Brown Trout Perception of Ultraviolet Radiation and Possible Influence on Distribution

Terrence H. Lee
Utah State University

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BROWN TROUT PERCEPTION OF ULTRAVIOLET RADIATION
AND POSSIBLE INFLUENCE ON DISTRIBUTION

By

Terrence H. Lee

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Fisheries and Wildlife

Approved:

UTAH STATE UNIVERSITY
Logan, Utah
1983
ACKNOWLEDGEMENTS

This study was under the direction of Dr. William Helm. I would like to express my appreciation to Dr. Helm for his encouragement and guidance.

I would also like to thank Dr. Inge Dirmhirn and Mr. G. Venugopal, Department of Soil Science and Biometeorology, for their unselfish contribution of time and expertise regarding the solar elements of the study.

I also want to express my appreciation to my parents, Mr. and Mrs. Orvis Lee, for their support. Finally, with utmost appreciation, to my wife, Sandy, whose steadfastness and support were beyond measure in fulfilling this project, I graciously thank my better half.

Terrence H. Lee
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ABSTRACT

Brown Trout Perception of Ultraviolet Radiation
and Possible Influence on Distribution

by

Terrence H. Lee, Master of Science
Utah State University, 1983

Major Professor: Dr. William Helm
Department: Fisheries and Wildlife

Brown trout (Salmo trutta), demonstrated an avoidance response to a range of intensities of artificial ultraviolet radiation in a laboratory setting. UV field measurements were made under a variety of riparian canopies in a mountain river system. UV values at various depth regimes were compared with laboratory response values. Results suggested that ultraviolet light could be a factor in the absence of brown trout in particular habitat types at various times during the daylight hours. Visible light intensity response values were also obtained under the same experimental and field conditions. These data suggested that visible light also could be a contributing factor in the absence of brown trout in different habitat types. Visible light may be of equal importance to ultraviolet light in eliciting an avoidance response in brown trout. (60 pages)
INTRODUCTION

Ecologically, many factors contribute to the presence of an organism in a particular niche. Distribution of brown trout in the aquatic ecosystem is influenced by such factors as water chemistry, flow regime, bottom type, water temperature, interspecific competition, food type and its availability, and light intensity.

A difference in behavior seems to appear between brown trout in Pennsylvania (Bachman 1982) and those in Utah (Gosse and Helm 1982). This difference involves the reaction of brown trout toward sunlight. They either: (1) avoid direct sunlight (Gosse and Helm 1982) or; (2) occupy feeding positions in direct sunlight (Bachman 1982), thus apparently ignoring or at least not avoiding bright light.

Moisture and particulates absorb and diffuse UV wavelengths, consequently the amount of UV reaching the earth could be reduced in industrial areas under cloud cover. Additionally, distance traveled through the atmosphere could decrease UV intensity even further. Since the study by Bachman (1982) was developed by workers in Pennsylvania at lower elevations and with more moisture and particulates in the atmosphere, along with more consistent cloud cover, ultraviolet radiation was suspected as a major contributing factor to the differences in brown trout response in the two areas.

This study addressed the question of whether ultraviolet light could be the reason for the apparent difference in behavior of brown trout between Pennsylvania and Utah. The major objectives were to
explore brown trout reactions to light to determine whether one portion of the spectrum, UV or visible, was more responsible than the other for an avoidance reaction.

Three hypotheses were tested:

\( H_1 \) Brown trout cannot detect ultraviolet radiation.

\( H_2 \) Brown trout will avoid ultraviolet radiation above some threshold intensity.

\( H_3 \) Brown trout will avoid visible light above some threshold intensity.

Light is a popular denominator in the determination of brown trout behavior. Bachman et al. (1979) while determining activity patterns of brown trout noted 48 percent of its 24-hour activity occurred during dawn, 45 percent during dusk (the remainder occurring during adjacent periods). Free-running experiments in constant darkness did not show such a pattern, suggesting this activity is exogenously controlled by changing light intensity. The authors concluded from the evidence taken as a whole, that changing light intensity at dawn and dusk is largely responsible for stimulating the increased activity, and neither a circadian rhythm nor food availability are involved in the diel activity pattern of this species.

Field and laboratory studies involving different methodologies have been conducted on brown trout to measure their activity patterns and the environmental factors which influence them (Swift 1962, 1964; Chaston 1968). Collectively, these studies show feeding does not
affect diel activity patterns of this species, that the activity is not influenced by an endogenous circadian rhythm, and light levels or changing light intensity are important environmental factors which influence brown trout behavior.

The rapid alteration of the activity pattern after only 24 hours under reversed light conditions suggested the effect of light is entirely exogenous and not at all related to the phasing of a biological clock (Chaston 1968). These results substantiate Swift's (1964) suggestion in which light could be an important factor in the control of the activity pattern of *Salmo trutta*. Light and not food is the prime stimulus to locomotive activity in brown trout, according to Swift (1964).

Therefore, the influence of light on the behavioral pattern of brown trout is well established. The question remains, is the brown trout reaction based on the entire light spectrum or are the fish cuing on a particular segment of the energy spectrum? If in fact the trout could not perceive UV, they could not respond to it.

