft.-c.			20.0 ft.-c.						200.0 ft.-c.					
										Series I			Series II			Series I			Series II		
	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"
1	40	28	16	44	20	24	32	20	4	40	32	20				32	24	20			
2	44	28	16	48	36	28	36	28	16	48	44	36				32	24	32			
3	52	36	28	48	36	28	44	36	32							40	40	36			
4	52	40	28	52	40	32	48	52	32							52	40	40			
5	56	40	32	52	44	32	52	52	56							64	52	52			
6	60	44	36	56	44	40															
7	60	44	40	56	48	40							43 - 51	48 - 56	47 - 65				47 - 53	47 - 53	47 - 53
8	60	48	40	60	48	44															
9	64	48	44	60	52	52															
10	68	56	48	72	56	52															
Range in per cent	28	28	32	28	36	28	20	32	52	8	12	16	8	8	18	32	28	32	6	6	6
Range in actual fish	1.4	1.4	1.6	1.4	1.8	1.4	1.0	1.6	2.6	0.4	0.6	0.8	0.8	0.8	1.8	1.6	1.4	1.6	0.6	0.6	0.6
No. of averages	10	10	10	10	10	10	5	5	5	2	2	2	20	20	20	5	5	5	40	40	40

stimulus or between stimulus and after stimulus).

No. of fish in light	0.1 ft.-c.			0.2 ft.-c.			2.0 ft.-c.			20.0 ft.-c.						200.0 ft.-c.					
										Series I			Series II			Series I			Series II		
	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"	10"	30"	60"
0	3	6	6	0	1	2	1	2	6	1	2	1	4	5	5	4	3	4	1	0	1
1	3	13	19	8	14	20	6	7	8	1	1	5	15	13	11	2	7	8	29	30	31
2	16	11	14	12	18	14	8	10	8	5	4	3	32	30	30	9	7	5	35	33	36
3	13	12	9	16	12	11	9	4	2	1	2	1	29	23	23	5	8	6	63	67	64
4	10	8	2	13	5	3	1	2	0	2	1	0	17	20	15	5	0	1	48	45	46
5	5	0	0	1	0	0	0	0	1	0	0	0	13	14	16	0	0	1	50	51	52
6													23	19	20				49	48	46
7													20	20	19				63	69	66
8													31	40	42				35	31	32
9													11	14	16				26	25	25
10													5	2	3				1	1	1
Total (N)	50	50	50	50	50	50	25	25	25	10	10	10	200	200	200	25	25	25	400	400	400
Average	2.78	2.06	1.64	2.74	2.12	1.86	2.12	1.88	1.40	2.20	1.90	1.40	4.870	5.060	5.215	2.20	1.80	1.80	4.973	4.965	4.920
%	55.6	41.2	32.8	54.8	42.4	36.2	42.4	37.6	28.0	44.0	38.0	28.0	48.7	50.6	52.2	44.0	36.0	36.0	49.7	49.6	49.2
t	2.2	3.4	8.2	2.2	3.8	6.3	2.8	4.2	6.5	1.1	2.1	5.8	.97	.44	1.6	1.6	4.7	3.7	0.3	0.4	1.0
P	.02	<.001	<.001	.03	<.001	<.001	<.01	<.001	<.001	.30	.05	<.001	.31	.65	.11	.10	<.001	<.001	.75	.70	.30

Table 7. Comparisons and statistical analyses of the responses of Salmo gairdneri (light exposed) to a light stimulus of the different light intensities (Values are average number of fish in the light compartment at 10", 30" and 60" after stimulus).

Light intensities compared ft.-c.	10 Seconds						30 Seconds						60 Seconds					
	Series I			Series II			Series I			Series II			Series I			Series II		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
0.1	2.78	0.17	0.9	--	--	--	2.06	0.26	0.8	--	--	--	1.64	1.07	.30	--	--	--
0.2	2.74			--	--	--	2.12			--	--	--	1.86			--	--	--
0.2	2.74	2.4	.02	--	--	--	2.12	0.96	.35	--	--	--	1.86	1.75	.08	--	--	--
2.0	2.12			--	--	--	1.88			--	--	--	1.40			--	--	--
2.0	2.12	0.20	0.8	--	--	--	1.88	0.05	>0.99	--	--	--	1.40	0.00	∞	--	--	--
20.0	2.20			--	--	--	1.90			--	--	--	1.40			--	--	--
20.0	2.20	0.00	∞	4.870	0.48	.65	1.90	0.24	.80	5.060	0.45	.65	1.40	0.87	.40	5.215	1.37	.17
200.0	2.20			4.973			1.80			4.965			1.80			4.920		

Table 8. Comparisons and statistical analyses of the responses of *Salmo salar* L. to a light stimulus at the three different time levels (10, 30 and 60 seconds) (Light-exposed fish).

Time Levels Compar.	0.1 ft.-c. $\bar{X}$	t	P	0.2 ft.-c. $\bar{X}$	t	P	2.0 ft.-c. $\bar{X}$	t	P	20.0 ft.-c. Series I $\bar{X}$	t	P	20.0 ft.-c. Series II $\bar{X}$	t	P	200.0 ft.-c. Series I $\bar{X}$	t	P	200.0 ft.-c. Series II $\bar{X}$	t	P
10 Sec.	2.78	2.8	<.01	2.74	3.0	<.01	2.12	0.8	.38	2.20	0.5	.60	4.87	0.7	.45	2.20	1.2	.22	4.97	0.05	.999
30 Sec.	2.06			2.12			1.88			1.90			5.06			1.80			4.96		
30 Sec.	2.06	1.8	.18	2.12	1.3	.20	1.88	1.5	.12	1.90	1.0	.30	5.06	0.6	.55	1.80	0.0	∞	4.96	0.28	.78
60 Sec.	1.64			1.86			1.40			1.40			5.21			1.80			4.92		
10 Sec.	2.78	4.8	<.001	2.74	4.2	<.001	2.12	2.3	.02	2.20	2.3	.02	4.87	1.3	.20	2.20	1.1	.30	4.97	0.33	.75
60 Sec.	1.64			1.86			1.40			1.40			5.21			1.80			4.92		

Table 9. Comparisons and statistical analyses of the responses of control and light-exposed Salmo salar L. to a light stimulus of various light intensities (Values are average numoer of fish in the compartment at 10", 30" and 60" after stimulus).

Type of fish compared	0.1 ft.-c.									0.2 ft.-c.									2.0 ft.-c.								
	10 sec.			30 sec.			60 sec.			10 sec.			30 sec.			60 sec.			10 sec.			30 sec.			60 sec.		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
Control	2.56	0.9	.35	2.88	3.3	.001	2.70	4.6	<.001	2.60	0.6	.55	2.38	1.2	.22	2.16	1.3	.20	2.24	0.4	.70	2.00	0.4	.70	1.80	1.3	.20
Light exposed	2.78			2.06			1.64			2.74			2.12			1.86			2.12			1.88			1.40		

Table 9 (continued).

Type of fish compared	20.0 ft.-c. Series I 10 Sec. $\bar{X}$	t	P	30 Sec. $\bar{X}$	t	P	60 Sec. $\bar{X}$	t	P
Control	2.48			1.96			1.60		
		0.6	.52		0.1	.90		0.5	.65
Light exposed	2.20			1.90			1.40		

Type of fish compared	20.0 ft.-c. Series II 10 Sec. $\bar{X}$	t	P	30 Sec. $\bar{X}$	t	P	60 Sec. $\bar{X}$	t	P
Control	5.05			4.90			4.57		
		0.7	.45		0.6	.52		2.5	.01
Light exposed	4.87			5.06			5.21		

Type of fish compared	200.0 ft.-c. Series I 10 Sec. $\bar{X}$	t	P	30 Sec. $\bar{X}$	t	P	60 Sec. $\bar{X}$	t	P
Control	1.48			1.00			0.40		
		2.0	.05		2.7	<0.01		4.9	<.001
Light exposed	2.20			1.80			1.80		

Type of fish compared	200.0 ft.-c. Series II 10 Sec. $\bar{X}$	t	P	30 Sec. $\bar{X}$	t	P	60 Sec. $\bar{X}$	t	P
Control	5.08			4.84			4.58		
		0.7	.45		0.8	.42		2.2	.04
Light exposed	4.97			4.96			4.92		

Table 10. Variations in the reactions of Salmo salar L. to a continuous light stimulus (Values are average number of fish in the light during a 15 minute period of observation; d - refers to duplicate experiments).

Exp. No.	Control fish		Light-exposed fish	
	20.0 ft-c	200.0 ft-c	20.0 ft-c	200.0 ft-c
1	0.000	1.400	3.333	3.467
2	0.100	0.667	2.567	2.867
3	2.500	1.600	3.333	4.033
4	0.000	0.900	3.367	2.200
5	1.000	0.867	4.200	4.033
6	1.500	1.630	4.500	5.067
7	1.700	1.500	3.733	4.400
1d	2.933	0.000	0.000	4.667
2d	2.500	0.000	5.067	2.133
3d	2.100	0.000	2.000	2.433
4d	3.000	0.000	2.133	2.533
5d	4.000	1.300	2.100	1.433
6d	2.267	2.933	4.000	1.900
7d	4.533	0.000	1.000	1.600
1dd		0.000		
2dd		1.000		
3dd		2.333		
4dd		0.000		
5dd		0.600		
6dd		0.000		
7dd		1.433		
1ddd		0.000		
2ddd		0.000		
3ddd		0.133		
4ddd		1.967		
5ddd		1.200		
6ddd		2.000		
7ddd		0.967		
Range	4.533	2.933	5.067	3.634
No. of fish	10	10	10	10

e 11. Frequency distributions and statistical analyses of the reactions of Salmo r L. to a continuous light stimulus (Values are frequencies of occurrence of particular number of fish in the light at 30" intervals for 15 minute periods licate experiments combined)).

of sh	Control fish		Light-exposed fish	
	20.0 ft-c	200.0 ft-c	20.0 ft-c	200.0 ft-c
0	87	377	30	6
1	65	241	39	41
2	107	177	95	110
3	95	42	82	117
4	50	3	109	70
5	16		62	65
6			3	11
7				
8				
9				
0				
al	420	840	420	420
r-	2.009	0.873	2.950	3.055
r nt	20.09	8.73	29.50	30.55
	59.94	573.19	39.88	41.38
	<0.001	<0.001	<0.001	<0.001

Table 12. Comparison and statistical analysis of the per cent of Salmo salar L. in the light at 20.0 and 200.0 ft-c during experiment with continuous light. (Based on 420 and 840 counts).

Light Intensity Compared	Control fish			Light-exposed fish		
	$\bar{X}$	t	P	$\bar{X}$	t	P
20.0 ft-c	2.009	16.96	<0.001	2.950	1.07	0.300
200.0 ft-c	0.873			3.055		

Table 13. Comparison and statistical analysis of the per cent of control and light-exposed Salmo salar (L.) in the light. (Based on 420 and 840 counts).

Type of fish Compared	20.0 ft-c			200.0 ft-c		
	$\bar{X}$	t	P	$\bar{X}$	t	P
Control	2.009	9.54	<0.001	0.873	34.39	<0.001
Light Exposed Fish	2.950			3.055		

Table 14. Variations in reactions of *Salmo salar* L to currents of different intensities. (Values are per cent of fish in current channel, and are based on 85 counts on 50 fish, the counts being 17 per experiment, in 5 experiments).

Exp. No.	Light-exposed fish					Control fish				
	2000 ml/min.	4000 ml/min.	8000 ml/min.	16000 ml/min.	32000 ml/min.	2000 ml/min.	4000 ml/min.	8000 ml/min.	16000 ml/min.	32000 ml/min.
1	70.59	74.12	65.29	64.12	54.71	55.30	57.65	55.88	45.30	52.35
2	71.18	76.47	70.00	64.70	56.47	56.47	59.41	57.65	52.94	52.94
3	77.65	81.18	73.53	67.65	63.53	65.30	65.29	60.00	59.41	59.47
4	78.82	84.71	74.12	69.41	65.29	68.24	70.00	60.59	60.00	62.94
5	80.59	87.65	76.47	72.94	--	71.76	74.71	65.29	66.47	--
Total	378.83	404.13	359.41	338.82	240.00	317.07	327.06	299.41	284.12	227.70
No.	5	5	5	5	4	5	5	5	5	4
Average per cent	75.76	80.83	71.88	67.76	60.00	63.41	65.41	59.88	56.82	56.92
Range per cent	10.00	13.53	11.28	8.82	10.58	16.46	17.06	9.41	21.17	10.59

of the experimental tank (current preference) (duration of experiment 24 hours daily).

No. of fish	Control fish					Light-exposed fish				
	2000 ml/min.	4000 ml/min.	8000 ml/min.	16000 ml/min.	32000 ml/min.	2000 ml/min.	4000 ml/min.	8000 ml/min.	16000 ml/min.	32000 ml/min.
0										
1										
2										
3		1			5					
4	3	3	4	14	5					
5	18	16	27	30	15	1	1	1	6	17
6	27	21	25	20	25	7	3	18	27	35
7	25	23	26	13	17	24	20	37	34	15
8	8	16	1	6	1	48	31	23	16	1
9	4	4	2	2		5	24	5	2	
10		1					6	1		
Total	85	85	85	85	68	85	85	85	85	68
Average	6.341	6.541	5.988	5.682	5.692	7.576	8.083	7.188	6.776	6.000
per cent	63.41	65.41	59.88	56.82	56.92	75.76	80.83	71.88	67.76	60.00
t	14.90	14.50	12.37	7.07	6.79	43.19	39.15	31.01	25.21	15.91
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 16. Comparison and statistical analysis of the numbers of Salmo salar L. in the current channel (Values based on 5 experiments of 17 counts each).

Currents compared ml/min.	Control fish			Light-exposed fish		
	X	t	P	X	t	P
2000	6.341	1.04	0.30	7.576	3.63	<0.001
4000	6.541			8.083		
4000	6.541	3.00	0.001	8.083	6.00	<0.001
8000	5.988			7.188		
8000	5.988	1.73	0.10	7.188	2.90	$0.01>P>0.001$
16000	5.682			6.776		
16000	5.682	0.05	0.999	6.776	5.68	<0.001
32000	5.692			6.000		

Table 17. Statistical comparison of the preference of control and light-exposed fish for water currents of various intensities (Values are average numbers of fish in the current channel and are based on 85 (2000-16000 ml/min.) and 68 (32000 ml/min.) counts on 40-50 fish - see text).

Type of fish	2000 ml/min.			4000 ml/min.			8000 ml/min.			16000 ml/min.			32000 ml/min.		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
Control	6.341			6.541			5.988			5.682			5.692		
		8.15	<.001		8.41	<.001		7.96	<.001		6.48	<.001		1.82	.05
Light Exposed	7.576			8.083			7.188			6.776			6.000		

18. Relationship between right and left channels in current preference experiments *Salmo salar* L. (Values are per cent of fish in right and left channels) + refers to R. END > L. END, - refers to L. END > R. END.

CONTROL FISH

2000 ml/min.		4000 ml/min.		8000 ml/min.		16000 ml/min.		32000 ml/min.	
R.END	L.END	R.END	L.END	R.END	L.END	R.END	L.END	R.END	L.END
71.76	65.30	59.41	74.71	60.00	60.59	59.41	45.30	52.94	59.47
56.47	68.24	70.00	57.65	65.29	57.65	52.94	60.00	62.94	
	55.30	65.29			55.88		66.47	52.35	
2	3	3	2	2	3	2	3	3	1
64.12	62.95	64.90	66.18	62.65	58.04	56.18	57.65	56.08	59.47
+1.17		-1.28		+4.61		-1.08		-3.39	
Diff.				+0.03					

LIGHT-EXPOSED FISH

2000 ml/min.		4000 ml/min.		8000 ml/min.		16000 ml/min.		32000 ml/min.	
R.END	L.END	R.END	L.END	R.END	L.END	R.END	L.END	R.END	L.END
80.59	78.82	84.71	74.12	70.00	74.12	69.41	72.94	54.71	65.29
77.65	71.18	87.65	81.18	73.53		67.65		63.53	56.47
	70.59		76.47	65.29		64.12			
				76.47		64.70			
2	3	2	3	4	1	4	1	2	2
79.12	73.53	86.18	77.26	71.32	74.12	66.47	72.94	59.12	60.88
+5.59		+8.92		-2.80		-6.47		-1.76	
Diff.				+3.48					

Table 19. Variations in the surfacing reactions of Salmo salar L. at different light intensities (values are per cent of fish in the upper one-third of an 86 cm high tank).

