Direct effects of solar ultraviolet radiation on fighting and foraging in juvenile coho salmon (*Oncorhynchus kisutch*)

by

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B.A., University of California at Berkeley, 1985
Ph.D., University at Buffalo, 1997

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ABSTRACT

In young coho salmon (*Oncorhynchus kisutch*), UVR is known to elicit exposure avoidance behavior and suppress aggressiveness. The latter observation has been attributed to the indirect effect of fish seeking shade from solar UVR under rocks consequently losing sight of prospective rivals. The present study quantified the direct impacts of UVR on agonistic (Strikes, Chases, Approaches) and feeding behaviors in juvenile coho salmon by furnishing outdoor aquaria with structural elements (i.e., inverted funnels) that provided habitat complexity without generating shade during midday experimental trials. Frequencies and durations of behaviors were compared between conditions that excluded or included natural solar UVR. Results indicated that hostile pursuits (Chases) persisted significantly longer under UVR illumination. Likewise, the frequencies of more belligerent interactions (Strikes, Chases) tended to increase under UVR, while milder territorial assertions (Approaches) and foraging (Feeding Efforts) tended to decline. However, none of the latter four outcomes tested as significant.

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INTRODUCTION

In the last thirty years, a compelling empirical literature has brought to light the diverse influences of ultraviolet radiation (UVR) in the lives of fish. The preponderance of this knowledge has regarded the deleterious aspects of UVR exposure, to which the earliest life stages appear most vulnerable (Battini et al 2000; Charron et al 2000). Catastrophic mortality rates (e.g., Dey and Damkaer 1990; Beland et al 1999; Vetter et al 1999) and severe anatomical and behavioral abnormalities (e.g., Hunter et al 1979; Dethlefsen et al 2001; Hakkinen and Oikari 2004) have been reported in the UVR-irradiated eggs and larvae of many fish species. By comparison, significant but typically sublethal outcomes predominate later in development, such as ocular damage (Cullen and Monteith-McMaster 1993; Cullen et al 1994), skin lesions (Noceda et al 1997; Ewing et al 1999), immunological changes (Salo et al 1998; Jokinen et al 2000), and suppressed rates of both heart function (Awaiwanont and Kawamura 1994) and metabolism (Winckler and Fidhiany 1996). Molecular evidence of UVR-induced oxidative stress (Charron et al 2000) and DNA injury (Vetter et al 1999; Meador et al 2000; Mitchell et al 2004) has also been detected in tissues across the lifespan.

Countermeasures mounted by fish against such exposure hazards include the enhanced synthesis of melanin (Hakkinen et al 2002), a pigment absorbing notably in the UVB (280-320 nm; Lowe and Goodman-Lowe 1996), and the selective retention in tissues and mucous of diet-acquired, mycosporine-like amino acids (Dunlap et al 1989), photo-protective compounds shielding towards the UVA (320-400 nm; Mason et al 1998). At the molecular level, the biochemically harmful products of irradiation are scavenged by antioxidants such as superoxide dismutase (Fitzgerald 1992; Hakkinen et al 2004), while multiple enzyme systems promote the repair of damaged DNA (Olson and Mitchell 2006).

Some species of fish have further demonstrated behavioral defenses against UVR protective both of self and of progeny. Juveniles of coho salmon (*Oncorhynchus kisutch*; Kelly and Bothwell 2002), Pacific herring (*Clupea pallasi*; Speekmann et al 2000), vendace (*Coregonus albula*), and whitefish (*Coregonus lavaretus*; Ylonen et al 2004) will actively retreat from high UVR intensities to shaded positions or deeper water. In turn, mature, spawning yellow perch (*Perca flavescens*; Williamson et al 1997; Huff et al 2004) and bluegill sunfish ((*Lepomis macrochirus*; Gutierrez-Rodriguez and Williamson 1999) have been noted to select deeper egg deposition sites in lakes with greater UVR penetration.

Such apparent UVR-discriminative and -evasive abilities are supported by microscopic and electrophysiological evidence of primarily UVA retinal photosensitivity in a number of fishes (Novales Flamarique 2000; Allison et al 2003; Hawryshyn et al 2003), including coho salmon (Beaudet et al 1997). UVR has also been found in some species to serve a valuable role in prey detection (Browman et al 1994), social signaling (Losey 2003; Siebeck 2004), mate selection (Kodric-Brown and Johnson 2002; Boulcott and Braithwaite 2005; Rick et al 2006), shoal choice (Modarressie et al 2005), and possibly migratory geo-orientation (Hawryshyn et al 1990).

With respect to intraspecific aggressiveness among juvenile salmonids in their natal streams, dispersive social interactions are evident as space and dominance disputes within a week of emergence (Puckett and Dill 1984; Armstrong et al 1999). Framed by notably fluid boundaries, individual territories typically broaden progressing upstream – to widths roughly sevenfold the lengths of their residents (Grant and Kramer 1990).

A number of ecological, situational, and individual variables are known to influence territorial activity in young salmon. Among the ecological factors, lotic habitats tend to foster higher levels of antagonism than lentic environments. This trend has been identified both between allopatric populations (Swain and Holtby 1989; Wessel et al 2006) and by local current conditions (Hartman 1965; Dill 1978; Zhivoglyadov 2003). Duration of stream habitation has also shown a positive correlation with aggressiveness (Taylor and Larkin 1986). Thus, non-migratory, freshwater forms have generally been assessed most belligerent (Hutchison and Iwata 1997). In comparison, anadromous coho salmon, typified by single-year stream occupancies (Kahler et al 2001), have been judged moderately aggressive (Hutchison and Iwata 1997), offering a favorably intermediate species for study.

Both the above ecological trends are consistent with energetic models (e.g., Dill 1978; Ryer and Olla 1996) predicting territorial aggression to be advantageous and selected for when its twofold or greater metabolic costs (Puckett and Dill 1984) are exceeded by its competitive benefits. This dynamic may be seen to prevail where food resources are limited, localized, and defensible

(Ryer and Olla 1995; Vollestad and Quinn 2003). Such conditions well describe the socioecology of drift-feeding young salmon, for which upstream positions near rapid flow provide best access to forage (Puckett and Dill 1984; Hutchison and Iwata 1997). Indeed, when food monopolization was prevented experimentally among coho salmon, aggressiveness tended to hinder physical development (Vollestad and Quinn 2003).

Circumstances of diminishing rewards for territorial defense, as encountered under intensifying intruder pressure or enhanced overall food abundance (Imre et al 2002), have been found to reduce territory dimensions (Dill et al 1981; McNicol and Noakes 1981; Vollestad and Quinn 2003). A non-metabolic cost also lies in the conspicuousness of hostile interactions to predators, such that individuals will generally subdue their aggressiveness in the presence of large predatory fish (Ryer and Olla 1996; Reinhardt 1999) and waterfowl (Martel and Dill 1993; Martel 1996). Regular reports of hatchery stocks exceeding wild fish in belligerence (e.g., Swain and Riddell 1990; Rhodes and Quinn 1998; Wessel et al 2006) have further implicated the artificial convergence of exaggerated densities, scheduled feedings, and negligible risks of predation in reinforcing otherwise overassertive and potentially hazardous, competitive responses (Swain and Riddell 1990; Young 2003; Wessel et al 2006). Such behavioral tendencies may be genetically incorporated over as few as four generations (Berejikian et al 1996).

Finally, individual characteristics observed to promote belligerence include superior condition and size (Holtby et al 1993; Young 2003), hunger (Dill

1978; Dill et al 1981), past successes in dominance challenges (Rhodes and Quinn 1998; Gilmour et al 2005), and prior residence at the contested site (Rhodes and Quinn 1998; Cutts et al 1999). Conversely, close genetic relatedness between potential combatants tends to inhibit antagonism (Brown and Brown 1993).

The territorial dynamics of juvenile salmon have been found to effect consequences from the physiological to the ecological. At the individual level, recurrent defeats are known to induce hormonal changes (Larson et al 2004) and declines in physical activity, growth, condition, disease resistance, and survivorship (Ryer and Olla 1995; Gilmour et al 2005). Competitively dominant fish, by contrast, will characteristically monopolize shelter and food resources (Ryer and Olla 1995; Vollestad and Quinn 2003; Gilmour et al 2005), feed more actively (Rhodes and Quinn 1998), and boast faster growth rates (Martel 1996; Cutts et al 1999; Reinhardt 1999; O'Connor et al 2000), even when restricted to the same daily rations as subordinates (Gilmour et al 2005). Such favorable outcomes have been discovered conducive to successful overwintering, early smolting and migration, and eventual oceanic and reproductive success (Dill et al 1981; Martel and Dill 1993; Quinn et al 1994; Cutts et al 1999).

In populations, territoriality shapes such processes and parameters as distribution, dispersal, density, and carrying capacity (Mikheev et al 1994; Bujold et al 2004). Larger individual territories, for example, have proved a reliable indicator of lower achievable densities in modeling research, with the degree of habitat saturation in turn predicting slowed growth and increased rates of emigration and mortality (Grant and Kramer 1990). Further, territorial competitive exclusion has been identified as a primary precursor to downcurrent dispersal in stream experiments (Quinn et al 1994), and been posited centrally responsible for the up to 80% reductions in density recorded between spring fry emergence and autumn (Lahti et al 2001). In summary, considerable research has upheld the influential position of juvenile agonistic interactions in the ecology of stream-rearing salmonids, and implied, by extension, significant consequences in the event of their disruption.

Although the induction of exposure avoidance behaviors by UVR has been documented in several salmonid species (Kelly and Bothwell 2002; Ylonen et al 2004), the prospect of any social impacts remained unappreciated until the recent observation of reduced agonistic activity among UVR-exposed juvenile coho salmon (Holtby and Bothwell 2008). This diminution in aggressiveness was ascribed to a mediating, visual isolation effect as experimental animals sought out refuge from solar UVR under sizable rocks. However, the ecological relevance and applicability of this inhibitory finding were achieved at an unavoidable empirical cost. That is, the inclusion of naturalistic substrates granting animals opportunities for UVR evasion also precluded the isolation of any direct UVR exposure effects.

Towards examining the direct irradiative impacts of UVR, the present investigation deliberately tipped the methodological balance in the opposing direction, surrendering a degree of environmental realism by employing artificial bottom features that entirely denied fish shelter from overhead UVR exposure. Thus, inverted plastic funnels were positioned over sand to furnish habitat complexity in the absence of any shadows cast during the midday. Agonistic and foraging events were then quantified under conditions that excluded or included solar UVR. Preliminary trials with a sand substrate alone produced an unusual aggregation of animals near aquarium walls, and were discontinued. This behavior was consistent with observations that visually uniform conditions in the laboratory tend to subdue antagonism and promote shoaling in young salmonids (Mikheev 1995).

No outcome predictions were inferred from the noted UVR behavioral research by Holtby and Bothwell (2008) on juvenile coho salmon given the disparities in methods and principal mechanisms of interest between that study and the present examination. Although UVR was determined to have imposed behaviorally inhibitory, indirect effects in that experiment, its direct irradiative impacts may yet be stimulatory, but have eluded detection as a consequence of animals' successful evasion of intensive UVR exposure.

Within the broader behavioral literature, sociological research has suggested the aggravation of human aggressive potential by an aversive environmental condition, as would describe UVR exposure for coho salmon on evidence of their avoidance reactions. The observation of rising violent crimes in hot weather, for example, has been much replicated (e.g., Anderson and Anderson 1984; Anderson 1987; Rotton and Cohn 2000). However, other human (Baron 1972; Baron and Bell 1976) and primate studies (Nunn and Deaner 2004) have reported declines in social antagonism with increasing temperature, the latter research addressing territoriality in ringtailed lemurs (*Lemur catta*). In view of such contrasting findings, the present inquiry proceeded without clear expectations as to the directional nature of any prospective UVR impacts. Therefore, two-tailed (i.e., non-directional) inferential tests were applied in statistical analyses.

