

THE SCOTOPIC VISUAL SENSITIVITY OF FOUR SPECIES OF TROUT: A COMPARATIVE STUDY

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ABSTRACT.—We compared the maximum scotopic visual sensitivity of 4 species of trout from twilight (mesotopic) to fully dark-adapted vision. Scotopic vision is the minimum number of photons to which a fully dark-adapted animal will show a behavioral response. A comparison of visual sensitivity under controlled laboratory conditions showed that brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) had maximum scotopic thresholds ($1.1 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.005 lux) 2 times lower than rainbow trout (*Oncorhynchus mykiss*) and Snake River cutthroat trout (*Oncorhynchus clarki bowieri*), which did not differ from each other ($2.1 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.01 lux). A literature review tended to corroborate these results in that brown trout and brook trout were reported to be more active during the night and at twilight than cutthroat trout and rainbow trout. We also measured light intensity within open versus shaded reaches during the day, dusk, and night in 3 Rocky Mountain streams. The scotopic sensitivity of brown trout and brook trout was sufficient to allow foraging during all twilight periods and under average nighttime light intensities in open and shaded reaches, whereas the scotopic sensitivity of rainbow trout and cutthroat trout may restrict their foraging to relatively bright nocturnal conditions (twilight or a moonlit night). Native cutthroat trout restoration efforts may have greater success in open versus shaded stream reaches in the Rocky Mountains and elsewhere.

Key words: light sensitivity, scotopic vision, cutthroat restoration, salmonids.

Three attributes of light can affect trout vision: (1) intensity (photons \cdot area⁻¹time⁻¹), (2) spectral composition (wavelength [nm]), and (3) polarization (the major plane of vibration in which most photons oscillate). Recent research has demonstrated that representatives of the major extant clades of Salmoninae (i.e., rainbow trout, cutthroat trout, brook trout, brown trout, and Atlantic salmon) are able to detect polarized light (Coughlin and Hawryshyn 1995, Novales-Flamarique and Hawryshyn 1997, Parkyn and Hawryshyn 2000) and can see light of varying irradiance and spectral composition, including ultraviolet, blue, green, yellow, and red (e.g., Douglas 1982, Bowmaker and Kunz 1987, Hawryshyn et al. 1989, Deutschlander et al. 2001). Most of these studies have examined the mechanisms underlying trout vision at the cellular/physiological level using isolated tissues or induced immobilization of whole organisms (e.g., Hawryshyn and McFarland 1987, Hawryshyn et al. 1989), whereas far fewer studies have examined the behavioral effects of these physiological differences in trout vision. Douglas and Hawryshyn (1990) emphasized that

electrophysiological studies, although valuable, were not reliable indicators of the response of the whole animal: “Only behavioural (psycho-physical) studies can tell us what the animal’s visual system is truly capable of achieving.”

Photoreceptor cells (rods and cones) respond to the number of photons striking the retina. Scotopic vision is not possible until sufficient photons have struck the retina to excite a nervous impulse (e.g., Partridge 1990). Maximum sensitivity to dim light has been defined as the minimum number of photons to which a fully dark-adapted animal will show a behavioral response (Douglas and Hawryshyn 1990). Dark-adapted scotopic vision is produced by a number of electrophysiological and biomechanical changes in the retina (e.g., Bowmaker 1990, Wagner 1990). Photopic vision occurs during the day, whereas mesotopic vision is intermediate between photopic and scotopic vision. Twilight periods span the transition from photopic to scotopic vision. We compared the maximum scotopic sensitivity of 4 species of trout from twilight (mesotopic) to fully dark-adapted vision. Maximum scotopic sensitivity

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in dark-adapted specimens of 4 species of trout was determined by the earliest commencement of visual behavior during a simulated dawn.

In the Rocky Mountains, introduced brook trout, brown trout, and rainbow trout (common names follow Nelson et al. 2004) have displaced native cutthroat trout, reducing their distribution to a small fraction of their historic range (e.g., Young et al. 1996). Introduced trout may grow faster and achieve a greater reproductive output than native cutthroat trout if they can feed longer because of a greater scotopic sensitivity. Thus, scotopic sensitivity may partially explain the ability of introduced trout to exclude native cutthroat trout.

We are aware of only 3 behavioral studies using whole organisms to compare the scotopic vision of different salmonid species. Henderson and Northcote (1985) found that lake populations of Dolly Varden (*Salvelinus malma*) foraging under dim light were better at detecting prey than cutthroat trout (*Oncorhynchus clarki clarki*). Similarly, Robinson and Tash (1979) found that brown trout (*Salmo trutta*) were more efficient at eating brine shrimp at lower light levels (starlight > 0.001 lux) than Apache trout (*Oncorhynchus gilae apache*). These data indicate that at least 1 species of brook trout and brown trout have greater scotopic sensitivity than cutthroat trout. Confer et al. (1978) found that the reaction distance of lake trout (*Salmo namaycush*) and brook trout (*Salmo fontinalis*) to planktonic prey was similar at illuminances equal to 1.0 lux, suggesting that different species in the same genus may have similar scotopic sensitivity.

Thus, we hypothesized that the scotopic vision of brown trout and brook trout would be more sensitive than that of fine-spotted Snake River cutthroat trout (*Oncorhynchus clarki bouvieri*). However, we had no basis for predicting possible differences in the scotopic sensitivity among rainbow trout (*Oncorhynchus mykiss*), fine-spotted Snake River cutthroat trout, brown trout, and brook trout, because of the absence of previous research. Similarly, there are no studies documenting 24-hour fluctuations in light intensity in stream ecosystems (day, twilight, and night). Field measurements, combined with laboratory experiments to determine the scotopic sensitivity of these trout, allowed us to determine the percentage of time that light levels are greater than scotopic thresholds for each species. These percentages

determine the maximum amount of time different species can forage in different reach types.