Ft-c	Control fish					Light-exposed fish				
	0.00	0.04	0.20	1.00	5.00	0.00	0.04	0.20	1.00	5.0
	0	0	6	11	1	2	32	12	9	0
	4	7	10	14	10	7	33	13	15	6
	5	10	14	24	14	14	36	19	18	6
		14	16	30	15		48	22	18	8
		18	18	32	17		49	23	22	16
Total	9	49	64	111	57	23	198	89	82	36
No.	(3)	(5)	(5)	(5)	(5)	(3)	(5)	(5)	(5)	(5)
Average %	3.00	9.80	12.80	22.20	11.40	7.67	39.60	17.80	16.40	7.20
Average	0.30	0.98	1.28	2.22	1.14	0.77	3.96	1.78	1.64	0.72
Range %	5	18	12	21	16	12	17	11	13	16

10. Frequency distributions and averages of the numbers of Salmo salar L. in the one-third of an 86 cm. high tank (surfacing reaction) at various light intensities based on 5 experiments of 10 counts each, at each light intensity).

Control fish					Light-exposed fish				
0 ft-c.	0.04 ft-c.	0.2 ft-c.	1.0 ft-c.	5.0 ft-c.	0 ft-c.	0.04 ft-c.	0.2 ft-c.	1.0 ft-c.	5.0 ft-c.
21	22	13	4	12	13	0	4	9	26
9	10	17	12	21	12	2	19	15	15
	15	14	15	15	4	5	15	15	6
	3	5	11	2	1	12	8	8	3
		1	5			13	4	2	
			2			12		1	
			1			4			
						2			
30	50	50	50	50	30	50	50	50	50
0.30	0.98	1.28	2.22	1.14	0.77	3.96	1.78	1.64	0.72
3.00	9.80	12.80	22.22	11.40	7.70	39.60	17.80	16.40	7.20

21. Statistical comparison of the per cent of Salmo salar L. in the upper one-of an 86 cm high tank (surfacing reaction) at different light intensities (Values on 5 experiments of 10 counts each, at each light intensity).

ht ities ared	Control fish				Light-exposed fish			
	$\bar{X}$	ΣX^2	t	P	$\bar{X}$	ΣX^2	t	P
t-c.	0.30	6.30	3.50	<0.001	0.77	9.37	11.34	<0.001
t-c.	0.98	48.98			3.96	95.92		
t-c.	0.98	48.98	1.48	0.2	3.96	95.92	8.68	<0.001
t-c.	1.28	52.08			1.78	58.58		
t-c.	1.28	52.08	3.89	<0.001	1.78	58.58	0.61	0.50
t-c.	2.22	90.58			1.64	69.57		
t-c.	2.22	90.58	4.79	<0.001	1.64	69.57	4.35	<0.001
t-c.	1.14	34.02			0.72	40.08		
t-c.	0.98	48.98	0.87	0.4				
t-c.	1.14	34.02						
t-c.	1.28	52.08	0.75	0.45				
t-c.	1.14	34.02						

Table 22. Comparison of the per cent of control and light-exposed fish in the upper one-third of an 86 cm high tank at the particular light intensity (Values are based on 5 experiments of 10 counts each, at each light intensity).

Type of fish compared	0 ft-c.			0.04 ft-c.			0.2 ft-c.			1.0 ft-c.			5.0 ft-c.		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
Control	0.30			0.98			1.28			2.22			1.14		
		3.66	<0.001		12.25	<0.001		2.35	0.02		2.27	0.02		2.42	0.015
Light-exposed	0.77			3.96			1.78			1.64			0.72		

Table 23. Frequency distributions and averages of the numbers of control Salmo salar L. in each compartment at successive distances from the light source in a horizontal light gradient (Roman numerals are compartments at successive distances from the light source).

No. of fish	7½ Watt							100 Watt							300 Watt						
	Series I							Series I							Series I						
	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
0	6	22	22	28	14	10	4	27	27	11	15	14	13	5	33	44	38	43	30	11	0
1	13	11	14	13	19	11	2	4	13	19	27	11	23	15	8	6	18	14	19	9	3
2	6	12	7	6	10	25	26	2	3	10	7	8	4	12	17	8	3	3	8	9	4
3	14	5	7	2	6	4	12	6	6	6	1	5	5	15	2	0	1		3	17	7
4	8			1	1		5	7	1	0		7	3	1		0				8	13
5	0						1	4		1		5	2	2		2				2	15
6	3									3										2	5
7																				2	8
8																					5
9																					
10																					
Total	50	50	50	50	50	50	50	50	50	50	50	50	50	50	60	60	60	60	60	60	60
Average	2.34	1.00	0.98	0.70	1.22	1.46	2.30	1.48	0.82	1.60	0.88	1.90	1.36	1.96	0.80	0.50	0.45	0.33	0.73	2.43	4.75

Table 23 (Continued) - Series II

No. of fish	7½ Watt							100 Watt							300 Watt						
	Series II							Series II							Series II						
	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
0	43	302	234	221	140	12		46	288	100	126	71	6	0	27	234	90	152	61	87	0
1	156	238	193	254	256	99		280	185	280	237	134	75	6	131	199	314	239	149	160	0
2	349	92	83	126	125	197		186	82	184	155	162	143	36	314	152	133	185	308	263	16
3	81	7	105	39	66	269	17	80	44	36	74	180	279	195	125	39	96	24	99	98	135
4	11	1	23		46	56	190	8	1		8	34	82	156	36	11	7	34	20	24	131
5			2		7	7	186					19	13	65	7	5		6	33	7	200
6							96						2	95						1	129
7							60							11							26
8							65							3							3
9							26							8							
10														16							
11														4							
12																					
13																					
14																					
Total	640	640	640	640	640	640	640	600	600	600	600	600	600	600	640	640	640	640	640	640	640
Average	1.78	0.70	1.21	0.97	1.44	2.44	5.45	1.58	0.81	1.26	1.34	2.02	2.67	4.31	2.05	1.08	1.40	1.32	1.81	1.75	4.59

successive distances from the light source (Roman numerals are compartments at successive distances from the light source).

No. of fish	7½ Watt							100 Watt							300 Watt						
	Compartment							Compartment							Compartment						
	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
0	15	9	15	13	12	11	6	27	38	22	20	9	0	1	31	33	23	26	18	2	0
1	18	16	15	18	17	30	4	14	9	15	18	25	10	4	9	17	16	17	17	15	0
2	15	20	20	14	10	9	13	7	3	4	9	11	18	9	10		7	6	11	12	2
3	2	5		5	8		6	2		6	2	4	12	13			4	1	3	17	13
4					2		16			3	1	1	9	15					1	4	9
5					1		5						1	3							15
6														5							9
7																					2
8																					
9																					
10																					
Total	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50
Average	1.08	1.42	1.10	1.22	1.48	0.96	2.74	0.68	0.30	1.06	0.92	1.26	2.46	3.32	0.58	0.34	0.84	0.64	1.04	2.12	4.44

No. of fish	7½ Watt							100 Watt							300 Watt						
	Compartment							Compartment							Compartment						
	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
0	173	323	231	122	24	2	0	60	466	259	432	220	162	0	5	259	213	333	159	43	0
1	445	221	153	249	86	68	49	220	119	269	135	203	187	0	442	302	267	209	271	288	5
2	22	86	167	173	111	119	131	199	15	66	32	63	143	0	65	37	119	27	76	100	22
3		10	88	87	252	166	55	120		6	1	97	35	0	88	2	1	18	72	108	45
4			1	9	118	199	168	0				17	8	32				11	16	55	39
5					32	46	106	1					32	77				2	6	6	45
6					14	40	73						33	90							19
7					3		48							95							46
8							10							24							93
9														42							115
10														57							153
11														64							18
12														118							
13														1							
14																					
Total	640	640	640	640	640	640	640	600	600	600	600	600	600	600	640	640	640	640	640	640	640
Average	0.76	0.66	1.18	1.39	2.81	3.23	3.96	1.61	0.24	0.70	0.34	1.15	1.61	8.32	1.39	0.64	0.85	0.62	1.22	1.77	7.51

Compartments compared	7½ Watt						100 Watt						300 Watt					
	Series I			Series II			Series I			Series II			Series I			Series II		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
I II	2.34 1.00	4.96	<.001	1.78 0.70	24.6	<.001	1.48 0.82	2.16	.02	1.58 0.81	14.7	<.001	0.80 0.50	1.70	.10	2.05 1.08	17.3	<.001
II III	1.00 0.98	0.09	.999	0.70 1.21	10.0	<.001	0.82 1.60	2.88	<.01	0.81 1.26	8.89	<.001	0.50 0.45	0.33	.74	1.08 1.40	5.71	<.001
III IV	0.98 0.70	1.36	.20	1.21 0.97	3.94	<.001	1.60 0.88	3.06	<.01	1.26 1.34	1.54	.13	0.45 0.33	1.05	.30	1.40 1.32	1.40	.15
IV V	0.70 1.22	2.56	>.01	0.97 1.44	7.95	<.001	0.88 1.90	3.97	<.001	1.34 2.02	10.6	<.001	0.33 0.73	2.95	<.01	1.32 1.81	8.56	<.001
V VI	1.22 1.46	1.22	.20	1.44 2.44	16.4	<.001	1.90 1.36	1.75	.08	2.02 2.67	10.1	<.001	0.73 2.43	6.82	<.001	1.81 1.75	1.06	.30
VI VII	1.46 2.30	3.29	.001	2.44 5.45	42.6	<.001	1.36 1.96	2.34	.02	2.67 4.31	19.4	<.001	2.43 4.75	7.10	<.001	1.75 4.59	43.9	<.001
I VII	2.34 2.30	0.13	.999	1.78 5.45	54.0	<.001	1.48 1.96	1.53	.15	1.58 4.31	33.3	<.001	0.80 4.75	14.6	<.001	2.05 4.59	41.4	<.001
II VII	1.00 2.30	4.89	<.001	0.70 5.45	71.2	<.001	0.82 1.96	4.89	<.001	0.81 4.31	41.9	<.001	0.50 4.75	15.7	<.001	1.08 4.59	54.6	<.001
III VII	0.98 2.30	4.93	<.001	1.21 5.45	54.3	<.001	1.60 1.96	1.29	.20	1.26 4.31	37.7	<.001	0.45 4.75	16.8	<.001	1.40 4.59	52.0	<.001
IV VII	0.70 2.30	6.15	<.001	0.97 5.45	64.6	<.001	0.88 1.96	5.66	<.001	1.34 4.31	35.3	<.001	0.33 4.75	15.9	<.001	1.32 4.59	50.1	<.001
V VII	1.22 2.30	4.06	<.001	1.44 5.45	52.4	<.001	1.90 1.96	0.20	.85	2.02 4.31	25.6	<.001	0.73 4.75	15.1	<.001	1.81 4.59	48.5	<.001

at successive distances from the light source. (Values are numbers of fish in each compartment. Roman numerals refer to compartments).

Compartments compared	7½ Watt						100 Watt						300 Watt					
	Series I			Series II			Series I			Series II			Series I			Series II		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
I	1.08	1.91	.05	0.76	2.76	<.01	0.68	2.5	>.01	1.61	31.1	<.001	0.58	1.80	.07	1.39	17.0	<.001
II	1.42			0.66			0.30			0.24			0.34			0.64		
II	1.42	1.83	.07	0.66	9.96	<.001	0.30	3.88	<.001	0.24	12.9	<.001	0.34	3.31	.001	0.64	5.26	<.001
III	1.10			1.18			1.06			0.70			0.84			0.85		
III	1.10	0.67	.50	1.18	3.64	<.001	1.06	.63	.54	0.70	9.5	<.001	0.84	1.15	.25	0.85	4.78	<.001
IV	1.22			1.39			0.92			0.34			0.64			0.62		
IV	1.22	1.17	.25	1.39	22.0	<.001	0.92	1.85	.05	0.34	14.9	<.001	0.64	2.23	.02	0.62	10.1	<.001
V	1.48			2.81			1.26			1.15			1.04			1.22		
V	1.48	2.62	<.01	2.81	5.8	<.001	1.26	4.96	<.001	1.15	60.2	<.001	1.04	5.22	<.001	1.22	8.22	<.001
VI	0.96			3.23			2.46			1.61			2.12			1.77		
VI	0.96	7.57	<.001	3.23	8.35	<.001	2.46	2.97	<.01	1.61	5.46	<.001	2.12	9.87	<.001	1.77	48.2	<.001
VII	2.74			3.96			3.32			8.32			4.44			7.51		
I	1.08	6.63	<.001	0.76	43.9	<.001	0.68	11.1	<.001	1.61	50.8	<.001	0.58	18.0	<.001	1.39	54.1	<.001
VII	2.74			3.96			3.32			8.32			4.44			7.51		
II	1.42	5.23	<.001	0.66	43.3	<.001	0.30	13.8	<.001	0.24	58.8	<.001	0.34	21.2	<.001	0.64	61.3	<.001
VII	2.74			3.96			3.32			8.32			4.44			7.51		
III	1.10	6.62	<.001	1.18	33.9	<.001	1.06	8.37	<.001	0.68	69.6	<.001	0.84	15.9	<.001	0.85	58.9	<.001
VII	2.74			3.96			3.32			8.32			4.44			7.51		
IV	1.22	5.95	<.001	1.39	32.1	<.001	0.92	9.84	<.001	0.34	66.4	<.001	0.64	17.9	<.001	0.62	59.9	<.001
VII	2.74			3.96			3.32			8.32			4.44			7.51		
V	1.48	4.50	<.001	2.81	13.3	<.001	1.26	8.72	<.001	1.15	65.4	<.001	1.04	14.7	<.001	1.22	53.7	<.001
VII	2.74			3.96			3.32			8.32			4.44			7.51		

Lights Compared	I $\bar{X}$	I t	I P	II $\bar{X}$	II t	II P	III $\bar{X}$	III t	III P	IV $\bar{X}$	IV t	IV P	V $\bar{X}$	V t	V P	VI $\bar{X}$	VI t	VI P	VII $\bar{X}$	VII t	VII P
7½ watt	2.34	2.8	<.01	1.00	.80	.40	0.98	2.3	.02	0.76	.70	.50	1.22	2.4	.02	1.46	0.4	.70	2.30	1.2	.2
100 watt	1.48			0.82			1.60			0.88			1.90			1.36			1.96		
100 watt	1.48	2.5	.01	0.82	1.5	.10	1.60	5.1	<.001	0.88	4.9	<.001	1.90	4.6	<.001	1.36	3.6	<.001	1.96	9.1	<.001
300 watt	0.80			0.50			0.45			0.33			0.73			2.43			4.75		
7½ watt	2.34	6.2	<.001	1.00	2.6	<.01	0.98	3.1	.001	0.76	2.9	<.01	1.22	2.7	<.01	1.46	3.6	<.001	2.30	7.4	<.001
300 watt	0.80			0.50			0.45			0.33			0.73			2.43			4.75		

Lights Compared	I $\bar{X}$	I t	I P	II $\bar{X}$	II t	II P	III $\bar{X}$	III t	III P	IV $\bar{X}$	IV t	IV P	V $\bar{X}$	V t	V P	VI $\bar{X}$	VI t	VI P	VII $\bar{X}$	VII t	VII P
7½ watt	1.78	3.8	<.001	0.70	2.3	.02	1.21	.95	.30	0.97	7.0	<.001	1.44	8.4	<.001	2.44	4.2	<.001	5.45	12.0	<.001
100 watt	1.58			0.81			1.26			1.34			2.02			2.67			4.31		
100 watt	1.58	9.1	<.001	0.81	4.7	<.001	1.26	2.8	.001	1.34	.30	.70	2.02	3.4	<.001	2.67	16.7	<.001	4.31	4.3	<.001
300 watt	0.80			1.08			1.40			1.32			1.81			1.75			4.59		
7½ watt	1.78	5.5	<.001	0.70	7.4	<.001	1.21	3.1	.001	0.97	6.3	<.001	1.44	6.1	<.001	2.44	12.2	<.001	5.45	11.2	<.001
300 watt	0.80			1.08			1.40			1.32			1.81			1.75			4.59		

Table 27. Comparisons and statistical analyses of the numbers of Salmo salar L. in each successive compartment at the three different watts used (Roman numerals refer to compartments). Series I - top table. Series II - bottom table. - Light-exposed fish.