MATERIALS AND METHODS

Experimental design

The direct and relatively immediate effects of UVR on agonistic and feeding behaviors in juvenile coho salmon were examined in a within-subjects investigation featuring 20 trials under each of two light conditions that either excluded or included direct solar UVR exposure, yielding 40 total trials. The spectral characteristics of summer sunlight were manipulated by passage through wavelength-selective, acrylic light screens placed above research aquaria. The UVR-absent experimental condition was achieved with OP-2 Acrylite screening (CYRO; Rockaway, New Jersey), which transmits UVB, UVA, and visible radiation (400-700 nm) at the approximate rates of 0%, 6%, and 90%, respectively, while OP-4 Acrylite, with corresponding transmittance values of 75%, 90%, and 93%, generated the UVR-present condition (Figure 1).

All behavioral trials were conducted under cloudless, midday conditions, July 3-26, 2006, at the University of Victoria, British Columbia. Experimental aquaria consisted of five, 80 cm x 30 cm, acrylic flume sections with their longer dimensions aligned east-west As flume side panels were constructed of the UVR-transmitting OP-4 acrylic, UVR-shielding OP-2 screens were oversized to impede direct, laterally-impinging UVR at lower solar elevations.

Trials were conducted at water depths of 10 cm, water temperatures of 12.0 ± 1.0°C, and approximate, unidirectional, west-to-east flow rates of 0.5 cm/sec. Linear flow velocities were estimated by measuring flume outflow volumes over ten, one-minute trials with a 10-liter plastic vessel graduated at 0.1-liter increments. Duplicate trials were executed on each of the five flumes, to yield an overall mean output rate of 8.9 ± 0.4 SD liter/min ($n = 10$, Appendix A) or 149 ± 6 ml/sec, converted to an approximated 0.5 cm/sec flow velocity through division by flumes' 300 cm^2 (i.e., 10-cm water depth x 30-cm flume width) cross-sectional areas.

In each aquarium, four inverted, white plastic funnels were arrayed in a zigzag configuration over a 2-cm layer of coarse sand (Figure 2). All funnels tapered linearly from diameters of 13 cm at base to 2 cm at water's surface, and were sufficiently squat in profile to not cast shadows during experimental times of the day.

The absence of shading by funnels in trials was established by visual inspection. Of course, this direct determination could only be achieved for visible wavelength radiation. In possessing shorter wavelengths, UVR would diverge from visible light upon refraction at the air-water interface and cast discrepant, non-visible shadows. The positions of such UVR shadows relative to that produced in the visible spectrum may be assessed using Snell's Law:

$$n_i \cdot \sin \theta_i = n_r \cdot \sin \theta_r$$

where: n_i = refractive index of air

θ_i = angle of incidence

n_r = refractive index of water

θ_r = angle of refraction

The refractive index of air approximates that of a vacuum, or unity, while the refractive index of water, roughly 1.345 for 400-nm wavelength radiation, increases with decreasing wavelength (Lynch and Livingston 2001). Therefore, shorter wavelength UVR would be subject to lesser sine values for θ_r, and experience a sharper refraction towards the vertical than visible light. Visual determinations of the lack of shading by funnels thus actually provide conservative assessments relative to shadows cast in the UVR spectrum.

Each 30-minute behavioral trial was preceded by a 20-minute allowance for light screen acclimation. Thus, given cloudless conditions between 1030 and 1500 hrs, experimentation progressed with an initial 20-minute acclimating period for the first spectral regime, followed immediately by a 30-minute experimental trial. This sequence was then repeated for the same group of fish with the second spectral environment. Fish groups invariably received both light conditions in the same aquarium, and were not handled between trials.

As a precaution against ordinal, stimulus presentation effects, light conditions were administered alternately first and second to successive experimental groups. With a single exception arising from electronic equipment failure, each group of fish was exposed to both spectral regimes on the same day.

All trials were videotaped with tripod-mounted, overhead cameras (Panasonic PV-704, SP speed) approximately 0.85 m above water's surface (Figure 3), positioned so as not to cast shade onto aquaria (Figure 4). Video-recordings were analyzed on a 27-inch (diagonal dimension) color television monitor for rates and durations of three agonistic interactions and one foraging behavior, applying the following classifications. Events marked by bodily attack were designated Strikes, and required the snout of the instigating fish advancing to within a quarter standard-length of the target individual; the targeted fish may or may not be displaced. In contrast, essentially expelling behaviors, identified as Chases, entailed both the aggressive displacement and pursuit of the second fish. Ritual displays and distinct movements towards other individuals in the absence of attack or pursuit were recorded as Approaches. Finally, thrusting motions of the snout into the surface drift, water column, or substrate constituted Feeding Efforts. Very similar classifications have been applied across a number of juvenile salmonid studies (e.g., Martel 1996; Young 2003; Wessel et al 2006). Behaviors were timed to the nearest second, with the exception that incident durations briefer than one-half second were rounded up to one-second; these occasions almost exclusively involved feeding.

Sunlight intensity during trials was measured as photosynthetically active radiation (PAR) in mmol/m^2/sec with a LiCor meter (LI-550B; Lincoln, Nebraska) fitted with a PAR quantum sensor (LI-190SB). Average values, determined from readings at the beginning, midpoint, and end of trials, were applied in analyses (Appendices B, C). Light attenuation by experimental aquarium water was measured with a spectrophotometer (Ultrospec 2000, Pharmacia-Biotech) at 5-nm intervals between 280 and 700 nm, inclusive. Percent reduction in incident light calculated for the 10-cm water depths of aquaria were low (3.8-6.0%) from 280 to 315 nm, very low (1.1-2.9%) from 320 to 335 nm, and negligible (< 0.7%) from 340 to 700 nm (Figure 5).

Experimental animals

One hundred and forty, juvenile coho salmon were captured by pole-seine in June 2006 from the Little Qualicum River on Vancouver Island, British Columbia. Animals were immediately transferred to the University of Victoria Aquatic Facility, to be maintained in an outdoor, continuous-flow, 100-gallon, opaque cylindrical tank with a translucent hood for diffuse natural illumination. Prior to study, fish were acclimated over 21 days to captive conditions and commercial rations (Skretting salmonid feed, Vancouver, British Columbia; twice daily, *ad libitum*). In the maintenance tank, feed was scattered randomly at water's surface. Following animals' transfer to research aquaria, food was introduced at surface near water inflows and permitted to disperse, simulating natural drift forage. Fish were not fed on experimental days.

Animals were distributed by non-selective netting into twenty successive groups (n = 20) of 7 individuals over the 24 days during which trials were conducted. The 7-fish group size both approximated the numbers at which young salmonids have been noted to spontaneously form social subsystems (Elliott 1990), and produced an experimental stocking level of 29.2 fish/m^2, approaching rates reported for comparable, juvenile salmon behavioral studies seeking to create intraspecific, competitive circumstances favoring territorial dynamics (40 fish/m^2; Lahti et al 2001), and to replicate typical population densities encountered near the time of fry emergence (46.3 fish/m^2; Imre et al 2002).

Fish were transferred to experimental aquaria at least 48 hrs before trials. Natural foraging and territorial behaviors were consistently observable within that interim; stable dominance hierarchies in young salmon have been known to develop within 4 hrs (Ryer and Olla 1995). After trials, fish were euthanized with a clove oil solution, wet-weighed by an electronic, digital scale to 0.01 g, and measured for fork-length using a ruler calibrated to 0.1 cm.

Data analyses

For each fish group, videotape analysis rate results represented all events meeting criteria for a given behavior classification, observed across all group members in 30-minute trials. Classifications were mutually exclusive. Each behavioral incident was, therefore, registered only once. Event durations were obtained by summing all recorded durations under a behavior classification for all group members, then dividing that total time by the number of observed events (i.e., the group's behavior rate).

Event frequencies and durations were then converted into their respective behavior change scores by subtracting values ascertained for UVR-absent trials from those for UVR-present trials. Positive change scores thus denoted behavioral increments with UVR exposure, and negative scores decrements. Seven behavior change variables thus resulted, reflecting incident rates and durations for Strikes, Chases, and Approaches, and incident rates alone for Feeding Efforts. Feeding duration change scores were not calculated as these behaviors were consistently less than one second and frequently briefer than one-half second under both light environments, though all recorded as one-second events at minimum in accordance with the stated scoring criteria. Score distributions for the seven final, behavior change variables were submitted to two-tailed t-tests for significant deviations from zero, with scores of zero representing null hypotheses asserting an absence of UVR exposure effects. All analyses were performed in SAS version 9.1 (2003).

RESULTS

Physical measurements of fish taken following trials indicated an overall mean fork-length of 5.5 ± 0.3 SD cm (range of individual fork-lengths: 4.0-6.8 cm, $n = 140$, Appendix D; range of group fork-length means: 5.1-6.1 cm, $n = 20$, Appendix E), and mean wet weight of 2.09 ± 0.33 SD g (range of individual wet weights: 0.84-3.74 g, $n = 140$, Appendix D; range of group wet weight means:

1.61-2.84 g, $n = 20$, Appendix E). No deaths or gross signs of disease were noted in research aquaria.

Mean levels of ambient sunlight were nearly identical between UVR-absent trials (mean: 1682 ± 66 SD mmol/m^2/sec, range: 1528-1752 mmol/m^2/sec, $n = 20$) and UVR-present trials (mean: 1684 ± 66 SD mmol/m^2/sec, range: 1528-1797 mmol/m^2/sec, $n = 20$; t (19) = 0.124, $p = 0.903$, two-tailed, Appendix F). Light readings taken at the beginning, midpoint, and conclusion of all trials – from which trial light levels were derived as averages – are shown in Appendix B for UVR-absent trials and in Appendix C for UVR-present trials.

Observed disparities in solar intensity between UVR-absent and UVR-present trials for each fish group did not exceed 132 mmol/m^2/sec – or an 8.3% difference. Further, the degree of disparity did not differ significantly between the equal number of groups for which light levels were greater under UVR-absent conditions (mean disparity: 4.3 ± 2.8 SD %, range: 0.3-8.3%, $n = 10$) and UVR-present conditions (mean disparity: 4.5 ± 2.6 SD %, range: 0.3-8.3%, $n = 10$; t (18) = 0.237, $p = 0.815$, two-tailed). Likewise, experimental times of the day were very similar for UVR-absent trials (mean: 1301 ± 0108 SD hrs, range: 1125-1455 hrs, $n = 20$) and UVR-present trials (mean: 1303 ± 0106 SD hrs, range: 1050-1455 hrs, $n = 20$; t (19) = 0.124, $p = 0.902$, two-tailed, Appendix F).

All mean change scores, standard deviations, skewness and kurtosis indices values, and two-tailed t-test results obtained for the seven final behavior change variables are shown in Table 1. Corresponding frequency distributions are presented in Figures 6-12. Graphic representations of score means and standard deviations are further displayed for the four rate change variables and three duration change variables in, respectively, Figures 13 and 14. Change scores did not require normalizing transformations; all skewness and kurtosis values fell between –1.00 and +1.25, suggesting a sufficient general conformity to parametric distributional assumptions.

Further, means and standard deviations representing source video-recording analysis results for rates and durations of aggressive and foraging events in UVR-absent and UVR-present trials – from which change scores were calculated – are presented numerically in Table 2, and graphically in Figures 15 and 16. All incident count and durational data tabulated from this study's 20 UVR-absent and 20 UVR-present trials are listed for, respectively, Strikes, Chases, Approaches, and Feeding Efforts in Appendices G-J.

No statistically significant, UVR exposure effects were evident in the comparative frequencies of all the behaviors quantified, although absolute change score means for more overtly aggressive Strikes and Chases did trend in positive values with UVR illumination. Conversely, mean rate change scores for less belligerent Approaches and Feeding Efforts trended negatively, but not significantly so, under UVR.

A single, significant UVR behavioral effect was observed, however, in analyses of event durations, with Chases persisting longer under UVR-present than UVR-absent conditions (t (19) = 2.618, $p = 0.017$, two-tailed, Tables 1, 2, Figures 14, 16). However, the absolute mean magnitude of this increase, 0.14 ± 0.24 SD sec ($n = 20$), was slight relative to both the mean Chase duration recorded across all trials, 1.69 ± 0.33 SD sec ($n = 40$), and the one-second durational increments applied in videotape analyses of agonistic events.

Exploratory, correlation analyses revealed a stronger, positive association between Chase durations and light levels under UVR-present conditions ($r = 0.324$, $p = 0.163$, $n = 20$) than in UVR-absent trials ($r = 0.086$, $p = 0.720$, $n = 20$), although neither relationship proved statistically meaningful. Similarly, a positive but statistically non-significant association between Chase durations and light intensities emerged at examining trial outcomes in full, combined across spectral conditions ($r = 0.218$, $p = 0.176$, $n = 40$). Event durations remained essentially unchanged for Strikes (t (19) = –0.321, $p = 0.752$, two-tailed) and Approaches (t (19) = –0.845, $p = 0.409$, two-tailed, Tables 1, 2, Figures 14, 16).