Our objectives were to (1) experimentally compare the scotopic visual sensitivity of brook trout, brown trout, fine-spotted Snake River cutthroat trout, and rainbow trout, (2) measure light intensity within open versus shaded reaches during the day, dusk, and night in 3 high-elevation mountain streams, and (3) review the literature on the diel activity of trout.

METHODS

Laboratory Tests of Scotopic Sensitivity

All fish used in this study, as in other studies on trout vision (e.g., Allen et al. 1973), were raised in fish hatcheries (2 in Wyoming and 1 in Colorado) because differences in the rearing environment in a natural setting might have led to variation in scotopic sensitivity. We selected hatcheries with similar temperatures (12°–15°C), water depths, water quality, food type, and structure (open raceways) to minimize environmental effects on differences in scotopic vision. None of the hatcheries was shaded. We selected fish of each species within the same size range (25–30 cm) because the number of visual receptors (rods and cones) and the concentration of scotopic pigments (rhodopsin and porphyropsin) increase as trout grow, making larger fish more sensitive to dim light than smaller fish (e.g., Allen et al. 1982).

We determined the scotopic sensitivity of 30 adult fish from each of the 4 salmonid species by recording the intensity of light at which individual fish first responded to a hand breaking the path of light directly overhead or to food floating at the surface of the water (hatchery pellets, Purina Trout Chow). Fish appeared to be startled by hand waving, which creates a shadow over the entire retina that can be perceived without highly acute vision. This startle response to hand waving should occur at lower light levels than a response that requires some level of acuity, such as the detection and location of drifting food. Also, trout may fail to respond to food after visual detection, even when they are starved, because of differences in individual behavior, whereas hand waving will elicit a consistent reaction, as if to a predator, and should provide a less variable signal of the threshold number of photons striking the retina to excite vision and a subsequent response.

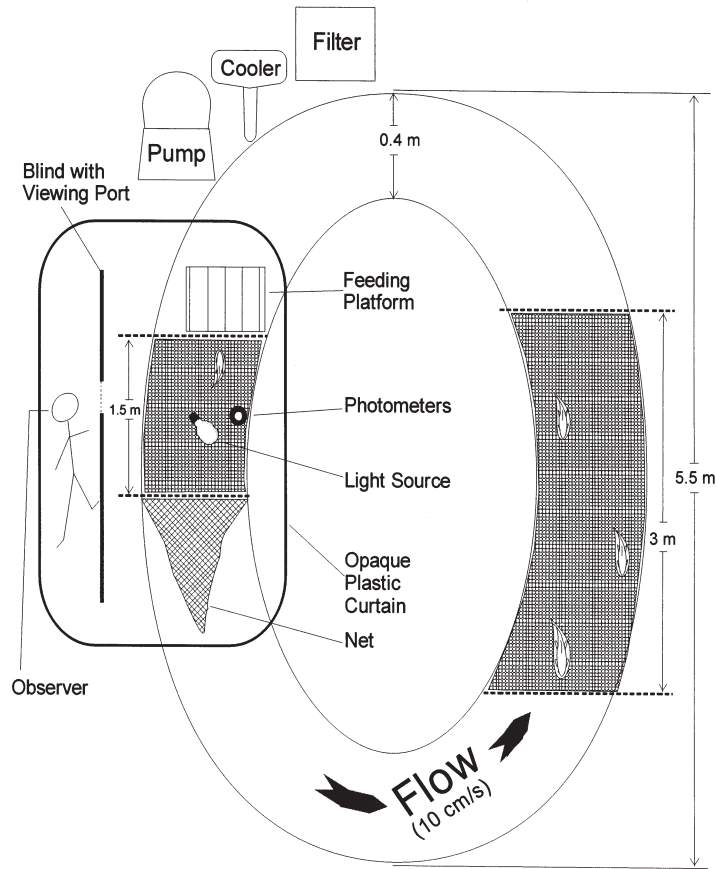


Fig. 1. Laboratory set-up for determining the maximum scotopic sensitivity of brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), fine-spot Snake River cutthroat trout (*Oncorhynchus clarki bowleri*), and rainbow trout (*Oncorhynchus mykiss*).

These experiments were conducted in an oval recirculating laboratory stream (Frigidunits Inc., Toledo, OH, www.frigidunits.com; Fig. 1). The experimental and nonexperimental sections were layered with natural gravels obtained from Nash Fork Creek in Wyoming. Water depth was 30 cm, current velocity $10 \text{ cm} \cdot \text{s}^{-1}$, and temperature 13° – 15°C . The stream was housed in a large room enclosed in a warehouse to block extraneous light. A window was blocked with three layers of black plastic during experimental observations. The laboratory stream, including the tent where we stood to make observations, was also enclosed in 3 layers of black plastic (Fig. 1). Observers were separated from the experimental section of the artificial stream by 3 additional layers of black plastic with a cutout viewing port ($25 \times 40 \text{ cm}$). Fish were observed and instruments were read

under complete darkness with the aid of a hand-held infrared flashlight (1000 nm–0.01 cm) and nightscope (model 260, ITT G3 Night Mariner Binoculars, www.ittnv.com) that magnified light ranging from 400 nm to 0.01 cm to 50,000 times brighter than ambient. Fish cannot see in the infrared spectrum (Ali 1961) and thus are not disturbed when observed with infrared radiation (Fraser et al. 1993).