Lights Compared	I			II			III			IV			V			VI			VII		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
7½ watt	1.08	2.3	.02	1.42	7.4	<.001	1.10	.2	.85	1.22	1.6	.12	1.48	1.0	.30	0.96	6.6	<.001	2.74	1.9	.06
100 watt	0.68			0.30			1.06			0.92			1.26			2.46			3.32		
100 watt	0.68	0.6	.55	0.30	0.4	.70	1.06	1.0	.30	0.92	1.6	.12	1.26	1.2	.18	2.46	1.3	.20	3.32	4.1	<.001
300 watt	0.58			0.34			0.84			0.64			1.04			2.12			4.44		
7½ watt	1.08	3.0	<.01	1.42	7.4	<.001	1.10	1.4	.15	1.22	3.3	.001	1.48	1.9	.07	0.96	6.6	<.001	2.74	6.0	<.001
300 watt	0.58			0.34			0.84			0.64			1.26			2.12			4.44		

Lights Compared	I			II			III			IV			V			VI			VII		
	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P	$\bar{X}$	t	P
7½ watt	0.76	23	<.001	0.66	13	<.001	1.18	10	<.001	1.39	25	<.001	2.81	26	<.001	3.23	21	<.001	3.96	38	<.001
100 watt	1.61			0.24			0.70			0.34			1.15			1.61			8.32		
100 watt	1.61	4.5	<.001	0.24	12	<.001	0.70	3.5	<.001	0.34	6.3	<.001	1.15	1.0	.30	1.61	1.9	.06	8.32	5.2	<.001
300 watt	1.39			0.64			0.85			0.62			1.22			1.77			7.51		
7½ watt	0.76	20	<.001	0.66	.57	.56	1.18	6.9	<.001	1.39	16	<.001	2.81	26	<.001	3.23	23	<.001	3.96	31	<.001
300 watt	1.39			0.64			0.85			0.62			1.22			1.77			7.51		

successive compartment of the light gradient tank. (Roman numerals refer to compartments). (Series I - top table. Series II - bottom table).

Type of fish compared	7½ Watt							100 Watt							300 Watt						
	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
Control	2.34	1.00	0.98	0.70	1.22	1.46	2.30	1.48	0.82	1.60	0.86	1.90	1.36	1.96	0.80	0.50	0.45	0.33	0.73	2.43	4.75
Light-exposed	1.08	1.42	1.10	1.22	1.48	0.96	2.74	0.68	0.30	1.06	0.92	1.26	2.46	3.32	0.58	0.34	0.84	0.64	1.04	2.12	4.44
t	4.9	2.1	.62	2.7	1.1	3.1	1.4	2.7	3.0	2.0	.25	2.3	4.0	5.1	1.3	1.1	2.5	2.4	1.7	1.1	.99
P	<.001	.03	,55	<.01	.30	.001	.15	<.01	<.01	.05	.80	.02	<.001	<.001	.20	.30	.01	.02	.08	.30	.30

Series II

Type of fish compared	7½ Watt							100 Watt							300 Watt						
	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
Control	1.78	0.70	1.21	0.97	1.44	2.44	5.45	1.58	0.81	1.26	1.34	2.02	2.67	4.31	2.05	1.08	1.40	1.32	1.81	1.75	4.59
Light-exposed	0.76	0.66	1.18	1.39	2.81	3.23	3.96	1.61	0.24	0.70	0.34	1.15	1.61	8.32	1.39	0.64	0.85	0.62	1.22	1.77	7.51
t	27	.94	.46	8.0	20	12	16	.58	13	2.7	21	12	13	30	14	8.8	11	12	10	.31	26
P	<.001	.32	.65	<.001	<.001	<.001	<.001	.55	<.001	<.01	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	.75	<.001

Legend for Figure 1 and Figure 2

a. Reservoir tank

b. Overflow pipe in reservoir

c. Refrigeration plate

d. Refrigeration pipe

e. Refrigeration motor

f. Refrigeration fan

g. Wall

h. Plastic pipe draining first three holding tanks

i. Plastic pipe draining remaining three holding tanks

j. Plastic pipe from reservoir to pump

k. Pump

l. Pump-motor

m. Holding tank

n. Screen to keep fish from overflow end

o. Overflow pipe

p. Plastic pipe joining overflow pipe and drainage duct

q. Hose supplying water to holding tanks

r. Stand supporting pump

s. Bench supporting holding tanks

t. Copper pipe conducting air to valve

u. Glass pipe to tap off air to holding tanks

v. Valve controlling air supply

w. Light shade supporting lights over holding tanks

x. Flourescent light bulb

y. Air-stone

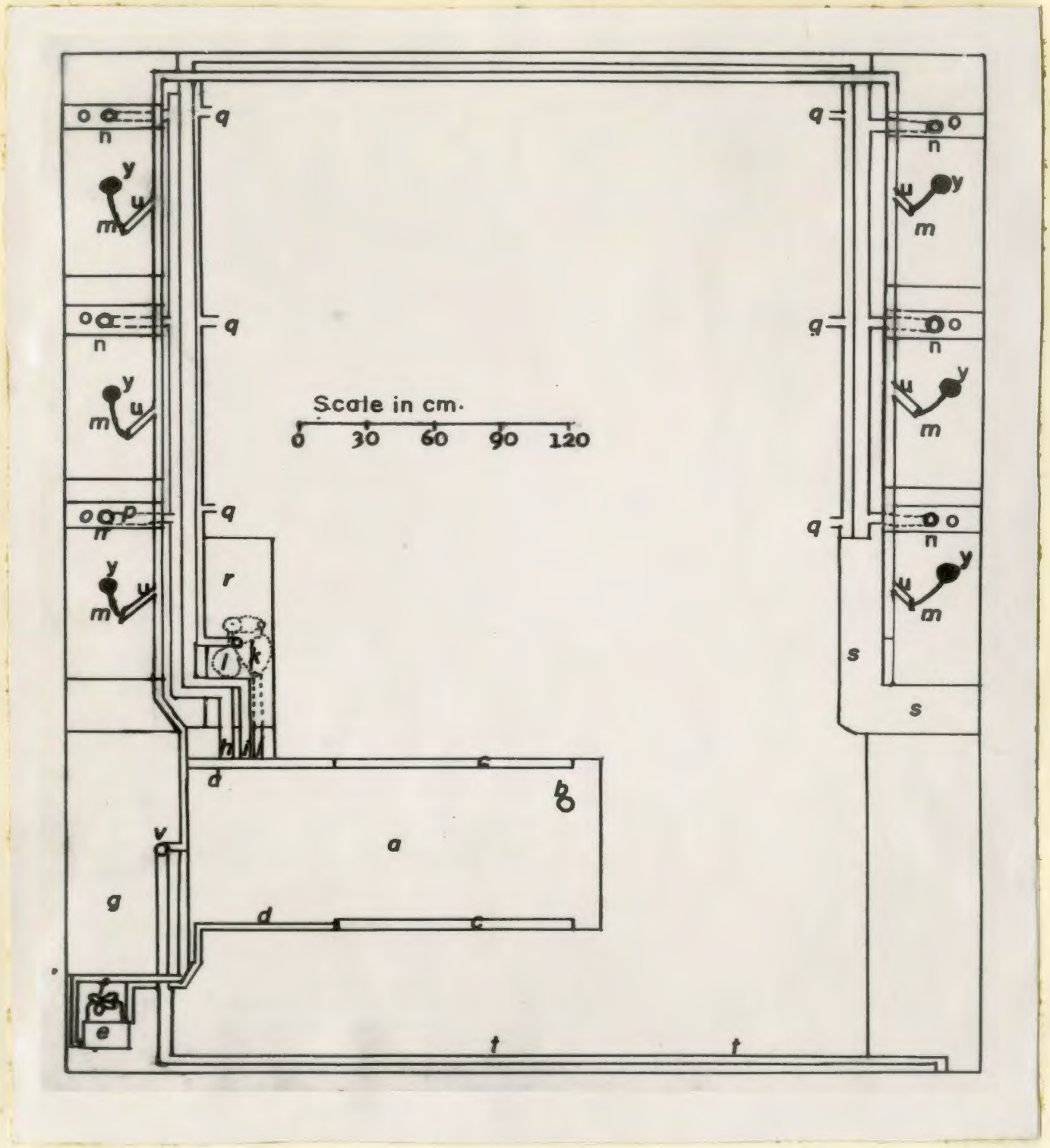


Figure 1. Diagram of tanks and associated apparatus for holding Salmo salar L. during the experimental study of behaviour patterns (Top view to show general layout).

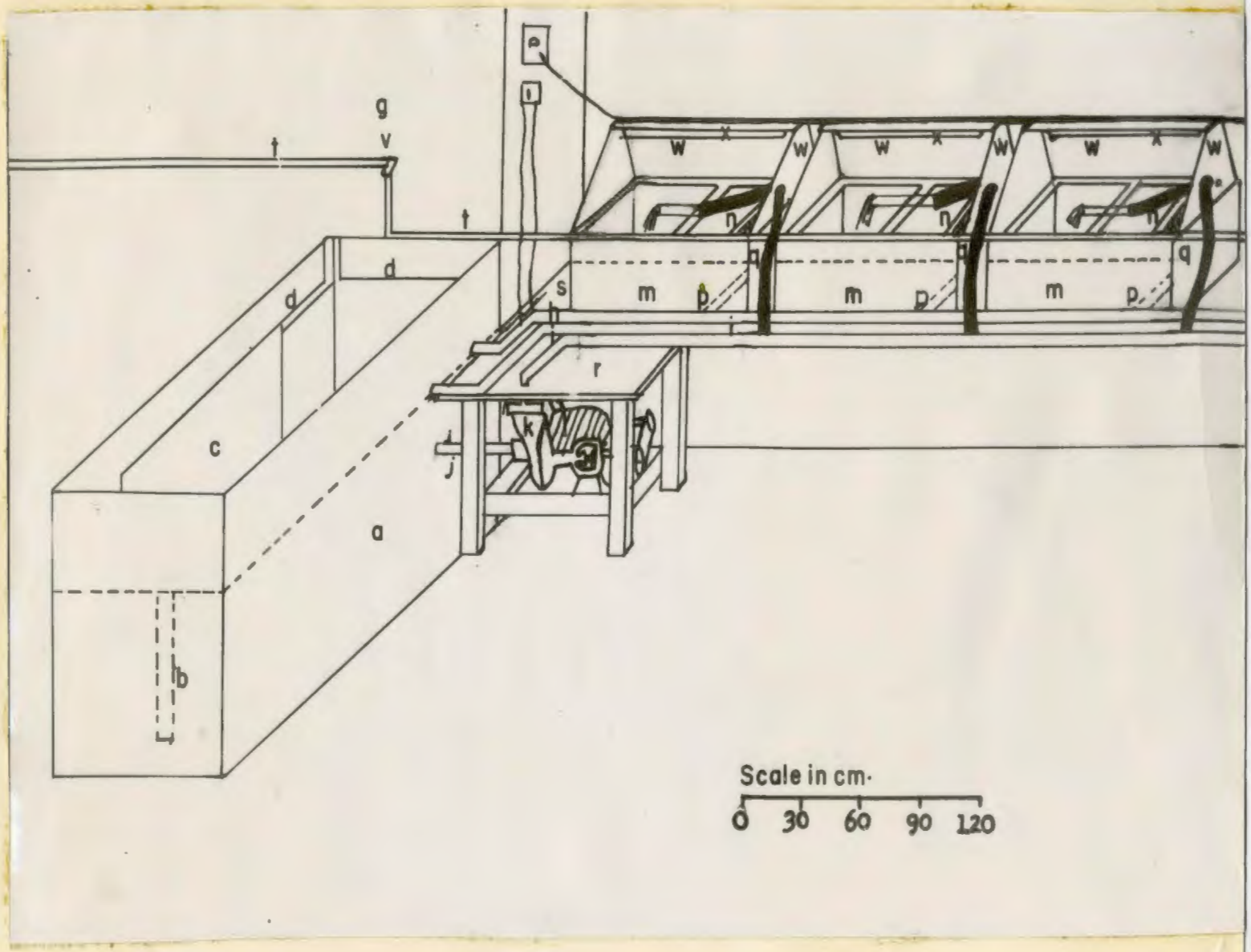


Figure 2. Diagram of a section of the apparatus for holding Salmo salar L. during the experimental study of behaviour patterns (Side view to show details of circulating water system and lighting system).

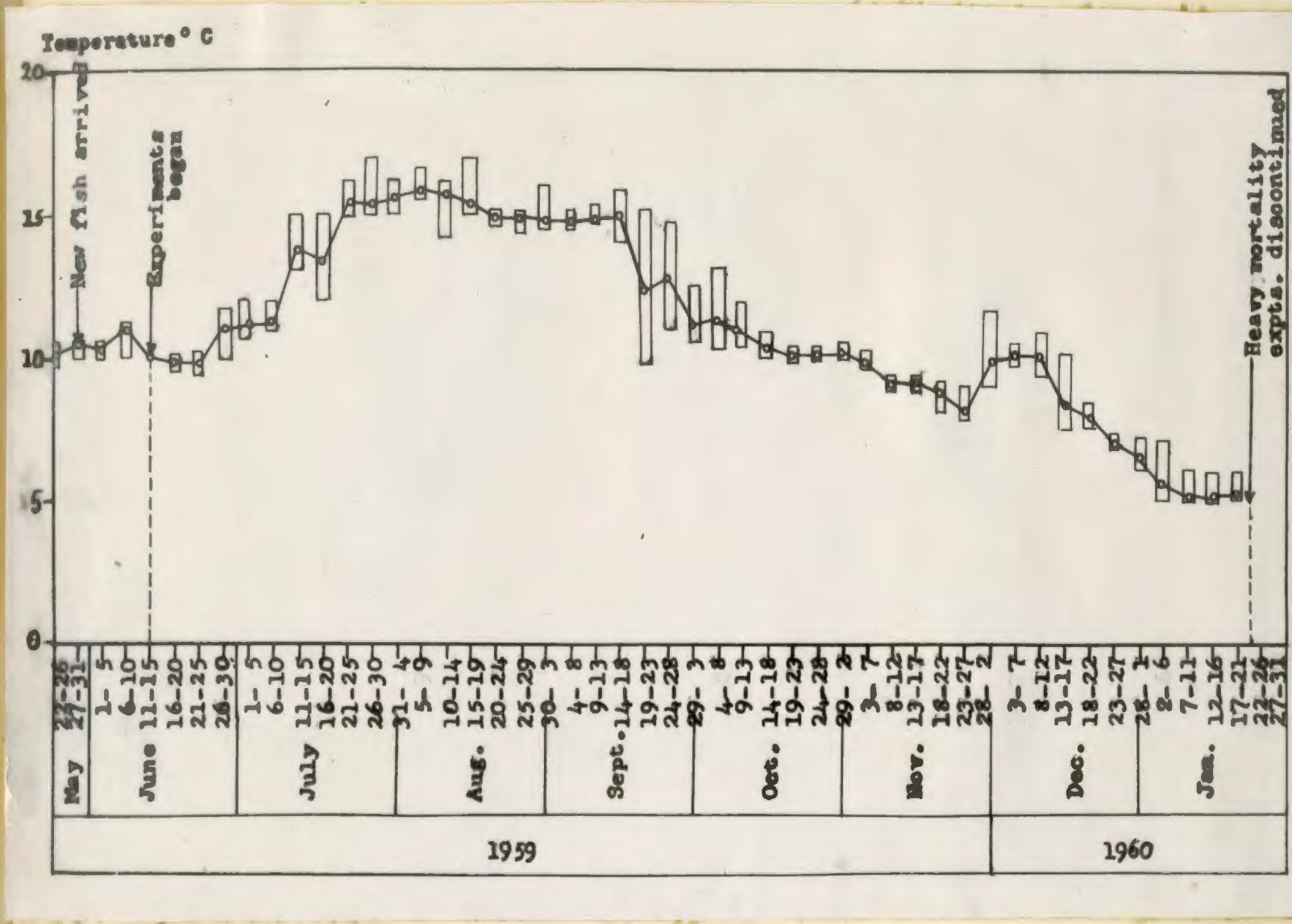


Figure 3. Variations in temperatures of water in holding tanks during experiments with Salmo salar L., 1959-1960 (Open circles are average temperatures during each five day period; rectangles are ranges of temperatures during each five day period).