As an unanticipated observation, one to several fish in a number of trials exhibited episodes of agitated swimming along aquarium sides, often in response to threatened or actual attack by rivals. While the behaviors resembled flight reactions, they frequently produced only limited lateral movement – due to the body and snout driving vigorously against aquarium walls. Although not formally quantified initially, the incidents appeared somewhat more prevalent under UVR conditions, suggesting some possible correspondence with the restless swimming against vessel sides witnessed during laboratory UVB irradiations of young rainbow trout (*Oncorhynchus mykiss*; Alemanni et al 2003).

Prompted by the concern that such behaviors may have interacted systematically across spectral conditions with the agonistic and foraging events under examination, all experimental video-recordings were reanalyzed with these swimming episodes documented as to their rates and nearest-second durations. The incidents were distinguished by animals' elevated tail-beat frequencies and sustained snout contact with aquarium side panels.

Results of the above reanalysis indicated that although frantic swimming episodes did show absolutely higher rates of occurrence in UVR-present trials (18.30 ± 21.21 SD, $n = 20$) than in UVR-absent trials (12.45 ± 19.80 SD, $n = 20$, Appendix K), as well as absolutely longer durations in UVR-present trials (5.44 ± 3.46 SD sec, $n = 20$) than in UVR-absent trials (4.65 ± 6.98 SD sec, $n = 20$, Appendix K), the observed differences failed to attain statistical significance for both event rates (t (19) = –1.664, $p = 0.113$, two-tailed) and event durations (t (19) = –1.315, $p = 0.204$, two-tailed). An additional comparison was performed examining the total duration of agitated swimming events summed across all group members in a trial. Results again showed an absolute but statistically non-significant increment in cumulative duration with UVR-present conditions (116.40 ± 139.28 SD sec, $n = 20$) as compared to UVR-absent trials (103.15 ± 200.30 SD sec, $n = 20$; t (19) = –1.320, $p = 0.203$, two-tailed). Agitated event rates, event durations, and cumulative durations were square-root transformed prior to analyses to normalize moderate levels of skewness and kurtosis.

DISCUSSION

Under artificial conditions where animals were denied refuge from direct solar UVR at summer, midday intensities, agonistic pursuits among young coho salmon persisted significantly longer than when this spectral region was experimentally excluded. With pursuits differentiated during behavioral analyses as the aggressive, territorial expulsion of rival individuals, this outcome spoke to UVR-exposed fish having exerted more sustained efforts in driving off conspecific intruders.

In non-naturalistic, experimental conditions designed to provide animals with structural complexity but prevent their characteristic avoidance of intense UVR exposure (Kelly and Bothwell 2002), agonistic pursuits among young coho salmon were found to persist significantly longer under direct, midday summer sunlight inclusive of UVR than when such wavelengths were excluded using spectral filters. With pursuits differentiated during behavioral analyses as the aggressive, territorial expulsion of rival individuals, this outcome spoke to UVR-exposed fish having exerted more sustained efforts in driving off conspecific intruders.

In possible explanation of this finding, it may be recalled that juvenile coho salmon have demonstrated both retinal UVR photoreceptive capacity (Beaudet et al 1997) and an aversion to UVR-rich environments (Kelly and Bothwell 2002), establishing, respectively, their sensory ability and motivation to select and defend a territory site partly on the basis of its UVR-protective benefit. This proposition finds support in their documented, preferential assumption of shaded positions when exposed to direct solar UVR (Kelly and Bothwell 2002; Holtby and Bothwell 2008). In such a circumstance, the instantaneous, protective value of a territory would appreciate in rough proportion to ascending, ambient

UVR levels, so justifying and eliciting increasingly vigorous and metabolically demanding behaviors, such as lengthier pursuits, in its defense. Such a process could feasibly operate even in shadeless environments – as in the present experiment – by inducing in UVR-irradiated individuals an aversive physiological state to lower their thresholds for aggressive expression and intensify their combativeness against intruders – much as hunger has been shown to heighten intraspecific belligerence in young coho salmon (Dill 1978; Dill et al 1981), and thus likely enhance animals' defense of their territorial foraging rights during periods of scarcity.

Juvenile coho salmon under predatory threat have likewise been noted to engage in more frequent and markedly aggressive chase behaviors despite a concurrent decline in their overall rate of hostile interactions (Reinhardt 1999). Might it more generally be the case, then, in circumstances where the overriding situational advantage of territoriality lies in self-protection – whether from predation or harmful radiation – that fish will constrain their movements within more conservative territorial boundaries but defend them more assertively, resulting in rarer but sharper encounters with neighbors? While speculative, this scenario plausibly gains evidence from a report of reduced territory size among coho salmon fry in the presence of piscivorous waterfowl (Martel 1996). Such dynamics would further help to bridge the discrepancy between prior findings of diminished overall agonistic activity in coho salmon under UVR (Holtby and Bothwell 2008) with the present determination of protracted pursuits.

Nonetheless, it warrants emphasis that the average extension in chase time detected under UVR illumination, 0.14 sec, while statistically significant, was brief in relation to both the one-second intervals applied in event duration assessments, and the average length of chases observed during behavioral trials, 1.69 sec. The former comparison would advise that the stated durational finding be viewed with some caution on metrical grounds, while the latter calls into question to what degree the pursuit increment recorded, if reliable, bears substantive, functional meaning, especially as applied to complex natural systems where diverse influences (e.g., population density, food abundance) are believed to interactively impinge on territorial processes (Imre et al 2002).

The above circumstances prove less problematic, however, on a conceptual basis. If a UVR-induced intensification of chase responses does, as suggested above, promote the defense of a territory's protective advantage under conditions of heightened environmental threat, then overlong pursuits that bear the resident animal farther from its territory would tend to escalate rather than moderate its vulnerability to that threat. Competing adaptive pressures may thus compress pursuit efforts within a narrow window of optimal lengths just in excess of that necessary to expel an intruder. This condition would render the only modest chase duration differences observed less surprising.

The present pursuit duration finding emerged in the absence of significant effects for the remaining behavioral dimensions examined (i.e., rates of Strikes, Chases, Approaches, and Feeding Efforts, and durations of Strikes and Approaches). Such null results tend to allay concerns that enhanced UVR intensities over rearing streams might impart large and pervasive changes in the social structures of young salmonids, at least in the short term.

However, other UVR-related behavioral changes could conceivably have arisen among the six remaining parameters but eluded detection as a consequence of the specific event classification and quantification procedures employed, or due to statistical considerations such as wide score variances or insufficient power perhaps obscuring subtler effects. Inadequate stimulus contrast between spectral conditions presents a further possibility, in that the incomplete transmission of UVR wavelengths by light screens imposed roughly 25% and 10% attenuations, respectively, of incident solar UVB and UVA during UVR exposure trials. These and other factors may have contributed to the absence of a broader pattern of coherent, statistically significant effects, although strict magnitude trends did suggest that UVR increased the general frequency of more belligerent interactions (i.e., attacks, pursuits; Young 2003; Wessel et al 2006) while subduing milder approach behaviors and foraging activity. Such an aggregate of outcomes would have aligned more closely with the position of aversive environmental conditions tending to aggravate (e.g., Anderson and Anderson 1984) rather than inhibit (e.g., Baron and Bell 1976) social aggression. The reflectance characteristics of the plastic funnels and sand used in trials were also not assessed. It remains unknown, therefore, to what extent these substrates' optical properties may have contributed to spectral and total luminance differences between light conditions.

A challenge might be issued that the isolated emergence of the above durational finding among seven quantified dimensions reasonably calls to question whether the effect may have arisen spuriously from simple chance factors or perhaps unidentified experimental confounds. While this possibility cannot be wholly discounted, if the prolongation of pursuits – regarded as principally repelling behaviors (Wessel et al 2006) – does in fact promote the ejection of trespassing rivals under conditions of UVR irradiative threat, then the absence of concomitant changes in attacks and approaches fails to pose a conceptual contradiction as these actions were not functionally distinguished by the displacement or expulsion of intruders.

Differing aspects of the present results conform to and depart from the closely applicable findings of Holtby and Bothwell (2008). For example, the above noted trend of diminished foraging under UVR would corroborate this earlier study's report of a statistically significant decrease in feeding activity, the latter, more robust effect perhaps having benefited from a concurrent process in which juvenile salmon evading UVR under rockwork were found less active overall. As for contrasting results, Holtby and Bothwell (2008) further reported UVR-related declines in both the frequencies and durations of agonistic behaviors, as opposed to the lengthened pursuits observed here. These investigators emphasized the indirect impact of UVR avoidance behavior, which led juvenile coho salmon to shaded positions beneath rocks, resulting in their visual isolation and diminished territorial activity. This mediated inhibition of aggressiveness by exposure avoidance may have been sufficient to render undetectable any UVR-induced increment in pursuit duration suggested in the present research.

Given that the above study (Holtby and Bothwell 2008) employed naturalistic experimental flumes which offered animals a level of shade access more reflective of wild rearing environments, its findings may be more ecologically applicable than those of the present study, where highly specialized and artificial conditions were established to examine the particular behavioral actions of direct solar UVR. This methodological divergence also suggests that the protraction of hostile pursuits observed in this investigation may only emerge with intensive and inescapable UVR irradiation.

In view of the complex climactic, seasonal, diurnal, and other factors modulating solar UVR intensities in the wild, gauging the magnitude of any prospective UVR behavioral impact presents a considerable challenge. Nevertheless, the ecological literature bears out the relevance and timeliness of this question in underscoring three anthropogenic environmental trends contributing to heightened UVR levels in streams. Of these, the global depletion of stratospheric ozone received the earliest and most widespread attention (Kerr and McElroy 1993), although local effects stemming from losses in riparian canopy vegetation (Brosofske et al 1997; Kiffney et al 2004) have been increasingly recognized. However, recent research has suggested most influential of all to be the diminished concentrations of UVR-absorbing organic solutes in stream water resulting from climate change and acidification effects (Schindler 2001; Molot et al 2004).

Some degree of caution is advisable in the interpretation and responsible application of the stated findings with respect to the methodological, statistical, and behavioral considerations enumerated below. Among methodological issues, the association of extended chases with direct UVR irradiation was identified at experimental stocking levels that approached natural stream densities near the period of fry emergence (Grant and Kramer 1990; Imre et al 2002). As such, this observation may be less instructive later in freshwater occupancy, when populations will have thinned considerably (Lahti et al 2001), although it remains unclear whether the effect might then be diminished or potentially magnified. Alternatively, in pertaining to the lengths of individual pursuit events rather than frequencies of intraspecific conflict, this result may prove fairly insensitive to fluctuations in population density.

A second methodological issue rests with the experimental use of artificial, conical structures (i.e., inverted funnels) deliberately chosen for their inability to provide animals with shade access during the midday. Given that river stones do not regularly assume such forms, wild fish residing over rocky substrates are likely to encounter far more opportunities to evade UVR than afforded fish in this research. Submerged woody debris (Dolloff and Reeves 1990) and bank overhangs (Zhivoglyadov 2003) may also be accessed for cover. Further, rearing coho salmon have been observed to selectively occupy deeper, pooled stream regions over shallows (Young 2003; Zhivoglyadov 2003) and, therefore, typically more sheltered habitats than the exposed, 10-cm depths permitted them here, although this consideration could reasonably be balanced against the noted, imperfect passage of UVR through experimental light screens – corresponding roughly to the absorptive effect of an additional 50-cm depth of aquarium water. While some rearing environments, such as unshaded stream riffles over bedrock, will approximate the fairly exacting, UVR exposure conditions administered in this study, they may not be widely representative. These various circumstances suggest that research animals likely endured greater UVR exposures than would wild individuals under comparable solar conditions. The stated findings may, therefore, tend towards overestimating behavioral impacts in the wild, and prove more valuable for their theoretical interest than broad ecological applicability.