We connected 2 custom-made dim-light sensors (Skye Instruments Ltd., Wales, U.K., www.skyeinstruments.com), 1 that measured total illuminance and 1 that measured total irradiance, to a data logger (LI-COR 1000, www.licor.com) and positioned them 5 cm above the water's surface to record the light intensity at which fish first responded to hand waving or food. The irradiance sensor had a flat spectral response across the entire range of detectable

wavelengths (400–720 nm) and a sensitivity of $2.0 \times 10^{-5} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$ to $1.6 \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, whereas the illuminance sensor had a sensitivity of 0.0001–80 lux with a bell-shaped spectral response curve across the range of wavelengths in this study (400–720 nm). This range from blue (400 nm) to deep red (720 nm) was appropriate for this study because trout cannot see infrared radiation (approximately >720 nm) and because there is very little light <400 nm (UV) in the natural environment during twilight or at night after the sun has dropped below the horizon (e.g., Williamson 1995, Rader personal observation). This is also the range of light most available at twilight and at night and is thus the most important range in dim-light studies.

We decided to report part of our results in lux because (1) the lux sensor allowed us to compare our results with previous behavioral studies on the visual response of salmonids (e.g., Robinson and Tash 1979, Mazur and Beauchamp 2003), (2) data from both sensors were highly correlated and provided similar results over the range of wavelengths used in this study (400–720 nm), and (3) illuminance allowed us to compare our lab results with our field measurements, which were recorded with lux sensors during the daylight hours. The critical information (the maximum scotopic sensitivity of these species) will be reported as both irradiance and illuminance.

Each trial began in complete darkness and light levels were gradually increased at a rate of $22.0 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{min}^{-1}$ ($0.005 \text{ lux} \cdot \text{min}^{-1}$). We collected preliminary data during 2 sunrises under clear skies in June 1997 to duplicate in the laboratory the natural rate at which light increases. We used our custom-made dim-light sensors to record light intensity every second for 90 minutes before the sun crested the horizon. Values varied between $6.1 \times 10^{-5} \mu\text{mol} \cdot \text{m}^{-2}\text{min}^{-1}$ ($0.003 \text{ lux} \cdot \text{min}^{-1}$), during the early transition from dark to light, to $2.5 \times 10^{-2} \mu\text{mol} \cdot \text{m}^{-2}\text{min}^{-1}$ ($1.2 \text{ lux} \cdot \text{min}^{-1}$), as the sky grew progressively lighter. We used the average rate of increase during the 1st and darkest half of the transition from dark to light, which is also consistent with the natural rate of change measured at early twilight (dusk and dawn) by Fraser and Metcalfe (1997). To duplicate the natural rate of irradiance increase in the laboratory, it was necessary to wrap the light source (15-watt incandescent tungsten bulb) in

3 pieces of neutral shade cloth. The light intensity of the bulb was controlled by a computer-operated rheostat (Solar 1000, Niche Engineering) that gradually increased the voltage and the irradiance at the specified rate. A similar method of gradually increasing light intensity to simulate a natural sunrise has been previously designed for a variety of laboratory uses (Allen 1980).

We used an SR9000 spectroradiometer (Macam Photometrics, www.macam.com) to compare the spectral composition of our incandescent bulb to the natural spectrum at dawn, dusk, and night at 3 levels of intensity: $2.0 \times 10^{-3} \text{ w} \cdot \text{m}^{-2}\text{nm}^{-1}$ ($\sim 0.5 \text{ lux}$), $3.8 \times 10^{-4} \text{ w} \cdot \text{m}^{-2}\text{nm}^{-1}$ ($\sim 0.1 \text{ lux}$), and $1.89 \times 10^{-4} \text{ w} \cdot \text{m}^{-2}\text{nm}^{-1}$ ($\sim 0.05 \text{ lux}$). A decrease in voltage at bright intensities can cause the spectrum of incandescent bulbs to change, progressively producing smaller proportions of blue light. However, decreasing the voltage from dim light to lower intensities of dim light did not change the spectrum, which was skewed toward a greater proportion of red light (Fig. 2).

We decided to use an incandescent bulb rather than a full-spectrum fluorescent light because we could gradually increase the intensity of the incandescent bulb using the computer-operated rheostat to simulate a natural dawn. The intensity of full-spectrum lights is often controlled with a wedge-shaped neutral density optic filter (e.g., Sontag 1971). However, this requires immobilizing an animal and restraining it to a specific area, thus precluding behavioral analyses. Also, a preliminary exercise showed that adding or removing single layers of fine shade cloth from a full-spectrum light provided a step-wise increase in light intensity that was too coarse for our objectives.

Each species was tested separately during the same time of year because previous research has shown that trout scotopic visual pigments increase during the winter and that this increase is associated with an increase in nocturnal behavior (e.g., Allen et al. 1982, Rimmer and Paim 1989). Cutthroat trout and brook trout trials were completed during August and September 1997, and rainbow and brown trout trials were completed in August and September 1999. Fish were transported from the hatcheries to our laboratory within 24 hours in a 3000-L aerated tank. Thirty individuals of each species were tested over a 10-day period (3 fish per day). All fish were tested from 09:00 to 16:00