Data were found indicating brown trout possessed the paired-pigments required for perception of ultraviolet radiation. Fish have pigments within their eye structure allowing them to sense particular wavelengths of the visible spectrum and possibly additional wavelengths beyond either end of the visible spectrum. Some species have one or the other of these pigments; other species have both. Munz and Beatty (1965) employed the terms "rhodopsin" and "porphyropsin" as convenient class names for the retinene,
retinene₂ visual pigments described. The presence of these visual pigments has been established in dozens of retinal extracts of rainbow trout (Salmo gairdneri), and cutthroat trout (Salmo clarkii). A few experiments have shown that these pigments are also present in the Atlantic salmon (Salmo salar), and the brown trout (Salmo trutta). It seems probable, therefore, that this pair of visual pigments is present in all species of Salmo (Munz and Beatty 1965). The presence of these paired-pigments in brown trout is well documented, and their importance in the detection of specific wavelength bands is evident (Wald 1941; Kampa 1953; Bridges 1956; Tsin 1979; Jacquest and Beatty 1972; Dartnall 1962).

Porphyropsin absorbs light at longer wavelengths than its rhodopsin counterpart and gives the fish the ability to perceive the red end of the visible spectrum and the longer wavelengths. Rhodopsin gives the fish the ability to perceive the blue end of the visible spectrum and possibly the shorter wavelength bands of UV.

A change in the proportions of a mixture of rhodopsin and porphyropsin will change the total absorption spectrum of the mixture, and may alter visual sensitivity (Northmore and Muntz 1970; Muntz and Northmore 1973). If the rhodopsin-porphyropsin ratio shifts toward a predominance of rhodopsin, an increase in the perception of the shorter wavelengths is presumed, and the possible increased perception of ultraviolet wavelengths might be implied. Likewise, a porphyropsin dominance would imply a greater perception of the longer wavelengths.
Different species of trout contain different relative proportions of these pigments. These differences may be related to niche selection of each species and are further complicated by seasonal variation, light intensity, and water temperature.

Cutthroat trout sampled from partially shaded areas have a lower proportion of porphyropsin when compared to open area fish (Allen et al. 1973). However, the rhodopsin-porphyropsin ratio of brown trout is stable under different light conditions. They further showed brown trout have a higher percentage of porphyropsin when compared to brook or rainbow trout. The preceding observation is somewhat clouded because the authors claimed the porphyropsin in brown trout is somewhat different than other trouts, and therefore a different type of analysis had to be used to quantify porphyropsin amounts. This method decreased the amount of rhodopsin pigment and should be noted when interpreting their conclusions. Additionally, Dartnall (1962) reported finding a larger proportion of rhodopsin in European brown trout when compared to American brown trout. He also indicated the rhodopsin-porphyropsin ratio was labile. The visual pigment system of the brown trout may be, in many respects, very different from the other trout examined. However, brown trout do possess a paired-pigment ratio suggesting the possibility of ultraviolet perception which may be altered by external factors.

In many fishes which possess paired rhodopsin-porphyropsin visual pigments, there is a winter-time increase in porphyropsin,
whereas in summer the dominant pigment was rhodopsin (Allen and McFarland 1973). Generally in trout, a seasonal variation occurs. There was a seasonal shift in porphyropsin from a high percentage during late winter and spring to a low percentage during midsummer and fall. The rhodopsin increased during midsummer and fall. This phenomenon was further linked with temperature or light.

Higher temperatures might favor a lower percent of porphyropsin and lower temperatures a higher percent of porphyropsin in paired-pigment species (Allen et al. 1973). In addition, these changes occur regardless of light conditions, and it seems clear that water temperature is an important factor in producing shifts in the rhodopsin-porphyropsin ratio. There is a possibility temperature may be an important factor in explaining comparable seasonal changes in visual pigment ratios among species which may respond differently to photic conditions (Beatty 1975). A study on rainbow trout (Salmo gairdneri), indicated the paired visual pigment species may increase the proportion of rhodopsin, in comparison to porphyropsin, as a response to warmer temperatures (Tsin and Beatty 1977). To complicate the data further, it was evident the proportions of the two components were not constant throughout the life cycle of salmon and trout (Beatty 1966).

Temperature may in part solve the paradox concerning the effect of light on different species of fishes, wherein light favors porphyropsin in some species (rudd, golden shiner, genus Belonesox) and favors rhodopsin in others (red-side shiner, several trouts),
according to Allen and McFarland (1973). Changes in the proportions of rhodopsin and porphyropsin can be shown by varying experimental conditions such as day length and intensity of light (Allen 1971; Dartnall et al. 1961). Experiments have shown a switch toward rhodopsin in rainbow and brown trout in response to light (Dartnall 1962). Additionally, visual pigments of fishes and spectral sensitivities are known to vary with the environmental light regime (Muntz 1975). Although light, at least indirectly, does influence the paired-pigment ratio according to some authors, water temperature may be more critical in shifting the ratio.

Assuming brown trout can perceive ultraviolet radiation because of possession of the paired pigments, is there indeed sufficient ultraviolet radiation penetrating the water for the fish to detect? Most of the ultraviolet penetration data have been salt water orientated; however, some of the data can be used as a reference or focal point regarding fresh water. Experiments in the uppermost 15 meters revealed sea water is much more transparent to ultraviolet radiation than has been previously assumed. Middle ultraviolet (MUV) radiation, 280 to 340 nm, can penetrate to ecologically significant depths in natural waters (Jerlov 1950; Lenoble 1956; Halldal and Taube 1972; Smith and Baker 1979). Ocean water was found to be much more transparent to ultraviolet radiation than had been assumed (Jerlov 1950). He also mentioned that in the East Mediterranean, where clarity of the water equals that of the Sargasso Sea, the ultraviolet radiation at 310 nm was reduced by only 14
percent per meter depth. For the ultraviolet at 375 nm, the corresponding value was 5 percent. In freshwater, UV of 360-365 nm at one meter depth in various lakes ranged from 60 to 20% of the surface intensity (Wetzel 1975).