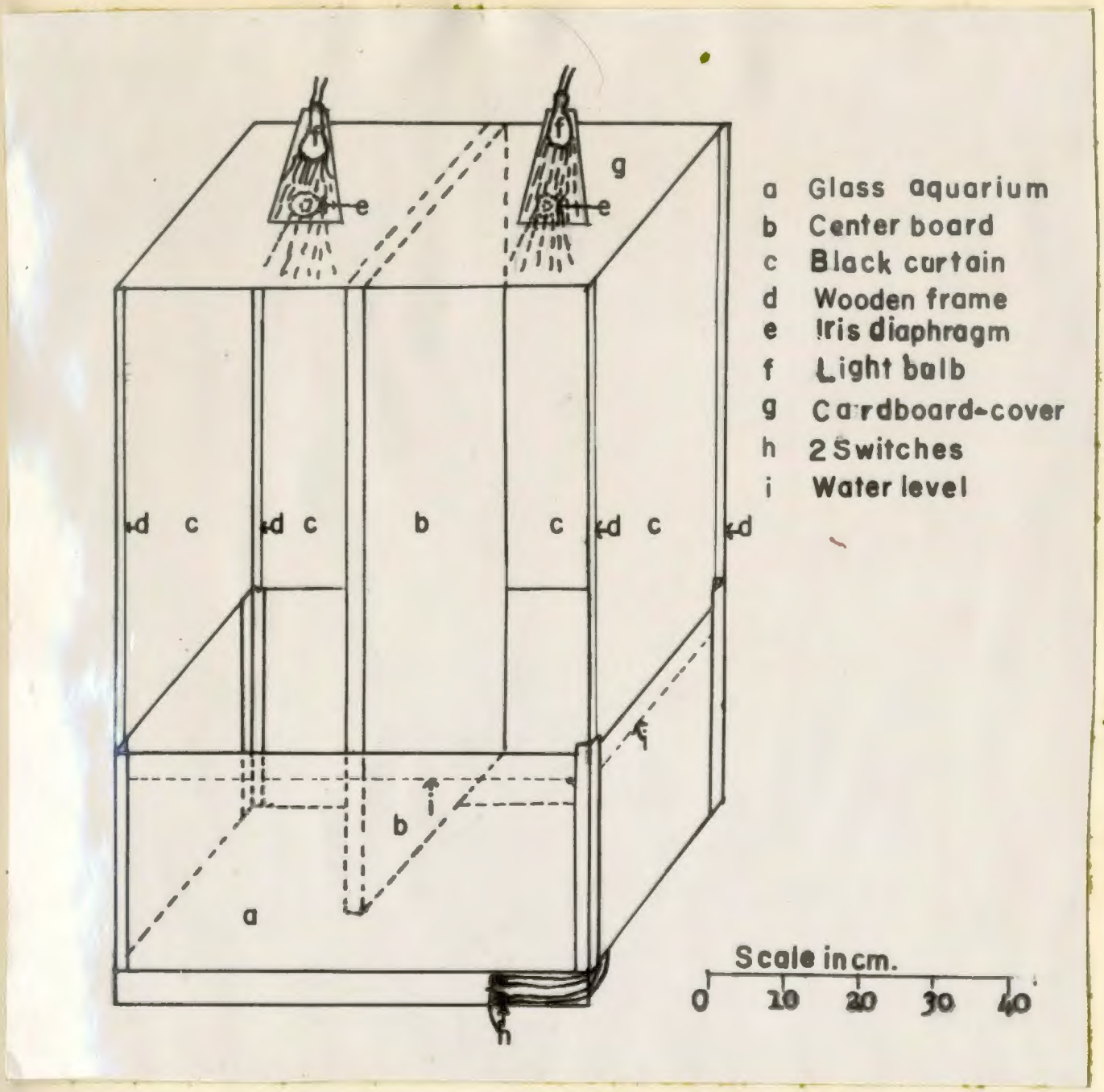


Figure 4. Diagram of apparatus used in positive-negative phototaxis experiments (Series I) with Salmo salar L.

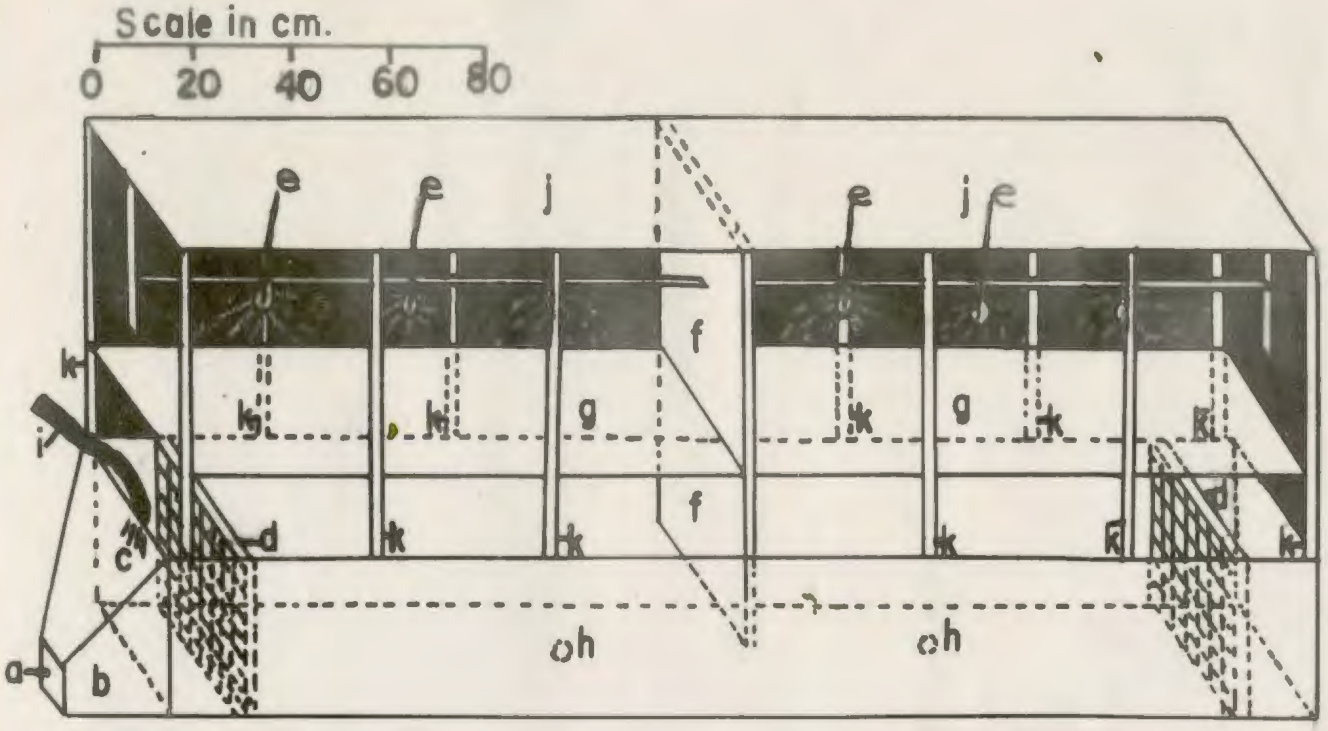
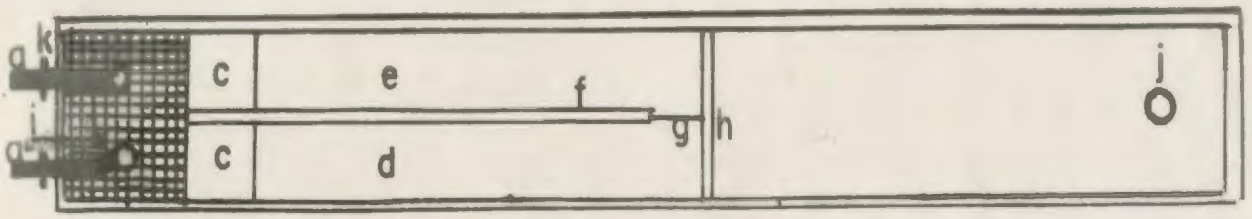
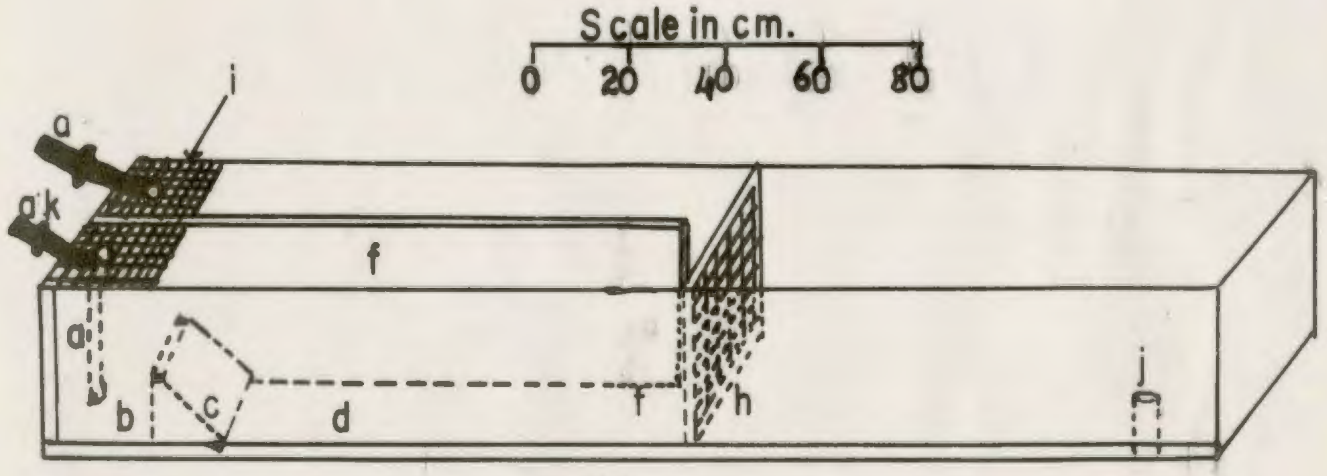


Figure 5. Diagram of apparatus used in positive-negative phototaxis experiments (Series II) with Salmo salar L.



(a)

a Inflow tube
b Resevoir
c Ramp
d Right channel
e Left channel
f Partition
g Line dividing common chamber
h Screen
i Wire screen for holding tubes
j Overflow pipe
k Clamp



(b)

Figure 6. Diagrams of tank used in experiments on current preference of Salmo salar L. (a) Top view (b) Side view.

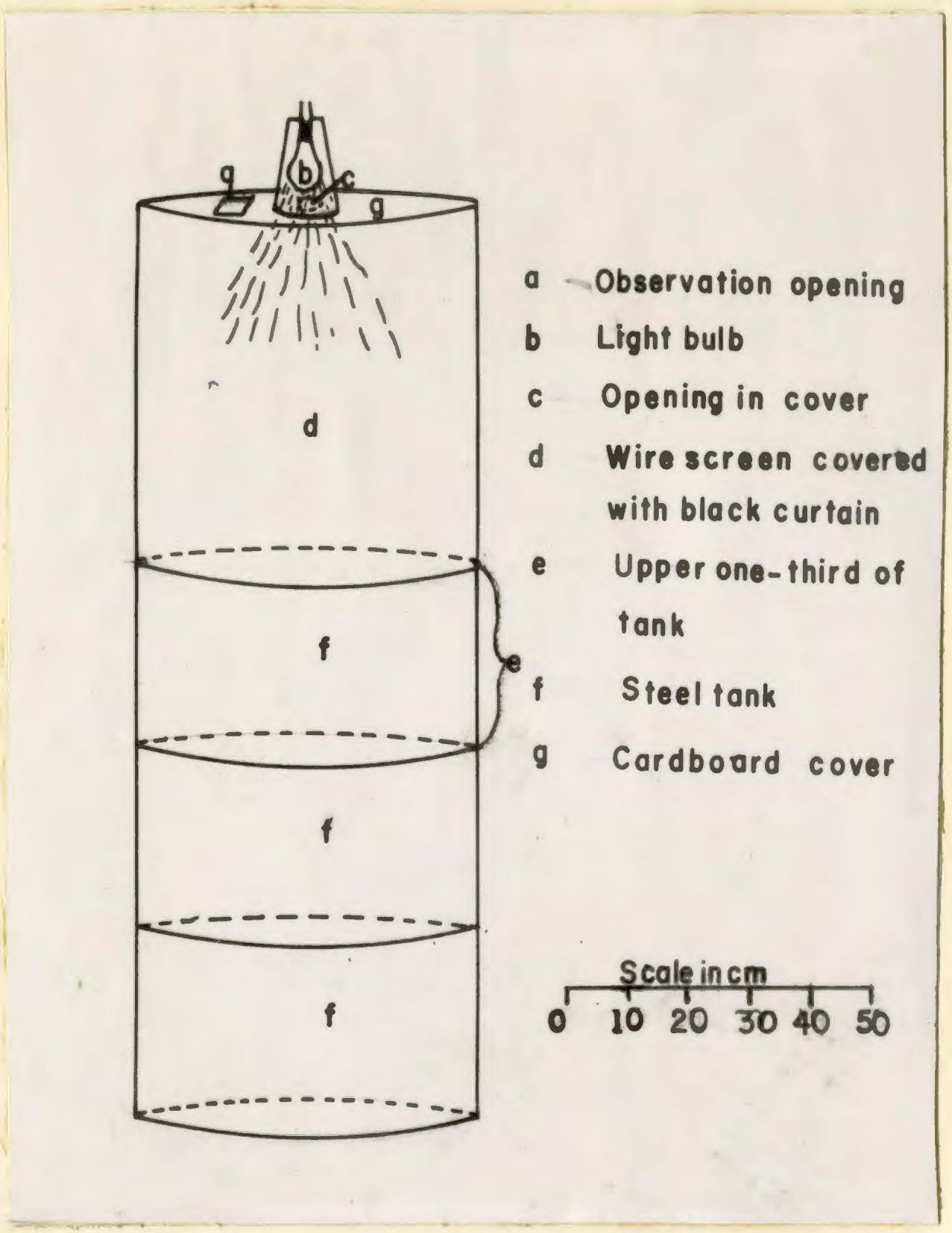


Figure 7. Diagram of apparatus used in surfacing experiments with Salmo salar L.