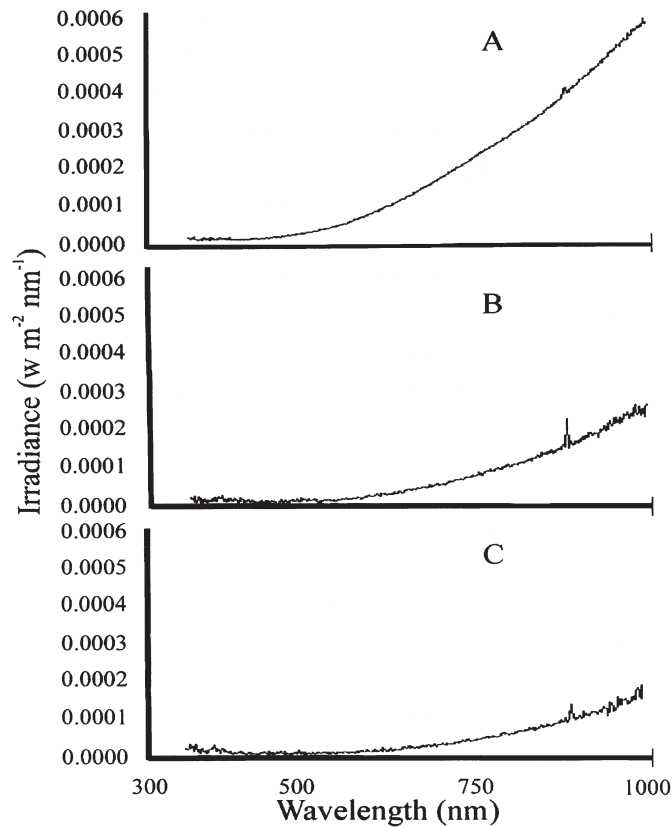


Fig. 2. Spectral composition of our laboratory light source (incandescent bulb) at 3 levels of intensity: $2.0 \times 10^{-3} \text{ w} \cdot \text{m}^{-2}\text{nm}^{-1}$, $\sim 0.5 \text{ lux}$ (A); $3.8 \times 10^{-4} \text{ w} \cdot \text{m}^{-2}\text{nm}^{-1}$, $\sim 0.1 \text{ lux}$ (B); and $1.89 \times 10^{-4} \text{ w} \cdot \text{m}^{-2}\text{nm}^{-1}$, $\sim 0.05 \text{ lux}$ (C).

during each trial. Before a trial, each fish was starved for 72 hours and dark-adapted for 8 hours. All fish were exposed to a diel cycle of 12 hours of night and 12 hours of day under full-spectrum fluorescent lights for at least 7 days prior to being dark-adapted. Under complete darkness, we removed a single fish from the holding section, placed it in the observation area, and provided a 40-minute acclimation period (Fig. 1). Trials did not begin until each fish was calm and facing upstream. Examining each fish alone eliminated the effects of intraspecific interactions on their behavior, which could cause some fish to fail to respond to a visual signal.

We also needed to determine if these fish could respond to food pellets by olfaction without a visual cue. Therefore, a trial began by adding 2 food pellets every 30 seconds upstream from the experimental section for 3 minutes under complete darkness to ensure that fish could not locate pellets by olfaction. Also, after 3

minutes and 6 feeding possibilities, the smell of food should have initiated a feeding response as the light levels increased. The fish had 15 seconds to locate the food during each 30-second interval before the pellet exited the experimental section. Every 30 seconds a hand was waved 4 times, without touching the water, directly above the fish. At the 4th minute, irradiance began to increase ($22.0 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{min}^{-1}$, $0.005 \text{ lux} \cdot \text{min}^{-1}$), and food additions and waving continued at 30-second intervals for 20 minutes. After 20 minutes irradiance reached $0.04 \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$ (0.1 lux), which is the approximate irradiance of a clear night with a full moon (Contor and Griffith 1995). We used a nightscope to record the light level when a fish first responded to either hand waving or when it first oriented toward and responded to food. In order to prevent disturbing the fish, waving stopped after the 1st response; however, food was added every 30 seconds throughout the 20-minute trial. If a fish failed to respond, it was

replaced with another fish and the trial was rerun.

Field Light Measurements

We measured light intensity in a shaded reach and in an open reach in 3 Rocky Mountain streams during the day, dusk, and night to estimate the amount of time different species can forage in different reach types. West St. Louis Creek is a 2nd-order tributary of St. Louis Creek, which is a 3rd-order mountain stream draining the USDA Fraser Experimental Forest in Grand County, Colorado (latitude 39°53'N, longitude 105°54'W). Nash Fork Creek is a 3rd-order stream draining the eastern slope of the Medicine Bow Mountains in Albany County, 65 km west of Laramie, Wyoming (latitude 41°21'N, longitude 106°13'W). Riparian vegetation along shaded stream reaches consisted of lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.), and fir (*Abies lasiocarpa*), but vegetation along reaches with an open canopy was dominated by low-growing willows (*Salix* spp.) and grasses. All reaches were located at similar elevations (~2800 m asl), and the open reaches were downstream from and adjacent to the steeper, shaded reaches.

We used our custom-made low light sensors (lux and $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$) to measure dim levels of light (last part of dusk and night) and a standard bright-light lux sensor (LI-210, LICOR Biosciences, www.licor.com) to measure illumination during the day and the 1st part of dusk. Although we were interested in dim-light differences in light intensity, the bright-light lux sensors (400–720 nm) were included to show relative differences between shaded and open reaches. Thus, dim and bright readings were expressed in lux because we only had lux sensors for bright light.

We evaluated light intensity with respect to (1) time of day, (2) cloudiness, (3) the lunar cycle, and (4) shading by riparian vegetation. Light intensity was measured during day (11:00–18:00), dusk (19:30–21:30), and night (23:00–02:00) once a week for 7 weeks (July and August 1999) at 3 stations in the shaded reaches and 3 in the open reaches in each stream. The mean, minimum, and maximum light intensity was recorded at each station every 5 seconds for six 15-second intervals evenly spaced over a 20-minute period during the times indicated above. The weather (e.g., cloudy versus clear) was noted during each

period at each station, and nighttime intensity was measured during each phase of the lunar cycle (no moon, part moon, or full moon). Sensors were leveled in the same position on the bank 0.5 m from the surface of the water at each station on each sampling date. These cylindrical sensors primarily detect light from directly overhead, which was appropriate because light arriving directly from its source (moon and stars) constitutes the majority of the total intensity at night (Endler 1993).

