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**STUDIES ON THE EFFECT OF BEHAVIOR ON FISH
GUIDANCE EFFICIENCY AT ROCKY REACH DAM:
AVOIDANCE TO STROBE LIGHT AND OTHER STIMULI**

by

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PREFACE

This report is a compilation of studies funded by Chelan County Public Utility District No. 1 over a two-year period from 1986 to 1987. The initial goal of the work was to determine how strobe lights could be deployed at Rocky Reach Dam to improve fish guidance efficiency. The approach included model, laboratory, and theoretical studies. The results were integrated with studies being carried out at Rocky Reach Dam by Chelan County Public Utility with the assistance of BioSonics Inc. We did not reach our goal and the use of strobe lights to improve fish guidance efficiency at Rocky Reach Dam has been abandoned for the immediate future. In retrospect, the success of the study is best measured through understanding why strobe lights were ineffective at the dam and how fish avoided guidance by the submersible traveling screen.

In this report, the studies conducted over the two year period are detailed. The direction of the research was in part affected by the results that were obtained in the field studies. To put this interaction between laboratory, model and field studies in context, a narrative of the hypotheses formulated during the study is presented in the introduction. This is followed by a summary of the results. Details of the studies are given in appendices.

ABSTRACT

Problems contributing to the low fish guidance at Rocky Reach Dam were investigated through laboratory experiments and a computer model. Particular attention was given to determining how strobe lights could be used to improve fish guidance efficiency.

In general, juvenile chinook and coho salmon and rainbow trout tended to avoid or escape strobe light at intensities between 0.1 and 5 $\mu\text{E}/\text{m}^2/\text{s}$. The EG&G strobe lights used at Rocky Reach Dam produced an intensity of about 1 $\mu\text{E}/\text{m}^2/\text{s}$ at a distance of 10 ft. Escape speed averaged about 7 bl/s and was dependent on strobe light intensity and the level of light that fish were adapted to. Escape speed increased with strobe flash rate, with a flash rate of 200/min or above being sufficient to induce speed near the maximum observed. Strobe intensity above 5 $\mu\text{E}/\text{m}^2/\text{s}$ and flash rates above about 500/min tended to stun fish. Juvenile steelhead were attracted to the low light intensities of the strobe's penumbra.

A computer model was developed to describe the trajectories of fish as affected by water currents and swimming to avoid strobe lights and the trashrack. A model suggested that trashrack passage was a critical factor in fish guidance efficiency. In laboratory experiments, strobe light could be used to force rainbow trout through a trashrack-like barrier. However, at Rocky Reach Dam, strobe lights were ineffective at forcing subyearling chinook through the trashrack. Thus, a hypothesis was formulated that the submersible traveling screen behind the trashrack may have generated sound stimuli that inhibited trashrack passage; moreover, it appeared that strobe lights were ineffective in counteracting this aversive stimuli.

INTRODUCTION

This report describes two years of research on the problems contributing to the low fish guidance efficiency (FGE) of a prototype submersible traveling screen (STS) at Rocky Reach Dam on the Columbia River. The immediate goal was to conduct studies on the feasibility of using strobe lights to improve the FGE of the prototype STS. To achieve this goal laboratory, theoretical and model studies were integrated with the field studies conducted at Rocky Reach Dam by Chelan County PUD. Laboratory studies were conducted at the Fisheries Research Institute (FRI) to determine the response of juvenile salmonids (chinook, coho and rainbow) to strobe light intensity and flash rate. In theoretical studies important behavioral responses observed in the laboratory were described with equations based on known principles in biology and psychology. A computer model was developed to describe the trajectories of fish passing through the dam. The results of the laboratory and field studies were considered in the model. Accordingly, the model was used to help design the field program at the dam. Over the course of the project three strobe light configurations were tested and a number of basic behavioral responses of fish to strobe lights were described and quantified. The sequence of studies and the major results obtained are illustrated in Table 1. All aspects of the work are summarized in the body of the report detailed in eight appendices. Appendices 3, 4, and 6 are in press.

Over the two-year period, strobe lights, incandescent lights and a deflector projecting outwards from the trashrack were deployed at Rocky Reach Dam in an attempt to improve FGE. In the spring of 1986, two strobe lights facing up into the water column were fixed on the trashrack (Fig. 1) to determine if the lights would drive fish upwards in the water column where they would intercept the trashrack above the level of the STS. This scenario, based on a fish trajectory model, was in its first stage of development. In the spring of 1986, field tests made at the dam by S. Hays of Chelan County PUD suggested that strobe lights produced a small improvement in FGE for some species in daylight conditions. Further model development and analysis in the autumn of 1986 suggested that strobe light would have a minimum effect on the upward movement of fish if they escaped by moving horizontally away from the strobe light beam. The field tests and model study suggested that strobe lights located on the trashrack and facing into the forebay would not significantly improve FGE.

Table 1. Major results obtained during the study.

	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
	1986				1987		
Laboratory Experiment Results	avoidance response increase with light intensity	stobes drive fish through trashrack	speed of escape increases by log of intensity	escape behavior changes over day	attraction to light depends on previous adaptation		
Theoretical Results			equation for distance of trashrack response		equation for escape speed and avoidance distance		equation for strength of attraction to solid light
Model Results				reasons for strobe light ineffectiveness			trashrack avoidance may be from sounds of STS
Field Results	strobe facing into forebay improved FGE	strobe facing up into trashrack degraded FGE			strobe facing trashrack plus front deflector had no effect on FGE		light behind trashrack had no effect on FGE

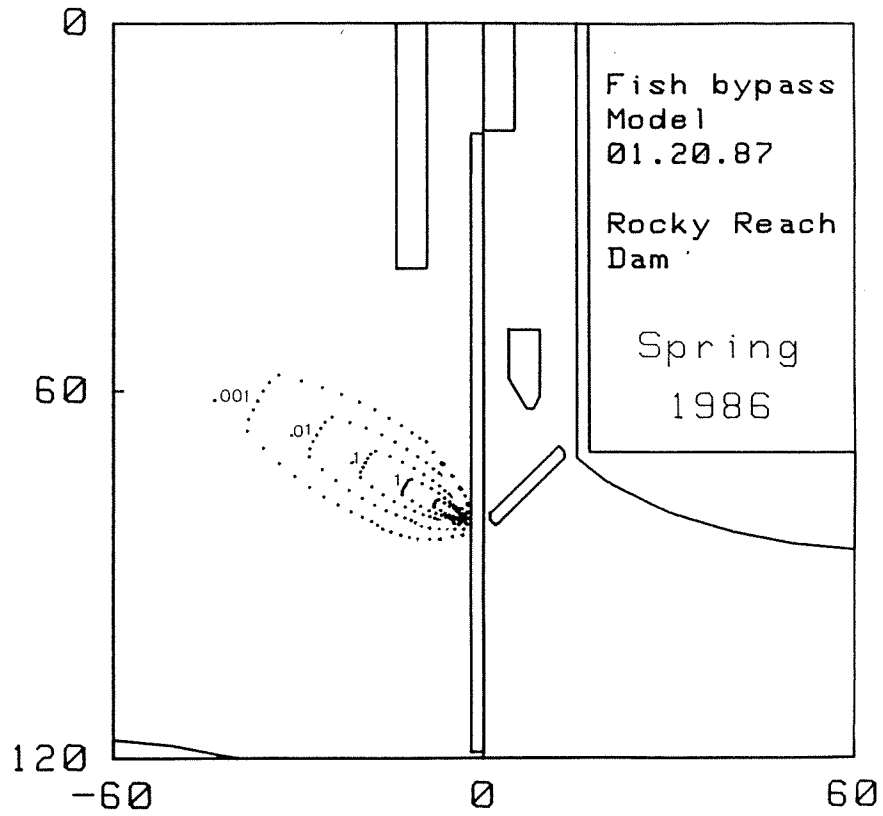


Fig. 1. Distribution of strobe light intensity during spring 1986 studies at Rocky Reach Dam. Strobe light intensities isopleths in $\mu\text{E}/\text{m}^2/\text{s}$. Strobe light distribution was calculated by fish trajectory model and calibrated with field observations. Horizontal and vertical dimensions are in ft.

In the summer of 1986, a new strategy was tried in which the trashrack was illuminated with strobe lights from below (Fig. 2). The idea here was that fish moving down the face of the trashrack would encounter the strobe lights and, to escape the light, they would pass through the trashrack and would be intercepted by the STS. Evidence from field tests indicated that lighting the trashrack did not improve trashrack passage.

In following up the results from the summer, model studies in 1986 indicated that the major problem appeared to be due to the reluctance of fish to pass through the trashrack above the level of the STS. Therefore, the focus shifted to find a way to improve fish passage through the trashrack above the STS. Hanson and Hiram (1983) published a study showing that salmon are reluctant to pass through a trashrack barrier. To follow up this observation, we conducted an experiment to determine if barrier passage could be improved with a strobe light. We determined that a strobe light could in effect force fish through a barrier if the light was on one side of the fish and the barrier was directly opposite the light on the other side of the fish. To follow up this scenario, a configuration was designed in which strobe lights were placed 10 ft out from the trashrack facing back towards the trashrack. A bar screen deflector on the front of the trashrack was constructed just below the level of the STS with strobe lights attached just above the bar screen (Fig. 3). The strategy was to box fish between the light and the deflector so their only route of escape was through the trashrack and into the STS. Field tests in the spring of 1986 demonstrated that the strategy was ineffective: Fish managed to pass around the front deflector with or without the strobe light on (S. Hays, Chelan County PUD, personal communication).

Having exhausted the immediate possibilities of driving fish through the trashrack, we turned our efforts to investigate ways to attract fish through the barrier. Laboratory studies were conducted in 1987 to quantify a well-known result that fish are, in some instances, attracted to solid lights. The study, detailed in Appendix 3, illustrated that the maximum attraction to light occurred when the light level was equal to the level fish were previously adapted to. In the summer of 1987, the region behind the trashrack was lit with incandescent lights (Fig. 4). The level of light at the trashrack was similar to the level of light fish experienced at depth during the day. The backlighting had no improvement on FGE (S. Hays, Chelan County PUD, personal communication).

While the field investigations were proceeding, our laboratory studies were revealing that strobe light was an aversive stimuli to fish. We measured avoidance strength in several ways including: the speed of escape, the distance of approach, and the distance at which fish turned from a light. We determined that the avoidance response increased as flash rate and strobe intensity increased. At the upper range of intensity and flash rate, avoidance

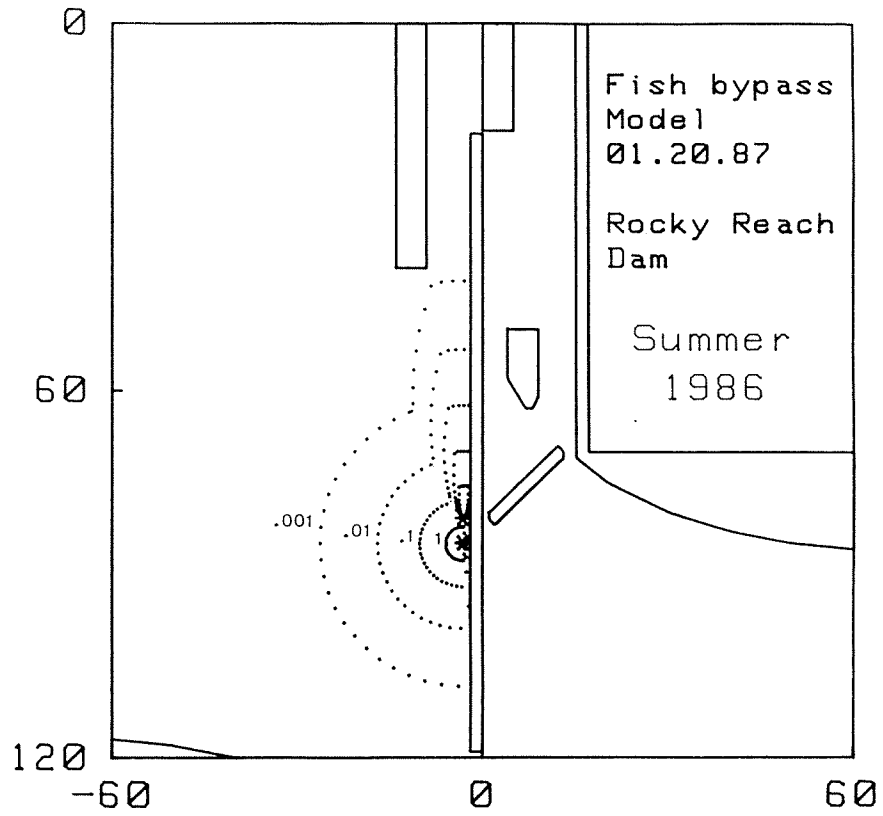


Fig. 2. Distribution of strobe light intensity during summer 1986 studies at Rocky Reach Dam. Same units as in Fig. 6.

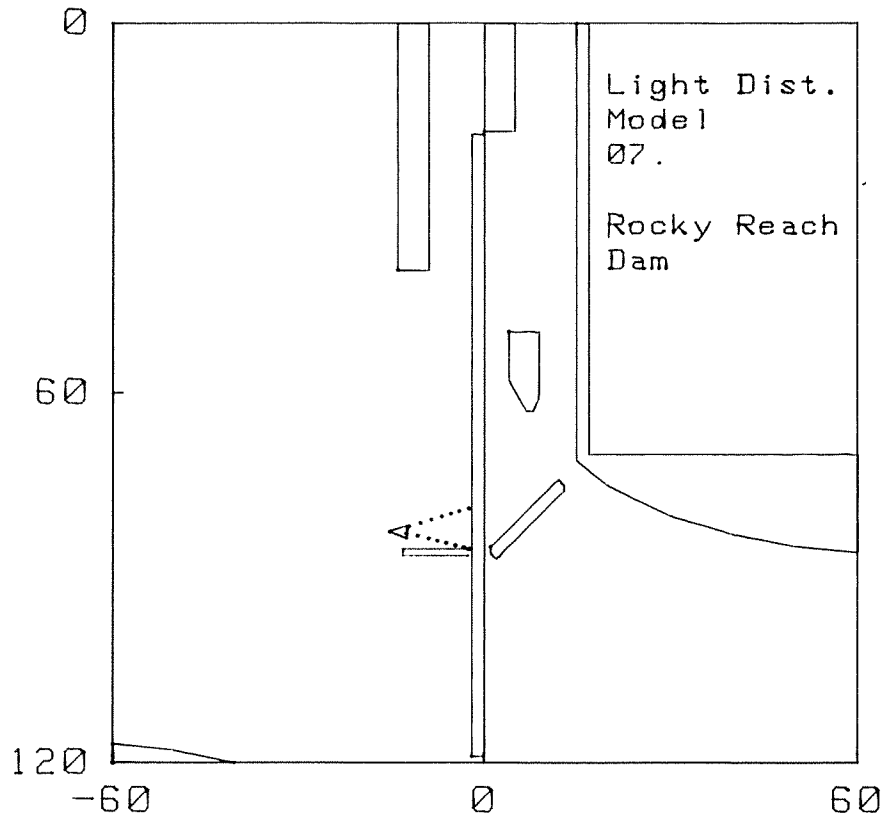


Fig. 3. Configuration in summer of 1987 showing strobe light facing trashrack with front bar screen deflector extending into forebay.

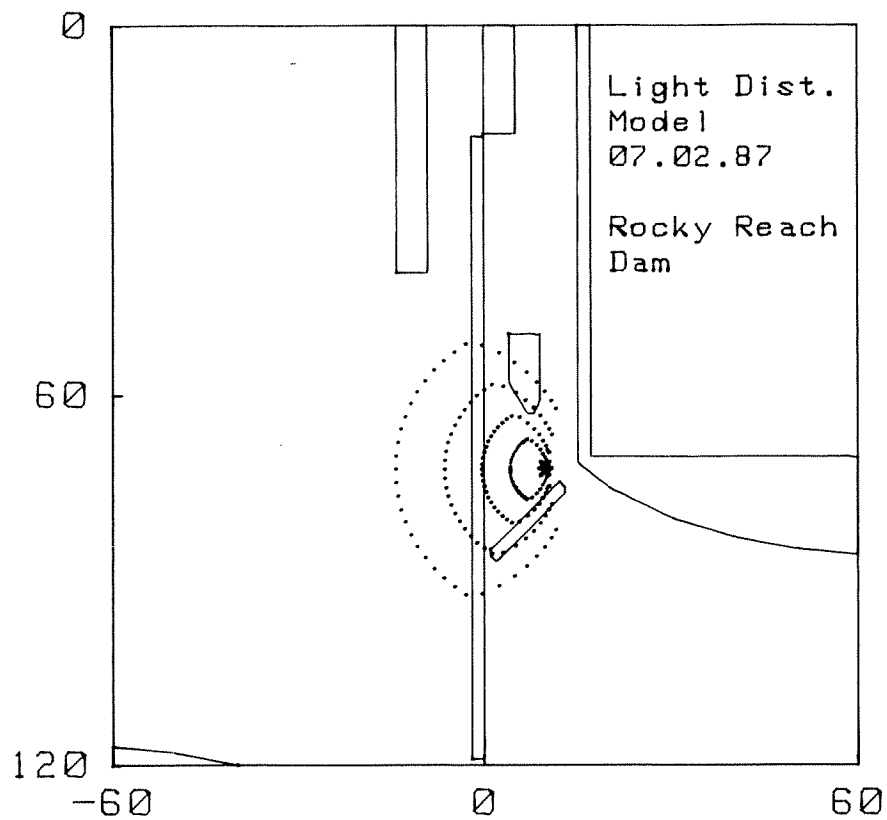


Fig. 4. Configuration in summer of 1987. Incandescent lights on STS projected back towards trashrack. Light isopleths extending from light on 1, 0.1, 0.01 and 0.001 $\mu\text{E}/\text{m}^2/\text{s}$.

behaviors appeared to weaken. With strong intensities, it appeared that a fish's ability to escape was impaired by the excessive stimuli of the light. This saturation phenomenon typically is observed in avoidance behavior studies.

Experiments conducted in a raceway at FRI (Appendix 2) indicated that fish could be attracted to the penumbra, or dim edge, of a strobe light. From these experiments we surmise that the response of fish to either strobe or solid lights depends on the intensities of the light they encounter and the intensities of light they were adapted to.

In the autumn of 1987, the model study was renewed and focused on investigating if trashrack passage was different with and without a STS behind the trashrack. A surprising result emerged from the study. We previously had assumed that the reluctance of fish to pass through the trashrack was due to a stimulus from the trashrack itself. The model indicated that fish only avoided passing through the trashrack when the STS was present, suggesting that the stimulus which fish avoided was associated with the STS and not the trashrack. With this hypothesis a new set of strategies to improve FGE emerged. To lessen the effect of an STS stimulus at the trashrack, the simplest strategy is to increase the distance between the trashrack and the STS. This scenario is supported by the observation that, in general, the dams on the Columbia River with the highest FGE also have the greatest distance between the STS and the trashrack. This hypothesis was independently formulated by S. Hays and R. Nason of Chelan County PUD. The trashrack has been moved about 10 ft out from the STS and the effect on FGE will be evaluated this spring.

2. LABORATORY STUDIES

In this section, laboratory experiments conducted (Table 2) to determine the response of fish to strobe lights are summarized. The experiments conducted with chinook salmon, steelhead, and rainbow trout indicated that escape- and avoidance-type behaviors could be quantitatively related to the intensity and flash rate of a strobe light. In addition, other factors were found to alter the behaviors, including: enclosure size, ambient light level, time of day, and the presence of trashrack like vertical bars. All experiments were performed in still water conditions. A summary of the major points revealed by the laboratory experiments follows.

Behavior and Enclosure Size

The behavior of fish to sudden and gradual introduction of a strobe light stimuli depended on the size of the enclosure (Appendix 1). In enclosures, up to about 1.5 m in length, individual fish swam against the glass towards the strobe light. In intermediate size enclosures, up to 3 m in length, fish would either turn away from the light, stop

Table 2. Summary of experiments conducted.

Stimuli variable	Behavioral response	Fish species	Fish length	Enclosure size	Water tem.	Appendix number
Flash rate and intensity	Speed and distance	Rainbow	135mm	8m x 2m	12	2
	Turn distance	Rainbow	135	3m x 0.3m	11	1
Flash rate	Angle	Rainbow	100	1m x 1m		1
	# turns	Chinook	60	3 liter	11	1
	Speed	Chinook	115	3m x 0.3m	21	1
	Delay time	Rainbow	150	3m x 0.3m	20	1
	Distance	Rainbow	150	3m x 0.3m	20	1
Flash intensity	Speed	Rainbow	140	3m x 0.3m	21	
	Distance	Rainbow	140	3m x 0.3m	11	1
	Speed	Chinook	70	3m x 0.3m	11	
Moving and fixed lights	Speed and angle	Chinook	100	1.3m x 1.3m	13	1
Enclosure size	Turn distance	Rainbow	135	3m x 0.3m	11	1
Time of day	Turn distance	Rainbow	130	3m x 0.3m	11	1
Barrier Distance	% passage	Rainbow	74 & 114 mm	4.5m x .4m	20	1

swimming, or swim toward the light. In a large enclosure, 8 m long, a group of fish would initially scatter in all directions when the strobe light was turned on. Immediately after the scatter response they swam away from the light and stopped in the light-dark boundary, which is known as the penumbra of the light (Appendix 2). In general, the escape speed increased with enclosure size. The freeze response, observed in individual fish in intermediate size enclosures, was never observed with schools of fish in large enclosures. Although the behaviors were dependent on the size of the enclosures the intensity of the behaviors exhibited similar patterns with respect to strobe intensity and flash rate. From this we may conclude that the results of the laboratory studies, identifying the optimum strobe characteristics, can be applied to the field setting.

Response to Flash Rate

The intensity of escape and avoidance behaviors increased with strobe flash rate when the strobe intensity was held constant at an intermediate level (Appendices 1 and 2). In general, maximum escape speed and avoidance distance were observed at 780 flashes/min and between 60 to 90% of the maximum response was observed at a flash rate of 200/min. The experiments included juvenile chinook salmon and rainbow trout (steelhead) ranging between 5 and 13 cm in length.

The effect of flash rate on angle of escape was investigated with rainbow trout. The angle at which fish swam to avoid a strobe light was greatest at 488/min. At a flash rate of 600/min fish did not appear to exhibit a clear preference for turning away from the light (Appendix 1).

Response to Strobe Light Intensity

The effect of strobe light intensity on the response of fish also was complicated by the difficulty in determining the actual intensity of light that fish received on their photoreceptors. Photoreceptor intensity was dependent on: (1) the source strength of the light, (2) the distance of the fish to the light, (3) the light absorption by the water, and (4) the photo-adaptation state of the fish. To control these variables strobe light intensities were reported at the location of a fish and in most experiments fish were dark adapted.

All light intensities were recorded with a LiCor light meter. Because of the slow response time of the instrument the light readings for a fixed light intensity did not reach the full reading at the lower strobe flash rates. The effective intensity at lower flash rates could be related to the intensity at higher rates through the equation:

$$(\text{Intensity at rate } x) = (\text{Intensity at rate } y) * (\text{rate } x/\text{rate } y).$$

In general, when fish were suddenly exposed to a strobe light, escape speed increased with strobe intensity and maximum escape speeds of between 5 and 10 body lengths per second (bl/s) were observed with strobe intensities of 1 to 4 $\mu\text{E}/\text{m}^2/\text{s}$. At strobe intensities $> 5 \mu\text{E}/\text{m}^2/\text{s}$ escape speeds appeared to decrease (Appendix 1). A model was developed relating the speed of escape to light intensity for intensities below the saturation level where speed declined (Appendix 2).

Experiments in an 8 m raceway demonstrated that fish exposed to a strobe light would hover a distance from the light in the region of the penumbra. This distance decreased in a linear manner with the logarithm of the strobe light intensity (Appendix 2).

Comparison of Light with Other Stimuli

The response induced by a strobe light was compared with the response that can be induced with other strong aversive stimuli. Escape responses in a 3 m tank were induced by throwing a lacrosse ball or a cement brick into the tank in front of the fish. The escape speeds and response times were statistically the same as the responses observed with strobe lights (Appendix 1). In general, a sudden encounter with a strobe light produced escape speeds of about 7 bl/s. In comparison maximum burst speeds of 10 to 13 bl/s can be produced with an electric shock (Webb and Corolla 1981).

Response to Vertical Bars

Experiments indicated that the passage of fish through vertical bars, simulating a trashrack, was affected by strobe light (Appendix 1). The experimental procedure was to force fish through vertical bars with a strobe light. In the base condition, without strobe light, only 28% of rainbow trout tested would pass through the vertical bar barrier. With a strobe light behind the fish, 75% of the fish would pass through the barrier. In both situations, fish that did not pass through the barrier swam towards it and turn away at a distance of about 0.2 m.

Diel Variations in Escape Behavior

A 24 hour study was conducted to determine if escape behavior varied over the time of day (Appendix 1). The escape behavior was quantified by the percent of fish that turned away from a strobe light. Fish displayed the least avoidance response at 0700 hr and the most response at 2300 hr.

3. THEORETICAL STUDIES

In theoretical studies, mathematical equations were developed describing the avoidance and escape responses of fish to strobe light, the startle response of fish encountering an approaching object, and the attraction of fish to solid lights. The equations for avoidance, escape and startle responses were incorporated into the models. The equation for light attraction was used to determine the level of light for backlighting the trashrack in the summer 1987 FGE studies.

Avoidance Response to Strobe Light

A mathematical model quantifying avoidance and escape responses of fish encountering a strobe light was developed (Appendix 2). The model assumed that the speed fish swim away from a strobe light is related to the difference in the perceived light intensity fish encounter and a light intensity fish prefer for their surroundings. For escape speed, v , the end results is:

$$v = V \log(I/I_a)$$

where I is the ambient light intensity, I_a is the preferred light intensity to which fish are adapted, and V is a velocity coefficient. The avoidance distance, that is the distance at which fish will hover from a strobe light, was expressed by the equation:

$$x_0 = (1/k) \log(I_0/I_a)$$

where I_0 is the intensity of light at its source and k is the extinction coefficient of light in water. The model has been evaluated with experiments on rainbow trout, and coefficients describing the speed and avoidance distance of fish as a function of light intensity have been determined.

Startle Response to Objects

The basis of the visual activation of the startle response was modeled to help understand the factors that effect the behavior of fish at the trashrack (Appendix 4). The model was developed to identify factors that might be important in avoidance of a trashrack perceived visually. The study indicated that the distance at which a fish initiates an avoidance response, if induced by the visual siting of the trashrack, may be defined:

$$D = (kV)^{1/3}$$

where D is the avoidance distance, V is the approach speed to the object, and k is a constant. The model was tested with published results on the startle response of zebra danio (*Brachydanio rerio*), a small tropical fish.

Attraction to Solid Light

Experiments were conducted showing that the strength of attraction of fish to a solid, non-flashing light, was dependent on the intensity of the light and the level of light the fish were adapted to (Appendix 3). A mathematical expression describing the strength of the attraction was developed from basic psychological principles. In dark surroundings, the percentage of fish attracted to a light over a specified time interval was expressed by the formula:

$$\text{Percent attraction} = A - k \text{ Abs}(\log I_s/I_a)$$

where A is a constant expressing the percent of fish attracted under the best conditions, k is a constant, Abs is the absolute value operator, \log is the logarithm to the base e , I_s is the intensity of light that fish encounter, and I_a is the intensity of light that fish were adapted to. The maximum attraction occurs when $I_s = I_a$.

4. MODEL DESCRIPTIONS

The low fish guidance at Rocky Reach Dam was investigated with a computer model. The study combined the results of the laboratory experiments and theoretical behavior models with field investigations of FGE, hydroacoustic distributions of fish and currents.

The computer model evolved over the project in three stages. In all stages the movements of fish were described by the summation of finite increment displacements resulting from water flow and any avoidance behavior to strobe light or a trashrack (Fig. 5).

Stage I Model

Initially a deterministic model was developed in which the movements of fish were described by an nonrandom flow field and simple nonrandom swimming movements that characterized the response of fish to a trashrack and strobe light. Flow streamlines were calibrated with average flow conditions determined by Hays (1986). Fish avoidance to strobe light and a trashrack were assumed to follow basic startle and avoidance type responses as described by Eaton and Hackett (1985), Weihs and Webb (1984) and Patrick et al. (1985). In the model, a fish's response to strobe light was to swim directly away from the source of the light. In response to a trashrack, the model assumed fish swam perpendicular to the face of the trashrack. The maximum escape speed was fixed at 2 ft/s.

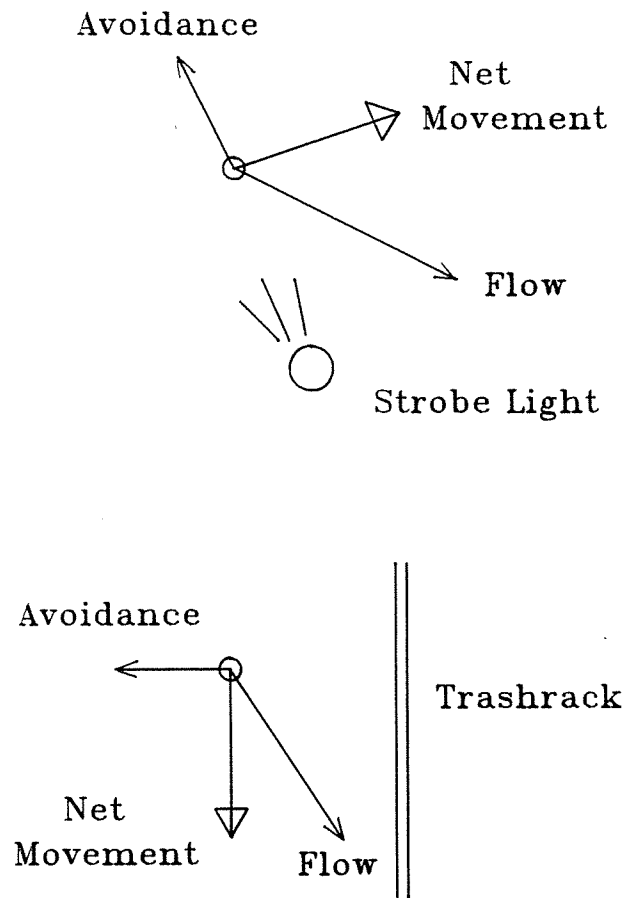


Fig. 5. The net movement of fish over a small increment of time is shown to be the vectorial sum of movement from flow and an avoidance behavior.

An avoidance response was assumed to occur at approximately $1 \mu\text{E}/\text{m}^2/\text{s}$. The distribution of light was calculated using radiative equations described in Preisendorfer (1976). Accurate field measurements of strobe light had not been made when the stage I model was developed, so the strobe light intensity was fixed to provide an initial avoidance response 20 ft from a light source. The distance for trashrack avoidance was fixed at 6 ft.

The model predicted that fish avoiding the trashrack would be pulled down the face of the trashrack by the flow and would eventually be pulled through the trashrack when the water flow exceeded the swimming speed of the fish. A model sensitivity analysis indicated that the FGE was highly sensitive to the trashrack avoidance distance. In the model, the FGE also was highly dependent on the strobe position. In general, the stage I model indicated that FGE was very sensitive to the avoidance responses of fish to a trashrack and strobe lights. With the limited information available at the time it appeared that an optimum strobe light location was below the level of the STS facing into the forebay at an angle of 20 degrees off horizontal (Fig. 1). This configuration was tested in the spring of 1986.

Stage II Model

In stage II of the model a number of alterations were made to improve its realism (Appendix 5). The description of the flow field was improved by including a random component to the direction of the flow. Avoidance behaviors to a trashrack and strobe light were also changed. The model distribution of strobe light was calibrated *in situ* with a strobe light used in the field tests at Rocky Reach Dam. Swimming speed during strobe light avoidance was described in terms of the light intensity equation developed in the laboratory and theoretical studies described in Appendices 1 and 2. Strobe light avoidance was characterized by the level of light fish were adapted to and a base escape velocity. The response to a strobe light was expressed in three dimensions. Thus, fish would initiate an escape response that moved them up, down, or to the side according to their location relative to the strobe light. Variability in the response to a trashrack was expressed in terms of an escape swimming speed that randomly deviated from a mean value according to a normal distribution. Trashrack avoidance was thus characterized by three components: the avoidance distance at which an escape response was initiated, the mean swimming speed of an escape, and the standard deviation of the speed. The model estimated FGE and catch by fyke nets in the turbine entrance.

Model parameters, describing trashrack avoidance, were adjusted so that model FGE and fyke net distributions were in approximate agreement with the distributions observed in the field test. Coefficients for the strobe light response were estimated from the results of the laboratory experiments discussed in Appendices 1 and 2. An analysis of the model

response characteristics indicated that the vertical movement of fish in response to strobe light would be reduced by avoidance movements in the lateral direction. This suggested that, with only a few strobe lights on a trashrack, the effect on the fish distribution would be minimal. The analysis also suggested that FGE was strongly dependent on trashrack avoidance distance and fish swimming speed. A change in avoidance distance of 2 feet resulted in an absolute change in FGE of 50%. Differences in FGE between species and conditions were analyzed in terms of changes in avoidance distance and swimming speed.

The model provided a plausible explanation for the observed variability in FGE and fyke net distributions, but there were problems in identifying a behavioral mechanism responsible for the responses. The avoidance distance was a critical parameter that could vary between about 1 and 5 ft. It was not clear what stimulus could produce an avoidance response in fish 5 ft from a trashrack. Also, the laboratory experiments suggested avoidance responses may occur at much closer distances.