The UV band is composed of wavelengths below 400 nm. Caldwell (1979) defined UV-C as UV radiation less than 280 nm, UV-B as 280 to 320 nm, and UV-A is 320 to 400 nm. UV-C in quantities lethal to unprotected organisms not only have reached the surface of the earth but have penetrated 5 to 10 meters into water (Berkner and Marshall 1965).

Some authors have ignored the evidence indicating ultraviolet radiation penetrates further into natural waters than previously suspected. Optical properties of natural waters are known only roughly in the ultraviolet region of the spectrum (Smith and Tyler 1976). The lack of sensitivity of the fish eye to infrared and ultraviolet radiations is proportional to the rapid extinction of these wavelengths in water (Brett 1957). Tyler and Smith (1967) allude to the difficulty in measuring transmittance within the wavelength range 350-750 nm because of water differences.

Water differences aside, a great deal is known about ultraviolet radiation penetration in natural waters. However, there does exist a notable difference between fresh and salt water which is influenced by several factors. The absorbances by river waters of wavelengths from 250 to 350 nm are consistently greater than those of sea water (Foster and Morris 1974). They added this can be attributed to
the relatively large amount of dissolved organic matter in rivers in comparison with sea water. In addition, it is also apparent from river water spectra that variations occur in the relative absorbance of wavelengths among streams. This is particularly obvious when the absorbance at longer wavelengths, in which only organic matter contributes, is compared with the absorbance at shorter wavelengths where inorganic species also absorb. At wavelengths below 250 nm, both inorganics and organics contribute towards the absorbance by natural waters, whereas above this wavelength, only organic materials strongly absorb (Foster and Morris 1974).

Armstrong and Boalch (1961) maintain that within the spectral region, 250-350 nm, organic compounds of diverse nature and low individual concentrations which comprise the total dissolved organic matter in natural waters, make the most significant contribution to the total ultraviolet absorbance. In sea water, only nitrate and bromide were of any importance in the absorbance of wavelengths below 235 nm (Ogura and Hanya 1966, 1967). Any remaining absorption was attributable to the dissolved organic matter present, which usually accounted for only a small fraction of the total absorbance below 230 nm, but was predominant at longer wavelengths. This is in agreement with Foster and Morris (1974). Siebeck (1978) stated "ultraviolet measurements recently conducted in a very turbid mountain puddle demonstrate that at a depth of 3 cm at 313 nm 25%, at 320 nm 35% and at 365 nm 40% of the radiation which penetrated the water was still present."
It appears that ultraviolet radiation penetration in fresh water is dependent on the water quality and particularly on its organic load. Variation in UV radiation reaching the earth's surface also occurs. Berger et al. (1975) compare the differences in measurements of UV-B between different geographic locations. When Philadelphia and Albuquerque data are compared (east coast to intermountain area), it is evident that more UV-B radiation reaches the intermountain area than the east coast area. In many instances the intensity level in Albuquerque is double or more than that of Philadelphia.

Another consideration is whether UV will pass through the cornea, lens and vitreus humor of a fish eye, to be detected by the visual pigments. Humans do not detect UV because of pigments in the cornea and lens (Lythgoe 1979). Fish lenses are transparent to radiation down to 340 nm, and the oil droplets in fish eyes are transparent down to 350 nm (Lythgoe 1979). There is some indication that while fish may detect UV-A, they may not detect UV-B.

**METHODS**

**Instruments**

*Standardization of Underwater UV Photometer*

For the purposes of this study, the accuracy of ultraviolet radiation measurements was paramount. Instrument capability including reliability was of extreme importance. An underwater photo-
meter (Schenk, Instrument No. 9019) possessing the detection sensitivity capability of the UV wavelength band below 400 nm was used. The photometer was equipped with UV-sensitive photocells from Falkenthal and Presser, a leading company in this range of production. This instrument coupled with specific filter (Schott selective filters) combinations gave it the capability to measure UV wavelengths below 400 nm. The photometer output in total UV energy was measured in microamps with a Keithley 130 digital multimeter. The internal resistance of the multimeter was less than 100 ohms, which was necessary for accuracy when obtaining such low output in microamps.

**Visible Light Meter**

Visible light measurements were taken with a visible light meter (Whitney, Model LMD-8A with a response curve capability of approximately 400 to 720 nm, with output measured in foot-candles). The instrument's output capability could only be measured in foot-candles, thus the departure from the underwater photometer output in microwatts cm$^{-2}$. Conversion of foot-candles to microwatts cm$^{-2}$ was not done because of each instrument's response to different criteria; foot-candles is a measure of illuminance, while microwatts cm$^{-2}$ is a measure of energy. A cosine error correction curve was established for this instrument because of its variability in sensitivity when light was measured at different sun angles. Both the photometer and the visible light meter were read at horizontal position, which was maintained by a bubble level attached to each instrument.
Methods of standardizing the UV photometer, deriving a cloud intensity UV curve, determining a cosine error for the visible light meter, and correcting visible light readings for refraction are presented in Appendix B.