The averages of flow, width, percent shade, gradient, and maximum pool depth were calculated for each reach in each stream. Average percent shading was digitally calculated using photographs taken from the same height (1.83 m) in the middle of the stream with a wide-angle lens aimed directly overhead into the canopy at 6 locations in each reach.

Literature Review on the Diel Activity of Trout

We reviewed the literature describing the diel activity of trout because differences in the time at which fish are most active should reflect differences in scotopic visual sensitivity. For each study we recorded the primary period(s) of activity and indicated the strength of evidence supporting the conclusions. Results from casual or haphazard observational data were less conclusive than systematic 24-hour observations, day versus night gut analyses, tracking of 24-hour activity patterns using radiotelemetry, or laboratory experimental data.

Statistical Analysis

A 1-way ANOVA and Tukey's multiple comparison tests (SAS Institute, Inc. 1997) with 4 levels (salmonid species) were used to compare the average light intensity of the 1st response of individual fish to either hand waving or food in our laboratory experiment. Tests for normality and homoscedasticity indicated that the data were skewed for 2 of the 4 species. Therefore, analyses were run after a \log_e transformation.

RESULTS

Laboratory Tests of Scotopic Visual Sensitivity

No fish responded to food (or waving) during the 3-minute dark phase at the beginning of each trial. This indicated that subsequent

TABLE 1. Physical attributes of shaded and open reaches in 3 Rocky Mountain streams.

	St. Louis Creek		West St. Louis Creek		Nash Fork Creek	
	Shaded	Open	Shaded	Open	Shaded	Open
Mean flow ($\text{m}^3 \cdot \text{s}^{-1}$)	0.093	0.098	0.039	0.055	0.072	0.068
Mean bankfull width (cm)	687	1740	273	320	635	830
Mean percent shade	41	0	70	0	64	0
Mean gradient (%)	2.1	1.5	3.1	1.7	3.6	0.6
Mean maximum pool depth (cm)	51	59	29	45	34	63

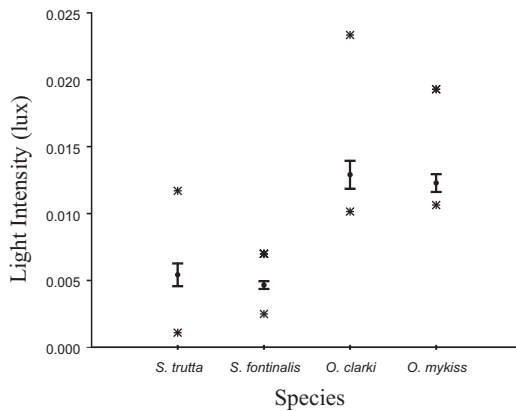


Fig. 3. Differences in the mean maximum scotopic sensitivity of 4 species of trout. Bars represent 1 standard error about the mean, and stars are the extreme high and low responses of individual trout within each species.

responses as light intensity increased were visual and not olfactory. Twelve fish (2 cutthroat trout, 4 brown trout, and 6 brook trout) out of 120 failed to respond during this experiment, and each was replaced by another fish. As expected, all 4 species were startled and reacted first to waving rather than food. Thirty-eight percent of the fish did not feed at any point during a trial, although 21% rose to a floating pellet without actually feeding. Because of this variation we did not analyze their response to food as a reliable indication of the maximum dim-light intensities at which these species could first detect food floating at the surface. However, the dim-light threshold showing a startle response was consistent across each species. Thus, the startle response was the basis for our dim-light comparisons in this study.

The irradiance at which fish first reacted to waving was significantly lower ($F_{3,116} = 64$, $P < 0.0001$) for brown trout and brook trout than for cutthroat trout and rainbow trout (Fig. 3). The average light intensity of the 1st response of brown trout ($1.1 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$,

~ 0.0054 lux) and brook trout ($9.4 \times 10^{-5} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.0047 lux) was approximately half that of cutthroat trout ($2.5 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.013 lux) and rainbow trout ($2.2 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.012 lux). The brightest intensity at which brook trout first responded ($1.5 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.0068 lux) was less than the dimmest intensity at which cutthroat trout ($1.9 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.01 lux) and rainbow trout ($1.9 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.01 lux) first responded (Fig. 3). Also, brown trout's first response was at a dimmer light level ($2.36 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.00012 lux) than for any of the other fishes' first responses, whereas cutthroat trout's first response was at the brightest ($4.2 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.02 lux).

The spectral composition of our lab light was shifted toward longer wavelengths: orange and especially red (Fig. 2). Blue and green wavelengths were poorly represented. Thus, differences in dim-light sensitivity between the 4 species in this study are based primarily on their response to light with longer wavelengths.

Field Light Measurements

As expected, shading and light intensity varied by stream and time of day (Fig. 4). St. Louis Creek was the largest stream and had the least shade, whereas West St. Louis Creek and Nash Fork Creek were smaller with a dense canopy over the shaded reaches (Table 1). Pool depth is important because most trout in these streams (brook trout) reside in pools and because light can rapidly attenuate with an increase in water depth (e.g., Wetzel 2001). However, there were no pools deeper than 75 cm in any of the reaches, and most were <60 cm deep. Thus, our light sensors, which were positioned just above the surface of the water, provided a good estimate of the relative differences in the light available to fish in the different reaches.