Stage III Model

In the third stage of the model development the effects of light were disregarded and the work focused on the trashrack avoidance with and without an STS behind the trashrack (Appendix 6). More detail was given to accurately describing water flow. Both the angle and speed of flow were described in terms of average and random components. The current components were calibrated for conditions with and without an STS using current meter data given by Hays (1986). Because evidence supporting the avoidance distance hypothesis was lacking a different approach was developed. In the new approach, trashrack passage was described in a probabilistic manner, taking into account fish swimming ability and variations in current flow at the trashrack. The approach allowed the trashrack behavior to be expressed by a single variable: the probability of trashrack passage. By comparison, in the stage II model three parameters were required to describe trashrack passage. The stage III model also included upward swimming behind the trashrack and the depth distributions of fish in the forebay were identified by species and day-night period.

The model parameters were determined on a species specific basis for day and night conditions and for configurations with and without a STS. Model parameters were obtained by minimizing a chi-square statistic between predicted and observed FGE and fyke net distributions. The analysis suggested that trashrack passage probability was 100% in the absence of the STS. That is, fish passed directly through the trashrack in their initial encounter with the structure. With an STS behind the trashrack passage probability dropped to zero above the depth of the STS and was 30% below the STS. In this case fish only passed through the trashrack above the depth of the STS when the current speed

momentarily exceeded their maximum swimming speed. Below the STS fish passed through the trashrack in about 1 out of 3 encounters.

These results suggested that some factor associated with the STS actively produced avoidance at the trashrack. The avoidance occurred during the night and day which suggested that the stimulus inducing avoidance was not visual. A brief review of the behavioral literature suggested that low frequency sound was a likely candidate for the postulated aversive stimulus. It is possible that a STS behind a trashrack could generate sufficient sounds to inhibit fish passage. The trashrack itself might have served as a reference marker that fish used to direct their escape. A second possibility is that fish were responding to rheotactic stimuli produced by turbulence caused by the STS. Turbulence and sound can be generated by the same dynamical processes but are measured with different instruments. In either case the model studies suggested that the STS might have produced aversive stimuli that contributed to the low FGE at Rocky Reach Dam.

5. CONCLUSIONS

Depending on the conditions in our experiments, we concluded that salmonids exhibit four basic responses to strobe light: (1) escape, (2) attack, (3) stun or (4) attraction. Escape responses were observed when the stimulus was of intermediate strength and the fish perceived an escape route. If escape was not possible, they often seemed to attack the light. The occurrence of these two behaviors could be controlled by altering the size of the test chamber. In small chambers, they swam towards the light and appeared to attack the strobe, while in larger chambers they swam to the opposite end of the chamber. Stun behaviors or reduced escape performance were observed if the strobe intensity was above $5 \mu\text{E}/\text{m}^2/\text{s}$ and the flash rate was above 500/m. At low light intensities, such as a strobe light appears at a distance, fish were attracted and would hover at the penumbra of the light. In general, avoidance and escape responses were observed with strobe light intensities of 0.1 to $5 \mu\text{E}/\text{m}^2/\text{s}$. The EG&G strobe lights used at Rocky Reach Dam produced a local intensity of about $1 \mu\text{E}/\text{m}^2/\text{s}$ at a distance of 10 ft.

A simple equation was used to quantify escape speed (typically 7 bl/s) in terms of light intensity. Evidence suggested that the escape speed was probably dependent on the level of light that fish were adapted to. When adapted to higher light levels, fish exhibited weaker responses to light than when they were adapted to lower light levels. The experiments also demonstrated that number of fish exhibiting an avoidance response changed with the time of day. Fish were least active at 7:00 and most active at 23:00.

From the laboratory experiments conducted in the spring and summer of 1986, we surmised that fish consistently respond and, for the most part, tend to move away from strobe light. Concurrent hydroacoustic measurements at Rocky Reach Dam provided evidence that strobe lights altered the vertical distribution of fish in front of the dam, but dip net and fyke net studies indicated that the effect on FGE was minimal. The model and laboratory studies provided a reasonable explanation for these observations: Inhibition of passage through a trashrack appeared to make FGE insensitive to the vertical distribution of fish in front of the trashrack.

The trashrack passage appeared to be a critical factor in determining FGE, and further studies suggested that fish were reluctant to pass through barriers. In the laboratory, with daylight condition, strobe light could be used to force rainbow trout through a trashrack-like barrier. But at Rocky Reach Dam, strobe light were ineffective at forcing subyearling chinook through the trashrack when the STS was directly behind it. This limited analysis suggests that strobe light stimulus could not counteract the aversive stimulus inhibiting trashrack passage at Rocky Reach Dam in 1986 and 1987.

How then can the trashrack passage, and consequently FGE, be improved? From our studies, we formulated the hypothesis that the STS may have generated sound stimuli that inhibited trashrack passage. This spring, the trashrack at Rocky Reach Dam will be moved about 10 feet away from the STS to decrease the level of STS-generated sound at the trashrack, which in turn should increase trashrack passage and improve FGE. The results of this study will provide an indirect test of the aversive sound stimulus hypothesis. A more direct evaluation will be conducted this year by studying the distribution of low frequency sound at the Bonneville Dam Second Powerhouse. If the results of both studies support the above hypothesis, the problem of improving FGE might be formulated as a problem in noise control. If the trashrack modifications at Rocky Reach Dam do not significantly improve FGE and the study of low frequency sound at Bonneville Dam is inconclusive, then we will be forced to reassess this line of fish passage research. In any case, it is our opinion that to obtain cost efficient improvements of FGE we must consider the behavior of fish toward the stimuli they encounter during passage. We also conclude that the trashrack is the region of prime importance, so studies should identify stimuli in the trashrack vicinity and the response of fish to the stimuli.

REFERENCES

- Eaton, R.C. and J.T. Hackett. 1985. The role of the Mauthner Cell in fast-starts involving escape in teleost fishes. Ch.8. in "Neural Mechanisms of Startle Behavior," Eaton, ed. Plenum Press New York. pp. 213-266.
- Hanson, C.H. and W.L. Hiram. 1983. Behavioral response of juvenile chinook salmon, *Oncorhynchus tshawytscha*, to trash rack bar spacing. Cal. Fish Game 68(1):18-22.
- Hays, S. 1986. Developmental testing of a prototype fish guidance system for turbine intakes at Rocky Reach Hydroelectric Project. Draft Report Chelan County Public Utility District No. 1. January 6 1986.
- Patrick, P.H., A.E. Christie, D. Sager, C. Hocutt, and J. Stauffer Jr. 1985. Responses of fish to a strobe light/air-bubble barrier. Fish. Res. 3:157-172.
- Preisendorfer, R.W. 1976. Hydrologic Optics. Volume I. Introduction. U.S. Department of Commerce, National Oceanic and Atmospheric Administration. 218 pp.
- Webb, E. H. and R.T. Corolla. 1981. Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. Fishery Bulletin 79:143-150.
- Weihs, D. and P.W. Webb. 1984. Optimal avoidance and evasion tactics in predator-prey interactions. J. Theor. Biol. 106:189-206.

APPENDIX 1:

General Studies on Responses to Strobe Light

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SUMMARY

1. Laboratory experiments characterized the response of juvenile salmonids to strobe light and to a trashrack-like structure. In general, fish strongly attempt to avoid both stimuli.
2. Strobe avoidance was a function of flash frequency. Regardless of experimental procedure or the parameter measured, 70-80% of maximum avoidance is obtained at 200 flashes per minute. This result, obtained in the laboratory, is in close agreement with the experiments in the 8-m-long raceway.
3. Avoidance was strongest at intermediate strobe intensities. At twilight background light intensities, the strongest avoidance response occurred between 1 and 4 $\mu\text{E}/\text{m}^2/\text{s}$. Under darker background conditions, lower strobe light intensities produced the strongest response. Very bright strobe intensities (4 $\mu\text{E}/\text{m}^2/\text{s}$) tended to 'stun' dark adapted salmonids in small tanks.
4. Some behaviors apparently related to strobe light were actually the result of confinement. We call this the 'box effect'. The most noteworthy behavior associated with enclosure size was inhibition of escape swimming.
5. Nonetheless, data collected in relatively small troughs (at least 3 m long x 0.3 m wide) appeared to be a reliable index of the behavior of salmonids in very large troughs (i.e., space unrestricted). Thus, while absolute parameter values obtained in a small tank were arbitrary, any changes in response were the same as those identified under unrestricted space conditions. This means that studies incorporating flowing water and, of necessity, performed in small tanks, should yield reliable data when interpreted properly.
6. Time of day affected strobe avoidance. Avoidance was strongest around 11 PM and weakest at 7 AM.
7. Young salmon avoided strobe lights as strongly as they avoided disturbances produced by dropping large, heavy objects in front of them.
8. In still water, vertical bars acted as a partial barrier. Vertical bars could either reinforce or inhibit the escape response from strobe light. The effect depended upon fish size, and the relative positions of the strobe, fish, and vertical bars.
9. Fish that suddenly encountered a strobe light would turn toward or away from the light. The probability of turning away from the light increased with flash rate of the light up to an intermediate level of 488/min. At 600/min, the probability of turning away from the light decreased.
10. Fish held in a pen in the forebay of Rocky Reach Dam that were inactive in the dark exhibited momentary activity when subjected to a strong strobe light. No general behavior toward or away from the light was evident.

1.0 DEFINITION OF TERMS AND ABBREVIATIONS

Terms and abbreviations used in Appendix 1 are defined below.

<i>approach speed</i>	refers to the swimming speed of a fish as it approaches the area where the strobe light is turned on
<i>BI</i>	background light intensity
<i>bl/s</i>	body lengths per second
<i>box effect</i>	behaviors resulting from enclosure size
<i>delay time</i>	time elapsed from first flash of strobe to first movement across a specified line.
<i>naive</i>	not previously exposed to strobe light
<i>SI</i>	strobe light intensity, as measured by a light meter in $\mu\text{E}/\text{m}^2/\text{s}$
<i>SI setting</i>	an arbitrary scale of strobe light intensity
<i>VBs</i>	vertical bars forming a trashrack-like barrier
<i>xx meter mark</i>	the distance from the strobe light designated as the starting point for an escape response. This distance (usually 0.3-0.4 m) depended upon enclosure size and was used because behavior very near the strobe was often difficult to quantify.
<i>zero fish</i>	those fish that failed to cross the 0.3 m (or as stated) mark within a specified time limit, usually 1 minute from strobe onset

2.0 GENERAL METHODS

In this appendix, a number of experiments designed to quantify the response of fish to strobe light characteristics are described. Special experiments are discussed in Appendices 2, 3 and 4.

The basic experimental design was to place individual fish in a trough and manipulate their behavior so that they remained in the desired area or performed the desired task. The strobe light was then turned on and escape velocity and general behavior were noted.

The experimental trough was approximately 3 m long and 0.3 m wide. Water depth was about 5 cm and water temperatures varied between 11 and 22°C. Lake Washington water was pumped into one end of the trough and exited the other end, producing a small current. The bottom of the trough was marked off at 30 cm intervals for recording swim distances. The entire trough area was shielded with black plastic and all fish viewing was done through a video camera mounted above the trough. The trough was illuminated from above by a 25-W red incandescent bulb and provided a background light intensity of $0.002 \mu\text{E}/\text{m}^2/\text{s}$ (~0.1 lux), as measured with a Biospheri-

cal Instruments Model# QSL-100 light meter. By comparison, full sunlight is approximately 2,000 $\mu\text{E}/\text{m}^2/\text{s}$.

A Diversitronics Luma Power Strobe Light Model 50 was placed directly above the upstream end of the trough. Both strobe light intensity and flash rate could be varied. The strobe light face plate was sometimes covered with neutral density filters to reduce light levels further. Approximate strobe light intensity was measured as quantum flux with a Lambda LiCor Model LI-185 light meter attached to an underwater quantum sensor (LI-192S) strobe light.

Juvenile chinook salmon (*Oncorhynchus tshawytscha*) and rainbow trout (*Salmo gairdneri*) were obtained from the University of Washington Hatchery and were held in flow-through tanks fed by Lake Washington water for several months prior to the experiments. Many had been exposed to strobe light before. All fish appeared healthy and were dark adapted for at least one hour before testing, unless otherwise stated.

Tests were recorded on a Panasonic AG-6200 VCR with a low light Dage-MTI Model 60 video camera. The camera was capable of resolving faceplate illuminations to $2 \times 10^{-6} \mu\text{E}/\text{m}^2/\text{s}$. Time to 0.01 s was recorded onto the video tape with a Panasonic Time Date Generator Model WJ-810. The video tapes were analyzed to obtain escape speed, time of first reaction to the light, percentage of fish moving away from the light, total distance traveled away from the light, and other variables. At least seven replicates were run for each condition, unless stated otherwise. Two basic experimental procedures (Cruise and Blast) were used and each is discussed below.

Cruise Procedure. Fish over 100 mm long tend to "cruise" from one end of the tank to the other. This natural swimming behavior was utilized to gain insight into the effect of strobe lights on moving fish.

Fish were allowed to cruise for a few minutes before exposure to the light. As the fish swam toward the strobe light end of the tank, the light was turned on when they passed a mark 1.2 m in front of the strobe. This design allowed the fish to respond to the light before reaching the highest intensity zone. Also, the design caused fish to swim into the lighted region for some distance before turning away. Approach speed (swimming speed prior to light exposure), initial response, percentage of fish traveling less than 1.2 m into the light before turning away from the light, average turn position, and escape speed were noted.

Blast Procedure. Here, the fish were manipulated (using light, visual references, or overhead refuge) to remain in a specified area directly beneath the strobe. All fish faced the light and were either stationary, or swam in a small current, when the strobe light was turned on; thus they suddenly were 'blasted' by light and could either move directly away from the light or remain in the bright region. Measurements included delay time, total distance traveled away from the light, escape speed, and response type.

3.0 EXPERIMENTAL REVIEWS

3.1 The Response of Salmonids to Vertical Bars

We investigated the response of rainbow trout to a trashrack-like barrier (henceforth called vertical bars (VBs)). Individual fish were placed at the end of a trough near the strobe light. The strobe light was turned on forcing the fish to swim through the VBs to escape from the flashing light. We observed their behavior as they attempted to deal simultaneously with both of these aversive stimuli.

Methods

The experimental trough was approximately 4.5 m long and 0.4 m wide. Water depth was 0.1 m and water temperatures ranged between 19 and 20°C. The bottom of the tank was marked off in 0.4 m increments for recording fish position. The trough was shielded with black plastic. All work was done at ambient light levels and the fish were all light adapted.

The VBs were made of one by three wooden slats held 0.15 m apart by a horizontal cross board. Two wooden slats, 0.025 m wide and 0.08 m deep, were placed 0.15 m from one another and 0.13 m from the tank walls. Five different VBs positions were investigated: 0.8, 1.2, 1.6, 2.1, and 2.5 m from the strobe light. Control tests were also conducted with no VBs. Several replicates were made for each position.

The strobe was placed inside an aquarium submerged in the trough. In the experiments, the strobe light was turned on and intensity was continuously and evenly increased until the fish swam 0.4 m from the strobe light, or until one minute elapsed. The strobe light flash rate was 600 per minute.

Experiments were conducted with two different trout size groups (large = $(x + SE \text{ mm}) 113 \pm 1.2$, small = 74 ± 1). Fish were allowed to acclimate for 3 minutes after being placed into the trough directly beneath the strobe and before being exposed to light. We recorded the percentage of fish that swam through the VBs at least once during the acclimation time. The strobe light was turned on when a fish was underneath and facing into the light.

The following data were collected by direct observation and video:

Strobe Off

percentage of fish retained by the VBs

Strobe On

percentage of fish passing the 0.4 m line
delay time

percentage of fish retained by the VBs

number of times a fish turned back toward the light

position of turn back toward light with respect to VBs

total distance traveled away from the light

escape speed

Only fish that moved past the 0.4-m mark were included in the presentation of the last six parameters above.

Results

Strobe Off. Thirty-eight per cent of the small fish and 30% of the large fish did not swim to the opposite end of the trough (4 m) within the first three minutes. At VB positions of 0.8 m, 1.2 m and 1.6 m, 48%, 55%, and 65% of the small fish, and 80%, 60%, and 82% of the large fish, respectively, were retained on the strobe light side of the VBs (Fig. 1). These data suggest that the presence of VBs inhibit fish motion.

Strobe On. Some fish did not move away from the strobe light; they either appeared stunned or they swam frantically from wall to wall beneath the light. Fish that failed to move away from the light and never passed the 0.4 m mark were designated 'zero fish'. Ten per cent of the large fish and 28 per cent of the small fish fell into this category in the absence of any VBs. The VBs had no clear effect on this parameter.

Of the fish that swam past the 0.4 m mark, some number did not pass the VBs:

% Retained by VBs

VB DIST from Strobe (m)	0.8	1.2	1.6	2.0	2.5	none
Large trout	10	10	25	0	0	0
Small trout	25	20	29	25	0	0

In the absence of VBs, all (non-zero) fish swam to the end of the tank. Thus, the VBs acted as a complete barrier to 10-30% of the fish if the bars were less than 2 m from the strobe.

The VBs inhibited the small fish from moving away from the strobe light and the closer the bars to the light, the longer the delay (Fig. 2). VB positions of 1.2 and 1.8 m from the light caused the greatest delay among the larger fish.

Delay time was related to the average strobe intensity setting at which the fish moved past the 0.4 m mark. A higher light intensity was needed to move the fish down the trough when the VBs were closer to the strobe (Fig. 3). The aberrant point (circled in Figs. 2 & 3) was consistently found with all parameters, and suggests that a size dependent critical distance between the strobe light and the VBs, caused a qualitative shift in the escape response.

As the fish approached the VBs they often turned back toward the light and circled in front of the VBs before actually passing. The number of times the fish turned back toward the light is presented below.

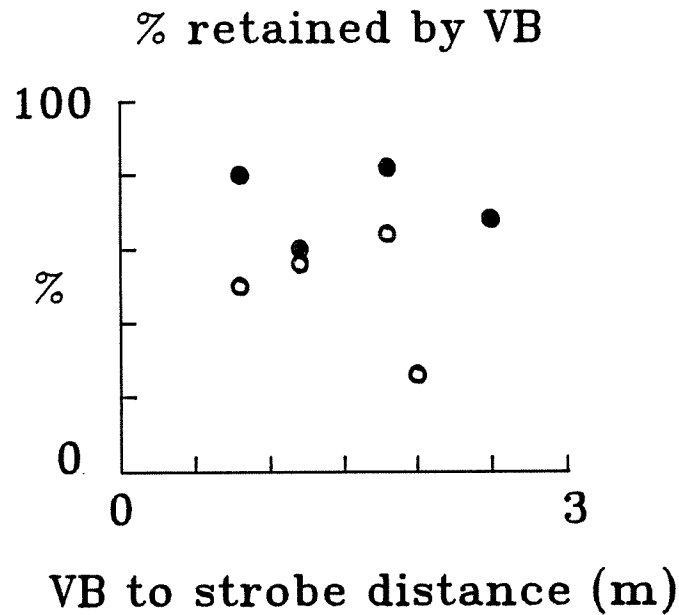


Fig. 1. Percentage of rainbow trout retained by vertical bars (VBs) with the strobe light off. Data are shown separately for two different trout size groups: ● (x = 113 mm) and ○ (x = 74 mm).

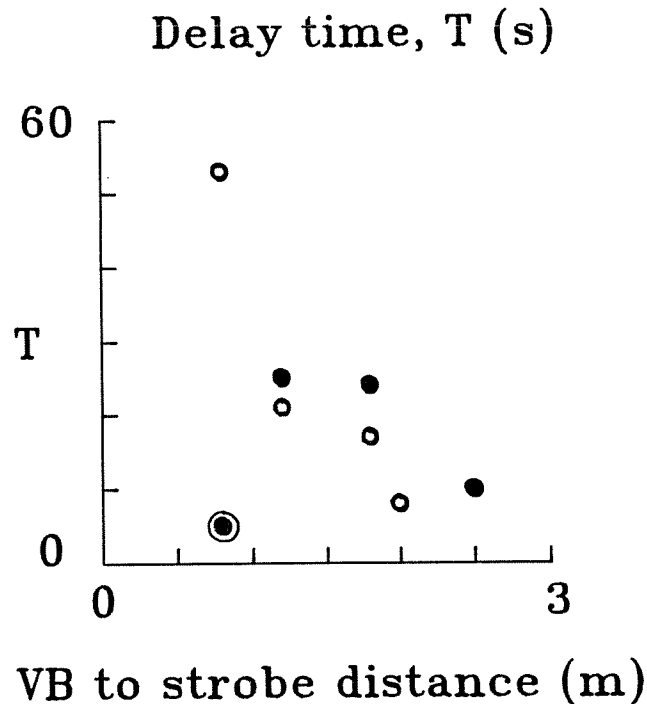


Fig. 2. Avoidance response delay time as a function of VB distance from the the strobe light. The circled datum does not fall along the otherwise decreasing function between delay time and VB position.

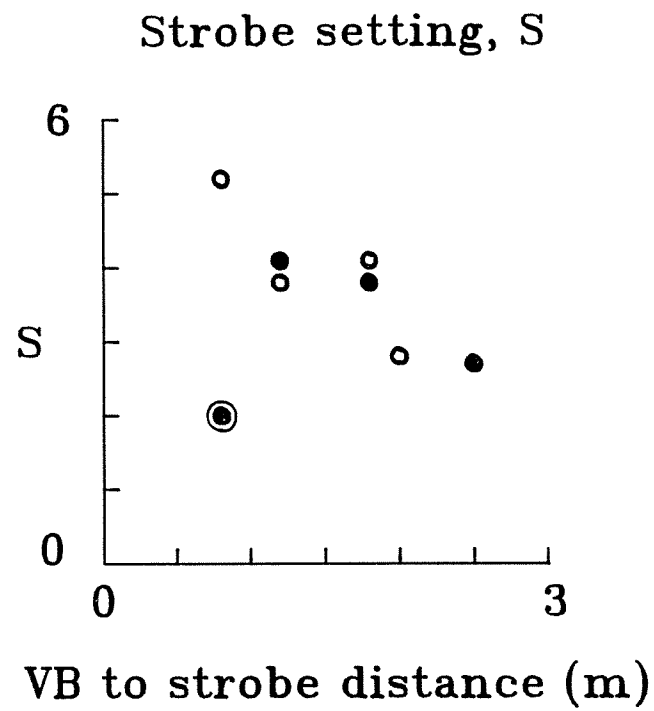


Fig. 3. Arbitrary strobe light intensity setting at which trout first swim away from the light as a function of VB position. The circled datum does not fall along the otherwise decreasing function between SI setting and VB position.

Number of Times Trout Turn Back Toward Light

VB DIST from Strobe (m)		0.8	1.2	1.6	2.0	2.5	no VBs
Large:	mean	0.6	1.3	1.3		0.1	0
	SD	1.1	1.3	1.4		0.3	0
Small:	mean	2.3	0.9	1.0	1.7		1.2
	SD	1.5	1.4	1.8	2.6		1.3

The position at which a fish turned back toward the strobe light was highly dependent upon VB position (Fig. 4).

Fish speed in front of the VBs seemed to be independent of VB position, except when the VBs were close to the light. In that case, the small trout swam slower and the large trout swam faster than at other VB positions.

Speed in Front of the VB (Body Lengths/s)

VB DIST from Strobe (m)		0.8	1.2	1.6	2.0	2.5	no VBs
Large:	mean	7.8	5.6	5.7		6.6	5.7
	SD	4.4	5.0	3.6		2.3	1.9
Small:	mean	0.7	6.3	3.8	6.2		4.5
	SD	0.5	4.4	3.0	0.9		1.7

Total escape speed showed similar patterns for both large and small fish (Fig. 5). Total escape speed was higher with VBs than without VBs, and highest when the VBs were close to the fish.

Total distance travelled away from the light appeared to be independent of VB position with all trout moving about 2.5 m away from the light.

Summary

In still water, the presence of VBs inhibited the natural movement of rainbow trout. In the absence of VBs, 30% of the large fish and 25-38% of the small fish remained within 0.8 m of the strobe. In contrast, on average, 72% of the large fish, and 58% of the small fish were contained in the area to the strobe side of the VBs.

When trout were forced to choose between swimming away from the strobe light and toward the VBs they reacted as if to balance two opposing forces. About 25% of the small fish and 10-25% of the large fish swam away from the light only to turn back toward it upon reaching the VBs. These fish continued to circle in front of the VBs, apparently alternately reducing the stimulus from each source.

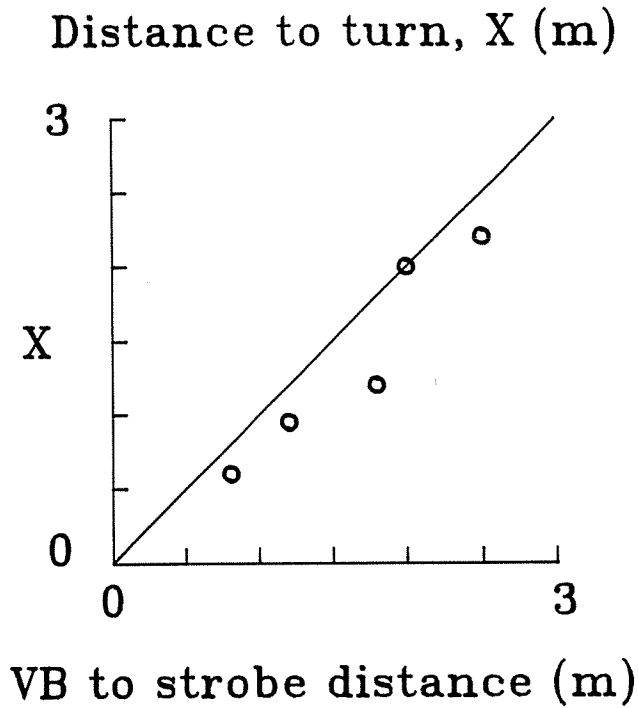


Fig. 4. Average position at which trout turn back toward the strobe light as a function of VB position. If trout were turning at the VB, data would fall on the line; the displacement below the lines shows that trout consistently turn back toward the light about 0.2 m in front of the VB.

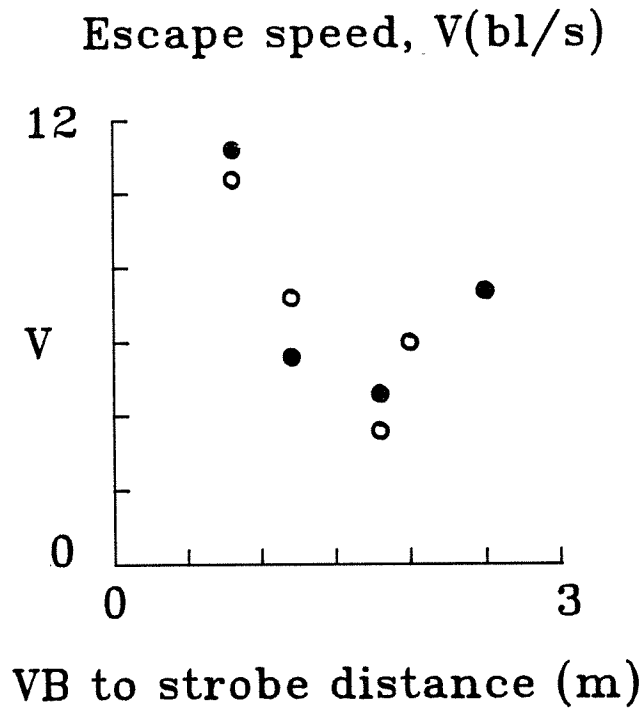


Fig. 5. Trout avoidance speed as a function of VB distance from the strobe light.

Trout were driven through the VBs with a strobe light. When the VBs were near the strobe, the large trout swam away from the light faster, with less delay, and at a lower illumination than when no VBs were present. Small trout responded in the opposite fashion:

Response Ratio (VB/no VB) for Various Parameters

	SPEED	DELAY TM	THRESHOLD SI
Large trout	1.4	0.5	0.8
Small trout	0.2	7.6	3.1

These parameters were not independent and the values were also highly variable. Nonetheless, this difference in initial response seems noteworthy, particularly since large trout showed the same response direction as small trout when the VBs were further from the strobe. These results suggest that the response to the VBs depended upon fish size and the relative positions of the strobe, fish, and VBs. If the VBs were closer to the strobe than a critical distance, then the VBs acted to reinforce the strobe avoidance response. Once the VBs were beyond the critical distance, they inhibited avoidance of the strobe. Furthermore, strobe avoidance inhibition decreased as a function of distance between the two stimuli (Fig. 6).

3.2 Effect of Flash Rate

Experiments designed to investigate the influence of flash rate on fish response to strobe light are summarized in the following table and discussed below in reverse chronological order.

Summary of Flash Rate Experiments

EXP#	SPECIES	LTH (mm)	T °C	FLASH RATES (1/min)	EXPERIMENTAL PROCEDURE
1	chinook	60	11	78, 200, 720	Fish in bowl, hi light, turns counted
2	chinook	115	21	78, 180, 240 300, 420, 600 780	Blast Procedure
3	rainbow	150	20	79, 99, 128, 173, 269	Blast Procedure
4	rainbow	135	11	78, 110, 140 180, 780	Cruise Procedure

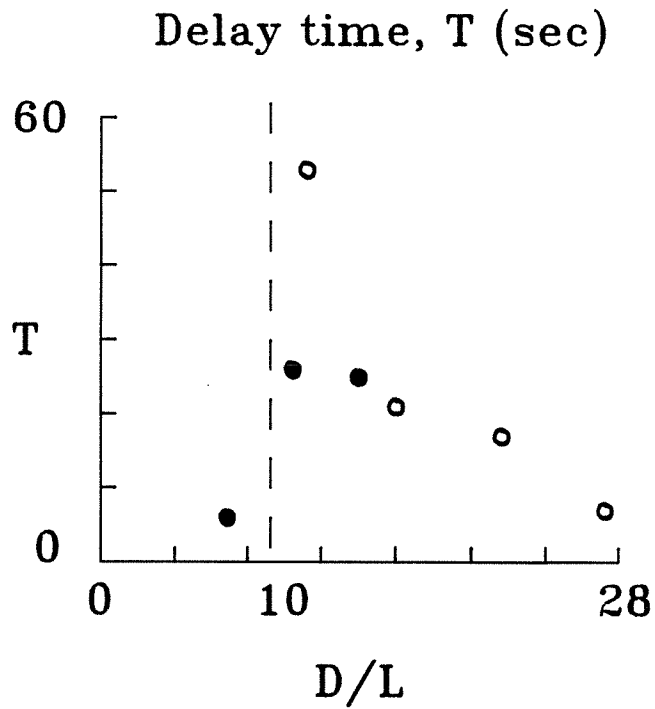


Fig. 6. Trout delay time is plotted vs the ratio of the distance (D) between the VBs and the strobe light to trout length (L). It is suggested that a size-dependent critical distance defines whether the VBs act to reinforce or inhibit avoidance of the strobe light. Dotted line indicates threshold region. o = small trout; o = large trout.

Experiment 4:*Methods*

Rainbow trout were tested for response to various strobe flash rates in a 3 m long trough. The strobe light was turned on as the trout swimming toward the strobe passed a mark 1.2 m in front of the strobe.

Results

The average distance traveled toward the light before turning varied as a function of strobe flash rate (Fig. 7). The greatest difference occurred between 78 and 180 flashes per minute. Each of these flash rates was associated with a different overall light intensity even though the intensity setting remained the same.

The major response change occurred between 0.12 and 0.22 $\mu\text{E}/\text{m}^2/\text{s}$ (very small light intensity range), suggesting that it was associated with rate, not intensity (Fig. 8).

Experiment 3:*Methods*

Rainbow trout were encouraged to swim directly in front of the strobe light and were then suddenly blasted with light at flash rates ranging from 79 to 269 per minute.

Results

Regardless of flash rate, about 50% of the fish moved 0.9 m away from the strobe within 5 seconds of the first flash. Other data are reported below.

Experiment 3 Data Table

Flash Rate	(1/min)	79	99	128	173	269
Delay Time (s)	mean	1.3	1.4	2.4	1.6	0.4
	SD	3.6	1.7	5.3	2.7	0.8
	N	13	8	13	11	9
Distance (m) moved in 5 sec	mean	0.9	0.9	1.0	1.1	1.1
	SD	0.4	0.4	0.4	0.2	0.2
	N	13	9	13	11	9
Speed (BL/s)	mean	2.4	2.3	2.0	1.7	1.8
	SD	16.2	11.4	8.3	6.7	9.5
	N	13	9	12	11	9

All of these fish moved away from the light (i.e., no zero fish).

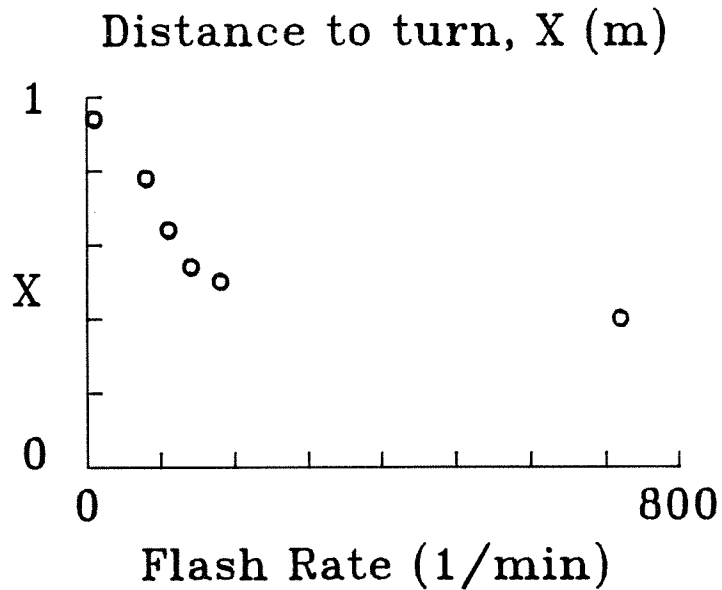


Fig. 7. Average distance that rainbow trout swam toward the light before turning, as a function of flash rate. Low values on the ordinate represent the strongest avoidance response.