A question central to the valid interpretation of trial results emerged at the interaction of research aquaria's physical limitations with the behavioral tendencies of experimental animals. That is, episodes of escape-like, agitated swimming marked by accelerated tail-beat frequencies were observed in a number of trials – evidently as artifacts of experimentation insofar as they occurred exclusively along the transparent panels of aquaria and would not thus generalize to natural conditions. At their initial, casual observation, the incidents appeared more prevalent during UVR trials, suggesting some relation to the UVR evasion behaviors described in coho and other salmon species (Kelly and Bothwell 2002; Alemanni et al 2003; Ylonen et al 2004). With subsequent, formal quantification, however, this behavioral disparity between spectral conditions was confirmed only at an absolute but not statistically significant level. Nevertheless, given the only modest, average increment in chase time observed with UVR illumination, and the possibility that agitated events could have precipitated deeper territorial intrusions and, therefore, lengthier retaliatory pursuits, this trend in an artifact trial behavior cannot be confidently excluded as a potential, confounding contributor to the greater chase durations recorded in UVR trials.

Beyond the metrical and effect magnitude discussions pursued earlier, an additional, noteworthy statistical issue regards this study's application of two-tailed (i.e., non-directional) inferential tests throughout its principal analyses. The significant result obtained for pursuit times, therefore, more properly supports the conclusion that UVR exposure induced an alteration in pursuit durations than it does their specific prolongation. Conceptual and practical extrapolations from the latter, directional interpretation should thus be made guardedly and with this acknowledgement. It bears re-emphasizing at this time that translating the admittedly slim, pursuit length differential isolated here under highly controlled conditions to the complexities of natural systems may present an imposing and ultimately humbling exercise. Given the intricate, interacting factors known to shape salmonid territorial behavior in streams, such as current velocity (Dill 1978; Zhivoglyadov 2003), risk of predation (Martel and Dill 1993; Ryer and Olla 1996), prey abundance, and conspecific density (Imre et al 2002), any achieved impact on agonistic interactions in the wild may finally be negligible.

Two other, possible alternative explanations for the stated outcomes warrant comment. First, the relative optical properties of light screens applied over contrasting spectral environments resulted essentially in an incremental administration of UVR above visible radiation – and thus greater total luminance – in UVR exposure trials. While it is therefore possible that the recorded behavioral disparities derived significantly from this quantitative difference in overall solar intensity rather than from the qualitative, specific inclusion of UVR, this alternative appears improbable from the viewpoint of the current empirical literature. A number of studies have examined juvenile salmon aggressiveness over a range of light levels, and found behavioral changes – when observed at all – to be associated with low rather than high irradiative intensities (Gregory and Griffith 1996; Kadri et al 1997; Nicieza and Metcalfe 1999). For example, antagonism among young Atlantic salmon (*Salmo salar*) was shown to decrease at very dim, starlight levels of illumination, presumably due to reduced visibility between animals (Valdimarsson and Metcalfe 2001). A more recent investigation (Holtby and Bothwell 2008) did identify behavioral differences across a broader range of light levels, although greater solar intensities tended to predict declines in aggressiveness, rather than the longer pursuits noted here. Further, the question of actual solar intensity differences between similarly manipulated, experimental light conditions was previously addressed by Kelly and Bothwell (2002). Employing optically identical spectral screening materials under cloudless, midday, summer sun at a nearby site (Nanaimo, British Columbia), these researchers measured incident light energy in the UVB, UVA, and visible regions, and determined the cumulative solar intensity under full spectrum (i.e., UVR-present) conditions to exceed that for UVR-absent conditions by only 5.4%. Lastly, in ancillary correlation analyses that addressed, successively, UVR-absent trials alone, UVR-present trials alone, and all trials collectively, pursuit times failed to display significant associations with light intensity, although correlation coefficients may have been attenuated somewhat by the narrow span of solar intensities under which trials were executed (i.e., statistical range restriction effects).

A final, interpretative challenge would hold that behavioral findings evolved not chiefly from UVR exposure but indirectly, by way of animals' innate, aggressive reactions to potentially antagonizing physical markings on conspecifics that may only be visible under UVR illumination. Facial patterns in certain damselfishes, for example, have been shown to trigger more vigorous intraspecific attacks in the presence of UVR (Siebeck 2004). Such research has customarily contrasted UVR conditions against those presenting optic barriers to both direct and indirect UVR penetration. In the present study, however, all aquarium sides were constructed from UVR-transmitting acrylic panels, enabling the lateral passage of indirect UVR that would have illuminated any UVR-dependent body markings present, even in UVR-absent trials – if less prominently than under direct UVR irradiation. This circumstance tends to decrease the likelihood that the documented behavioral changes arose simply as a function of UVR-reliant visual cues.

With behavioral trials consistently completed within an hour of initial spectral regime exposure, it is important to recognize that study protocols stressed the detection of fairly immediate irradiative impacts. The various null findings reported should not, therefore, be taken to exclude the possibility of corresponding, extended exposure effects, perhaps as behavioral correlates to the diverse conditions identified in UVR-irradiated fish (e.g., Winckler and Fidhiany 1996; Jokinen et al 2000).

With food and mate access offered in illustration, it has been reasonably contended that the adaptive economics underlying territorial aggression fundamentally rest in the quality, distribution, and defensibility of limited resources across spatial and temporal dimensions (Valdimarsson and Metcalfe 2001). In view of the germinal research establishing the presence of UVR-evasive behaviors in salmonid fishes (Kelly and Bothwell 2002; Ylonen et al 2004) alongside the recent (Holtby and Bothwell 2008) and present findings to suggest the influence of UVR in shaping juvenile salmon agonistic activity, shelter from UVR exposure clearly merits further examination as a potential resource factor driving salmonid territoriality in streams. The prospect is especially intriguing from the standpoint of resource quality and distribution over space and time. Given that a territory's UVR-protective capacity may undergo dramatic fluctuations due to, one, predictable diurnal shifts in solar intensity and direction of incidence relative to shading elements, and, two, drastic and erratic variations in luminance as a result of weather changes, a momentarily favorable, well-shaded territorial site could very rapidly deteriorate into a UVR-inundated hazard. Might this inherent instability of UVR-protection as a spatial resource and potential basis for territory selection be a significant contributor in the well-known, pronounced spatial variability of salmon territorial systems in rearing streams (Puckett and Dill 1984; Grant and Kramer 1990)?

Table 1. Mean behavior change scores observed with UVR illumination, standard deviations, skewness and kurtosis values, and associated two-tailed, t-test results for event rates (per 30-minute trial) and event durations (sec) of Strikes, Chases, and Approaches, and event rates of Feeding Efforts, determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon. Bolded type indicates $p < 0.05$.

Behavior dimension	Change score	Skewness	Kurtosis	*t* (19)	*p*
Strikes					
Rate	5.30 ± 32.22	0.448	0.255	–0.736	0.471
Duration	–0.02 ± 0.24	0.247	0.909	–0.321	0.752
Chases					
Rate	8.90 ± 37.83	0.587	1.230	–1.052	0.306
Duration	0.14 ± 0.24	0.446	0.323	2.618	**0.017**
Approaches					
Rate	–7.95 ± 23.32	–0.024	–0.546	1.525	0.144
Duration	–0.06 ± 0.33	–0.860	0.572	–0.845	0.409
Feeding Efforts					
Rate	–4.70 ± 17.54	–0.962	1.061	1.198	0.246

Table 2. Mean event rates (per 30-minute trial), mean event durations (sec), and standard deviations for Strikes, Chases, Approaches, and Feeding Efforts observed in 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

Behavior dimension	UVR-absent	UVR-present
Strikes		
Rate	48.25 ± 25.89	53.55 ± 29.73
Duration	1.24 ± 0.20	1.23 ± 0.22
Chases		
Rate	56.10 ± 32.24	65.00 ± 45.88
Duration	1.62 ± 0.28	1.76 ± 0.37
Approaches		
Rate	84.05 ± 25.40	76.10 ± 28.51
Duration	1.57 ± 0.23	1.51 ± 0.25
Feeding Efforts		
Rate	36.45 ± 26.56	31.75 ± 16.28
Duration	1.02 ± 0.04	1.01 ± 0.02

Figure 1. Light transmittance (%) profiles for OP-2 (UVR-absent) and OP-4 (UVR-present) Acrylite screens, assessed by spectrophotometer (Perkin Elmer Lambda II) from 280 to 700 nm, inclusive; adapted from Holtby and Bothwell (2008).

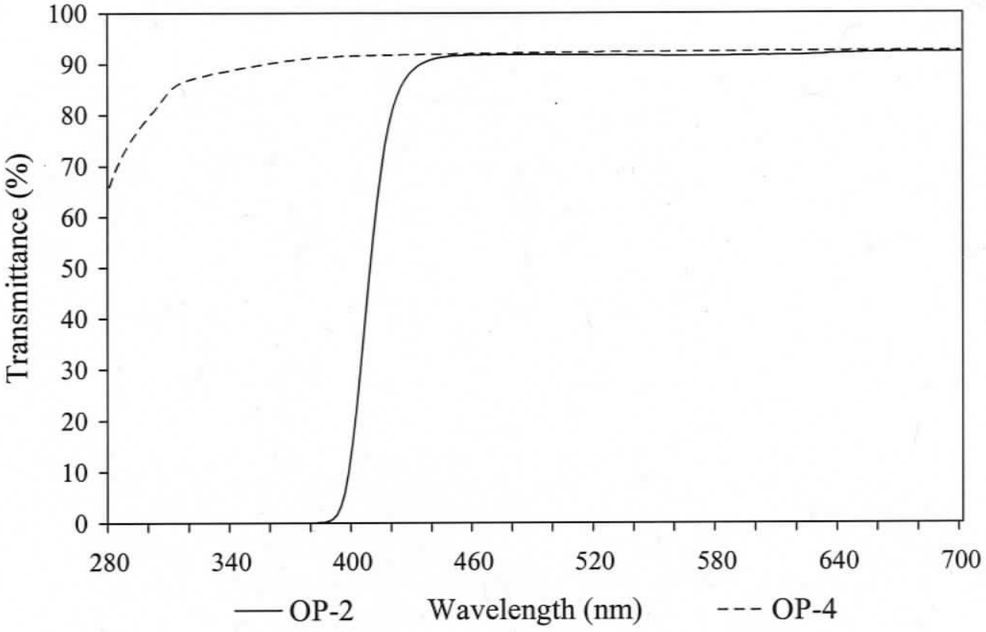
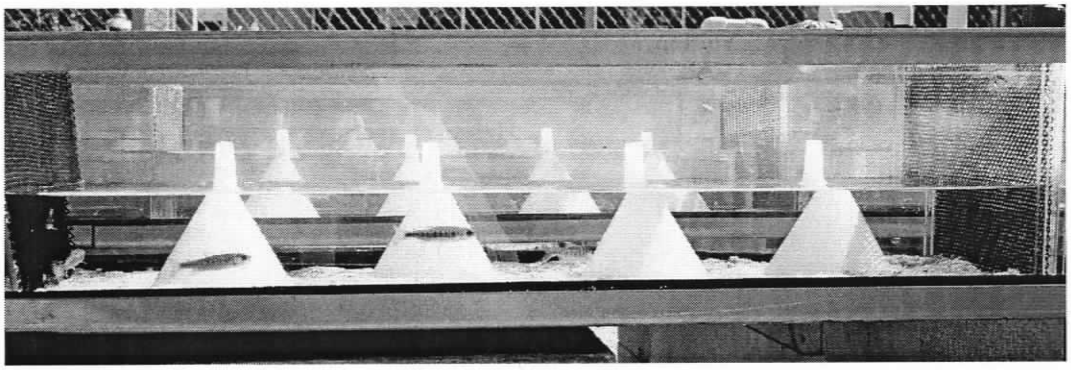


Figure 2. Photograph of outdoor, unidirectional-flow, experimental aquarium featuring four inverted, plastic funnels arrayed in a zigzag configuration (represented schematically below) over coarse sand – with juvenile coho salmon visible.