Light intensity varied 9 orders of magnitude between extreme conditions: a clear sunny day

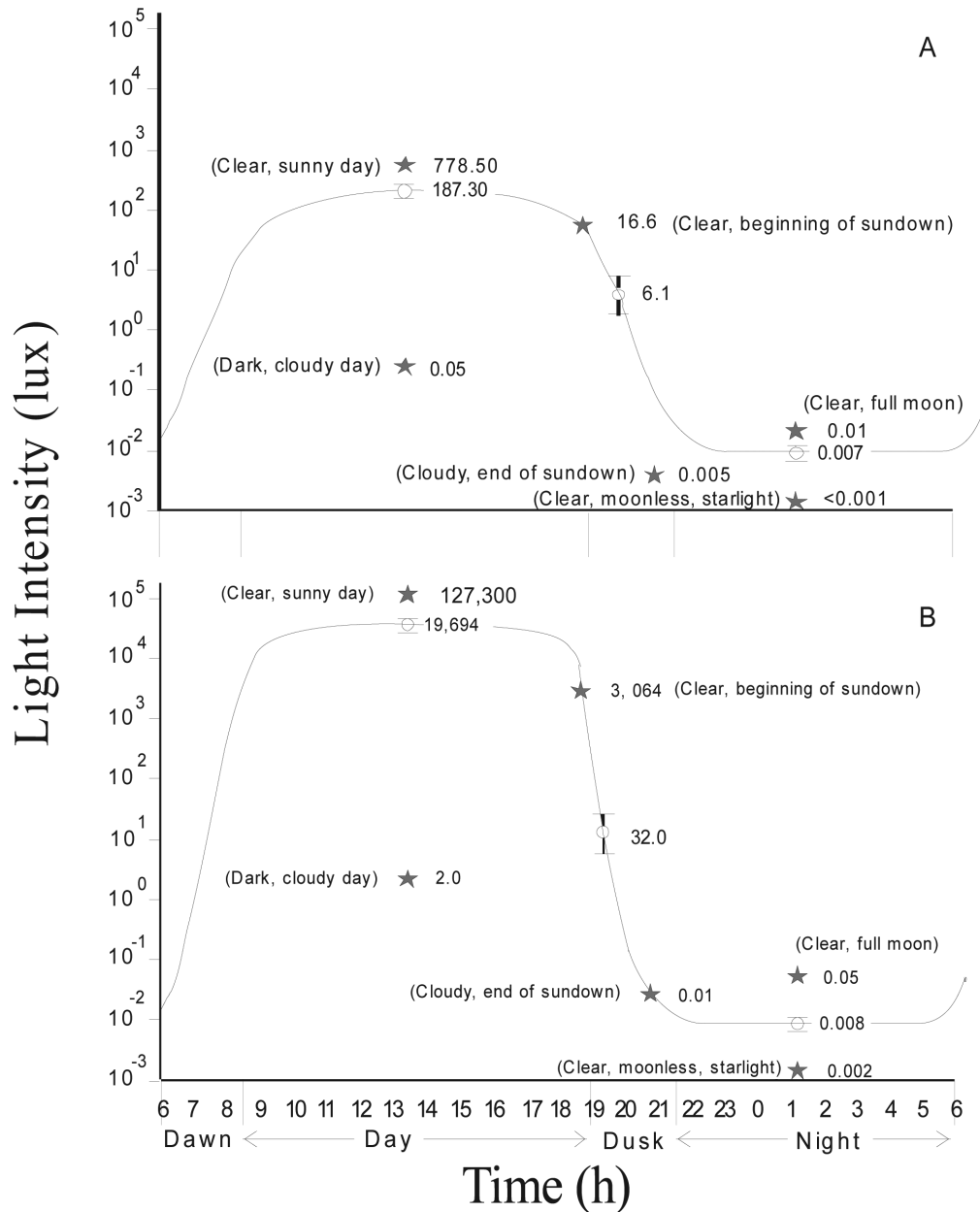


Fig. 4. Mean differences in light intensity during the day, dusk, and night between reaches with a closed (A) and open (B) canopy in 3 mountain streams. Bars represent 1 standard error about the mean, and stars are the extreme high and low values for each period. The line is a generalized curve for a 24-hour period.

in the open versus a clear moonless night in the shade. However, the level of starlight on a clear moonless night in the shade was below the detection limit of our dim-light sensors. Average irradiance at dusk and the brightest nighttime conditions (clear, full moon) were both 5 times greater in the open than in the shade (Fig. 4).

As expected, cloudiness greatly reduced irradiance in both open and shaded reaches. Contrary to expectations, however, average light intensities at night were similar in the open and shaded reaches ($1.61 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.008 lux and $1.47 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, ~ 0.007 lux, respectively) because, by chance,

we made more nighttime measurements under cloudy conditions in the open than in the shade. Our results are consistent with the summary provided by Contor and Griffith (1995) in which the intensity of starlight and moonlight in the open can vary between 0.0005 lux and 0.001 lux and between 0.05 lux and 1.0 lux, respectively.

Trout Diel Activity

We found 28 studies that reported the diel activity of brown trout, 23 for cutthroat trout and rainbow trout, and 10 for brook trout (Table 2). Brown trout and brook trout had the most frequent occurrence of activity under dim-light conditions. Seventy-five percent of the studies reported twilight and/or nocturnal activity for brown trout, 70% for brook trout, and 39% for cutthroat trout + rainbow trout. Also, brown trout had the highest percentage of reported nighttime activity (64%) followed by brook trout (30%) and cutthroat trout + rainbow trout (13%).