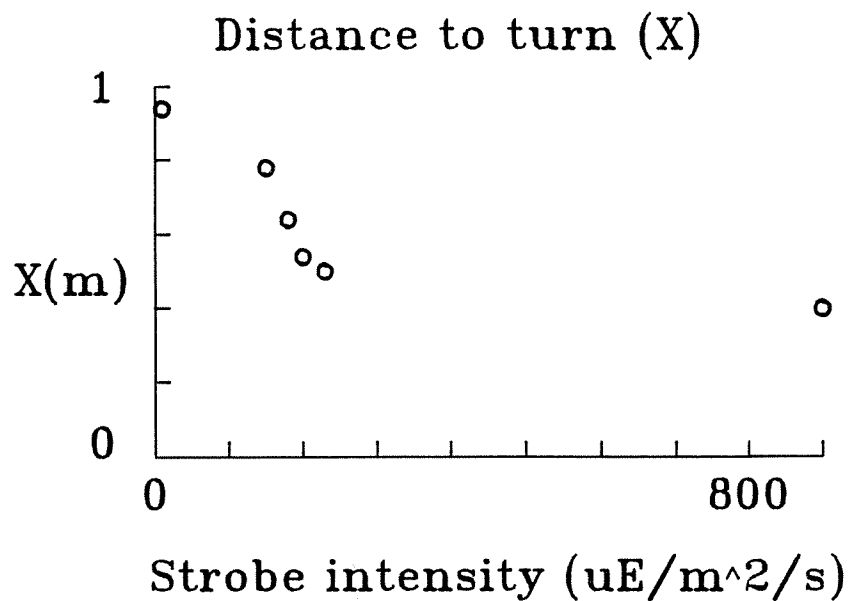


Fig. 8. Average distance rainbow trout swam toward the light before turning vs measured strobe intensity (increasing due to flash rate). Seventy percent of the response change occurs over an intensity range of $0.1 \mu\text{E}/\text{m}^2/\text{s}$, suggesting that the response change is due to flash rate.

Experiment 2:*Methods*

Young chinook swam directly in front of the strobe in a 3 m long trough and were then blasted with light at rates ranging from 78 to 780 flashes per minute.

Results

These salmon showed a consistent difference in their response to all flash rates. Only 30% of the fish moved beyond the 0.3 m line at 78 flashes/min (Fig. 9); most fish circled about and appeared to be 'stunned.' The chinook exposed to 78 flashes per minute endured high strobe light intensity, delayed their response (Fig. 10), and didn't move very far.

Experiment 1:*Methods*

Small chinook were placed into a 3 liter cylindrical tank and subjected to very high strobe intensities. The number of turns counted per unit time provided an index of the need to escape.

Results

This group of 60 mm chinook showed a sharp increase in response between 78 and 200 flashes/min (Fig. 11).

3.3 Effect of Strobe Intensity

Experiments were conducted to investigate the affect of strobe intensity on the avoidance response of juvenile salmonids. These will be described in reverse chronological order and a summary table is provided below.

Summary of Strobe Intensity Experiments

EXP#	SPECIES	LTH (mm)	T °C	FLASH RATE	INTENSITIES TESTED ($\mu\text{E}/\text{m}^2/\text{s}$)	PROCEDURE
1	chinook	70	11	780	0.23, 1.23, 3.7, 4.0, 7.9	Cruise
2	rainbow	140	21	180	0.03, 0.06, 0.07, 0.13, 0.88, 9	Cruise
3	rainbow	135	11	180	<<0.02, 0.02, 0.2, 1.2 3.3	Blast

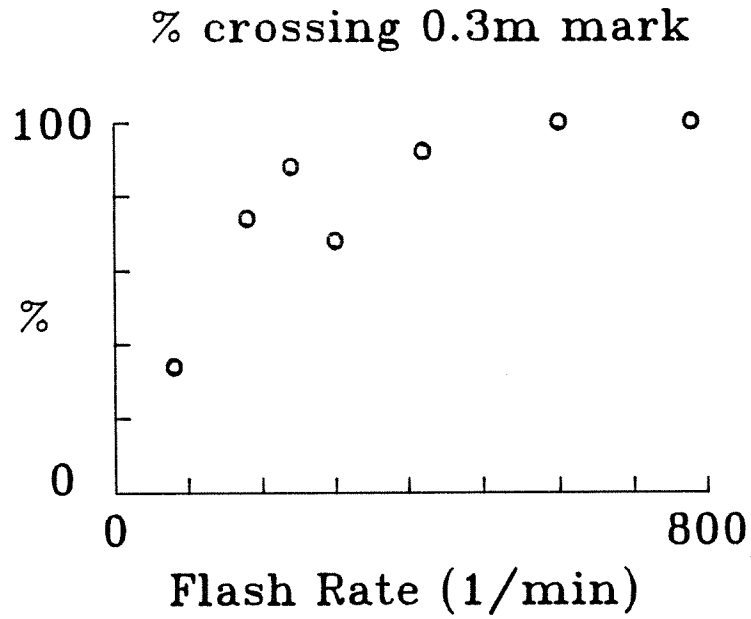


Fig. 9. Percentage of chinook crossing the 0.3 m mark after onset of the strobe light. A number of fish did not swim away from the light at the lowest flash rates.

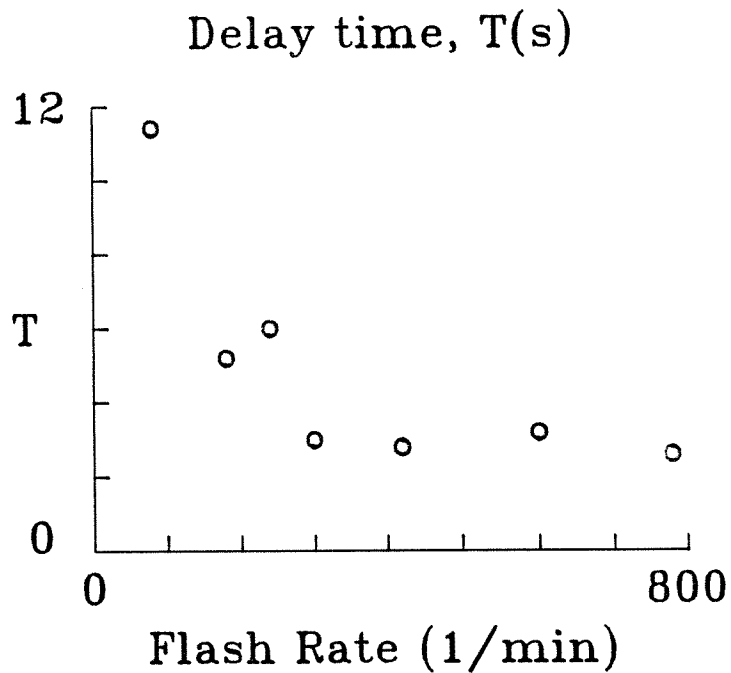


Fig. 10. Chinook avoidance response delay time vs flash rate.

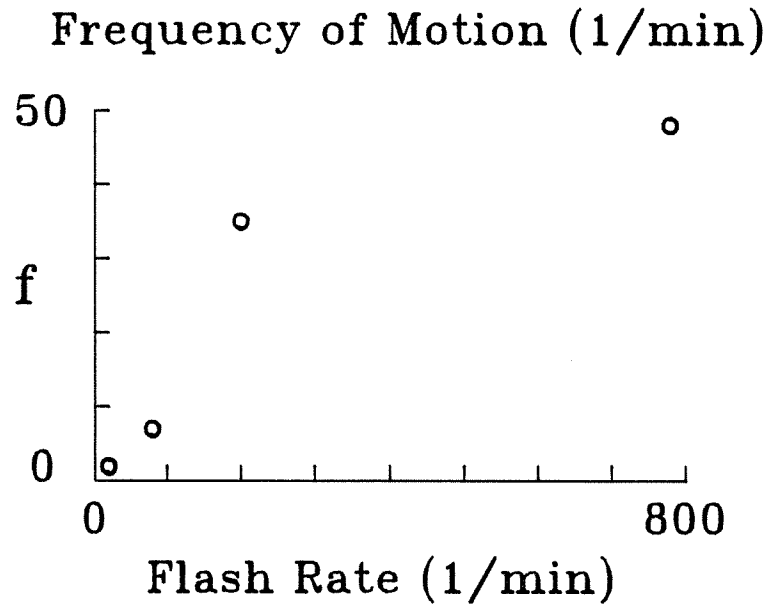


Fig. 11. Mean frequency of 'avoidance motions' of chinook as a function of flash rate.

Experiment 3:*Methods*

Rainbow trout were placed into a 3 m long trough and allowed to 'cruise' from one end of the tank to the other end. As the trout swam past a mark 1.2 m in front of the strobe, they were suddenly subjected to flashing light, which varied in intensity from less than 0.02 $\mu\text{E}/\text{m}^2/\text{s}$ to 3.3 $\mu\text{E}/\text{m}^2/\text{s}$.

Results

The number of startle responses differed dramatically as a function of strobe intensity. For example, over 70% of the fish startled as the light was turned on at 0.02 $\mu\text{E}/\text{m}^2/\text{s}$ and over 40% of the fish startled at 0.2 $\mu\text{E}/\text{m}^2/\text{s}$. No startles occurred at any other intensities.

Regardless of intensity, 10 to 60 per cent of the trout stopped swimming once the light was turned on. Approximately one-half of the fish swam forward less than 1/2 m before turning away from the strobe light, except at very low light levels. The highest light intensity seemed to inhibit the escape response.

The average approach speed of the trout was 2.2 bl/s. The average speed in the 2-second interval after the light was turned on was slower than the approach speed if the fish were traveling toward the light in the escape, and faster than the approach speed if the fish were traveling away from the light in the escape (Fig. 12).

Avoidance Speed
(bl/s)

SI	($\mu\text{E}/\text{m}^2/\text{s}$)	0	<0.02	0.02	0.2	1.2	3.3
Toward	mean	2.1	1.7	2.3	1.5	1.8	2.7
	SD	1.1	0.6	0.8	1.2	0.5	2.5
	N	7	5	5	4	3	4
Away	mean		1.7	2.7	1.9	3.0	2.9
	SD		0.8	0.6	0.8	1.1	1.5
	N		2	2	3	4	3

Experiment 2:*Methods*

Rainbow trout were placed in a 3 m long trough. When they were directly in front of the strobe, they were "blasted" with light.

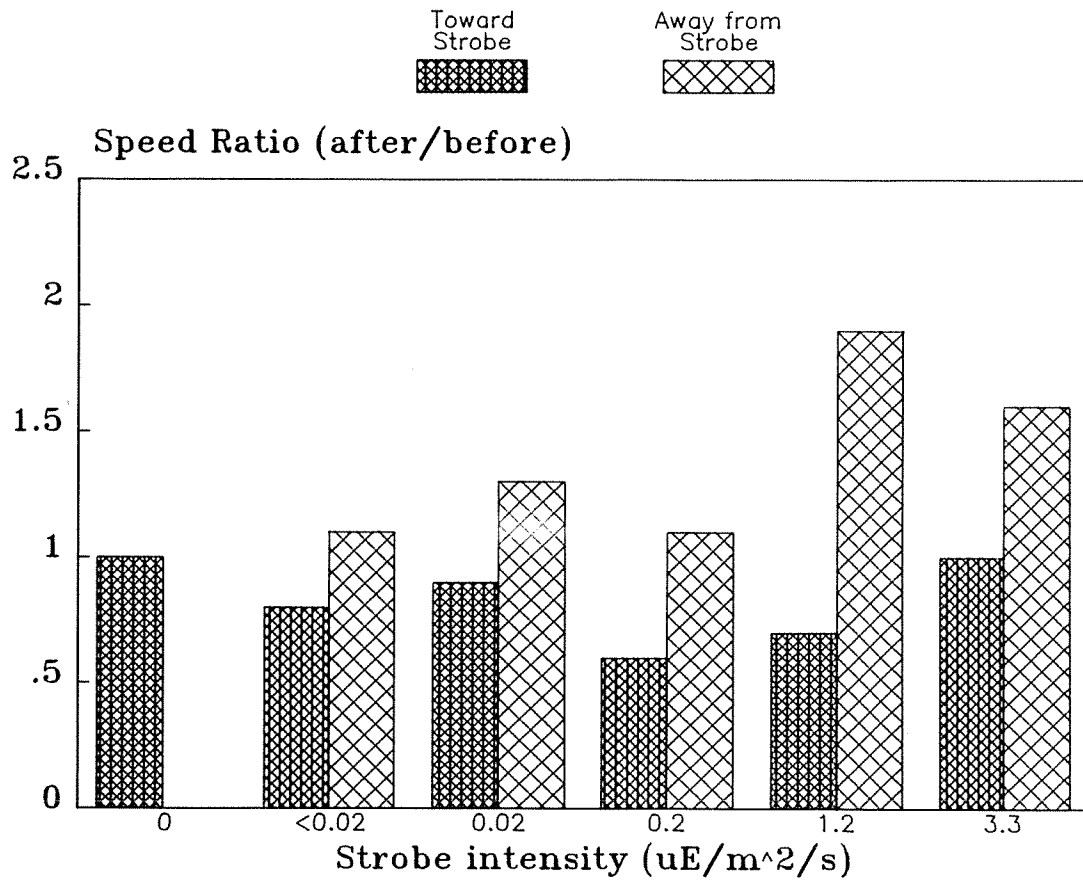


Fig. 12. The ratio of speed before turning on strobe light to speed after turning on strobe light for trout. The graph demonstrates that if the fish turned away from the light, they traveled faster with the light on; if the fish continued toward the light, their speed was slower with the light on.

Results

An analysis of variance showed that the total distance traveled away from the strobe light, and the speed over the total distance traveled, were both related to strobe light. Trout swam further away from the light at the lower intensities. More "zero fish" occurred at the high light intensities than at the low intensities. These data are presented below along with speed measurements.

Intensity Experiment 2 Results

SI ($\mu\text{E}/\text{m}^2/\text{s}$)		0.03	0.08	0.07	0.13	0.88	9.1
% zero fish		0	0	0	11	22	11
Distance (m)	mean	0.9	1.2	1.0	0.6	0.7	0.8
	SD	0.4	0	0.3	0.4	0.4	0.4
	N	8	7	10	11	9	9
Speed (BL/s)	mean	1.5	3.0	2.3	1.6	2.5	1.6
	SD	10	8.9	13.0	15.7	12.8	8.1
	N	8	7	10	10	7	8

Experiment 1:*Methods*

Juvenile chinook swam in a small current directly in front of the strobe light and were "blasted" at strobe intensities ranging from $0.23 \mu\text{E}/\text{m}^2/\text{s}$ to $7.9 \mu\text{E}/\text{m}^2/\text{s}$.

Results

In approximately one half of all the experiments, the fish swam toward the strobe light within the first ten seconds of exposure. Chinook appeared to be either stunned or in a state of panic. Swimming directly away from the strobe light did not often occur, but was most likely under higher light levels in the background.

The average escape speed ($\bar{x} \pm 1\text{SE}$, $n = 66$) was 0.92 ± 0.10 ft/s (28 cm/s or about 4 body lengths/s). Mean escape velocities were a function of strobe intensity (Fig. 13). Fish responded most strongly between strobe intensities of 1 and $3.9 \mu\text{E}/\text{m}^2/\text{s}$.

Summary

The following table summarizes the results of the three experiments designed to investigate the effects of strobe intensity on the response of salmonids to flashing light.

Results of Strobe Intensity Experiments

Showing light levels that induced maximum values of parameters

EXP#	PARAMETER	MAR*	PARAMETER	MAR	PARAMETER	MAR
1	speed	1.23-3.7				
2	speed	0.06-0.9	distance	0.03-0.07	%zero fish	0.03-0.7
3	speed	1.2,3.1	turn dist	0.02-1.2	% turning	0.02-3.3

*Range of light ($\mu\text{E}/\text{m}^2/\text{s}$) for maximum response.

3.4 "Box" Effect

An experiment was conducted to determine whether the salmonid response to strobe light was altered by the walls of the experimental trough.

Methods

Rainbow trout (135 mm) were placed into several different sized enclosures, produced by placing a clear plexiglass plate (strobe facing end) and a metal grate (back end) between the walls of the trough. The distance between the front end of a box and the strobe light was also varied. The "cruise procedure" was followed and box lengths were: 0.6, 0.9, 1.2, 1.5, 1.8, 2.1, and 2.4 m.

Results

Nearly all fish swam actively against the clear plate facing the strobe light for box lengths ranging from 0.6 to 1.8 m. Many fish swam away from the light once the box was expanded to 2.1 m (Fig. 14). The distance of the plexiglass box front to the strobe did not cause any response differences.

A second experiment, using methods outlined in the vertical bars section, revealed that the size of the holding tank altered the response of the fish. Fifty per cent of the rainbow (N = 6) held in a 0.7 m long trough and then placed into the 4 m long experimental trough never moved away from the strobe light. In contrast, all fish (N = 7) held in a 4 m long trough and then transferred to the experimental trough moved away from the light.

In an experiment at Rocky Reach Dam, 100 mm chinook held in a 1.3 m by 1.3 m net pen did not consistently swim away from the strobe light (see Section 3.9). Fifty percent of the chinook, rainbow and steelhead trout tested in a 3 m long trough consistently swam away from strobe light. In contrast, all rainbow trout tested in an 8 m long raceway consistently swam away from strobe light (see Appendix 2).

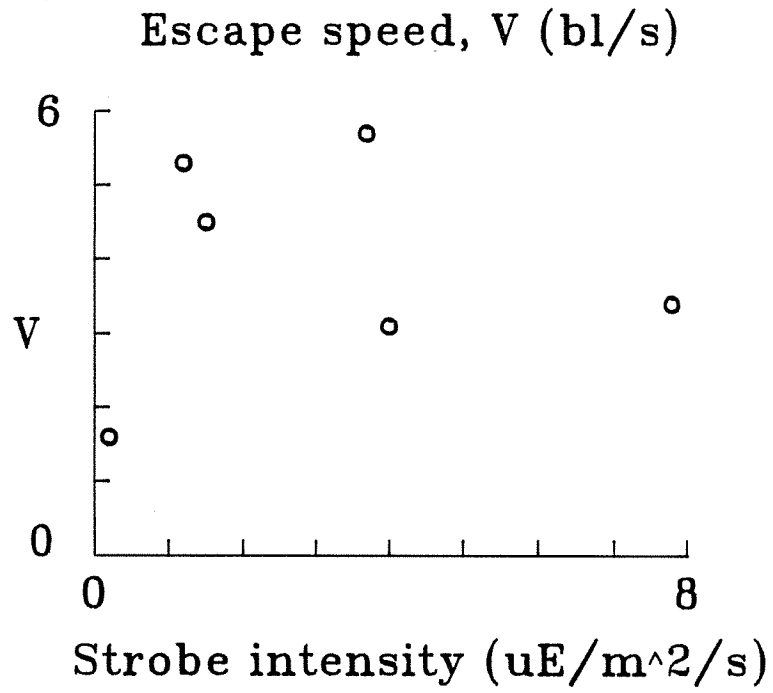


Fig. 13. Chinook avoidance speed as a function of strobe light intensity.

Those fish which avoided strobe light in the 3 m long trough showed the same response curve as fish tested in the 8 m long raceway. For example, 70-80% of the maximum avoidance response was obtained at a flash rate of 200/min in both the 8 m long raceway and the 3 m long trough. Thus, fish which avoid strobe light in a relatively small trough provide a reliable index of behavior in a large raceway.

These results indicate that enclosure size affects the avoidance behavior of salmonids to strobe lights. Furthermore, it appears that in circumstances when the use of large troughs is impractical or impossible, the effect of enclosure size can be accounted for.

3.5 The Effect of Time of Day

An experiment was conducted demonstrating that the response to strobe light may change depending upon time of day.

Methods

Rainbow trout were placed into a 3 m long trough and tested for movement away from strobe light using the cruise procedure. The experiment was repeated at eight different times during one 24 hour period. Seven naive fish were tested at each time (i.e., N = 56).

Results

The most striking result was a complete inhibition of the avoidance response at 7:00 AM (Fig. 15). Steelhead tested at 7:00 A.M. (in a similar experiment) also showed 0% turning within 1/2 m.

3.6 Effect of Experience

An experiment was conducted to test the affect of previous exposure to strobe light on the avoidance response. The general behavior of 7 naive rainbow trout was compared to the behavior of 7 previously exposed rainbow trout.

Methods

Fish were placed individually into a 3 m long trough and allowed to cruise past the 1.2 m mark before exposure to strobe light. The strobe intensity setting and flash rate were set at 5 and 180, respectively.

Results

Prior exposure to strobe light did not alter the escape response as measured by the percentage of fish turning away from the light before traveling 1/2 m toward the light, or the average distance traveled before turning away from the light.

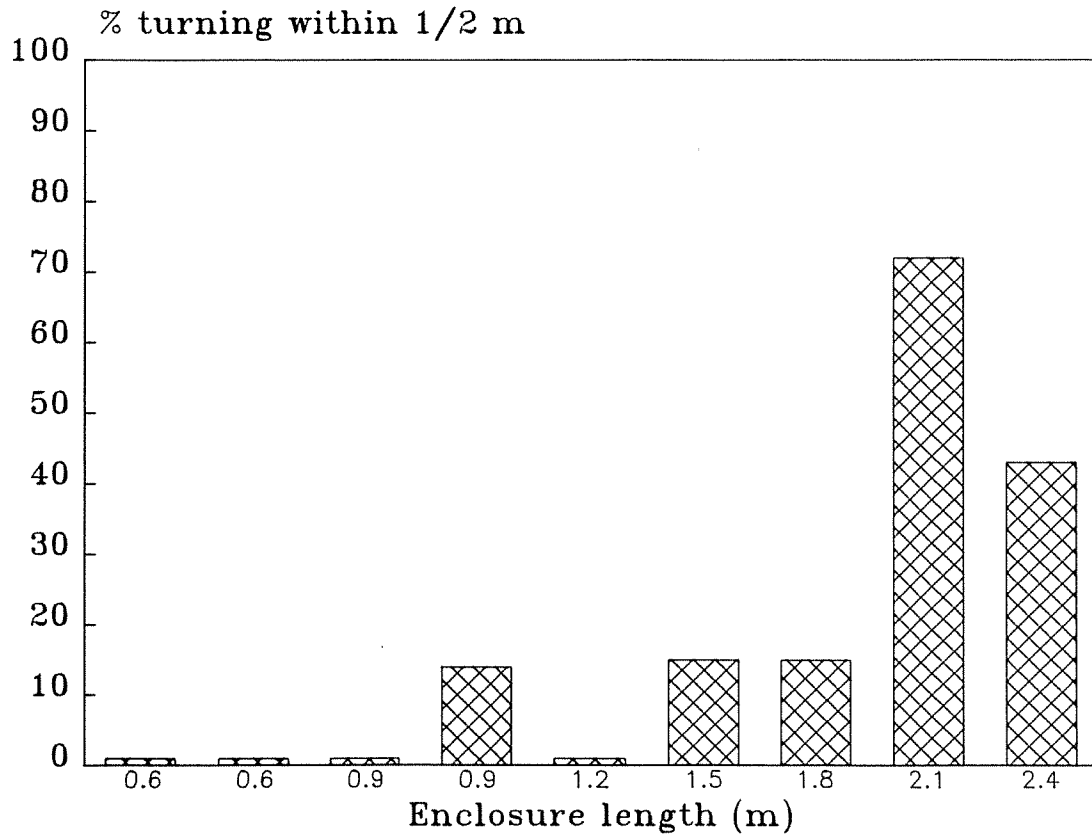


Fig. 14. Percentage of rainbow trout turning away from the strobe before traveling 1/2 m toward the light as a function of enclosure length. Seven replicates were run for each condition (N=63). Equal box lengths indicated on the abscissa were experiments run with the front box edge at different distances from the strobe light. The 2.4 m box length was used in many experiments presented in this report.

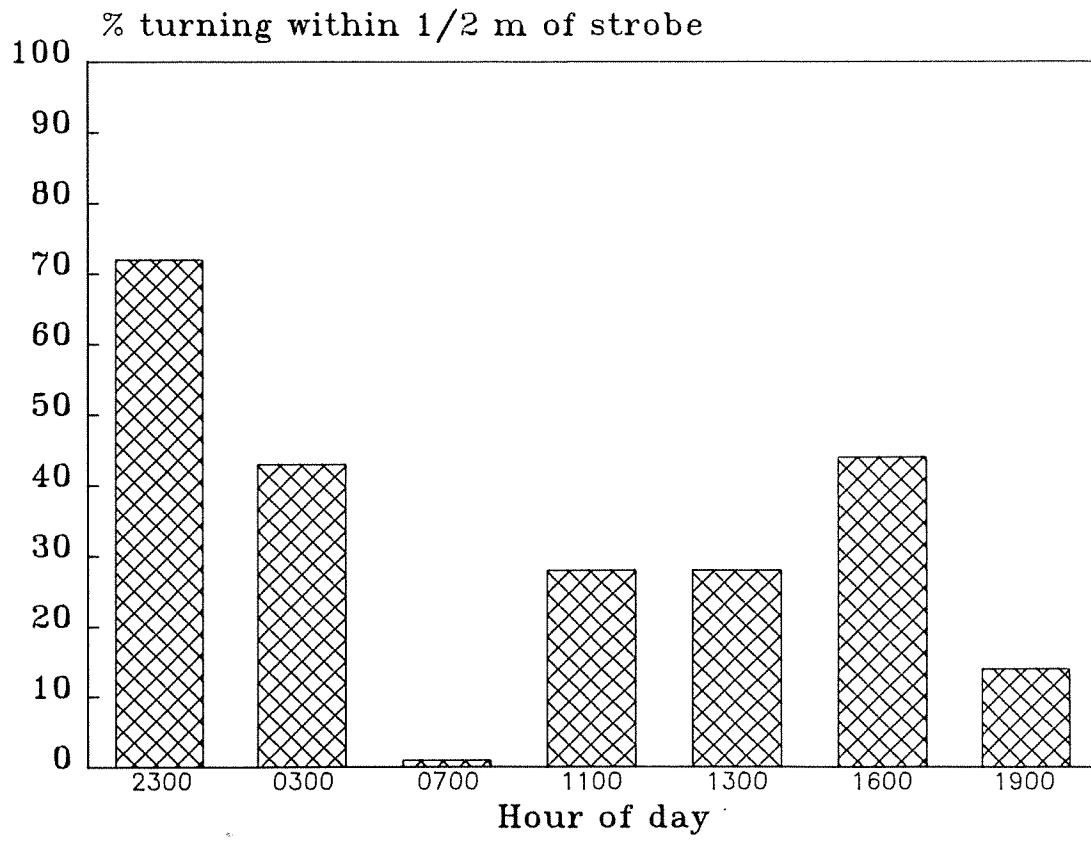


Fig. 15. Percentage of rainbow trout turning away from the strobe light as a function of time of day. N=7 for each time period. No fish turn away from the light quickly at 7:00 AM.

		Naive	Non-naive
% turning within 1/2 m		57	71
turn distance (m)	mean	0.5	0.5
	SD	0.3	0.3

3.7 Reference Experiments

Experiments were performed to identify how the response to strobe lights compared with other stimuli.

Methods

Rainbow trout and steelhead, about 135 mm long, were tested in a 3 m long trough using the cruise procedure. As a fish crossed the 1.2 m mark, it was subjected to strobe light, a lacrosse ball dropped from a height of 1.5 m, or a falling seven pound brick. The average turn position and the percentage of fish turning before traveling 1/2 m toward the light were recorded for each stimulus.

Results

No difference was apparent between the groups. This suggests that failure to swim away from strobe light was likely associated with enclosure size and did not mean that strobe light was a weak stimulus. Nearly as many trout failed to swim away from a falling ball or brick as from strobe light.

		RAINBOW TROUT		STEELHEAD	
		STROBE	BALL	BALL	BRICK
Turn position (m)	mean	0.5	0.5	0.5	0.6
	SD	0.5	0.5	0.6	0.3
	N	7	7	7	7
% Turning in 1/2 m		57	29	57	33

3.8 Effect of Flash Rate on Direction of Escape

Introduction

Laboratory experiments were conducted to determine if the direction of escape from strobe light was dependent on the flash rate. The experimental facility was designed to force fish down an approach alley into a test chamber containing a strobe light. Fish could see the reflection of the

strobe light in the approach alley, but they did not directly encounter the light until they entered the test chamber. This arrangement was used to partially mimic the experience of fish being drawn toward a trashrack and strobe lights.

Materials and Methods

Yearling steelhead trout (*Salmo gairdneri*) raised at the University of Washington's School of Fisheries hatchery were used in the experiments (Nov. 28-30, 1986). The average fish length was 118 mm. Fish were tested in a facility consisting of a tank divided into a holding chamber, an approach alley 1-m long, and square test chamber 1 m x 1 m x 0.2 m (Fig. 16). A constant flow of 11°C water from Lake Washington flowed through the system entering through the holding facility and exiting through the far end of the test chamber.

Fish were fed and held in the holding chamber overnight before the experiments. Individual fish entered the approach alley through a trap door in the alley wall. Fish were forced down the approach alley with a screen. Entering the test chamber, they encountered the strobe light.

Light intensity ($\mu\text{E}/\text{m}^2/\text{s}$) measured from the strobe (cm) for test chamber and alley for five different flash rates.

cm ⁺	0	144 ⁺⁺	288	488	600
			<u>Test chamber</u>		
0	0.05	8.40	13.50	21.60	27.60
10	—*	1.50	2.50	3.60	4.50
20	—	0.60	1.00	1.50	1.80
30	—	0.30	0.51	0.72	0.93
40	—	0.24	0.39	0.54	0.69
50	—	0.18	0.30	0.42	0.51
60	—	0.15	0.24	0.30	0.39
70	—	0.12	0.18	0.26	0.33
80	0.05	0.09	0.15	0.20	0.24
			<u>Alley</u>		
0	0.05	0.12	0.18	0.26	0.33
10	—	0.05	0.05	0.08	0.08
20	—	—	—	0.06	0.08
30	—	—	—	0.06	0.06
40	—	—	—	0.05	0.06
50	—	—	—	0.05	0.05
100	0.05	0.05	0.05	0.05	0.05

+Distance measured from strobe tube.

++Flash rates are 1/min.

*Values equal to ambient light levels ($0.05 \mu\text{E}/\text{m}^2/\text{s}$).

A xenon strobe light with variable flash rate (Tandy Company) was housed in a glass tube in one corner of the test chamber. A second inoperative tube was placed in the opposite corner to provide symmetry in the chamber. The strobe was switched between both tubes to test for behavioral preference for one side of the chamber or the other. No preference was observed.

An ambient light level of $0.05 \mu\text{E}/\text{m}^2/\text{s}$ was produced by two 25W red incandescent bulbs. Strobe intensity was measured with a Li-cor model LI-185 photometer. The light intensity decreased in a radial fashion with distance from the strobe tube. The approach alley light intensities were one to two orders of magnitude lower than in the test chamber (Fig. 17). Because of the response lag of the light meter, strobe intensity decreased with flash rate.

The tests were conducted in the day with fish adapted to the red background lights. At the beginning of a test, a fish was allowed to voluntarily enter the alley. The video recorder and strobe light were turned on and two guiding screens of perforated plexiglass were used to maneuver the fish along the alley. The test was completed when the fish had come in contact with a wall in the test chamber or had stopped moving. Individual fish paths were traced onto acetate sheets from the video monitor.

The experimental design was as follows. Four fish in succession were tested at each of four flash rates: 140, 288, 488 and 600/min. Between changes in flash rate, one fish was tested under control conditions (no light). This balanced design reduced variability from uncontrolled factors such as time of day or the hunger state of the fish.

A continuity-corrected chi-square analysis (.05 level of significance) was performed as a comparison between the control (no light) group and each flash rate group to determine if there was a relationship between response and flash rate. To categorize responses for the analysis, the test chamber was divided into two zones, A and B, in which zone A contained the flashing strobe. The junction of these zones corresponded to the midline of the test chamber (Figure 16). Responses were categorized as positive if fish stayed or moved into zone B within one second of entering the test chamber and negative if, after one second, fish were in zone A.

A one-way ANOVA (.05 significance level) was performed to detect differences between mean speeds of the responses to different flash rates.

Results

Fish tested under control (no light) conditions showed no preference for either side of the test chamber. Most fish exposed to the strobe light (flash rates of 140, 288, 488 and 600) showed a preference for zone B, although only the 488/min group resulted in a significant difference

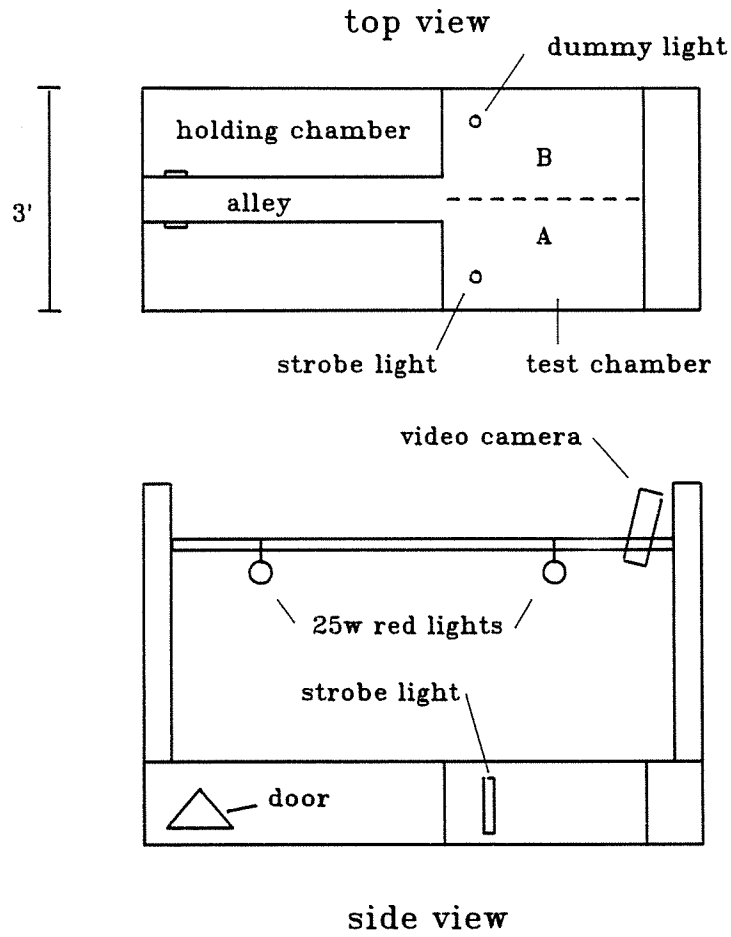


Fig. 16. Test facilities for angle experiments.