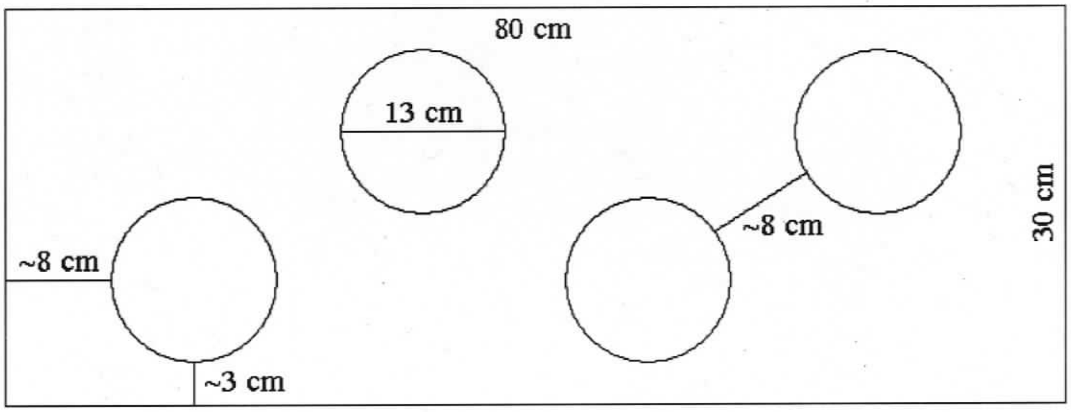


Figure 3. Photograph of two tripod-mounted cameras – directed downward to obtain overhead video-recordings of experimental aquaria, visible below.

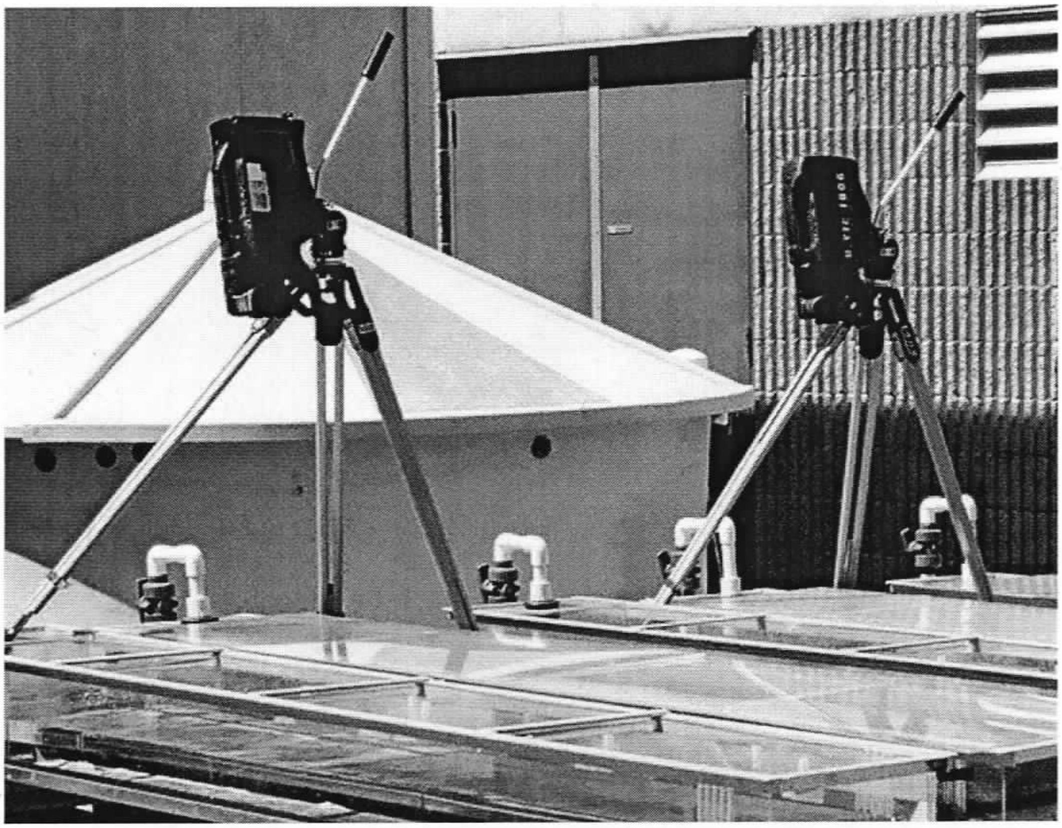


Figure 4. Sample frame from trial videotape illustrating vantage point of video-recording, absence of shading from overhead camera and tripod, zigzag configuration of four inverted funnels over sand, and experimental group of 7 juvenile coho salmon.

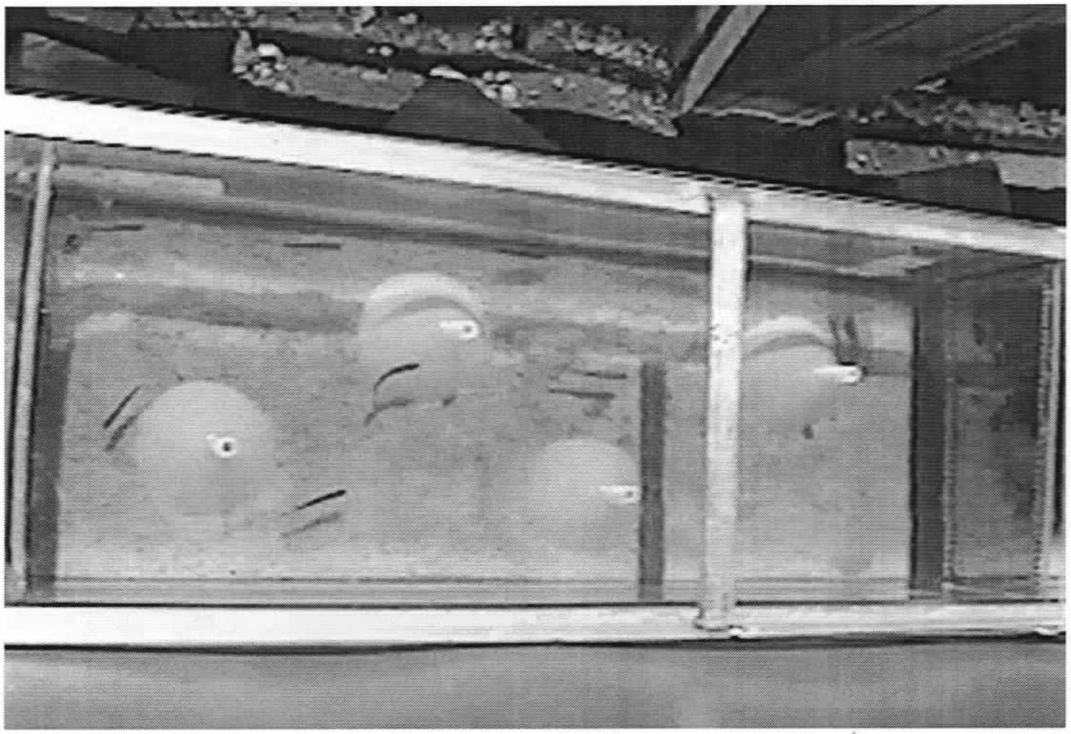


Figure 5. Light transmittance (%) profile for 10-cm water depth of experimental aquaria, assessed by spectrophotometer (Ultrospec 2000, Pharmacia-Biotech) from 280 to 700 nm, inclusive.

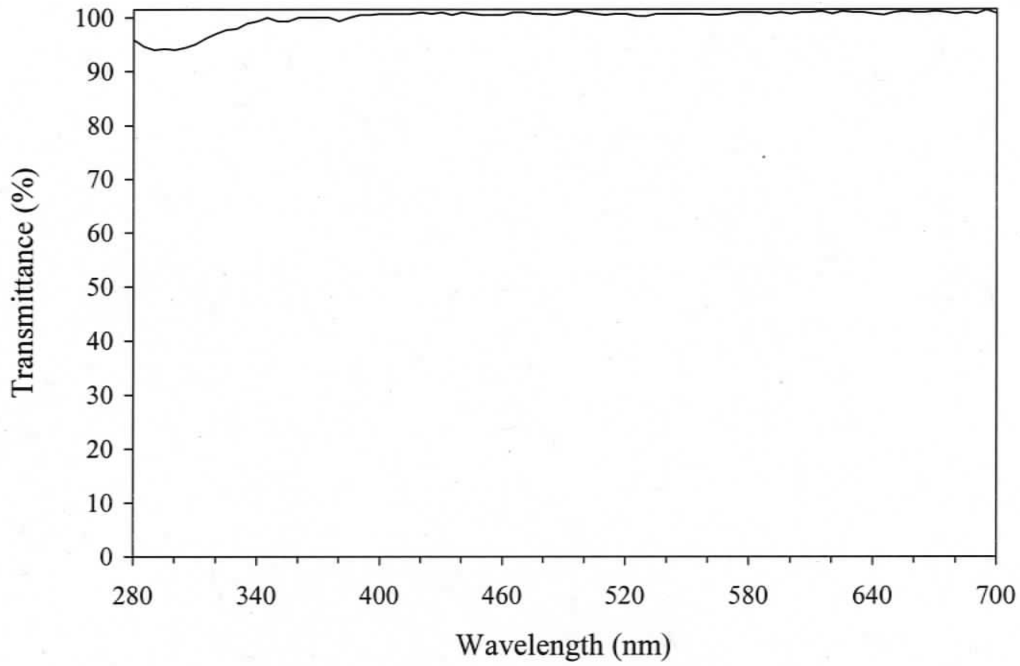


Figure 6. Frequency distribution for Strike rate change scores observed with UVR illumination – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

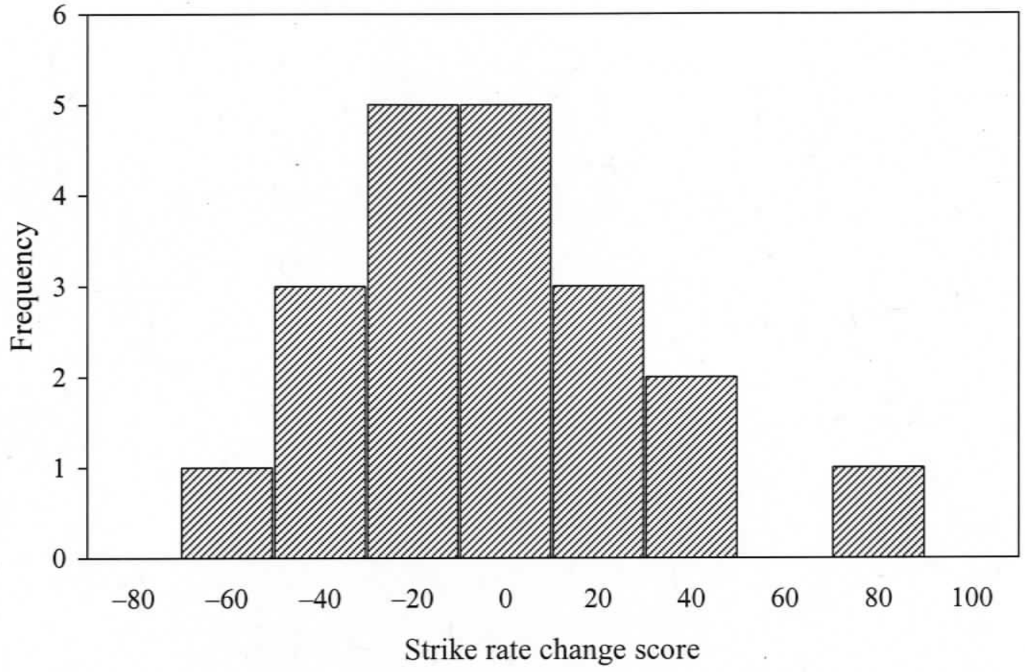


Figure 7. Frequency distribution for Chase rate change scores observed with UVR illumination – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

