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THE PHOTIC ENVIRONMENT OF A SALMONID NURSERY LAKE

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Summary

The spectral characteristics of Lake Cowichan (Vancouver Island) were examined using a LiCor underwater spectroradiometer. The results were analyzed in terms of salmonid vision with special emphasis placed on the ultraviolet part of the spectrum. Irradiance measurements were taken by SCUBA divers every 3 m from 18 m to the surface at each of seven locations. The measurements at each depth consisted of four scans from 300 to 850 nm of downwelling, upwelling and horizontal light in the sun and antisun directions. The study covered different times of day and variable atmospheric conditions. According to predictions from the absorptive properties of water molecules and scattering by these and suspended particulates, it was found that the ultraviolet part of the spectrum was the least transmitted. The light field varied in intensity and dominant wavelengths depending on direction and time of day. The relative proportion of ultraviolet, short and middle wavelengths with respect to the entire spectrum peaked during crepuscular periods; the opposite was true for long wavelengths. An analysis of the irradiance values with respect to salmonid vision showed that there was enough light to stimulate all the photoreceptor mechanisms found in juvenile salmonid retinae (sensitive to ultraviolet, short, middle and long wavelengths) at all depths studied. Nevertheless, 18 m was found to be the limiting depth for stimulation of the ultraviolet cone mechanism, which is required for perception of ultraviolet polarized light. This depth restriction may be linked to the observed salmonid movements close to the surface during crepuscular periods.

Introduction

Recent discoveries showing that salmonids possess ultraviolet photoreceptors (brown trout, *Salmo trutta*, Bowmaker and Kunz, 1987) and that they are capable of detecting ultraviolet radiation (rainbow trout, *Oncorhynchus mykiss* Hawryshyn *et al.* 1989) have led to hypotheses regarding its use in nature. Among these hypotheses, contrast enhancement between target and background through

Key words: spectral irradiance, ultraviolet light, photoreceptor, phytoplankton, salmonids, nursery lake.

ultraviolet vision has been suggested as a means for improving foraging performance in larval fishes (Bowmaker and Kunz, 1987; Loew and McFarland, 1990). Also, ultraviolet vision and, in particular, detection of ultraviolet polarized light, may be a navigational tool used by juvenile salmonids leaving nursery lakes and coastal areas on their way to the open ocean (Hawryshyn *et al.* 1990). The spectral characteristics of these inshore and coastal environments, however, have not been fully examined.

The study of ultraviolet transmission in water bodies has concentrated on the open waters of oligotrophic oceans (Smith and Baker, 1979). Instead, the juvenile stage of some salmonids (i.e. sockeye salmon, *Oncorhynchus nerka*, cutthroat trout, *Oncorhynchus clarki*, steelhead trout, *Oncorhynchus mykiss*) may take place in mesotrophic and/or eutrophic lakes. These water bodies usually contain high concentrations of chlorophyll and dissolved organic matter (DOM) which control the seasonal variations of light transmission in them (Prezelin *et al.* 1991). The visual environment experienced by juvenile salmonids of some species is very different from what they encounter as adults in the open ocean; the spectral characteristics of the open ocean are highly dependent on the water molecules alone (Jerlov, 1976; Kirk, 1983). Nevertheless, it is during their early life history in nursery lakes that juvenile salmonids possess ultraviolet vision, a property that appears to be lost during development (Hawryshyn *et al.* 1989; Beaudet *et al.* 1991). Thus, it is important to examine the availability of ultraviolet light in nursery lake environments of these Pacific salmonid species.

The validity of hypotheses regarding the use of ultraviolet vision in nature depends on the confirmation of two observations: first, the light stimuli to which fish respond in laboratory experiments must match the intensity cues present in the environment; second, the presentation of visual cues alone during laboratory experiments simulating natural conditions should result in the predicted fish behaviour. So far, none of these conditions has been met for waters representative of salmonid nursery lakes. Results from laboratory studies describing salmonid behaviour in response to light stimuli of defined energy and wavelengths (Hawryshyn *et al.* 1989, 1990) have not been compared to ecologically relevant light intensities present in the natural environment. It was therefore the goal of this study to characterize the spectra of available light in Lake Cowichan, a nursery lake for various species of Pacific salmonids. In the following study, we specifically examine the distribution of light from the various parts of the spectrum (ultraviolet, short, middle and long wavelengths) with respect to depth and direction of observation, how the light field varies with time of day, and how these observations relate to salmonid visual capabilities and hypotheses concerning utility of ultraviolet vision in nature.