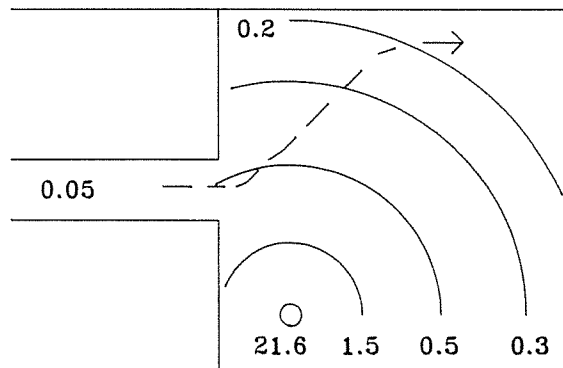


Fig. 17. Intensity of strobe light $\mu\text{E}/\text{m}^2/\text{s}$ in test chamber.

(Figure 18). At a .05 level of significance, the null hypothesis stating independence between fish direction and flash rate was rejected for 488 flashes/min but was not rejected for 140, 288, and 600 flashes/min. The continuity correction used in this chi-square analysis makes the significant result highly dependable.

Analysis summary showing the number of fish that moved toward or away from the strobe within one second during control (strobe off), 140, 288, 488 and 600/m flash rate tests. Chi-square critical value was 3.841 (df = 1, α = .05) and p-value is shown only for significant comparisons.

Strobe flash rate	No of fish		Chi-square	Conclusion
	Away	Toward		
0 (= control)	23	19	0.048	ns
140	11	8	0.002	ns
288	35	18	0.824	ns
488	14	2	4.052	.025 < p < .05
600	10	6	0.055	ns

Mean fish speeds at flash rates of 0, 140, 288, 488 and 600/min were 7.62, 7.42, 6.88, 8.04, and 6.69 bl/s, respectively. The computed ANOVA (.05 significance level) showed the differences between the mean fish velocities to be non-significant.

Mean velocity (bl/s) measurements and one-way ANOVA calculations (α = 0.05).

Strobe flash rate	Mean	(Std. dev.)	n	Source of variation	df	SS	MS	F	
0	7.62	(2.374)	42	BETWEEN GROUPS	4	28.44	7.11	1.49	
144	7.42	(1.672)	19						
288	6.88	(2.260)	53	WITHIN GROUPS	141	671.02	4.76		
488	8.04	(2.225)	16						
600	6.69	(1.818)	16						
TOTAL					145	699.46			
					(.10 < p < .25)				

Discussion

These data suggest that avoidance direction was affected by flash rate while the speed was not. The ANOVA performed on the mean fish speeds clearly showed no significant differences between control and flash rate groups.

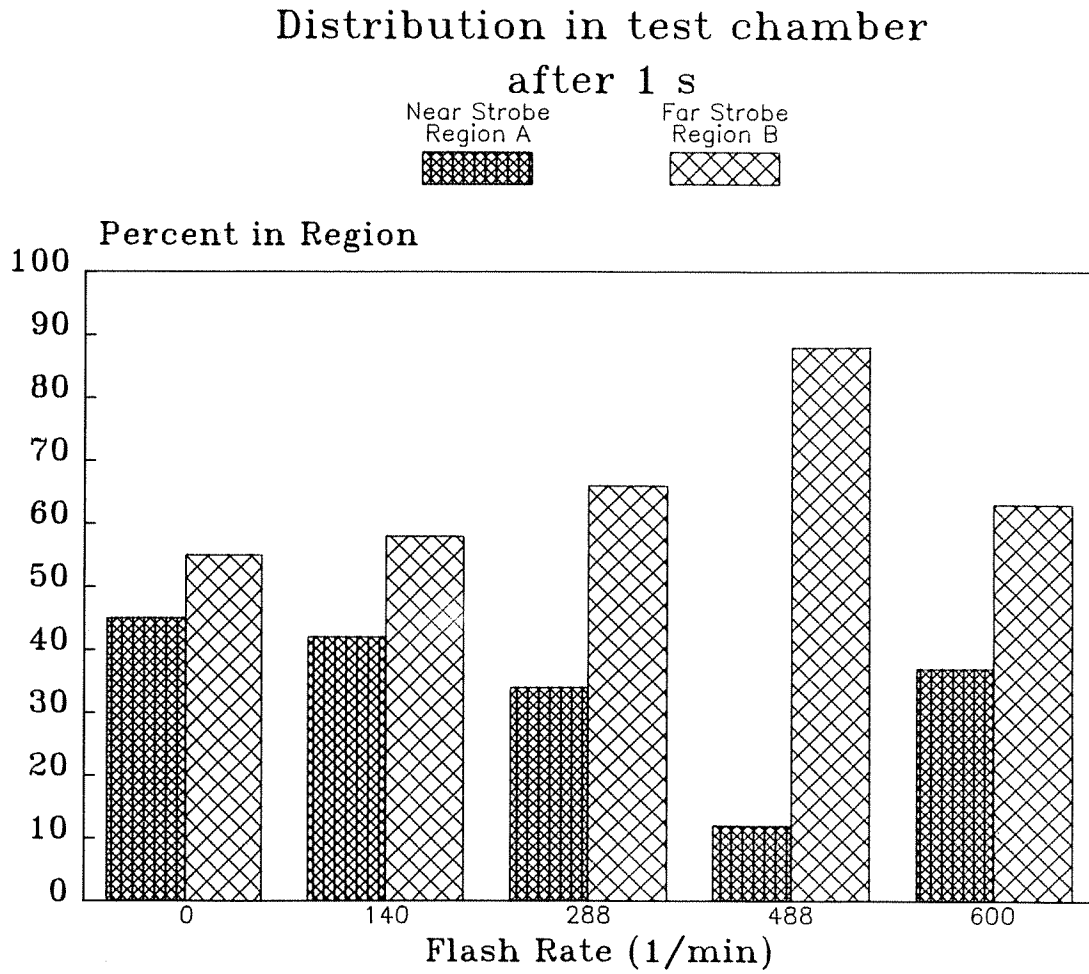


Figure 18. Percent of steelhead in regions A (near light) and B (away from light) after 1 s.

The chi-square analysis for the comparison between direction of movement and flash rate showed a significant difference in the 488/min flash rate. A graphical examination of the results (Fig. 18) tends to suggest that greater avoidance was achieved with an increase in flash rate. The percentage of fish in zone B exposed to the 600/min flash rate was lower than expected. The high frequency flash rate may have stunned the fish, thus reducing their avoidance response.

3.9 Reaction of Juvenile Chinook Salmon in a Net Pen to Strobe Light

Introduction

To supplement our studies of the reaction of salmon to strobe light experiments were conducted at Rocky Reach Dam. The purpose of the experiments was to bridge the gap between our studies of fish behavior to strobe light in laboratory experiments and fish behavior to strobe lights 80 ft down a trashrack at the dam. The experiments were conducted in the surface waters of the forebay of the dam river using the strobe light that was also used on the trashrack.

Methods

On October 3 1986 experiments were conducted at night in the forebay of Rocky Reach Dam in a pen 4.2- x 4.2-ft wide and 1-ft deep held just below the surface. The bottom of the pen was covered with white plastic, which made the fish visible. The sides of pen were made of black plastic webbing that was essentially invisible in water. The pen was located next to a concrete wall on the east end of the dam. A strobe light (EG&G Fish Avoidance Xenon System, Model number FA-125) as positioned 10.4 ft away and produced a light intensity in the pen between 0.25 to 0.7 $\mu\text{E}/\text{m}^2/\text{s}$. The flash rate was 300/min. Fish movements were recorded from 8 ft over head by a Dage-MTI Intensified Silicon Diode low light camera, MK 11 Series camera. A red 25W background light was used to illuminate the area. With the background light fish in the pen were just distinguishable from the viewing platform 8 ft above the water surface.

Three groups of 8 fish subyearling chinook salmon (*Oncorhynchus tshawytscha*), approximate length 100 mm, were placed in the pen and subjected to a number of trial exposures to the strobe and an incandescent 40w light 6 ft directly above the pen.

Fish were transferred from the hatchery and the experimental area in a 5-gallon bucket. They were poured into the pen from a height of 6 ft and allowed to acclimatize to the pen for 20 min before beginning the experiments.

The fish in each group were subjected to four light conditions: swing, blast, solid and blast-solid. The conditions were tested in sequence with a 5-min period between each trial.

Description of the four light conditions fish

- (1) "Swing": The strobe light was turned on facing 90 degrees to the pen and was rotated towards the pen over a 6 s interval. This procedure was designed to mimic the pattern of light fish were expected to encounter when they were pulled into the trashrack by a turbine entrance flow.
- (2) "Blast": The strobe light was aimed directly at the pen and turned on.
- (3) "Solid": The overhead incandescent 40 w bulb over was turned on.
- (4) "Solid-Blast": The incandescent light and strobe light facing the pen were turned on together.

The fish position and movement were determined by plotting the video images on an acetate sheet over the video screen. The headings of fish relative to the strobe light and their movements were recorded for about 4 s after the light stimuli were activated. Time with a resolution of 0.01 s was superimposed on each video frame with a Panasonic time-date generator.

Results

Fish were inactive in dark. When the strobe was turned on they exhibited a variety of desultory movements including: darting behavior, freeze behavior, and slow swimming. A common pattern was for the fish to initially move when the light was first turned on and then after a few seconds they slowed or became still. In general, no behavioral pattern dominated in any group or with any set of light conditions.

For all trials the average velocity over the first 4 s interval was 2.4 bl/s. The average speeds varied between light conditions (Fig. 19), but there was no significant difference in speed at the 0.05 probability level. In several fish, the initial speed was large, reaching 15 bl/s within the first 0.06 s.

Mean velocity (bl/s) and ANOVA (alpha = 0.05)

Light conditions	Mean (std. dev.)	n	variation	df	SS	MS	F	
"Swing"	2.3 (1.3)	14	Between Groups	3	36.7	12.23	6.36	
"Blast"	1.6 (0.9)	22						
"Swing"	3.6 (2.0)	14	Within Groups	50	96.15	1.92		
"Blast & solid"	3.2 (1.2)	4						
			TOTAL	53	132.85			
							P = .001	

The light stimulus often caused fish to move for the first second or two and then to freeze. To determine if the light stimuli altered their orientation in a consistent manner the initial heading when

the stimulus was activated was plotted against the fish heading when activity decreased (Fig. 20). In general, no consistent pattern emerged. Of the 33 fish facing the strobe when it was turned on 51% turned away from the light (quadrant A, in Fig. 20) and 49% remained facing the light (quadrant C, Fig. 20). Of the 16 fish facing away from the light when the stimulus was activated 56% remained facing away from the light (quadrant B) while 43% turned towards the light (quadrant D). More fish started the experiments facing the direction of the strobe light. This was a result of fish tending to face towards the strobe light after their first exposure to light.

Velocity Comparison Between Groups

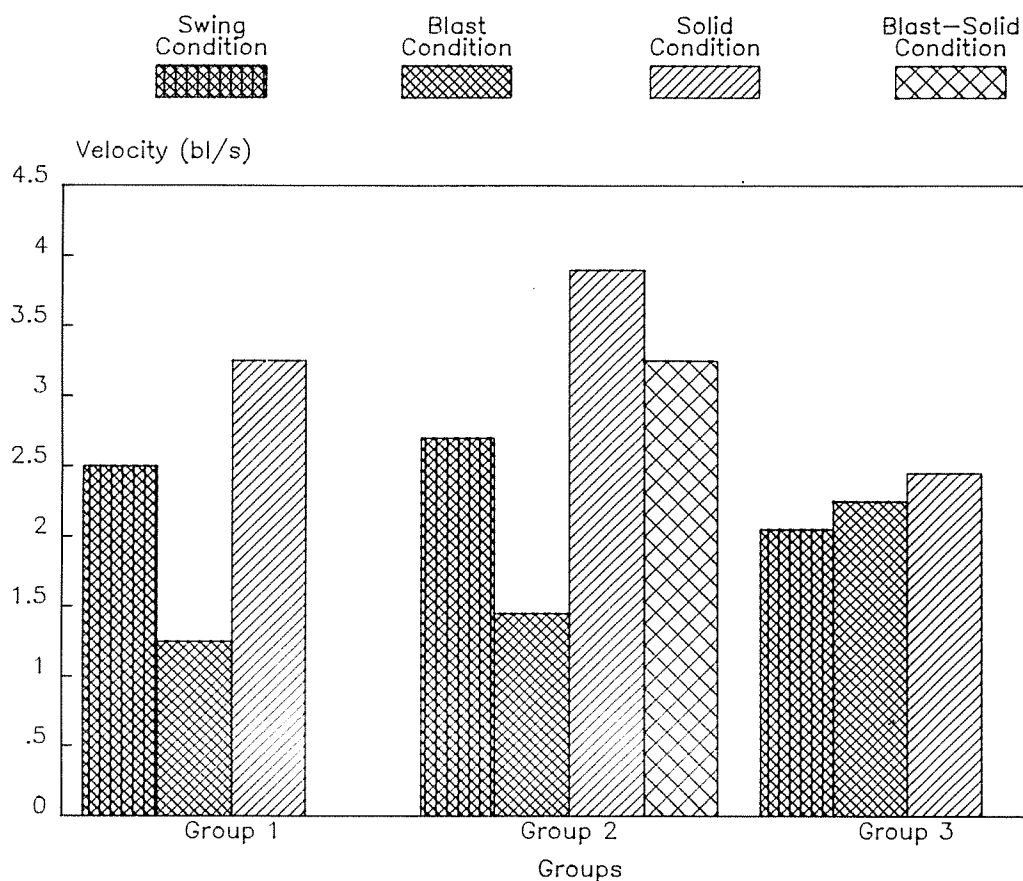


Fig. 19. Speed of groups of juvenile chinook salmon exposed to light.

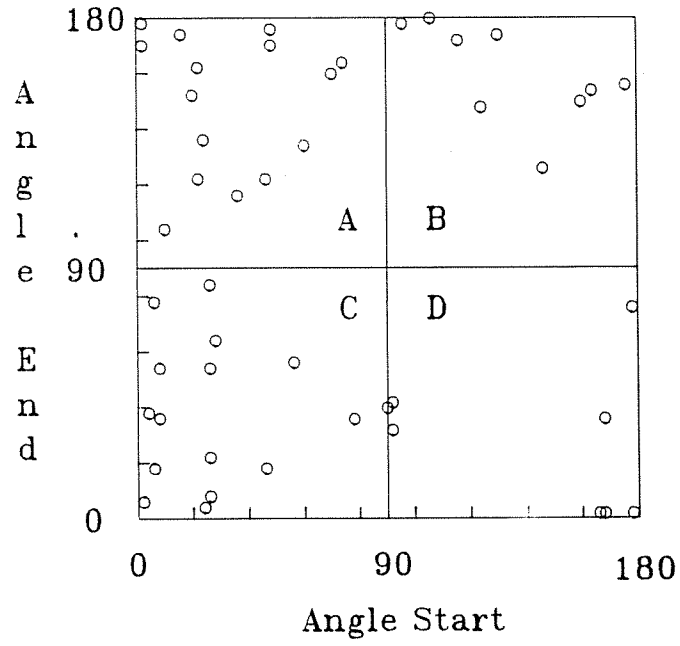


Fig. 20. Direction of fish before and after exposure to strobe light.

APPENDIX 2:

Response of Rainbow Trout in a Raceway to Strobe Light

INTRODUCTION

Experiments were conducted to determine the response of rainbow trout in a large raceway to strobe lights at night. The experiments were used to develop a quantitative model for the response of fish to strobe light.

METHODS

Experiments were conducted at the University of Washington Hatchery in an outdoor raceway 8.3 m (27 ft) in length, 1.6 m (5.25 ft) wide, and 1.07 m (3.5 ft) deep. The water depth was 0.6 m (2 ft). The raceway was painted a dark green. During the experiments all flow through the raceway was shut off.

A Diversitronics Luma Power Strobe Light Model 50 was placed at the downstream end of the raceway and was pointing down into the water from a height of 4 feet from the bottom of the raceway (Fig. 1). The flash rate was adjustable between 78 and 780/min and strobe intensity in the water was adjustable between 0.05 to 5.3 $\mu\text{E}/\text{m}^2/\text{s}$.

Strobe intensity was determined with a Lambda LiCor Underwater Quantum Sensor Model LI-185 with an Underwater Quantum Sensor Model LI-192S. The distribution of light intensity was measured at the bottom down the axis of the raceway. The sensor was aimed at the strobe to obtain the maximum reading at each location. The zero distance position was directly under the strobe with the sensor directed up at the strobe. Strobe intensity at the zero position position was designated I_0 . At a distance of 1 m and beyond the intensity decreased in an exponential like manner down the raceway axis (Fig. 2) and could be described by the equation:

$$I = I_0 \exp(-kx) \quad (1)$$

where I_0 is the intensity at $x = 0$ and k is the light extinction coefficient in the raceway. A regression based on eq(1) gave $I_0 = 0.9$ ($\mu\text{E}/\text{m}^2/\text{s}$) and $k = 1.2$ (1/m). The difference between the measured I_0 and I_0 obtained from a regression results from the fact that close to the light the distribution does not follow the exponential equation.

Experiments were conducted during the nights of Nov. 24 and Dec. 1, 1986. In each experiment, fifty 135 mm yearling rainbow trout (*Salmo gairdneri*) raised at the University of Washington Hatchery were placed in the raceway and dark adapted for 1 hour at an ambient light level of about 0.05 $\mu\text{E}/\text{m}^2/\text{s}$. At this light level the location of the fish could not be detected unless the strobe light was operating.

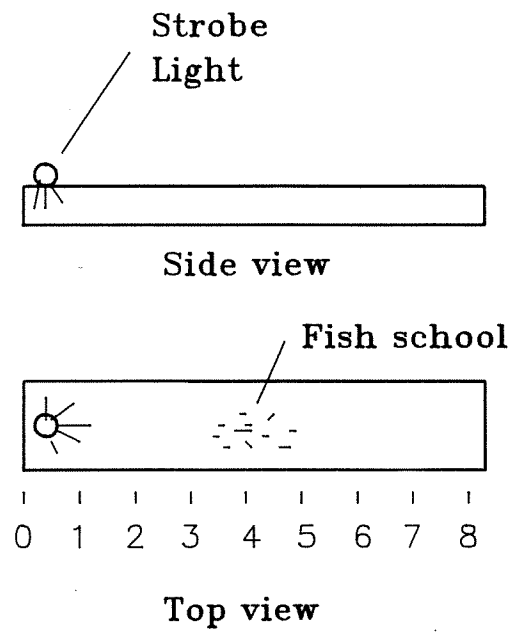


Fig. 1. Location of strobe light and meter marks in raceway. Position of fish illustrated at 4-m mark.

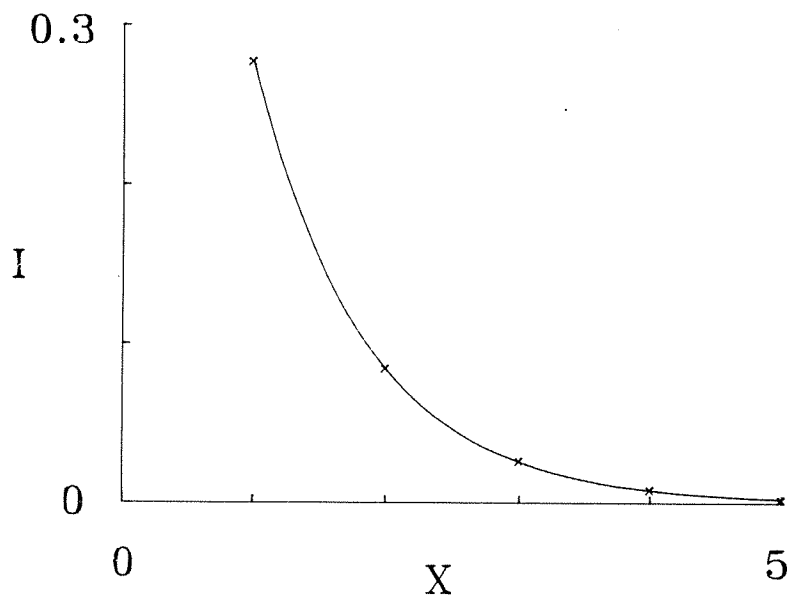


Fig. 2. Strobe intensity, I ($\mu\text{E}/\text{m}^2/\text{s}$) down the axis of the raceway, X (m).

Before each trial fish were herded to the strobe end of the raceway with a flashlight. The fish were light averse and moved readily to the desired end of the raceway. Turning off the flashlight they would slowly move back towards the center of the raceway at a speed of about 0.1 m/s (0.7 bl/s).

The average position of fish in the raceway was determined by visual observation of the center of mass of the school by a person looking over the edge of the raceway. Fish behavior did not appear to be affected by the presence of the observer. The times at which the school crossed meter marks on the side of the raceway were recorded. Zero time was designated as the moment the strobe light was turned on.

Escape speed was calculated from the time-distance information collected by visual observation. Time-distance data were fit with an exponential regression of the form:

$$x = a \exp(bt) + c \quad (2)$$

where a , b and c are coefficients obtained from regression, t is time and x is the position of the school in the raceway at time t . A typical example of the exponential regression of distance to time for a single trial is illustrated in Fig. 3. The equation gave good fits in virtually all trials.

Differentiating x with respect to t the speed is predicted by the equation:

$$v = v_0 \exp(bt), \quad (3)$$

where v_0 is the initial escape speed, defined with the coefficients as $v_0 = ab$, and b is a velocity deceleration coefficient.

EXPERIMENTS

Two experimental protocols were used: (1) Escape behavior was observed after herding fish under the strobe and turning the light on. The time to reach distance marks provided information with which to compute speed, and (2) avoidance behavior was determined as the stable position of the school with the strobe light on. In both protocols behavior was determined as a function of strobe intensity and flash rate. In each experiment replicate trials were conducted on the groups of fish so changes in behavior were the result of effects of controlled changes in the light and learning or habituation by the fish.

In all experiments the fish formed loose schools when undisturbed. They were light averse to both the strobe and the flashlight used to herd them. When the strobe light was turned on the fish elicited a classic startle response and moved randomly in the first second. They quickly oriented themselves and swam towards the dark end of the raceway. At some distance, which was always greater than 3 meters from the dark end of the raceway, they would stop and reform into a loose school.

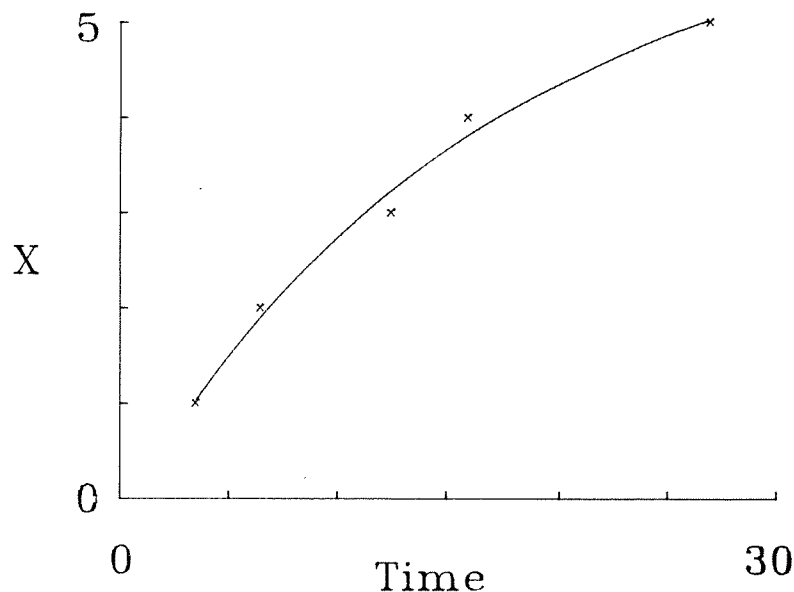


Fig. 3. Distance of an escaping school of trout, X (m) vs. time (s) since the strobe was turned on.

Speed vs Flash Rate

On Nov. 24, a total of 33 trials were conducted on a group of 50 fish to determine the affect of flash rate on escape speed. The strobe intensity was fixed at maximum (equivalent to $I_0 = 5.3 \mu\text{E}/\text{m}^2/\text{s}$ @ flash rate 780/min). Fish escape speeds were observed in 11 trials at 3 flash rates. The sequence of flash rates was randomized as follows: acbabcbacabcbacabcbacabcbacabcb, where a = 780/min, b = 180/min and c = 78/min. On Dec. 1 the experiment was repeated using a second group of fish and a flash rate of 290/min.

The escape speed decreased with experience. This resulted in a drastic change in time to reach distance markes between early and late trails (Fig. 4). Comparing the first trial at each flash rate with a latter trial when the fish were experienced it is evident that the initial escape speed increased significantly with experience (Table 1).

Table 1. Initial escape speeds of naive (N) and experienced (E) fish with strobe intensity on full. (*) designates trials conducted Dec. 1. All others trials were conducted Nov. 24.

Flash rate (1/min)	Initial speed v_0 (bl/s)	
	B	E
78	1.0	3.7
180	2.9	4.5
*290	1.6	3.6
780	5.0	7.6

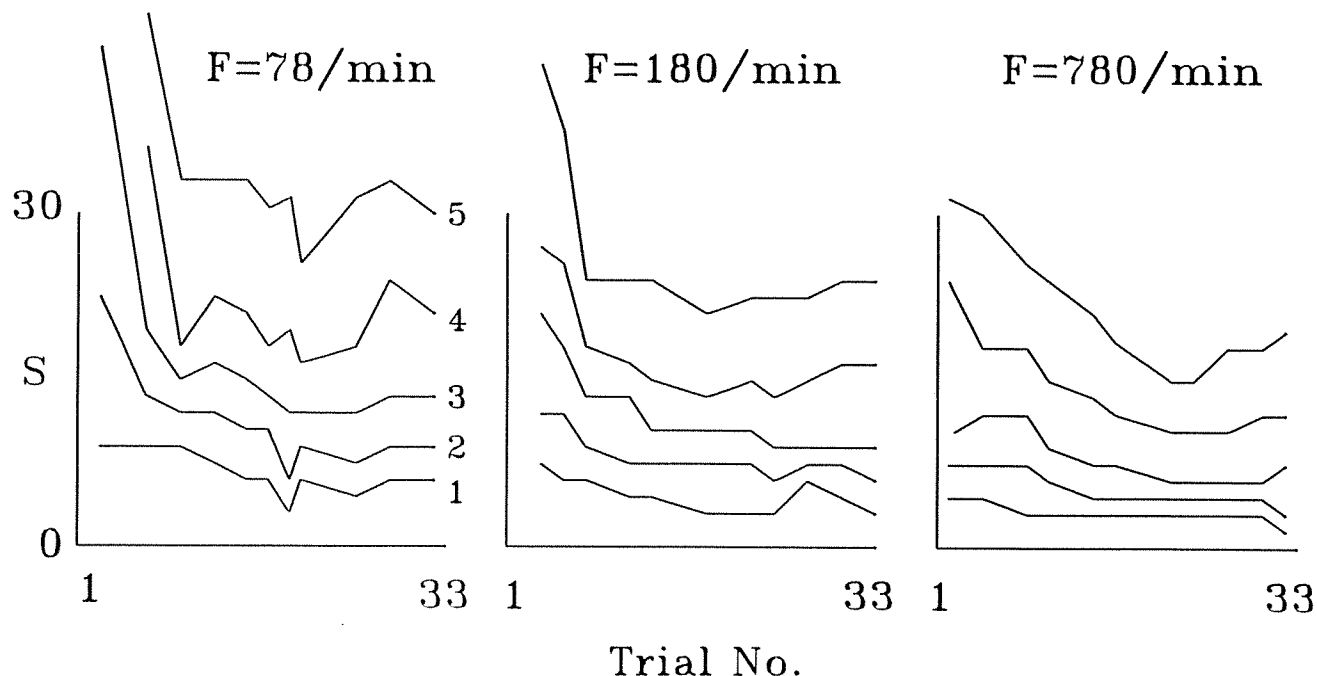


Fig. 4. Time to distance marks (1 to 5 m) vs. trial numbers for three flash rates (F). The flash rates were mixed and a total of 11 trials were conducted at each flash rate.

The data show that, for experienced fish, the initial escape speed increased with flash rate (Table 2). The data from the Dec. 1 experiment used a different group of fish and did not fit the pattern. This illustrates that differences in individual fish or differences from day to day can have a significant effect on the behavior. The escape speed increased in an approximate logarithmic fashion with flash rate as is illustrated by the linear regression of v_0 to the log of flash rate using the data from Nov. 24 given in Table 2 (Fig. 5).

Table 2. Escape response regression coefficients for different strobe flash rates. Strobe intensity fixed at $5.3 \mu\text{E}/\text{m}^2/\text{s}$ @ 780/min. (*) designates trials conducted Dec 1; other data collected Nov. 24. For each regression $n = 45$.

Strobe flash rate (1/min)	Initial speed v_0		Eq. 2 Coefficients	
	(m/s)	(bl/s)	Speed b (1/s)	Distance c (m)
78	0.52	3.7	-0.073	6.6
180	0.63	4.5	-0.085	7.0
*290	0.50	3.6	-0.085	6.4
780	1.05	7.6	-0.176	5.5

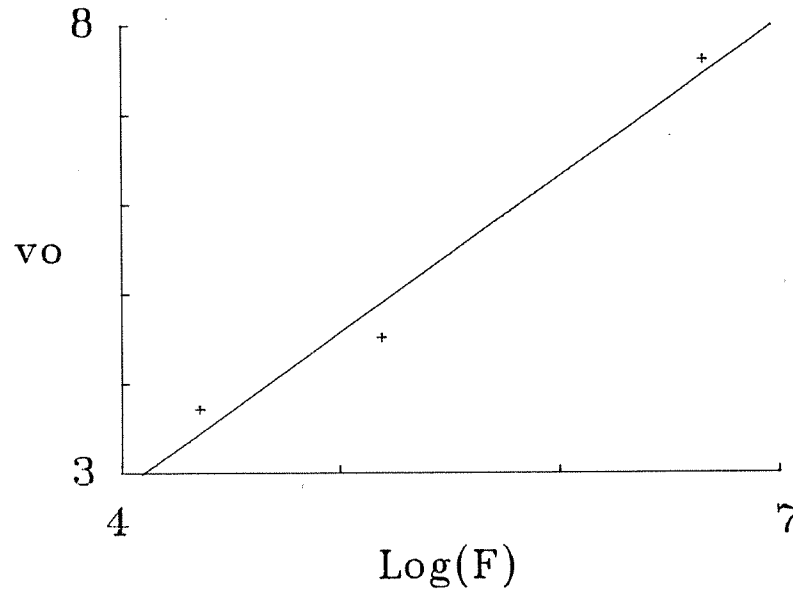


Fig. 5. Initial escape speed v_0 (bl/s) vs. the logarithm of flash rate F (1/min) for data collected Nov. 24.

Speed vs Strobe Intensity

Experiments to determine the effect of strobe intensity and experience on escape response were run Dec. 1. A group of 50 fish was used in a sequence of 32 trials. The flash rate was 290/min. Strobe intensity was fixed in groups of 7 sequential trials. The strobe intensities in order of presentation were 2, 0.05, 0.5 and $0.03 \mu\text{E}/\text{m}^2/\text{s}$. The time to reach the meter distance marks as a function of trial number is shown for the three strobe intensities in Fig. 6.

The effect of strobe intensity on escape speed was also determined with a fixed flash rate of 780/min. The fish were experienced during these trials and escape speed increased as a function of strobe intensity (Table 3; Fig. 7).

Table 3. Escape speed coefficients for different strobe intensities. Flash rate fixed at 780/min.