DISCUSSION

We have shown that the maximum scotopic threshold of brown trout and brook trout was more sensitive than that of cutthroat trout and rainbow trout. Confounding factors did not compromise these results because all of these fish were (1) raised in hatcheries under similar light conditions, (2) similar in size, and (3) tested during the same season at the same temperatures. Also, these results were generally supported by our literature review in that a greater percentage of studies reported dim-light activity for brown trout and brook trout than for cutthroat trout and rainbow trout, which were primarily diurnal. Brook trout and brown trout had average scotopic thresholds near $1.0 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$ (~ 0.005 lux), whereas Snake River cutthroat trout and rainbow trout had average thresholds near $2.0 \times 10^{-4} \mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$ (~ 0.01 lux). These thresholds underestimated the scotopic sensitivity of these fish because intensity was measured near the surface of the water and not in the water where the fish were swimming. However, actual thresholds should be only slightly lower because the water in our experimental stream was shallow, clear, and produced a minimum amount of attenuation.

The light source in our laboratory experiment was skewed toward longer wavelengths of

orange and especially red at all of the dim-light intensities used in this study. Thus, in order to place these findings in their correct environmental context, we need to discuss the availability of light with longer wavelengths under dim-light conditions in the natural environment. That is, the application of our lab results to a natural setting depends on whether the predominant wavelengths in the field under dim light (twilight, moonlight, starlight) are often skewed toward longer wavelengths, especially red.

Although longer wavelengths attenuate rapidly with increasing water depth (Wetzel 2001), red light should be plentiful in most mountain streams because fish habitats (pools and runs) are often <50 cm deep. In distilled water, 50% of red light remains at approximately 1 m in depth (Wetzel and Likens 1991). Thus, 75% or more of the ambient red light should remain after attenuation in most pool habitats in these streams.

During twilight as the sun approaches and initially drops below the horizon the spectrum is skewed towards red and blue light with a 33% reduction in green, yellow, and orange light (Johnson et al. 1966, McFarland and Munz 1976). However, as the sun continues to drop below the horizon, red light decreases and the spectrum becomes increasingly blue because blue light is the dominant color of skylight. Thus, early twilight is dominated by red light directly from the sun and blue skylight, and late twilight is dominated by blue skylight unless there are clouds overhead. Reddish light from the setting sun will reflect off of the undersurface of clouds onto the surface of a stream, prolonging the period when wavelengths are skewed toward red (Endler 1993). Clouds produce a flat, white spectrum on the surface of a stream only if the sun shines through them from above (McFarland and Munz 1976, Endler 1993).

Although the moon reflects sunlight and has a fairly flat spectrum, it is enriched in red wavelengths relative to full sunlight (McFarland and Munz 1976). Also, when the moon is low on the horizon, its light must pass through more of the Earth's atmosphere, causing an additional shift towards the red end of the spectrum. The spectrum of starlight is also skewed toward red wavelengths (Munz and McFarland 1973). Additionally, McFarland and Munz (1976) measured the daylight spectrum of Carrabelle River

TABLE 2. Literature review of the diel activity of several salmonid species. Strength of evidence is recorded in the last column (1 = haphazard observational data, 3 = systematic observational data / diel gut analysis, 5 = telemetry/experimental data).

Species	Diel periodicity	Citation	Evidence
<i>Oncorhynchus apache</i>	Diurnal	Robinson and Tash 1979	5
<i>Oncorhynchus clarki</i>	Diurnal	Griffith 1974	1
<i>O. clarki</i>	Diurnal	Edmundson et al. 1968	1
<i>O. clarki pleuriticus</i>	Diurnal	Young et al. 1997a	5
<i>O. clarki clarki</i>	Nocturnal	Schutz and Northcote 1972	5
<i>Oncorhynchus mykiss</i>	Crepuscular	Newman 1956	1
<i>O. mykiss</i>	Crepuscular	Elliott 1970	3
<i>O. mykiss</i>	Crepuscular	Elliott 1973	3
<i>O. mykiss</i>	Crepuscular	Douglas 1982	5
<i>O. mykiss</i>	Crepuscular	Jenkins et al. 1970	5
<i>O. mykiss</i>	Crepuscular	Landless 1976	5
<i>O. mykiss</i>	Diurnal	Edmundson et al. 1968	1
<i>O. mykiss</i>	Diurnal	Eggers 1977	1
<i>O. mykiss</i>	Diurnal	Hoar 1953	1
<i>O. mykiss</i>	Diurnal	Angradi and Griffith 1990	3
<i>O. mykiss</i>	Diurnal	Tippets and Moyle 1978	3
<i>O. mykiss</i>	Diurnal	Campbell and Neuner 1985	3
<i>O. mykiss</i>	Diurnal	Young et al. 1997a	5
<i>O. mykiss</i>	Diurnal	Bisson 1978	5
<i>O. mykiss</i>	Diurnal	Boujard and Leatherland 1992	5
<i>O. mykiss</i>	Fed at light levels >0.035 lux	Tanaka 1970	5
<i>O. mykiss</i>	Nocturnal	Elliott 1973	3
<i>O. mykiss</i>	Nocturnal	Jenkins 1969	5
<i>Salvelinus alpinus</i>	Nocturnal	Dervo et al. 1991	3
<i>Salvelinus fontinalis</i>	Crepuscular	Newman 1956	1
<i>S. fontinalis</i>	Crepuscular	Boisclair 1992	3
<i>S. fontinalis</i>	Crepuscular	Hoar 1942	5
<i>S. fontinalis</i>	Crepuscular	Gibson and Keenleyside 1966	5
<i>S. fontinalis</i>	Diurnal	Griffith 1974	1
<i>S. fontinalis</i>	Diurnal/crepuscular	Allan 1981	3
<i>S. fontinalis</i>	Continuously active	Rader unpublished data	3
<i>Salvelinus malma</i>	Diurnal	Edmundson et al. 1968	1
<i>S. malma</i>	Nocturnal	Schutz and Northcote 1972	5
<i>Salmo salar</i>	Crepuscular	Hoar 1942	5
<i>S. salar</i>	Diurnal	Fraser et al. 1993	5
<i>S. salar</i>	Diurnal	Gibson and Keenleyside 1966	5
<i>Salmo trutta</i>	Continuously active	Tuša 1968	1
<i>S. trutta</i>	Continuously active	McIntosh and Townsend 1995	5
<i>S. trutta</i>	Continuously active	Oswald 1978	5
<i>S. trutta</i>	Crepuscular	Eriksson 1978	1
<i>S. trutta</i>	Crepuscular	McCormack et al. 1989	5
<i>S. trutta</i>	Diurnal	Bachman 1984	3
<i>S. trutta</i>	Diurnal	Borja et. al 1990	5
<i>S. trutta</i>	Diurnal/crepuscular	Swift 1962	3
<i>S. trutta</i>	Diurnal/crepuscular	Swift 1964	3
<i>S. trutta</i>	Diurnal/crepuscular	Elliott 1970	3
<i>S. trutta</i>	Nocturnal	Brynildson et al. 1963	1
<i>S. trutta</i>	Nocturnal	Butler and Hawthorne 1968	1
<i>S. trutta</i>	Nocturnal	Jenkins 1969	1
<i>S. trutta</i>	Nocturnal	Lewis 1969	1
<i>S. trutta</i>	Nocturnal	Dervo et al. 1991	3
<i>S. trutta</i>	Nocturnal	Shuler et al. 1994	3
<i>S. trutta</i>	Nocturnal	Chaston 1968	3
<i>S. trutta</i>	Nocturnal	Chaston 1969	3
<i>S. trutta</i>	Nocturnal	Elliott 1967	3
<i>S. trutta</i>	Nocturnal	Elliott 1973	3
<i>S. trutta</i>	Nocturnal	Young et al. 1997b	5
<i>S. trutta</i>	Nocturnal	Clapp et al. 1990	5
<i>S. trutta</i>	Nocturnal	Schutz and Northcote 1972	5
<i>S. trutta</i>	Nocturnal	Robinson and Tash 1979	5