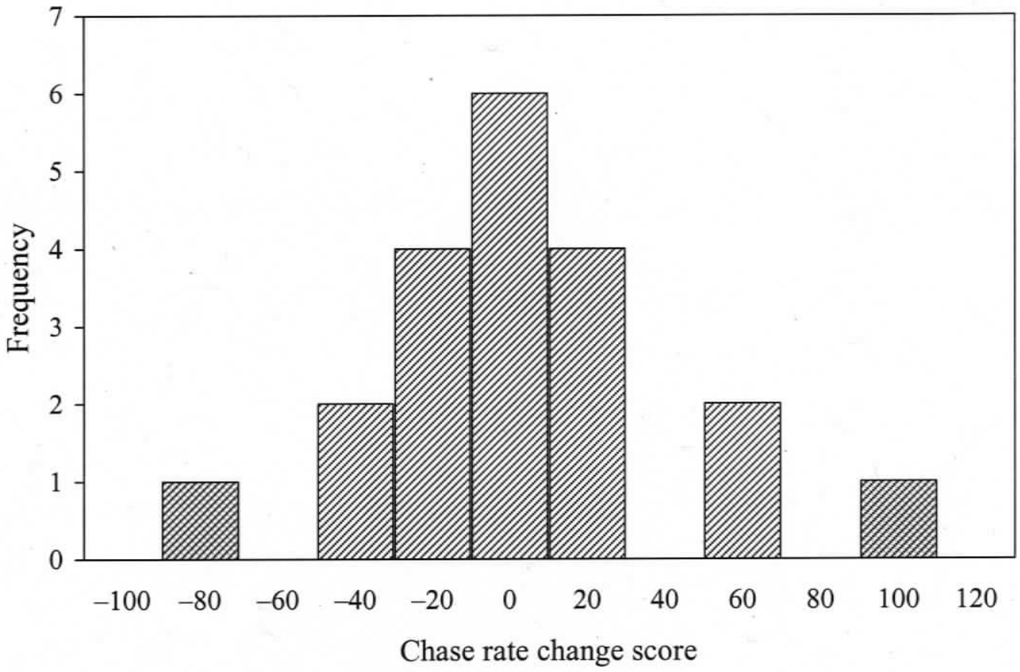


Figure 8. Frequency distribution for Approach rate change scores observed with UVR illumination – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

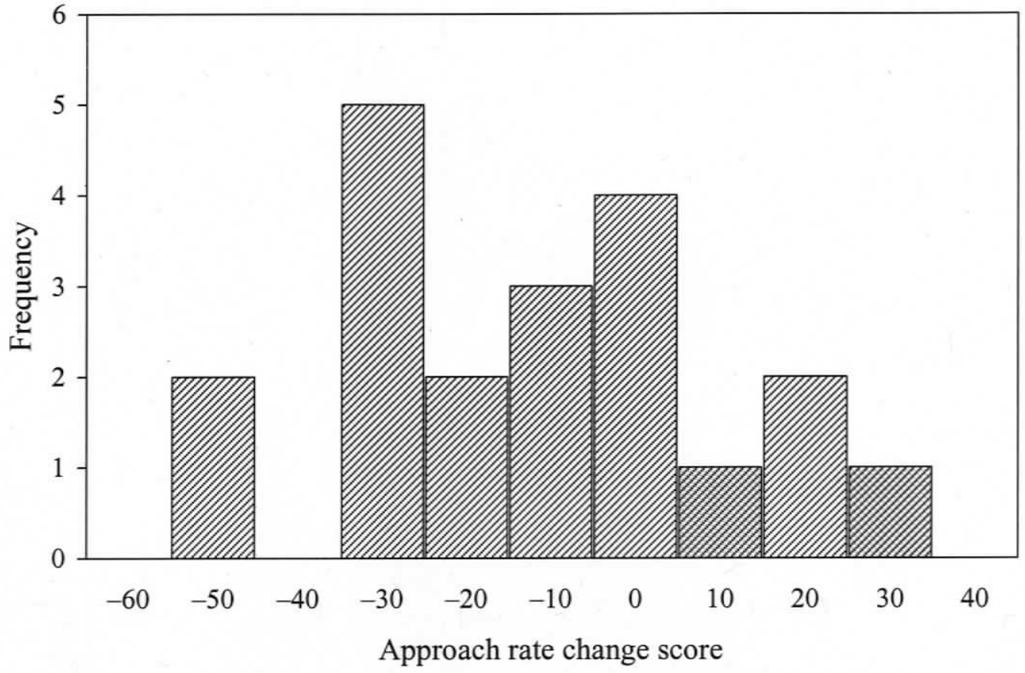


Figure 9. Frequency distribution for Feeding Effort rate change scores observed with UVR illumination – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

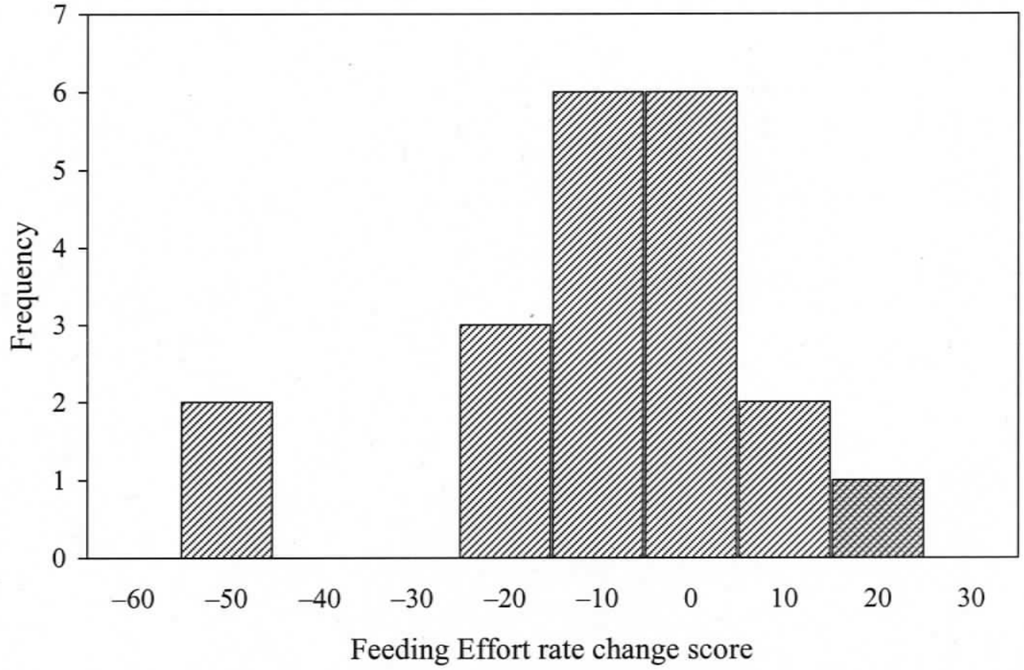


Figure 10. Frequency distribution for Strike duration change scores (sec) observed with UVR illumination – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

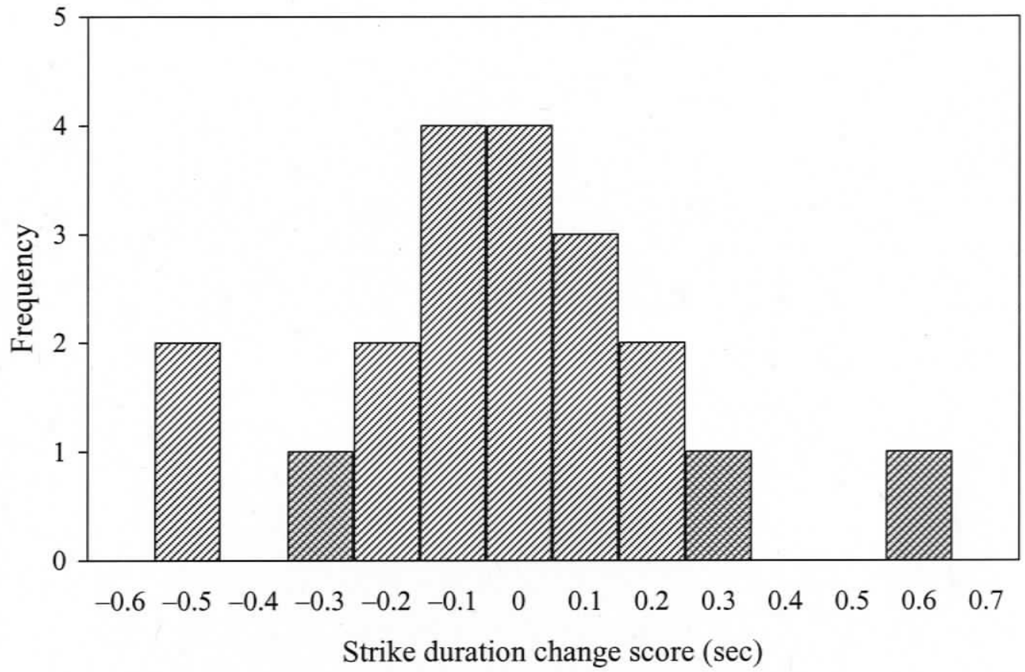


Figure 11. Frequency distribution for Chase duration change scores (sec) observed with UVR illumination – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

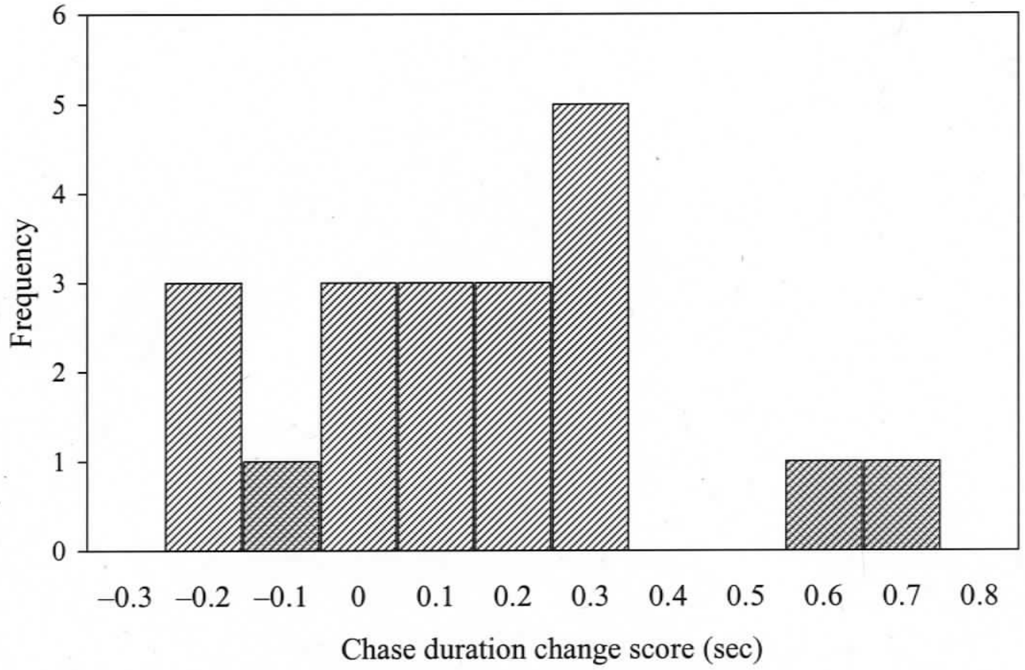


Figure 12. Frequency distribution for Approach duration change scores (sec) observed with UVR illumination – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

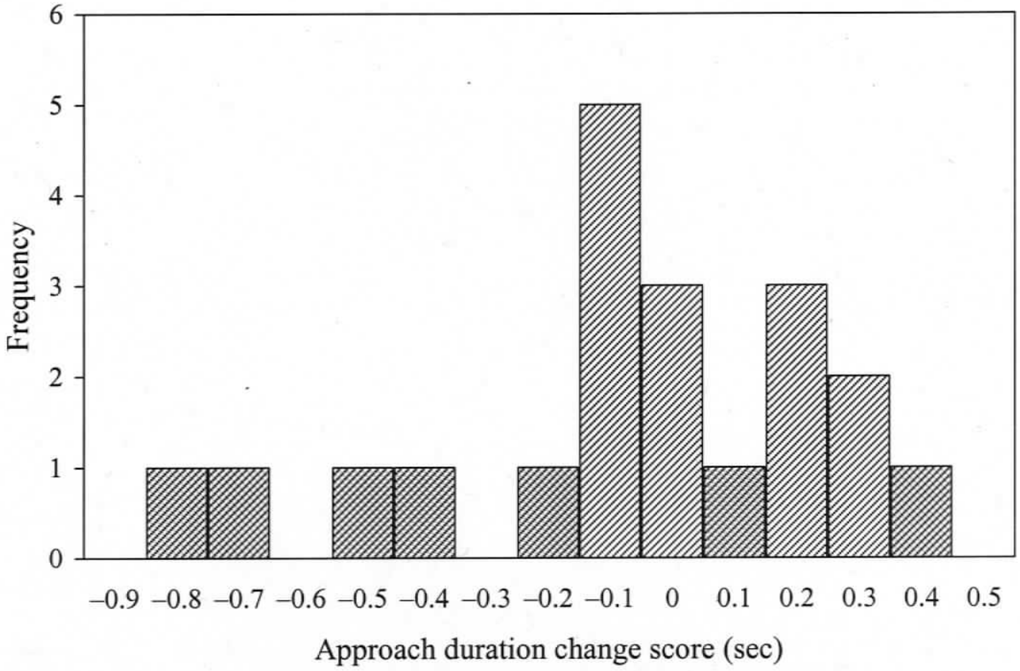


Figure 13. Behavior rate change score means (points) and standard deviations (lines) observed with UVR illumination for Strikes, Chases, Approaches, and Feeding Efforts – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