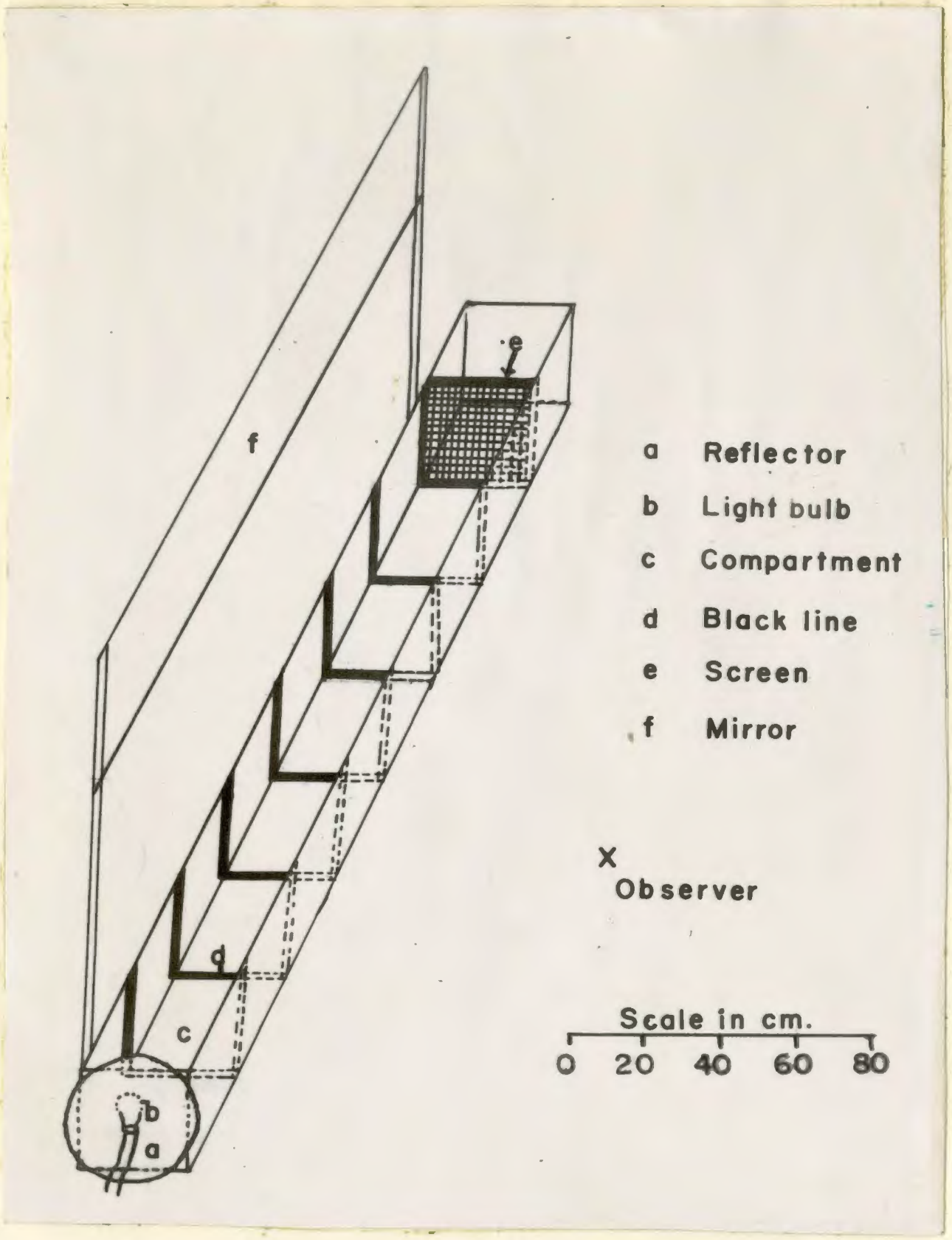


Figure 8. Diagram of apparatus used in light gradient experiments with Salmo salar L.

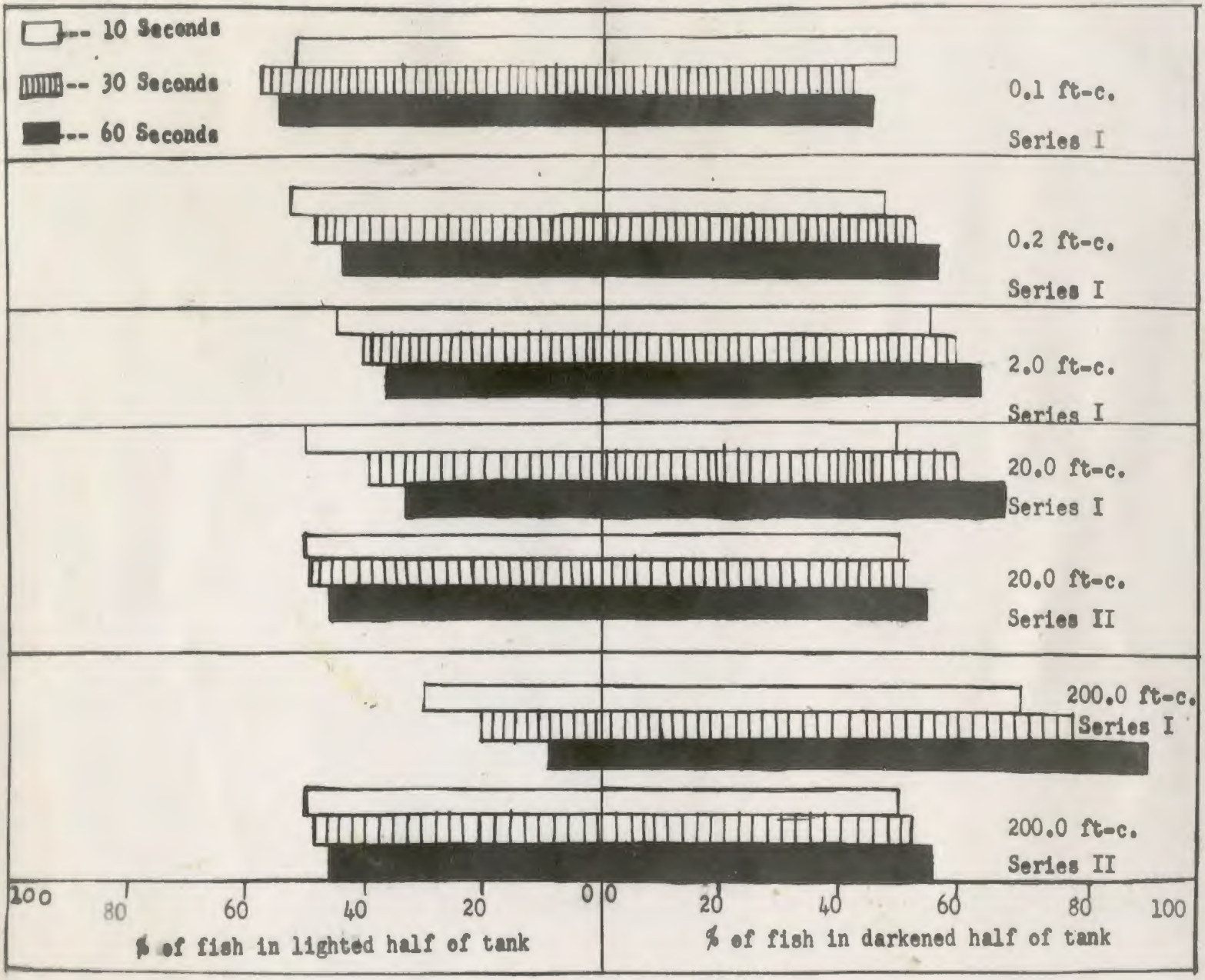


Figure 9. Reactions of Salmo salar L. (control) to a light stimulus of various intensities (See text for definition of Series I and Series II and explanation of 10, 30, and 60 seconds. Acclimation temperature ^{o}C-- Series I - 15.0, Series II - 10.0-5.0).

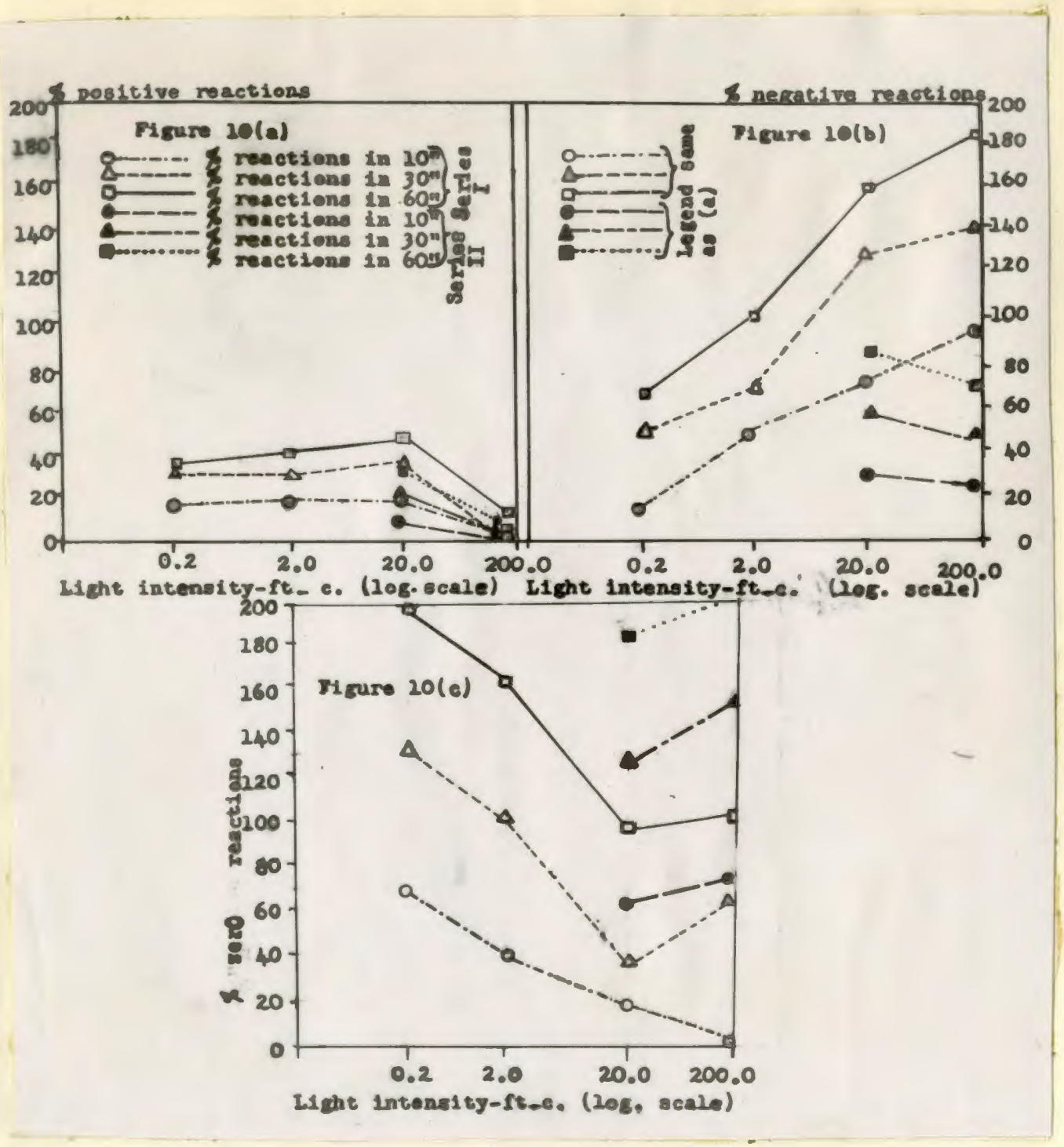


Figure 10. Graphs showing variations in reactions of control Salmo salar L. to a light stimulus of various intensities (The legend is the same for all three figures. Figure 10(a)--positive reactions; Figure 10(b)--negative reactions; Figure 10(c)--zero reactions. Acclimation temperature °C.-- Series I - 15.0, Series II - 10.0-5.0).

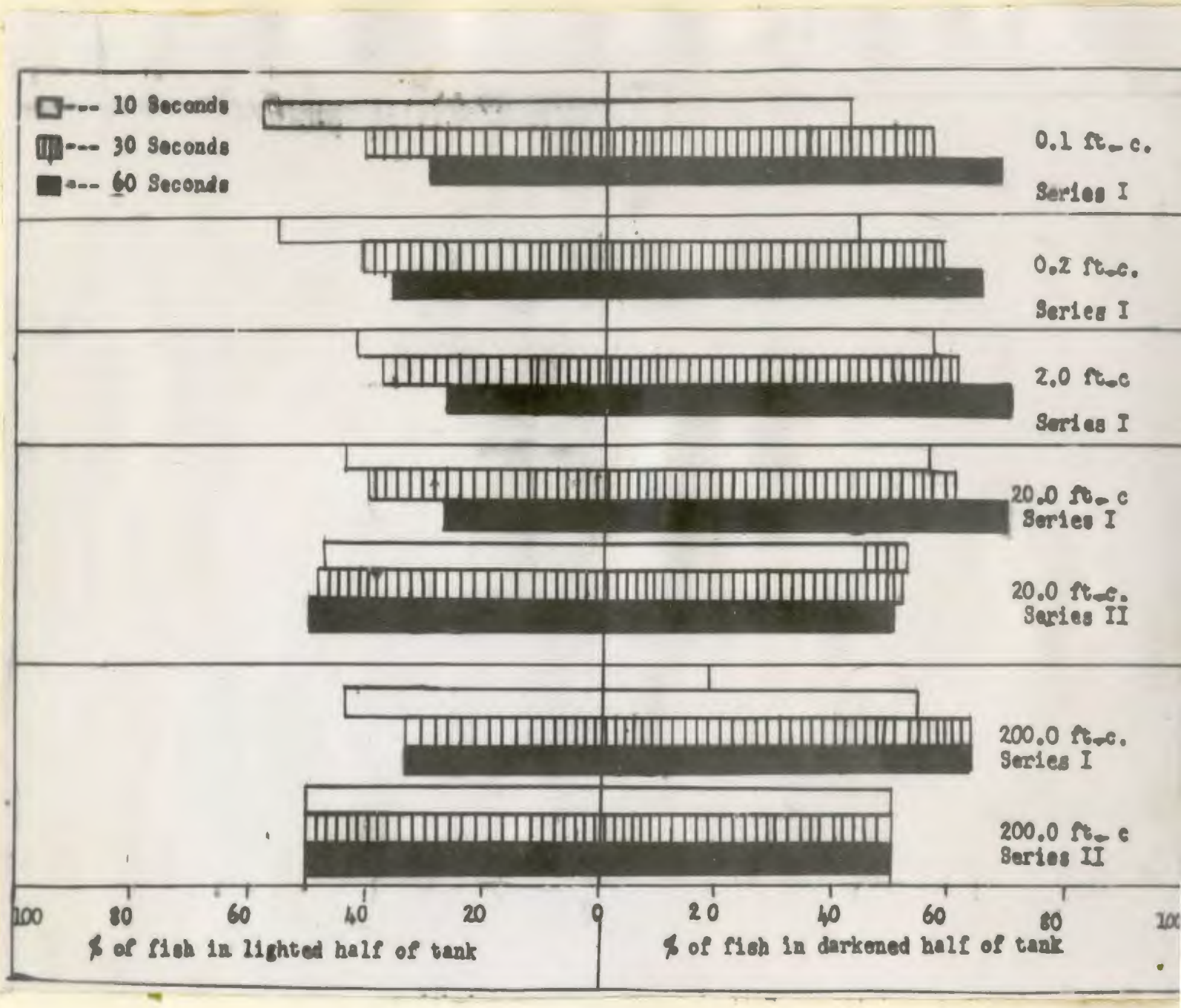


Figure 11. Reactions of Salmo salar L. (light-exposed) to a light stimulus of various intensities (See text for definition of Series I and Series II and explanation of 10, 30, and 60 seconds. Acclimation temperature °C. -- Series I - 15.0, Series II - 10.0-5.0).