Strobe intensity ($\mu\text{E}/\text{m}^2/\text{s}$)	Initial speed v_0		Eq. 2 coefficients		Number of trials
	(m/s)	(bl/s)	Speed b (1/s)	Distance c (m)	
0.1	0.77	5.7	-0.186	4.62	2
0.5	0.94	6.9	-0.191	5.21	2
1.3	1.28	9.4	-0.268	5.27	5
3.5	1.56	11.5	-0.323	5.11	2
5.3	1.60	11.8	-0.347	5.06	4

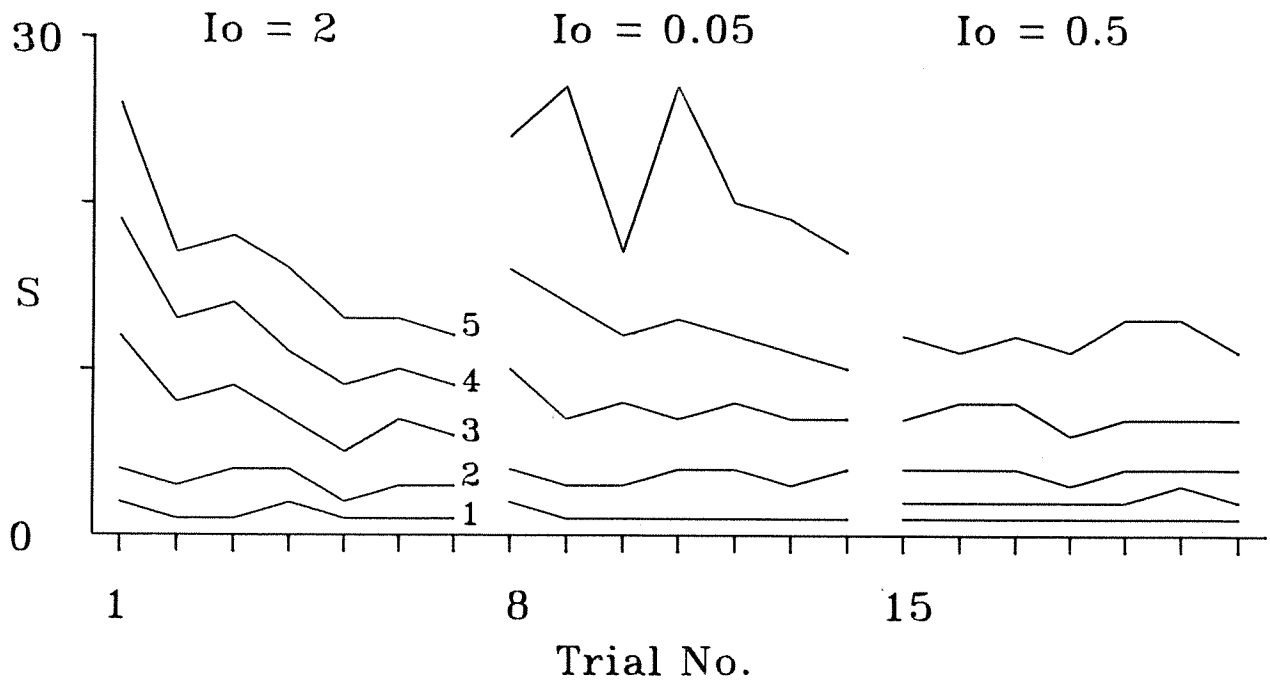


Fig. 6. Time (s) to reach distance marks (1 to 5 m) as a function of trial number for three strobe intensities, I_0 ($\mu\text{E}/\text{m}^2/\text{s}$).

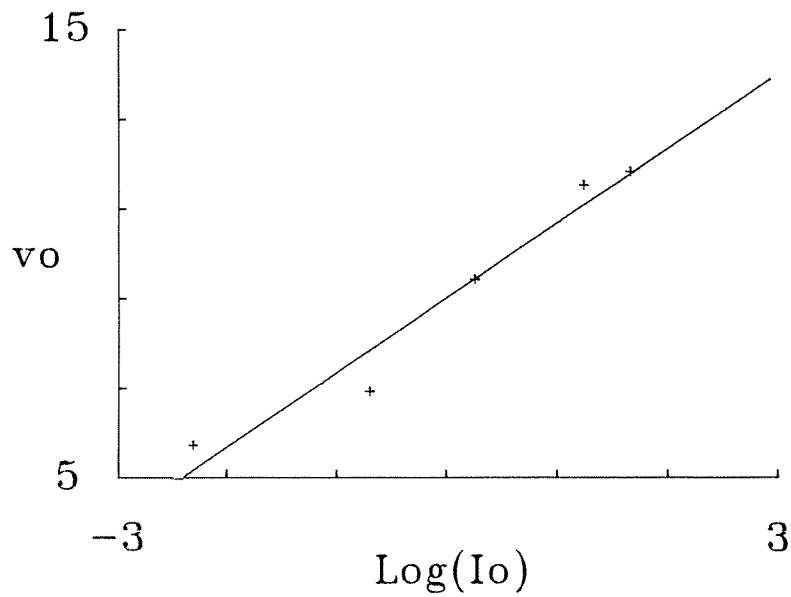


Fig. 7. Initial escape speed, v_0 (bl/s) as a function of the logarithm of the strobe intensity, I_0 ($\mu\text{E}/\text{m}^2/\text{s}$).

Distance vs Intensity and Flash Rate

Experiments were conducted Dec. 1 to study the avoidance behavior of experienced fish. The response of avoidance distance to strobe intensity was measured at 5 flash rates. In each sequence, flash rate was fixed and the initial strobe intensity was set to the minimum value. The position of the fish was noted and the intensity increased one setting. A total of 10 strobe intensities were used. At each setting the fish moved and stabilized at a new position within about 10 s. At all flash rates the fish distance to the strobe light increased in a linear manner with the logarithm of the light intensity (Fig. 8). A similar result was obtained when strobe intensity was held constant and flash rate was increased in increments (Fig. 9).

Evidence for Attraction to Strobe

The avoidance experiments described above illustrated that fish moved away from the light as the strobe intensity or flash rate was increased. To determine if fish would move towards the light if the intensity or flash rate was decreased the strobe settings were decreased after the maximum settings were reached in a number of experiments. In each case, if the flash rate or strobe intensity was dropped from the maximum to minimum setting the fish moved from their maximum distance to a new position with 10% of the minimum distance observed at the beginning of the sequence. The sequence numbers, distance and strobe settings for 4 sequences are given in Table 4.

Table 4. Avoidance distance as a function of flash rate and intensity in four sequences.

Sequence number	Flash rate (1/min)	Intensity ($\mu\text{E}/\text{m}^2\text{s}$)	Distance (m)
1	78	0.01	2.5
11	78	0.35	4.2
12	78	0.01	2.5
15	78	0.35	4.2
1	290	0.05	2.5
11	290	1.9	4.5
12	290	0.05	2.5
16	290	1.9	4.5
1	780	0.05	2.7
11	780	5.0	5.0
12	780	0.05	3.0
15	780	5.0	5.0
1	78	0.29	3.0
10	780	1.3	4.0
11	78	0.29	3.0
13	780	1.3	4.0

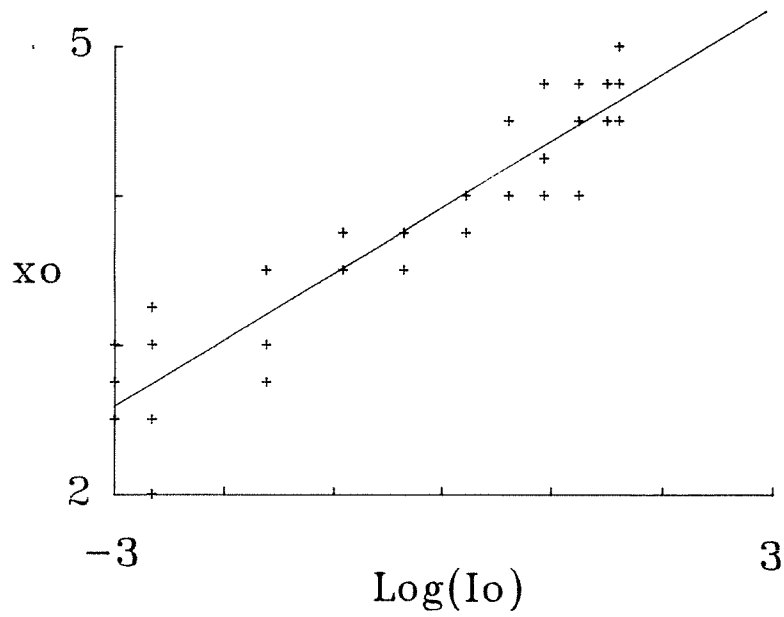


Fig. 8. Fish avoidance distance x_0 (m) from strobe as a function of the logarithm of strobe intensity, I_0 ($\mu\text{E}/\text{m}^2/\text{s}$).

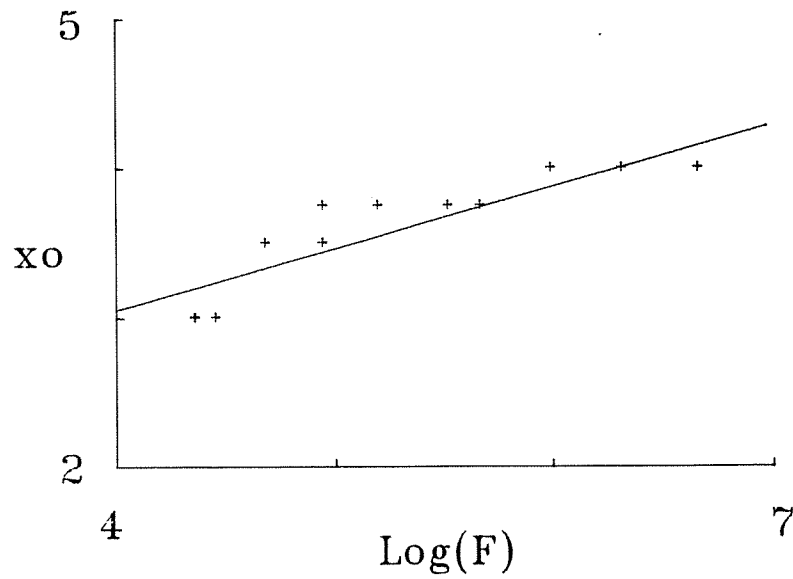


Fig. 9. Fish avoidance distance x_0 (m) from strobe as a function of the logarithm of strobe flash rate, F (1/min).

DISCUSSION

Effect of Learning on Escape Behavior

Plots of time-to-distance isopleths vs trial number (Fig. 4) demonstrated that speed of escape increased with experience. The increase reached an asymptote after about 15 trials. A comparison of initial escape speed in naive and experienced fish (Table 1) suggests that the initial escape speed might increase on the order of 60% with experience. This is a commonly observed phenomenon in psychological studies where the speed with which an animal carries out a task increases with practice.

Effect Due to Individual Difference

The escape responses exhibited differences which can not be attributed to experimental conditions or the effects of learning. To illustrate this difference, compare tests under the same conditions with different groups of experienced fish. On Nov. 24, the initial escape speed of 7.6 bl/s was obtained from a regression of 9 trials with a flash rate 780/min and an intensity of 5.3 $\mu\text{E}/\text{m}^2/\text{s}$. On Dec. 1, under the same conditions, a regression of 4 trials gave an initial escape speed of 11.8 bl/s. The difference in speeds is about 50%. This variation is on the same order as was observed with the effect of experience.

Escape Speed

In all trials, speed during an escape response decreased exponentially with time according to eq(1). A plausible explanation for this response can be formulated in terms of a fish's preception of light intensity. We begin with Fechner's Law (1860), which state that the perceived intensity of a stimulus, P , is proportional to the logarithm of the physical intensity of the stimulus, I , so:

$$P \sim \log(I).$$

Assuming that the motivation to escape is proportional to the difference between the perceived light intensity and a perceived light intensity to which fish were adapted, P_a , then speed can be expressed:

$$v \sim P - P_a.$$

Including Fechner's Law, the escape speed in terms of the physical intensity of the light is:

$$v = V \log (I/I_a), \quad (4)$$

where V is a physiologically based coefficient that factors into the equation the fish's swimming ability during an escape response, and I_a is the light level to which the fish is adapted at the time of the response.

The hypothesis formulated by eq(4) is that fish will seek a light level to which they were previously adapted. If they encounter a light brighter than the adaptation level, they move away from the light. If they encounter a light level that is darker than the adaptation level, they move towards the light. The motivation to move vanishes when the ambient light level and the adaptation light level are equal. Evidence collaborating this hypothesis was obtained from an experiment where the number of fish attracted to a circle of light followed the same logarithm law (Appendix 3). Equation (4) predicts that strobe light at low intensities could attract fish. This prediction is supported by the avoidance experiments presented in Table 4.

To express the speed equation in terms of distance and eventually time note that the distribution of light down the axis of the raceway can be approximated by the exponential distribution according to eq(1). Combining eq(1) and eq(4) and recalling that speed is the derivative of distance with time gives:

$$dx/dt = V \log (I_0/I_a) - V k x. \quad (5)$$

Solving eq(5) for x , the distance of escape as a function of time is:

$$x = -(x_0 - x_s) \exp(-Vkt) + x_0 \quad (6)$$

where x_s is the initial position of the school and x_0 is the final position. By definition x_0 is the avoidance distance and is defined:

$$x_0 = (1/k) \log(I_0) - (1/k) \log(I_a). \quad (7)$$

Assuming that the initial position is $x_s = 0$ and noting that eq(6) is equivalent to eq(2), then the initial escape speed can be expressed:

$$v_0 = V \log (I_0) - V \log (I_a). \quad (8)$$

Equation (8) suggests that the initial escape speed should have a linear relationship with the log of stimulus intensity if all other factors are constant. The regression of $\log(I_0)$ against v_0 (Fig. 7) supports this hypothesis. The slope and intercept of the linear regression in Fig. 7 are 1.66 and 9, respectively. The parameter values in eq(8) are accordingly $V = 1.66$ and $I_a = 0.004 \mu\text{E}/\text{m}^2/\text{s}$. From the model, the escape speed can be approximated with four coefficients as:

$$v = V \log(I_0/I_a) \exp(-kVt), \quad (9)$$

where V is a coefficient determined by the fish's physiology, k is the light extinction coefficient in the water, I_0 is the strobe light intensity, and I_a is the light level to which fish are adapted.

Avoidance Distance

Figure 8 illustrates that avoidance distance increased in a linear manner with the logarithm of strobe intensity. Equation (7) predicts the same linear relationship under certain conditions. The

regression coefficients for Fig. 8 are $1/k = 0.445$ and $(1/k) \log(I_a) = -3.93$. According to eq(7) the model parameters are $k = 2.45$ (1/m) and $I_a = 0.00015 \mu\text{E}/\text{m}^2/\text{s}$. In comparison, the regression of light with distance from eq(1) gave $k = 1.97$ and the regression of distance with time from eq(8) gave $I_a = 0.004$.

SUMMARY

In this study a hypothesis for the response of rainbow trout to strobe lights was developed and evaluated with experiments. We concluded that, in principle, escape behavior characteristics can be determined by strobe light intensity and flash rate. Other factors enter into the prediction that, as yet, have not been evaluated (see eq.(9)). Clearly the propagation of light through water is an important factor. The model also suggests that the level of light that fish were previously adapted to also affects their response. Finally the escape response should involve a physiological factor related to a fish's swimming ability. The study indicated that strobe light is an aversive stimulus under most conditions and the avoidance distance may range between about 3 to 9 meters depending on strobe intensity and the above mentioned factors. The theory and experimental evidence also suggested that strobe light may attract fish under certain circumstances.

REFERENCES

Fechner.H. (1860). Elemente der Psychophysik. Leipzig: Breikopf and Haertel.

APPENDIX 3:
**CONDITIONS UNDER WHICH LIGHT ATTRACTS
JUVENILE SALMON**

by

K. J. Puckett and James J. Anderson

**Electric Power Research Institute Conference
on Fish Protection at Stream and Hydropower Plants
San Francisco, California
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ABSTRACT

When juvenile salmon encounter a sudden decrease in ambient light intensity, they may exhibit attraction to light. This response was investigated by adapting age 0 chinook salmon (*Oncorhynchus tshawytscha*) to a constant ambient light intensity (I_a), followed by simultaneously reducing ambient light and producing a small spot of light (intensity I_s) at the center of the test tank. Maximum attraction to the light, evidenced by the number of fish above the light spot, was observed when $I_s = I_a$. When I_s was 100 times I_a , chinook actively avoided the light spot. The study indicates that ambient light levels must be considered when attempting to guide fish with lights.

INTRODUCTION

It has long been recognized that light might be used to guide fish away from hazards at hydroelectric facilities. Recent studies have demonstrated that mercury light attracts fish both in experimental field and laboratory settings (1). Light can attract (2) or repel (3) salmonids, but guidance effectiveness under operational field conditions has been variable (4, 1). This variability is partially attributable to an insufficient understanding of the behavioral response of salmon to light.

Many studies have investigated the effects of light intensity on the behavior of juvenile salmon (5, 6, 7, 8, 9, 10, 11) and other fish (12, 13). Fields (14) concluded that juvenile salmon swam away from, or toward, a light stimulus to maintain that light level to which they were adapted. This hypothesis suggests that salmon evaluate the difference between adaptation light intensity and stimulus light intensity. In this context, "adaptation light intensity" refers to the intensity to which the salmon's eyes were physiologically adjusted (15). If Fields' hypothesis were correct and could be quantified, then our ability to anticipate the response of salmon to light would be enhanced.

Although the response of fish to light is complex, evidence suggests that some aspects of the stimulus-response relationships can be quantified. Fechner (16), discussed by Rapoport (17), demonstrated that the perception of a stimulus is proportional to the log of the physical intensity of the stimulus:

$$P = (k) \log I \quad (1)$$

where P is perceived intensity, I is physical intensity, and k is a constant. It is likely that response to light is dependent upon an organism's perception of that light. Studies on the perception of light by fish have demonstrated that the retinomotor responses of rods and cones in the fish eye approximately follow the Fechner law (18). In addition, some salmonid behaviors, such as feeding rate, obey the Fechner law, at least within certain light intensity ranges (19). This evidence

suggests that behavioral response may be proportional to perceived stimulus intensity. To formulate Fields' hypothesis mathematically, we assume that the attraction of fish to light (R) is proportional to the difference between the perceived intensity of the stimulus light and the perceived intensity of the adaptation light:

$$R = R_m - k (P_s - P_a) \quad \text{when } I_s > I_a$$

and

$$R = R_m + k (P_s - P_a) \quad \text{when } I_s < I_a \quad (3)$$

where R_m is maximum attraction, k is a constant, P_s is the perceived intensity of the stimulus, P_a is the perceived intensity of the adaptation light, I_s is the physical intensity of the stimulus light, and I_a is the physical intensity of the adaptation light. Our mathematical formulation of Fields' hypothesis (Fig. 1) implies that maximum attraction will occur when the perceived intensity of the stimulus light is equal to the perceived intensity of the adaptation light. Furthermore, attraction decreases linearly when P_s and P_a are different.

To test Fields' hypothesis, we measured physical stimulus intensity rather than perceived stimulus intensity. Therefore, we rearranged the above equations by applying Fechner's law to get the expression:

$$R = R_m - k \log (I_s/I_a), \quad \text{when } I_s > I_a \quad (4)$$

and

$$R = R_m + k \log (I_s/I_a), \quad \text{when } I_s < I_a \quad (5)$$

On the basis of this formulation, we designed our experiments to test the response of fish to different ratios of I_s to I_a . Juvenile chinook salmon (*Oncorhynchus tshawytscha*) were adapted to specified light levels (I_a). Simultaneously, the ambient light level was reduced, and the fish were exposed to the stimulus light (I_s). We counted the number of fish attracted to the light at several different ratios of I_s to I_a . Throughout this paper, we refer to the ratio I_s/I_a as "contrast."

METHODS

Experiments were conducted with 2-month-old juvenile chinook (average length = 53 mm) that were raised at the University of Washington hatchery under artificial and natural light. For each test, a new group was randomly selected from several hundred thousand well-fed fish being held in an outdoor raceway.

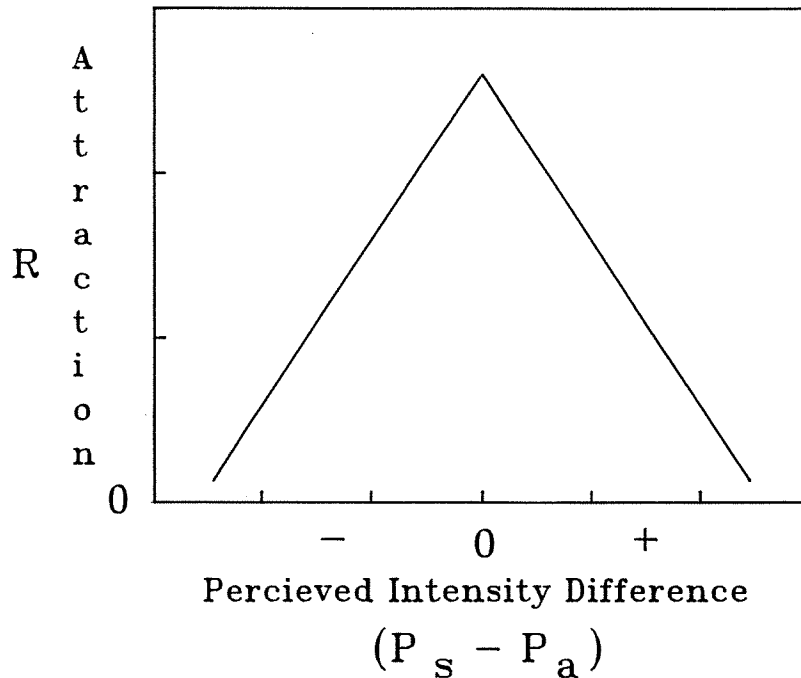


Figure 1. Mathematical formulation of Fields' hypothesis.

The experimental tank, 2.4-m long by 0.9-m wide, was enclosed by black plastic to reduced outside interference and was filled to a depth of 0.2 m with flowing water from Lake Washington (10°C). All lights, other than the stimulus or adaptation lights, were off during tests. Adaptation lighting over the test tank was provided by two 100-W incandescent bulbs controlled by a rheostat; intensities could be varied between 0.1 and 1 $\mu\text{E m}^{-2} \text{ s}^{-1}$. The stimulus light consisted of a 200-, 40- or 15-W bulb located inside, and at the top of, a 0.6-m long by 0.18-m diameter black stove pipe. The pipe was sealed at the top and hung down to within 0.18 m of the water surface. This projected a well-defined cylinder of light through the water, creating a 0.27-m diameter spot of light on the bottom of the tank. This spot of light was bounded by another dim light zone. Light intensity measurements were taken with a LiCor Model LI-192S underwater quantum sensor connected to an LI-185 light meter. Measurements were taken 5 cm from the bottom of the tank, underwater, and with the sensor facing straight up. All light measurements reported throughout this paper are in units of $\mu\text{E m}^{-2} \text{ s}^{-1}$. The sensor was not sensitive enough to obtain readings at the two lowest stimulus intensities; consequently, they were determined by regressing measured light intensity on rheostat position and extrapolating. Tests were recorded on a Panasonic AG-6200 VCR with a low-light Dage-MTI Model 60 video camera. Time to 0.01 s was recorded on the video tape with a Panasonic Time Date Generator Model WJ-810.

At the beginning of a test, 15 salmon were placed in the experimental tank for 20 min of acclimation under a specified adaptation light intensity. The adaptation lights were then turned off, the stimulus light was turned on at a predetermined intensity, and fish behavior was video-taped for 2 min. Video tapes were later reviewed in slow- and stop-motion, and the number of fish above the light slope 10 s after the first entry of a fish into that area was counted. Six replicates were completed for each combination of I_s and I_a tested. Tests were conducted in March 1987 between the hours of 9 AM and 5 PM.

RESULTS

During acclimation, the chinook usually formed a school and swam throughout the tank. Sometimes, especially at the lowest adaptation light levels, the fish remained in a motionless group in part of the tank. In either case, the fish rarely spent time, except in passing, in the area under the stimulus light. If uniformly distributed, 3% of the fish would inhabit the area under the stimulus light.

Response Depends on I_s/I_a

Two groups of data were used to verify that fish respond to the ratio I_s/I_a , rather than I_s or I_a . Attraction was determined for a range of light intensities, but with I_s/I_a constant and equal to one (Table 1). If response was dependent on either I_s or I_a , and not their ratio, then the standard deviations and means of the groups should be different. However, no significant differences were found between the means (t-test: $t = 0.4$, $P = 0.7$) or variance.

Response Form as a Function of I_s/I_a

The experiments show that attraction was strongest at $I_s/I_a = 1$ and decreased when I_s/I_a was greater or less than 1 (Table 2). At $I_s/I_a = 100$, no chinook were attracted to the light spot. The number of fish attracted to the light varied linearly with the log of physical stimulus contrast (Fig. 2). The slope (k) was slightly steeper when I_s/I_a was greater than 1, and much of the variability in number of fish attracted to the light spot can be explained by contrast (Table 3). The regression coefficients, k and R_m , are as defined in Eqs. 4 and 5. R_m is close to the maximum number of fish (15) that could be attracted to the light in these experiments.

DISCUSSION

This study demonstrated that juvenile chinook salmon were attracted to light, and that the strength of attraction was proportional to the logarithm of the contrast between stimulus light intensity and adaptation light intensity. This concept of contrast is similar to that discussed by Finger and Fields (20) and partially tested by Ali (21).

Table 1
Data to test for importance of I_a or I_s

Rep#	Group 1			Group 2		
	I_s	I_a	No. fish above light spot	I_s	I_a	No. fish above light spot
1	0.5	0.5	13	0.1	0.1	11
2	0.5	0.5	8	0.3	0.3	10
3	0.5	0.5	12	0.5	0.5	12
4	0.5	0.5	11	0.6	0.6	9
5	0.5	0.5	9	0.8	0.8	9
6	0.5	0.5	8	1.0	1.0	10
MEAN			<u>10.7</u>			<u>10.3</u>
SD			1.86			1.21

Table 2
Light attraction as affected by I_a/I_s

I_s	I_a	I_s/I_a	No. fish above light spot	
$\mu\text{E m}^{-1} \text{s}^{-2}$			(mean)	(SD)
10	0.1	100	0.0	0.00
5	0.1	50	1.7	2.42
1	0.1	10	5.3	4.96
0.5	0.5	1	12.7	1.21
0.05	0.5	0.1	8.3	1.86
0.02*	1	0.02	5.5	2.07
0.005*	1	0.005	0.5	0.70

We noted that when the stimulus light was brighter than the adaptation light, the chinook were attracted to the dim zone that bounded the light spot above which fish were counted. Thus, behavior seemed to be consistent with Fields' hypothesis. In theory, as the contrast between stimulus and adaptation increases, the chinook must swim farther from the light spot to maintain their adaptation level. In fact, during experiments at $I_s/I_a = 100$, chinook were observed to swim to corners farthest from the light and appeared to actively avoid the light. The chinook exhibited weak attraction when I_s/I_a was less than 1. This response may have resulted from their inability to detect a dim stimulus light after exposure to relatively bright light.

In their natural stream or ocean habitat, salmonids use light to gain information about the environment. They are visual predators and thus depend upon light to obtain energy for growth and reproduction. Light intensity, and diel and seasonal light cycles, influence the development,

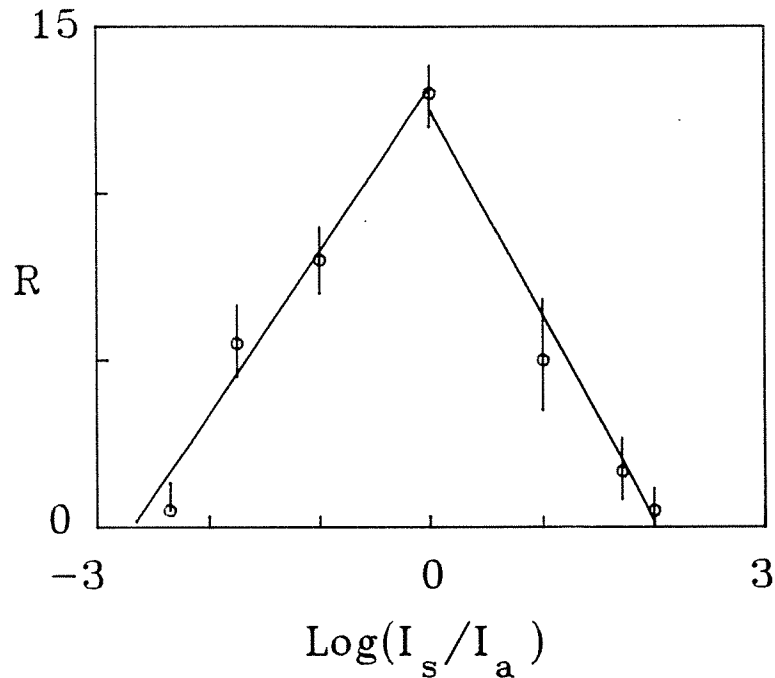


Figure 2. R represents the average number (± 1 SE) of chinook salmon attracted to the light spot. Lines fitted by least squares regression.

Table 3
Regression coefficients

Contrast	k	R _m	r	P
I _s /I _a > 1	6.3	12.3	-0.88	<0.01
I _s /I _a < 1	5.1	13.1	0.93	<0.01

physiology, and ecology of salmon (22, 12). It is no wonder that researchers have had difficulty describing and quantifying the response of fish to light. This difficulty increases when adaptation is not accounted for, or when results are reported as response averaged across time. Very often this is the time during which adaptation occurs.

Many studies have attempted to identify life stage and species specific phototaxis (e.g., 6, 7, 8). We suggest that most fish are not strictly photopositive or photonegative, even within a species or life stage, and that phototaxis depends upon, among other factors, immediate past exposure to light.

DOWNSTREAM MIGRANT GUIDANCE APPLICATIONS

Both the results and the experimental design of this study are directly applicable to diversion problems for downstream migrants at hydroelectric facilities. If these results can be repeated, especially with other species and life stages, then the use of light to attract fish away from hazardous areas shows great potential.

Our study suggests that bypass efficiency will improve when the response of fish to light and other relevant stimuli is better understood. We suggest that the long-term goal of fish guidance work should be to achieve an adequate level of understanding. Optimum fish bypass efficiency can then be facilitated by the application of fish behavior principles in an engineering context.

ACKNOWLEDGMENTS

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REFERENCES

1. Assessment of Downstream Migrant Fish Protection Technologies for Hydroelectric Application. Palo Alto, CA: Electric Power Research Institute, EPRI AP-4711, September 1986.
2. D. E. Johnson, P. E. Fields, P. S. Karekar, and G. L. Finger. "Conditions Under Which Light Attracts and Repels Pre-Migratory Salmon in Clear and Turbid, Still and Running Water." University of Washington College of Fisheries Tech. Rept., No. 42, March 1958.
3. P. E. Fields, G. L. Finger, R. J. Adkins, and R. Pyke. "Factors Influencing the Efficiency of Light Barriers in the Guidance of Young Salmonidae." University of Washington College of Fisheries Tech. Rept., No. 8, 1954.
4. C. H. Hocutt. "Behavioral Barriers and Guidance Systems." Effects on Fish and Shellfish Behavior. New York: Academic Press, 1980. C.H. Hocutt, J. R. Stauffer, Jr., J. E. Edinger, L. W. Hall, Jr., and R. P. Morgan II (eds.). pp. 183-205.
5. E. Fields and G. L. Finger. "The Reaction of Five Species of Young Pacific Salmon and Steelhead Trout to Light." University of Washington College of Fisheries Tech. Rept., No. 7, 1954.
6. W. S. Hoar, M. H. A. Keenleyside, and R. G. Goodall. "Reactions of Juvenile Pacific Salmon to Light." J. Fish. Res. Board Canada, Vol. 14, 1957, pp. 815-830.
7. A. T. Pinhorn and C. W. Andrews. "Effects of Photoperiod on the Reactions of Juvenile Atlantic Salmon (*Salmo salar* L.) to Light Stimuli." J. Fish. Res. Board Canada, Vol. 20, 1963, pp. 1245-1266.
8. A. T. Pinhorn and C. W. Andrews. "Effect of Photoperiods on the Behavior of Juvenile Atlantic Salmon in Vertical and Horizontal Light Gradients." J. Fish. Res. Board Canada, Vol. 22, 1965, pp. 369-383.

9. R. J. Gibson and M. H. A. Keenleyside. "Responses to Light of Young Atlantic Salmon (*Salmo salar*) and Brook Trout (*Salvelinus fontinalis*)." J. Fish. Res. Board Canada, Vol. 23, 1966, pp. 1007-1024.
10. H. MacCrimmon and Wen-Hwa Kwain. "Use of Overhead Cover by Rainbow Trout Exposed to a Series of Light Intensities." J. Fish. Res. Board Canada, Vol. 23, 1966, pp. 983-990.
11. W. Kwain and H. MacCrimmon. "Further Observations on the Response of Rainbow Trout, *Salmo gairdneri*, to Overhead Light." J. Fish. Res. Board Canada, Vol. 26, 1969, pp. 3233-3237.
12. J. H. S. Blaxter. "Light-Fishes." In: Marine Ecology, Vol. 1. New York: Wiley-Interscience, 1970, O. Kinne (ed.), pp. 213-320.
13. V. R. Protasov. Vision and Near Orientation of Fish. Jerusalem: Israel Program for Scientific Translations, 1970.
14. P. E. Fields. Final Report on Migrant Salmon Light Guiding Studies (Contract No. D.A. - 45 - 108 Civeng - 63 - 29) at Columbia River Dams. Portland, OR: United States Army Corps of Engineers. February 1966.
15. M.A. Ali. "Retinomoter Responses." In: Vision in Fishes. New York: Plenum Press, 1975, M. A. Ali (ed.), pp. 313-355.
16. G. T. Fechner. "Elemente der Psychophysik." Leipzig: Breikopf und Haertel, 1860.
17. A. Rapoport. Mathematical Models in the Social and Behavioral Sciences. New York: John Wiley & Sons, 1983, pp. 118-125.
18. M. A. Ali. "The Ocular Structure, Retinomotor and Photo-Behavioral Responses of Juvenile Pacific Salmon." Can. J. Zool., Vol. 37, 1959, pp. 965-996.
19. J. R. Brett and C. Groot. "Some Aspects of Olfactory and Visual Responses in Pacific Salmon." J. Fish. Res. Board Canada, Vol. 20, 1963, pp. 287-303.
20. G. L. Finger and P. E. Fields. "The Role of Light Adaptation on Negative Phototaxis in Silver Salmon (*Oncorhynchus kisutch*). University of Washington College of Fisheries Tech. Rept., No. 34, 1957.
21. M. A. Ali. "Light Preference of Control, Light- or Dark-Adapted Sockeye Salmon (*Oncorhynchus nerka*) Juveniles." Am. Zool., Vol. 2, 1962, p. 385.
22. P. M. J. Woodhead. "The Behaviour of Fish in Relation to Light in the Sea." Oceanogr. Mar. Biol. Ann. Rev., Vol. 4, 1966, pp. 337-403.