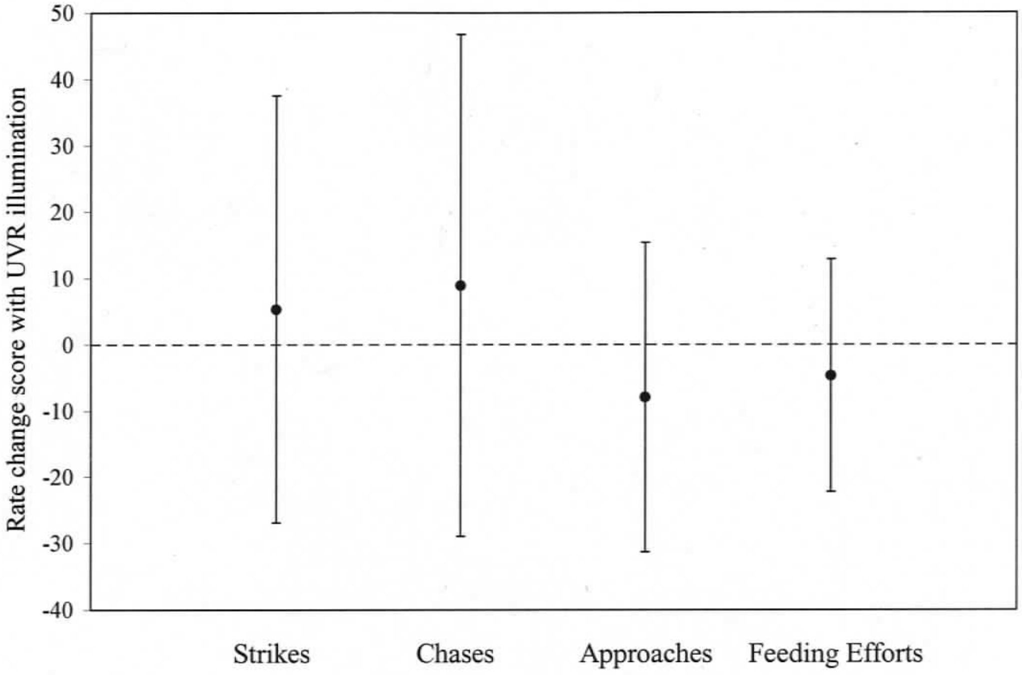


Figure 14. Behavior duration change score (sec) means (points) and standard deviations (lines) observed with UVR illumination for Strikes, Chases, and Approaches – determined over 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

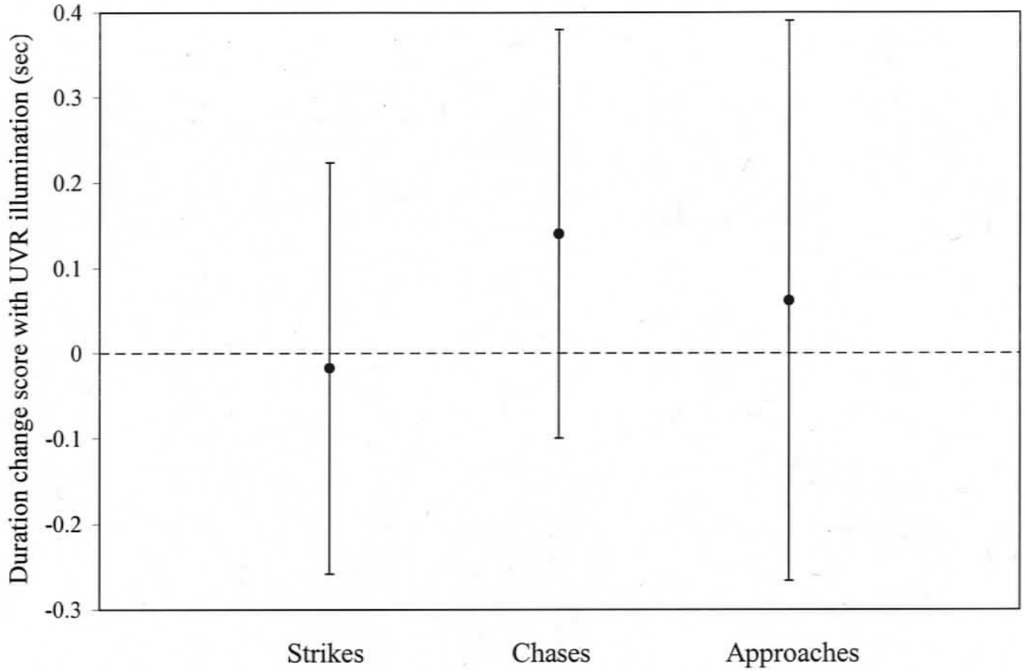


Figure 15. Behavior rate means (bars) and standard deviations (lines) for Strikes, Chases, Approaches, and Feeding Efforts observed in 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.

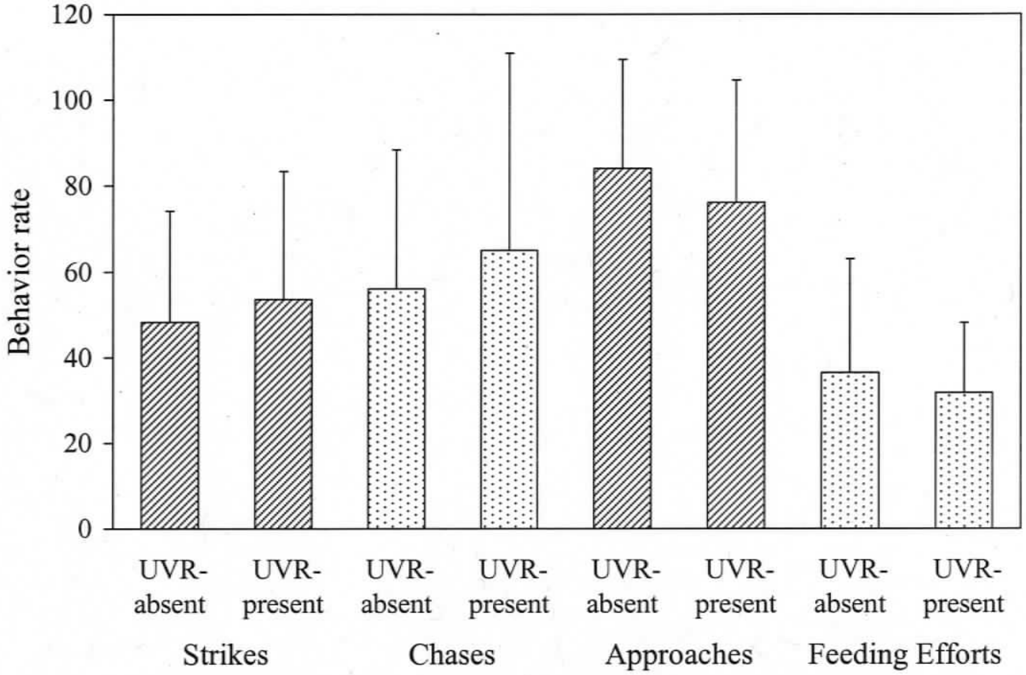
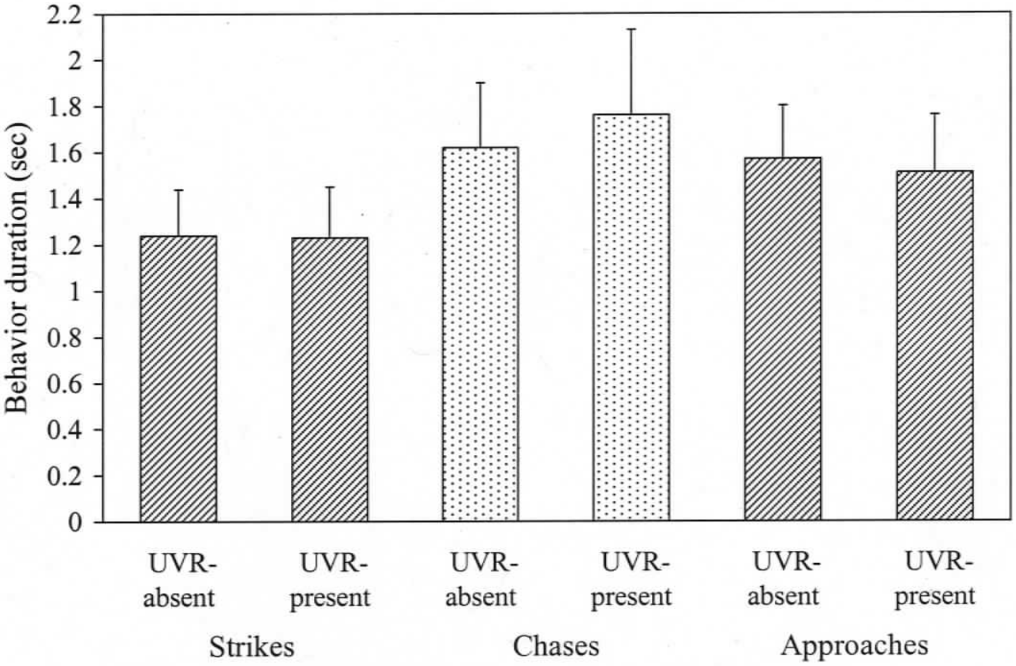


Figure 16. Behavior duration (sec) means (bars) and standard deviations (lines) for Strikes, Chases, and Approaches observed in 20 UVR-absent and 20 UVR-present, 30-minute trials for 20 groups of juvenile coho salmon.



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Appendix A. Output volumes (l) for duplicate, one-minute, flow measurement trials conducted on five experimental flumes (*n* = 10).

Flume	Trial	Output volume (l)
A	1	9.1
	2	9.2
B	1	8.4
	2	8.3
C	1	9.0
	2	9.0
D	1	8.8
	2	8.7
E	1	9.3
	2	9.5

Appendix B. Ambient photosynthetically active radiation (PAR) levels (mmol/m^2/sec) at the beginning (0'), midpoint (15'), and conclusion (30') of 30-minute, UVR-absent trials for 20 experimental groups of juvenile coho salmon.

	PAR level (mmol/m^2/sec)		
Group	Beginning	Midpoint	Conclusion
1	1647	1605	1570
2	1733	1720	1700
3	1700	1708	1720
4	1774	1758	1725
5	1805	1713	1730
6	1733	1701	1650
7	1740	1729	1711
8	1805	1713	1730
9	1556	1520	1507
10	1706	1684	1590
11	1662	1688	1715
12	1747	1752	1751
13	1711	1726	1730
14	1768	1746	1727
15	1717	1696	1660
16	1660	1660	1665
17	1669	1659	1643
18	1694	1673	1674
19	1547	1566	1610
20	1547	1566	1610

Appendix C. Ambient photosynthetically active radiation (PAR) levels ($mmol/m^2/sec$) at the beginning (0'), midpoint (15'), and conclusion (30') of 30-minute, UVR-present trials for 20 experimental groups of juvenile coho salmon.

	PAR level ($mmol/m^2/sec$)		
Group	Beginning	Midpoint	Conclusion
1	1733	1720	1700
2	1761	1778	1782
3	1631	1649	1580
4	1660	1662	1607
5	1688	1612	1638
6	1810	1798	1782
7	1805	1713	1730
8	1740	1729	1711
9	1706	1684	1590
10	1556	1520	1507
11	1747	1752	1751
12	1662	1688	1715
13	1727	1710	1708
14	1655	1663	1697
15	1768	1746	1727
16	1669	1659	1643
17	1660	1660	1665
18	1547	1566	1610
19	1694	1673	1674
20	1694	1673	1674

Appendix D. Fork-lengths (cm) and wet weights (g) for 20 experimental groups of 7 juvenile coho salmon ($n = 140$).