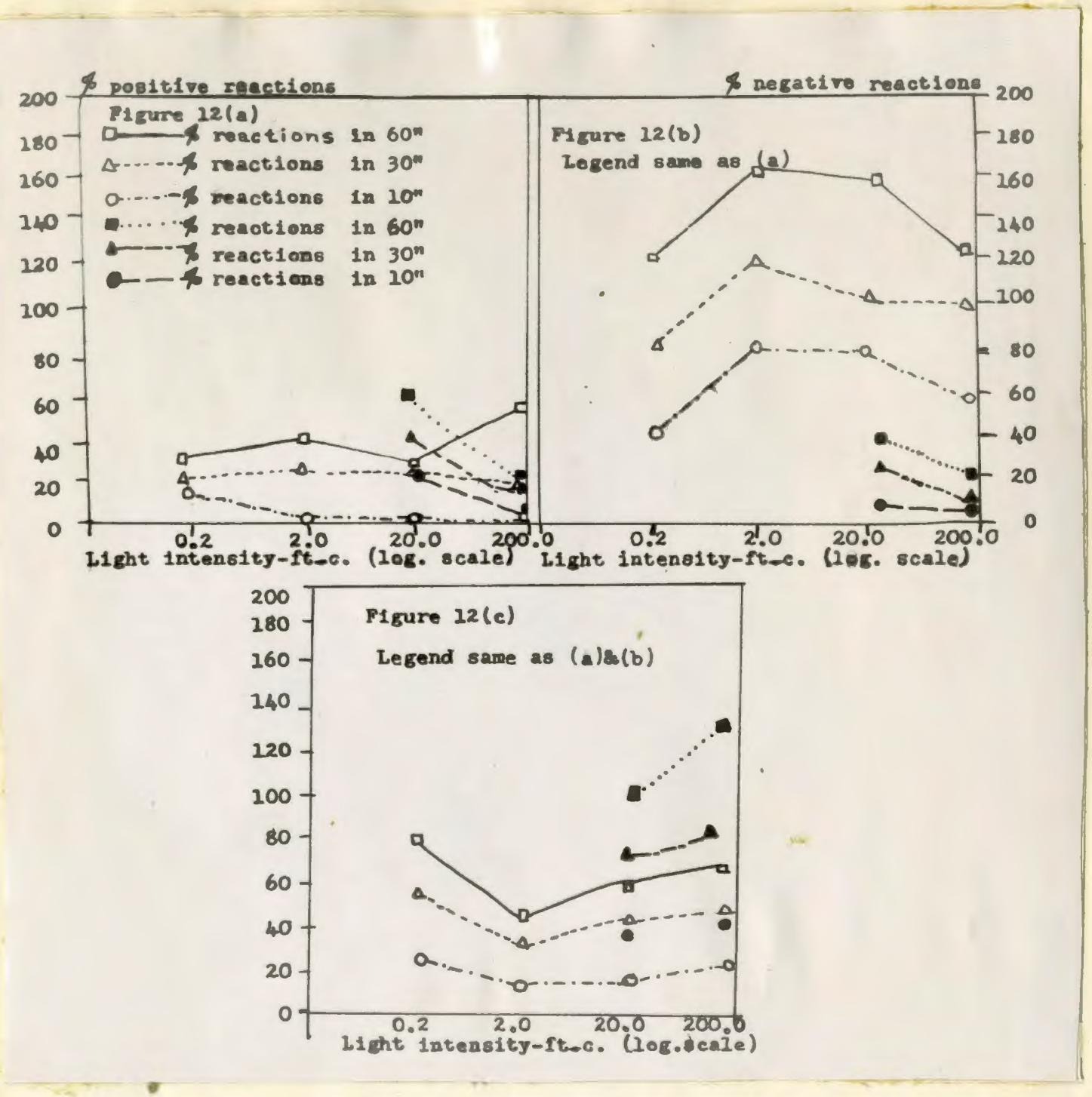


Figure 12. Graphs showing variations in reactions of light-exposed Salmo salar L. to a light stimulus of various intensities (The legend is the same for all three figures. Figure 12(a)-positive reactions, Figure 12(b)-negative reactions, Figure 12(c)-zero reactions. Acclimation temperature ^{o} C. -- Series I - 15.0, Series II - 10.0-5.0).

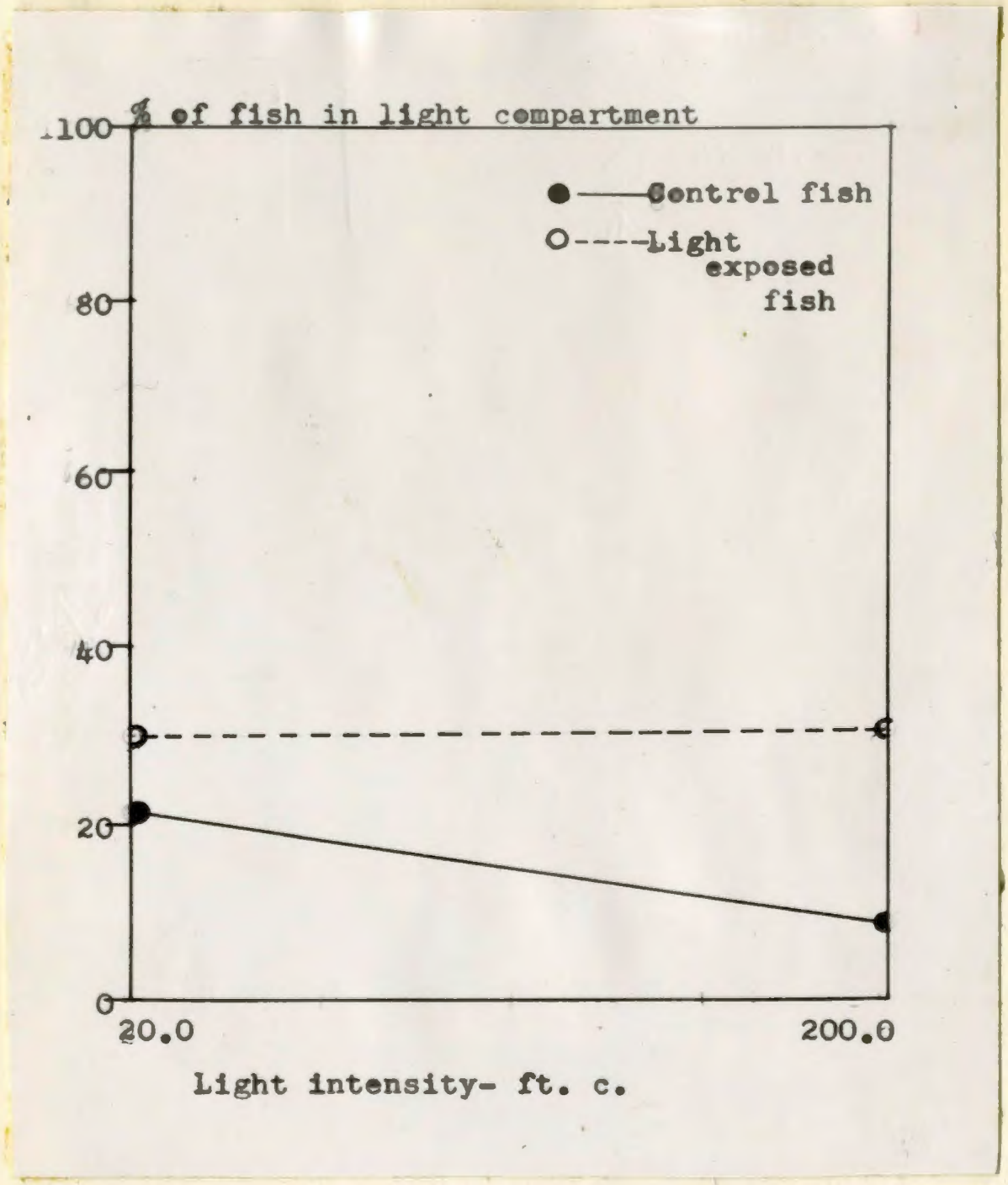


Figure 13. Graphs showing reactions of control and light-exposed fish to continuous light. Acclimation temperature° C. -- 10.0-5.0.

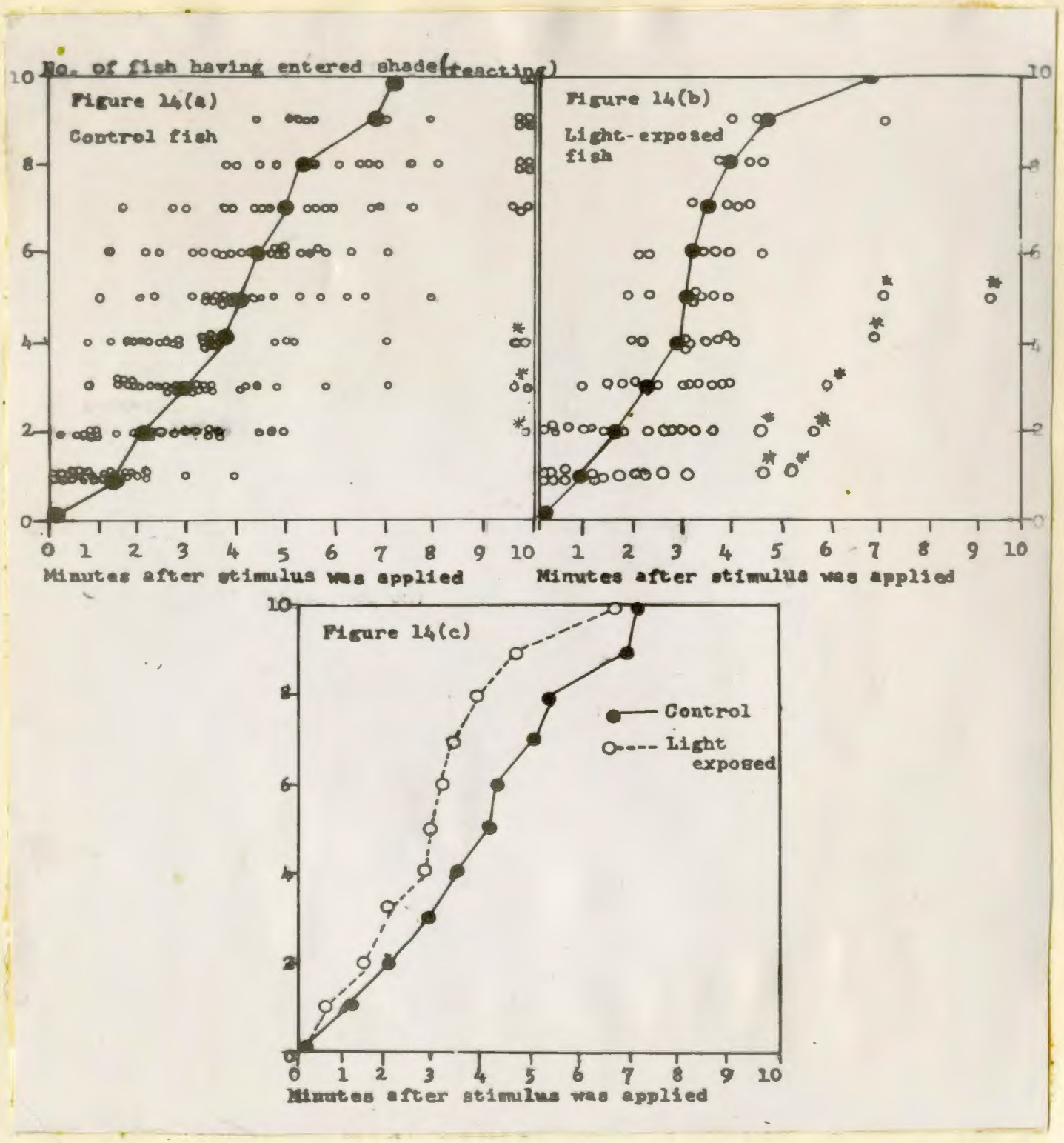


Figure 14. Graphs showing reaction times of Salmo salar L. to a light stimulus (Open circles are averages of individual experiments; solid circles are averages of the total experiments. Stimulus was applied by suddenly exposing fish to 200.0 ft-c).

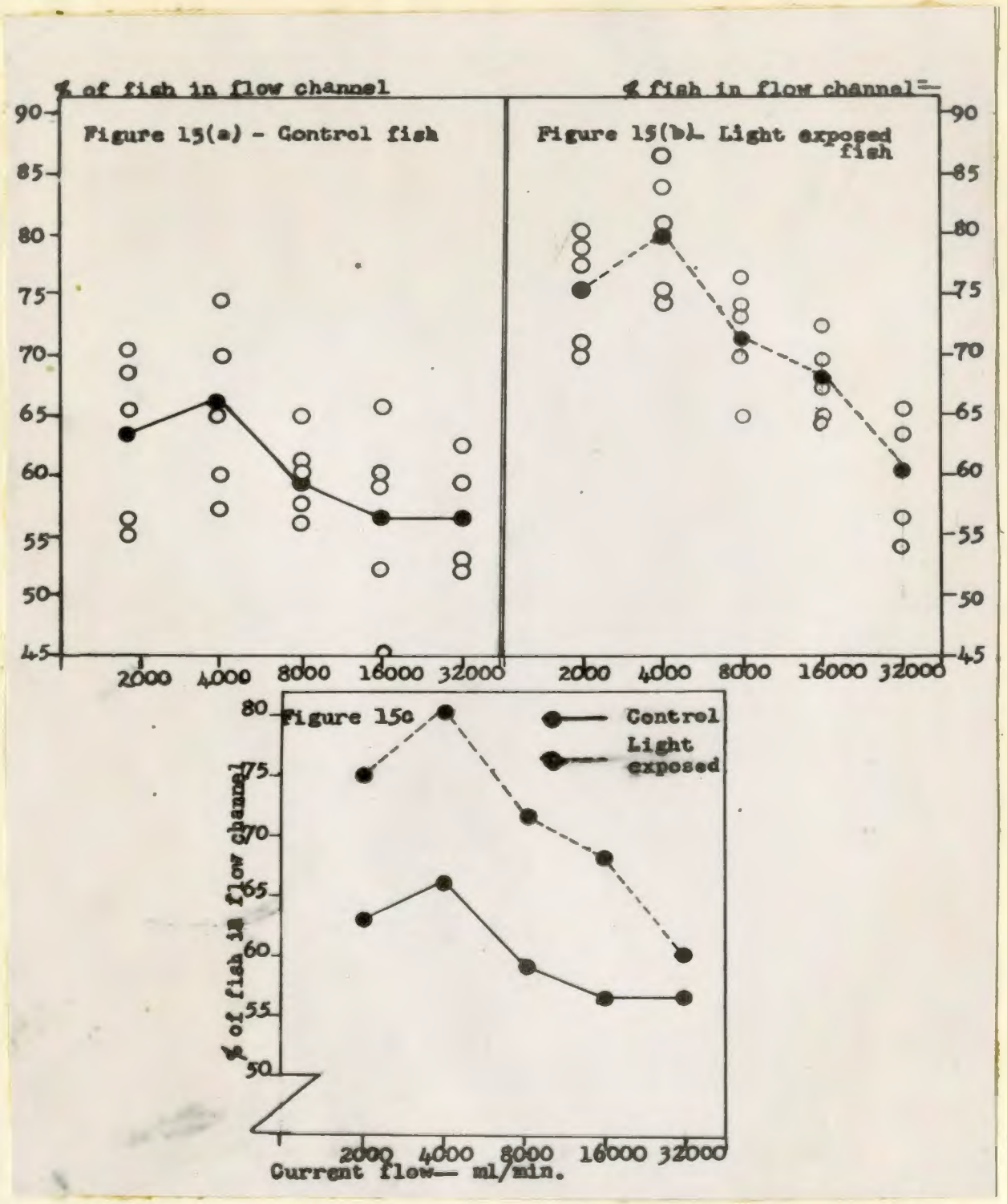


Figure 15. Preference of Salmo salar L. for water currents of various intensities (Open circles - averages of individual experiments; solid circles - averages of the total experiments. Currents are ml/min of water flowing into the upper reservoir of experimental tank. Acclimation temperature °C.-15