APPENDIX 4:
**A NEURAL MODEL FOR VISUAL ACTIVATION
OF STARTLE BEHAVIOR IN FISH**

by

James Jay Anderson

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ABSTRACT

The startle response of a fish to an attacking predator is modeled with a Mauthner cell spike initiated by inputs from ganglion cells that sense the expansion of the predator's image on the fish's retina. The image expansion rate is dependent on the predator's distance (D), speed (V) and silhouette area (A). The Mauthner cell fires when the expansion rate reaches a threshold value. The model defines a startle response reaction distance as $D = (k A V)^{1/3}$, where k depends on the eye morphology and Mauthner cell electrical properties. The equation is fit to published data on the reaction distance of zebra danio (*Branchydanio rerio*).

INTRODUCTION

Fish typically exhibit a variety of escape maneuvers in response to predators. The quickest escape behavior is the startle response in which a fish performs a fixed action pattern to a sudden stimulus. The behavior has been described as a fixed action pattern in three stages (Eaton & Hackett, 1984). Stage 1 is highly stereotypic. Over a 30 msec time increment, the fish initiates a tail flip in which, depending on the species, the body either forms the shape of a C or S with its head directed away from the aversive stimulus. In stage 2 the bend in the fish proceeds down the body adjusting the escape trajectory and the fish moves either forward or to the side over about a 100 msec interval. Stage 3 varies from unpowered glides to periodic lateral movements of the body and tail, which are usually associated with steady swimming.

The evolutionary significance of a startle response is through its survival value. Even a small movement of a fish may be enough to allow it to escape an attacking predator. A fast reflexive response, although simple, may provide the time necessary for a fish to evaluate the situation and follow up the startle response with an appropriate defensive behavior. An attacking predator may approach from any angle and so it is critical that a fish can reliably assess an attack from any angle. The binocular vision of a fish covers only a small portion of its total field of vision so an effective startle response must be activated with a fish's monocular vision. A variety of senses may be activated by an predator's attack including the lateral line (Blaxter, Gray & Denton, 1981) and vision (Dill, 1974). In this model we consider the activation of the startle response by vision. The visual input of an attack is a change in the size and position of the image of the predator on the retina of the fish. Through this input a fish must be able to distinguish the predator's distance, speed and direction. Evidence suggests fish have these abilities. Objects moving away from a fish will not generally elicit a startle response, while objects moving towards a fish will. This response can be easily observed with fish in a tank by moving your hand quickly toward or away from the tank. Dill (1974) showed that fish make an assessment of a predator's size and attack velocity by demonstrating that the distance at which a fish elicits a startle-type escape response is related to the

apparent size and velocity of an attacking predator. Webb (1981) found that this response varies with fish length.

The startle response is predominantly initiated by a pair of prominent neurons called Mauthner cells that descend into the spinal cord where excitatory connections are made with motoneurons innervating the trunk musculature (Kimmel & Eaton, 1976). Startle responses can be initiated by other neuronal pathways but they appear to be of secondary importance. Mauthner cells have conspicuously large soma that, in some fish species, have a diameter of 0.1 mm and may have approximately 200,000 synaptic terminals from a variety of sensory inputs including sound, gravity, angular acceleration, vibration, water flow, electric fields and vision (Cochran, Hackett, & Brown, 1980). Recent work with goldfish has shown that the optic nerve has inputs to the Mauthner cell via projections from the tectum (Zottoli, Hordes & Faber, 1987). A startle response is activated when the membrane potential of a Mauthner cell is driven to its threshold by the summed activity of synaptic terminals on the cell from the afferent nerve pathways. When the potential reaches its threshold level, the cell fires through a membrane depolarization, which in turn fires motoneurons of the muscular system. Startle response latencies of between 5 to 40 msec after the introduction of vibration and electric shock stimuli have been observed in a number of fish species (Eaton & Hackett, 1984). The latency to visual stimuli has not been carefully studied, but evidence suggests the speed of the visual response is on the same order. A filmed sequence of a cyprinid escaping a predatory snake suggests the startle response latency was within 40 msec of the snake attack (Eaton & Hackett, 1984). This action must be carried out with a minimum of neural processing because the response times of individual neurons typically required a few msec (Kandel, 1981). Stimulating the optic nerve evokes a postsynaptic potential in the Mauthner cell with a latency of about 1 msec (Zottoli, Hordes & Faber, 1987). Thus, a visually induced startle response neural pathway should involve the firing of a small number of neurons in series. To develop a startle response model we disregard the details of the process between the retina and the Mauthner cell and focus only on the inputs and outputs of the system. We consider concepts developed in the study of amphibian behavior and neurobiology.

Studies of the visual prey-predator discrimination in frogs provide a good basis for a model of the startle response visual activation in fish. The neural pathway of visual discrimination behavior in frogs has been traced from the retina to the optic tectum (Ewert, 1976; Ingle, 1981). How the animals discriminate prey from predators has been the topic of a series of models involving the interactions of the retina, optic tectum and pretectum (Cervantes-Perez, Lara & Arbib, 1985). We shall consider a similar model based on the interaction of the retina and spinal cord neurons involved with the startle response. To simplify, the model shall focus on the Mauthner cell as a major motoneuron activator of the startle response and will not consider alternative pathways by which retinal signals reach the motoneurons.

MODEL DEVELOPMENT

The model includes basic structural and neural characteristics of a fish eye. In vertebrate eyes, visual images are focused through the lens onto the retina, which is composed of three tiers of cells- rod and cone photoreceptors, bipolar cells, and ganglion cells- which are laterally connected by horizontal cells and amacrine cells (Polyak, 1955; Protasov, 1968; Ali, 1975). Ganglion cells connect through the optic nerve tract to the optic tectum of the midbrain. The densities of photoreceptor and ganglion cells are not uniform over the retina and the highest densities are found in the area corresponding to the major binocular fixation point on the retina. There are about four to five times as many cones and ganglion cells per unit area in the upper temporal part of the retina as in the anterior regions (Guthrie, 1986). Over the monocular visual field, variations in the densities of rods, and presumably ganglion cells, are less and are generally within a factor of two (Ahlbert, 1970). Signals from groups of photoreceptors are processed through the system of bipolar, amacrine, and horizontal cells to activate specific types of ganglion cells. In effect each ganglion cell is sensitive to a region of photoreceptor cells and is activated when a specific pattern of light falls on the field. Several general types of ganglion cells are found in mammals: X type ganglion cells respond to a pattern of a dark center surrounded by a light field; Y type cells respond to a light center surrounded by a dark field; and W type of ganglion cells seem to detect motion across their receptor fields. About 40% of the retinal ganglion cells are W type although within this category differences exist in the type of motion that can be detected (Kandel, 1981). Generalizing from mammals we assume these motion-sensing cells may provide a simple mechanism to initiate the startle response in fish. To this end, the startle response model assumes that the firing of a Mauthner cell is determined by the rate of firing of W type ganglion cells which, in turn, are determined by the rate of expansion of a predator's image on the retina (Fig. 1).

Mauthner Cell Dynamics

A Mauthner cell action potential is produced when the cell membrane potential, u , reaches the threshold value U . The dynamics of the potential will be modeled in the style of the "classical neurodynamics" model (Hopfield, 1982; Hopfield & Tank, 1986). The membrane current will be described by the equation;

$$C \frac{du}{dt} = P - \frac{u}{R} + I \quad (1)$$

This equation expresses the net input of current charging the input capacitance, C , of a neuron to potential u as the sum of three sources: (1) a phasic synaptic current from the ganglion cells, P ; (2) leakage current due to the Mauthner cell membrane resistance R ; and (3) a tonic current from other neurons external to the circuit, I .

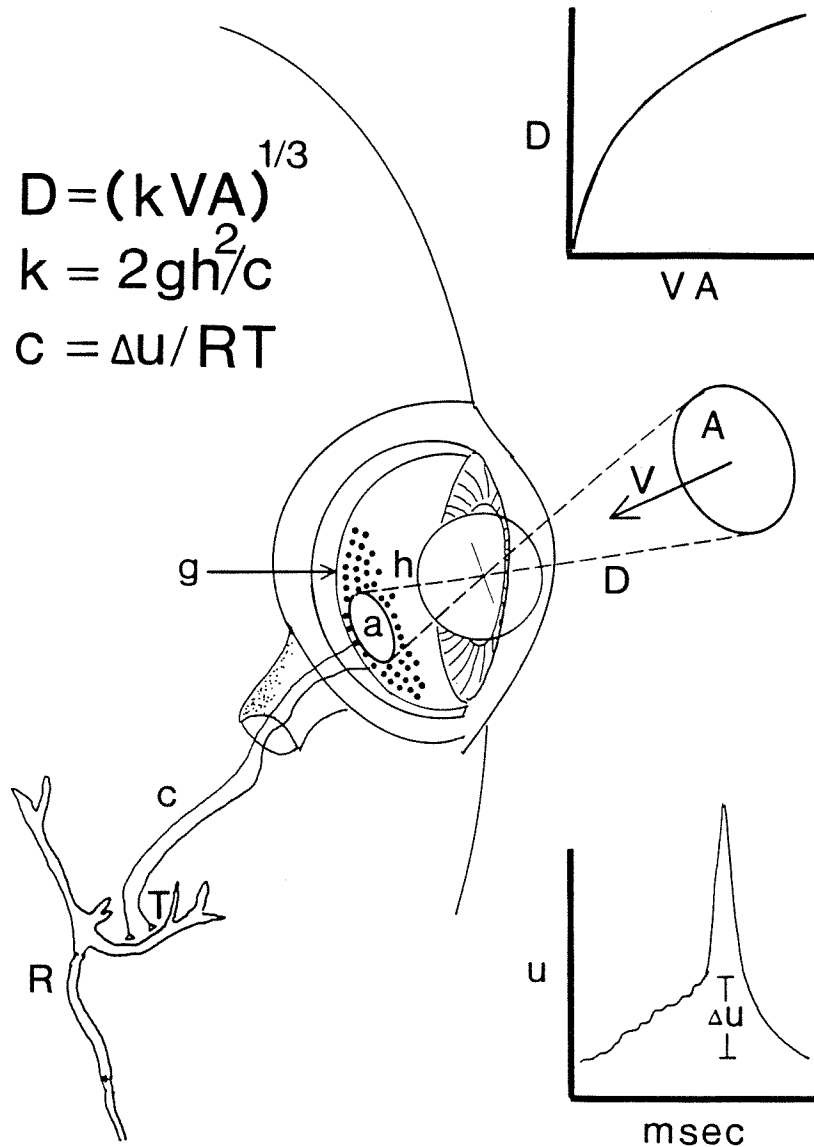


Fig. 1. Model for visual activation of startle response involving fish eye and Mauthner neuron. Reaction distance, D , at which startle response is initiated is proportional to the $1/3$ power of the predator's area, A , times velocity, V (upper righthand curve). Parameter, k , depends on motion-sensing ganglion cell density, g , eye focal length, h , and critical ganglion firing rate, c , which is controlled by the expansion rate of the retinal image area, a . Mauthner cell spike is generated when cell membrane potential, u , reaches threshold Δu (lower righthand curve). Threshold ganglion firing rate, c , depends on, Δu , Mauthner cell resistance, R , and ganglion-Mauthner cell synaptic strength, T .

This model assume that the phasic current to the Mauthner cell is produced by the firing of motion-sensing ganglion cells. If these cells only fire with image motion across their receptive fields, then the phasic current changes as the number of motion-sensing ganglion cells which are firing changes. This relationship can be expressed as

$$P = T \frac{dw}{dt} \quad (2)$$

where w is the number of ganglion cells firing and T is the average synaptic strength, which expresses the electric charge that a Mauthner cell receives when a ganglion cell detects retinal image motion.

The equilibrium membrane potential, where $du/dt = 0$, can be expressed as

$$u(\infty) = R \left(T \frac{dw}{dt} + I \right) \quad (3)$$

The minimum possible firing rate that can induce a Mauthner cell action potential can be determined by setting $u(\infty) = U$ in eqn(3) and solving for dw/dt giving

$$c = \frac{1}{T} \left(\frac{U}{R} - I \right). \quad (4)$$

where $dw/dt = c$ is the summed rate produced by the combined firing of ganglion cells.

The rate of firing of motion-sensing ganglion cells, dw/dt , is determined by the size and movement of a predator's image across the receptive fields of the ganglion cells. When the summed firing rate exceeds the critical rate, c , the charge input to the Mauthner cell exceeds the leakage rate and the Mauthner cell potential rises and eventually reaches the threshold level U and the cell fires, inducing a signal to the motoneurons responsible for activating the startle response. Thus, in the model, a startle response is dependent on the rate of expansion of a predator's image on the fish's retina.

To formulate the summed firing rate of ganglion cells, define the number of ganglion cells with receptive fields covered by the retinal image of a predator as

$$w = \int_0^a g(a') da' \quad (5)$$

where a is the area of the predator's image on the retina and $g(a)$ is the areal density of ganglion cell connections to the Mauthner cell. Ganglion cell density varies over the retina (Guthrie, 1986) but the effect may be relatively minor due to the small changes in cell density across the actual area covered by a retinal image.

The rate of summed firing of ganglion cells corresponds to the rate at which the area of the predator image expands over the retina. This rate can be expressed by differentiating eqn(5) over time and using Leibnitz's rule to obtain

$$\frac{dw}{dt} = g(a) \frac{da}{dt} + \int_0^a \frac{dg(a)}{dt} da \quad (6)$$

where the rate of firing of ganglion cells equals the contribution to the rate from the expansion of the predator's image on the retina plus a contribution by the change in the density of ganglion cells.

The Retinal Image

The rate of expansion of the image of the predator on the retina of the fish can be developed in terms of the size, speed and distance of the predator. Assume that all information sufficient to determine a predator's attack is contained in the movement of the predator's silhouette image on the retina. The actual silhouette of the predator can be defined by a polar coordinate equation, $R(O)$, describing the distance of the silhouette's edge from its center of mass as a function of the rotation angle, O . The projection of the predator's silhouette on the retina is inverted and reduced and can be sufficiently defined by the polar equation;

$$r(O)/h = R(-O)/D \quad (7)$$

where D is the distance from the fish to the predator and h is the focal distance of the fish eye (Fig. 1).

The area of the silhouette can be expressed as

$$A = \frac{1}{2} \int_0^{2\pi} R^2(O) dO. \quad (8)$$

and using eqn(7) the area of the retinal image can be expressed

$$a = (h/D)^2 A. \quad (9)$$

The rate of change of the image area on the retina is obtained by differentiating eqn(9) with respect to time and noting that h and A are constant

$$\frac{da}{dt} = 2 \frac{A V h^2}{D^3} \quad (10)$$

where $V = -dD/dt$ is the velocity of the predator moving toward the fish and is assumed constant in the model.

The summed rate of ganglia firing depends on $g(a)$, which expresses the density of ganglion cell connections to the Mauthner cell as a function of retinal area. Evidence (Ahlbert, 1970; Guthrie, 1986) suggests that the density of photoreceptors and ganglion cells is relatively constant over the majority of the retina and only increases in the periphery corresponding to the binocular field. Predators attack from all angles and their retinal images usually cover a small portion of the

retinal field. Thus, the essential dynamics of the ganglion firing rate can be modeled assuming a constant ganglion density

$$g(a) = g. \quad (11)$$

Using eqn(10) and (11) in (6) gives

$$\frac{dw}{dt} = 2 \frac{g A V h^2}{D^3} \quad (12)$$

Incorporating the minimum threshold firing rate, $dw/dt = c$, the reaction distance for the startle response escape is defined from eqn(12) as

$$D = (k A V)^{1/3} \quad (13)$$

where k is a time constant defined as

$$k = 2 g h^2 / c \quad (14)$$

and the critical ganglion summed firing rate c is defined as

$$c = \Delta u / R T \quad (15)$$

where $\Delta u = U - IR$ is the Mauthner cell spike generation threshold potential relative to the resting potential IR .

Equations (13), (14), and (15) together comprise the model of the visual activation of the startle response in terms of behavioral, morphological, and neurobiological factors. Equation (13) describes the behavioral interaction between predator and prey with one free parameter, the startle response time factor k . This factor defines the image expansion rate needed to induce a startle response in terms of the time in which the image would expand into a unit area equal to twice the square of the focal length. The response time factor, defined by eqn(14), contains retinal morphological properties g and h and the summed firing rate c . Both g and h are dependent on fish length and species. The dynamic factor c is dependent on the Mauthner cell electrical properties according to eqn(15). The membrane resistance, R , is most likely a fixed property of the Mauthner cell. The relative critical threshold, Δu , is influenced by the input of other neurons to the Mauthner cell and, as such, this property may change according to the inhibition or excitory inputs from other systems which may be altered by the mental or physiological state of the fish. The synaptic strength, T , describes the number of coulombs of electric charge that the Mauthner cell receives when a ganglion cell fires. Mauthner cells will show a form of habituation with repeated responses (Eaton & Hackett, 1984) and, in terms of the model, the habituation could be expressed as a temporary decrease in T .

MODEL EVALUATION

Several factors of the model can be evaluated using experimental data from the literature. The behavioral prediction of eqn(13) can be evaluated using data published by Dill (1974) on the escape response of zebra danio (*Branchydanio rerio*). Dill found that the reaction distance at which fish attempted to escape the direct attack of a model predator was a function of both predator size and velocity. His data (Dill, 1974; Table 1) is reproduced in Table 1 with model size expressed as frontal area. The best fit of eqn(13) to the data is through the linear form

$$X = a_0 + a_1 Y \quad (16)$$

Table 1. Mean escape reaction distance D (cm) of naive zebra danios to model predators of different sizes and velocities (From Dill, 1974).

Predator velocity U (cm/s)	Predator silhouette area, A (cm ²)		
	5.0	11.3	20.3
11.6	11.5	18.2	9.9
43.6	13.8	22.4	24.8
62.8	20.4	25.0	26.5
108.5	25.2	33.0	31.3

where $X = D$, $Y = (A V)^{1/3}$, the slope is $a_1 = k^{1/3}$, and a_0 is a free parameter which should equal zero (Fig. 2). Dill's control experiment, the test apparatus without a model predator attached, produced no fright response. This observation was included in the regression as a point at the origin, by specifying that $D = 0$ when $A = 0$. This quantifies the obvious, but important, observation that fish do not startle when the predator is invisible. The regression coefficients and 90% confidence interval limits are given in Table 2. The R-squared of the regression with 13 points is 0.88.

An approximate estimate of the threshold ganglia summed firing rate, c , that initiates the model escape response can be obtained from eqn(14) with the estimate of k and literature estimates of the g and h . The zebra danio used in Dill's experiments were 20 mm in length. Since g and h are dependent on fish length and no estimates are available for the danio, representative estimates must be obtained from fish of similar size but of different species. In 40 mm goldfish, a typical ganglion cell density is 6000 cells/mm (Johns & Easter, 1975). Assuming that 40% of these ganglion detect motion, an estimate of the effective cell density is $g = 2400$ cells/mm. Assuming that the distance from the center of the lens to the retina is a measure of focal length, then a representative estimate is $h = 0.9$ mm, which is the distance from the center of the lens to the retina in a 22 mm guppy (Protasov, 1968). From eqn(14) the summed firing rate needed to produce a startle response is about 200 cells/s (Table 2).

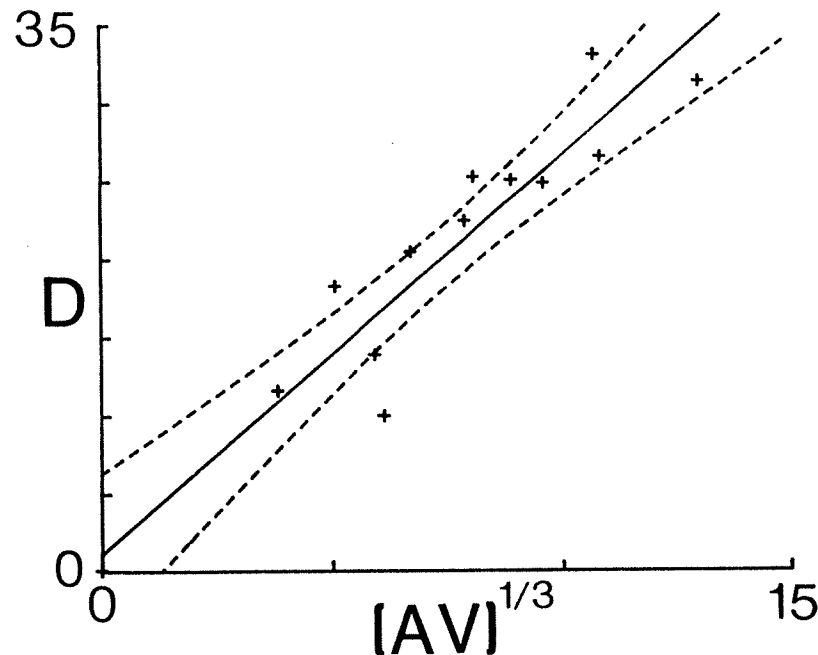


Fig. 2. Regression of Dill's (1974) data of reaction distance of zebra danio vs. the $1/3$ power of predator's area, A , times velocity, V . Dashed lines depict 90% confidence interval of regression.

Table 2. Regression coefficients, 90% confidence interval limits, T-values, and regression R-squared for regression of eqn(16) to Table 1 data. Model parameters c , T and k calculated from eqns(14), (15), and (16).

	a_0	a_1	k (sec)	c (cells/s)	T (coulombs)
Coefficient	1.07	2.56	16.8	231	0.6×10^{-12}
Lower limit	-3.15	2.04	8.5	457	0.3×10^{-12}
Upper limit	5.29	3.08	29.2	133	0.9×10^{-12}
T-value	0.45	8.86			
					R-squared = 0.88

A very rough value for the synaptic strength, T , can be estimated from Mauthner cell electrical properties using eqn(15). Assuming the cell resistance is 10^8 ohms and the relative potential to fire a cell is 15 mV (Kandel, 1981), a first order estimate of the synaptic strength is $T = 10^{-12}$ coulombs/ganglion. To put this value into perspective, a postsynaptic potential introducing 10^{-11} amps into a cell over a period of about 1 ms requires a charge input of about 10^{-14} coulombs at the synapse. Thus, the average synaptic strength, T , associated with a ganglion cell firing should be about 100 times the strength of a single synapsis. Assuming that the retina has on the order of 10,000 motion sensing ganglion cells and each one affects an individual synapse on the Mauthner cell then 5% of the Mauthner cells synapses are associated with the vision system. Because T is

estimated to be 100 times the strength of a single synapse each connection should fire a number of times for each ganglion cell activation. The Mauthner cell receives a variety of afferent inputs indicating the fish's sense of sound, acceleration, touch, and vision so the surmise that each sense might account for 5 or 10% of a cell's synapses does not seem unreasonable.

DISCUSSION

The model describes the activation of the startle response through the interactions of the retina and Mauthner cell using neurodynamics developed by Hopfield (1982) and Cervantes-Perez et al.(1985) and others. When the expansion rate of an attacking predator's image on the fish's retina reaches a threshold level the Mauthner cell fires producing a startle response. The model is an extension of Dill's (1974) model in which reaction distance of the escape response is expressed in terms of the predator's speed and size. The model provides a good fit to Dill's (1974) data on the reaction distance response by zebra danio. More importantly, the model provides further testable hypotheses on how the startle response may be related to: (1) fish size, through the eye focal length and ganglion density; (2) to habituation, through the Mauthner cell afferent synapse strengths; and (3) to learning, through the Mauthner cell tonic potential.

The possibility of developing a basic equation to describe the startle response distance to visual objects has great value. Webb (1981) demonstrated that the reaction distance is an important factor in determining the success of northern anchovy larvae escaping from predators. Of larvae responding to an attack by a clown fish, 26% attempted to escape too late and were caught. In ecological theories the reaction distance in predator-prey encounters is a fundamental factor which determines the outcome of encounters. A simple equation describing the reaction distance can be of great use in understanding and modeling ecosystems. The startle response of fish also has a significant role in how fish behave in fish diversion structures. At the present time, little is known about how fish respond to screens and lights used to divert fish from power plant water intakes. The proposed model may provide part of the fundamental understanding that is needed to design efficient fish diversion structures.

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REFERENCES

- AHLBERT, I. (1970). *Arkiv for Zoologi* 22, 445.
- ALI, M.A. (1975). "Vision in Fishes." NATO Advanced Study Institute Series. New York: Plenum Press.
- BLAXTER, J.H.S., GRAY, J.A.B & DENTON, E.J. (1981). *J. mar. biol. Ass. U.K.* 61, 851.
- CERVANTES-PEREZ, F., LARA, R. & ARBIB, M. (1985). *J.theor.Biol.* 113, 117.

- COCHRAN, S.L., HACKETT, J.T. & BROWN, D.L. (1980). *Neuroscience* 5, 1629.
- DILL, L.M. (1974). *Anim. Behav.* 22, 711.
- EATON, R.C. & HACKETT, J.T. (1984). In: "Neural Mechanisms of Startle Behavior" (Eaton, R.C. ed.). New York: Plenum Press.
- EWERT, J.-P. (1976). In: "The Amphibian visual System" (Fite, K. ed.). New York: Academic Press.
- GUTHRIE, D.M. (1986). In: "The Behavior of Teleost Fishes" (Pitcher, T.J. ed.). Baltimore: Johns Hopkins University Press. HOPFIELD, J.J. (1982). *Proc. Nat. Acad. Sci.* 79, 2554.
- HOPFIELD, J.J. (1982) *Proc. Nat. Acad. Sci.* 79, 2554.
- HOPFIELD, J.J. & TANK, D.W. (1986). *Science* 233, 625.
- INGLE, D.J. (1981). In: "Handbook of Motivation". (Teitelbaum & Satinoff, eds.). New York: Plenum Press.
- JOHNS, P.R. & EASTER, S.S. (1975). In: "Vision in Fishes" (Ali, M.A. ed.). NATO Advanced Study Institute Series. New York: Plenum Press.
- KANDEL, E.R. (1981). In: "Principles of Neural Science" (Kandel, E.R. & Schwartz, J.H. eds.). New York: Elsevier/North-Holland.
- KIMMEL, C.B. & EATON, R.C. (1976). In: "Simpler Networks and Behavior" (Frentress, J.C. ed.). Sunderland: Sinauer Associates Publishers.
- POLYAK, S. (1955). "The Vertebrate Visual System." Chicago: University of Chicago Press.
- PROTASOV, V.R. (1968). "Vision and Near Orientation of Fish." (Translated from Russian-Israeli Program for Scientific Translations.)
- WEBB, P.W. (1981). *Fish Bull.* 79, 727.
- ZOTTOLI, S.J., HORDES, A.R. & FABER, D.S. (1987). *Brain Res.* 401,113.

APPENDIX 5:
COMPUTER MODEL STUDIES STAGE II

MODEL DESCRIPTION

In the second stage of development, the model describes fish paths from movements produced by water flow and swimming behavior in response to stimuli from strobe lights and a trashrack. For strobe light avoidance, swimming speed is defined in terms of light intensity and the direction is directly away from the light. For trashrack avoidance, the swimming speed is assumed to vary with a normal distribution and the direction is taken to be perpendicular to the trashrack. Trashrack avoidance is initiated when the fish comes within a critical distance of the trashrack. The component of fish movement from water flow is defined in terms of an empirical equation describing the streamlines of the water flow. Over small increments of time, components of displacement from water flow, strobe light avoidance, and trashrack avoidance are summed vectorially. With a fixed flow and strobe light configuration, fish trajectories are dependent on five parameters: V and I_a describe the strobe light avoidance response according to eq. (4) (Appendix 2), D is the critical distance from the trashrack at which avoidance occurs, V_1 is the mean speed of the trashrack avoidance and S_1 is the standard deviation of the speed.

FISH TRAJECTORIES

Figure 1 illustrates the general types of paths generated by the model. Path A shows the effect of trashrack avoidance. Fish follow the water path to the critical distance where they swim away from the trashrack. This avoidance behavior counteracts the horizontal component of the flow, but not the vertical component, so fish move down the trashrack at a velocity equal of the vertical component of the flow. Variations in the trashrack avoidance speed causes some fish to pass through the trashrack above the depth of the submersible traveling screen (STS). Below the STS the horizontal component of the flow exceeds the maximum avoidance speed and fish are pulled through the trashrack. Path B illustrates the behavior of fish in the strobe light. When encountering the light, fish swim directly away from the source. For the configuration in Fig. 1, this counteracts the vertical component of the water flow and fish generally move horizontally to the side of the light beam and towards the trashrack. Path C illustrates the behavior of fish in a high flow region deeper in the water column. They move with the flow and pass directly through the trashrack.

SENSITIVITY ANALYSIS

A model sensitivity analysis indicated that trashrack avoidance behavior was the most important factor controlling the level of FGE. The FGE increased with a decrease in the critical distance, D , and the trashrack avoidance speed, V_1 (Fig. 2). The variability factor, S_1 , had a secondary effect on FGE. The light avoidance parameters, V and I_a , and the depth distribution of fish in the

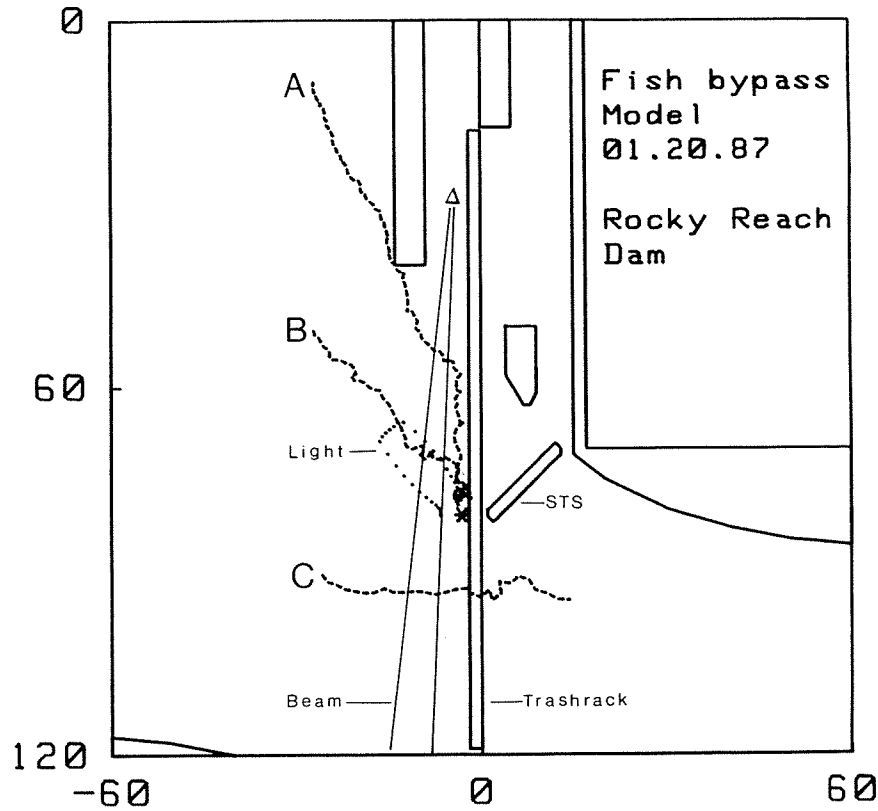


Fig. 1. Examples of fish trajectories, A, B, and C, at Rocky Reach Dam calculated with computer model. Includes hydroacoustic beam within 5 ft of trashrack a $0.1 \mu\text{E}/\text{m}^2/\text{s}$ strobe light intensity isopleth, and the submersible traveling screen (STs).

forebay also had a small effect on FGE. A change in the average depth of fish in the forebay of 10 ft caused only about a 5% decrease in FGE. A 50% variation in V or a three order of magnitude change in I_a , only change the FGE by a few percent.

RESULTS

An analysis of the field results from the spring and summer of 1986 and laboratory experiments with the computer model present a consistent set of hypothesis on the behavior of fish in front of the dam. To develop this synthesis major field and laboratory observations are first outlined and then interpreted in terms of the model.

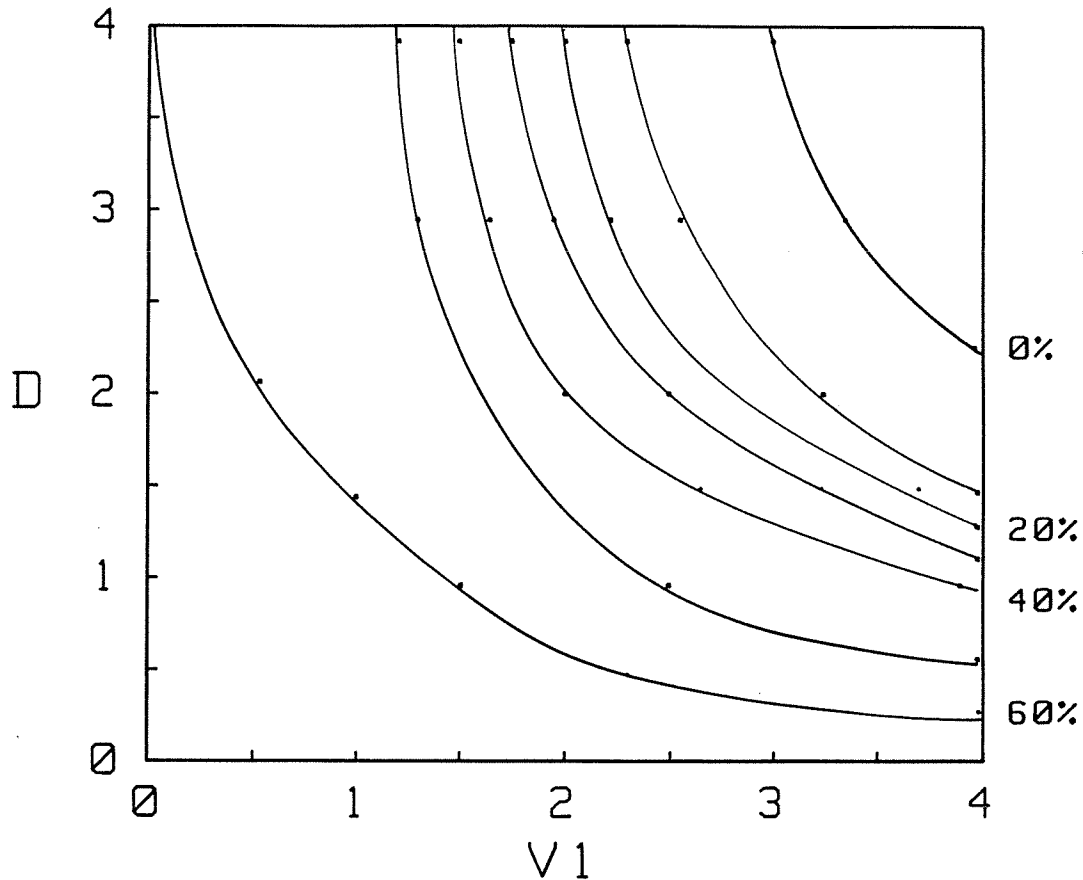


Fig. 2. Fish guidance efficiency isopleths (10% intervals) as a function of trashrack critical avoidance distance, D , in ft and escape velocity V_1 , in ft/s.