Group	Fish	Fork-length (cm)	Wet weight (g)
1	1	5.7	1.85
	2	5.8	2.23
	3	5.2	1.45
	4	5.5	1.88
	5	5.4	1.85
	6	5.6	2.14
	7	5.3	1.82
2	1	5.9	2.85
	2	4.9	1.64
	3	4.9	1.52
	4	4.8	1.86
	5	5.5	2.03
	6	5.5	2.05
	7	5.4	1.94
3	1	5.4	1.75
	2	5.6	1.88
	3	5.5	1.69
	4	5.7	2.00
	5	5.5	1.89
	6	6.1	2.23
	7	5.7	1.95

Appendix D (Continued). Fork-lengths (cm) and wet weights (g) for 20 experimental groups of 7 juvenile coho salmon (*n* = 140).

Group	Fish	Fork-length (cm)	Wet weight (g)
4	1	5.0	1.41
	2	5.4	1.77
	3	5.5	2.01
	4	4.9	1.38
	5	6.1	2.40
	6	5.0	1.36
	7	5.6	1.88
5	1	5.4	1.96
	2	5.4	2.06
	3	4.9	1.38
	4	5.8	2.02
	5	5.5	1.92
	6	5.9	2.43
	7	5.4	1.99
6	1	6.7	3.21
	2	5.6	1.86
	3	4.9	1.05
	4	5.3	1.81
	5	5.8	2.33
	6	5.3	1.69
	7	5.4	1.86

Appendix D (Continued). Fork-lengths (cm) and wet weights (g) for 20 experimental groups of 7 juvenile coho salmon ($n = 140$).

Group	Fish	Fork-length (cm)	Wet weight (g)
7	1	5.9	2.07
	2	5.3	1.57
	3	5.7	2.24
	4	5.7	2.39
	5	5.3	1.71
	6	6.3	2.91
	7	6.1	2.87
8	1	5.6	1.75
	2	6.1	2.40
	3	5.1	1.22
	4	5.2	1.55
	5	6.2	2.64
	6	5.7	1.93
	7	5.4	1.73
9	1	5.8	2.19
	2	5.4	1.73
	3	5.8	1.99
	4	5.7	1.99
	5	5.4	1.77
	6	5.4	1.60
	7	5.3	1.60

Appendix D (Continued). Fork-lengths (cm) and wet weights (g) for 20 experimental groups of 7 juvenile coho salmon (*n* = 140).

Group	Fish	Fork-length (cm)	Wet weight (g)
10	1	4.9	1.29
	2	5.5	1.73
	3	5.2	1.54
	4	5.6	1.76
	5	5.8	2.01
	6	4.5	0.94
	7	5.7	1.99
11	1	5.6	2.41
	2	4.3	0.90
	3	5.7	2.51
	4	5.8	2.52
	5	5.6	2.37
	6	4.0	0.84
	7	5.0	1.50
12	1	6.2	3.28
	2	5.5	2.16
	3	5.5	2.20
	4	4.7	1.32
	5	5.2	1.86
	6	5.3	1.90
	7	4.2	0.98

Appendix D (Continued). Fork-lengths (cm) and wet weights (g) for 20 experimental groups of 7 juvenile coho salmon (*n* = 140).

Group	Fish	Fork-length (cm)	Wet weight (g)
13	1	5.4	2.08
	2	5.8	2.59
	3	5.1	1.61
	4	5.4	1.94
	5	5.7	2.07
	6	6.0	2.55
	7	4.8	1.38
14	1	6.4	3.49
	2	5.5	2.10
	3	5.6	2.15
	4	5.2	1.72
	5	4.4	1.13
	6	4.7	1.40
	7	5.1	1.62
15	1	5.3	1.74
	2	4.6	1.17
	3	5.4	1.77
	4	5.9	2.75
	5	5.7	2.31
	6	4.7	1.31
	7	5.8	2.56

Appendix D (Continued). Fork-lengths (cm) and wet weights (g) for 20 experimental groups of 7 juvenile coho salmon ($n = 140$).

Group	Fish	Fork-length (cm)	Wet weight (g)
16	1	6.2	3.24
	2	5.4	2.39
	3	6.6	3.35
	4	5.0	1.79
	5	5.8	2.61
	6	6.1	3.01
	7	5.5	2.13
17	1	6.2	3.05
	2	5.4	2.07
	3	6.5	3.57
	4	5.1	1.74
	5	5.6	2.50
	6	5.0	1.71
	7	6.0	2.83
18	1	6.8	3.55
	2	5.4	1.92
	3	6.1	2.84
	4	6.2	3.12
	5	6.1	2.85
	6	5.7	2.18
	7	6.3	3.44

Appendix D (Continued). Fork-lengths (cm) and wet weights (g) for 20 experimental groups of 7 juvenile coho salmon ($n = 140$).

Group	Fish	Fork-length (cm)	Wet weight (g)
19	1	5.6	2.10
	2	6.2	2.89
	3	6.5	3.55
	4	5.4	1.90
	5	5.4	1.84
	6	5.9	2.52
	7	5.7	2.43
20	1	5.7	2.28
	2	6.3	3.41
	3	5.3	1.69
	4	6.7	3.74
	5	6.0	2.54
	6	5.2	1.37
	7	5.9	2.69

Appendix E. Means and ranges of fork-lengths (cm) and wet weights (g) for 20 experimental groups of juvenile coho salmon.

	Fork-length		Wet weight	
Group	Mean	Range	Mean	Range
1	5.5	0.6	1.89	0.78
2	5.3	1.1	1.98	1.33
3	5.6	0.7	1.91	0.54
4	5.4	1.2	1.74	1.04
5	5.5	1.0	1.97	1.05
6	5.6	1.8	1.97	2.16
7	5.8	1.0	2.25	1.34
8	5.6	1.1	1.89	1.42
9	5.5	0.5	1.84	0.59
10	5.3	1.3	1.61	1.07
11	5.1	1.8	1.86	1.68
12	5.2	2.0	1.96	2.30
13	5.5	1.2	2.03	1.21
14	5.3	2.0	1.94	2.36
15	5.3	1.3	1.94	1.58
16	5.8	1.6	2.65	1.56
17	5.7	1.5	2.50	1.86
18	6.1	1.4	2.84	1.63
19	5.8	1.1	2.46	1.71
20	5.9	1.5	2.53	2.37

Appendix F. Times (hrs) and ambient photosynthetically active radiation (PAR) levels (mmol/m^2/sec) of UVR-absent and UVR-present trials for 20 experimental groups of juvenile coho salmon.

	Time of trial		PAR level	
Group	UVR-absent	-present	UVR-absent	-present
1	1445	1345	1607	1718
2	1345	1255	1718	1774
3	1135	1050	1709	1620
4	1345	1445	1752	1643
5	1145	1410	1749	1646
6	1430	1330	1695	1797
7	1245	1145	1727	1749
8	1145	1245	1749	1727
9	1455	1400	1528	1660
10	1400	1455	1660	1528
11	1150	1250	1688	1750
12	1250	1150	1750	1688
13	1240	1335	1722	1715
14	1300	1150	1747	1672
15	1355	1300	1691	1747
16	1235	1335	1662	1657
17	1335	1235	1657	1662
18	1330	1125	1680	1574
19	1125	1330	1574	1680
20	1125	1330	1574	1680

Appendix G. Rates and mean durations (sec) of Strikes in 30-minute, UVR-absent and UVR-present trials for 20 experimental groups of juvenile coho salmon.

	Rate of Strikes		Mean Strike duration	
Group	UVR-absent	-present	UVR-absent	-present
1	55	37	1.073	1.027
2	24	79	1.167	1.000
3	39	65	1.077	1.015
4	49	60	1.224	1.217
5	39	9	1.051	1.000
6	29	44	1.862	1.409
7	83	89	1.494	1.034
8	75	46	1.347	1.435
9	9	53	1.444	1.528
10	25	15	1.200	1.000
11	62	23	1.532	1.261
12	40	36	1.125	1.083
13	63	88	1.238	1.148
14	89	92	1.112	1.337
15	79	103	1.177	1.359
16	19	99	1.211	1.192
17	51	36	1.196	1.750
18	13	10	1.154	1.100
19	29	44	1.000	1.114
20	93	43	1.204	1.535

Appendix H. Rates and mean durations (sec) of Chases in 30-minute, UVR-absent and UVR-present trials for 20 experimental groups of juvenile coho salmon.

	Rate of Chases		Mean Chase duration	
Group	UVR-absent	-present	UVR-absent	-present
1	59	69	1.780	1.754
2	53	153	1.642	1.464
3	83	67	1.398	1.164
4	43	73	1.651	1.918
5	42	7	1.452	1.571
6	22	42	1.864	2.476
7	85	64	2.200	2.391
8	53	76	1.830	2.066
9	20	42	1.900	1.833
10	34	28	1.676	1.964
11	65	50	2.031	2.300
12	105	36	1.752	1.917
13	67	69	1.582	1.536
14	142	208	1.352	1.606
15	70	70	1.586	1.629
16	22	91	1.045	1.121
17	27	30	1.593	1.367
18	14	16	1.214	1.875
19	37	45	1.351	1.644
20	79	64	1.405	1.516

Appendix I. Rates and mean durations (sec) of Approaches in 30-minute, UVR-absent and UVR-present trials for 20 experimental groups of juvenile coho salmon.

	Rate of Approaches		Mean Approach duration	
Group	UVR-absent	-present	UVR-absent	-present
1	91	44	1.374	1.318
2	115	85	1.748	1.082
3	76	89	1.237	1.135
4	103	88	1.573	1.364
5	76	46	1.500	1.696
6	63	66	1.794	1.803
7	44	17	1.750	1.294
8	61	98	2.246	1.398
9	59	66	1.678	1.697
10	70	52	1.414	1.827
11	109	114	1.716	1.702
12	94	44	1.574	1.864
13	90	114	1.511	1.412
14	105	82	1.476	1.329
15	110	109	1.482	1.817
16	69	89	1.565	1.191
17	70	77	1.714	1.805
18	63	62	1.302	1.532
19	64	54	1.203	1.426
20	149	126	1.550	1.476

Appendix J. Rates and mean durations (sec) of Feeding Efforts in 30-minute, UVR-absent and UVR-present trials for 20 experimental groups of juvenile coho salmon.

	Rate of Feeding		Mean Feeding duration	
Group	UVR-absent	-present	UVR-absent	-present
1	26	17	1.038	1.059
2	18	27	1.056	1.000
3	33	51	1.000	1.000
4	42	24	1.000	1.000
5	13	17	1.154	1.000
6	11	15	1.000	1.000
7	12	14	1.000	1.000
8	9	29	1.000	1.000
9	27	25	1.074	1.000
10	39	29	1.000	1.000
11	19	27	1.000	1.037
12	42	37	1.000	1.000
13	41	23	1.024	1.000
14	28	28	1.000	1.000
15	42	27	1.024	1.000
16	124	79	1.008	1.025
17	47	64	1.000	1.000
18	81	37	1.000	1.000
19	42	36	1.000	1.000
20	33	29	1.000	1.069

Appendix K. Rates and mean durations (sec) of agitated swimming episodes in 30-minute, UVR-absent and UVR-present trials for 20 experimental groups of juvenile coho salmon.

	Rate of episodes		Mean episode duration	
Group	UVR-absent	-present	UVR-absent	-present
1	33	70	4.909	4.571
2	17	1	5.647	2.000
3	1	0	5.000	0.000
4	0	63	0.000	6.159
5	11	6	5.727	5.000
6	0	3	0.000	7.333
7	12	21	3.417	6.190
8	79	34	5.342	5.559
9	2	14	3.000	6.286
10	8	12	5.625	3.667
11	44	13	8.864	13.231
12	24	38	32.292	10.711
13	1	6	1.000	7.667
14	0	12	0.000	6.083
15	6	49	4.333	5.490
16	2	4	1.500	1.250
17	5	8	3.000	2.750
18	4	11	3.250	3.273
19	0	1	0.000	10.000
20	0	0	0.000	0.000