Laboratory Experiments

Wild brown trout ranging from 12 to 30 cm in total length were obtained from the Right Fork of the Logan River by electro-fishing. The fish were fed a natural diet of sectioned night crawlers every other day throughout the duration of the experiment. Holding facilities consisted of a circular fiberglass tank with flow-through capabilities. Municipal water was run through a two-staged filter system located above the tank. The filter system consisted of 0.3 meter of activated charcoal for chlorine elimination and 0.6 meter of plastic shotgun shell wads providing a trickledown splash system which eliminated oxygen and nitrogen supersaturation. The water exchange rate was quite rapid and the dissolved oxygen level was maintained at 4.5 to 5.0 ppm; the water temperature was maintained at 13 to 16 C. Scheduled lighting was maintained throughout the holding period. Overhead cover was provided with floating boards.

Permanent tags were not attached to avoid traumatizing the fish. Bachman's (1982) procedure of diagramming the arrangement of dark pigment spots on the back of the fish in the vicinity of the dorsal fin was used to identify individual fish.
Laboratory Experimental Procedures

The experimental unit consisted of a 213 cm X 61 cm X 56 cm deep tank system which provided a controlled environment maintaining a 13 to 16 C temperature and a dissolved oxygen concentration of 5.5 ppm. An opaque section of plexiglass was used to bisect the tank, with an opening on the bottom for fish passage between the two chambers.

Visible light (300 watt source), with intensity controlled with a rheostat, was positioned above one chamber of the tank. Visible light readings were measured and recorded throughout the bottom of the test chamber in 25 cm of water at various rheostat voltages ranging from 20 to 120 volts. A fish's position could then be related to the intensity of visible light at any specific position.

The UV radiation source was obtained from two blacklight fluorescent bulbs positioned above the other test chamber. The blacklight UV emission band was measured with a spectrophotometer to insure that the UV spectral output was similar to natural sunlight. The spectral band was similar, however, its intensity was less than that of sunlight. Alteration of UV intensity from these bulbs could only be achieved by varying the bulb height above the water surface. Again, as with the visible light, the UV intensities were measured and recorded at the bottom of the test chamber and the position of the fish was related to the previously recorded UV intensity for that specific location.
The blacklight spectral band consisted of not only UV radiation, but also a small amount of visible blue light. The UV and the visible blue light emissions from the blacklight had to be separated to determine if fish response was specific to either one of these components. To clarify this, a band specific filter material (Llumar, Martin Processing, Inc.) which transmitted 80% of the visible spectrum and blocked transmission of the UV spectral band was installed in one test chamber. The opposite chamber of the test tank consisted of blacklight only, no Llumar filter, and emitted both UV and the small amount of visible blue light.

Equal intensities of visible blue light were then maintained in both experimental units, the only difference being one unit was subjected to UV in addition to the blue light. In all tests, the fish avoided the UV-blue light chamber and positioned themselves in the blue light only chamber. Blue light intensity in the blue light only chamber was increased, and the test repeated. Again, the fish avoided the UV-blue light chamber and positioned themselves in the higher intensity visible blue only chamber. Therefore, the fish were avoiding the UV component of the blacklight emission and were not cuing on the small amount of visible blue the blacklight was also emitting. The following test sequence could then be initiated and responses noted.

**Tolerance Test Format**

Thirty fish were run three times each through a range in visible and UV light intensities such that an avoidance range of visible
and UV intensities could be identified from fish response. Each individual fish was run through the sequence three times in succession. Two minutes were allowed for response to each change in intensity; five minutes were allowed at position after response and before the next element of the sequence was initiated. The test sequence is outlined in Figure 1.

**Field Data Collection**

A segment of the Blacksmith Fork River with a variety of riparian habitat along a pool-riffle-pool-riffle sequence was chosen for the field data collection. These stations were chosen because of previous studies indicating areas where fish were observed or not observed. Seven sampling stations were located along this segment of the river. Ultraviolet and visible light measurements were taken ten times at each sampling station during the daylight hours of July 31, 1982, beginning at 8:00 am and ending at 7:00 pm. Data were taken on the hour with the exception of 12:00 and 3:00 pm. Data collection was done during clear, bright-sun, and intermittent windy conditions. Both UV and visible light intensities were measured at nearly the same time and same depth regime at each station. Visible light measurements were corrected by using the cosine correction factor in sun angle calculations.

The stations were described as follows:

Station 1 - Open riffle.

Station 2 - Intermittent shade - under river birch with branches several feet above the water.
Test Sequence Steps:

1. No light source in either test chamber.
2. Ambient visible room light present at the same intensity as in the holding tank room.
3. Fish inserted; allowed to wander through escape route into both chambers; allowed to acclimate for 30 minutes.
4. When fish positioned itself in test chamber of visible light emission only, test sequence was initiated.

<table>
<thead>
<tr>
<th>UV Test Chamber</th>
<th>Visible Light Test Chamber</th>
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<tr>
<td>UV-high intensities</td>
<td>Visible light intensities (were same)</td>
</tr>
<tr>
<td>UV-high intensities</td>
<td>Visible light - high intensities</td>
</tr>
<tr>
<td>UV-high intensities</td>
<td>Visible light - low intensities</td>
</tr>
<tr>
<td>UV decreased until fish moved to UV chamber.</td>
<td></td>
</tr>
<tr>
<td>UV-low intensities</td>
<td>Lower visible light</td>
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<tr>
<td>UV-low intensities</td>
<td>Visible light intensities (were same)</td>
</tr>
<tr>
<td>UV decreased to intensities lower than in Step 9.</td>
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<tr>
<td>UV-low intensities</td>
<td>Visible light intensities (were same)</td>
</tr>
<tr>
<td>UV-intensities increased</td>
<td>Visible light intensities (were same)</td>
</tr>
</tbody>
</table>

- Indicates fish position
- Indicates fish movement

FIGURE 1.—Tolerance test sequence.
Station 3 - Extended shade - under river birch with branches hanging close to the water.
Station 4 - Brush overhanging on bank area.
Station 5 - Lower pool - open area.
Station 6 - Brush and willow overhanging on bank area.
Station 7 - Pool - open area.