Field Observations

Fyke net catches behind the trashrack and hydroacoustic studies of fish distributions in front of the trashrack, with and without strobe lights, indicated several basic features of the fish trajectories:

- (1) In the hydroacoustic beams, which were as close as 5 ft to the trashrack, fish generally followed the water flow (Steig, Condiotty, and Raemhild 1986).
- (2) The median fish depth was always above the depth of the STS. Six ft from the trashrack the average median fish depth was 8 ft above the STS in the spring test and 14 ft above the STS in the summer test.
- (3) Fyke net catches behind the trashrack indicated the majority of fish passed below the STS in both the spring and summer tests (Hays and Truscott 1986).
- (4) In the spring period, the median fish depth generally was deeper closer to the trashrack (Tables 1 and 2).

Table 1. Median depth of fish distribution at 6 and 12 ft from trashrack. Data from hydroacoustic studies (Steig, Condiotty and Raemhild 1986). F= front deflector, R = rear deflector on trashrack. Spring study includes groups 1-12, summer study groups 13-20.

Group number	Deflectors	Time	Strobe	Median Depth		Depth change
				6ft	12ft	
<i>Spring</i>						
1	R	Day	no	73	69	4
2	R	Day	no	68	69	1
3	R	Night	no	71	68	3
4	R	Night	no	69	65	4
5	F & R	Day	no	74	70	4
6	F & R	Night	no	79	73	6
7	F & R	Day	no	71	66	5
8	F & R	Night	no	68	64	4
9	F & R	Day	no	75	67	7
10	F & R	Night	no	70	66	4
11	F & R	Day	yes	70	66	4
12	F & R	Night	yes	74	74	0
<i>Summer</i>						
13	F & R	Day	no	72	71	1
14	F & R	Night	no	67	69	-2
15	F & R	Day	yes	66	66	0
16	F & R	Day	no	70	65	5
17	F & R	Day	yes	62	69	-7
18	F & R	Night	no	62	65	-3
19	F & R	Day	yes	65	70	-5
20	F & R	Day	no	62	69	-4

Table 2. Summary of FGE and median fish depth with and without strobe light. Ch1 for yearling chinook, Ch0 for subyearling chinook, Z6 and Z12 are the median depths of the fish distribution at a distance of 6 and 12 ft in front of the trashrack. Yearling chinook, sockeye, steelhead, and coho data are from the spring study. Daylight results for subyearling chinooks are from summer. FGE data from Hays and Truscott (1986), depth data from hydroacoustic studies of Steig, Condiotty and Raemhild (1986).

Conditions	Spring period				Summer period					
	FGE				Depths					
	Ch 1	Sock	Steel	Coho	Z6	Z12				
No Strobe	Day	6.6	7.5	39.7	25.4	71	66	1.5	62	69
	Night	12.4	3.7	8.9	35.8	68	64	-	-	-
Strobe	Day	28.0	17.0	27.6	60.9	70	66	3.0	65	70
	Night	5.3	4.9	15.9	7.1	74	74	-	-	-

- (5) During the night time strobe test in the spring the median fish depth did not decrease towards the trashrack (Tables 1 and 2).
- (6) At night in the spring, the fish were deeper in the water column with strobe lights than without lights.
- (7) In the summer, test the median fish depth was generally more shallow closer to the trashrack (Tables 1 and 2).
- (8) The fyke net studies indicated that the effect of strobe lights on FGE was different from species to species (Table 3).
- (9) The majority of fish were caught in fyke net rows 3 and 4 (Table 4).

Model-field Comparisons

To reconcile the nine observations listed above with the model and laboratory studies, model parameters were first estimated. The laboratory experiments indicated that rainbow trout and chinook salmon exhibited escape speeds between 6 and 8 bl/s. Using representative fish length for the species in the spring and summer runs, a range of trashrack escape speeds were estimated (Table 4). Light avoidance parameters, obtained from experiments with rainbow trout, gave $V = 1$ ft/s and $I_a = 0.001$ to $0.1 \mu\text{E}/\text{m}^2/\text{s}$. Model trajectories representing spring coho, sockeye and yearling chinook trajectories (Fig. 3) and summer subyearling chinooks (Fig. 4) are generated with the model parameters given in Table 4.

To interpret observations (1), (2), and (3) above, note that in Figure 1 model trajectories A and B follow the flow within the region of the hydroacoustic beam and only drop rapidly in the region between the beam and the trashrack. The drop in median depth between (observations (4) and (5) listed above) are reproduced in the trajectories for the spring run (Fig. 3). Model fyke net distributions in Figure 3 are similar to the observed catches in the spring period with the majority of catch in row 3 (Table 3). Model trajectories for summer subyearling chinook (Fig. 4) suggest that a rise in the fish distributions as they approach the trashrack was due to a trashrack avoidance at a distance of about 5 ft. This feature is consistent with observation (7). The resulting fyke net catches were deeper than in the spring period with the majority of the catch in row 4. This feature is also evident in the observed catch (Table 3).

The model studies indicated that D and V_1 were the major factors affecting FGE and that slight changes in the parameters should have major effects on FGE (Fig. 2). The species-to-species differences with and without strobe lights in day and night conditions (Table 2) can be interpreted in terms of variations in D and V_1 . The species specific responses are uniquely defined in terms of FGE and V_1 (Table 2) and for each species, the parameters define distinct regions in a D vs. V_1 diagram. Conditions without strobe light parameter boundaries are set by the day and night

Table 3. Fyke net distribution from selected FGE tests. Percentage of catch for nets 1 through 7. From Hays and Truscott (1986).

Fyke net Number	Coho		Sockeye		Steelhead		Chinook 1		Chinook 0		Average	
	D	N	D	N	D	N	D	N	D	N	D	N
1	4	8	6	0	0	1	0	1	0	8	2	9
2	4	16	10	3	14	7	7	13	13	16	10	11
3	53	23	18	13	56	27	34	38	28	23	38	25
4	29	22	29	32	19	28	33	25	44	22	31	26
5	7	16	19	32	5	21	10	13	10	16	10	20
6	3	13	14	16	5	14	8	8	4	13	7	13
7	0	1	3	4	0	0	2	0	1	1	1	1

Table 4. Model parameters for selected standard model runs giving resulting FGE and fyke net percentage distributions. Fish length in inches, escape speed, V_1 , and standard deviation, S_1 , in ft/s are calculated assuming escape speed of 7 body lengths/s and $S_1 = 0.4 * V_1$. Critical trashrack avoidance distance, D , in ft.

Species	Model Parameters					Fyke net row percentages						
	Length	D	V_1	S_1	FGE	1	2	3	4	5	6	7
Coho	4.6	1.8	2.6	1	25	0	0	83	11	2	0	0
Sockeye	4.0	3.8	2.4	1	17	0	8	19	62	7	1	0
Steelhead	7.0	1.4	3.7	1.5	16	0	2	38	51	4	1	0
Chinook 1	5.0	2.4	2.9	1.2	7	0	0	69	24	3	1	0
Chinook 0	4.0	4.0	2.5	1	4	0	0	41	53	2	0	1

levels of FGE and the escape speed, which was assumed to have a mean value between 6 and 8 bl/s (Fig. 5). Observed variations in FGE, between day and night, can be explained by a variation in avoidance distance, D , of less than 1 ft, or by a variation in escape speed, V_1 , of less than 1 ft/s. The analysis suggests that steelhead, which were the fastest swimmers, had the smallest critical distance, that is they stayed closer to the trashrack. Subyearling chinook and sockeye were at the other extreme, with slower escape speeds they kept a greater distance from the trashrack.

With strobe light, the FGE exhibited greater differences between day and night conditions (Table 2). In the spring period possible causes for the increase in the day time FGE can be explained by a decrease in either D or V_1 . The decrease in FGE at night could result from an increase in either D or V_1 . The magnitude of the possible change, if one parameter changed while the other remained unchanged, is illustrated in Figure 6. The base conditions were taken as average D and V_1 values representing non-strobe light conditions (Table 4). Figure 6 suggests that the parameters for steelhead were least affected by strobe light and the parameters for coho were the most affected. For coho, either D changed by up to 2.5 ft or V_1 changed by up to 3 ft/s.

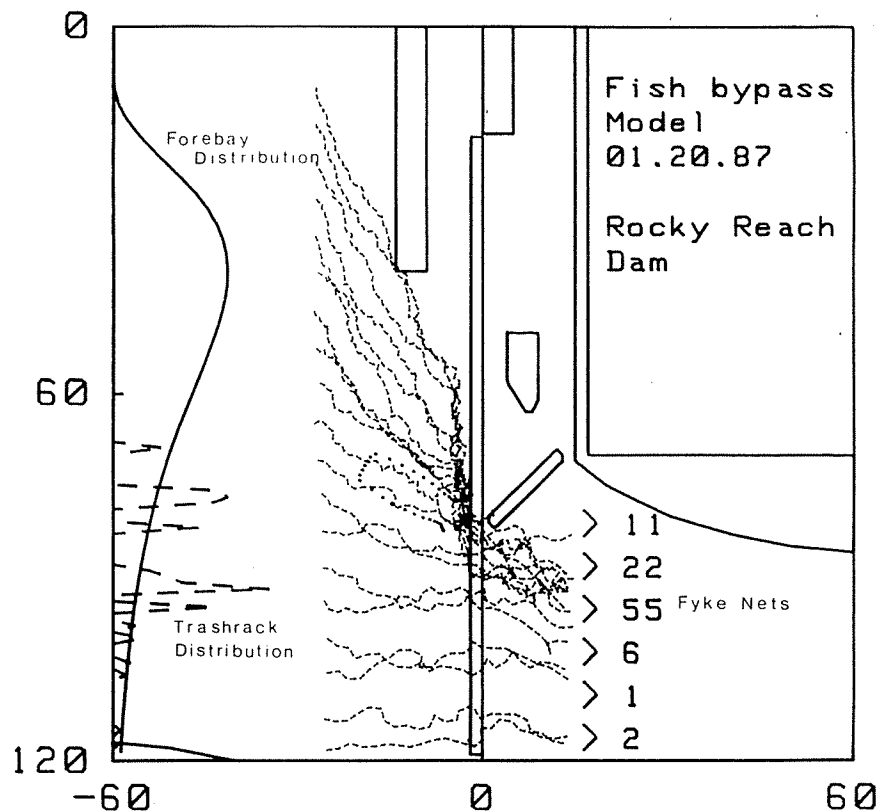


Fig. 3. Fish trajectories with vertical distributions of fish in forebay and at trashrack, and distribution of catch in fyke nets is expressed as percentages of the total fyke net catch. Model parameters represent spring run conditions.

The spring study results suggest that strobe light in the day either decreased the critical distance or the escape speed while at night strobe light appeared to have the reverse effect. Behavioral mechanisms to explain this hypothesis have not been identified at this time. The difference between day and night response may, in part, relate to the light level that fish are adapted to. The median depth data (Table 2) provides secondary evidence that fish response to the strobe light is dependent on the adaptation light level. For example, in the day strobe light apparently did not affect the depth distribution, since during the day the median depth was essentially the same with and without strobe light. At night the distribution with strobe light was 10 ft deeper than the distribution without strobe light (Table 2).

The summer studies on subyearling chinook presented a different picture. The subyearling chinook were smaller and had less swimming ability to escape the trashrack. The parameter diagram (Fig. 6) suggests that the low daytime FGE could have been the result of fish maintaining a greater critical distance from the trashrack. This could have been a result of the greater water

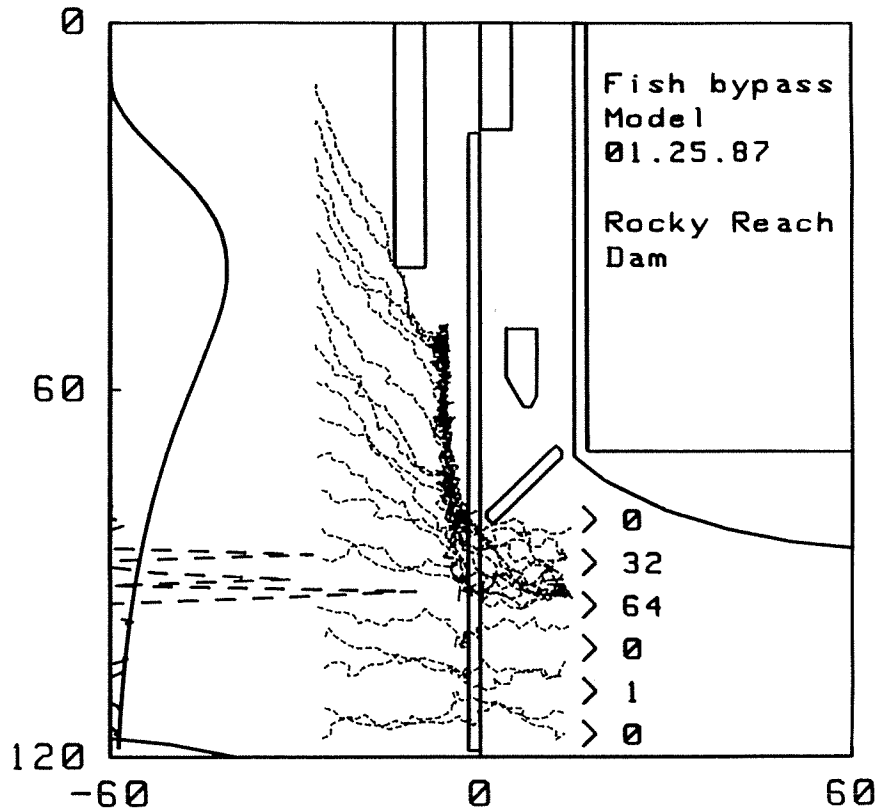


Fig. 4. Fish trajectories with vertical distributions of fish in forebay and at trashrack, and distribution of catch in fyke nets is expressed as percentages of the total fyke net catch. Model parameters represent summer run conditions.

transparency typically found in the summer, which would have made the trashrack more visible in the day. This mechanism could not affect the night FGE but unfortunately FGE studies were not conducted at night in the summer period. The summer period median depth distribution (Table 2) was also different than the spring distribution. In the summer period, the median depth was shallower closer to the trashrack, while in the spring period, the opposite condition existed and the median depth was deeper closer to the trashrack. The shallow median depth of the summer distribution could have been the result of fish swimming upwards to avoid the trashrack.

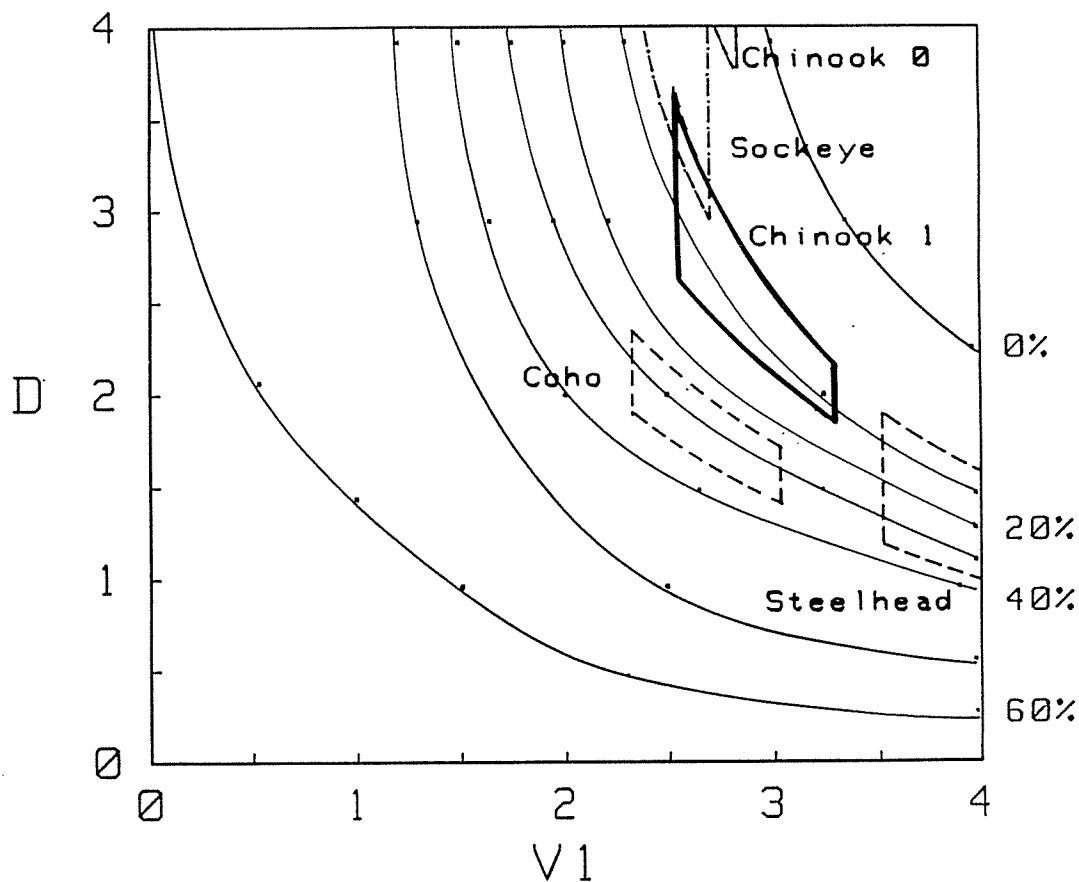


Fig. 5. Groupings of fish parameter sets showing differences in FGE as a function of escape speed, V_1 , and critical avoidance distance, D . Regions determined by FGE for configurations without strobe lights and V_1 , estimated from fish length and escape speeds from 6 to 8 bl/s.

REFERENCES

- Hays, S.G. and K.B. Truscott. 1987. Rocky Reach prototype fish guidance system—1986 developmental testing. Chelan County Public Utility District No. 1.
- Steig, T.W., J. Condiotty and G.A. Raemhild. 1986. Hydroacoustic assessment of downstream migrating salmon and steelhead at Rocky Reach Dam in 1986. Report to Chelan County P.U.D. No. 1. BioSonics, Inc.

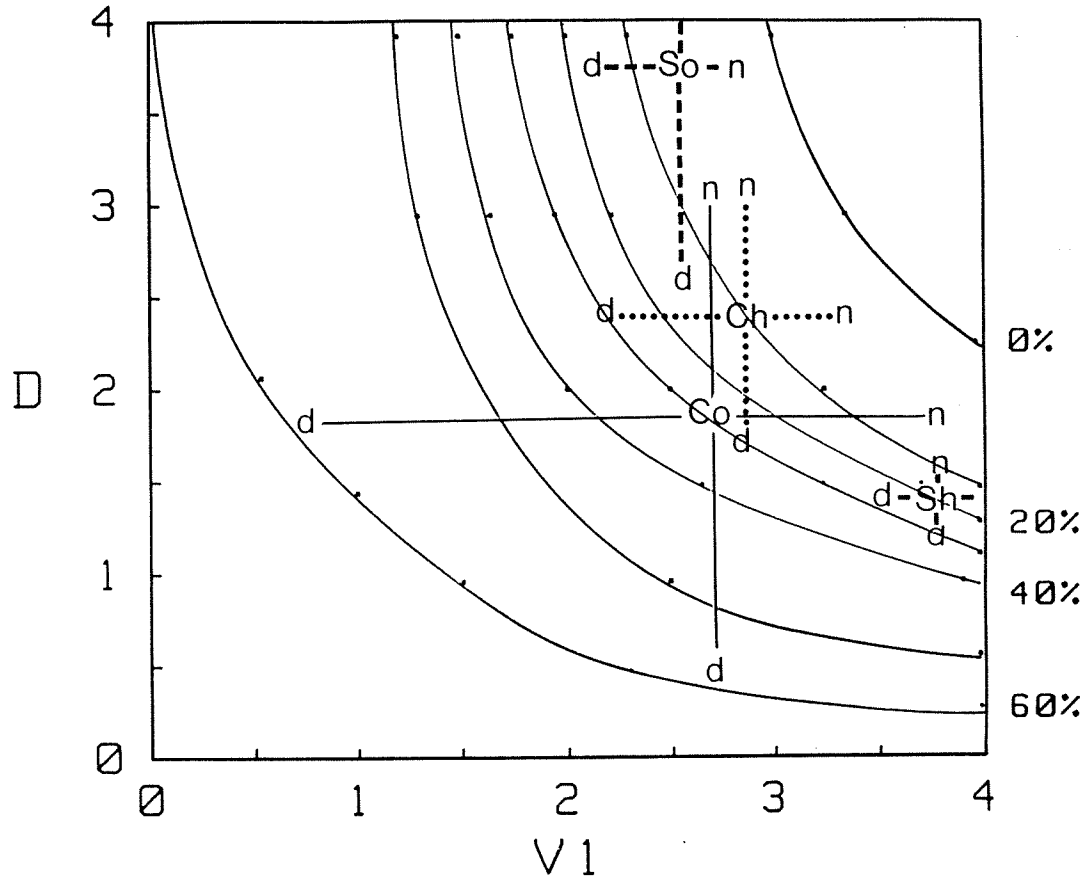


Fig. 6. Possible change in D and V1 associated with day and night FGE under strobe light conditions. D, V1 parameter locations for coho, sockeye, yearling chinook salmon, and steelhead trout designated Co, So, Ch, and Sh, respectively. d and n designated parameter positions for FGE observed in day and night.

APPENDIX 6:

**A COMPUTER MODEL FOR FISH TRAJECTORIES
AT ROCKY REACH DAM: INDICATIONS THAT
FISH AVOID LOW FREQUENCY SOUND MADE BY
THE SUBMERSIBLE TRAVELING SCREEN**

by

James J. Anderson

**Electric Power Research Institute Conference
on Fish Protection at Stream and Hydropower Plants
San Francisco, California
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ABSTRACT

Factors that affect fish guidance efficiency at Rocky Reach Dam were investigated using a computer model to describe the trajectories of fish in terms of movements by water flow and swimming in response to stimuli. Flow parameters were estimated from least-squares regressions on flow observations. Behavioral parameters were estimated by fitting the model to observed fish guidance efficiency and fyke net distributions using a chi-square minimization. The model analysis suggested that without a submersible traveling screen (STS) behind the trashrack, fish readily passed through the trashrack. When a STS was present, fish actively avoided the trashrack in front of the STS. The avoidance response caused fish to move down the face of the trashrack. Below the STS, avoidance decreased and fish passage through the trashrack increased. The low fish guidance efficiency obtained with the STS at Rocky Reach could be accounted for by random flow fluctuations exceeding the fish's escape velocities. The analysis suggested that the STS produced an aversive stimulus that caused active avoidance in the vicinity of the STS. A hypothesis is proposed that the STS generates low frequency sounds that fish avoid.

PREFACE

To develop a bypass facility to divert downstream migrating juvenile salmon from the turbine entrances at Rocky Reach Dam on the Columbia River, a prototype submersible traveling screen (STS) was installed immediately behind the trashrack in unit 1. Baseline studies of fish distributions in the forebay and the turbine entrance suggested that the potential fish guidance efficiency (FGE) approached 70%. When the STS was installed, the actual FGE was 10% or less. Hydroacoustic and fyke net studies indicated that fish essentially followed the flow lines to within 5 ft of the trashrack but then moved down, passing through the face of the trashrack below the level of the STS.

Although it was apparent that fish exhibited an avoidance response, it was not clear what produced the avoidance or what could be done to counteract it. Several competing explanations were considered, which attributed the avoidance to: the trashrack, a change in the flow due to the STS, or the STS itself. Fish sometimes avoid passing through trashrack-like barriers (1), and this principle is in fact the basis for hanging chain barriers. If trashrack avoidance were important, then in a flow reduced by a STS, fish avoidance responses might effectively exclude fish long enough for them to drop below the STS. In this case, the FGE might be controlled in a critical balance of flow and a trashrack avoidance response by the fish. An alternative scenario might attribute the low FGE to the STS itself, with fish response to the trashrack and flow being insignificant. A third

hypothesis suggested that large vortices in front of the dam might pull the fish deeper into the water column before they reached the trashrack.

Because the evaluation of each hypothesis would involve expensive and time-consuming field studies, a computer model was developed to evaluate possible causes of low FGE. The model, which is outlined in the following sections, combines information on flow with the behavior and ability of fish to avoid aversive stimuli. With the model, it was possible to gain both an intuitive and quantitative understanding of how different factors interact to control FGE.

The model related FGE and fyke net distributions to the flow conditions and behavior of fish in front of and behind the trashrack. Flow parameters were determined from observations using least-squares regressions. The behavioral parameters were then varied until the predicted and observed FGE and fyke net distributions had a minimum chi-square difference. This procedure, applied to the data with and without a STS, revealed that significant avoidance only occurred when the STS was present. This suggests that the STS generated a stimulus that fish strongly avoided. The ethological literature provides evidence that the stimuli could be low frequency noise generated by the STS.

THE MODEL

The trajectories of fish from the forebay through the trashrack and into the STS and turbine intake of unit 1 at Rocky Reach Dam (Fig. 1) were modeled with finite increment equations in which the movement of fish is expressed in terms of the water flow and the swimming movement of the fish in response to stimuli. The finite increment equations are written as follows:

$$x_{i+1} = x_i + (u_f + u_b) dt \tag{1}$$

$$z_{i+1} = z_i + (v_f + v_b) dt$$

where dt is the time increment, x_i and z_i are the horizontal and vertical coordinate positions of the fish at time $i \cdot dt$, u_f and v_f are the vertical and horizontal velocities due to the flow and u_b and v_b are swimming velocities. All velocities can change from one time increment to the next according to the flow regime and the stimuli encountered.

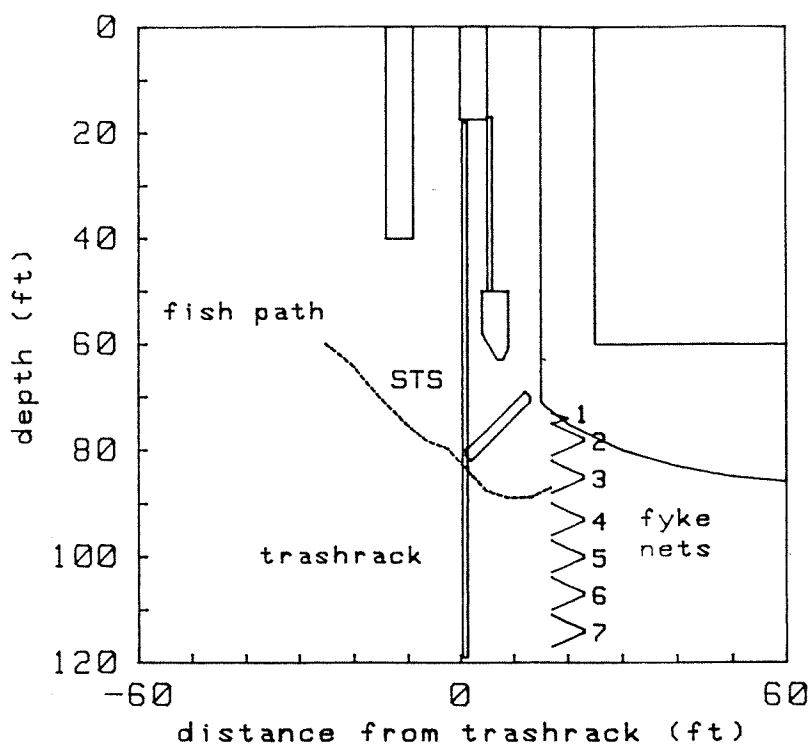


Figure 1. Cross-section of Rocky Reach Dam showing a fish trajectory from the forebay through the trashrack and into a fyke net.

Flow Contribution

Slope. The slope, or gradient of the water flow is described in terms of mean and fluctuating parts as follows:

$$\frac{dz}{dx} = \overline{\frac{dz}{dx}} + \frac{dz}{dx}' \quad (2)$$

The mean part is described by stream functions, which represent the mean flow path at any level. The stream functions to a first order are determined by the boundaries of the ceiling and floor of the turbine intake tunnel using equations of the form:

$$z = Z_t + c(x - X_t)^a \quad (3)$$

where $z = 0$ is the water surface in the forebay and $x = 0$ is the horizontal coordinate referenced to the trashrack, and Z_t and X_t are turbine reference points. The vertical coordinate is positive downwards and the horizontal coordinate is positive toward the turbine. Two stream-line regimes

are defined relative to the midpoint depth of the turbine, Z_t . For $z < Z_t$, the exponent, a , is a positive constant and for $z \geq Z_t$, the exponent is $a = 0$. The constant in Eq. 3 depends on the specific streamline. The exponent can be determined from 3 points on a streamline with the expression:

$$a = \ln \frac{(z_1 - z_2)(x_3 - x_2)}{(z_3 - z_2)(x_1 - x_2)} \quad (4)$$

The mean gradient of a streamline at any point is:

$$\frac{dz}{dx} = a \frac{z - Z_t}{x - X_t} \quad (5)$$

The fluctuations in the slope of the streamlines are estimated from observations of the range of the current speed fluctuations in front of the trashrack. Assuming that fluctuations exhibit a sinusoidal pattern with a random period, I can approximate the standard deviation of the fluctuations with the root mean square of their range in the vertical component, ΔS_z , divided by the mean speed of the current, S , so that:

$$\text{STD}(dz/dx) = (\Delta S_z / 2S)^{1/2} \quad (6)$$

The fluctuating slope is then expressed:

$$dz/dx' = \text{STD}(dz/dx) X(t) \quad (7)$$

where $X(t)$ is a Brownian motion stochastic process in which every increment, $X(t+dt) - X(dt)$, is normally distributed with mean 0 and a variance dt .

The vertical distribution of $\text{STD}(dz/dx)$ is estimated from the data on the vertical and horizontal fluctuation ranges at 5-ft depth increments. The ranges for each depth interval are put in Eq. (6), and the depth distribution of the result is determined by a least-square regression of the polynomial:

$$\text{STD}(dz/dx) = b_0 + b_1 z + b_2 z^2 \quad (8)$$

The mean slope of the flow trajectories described with Eq. 2 generally decreases with depth while the variations in the slope of the flow trajectories increase with depth (Fig. 2).

Speed. The current speed along a streamline is empirically described in terms of mean and fluctuating components as:

$$S = \bar{S} + S' \quad (9)$$

The mean current vertical profile is estimated from a least-squares regression of speed data using the polynomial (Fig. 3):

$$S = a_0 + a_1 z + a_2 z^2 + a_3 z^3 \quad (10)$$

The vertical distribution of the amplitude in the fluctuating component of the current speed is estimated in terms of the amplitude in the current fluctuation ΔS . The vertical distribution of ΔS is determined in an analogous manner to dz/dx' using Eqs.(6), (7) and (8), where ΔS_z is replaced with the range in the speed variation, which is defined as $\Delta S = (\Delta S_x^2 + \Delta S_z^2)^{0.5}$, where ΔS_x is the range of the horizontal component of the flow variation.

Behavior Contribution

The response to the trashrack is expressed in terms of the probability of eliciting an escape response directly away from the trashrack. To successfully avoid the trashrack, a fish first must be able to swim against the current and, second, must desire to do so. These two factors are expressed with a simple algorithm that is applied when the fish encounters the trashrack. If the current velocity, horizontal to the trashrack, S_x , is faster than the maximum escape speed, U , then the fish passes through the trashrack. If the escape speed is greater than the current horizontal velocity, then fish can avoid the trashrack; thus, the probability of the fish passing through the trashrack is set at P , where the escape speed is variable. Mathematically, this algorithm is expressed as follows:

$$\begin{aligned} &\text{IF } S_x > U \text{ or RND} < P \text{ THEN} \\ &\quad u_f + u_b = S_x - U \\ &\quad v_f - v_b = S_z \\ &\text{ELSE} \\ &\quad u_f + u_b = (-S_x + U) \text{ RND} \\ &\quad v_f - v_b = S_z \end{aligned} \quad (11)$$

where RND is a rectangular probability function of the type generated by a computer random number generator. Two trashrack passage probabilities are formulated: P_0 expresses the

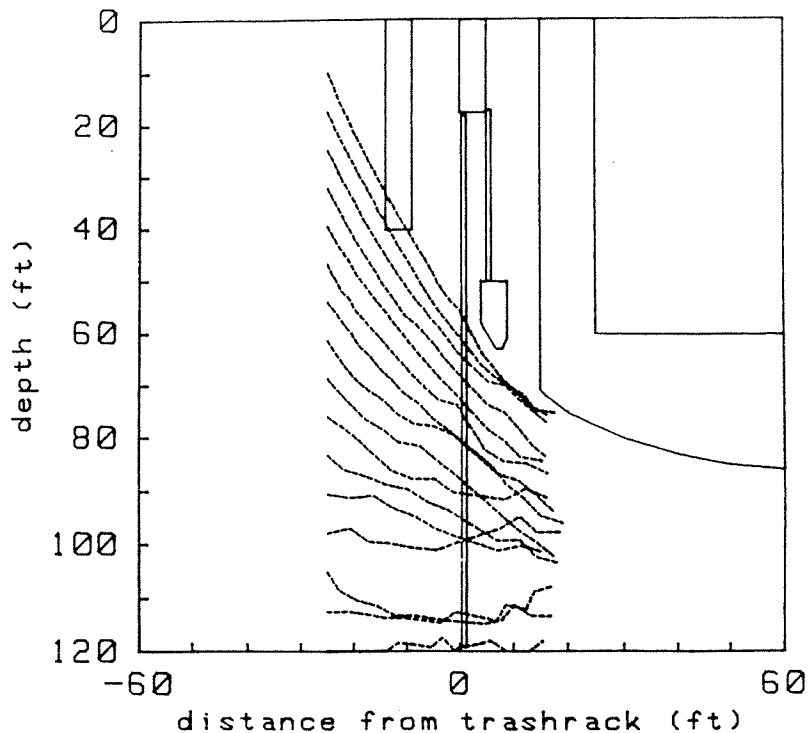


Figure 2. Model streamlines through trashrack.