in Florida and found that there was no light with a wavelength shorter than 600 nm during the day in this blackwater river. This redshift is caused by plant leachates (e.g., tannins) that are often abundant in the groundwater associated with stream ecosystems. Thus, the prevalence of a red-shifted spectrum in streams may also depend on the concentration of plant leachates in the groundwater and the amount of groundwater inflow. Overall, this information suggests that dim-light conditions in streams are often skewed toward red wavelengths. Thus, our lab results do represent differences in sensitivity between these species under frequent natural conditions. However, we cannot eliminate the possibility that the variation in scotopic sensitivity among these species could change if similar lab studies were conducted with predominantly blue light.

Trout are visual predators, and light is one of the most important factors determining prey detection (e.g., Wilzbach et al. 1986, Forrester et al. 1994). Over a 24-hour period, trout with sensitive scotopic vision will be able to forage longer than trout with poor scotopic sensitivity. Species with better dim-light vision could have higher 24-hour rates of consumption. Because food may limit trout populations (Chapman 1966, Richardson 1993), higher rates of consumption could produce faster growth and greater fecundity. The light intensity necessary to invoke a startle response was 2 times lower in brown trout and brook trout than in Snake River cutthroat trout and rainbow trout. Our literature review showed that cutthroat trout and rainbow trout were primarily active during the day, which suggests that cutthroat trout as a group may have poorer scotopic vision than brook trout or brown trout. If so, these 2 species may be able to forage longer over a 24-hour period and during the course of a growing season than most, if not all, cutthroat lineages. This may partially explain how brook trout and brown trout exclude most cutthroat trout populations in many mountain streams of the western United States (e.g., Behnke 1992).

Adult brook trout and brown trout spawn in the fall, and young fish hatch early in the spring, giving them a size advantage over the fry of cutthroat trout, which spawn during the spring and hatch later in the summer (e.g., Behnke 1992). For a variety of reasons, large body size is an important factor in determining differences in the fitness of stream salmonids (e.g., Fausch

1984, McIntosh et al. 1994). The ability of brook trout and brown trout to feed longer over a 24-hour period may allow them to sustain or even increase this initial size advantage, which allows them to maintain a greater overall fitness than cutthroat trout. This fitness advantage may be the best explanation for how introduced trout (brook trout and brown trout) can cause the local extirpation of native cutthroat trout.

Native cutthroat trout may be better able to compete with introduced trout in open reaches because brighter light intensities may reduce the foraging advantage of brook trout and brown trout. Light intensities from mid-twilight to a moonless, starlit night were about 5 times greater in open reaches than in shaded reaches of this study. In open reaches, cutthroat trout may be able to forage longer with greater efficiency during the growing season than in darker, shaded reaches. This suggestion is consistent with the observation that coastal cutthroat trout foraging efficiency and abundance were greater in logged headwater streams of the Oregon Cascades than in reaches shaded by stands of mature riparian vegetation (Hawkins et al. 1983, Wilzbach and Cummins 1986). If so, native cutthroat trout restoration efforts may have greater success in open versus shaded stream reaches in the Rocky Mountains and elsewhere.

Future research should extend the application of our results on the scotopic sensitivity of Snake River cutthroat trout to all cutthroat lineages. It should examine the underlying physiological mechanisms explaining differences in scotopic sensitivity among these species. Also, future research should explore the relationship between the maximum scotopic threshold of cutthroat trout, their foraging efficiency, and their overall fitness versus that of introduced trout in open and shaded reaches.

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