RESULTS AND DISCUSSION

Laboratory

The subsample of the brown trout population of the Right Fork of the Logan River did avoid visible light at various intensities under laboratory testing conditions. During the test sequence (Figure 1) described in the methods (step-6), the visible light chamber was increased in intensity until the fish moved to the UV chamber. The avoidance value in foot-candles of visible light at the location vacated by the fish was noted (Table 1). The visible light avoidance response intensity value was the overall mean ($\bar{X}$) of the 30 fish tested in three separate runs. In order to test the validity of the overall mean, the variance in the means obtained among the three separate runs was compared. This was accomplished by an analysis of variance-randomized block-two factor analysis.
TABLE 1.—Individual brown trout avoidance response to UV and visible light intensities during three successive sequence runs.

<table>
<thead>
<tr>
<th>Fish Identification</th>
<th>Ultraviolet radiation (uwatts cm$^{-2}$)</th>
<th>Visible light (foot-candles)</th>
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<td>30</td>
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<td>3500</td>
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$\bar{x} = 3500$ uwatts $^{-2}$  \hspace{1cm} $\bar{x} = 646$ foot-candles
TABLE 2.—Analysis of variance and corresponding F-test regarding visible light response values.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Sum of squares</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
<th>F value</th>
<th>Tabular F</th>
</tr>
</thead>
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<td>274,508</td>
<td>2</td>
<td>137,254</td>
<td>1.59</td>
<td>3.17</td>
</tr>
<tr>
<td>2 - Among fish</td>
<td>8,980,995</td>
<td>29</td>
<td>309,689</td>
<td>3.58*</td>
<td>1.69</td>
</tr>
<tr>
<td>3 - Residual</td>
<td>5,007,624</td>
<td>58</td>
<td>86,338</td>
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<td></td>
</tr>
<tr>
<td>Total</td>
<td>14,263,128</td>
<td>89</td>
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</tr>
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</table>

* F-test significant at 5%.

The three separate runs were not significantly different at the (F, .05) level (Table 2). Therefore, the overall mean visible light avoidance response intensity ($\bar{X} = 646$ foot-candles, with 95% confidence limits of 562 to 730 foot-candles), sample standard deviation ($S = 402$ foot-candles), and population standard deviation ($\sigma = 400$ foot-candles) were calculated on the total three-run data. The sample and population standard deviations were quite high, however, they were below the mean value. The variance in individual response was significant at the (F, .05) level (Table 2), but could be the true picture of the variability of the total population. A computed ($r$) value of 0.018 indicated there was little correlation between length of the fish tested (12 to 30 cm) and the fish response to visible light intensity, and therefore was not a factor in the significant individual variance. The histogram (Figure 2) suggests the variability in visible light response is similar to a normal distribution curve with extreme responses on each end.

Continuing with step-6, the UV intensities varied throughout the UV chamber and the fish typically sought a location of minimum...
FIGURE 2. — Visible light avoidance distribution.

FIGURE 3. — Ultraviolet avoidance distribution.
UV intensity. Thus far, the fish avoided a high visible light intensity, sought the lower visible light intensity in the UV chamber, and tolerated a UV intensity lower than the maximum in the chamber. The UV value in microwatts cm\(^{-2}\) at the location where the fish positioned itself was noted.

Step-8 of the test sequence consisted of the UV chamber now having a lower intensity of visible light than the visible light chamber and the fish could conceivably be cuing on the visible light intensity. At this point in the sequence, they tolerated low intensity UV to get to the lower intensity of visible light in the UV chamber. When the intensity in the visible light chamber was reduced to the same level as that in the UV chamber (step-9), the fish wandered between the two chambers. This implied that with similar low visible light intensities in both chambers, they did not respond to the low UV intensities. In other words, at low visible light intensities in both chambers, low UV was tolerated or not detected.

When the fish avoided the UV chamber (step-11), the lowest UV intensity in the chamber was then noted as the intolerance level of UV for that particular test fish (Table 1). Reiterating, both test chambers had the same amount of visible light, the only difference being the UV light in the chamber the fish avoided.

Therefore, the subsample of brown trout also avoided UV radiation at various intensities under similar laboratory testing conditions. The UV avoidance response intensity value was the overall mean ($\bar{x}$) of the 30 fish tested in three separate runs. Similarly, compared
to visible light data, the variance in the means obtained among the	hree separate runs was tested by an analysis of variance-randomized block-two factor analysis.