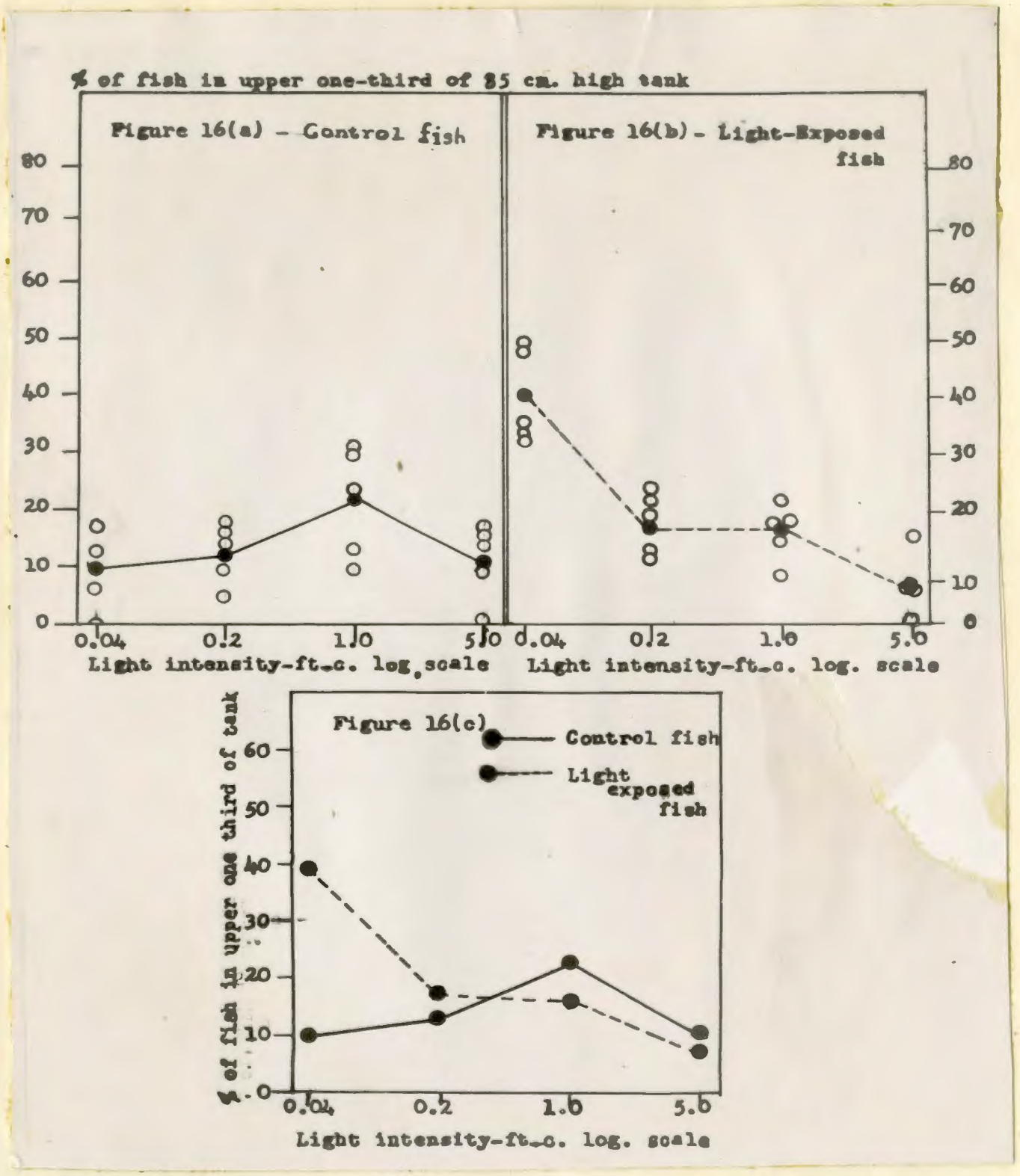


Figure 16. Surfacing reaction of Salmo salar L. (vertical distribution in a vertical light gradient) (Open circles - averages of individual experiments; solid circles - averages of the total experiments. Acclimation temperature ^{o} C.---15.0).

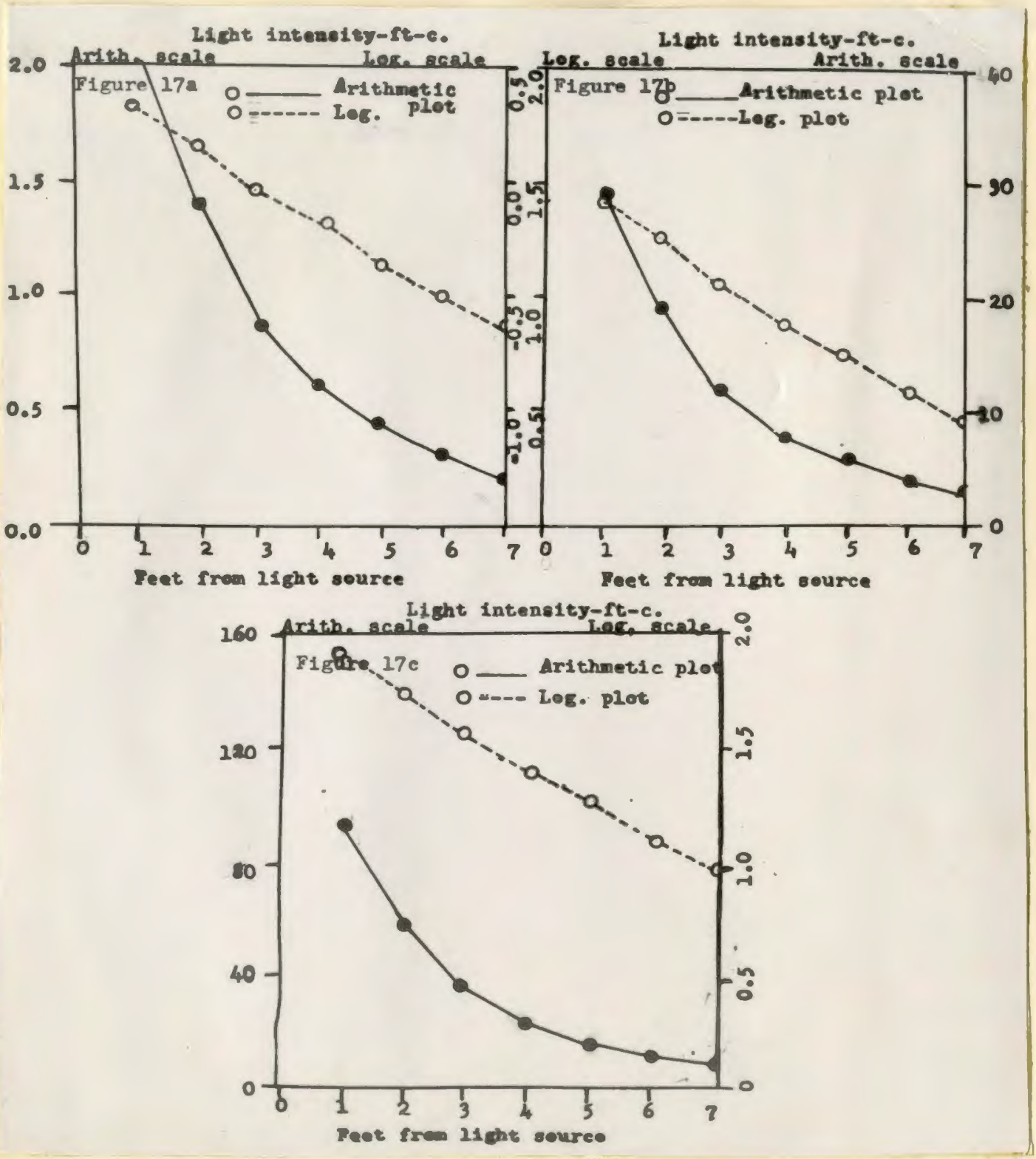
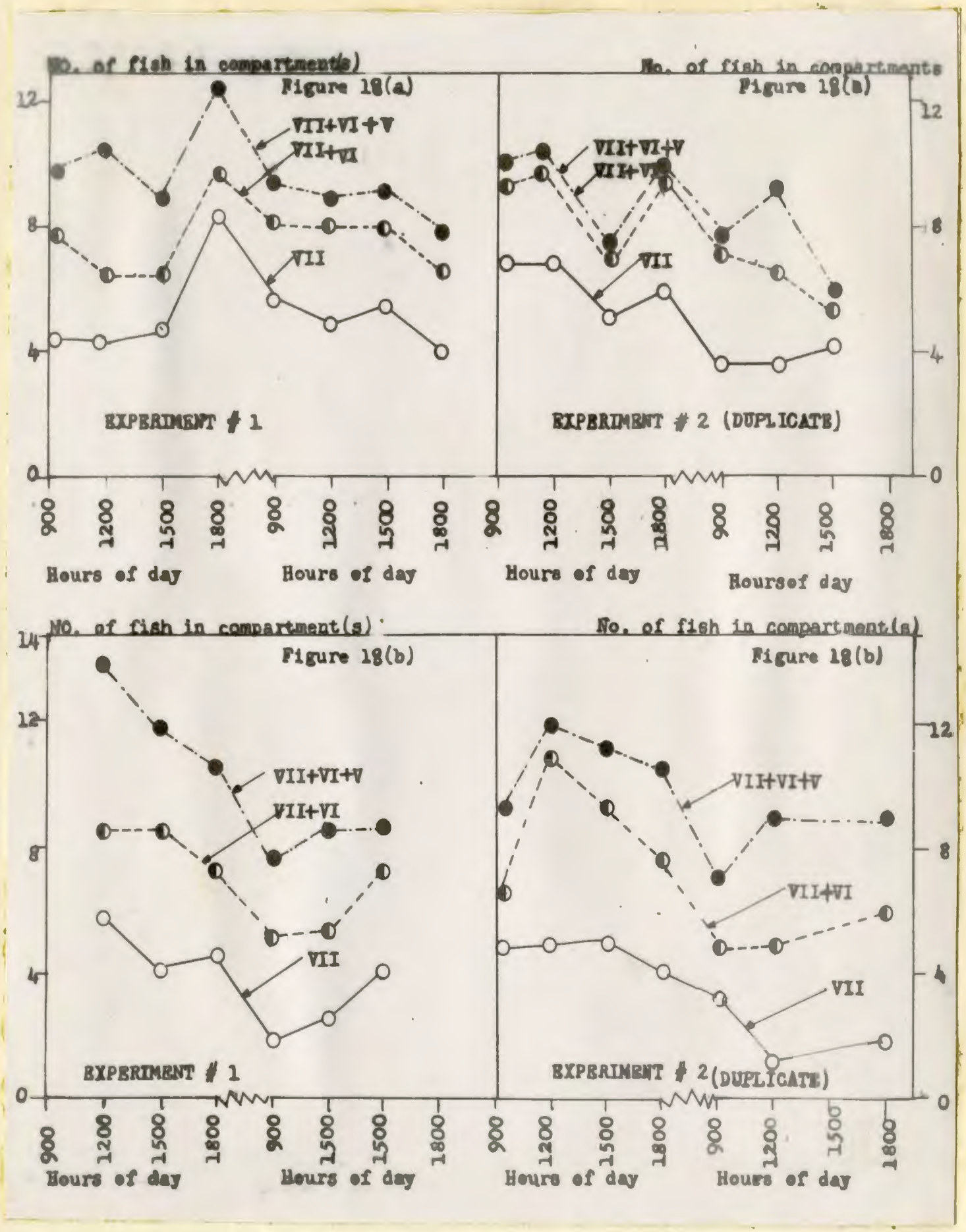
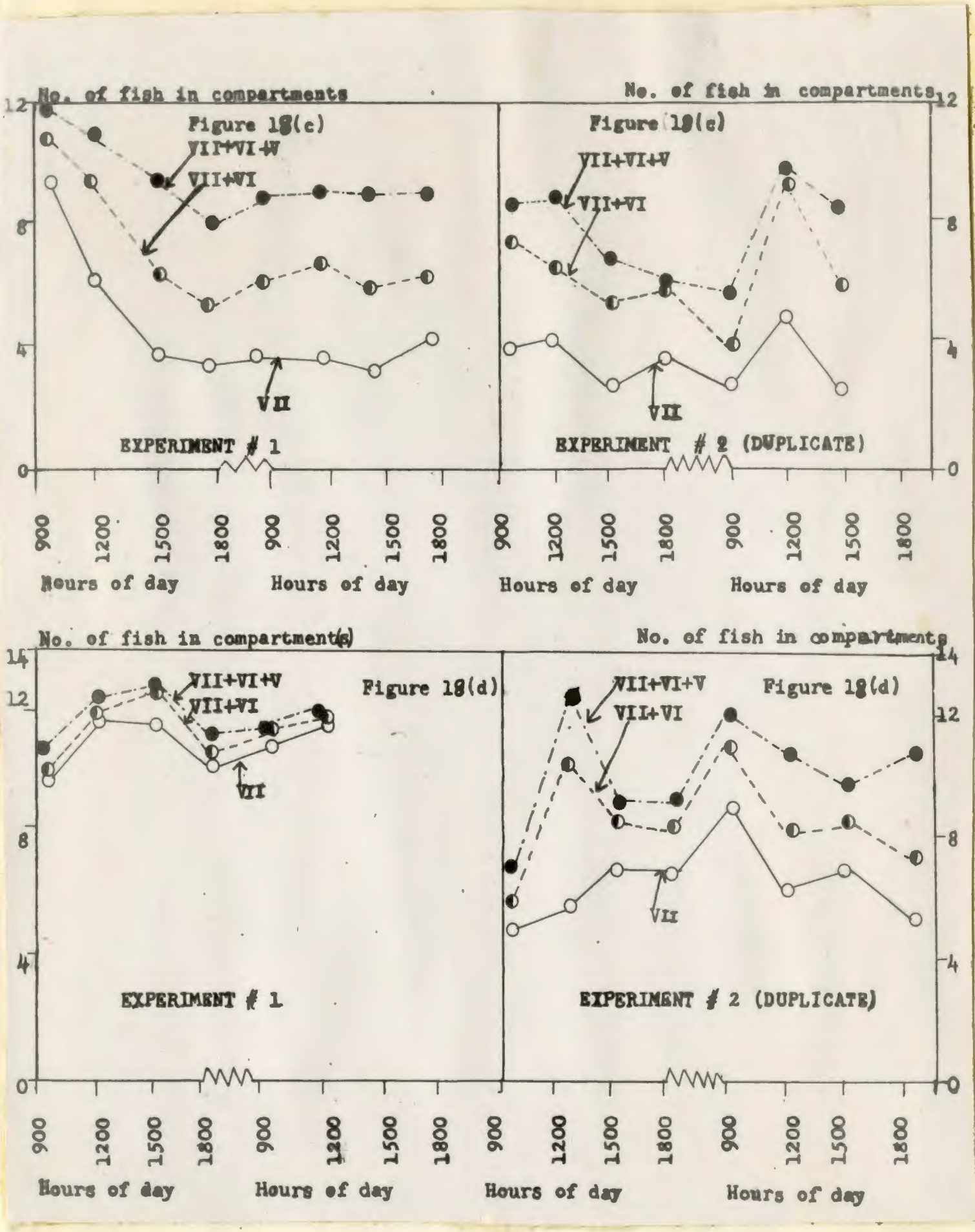


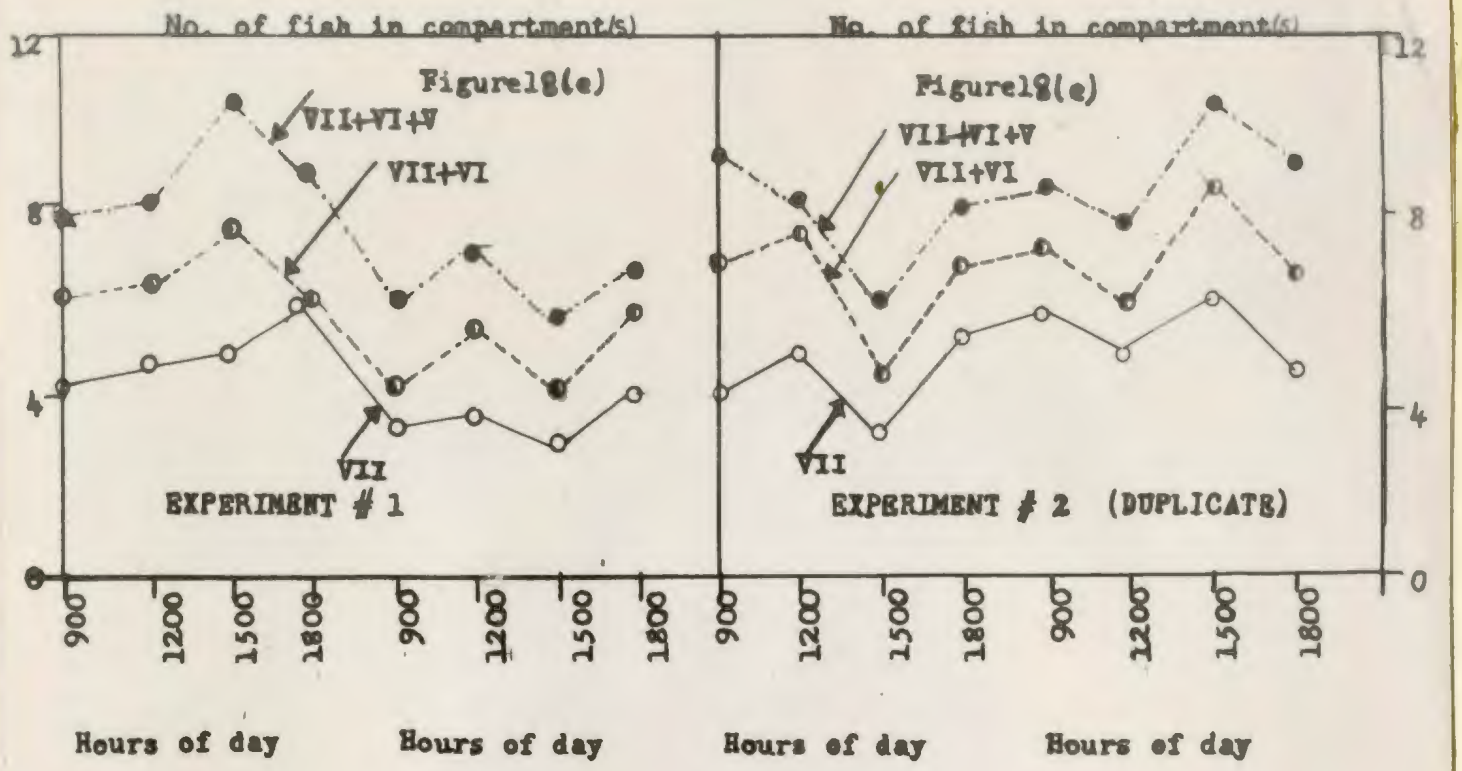
Figure 17. Graphs showing decrease in light intensities at one foot intervals from a light source, which was an incandescent light bulb, placed at one end of a rectangular wooden tank.(Figure 17a-7.5 watt bulb, Figure 17b-100 watt bulb, Figure 17c-300 watt bulb).