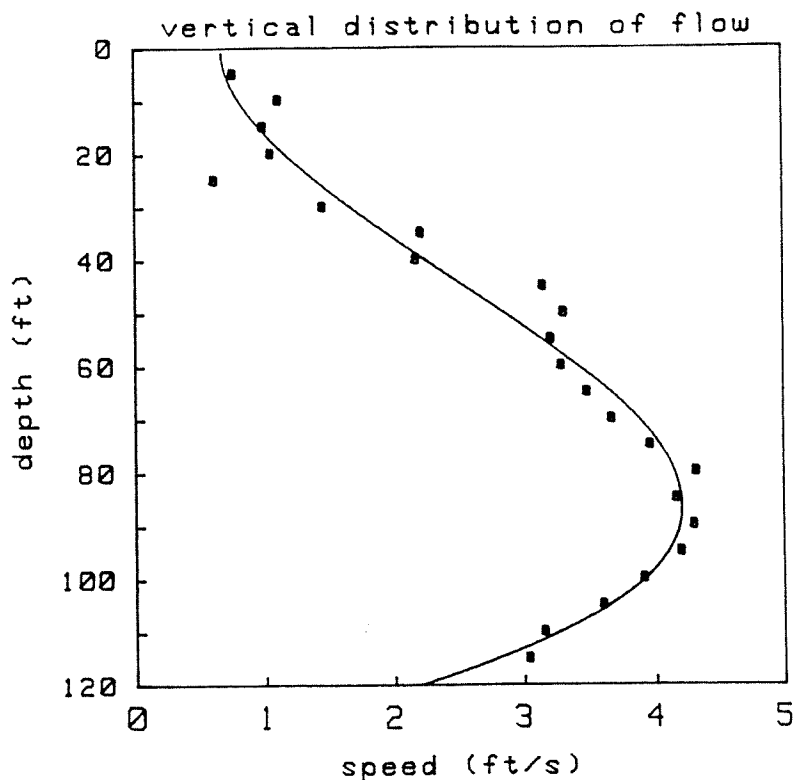


Figure 3. Vertical profile of current speed 12 ft in front of unit 1 with 100 MW load. Line represents regression of data using polynomial equation.

probability of avoiding passage through the trashrack when above the STS, and P_1 expresses the probability of avoiding passage when below the STS. With this algorithm, fish may contact the trashrack several times before they pass through it. With each avoidance behavior, fish are pulled deeper into the water column by the vertical component of the flow (Fig. 4).

After passing through the trashrack, the velocity components are expressed as follows:

$$u_f + u_b = S_x \quad (12)$$

$$v_f + v_b = S_z - V.$$

where V is a vertical swimming velocity that is included to model possible upward movements that are thought to occur in some instances (M. Bell, personal communication).

Fish Distribution in Forebay

The vertical distribution of fish in the forebay observed hydroacoustically (2; 3) can be described with a gamma density function (Fig. 5):

$$p(z) = \frac{(z/m)^{n-1} e^{(-z/m)}}{m \Gamma(n)} \quad (13)$$

where Γ is the gamma function and the constants m and n are determined from the mean depth, Z_{mean} , and the mode depth, Z_{mode} , of the vertical distribution of fish in the forebay by the equations:

$$\begin{aligned} m &= Z_{\text{mean}} - Z_{\text{mode}} \\ n &= Z_{\text{mean}} / (Z_{\text{mean}} - Z_{\text{mode}}) \end{aligned} \quad (14)$$

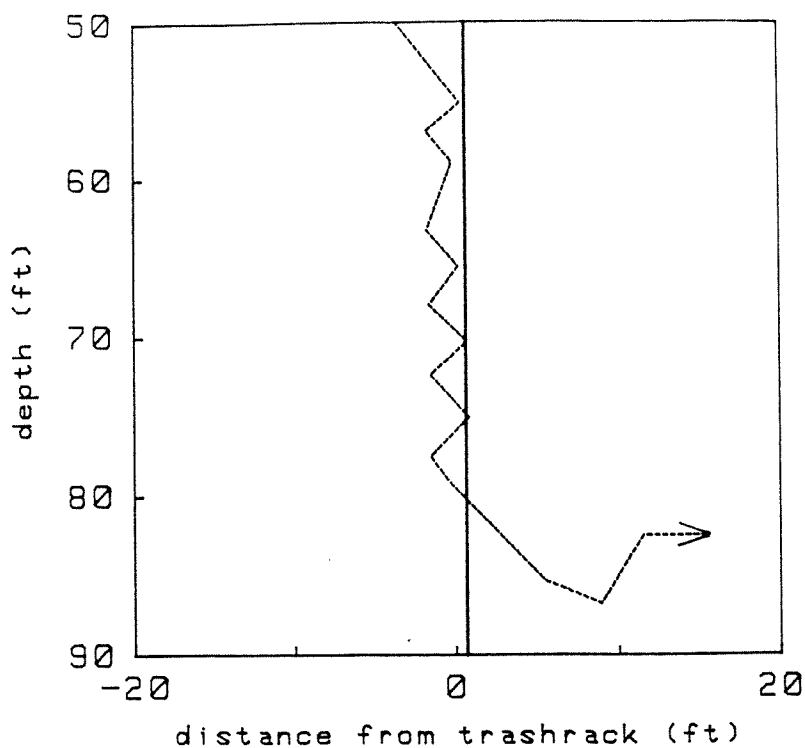


Figure 4. Model trajectory of fish at trashrack showing avoidance and eventual passage through the trashrack.

FGE Calculation

To calculate FGE and the distributions of fish in fyke nets, the water column is divided into N depth increments and trajectories are calculated from starting at depths $z_0(n)$, where $n = 1, 2, \dots, N$, at a distance x_0 from the trashrack. The endpoint depths of the trajectories are designated $z_e(n)$. Trajectories that pass through the trashrack above the depth of the STS are taken to be guided and contribute to the FGE according to the formula:

$$\text{FGE} = \frac{\sum_i^M p(z_0(i))}{\sum_n^N p(z_0(n))} \quad (15)$$

where $i = 1, 2, \dots, M$ is the set of guided trajectories.

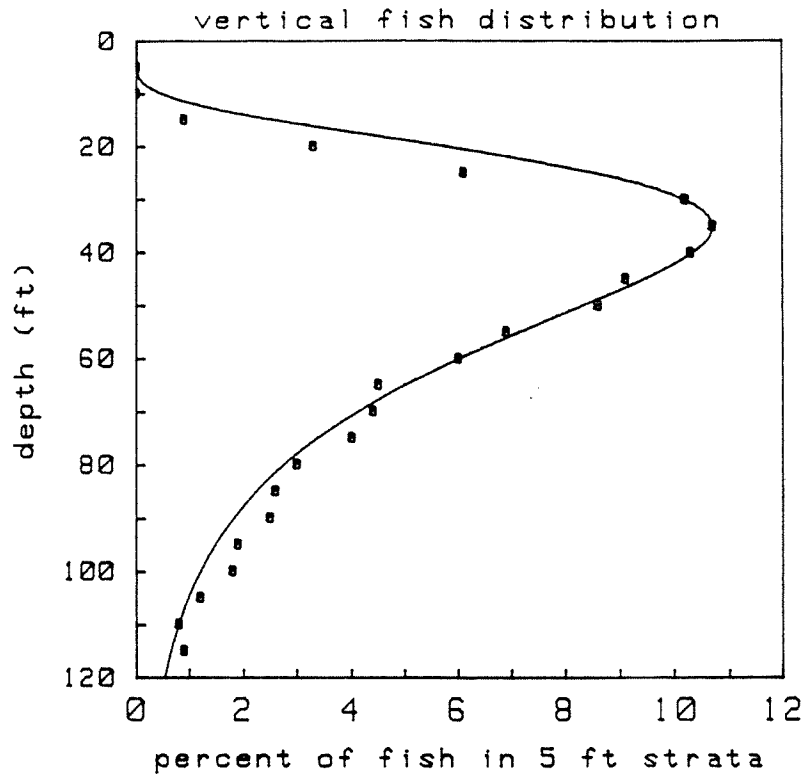


Figure 5. Vertical profile of fish in forebay determined with hydroacoustics. Line represents gamma function model of profile.

Fyke Nets

Trajectories that pass through the trashrack below the STS are unguided and contribute to the fyke net catches. The distribution of fish in fyke nets is expressed by the following equation as percentages of the total number not guided:

$$FYKE(j) = 100 \left\{ \frac{\sum_{k(j)}^{L(j)} p(z_0(k(j)))}{\sum_n^N p(z_0(n))(1-FGE)} \right\} \quad (16)$$

where $k(j) = 1, 2, \dots, L(j)$ is the set of trajectories terminating in fyke net j where $j = 1, 2, \dots, 7$.

MODEL RESPONSE

Model Fit

The model output includes the FGE and FYKE, which is the normalized distribution of fish in fyke nets 1 to 7. These measures are controlled by a number of flow and behavioral model parameters. The flow parameters were determined from statistical regressions of the polynomial equations on the mean and ranges of the vertical and horizontal components of flow made 12 ft in front of unit 1 with a 100 MW turbine load for conditions with and without a STS (3). The behavioral parameters were determined by adjusting their values to obtain a minimum chi-square of the difference between the observed and predicted levels of FGE and FYKE. The behavioral parameters were confined within limits. Probabilities were confined within the range 0 to 1, the maximum escape velocity was set at 12 body lengths per second (bl/s), and the forebay depth distribution modes were confined within ± 7 ft of the mode observed hydroacoustically. The hydroacoustically determined mode (Fig. 5) was not used as a fixed parameter because it represents a mixture of fish species, while the distributions in the model are species-specific. The time increment, dt , was set at 1 s, this being a time interval over which the change of flow and swimming speeds was expected to be minimal.

Conditions without STS

For the conditions without a STS, the best fit to the fyke net distributions was obtained when the probability of trashrack avoidance was zero and the fish exhibited upward swimming behind the trashrack (Table 1). The distributions were fine-tuned for each species and for day and night conditions (Table 2 and 3) by adjusting the parameters for forebay depth distribution. Yearling and subyearling chinook, coho and steelhead were caught in the upper three fyke nets in both day and night periods. The model depths in the forebay required to fit the fyke net distributions were within 7 ft of the mode, which was determined acoustically to be 35 ft. The pattern for sockeye was aberrant. During the day, the required forebay distribution mode was at the surface, while at night the mode was at the bottom (Fig. 6). In general, the picture presented with these parameters is of fish following the flow through the trashrack and moving upwards at a normal cruising speed of 3 to 4 bl/s on the back side of the trashrack (Fig. 7). There appeared to be little, if any, tendency for the fish to avoid the trashrack with the STS absent.

Conditions with STS

To model the conditions with a STS the depth distributions, determined from fitting the model to the fyke net distributions without a STS, and the flow parameters for the STS condition were used.

The behavioral parameters were adjusted to minimize the chi-square fit to the FYKE and FGE observations (Table 4). In general, the chi-square values obtained for the STS condition were one order of magnitude larger than were obtained for the condition without the STS (Table 5 and 6). In all cases, model fits required $P_0 = 0$, indicating that all fish actively avoided passing through the trashrack above the depth of the STS. Below the level of the STS, model fits to the data required that P_1 be between 0.3 and 0.5. Fish trajectories for these conditions followed the flow to the trashrack and then moved down the face of the trashrack. At the level of the STS, few fish passed through the trashrack; however, below the STS, fish passed through after about 3 encounters (Fig. 8).

With $P_1 = 0$ above the STS, fish were only guided when the random fluctuations in the current exceeded the burst speed of the fish. Assuming burst speeds of 12 bl/s, the maximum escape speeds would range between 4 and 5 ft/s for chinook, sockeye, and coho, and up to 7 ft/s for steelhead. In these ranges, the modeled FGE is critically dependent on the escape speed (Fig. 9), so essentially all guidance of subyearling chinook, sockeye, and coho could be the result of random current fluctuations pulling the fish through the trashrack. Yearling chinook and steelhead could, theoretically, swim against the flow. In any case, the estimated probability of trashrack passage above the STS was near zero for all species.

DISCUSSION

The model analysis suggests that fish actively avoided passing through the trashrack when the STS was directly behind the trashrack. Below the level of the STS, trashrack passage increased, and when the STS was absent the fish apparently exhibited little trashrack avoidance. These results strongly suggest it is the STS itself that was generating the avoidance. This conclusion is supported by recent studies conducted at Bonneville Dam Second Powerhouse, where the trashrack was removed and fish still avoided the STS and the bypass slot (J. Williams, personal communication). At both of these dams, the STS was close to the trashrack and FGE was low. At other projects with higher FGE, the STS location was further behind the trashrack. Together, these findings suggest that the STS, when located close to the trashrack, may generate stimuli that cause avoidance responses in downstream migrants. The role of the trashrack is unclear: It might play a secondary role such as providing a reference for the direction and timing of the avoidance responses, or perhaps it could have some importance in how a STS generates aversive stimuli. Speculating on the nature of the stimuli generated by a STS, I can immediately eliminate several possibilities. The stimulus was probably not visual because the STS was deep in the water column and low FGEs also occurred at night. Physical contact with the STS was probably not an

Table 1
PARAMETERS FOR MODEL FIT
(without STS)

	<u>Chinook 1</u>		<u>Chinook 0</u>		<u>Sockeye</u>		<u>Coho</u>		<u>Steelhead</u>	
	(D)	(N)	(D)	(N)	(D)	(N)	(D)	(N)	(D)	(N)
Z _{Mode}	29	30	32	42	1	200	31	28	27	39
Z _{Mean}	35	38	53	70	25	3000	35	69	50	81
U	4	4	4	4	4	4	4	4	4	4
V	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
PO	1	1	1	1	1	1	1	1	1	1
P1	1	1	1	1	1	1	1	1	1	1

Source: (4).

Note: (D) designated day conditions and (N) night conditions.

Table 2
SUMMARY OF FYKE NET DISTRIBUTIONS
(Day conditions without STS)

	<u>Chinook 1</u>		<u>Chinook 0</u>		<u>Sockeye</u>		<u>Coho</u>		<u>Steelhead</u>	
	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)
Net 1	41	41	22	24	36	37	41	42	26	27
Net 2	33	34	27	24	21	21	38	38	26	24
Net 3	15	19	23	25	16	19	13	17	21	24
Net 4	6	4	14	14	11	11	5	2	13	13
Net 5	3	1	8	9	9	8	1	0	7	8
Net 6	2	0	3	2	5	2	0	0	5	2
Net 7	0	0	0	0	0	0	0	0	0	0
Chi-square	6		5		5		5		6	

Source: (4).

Note: Results are from 1986 studies at Rocky Reach Dam. (O) observed values; (P) predicted values according to Eq. (16). Distributions are reported as percentages.

Table 3

SUMMARY OF FYKE NET DISTRIBUTIONS
(Night conditions without STS)

	<u>Chinook 1</u>		<u>Chinook 0</u>		<u>Sockeye</u>		<u>Coho</u>		<u>Steelhead</u>	
	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)
Net 1	32	36	15	17	11	9	23	23	17	18
Net 2	33	32	27	21	14	13	21	21	22	20
Net 3	17	22	24	27	18	23	24	24	23	26
Net 4	9	7	18	17	21	21	17	15	19	17
Net 5	5	3	11	12	20	21	10	11	11	13
Net 6	3	1	5	4	13	8	4	3	7	4
Net 7	0	0	0	0	0	0	0	0	0	0
Chi-square	14		13		14		2		7	

Source: (4).

Note: Results are from 1986 studies at Rocky Reach Dam. (O) observed values; (P) predicted values.

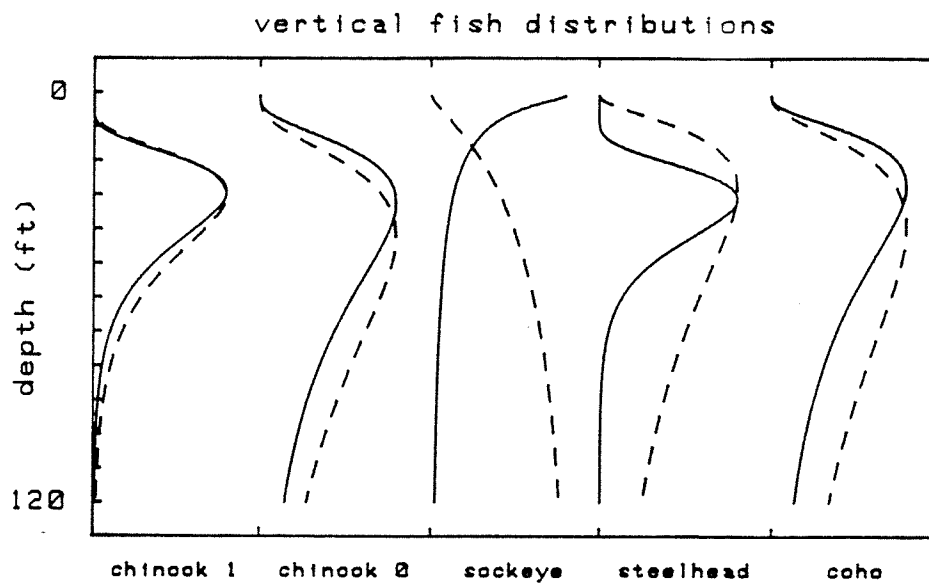


Figure 6. Model profiles of vertical distributions of fish in forebay by species. Solid lines for day profiles, dashed lines for night profiles.

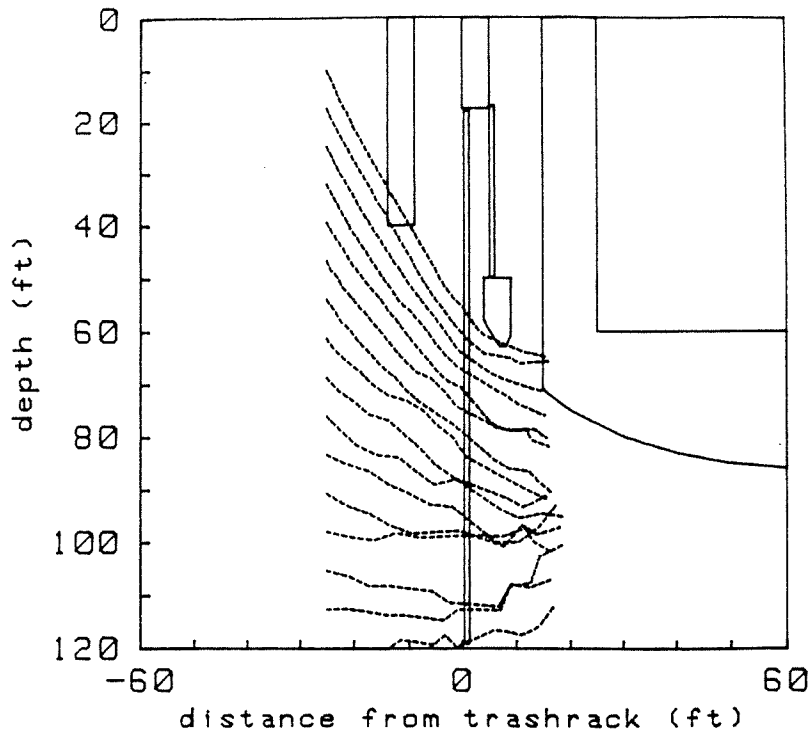


Figure 7. Trajectories of fish for conditions without a STS showing passage of fish through the trashrack and upward movement behind the trashrack.

Table 4

PARAMETERS FOR MODEL FIT
(with STS)

	<u>Chinook 1</u>		<u>Chinook 0</u>		<u>Sockeye</u>		<u>Coho</u>		<u>Steelhead</u>	
	(D)	(P)	(D)	(P)	(D)	(P)	(D)	(P)	(D)	(P)
Z _{Mode}	29	30	32	70	1	200	31	28	27	39
Z _{Mean}	35	38	53	42	25	3000	35	69	50	81
U	4.2	4.2	4.15	4.15	4	4	4	4	4.1	4.1
V	0	0	0	0	0	0	1	1	0	0
PO	0	0	0	0	0	0	0	0	0	0
P1	0.3	0.3	0.5	0.5	0.5	0.5	0.3	0.3	0.4	0.4

Source: (4).

Note: (D) designated day conditions and (N) night conditions.

Table 5

SUMMARY OF FGE AND FYKE NET DISTRIBUTIONS
(Day conditions with STS)

	<u>Chinook 1</u>		<u>Chinook 0</u>		<u>Sockeye</u>		<u>Coho</u>		<u>Steelhead</u>	
	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)
FGE	3	1	3	5	9	5	18	25	13	5
Net 1	1	0	0	0	6	0	13	3	4	0
Net 2	7	6	14	9	10	8	13	22	10	8
Net 3	36	40	28	21	18	26	44	40	31	21
Net 4	34	27	44	37	29	34	18	19	25	35
Net 5	11	15	10	21	19	22	7	12	16	20
Net 6	9	9	7	7	14	5	4	3	12	9
Net 7	2	1	0	5	4	4	1	0	2	6
Chi-square	21		72		58		71		81	

Source: (4).

Note: Results are from 1986 studies at Rocky Reach Dam. (O) observed values; (P) predicted values.

Table 6

SUMMARY OF FGE AND FYKE NET DISTRIBUTIONS
(Night conditions with STS)

	<u>Chinook 1</u>		<u>Chinook 0</u>		<u>Sockeye</u>		<u>Coho</u>		<u>Steelhead</u>	
	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)	(O)	(P)
FGE	9	1	0	4	4	3	30	15	6	4
Net 1	1	0	0	0	0	0	7	1	0	0
Net 2	13	6	8	8	3	6	16	15	2	6
Net 3	38	38	28	18	13	14	24	33	21	20
Net 4	26	28	43	36	32	30	22	21	22	31
Net 5	13	15	13	22	32	23	16	17	25	22
Net 6	8	9	7	8	16	12	14	9	26	12
Net 7	1	1	1	7	4	16	1	5	3	9
Chi-square	30		72		62		92		85	

Source: (4).

Note: Results are from 1986 studies at Rocky Reach Dam. (O) observed values; (P) predicted values.

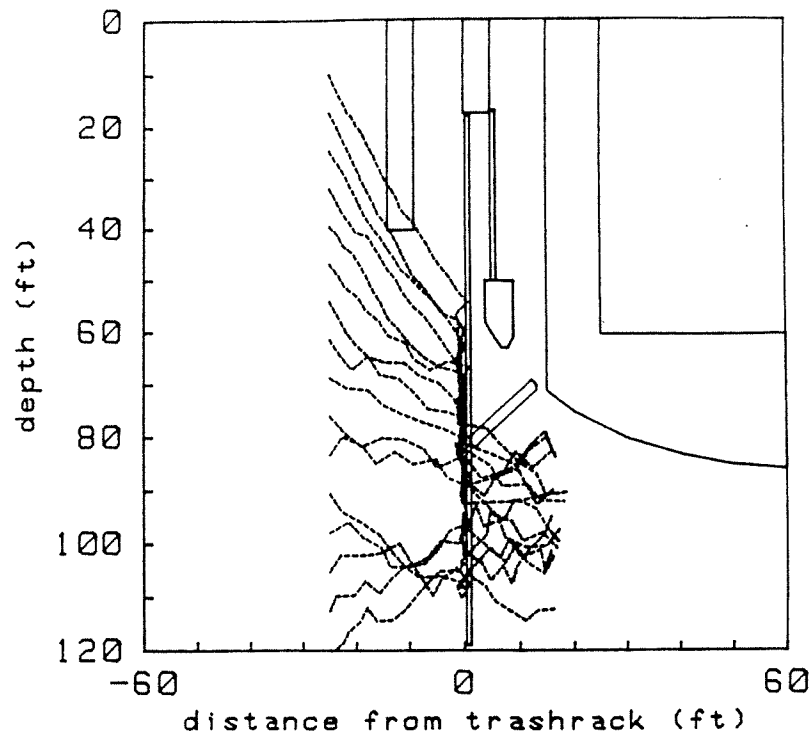


Figure 8. Trajectories of fish with a STS showing movement down the face of the trashrack and passage through the trashrack below the STS.

important source of aversive stimuli because the frequency of descaling was not significantly increased with the STS. The most interesting possibility is that sound was the aversive stimulus.

In general, the lateral line sensory system in salmon is sensitive to sound frequencies up to about 1,000 Hz, with a peak sensitivity at about 160 Hz (5, 6). Over this range of frequencies, fish exhibit a variety of responses, including startle, avoidance and attraction. Startle responses, in which the fish turn away from a stimuli within a 10-30 ms period, can be evoked readily by sound stimuli (7, 8). Herring startle to sound frequencies between 20 and 200 Hz (9) and are most sensitive at about 160 Hz (8). Following a startle, fish swim away from the stimuli and may reach burst speed for a few hundred ms. This response is often followed by a glide or steady swimming away from the stimulus (7). Avoidance responses, which are slower, might be initiated in the 60-400 ms interval. Both startle and avoidance responses would suffice to move fish away from a trashrack in flows of a few ft/s. Avoidance responses can be evoked in herring by continuous low frequency noise between 5-15 Hz, with threshold sound pressures between 3 and 55 Pa (10). Carp showed rapid movements in response to sounds between 6 and 12 Hz. These low frequency noises are generated when fish swim, and since fish apparently do not habituate to them, it is likely

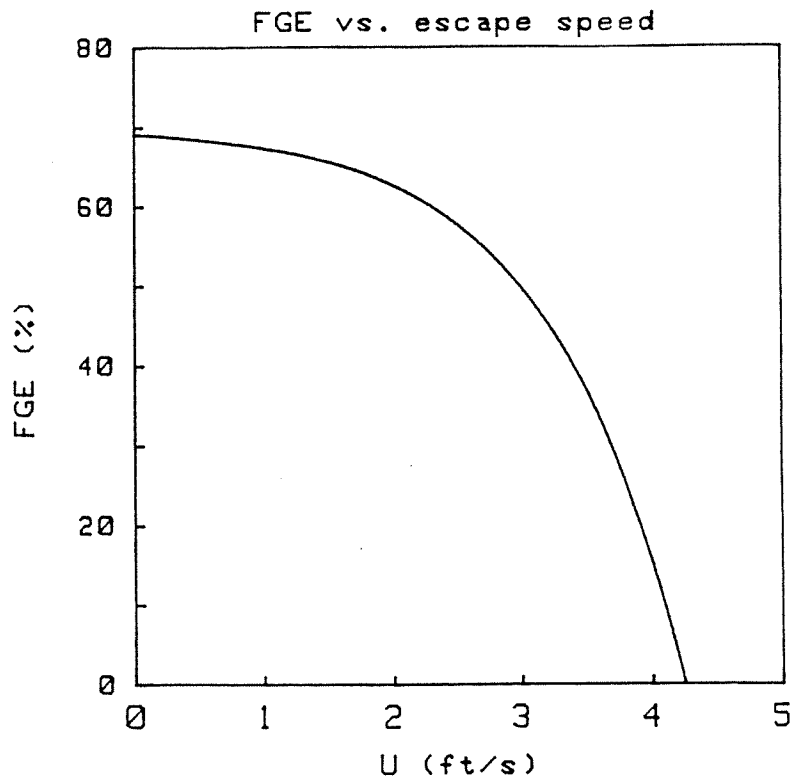


Figure 9. Model-derived relationship between FGE and fish escape speed for the conditions with a STS at Rocky Reach Dam.

that they use these frequencies for communication in synchronized swimming (11). Fish can habituate to sounds around 150 Hz (5), but when the intensity of the source rapidly increases, avoidance and startle responses can be induced (12). Studies on steelhead downstream migrants demonstrated avoidance at sound frequencies up to 80 Hz. The response occurred only in the near-field, and the greatest distance that fish moved from the source was 2 ft (5).

A detailed study of the hearing capabilities of Atlantic salmon (6) determined that the threshold of discrimination of Atlantic salmon has a maximum sensitivity at about -5 to 10 dB/ubar for frequencies between 20-100 Hz. In comparison, footsteps along the bank of a river reached up to 45 dB/ubar. At close distances, Atlantic salmon detect the particle displacement of sound more readily than the pressure wave. This was demonstrated in an experiment in which the threshold produced by a speaker was found to be 30 dB/ubar lower if the speaker was immersed in the water than if it was in the air. The masking of a signal by ambient noise raises the threshold of detection. To a first order, masking will occur if the ambient level is within 24 dB of the threshold. Thus, hearing impairment is expected in fast-flowing water. In general, the effect of ambient noise raises the threshold level in a linear manner; therefore a 10 dB shift in the ambient noise increases the

threshold by 10 dB, and the effect of the masking decreases as the frequency between the signal and the ambient noise increases.

The sound spectrum at a hydroelectric powerplant is unknown. In the absence of observations, we must estimate the possible range of frequencies of the ambient sound and the sound produced by a STS. To a first order, we expect the ambient noise is produced by the rotation of the turbines. Since the rotation speed is about 200 rpm (13), we expect the fundamental frequency of the ambient noise is about 10 Hz. To estimate the possible frequencies generated directly by a STS, I assume it is a rectangular membrane; consequently, the fundamental frequency of vibration is given by the equation:

$$f = \frac{c}{2} \sqrt{(1/l_x)^2 + (1/l_z)^2} \quad (17)$$

where c is the speed of sound through freshwater (4813 ft/s, 1480 m/s), and l_x and l_z are the dimensions of the membrane (14). The STS at Rocky Reach Dam has two sections, each with dimensions of about 10 x 13 ft, so by using Eq. 17, I determined that the fundamental resonating frequency of the STS is about 600 Hz. Lower frequencies could also be generated by the currents pulsating through and around the structure. In its location behind the trashrack, the STS frames a triangular shaped cavity with dimensions of several tens of ft. It might be possible that flow through this cavity produces a low frequency noise. In any case, current measurements indicate that the flow below the STS was considerably more variable when the STS was present (2).

A STS might generate low frequency sounds by one of several mechanisms. Although the ambient turbine noise might be in the range of frequencies generated by a STS, the turbine is about 70 ft from the trashrack; the intensity of the sounds might be diminished at the trashrack and the major source of low frequency sound might be from the STS. Although this hypothesis is only supported by circumstantial evidence, it warrants further consideration. If the low FGE is due to fish avoidance of low frequency sound, then the route to improving FGE could be through the abatement of this sound.

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REFERENCES

1. Hanson, C.H. and H.W. Li. "Behavioral response of juvenile chinook salmon, *Oncorhynchus tshawytscha*, to trash rack bar spacing." Calif. Fish Game, Vol. 69, 1983, pp. 18-22.
2. Raemhild, G.A., T.W. Steig, R.H. Riley and S. Johnston. "Hydroacoustic assessment of downstream migrating salmon and steelhead at Rocky Reach Dam in 1983." Seattle: Biosonics, Inc., Washington, 1984.
3. Hays, S.G. "Developmental testing of a prototype fish guidance system for turbine intakes at the Rocky Reach Hydroelectric Project." Chelan County Public Utility District No. 1, 1986, Wenatchee, Washington.
4. Hays, S.G. and K.B. Truscott. "Rocky Reach prototype fish guidance system—1986 developmental testing." Chelan County Public Utility District No. 1, 1987.
5. Vanderwalker, J.G. "Response of salmonids to low frequency sound." Marine Bio-Acoustics, Vol. 2, W.N. Tovolga, ed. New York: Pergamon Press, 1967.
6. Hawkins, A.D. and A.D.F. Johnstone. "The hearing of the Atlantic salmon, *Salmo salar*." J. Fish. Biol., Vol. 13, 1978, pp. 655-673.
7. Eaton, R.C. and J.T. Hackett. "The role of the Mauthner cell in fast-starts involving escape in teleost fish." Neural Mechanisms of Startle Behavior, R.C. Eaton, ed. New York: Plenum Press, 1984, pp. 213-262.
8. Blaxter, J.H.S., J.A.B. Gray, and E.J. Denton. "Sound and startle responses in herring shoals." J. Mar. Biol. Assoc. U.K., Vol. 61, 1981, pp. 851-869.
9. Blaxter, J.H.S. and D.E. Hoss. "Startle response in herring: the effect of sound stimulus frequency, size of fish and selective interference with the acoustico-lateralis system." J. Mar. Biol. Assoc. U.K., Vol. 61, 1981, pp. 871-879.
10. Blaxter, J.H.S. and R.S. Batty. "Herring behaviour in the dark: responses to stationary and continuously vibrating obstacles." J. Mar. Biol. Assoc. U.K., Vol. 65, 1985, pp. 1031-1049.
11. Konagaya, T. "Response of fish to low frequency sound." J. Jap. Soc. Sci. Fish., Vol. 46, No. 2, 1980, pp. 125-128.
12. Schwarz, A.L. and G.L. Gree. "Responses of Pacific herring, *Clupea harengus pallasii*, to some underwater sounds." Can. J. Fish. Aquat. Sci., Vol. 41, 1984, pp. 1183-1192.
13. Bell, M.C. Updated compendium on the success of passage of small fish through turbines. Contract No. DACW-68-76-C-0254, U.S. Army Corps Engineers, 1981.
14. Kinsler, L.E. and A.R. Frey. Fundamentals of Acoustics. New York: John Wiley & Sons, 1980.