TABLE 3.—Analysis of variance and corresponding F-test regarding ultraviolet response values.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Sum of squares</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
<th>F value</th>
<th>Tabular F</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 - Among runs</td>
<td>854</td>
<td>2</td>
<td>427</td>
<td>2.135</td>
<td>3.17</td>
</tr>
<tr>
<td>2 - Among fish</td>
<td>21,261</td>
<td>29</td>
<td>733</td>
<td>3.665*</td>
<td>1.69</td>
</tr>
<tr>
<td>3 - Residual</td>
<td>11,621</td>
<td>58</td>
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<tr>
<td>Total</td>
<td>33,736</td>
<td>89</td>
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</tr>
</tbody>
</table>

* F-test significant at 5%.

The three separate runs were not significantly different at the (F, .05) level (Table 3). Therefore, as with the visible light data, the overall mean UV avoidance response intensity ($\bar{X} = 3500$ microwatts cm$^{-2}$, with 95% confidence limits of 3003 to 4002 microwatts cm$^{-2}$), sample standard deviation ($S = 2789$ microwatts cm$^{-2}$), and population standard deviation ($\sigma = 2774$ microwatts cm$^{-2}$) were calculated on the total three-run data. In comparison to visible light values, the sample and population standard deviations were similarly high. The variance in individual response was significant at the (F, .05) level (Table 3). A computed ($r$) value of 0.1460 indicated there was little correlation between the length of the fish tested (12 to 30 cm) and the fish response to UV intensity, and therefore was not a factor in the significant individual variance. The variability was not unexpected, and the histogram (Figure 3) suggested that the UV response was similar to a normal distribution curve.
Field

Figures 4 through 10 represent the surface and subsurface values of visible (upper) and UV (lower) light at specific sampling stations during July 31, 1982. The solid lines in each figure represent the surface values of visible and UV light over time of day, and the broken lines represent the visible and UV light intensities at the maximum depth measured at that specific station. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.

Gosse and Helm (1982) report brown trout select locations for resting where visible light intensities do not exceed 5% (500 foot-candles) of full incident sunlight. The above measurements were not corrected for cosine error, and thus would be somewhat lower than measurements made during this study. Neither the mean avoidance visible light intensity (646 foot-candles) nor the lower confidence limit (562 foot-candles) is greatly different than the 500+ foot-candles value Gosse and Helm report for wild, free-ranging brown trout.

UV and visible light intensities measured near the substrate suggest that the fish would not use these areas for resting during the time when the respective critical avoidance intensities were exceeded as determined by the UV and visible light avoidance experiments. The difference in times when the two avoidance intensities
FIGURE 4.—Station 1 - Ultraviolet and visible light surface and penetration values during specific hours. Riffle - open area. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.
FIGURE 5.—Station 2—Ultraviolet and visible light surface and penetration values during specific hours. Riffle, midstream, mottled shade - branches overhead. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.
FIGURE 6.—Station 3 - Ultraviolet and visible light surface and penetration values during specific hours. Riffle, midstream, shade - under river birch. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.
FIGURE 7.—Station 4 - Ultraviolet and visible light surface and penetration values during specific hours. Right shoreline bank - shade area. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.
FIGURE 8.—Station 5 - Ultraviolet and visible light surface and penetration values during specific hours. Lower end of bush pool - open area. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.
FIGURE 9.—Station 6 - Ultraviolet and visible light surface and penetration values during specific hours. Right bank in shade - rest area. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.
FIGURE 10.—Station 7 - Ultraviolet and visible light surface and penetration values during specific hours. Big bend pool - open area. The horizontal lines are the overlays of the laboratory UV and visible light mean avoidance intensities (solid) and the 95% confidence limits (dashed) of the respective mean values.
first occurred in the morning or last occurred in the evening varied between a few minutes to about an hour, with visible light intensities always reaching avoidance values at the same time or prior to and lasting until the same time or later than UV (Figures 4-10). Since most time differences ranged from near zero to less than 30 minutes, it hardly appears justified to identify either visible or UV as the most important light component in regulating brown trout positions. However, the field measurements demonstrate the greater value of one riparian vegetation type over another. These observations are made with the qualification that UV and visible light intensities do indeed affect the daylight residence time of brown trout in specific habitat types.

Riffle or pool open area data (Figures 4, 8, 10) suggest that daylight residence time would be shorter than residence time at other stations based on UV and visible light avoidance experiments. Figure 6 illustrates the possible extention of residence time under an overhanging tree with branches close to the water surface. The high peaks in UV and visible light intensities are attributed to the changing sun angle. With low-hanging branches however, a fish could move a short distance and again find a location with light intensities below avoidance levels. A sparse overhanging canopy (Figure 5), or a dense overhanging canopy far above the water surface would not provide such an opportunity, and thus is less valuable in providing shade.
The importance of low overhanging riparian vegetation is illustrated by Figures 7 and 9. Both stations provided extended residence time based on UV and visible light mean avoidance intensities. The UV critical intensity was never reached throughout the daylight hours at these two sampling stations, and the visible light just reached critical intensity for only a short time at one station. Station 6 (Figure 9) was identified as a known resting area from previous studies.

When sun angle change was considered, low overhanging brush provided a more uniform sanctuary during the daylight hours compared to higher overhanging tree canopy. Calculated percent residence time during daylight hours at each station type (Table 4) illustrates the theoretical amount of time various habitats could be used under acceptable UV and visible light conditions. The increased value of low overhanging riparian vegetation over other riparian types is clearly evident.