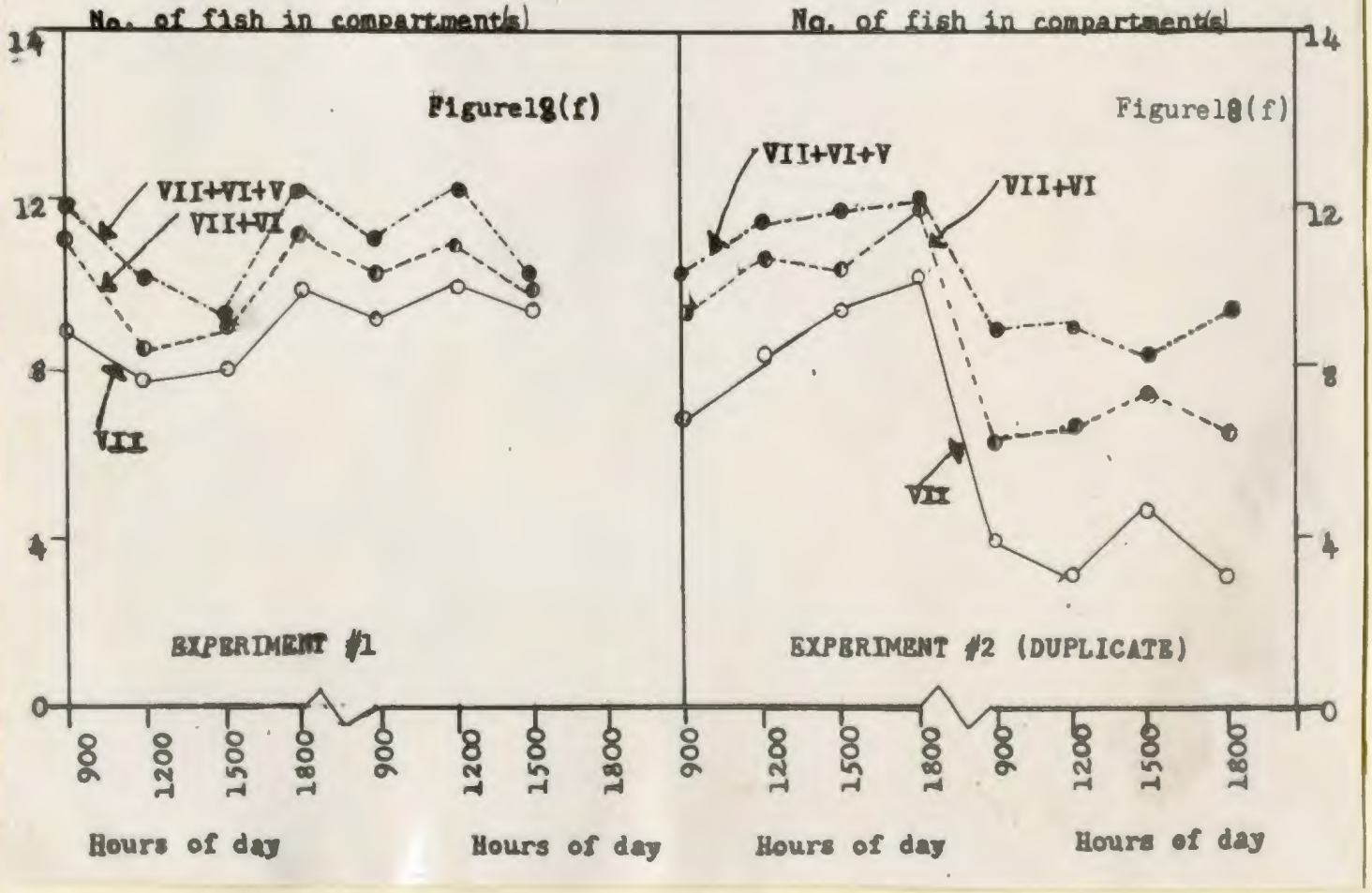
Figure 18. Graphs showing variations in the reactions of Salmo salar L. to horizontal light gradients with respect to the time of day (diurnal variations) and the time after the observations began. (Roman numerals refer to the compartments combined to obtain averages. Broken lines indicate the passage of darkness (6.00 P.M. to 9.00 A.M.). Acclimation temperature ° C. --15.0).

Legend--- Figure 18(a)--7.5 watt bulb--control fish
Figure 18(b)--7.5 watt bulb--light-exposed fish
Figure 18(c)--100 watt bulb--control fish
Figure 18(d)--100 watt bulb--light-exposed fish
Figure 18(e)--300 watt bulb--control fish
Figure 18(f)--300 watt bulb--light-exposed fish


No. of fish in compartment(s)
Figure 18(a)
VII+VI+V
VII+VI
VII
EXPERIMENT # 1
Hours of day
No. of fish in compartments
Figure 18(a)
EXPERIMENT # 2 (DUPLICATE)
Hours of day
Hoursof day
No. of fish in compartment(s)
Figure 18(b)
VII+VI+V
VII+VI
VII
EXPERIMENT # 1
Hours of day
No. of fish in compartment(s)
Figure 18(b)
EXPERIMENT # 2(DUPLICATE)
Hours of day


No. of fish in compartments
Figure 18(c)
VII+VI+V
VII+VI
VII
EXPERIMENT # 1
No. of fish in compartments
Figure 18(c)
VII+VI+V
VII+VI
VII
EXPERIMENT # 2 (DUPLICATE)
12
8
4
0
900
1200
1500
1800
Hours of day
No. of fish in compartments
Figure 18(d)
VII+VI+V
VII+VI
VII
EXPERIMENT # 1
No. of fish in compartments
Figure 18(d)
VII+VI+V
VII+VI
VII
EXPERIMENT # 2 (DUPLICATE)
14
12
8
4
0


No. of fish in compartment(s)
Figure18(e)
VII+VI+V
VII+VI
VII
EXPERIMENT # 1
No. of fish in compartment(s)
Figure18(e)
VII+VI+V
VII+VI
VII
EXPERIMENT # 2 (DUPLICATE)
12
8
4
0
900
1200
1500
1800
Hours of day


No. of fish in compartment(s)
Figure18(f)
VII+VI+V
VII+VI
VII
EXPERIMENT #1
No. of fish in compartment(s)
Figure18(f)
VII+VI+V
VII+VI
VII
EXPERIMENT #2 (DUPLICATE)
14
12
8
4
0
900
1200
1500
1800
Hours of day

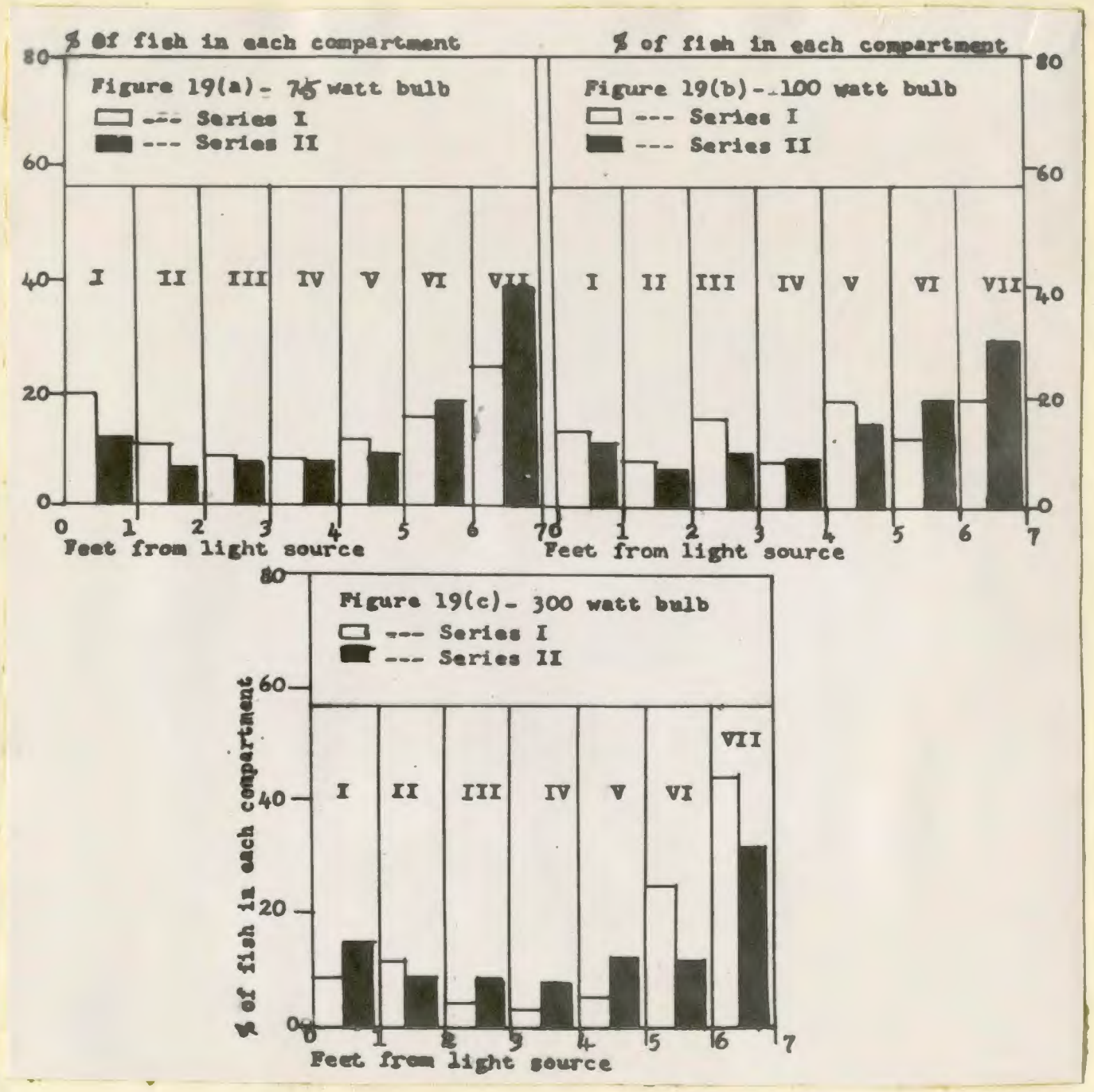


Figure 19. Behaviour of Salmo salar L. in a horizontal light gradient (Control fish. Roman numerals are successive compartments at one foot intervals from the light source, with the highest light intensity in I and the lowest in VII. Acclimation temperature °C. -- Series I - 15.0, Series II - 10.0-5.0).

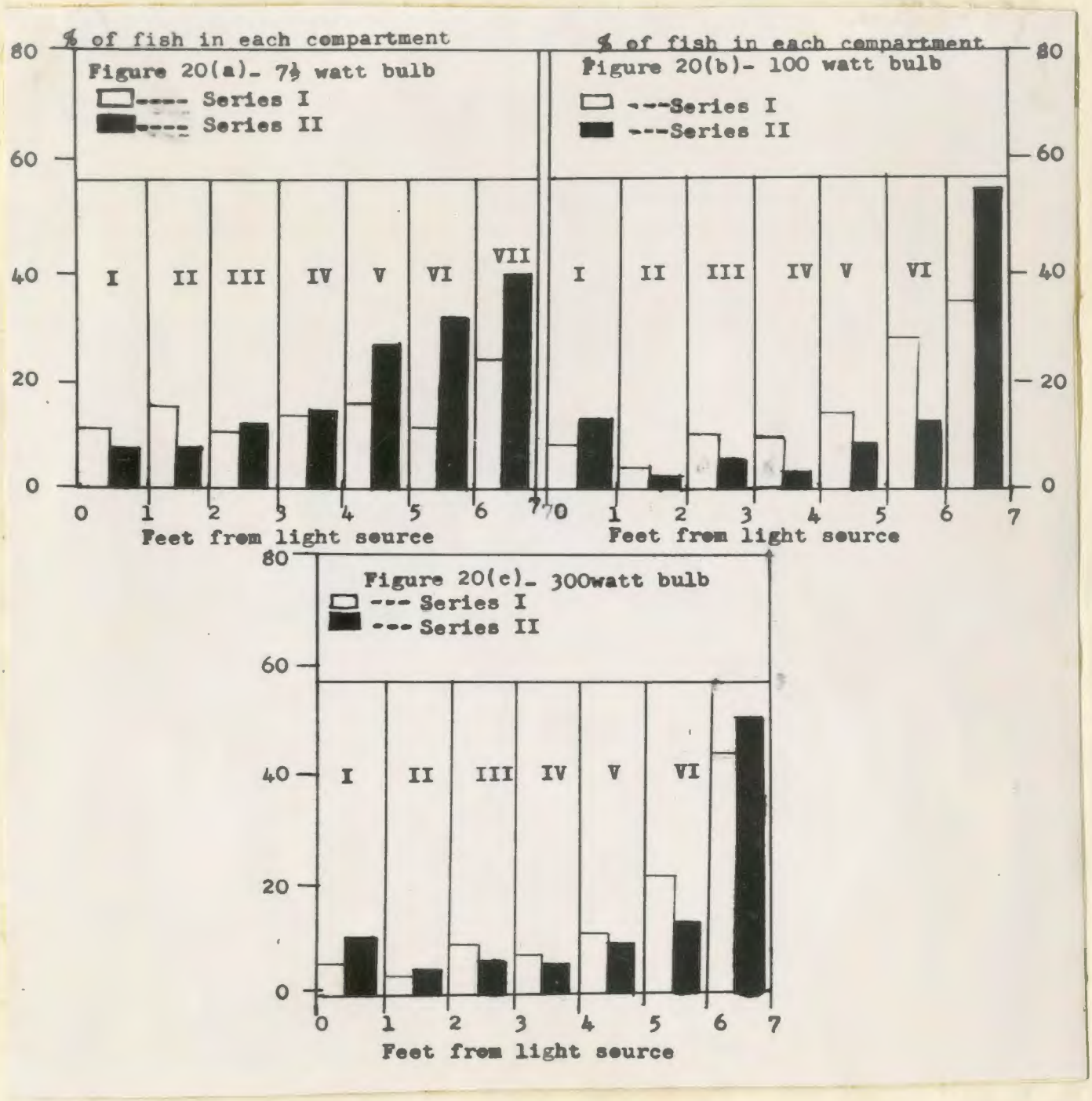


Figure 20. Behaviour of Salmo salar L. in a horizontal light gradient (Light-exposed fish. Roman numerals are successive compartments at one foot intervals from the light source, with the highest light intensity in I and the lowest in VII. Acclimation temperature ^{o}C. -- Series I - 15.0, Series II - 10.0-5.0).