Appendix B, Figure 12 illustrates the decline in visible light and UV intensities with respect to cloud cover above the surface of the water. As cloud intensity increased, UV values decreased more dramatically than visible light values. The broken horizontal lines are the critical avoidance response intensity values. Some inferences can be drawn on the affect of cloud cover on ultraviolet and visible light at locations near the stream bottom typically occupied by brown trout from an examination of Figures 4-10 (see also Appendix A, Tables 5-11). Light input depressed by cloud cover will
Table 4.—Theoretical percent residence time at each specific station based on subsurface UV and visible light mean avoidance values.

<table>
<thead>
<tr>
<th>Station</th>
<th>Ultraviolet Residence time in daylight hours</th>
<th>Percent residence time</th>
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<tbody>
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<td>6</td>
<td>11</td>
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<tr>
<td>4</td>
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<td>3</td>
<td>27</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>18</td>
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</table>

<table>
<thead>
<tr>
<th>Visible Light Residence time in daylight hours</th>
<th>Percent residence time</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>11</td>
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<tr>
<td>4</td>
<td>11</td>
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<td>7</td>
<td>2</td>
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<td>5</td>
<td>2</td>
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</table>

be further reduced by reflection and absorption, depending upon time of day, surface agitation and depth. The ultraviolet light values reported for Philadelphia and Albuquerque indicate that the values in Figures 4-10 and Appendix A, Tables 5-11, could be reduced by 0.5 or more to be representative of conditions in Pennsylvania.

Conclusions

Under laboratory testing conditions, the hypothesis stating brown trout cannot detect ultraviolet radiation was rejected. The hypotheses stating brown trout will avoid UV and visible light above some threshold intensity could not be rejected.
When the UV and visible light mean avoidance response intensities are overlaid onto the light penetration graphs at each field station, it is apparent the riparian vegetation type consisting of low overhanging brush provides a more consistent refuge of low UV and visible light intensities throughout the daylight hours when compared to the other riparian types. These areas harbor light intensities below the mean avoidance response intensities found in the laboratory experiments, and subsequently could be used by resting brown trout more consistently through the day than other habitat types.

Riparian types consisting of large overhanging trees may reduce the UV and visible light values in the stream beneath them to below the mean avoidance response levels intermittently during the day. However, sun angle and sunlight penetration under high overhanging limbs change these values during the course of the day.

It appears brown trout will avoid high and moderate levels of both ultraviolet and visible light. If brown trout in the wild are cuing on the mean avoidance levels of ultraviolet and visible light, the affects of the two can not be separated because the two avoidance levels are reached at nearly the same time of day.
REFERENCES


APPENDICES
Appendix A. Tables
TABLE 5.—Ultraviolet radiation and visible light penetration at designated time during daylight hours at specific sampling station.

<table>
<thead>
<tr>
<th>Time</th>
<th>Station 1 -- Riffle - open area</th>
<th>Depth (Feet)</th>
<th>Visible light (Foot-candles)*</th>
<th>Ultraviolet radiation (Microwatts cm⁻²)</th>
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### TABLE 5 - continued

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<thead>
<tr>
<th>Time</th>
<th>Depth</th>
<th>Visible light (Foot-candles)*</th>
<th>Ultraviolet radiation (Microwatts cm$^{-2}$)</th>
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</table>

* Cosine error corrected values based on sun angle for surface measurements and water refraction correction for below surface measurements.

** Visible light meter maximum measurement capability was 10,000 foot-candles.
TABLE 6.—Ultraviolet radiation and visible light penetration at designated time during daylight hours at specific sampling station.

<table>
<thead>
<tr>
<th>Time</th>
<th>Depth</th>
<th>Visible Light</th>
<th>Ultraviolet radiation</th>
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Note: When comparing surface values proportionally i.e., VL/UV, values were inconsistent because of the swaying over-hanging branches giving a mottled sun-shade effect on the water surface. Maximum depth measurements were a more consistent gauge of UV and VL values. Additionally, the proportion is also influenced by sun angle. At low sun angle (early morning and late afternoon) much less UV gets to the earth (proportional to visible light) than when the sun is at its zenith. This should be noted for all sampling stations.
TABLE 7.—Ultraviolet radiation and visible light penetration at designated time during daylight hours at specific sampling station.

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<th>Station 3 -- Riffle, midstream, total shade (under river birch)</th>
<th>Depth (Feet)</th>
<th>Visible light (Foot-candles)</th>
<th>Ultraviolet radiation (Microwatts cm(^{-2}))</th>
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  - 2.0: 17, 153
  - 2.5: 11, 153

### 9:10 am
- **Surface**
  - .5: 428, 755
  - 1.0: 114, 604
  - 1.5: 82, 453
  - 2.0: 80, 306
  - 2.5: 48, 306

### 10:10 am
- **Surface**
  - .5: 361, 1050
  - 1.0: 170, 906
  - 1.5: 128, 608
  - 2.0: 85, 608
  - 2.5: 70, 456

### 11:10 am
- **Surface**
  - .5: 374, 1341
  - 1.0: 229, 1200
  - 1.5: 146, 906
  - 2.0: 83, 755
  - 2.5: 83, 456

### 1:10 pm
- **Surface**
  - .5: 515, 1480
  - 1.0: 224, 1480
  - 1.5: 214, 1192
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  - 2.5: 184, 755

### 2:10 pm
- **Surface**
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* Value greater than previous hour because of sun coming in under canopy.
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### TABLE 10.—Ultraviolet radiation and visible light penetration at designated time during daylight hours at specific sampling station.

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TABLE 11.—Ultraviolet radiation and visible light penetration at designated time during daylight hours at specific sampling station.

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Appendix B. Instrument Standardization
INSTRUMENT STANDARDIZATION

Standardization and calibration of the underwater photometer was accomplished by the conversion of multimeter output in microamps to microwatts cm\(^{-2}\) by way of a UV constant curve derived in conjunction with a more sophisticated spectrophotometer of known standardization.

**Derivation of the UV Constant Curve**

Simultaneous UV measurements were taken by the spectrophotometer and the underwater photometer at three intervals during a clear bright-sun day. Ultraviolet spectral intensities were integrated over the 300-400 nm band using the standardized spectrophotometer. Total UV energy was measured with the underwater photometer and averaged over the same time frame as the spectral intensities measured by the spectrophotometer. The average underwater photometer output was expressed in microamps.

The spectrophotometer wavelengths were identified by comparing them with the "Fraunhofer" lines in the standard solar spectrum.

The following formula was then used to obtain UV irradiance in microwatts cm\(^{-2}\) for that particular wavelength:

\[ K_1 \times K_2 \times \text{wavelength height in cm}; \]

where \( K_1 \) is identified as a scale factor and \( K_2 \) is a calibration factor for the spectrophotometer which is determined for each wavelength.
The calculated irradiance value for each wavelength between 300-400 nm was then plotted on a graph. The curve was then integrated to obtain the total UV solar intensity in the field of 300-400 nm wavelength. The calculated total UV solar intensity was then divided by the average reading of the underwater photometer to obtain the constant for that time. The entire process was repeated at two other time intervals to obtain two additional constants. The value of each constant was expressed in microwatts cm$^{-2}$ microamp$^{-1}$.

The entire procedure seems quite lengthy, however, once the constant curve is obtained (Appendix B, Figure 11), photometer output in microamps is matched to the curve on the X axis, then transversed to the microwatts cm$^{-2}$ microamp$^{-1}$ on the Y axis to obtain the constant for that particular photometer microamp reading. The constant is then multiplied by the original photometer reading in microamps and the UV irradiance in microwatts cm$^{-2}$ is obtained. With the UV constant curve established, it takes one calculation to obtain the UV irradiance from the underwater photometer output.

**Derivation of Cloud Intensity UV Curve**

Derivation of the cloud intensity UV curve involved the convolution (integration of products), of the spectral response curves of the UV photometer and the absorbance filters used in conjunction with the photometer. This was necessary to obtain the instrument correction regarding UV sensitivity during cloudy conditions for the photometer used.
FIGURE 11.—Ultraviolet radiation constant curve.
The following formula was used:

\[ Z = Y_1 \lambda \times Y_2 \lambda \times Y_3 \lambda; \]

where \( Y_1, Y_2, \) and \( Y_3 \) are the response values for the UV photometer, filter-1, and filter-2 respectively, at a particular spectral wavelength (\( \lambda \)).

The (Z) values for each specific wavelength were further convoluted against standard curves of clear and cloudy conditions. The photometer curves for clear and cloudy conditions were plotted. The areas of the curves were measured and a ratio of cloudy-clear was obtained. The uncorrected UV irradiance was divided by the cloudy-clear ratio and further multiplied by a percent value obtained from a "percent UV of the total" standard curve. The value obtained was the corrected UV irradiance at that particular cloud cover intensity. Appendix B, Figure 12 illustrates the corrected UV irradiance values plotted against increasing cloud intensity.

A quartz beaded lens was fitted over the photocells and filters of the underwater photometer giving the instrument the capability to diffuse UV radiation onto the photocells and eliminate hotspots. Therefore, a cosine error correction curve was not needed in the calculation of UV irradiance from the instrument.

**Cosine Error Determination**

To obtain the cosine error due to the changing angle of the light source, an apparatus designed specifically for this purpose
FIGURE 12.— Cloud cover influence on ultraviolet and visible light intensities. Dashed lines are lab UV and visible light mean avoidance intensities.
was used. A beam of light, constant in irradiance, was directed onto the light meter. The irradiance remained constant while the light source was positioned at increasing angles and measurements were made at each angle. A ratio (light intensity-cosine of angle), was calculated for each angle and plotted on a graph. The calculated ratio of the specific angle was the cosine error of the instrument for that angle. The ratio was then divided into the instrument reading for that particular date and hour to give the corrected amount of energy at that location in time and sun angle.

Sun angle calculation for a specific date and hour was obtained from calculations derived from standard tables. Equation of time, declination, and Logan's latitude were obtained from tables. The zenith angle of the sun for a specific time was calculated from the formula:

\[ Y = \cos Z = \cos(15 \times (T_2 - 12)) \times \cos \delta \times \cos \phi + \sin \delta \sin \phi. \]

Then the zenith angle (Z) = \(\cos^{-1}(Y)\);

where \(T_2\) is the corrected time added to the equation of time; \(\delta\) is the declination of the sun; and \(\phi\) is Logan's latitude.

When the zenith angle was obtained, the angle was matched with the same angle on the cosine error curve to obtain the cosine error correction. The correction was then divided into the irradiance value determined from the light meter to obtain the corrected irradiance value for measurements taken at the surface of the water.

Measurements taken below the surface of the water were calculated and corrected with reference to the refractory index of water. The
following formula was used:

\[ \theta_2 = \sin^{-1} \left( \frac{\sin(\theta_1)}{1.33} \right) \]

where \( \theta_1 \) is the angle of the sun. Once the angle was obtained, the respective cosine error was obtained from the graph and the correction in irradiance was made.