We used an underwater spectroradiometer to measure irradiance at several depths and at different locations in Lake Cowichan. Some measurements lasted for periods of 24 consecutive hours to examine changes in the light field with time of day. In particular, we were interested in the spectral characteristics of Lake Cowichan during crepuscular periods since, at these times, the light field is expected to shift towards shorter wavelengths (Rayleigh and Mie scattering, Van de Hulst, 1957). To assess the amount of light available for stimulation of salmonid photoreceptors, the spectral irradiance values obtained were corrected for absorption of the four pigments found in juvenile salmonid retinae [ultraviolet, short wavelength (blue), middle wavelength (green) and long wavelength (red)] and for ocular media transmission of rainbow trout, *O. mykiss*. This provided us with values representative of the intensities of light available for photoreception in salmonids. The set of values obtained, therefore, constitutes an estimate of the region in the water column that can be used for cone photoreception. We then compared the amount of ultraviolet light available in nature for stimulation of salmonid photoreceptors to irradiance values used in the laboratory (Hawryshyn *et al.* 1989). This permitted us to determine whether there is enough ultraviolet light penetrating Lake Cowichan to drive visually mediated behaviour.

Materials and methods

The site of study was Lake Cowichan (Vancouver Island, latitude 48°40–55′N, longitude 124°5–25′W). We established seven sampling stations to compare regional differences in types of water that may arise from proximity to outflows, inflows or differing catchment areas (Fig. 1).

Spectral irradiance measurements were taken using an underwater LiCor spectroradiometer (LI-1800 UW model, LiCor instruments, Lincoln, Nebraska). This instrument consists of three major components: a filter wheel, a holographic monochromator and a silicon detector with related electronics. Light enters the LI-1800 through a standard cosine collector and is directed through the filter wheel before entering the monochromator. The filter wheel contains seven order-sorting filters which eliminate second-order harmonics. The use of the seven filters also enhances stray light rejection by filtering out light that is not in the same spectral region as that being examined. This results in improved performance compared to

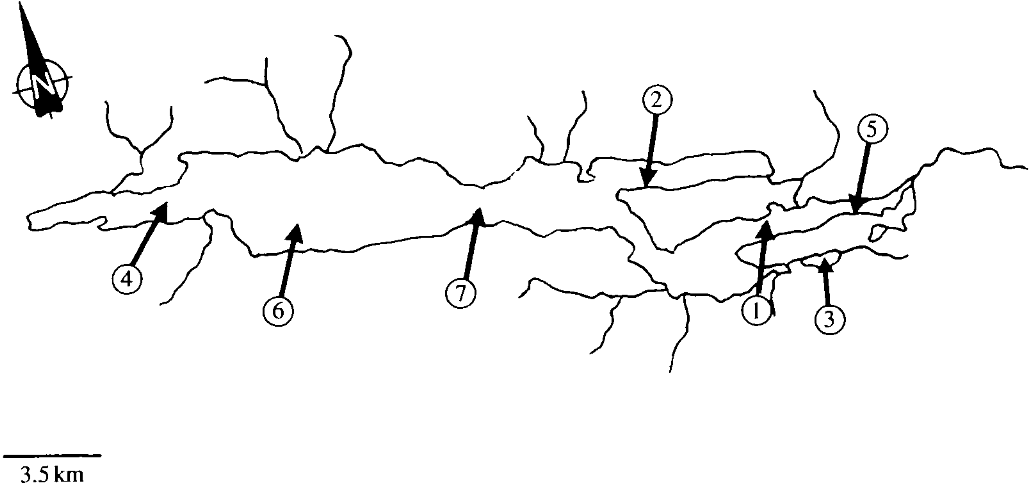

Fig. 1. Map of Lake Cowichan showing the seven stations of study.

normal, single-monochromator systems (Biggs, 1984). There is also a dark reference (zero reading) on the filter wheel that is substracted from any output from the detector. The data obtained thus contains minimal noise levels. Our LI-1800 has a holographic grating bandwidth of 4 nm; accurate measurements can therefore be obtained from 300 to 850 nm. The irradiance values obtained are in quantal units (photons $m^{-2} s^{-1} nm^{-1}$), each scan collecting light over an angle of 180° (spectral irradiance).

Spectral irradiance measurements were taken by SCUBA divers submerging the LiCor spectroradiometer to 18 m depth and bringing it towards the surface at 3 m intervals. Four scans ranging the spectrum from 300 to 850 nm were taken at each depth. The scans show spectral irradiance of downwelling, upwelling and horizontal light in the sun and antisun directions at 5 nm intervals (Fig. 2). The spectroradiometer was connected to a portable computer situated at the surface and operated by the boat tender/researcher. This person communicated with the divers using a surface-to-diver communication system and controlled the execution of the scans through the computer. An air scan was taken at the end of each dive and used to correct the irradiance values found under water for differences in weather conditions among stations. This was done by dividing the irradiance values at each depth by the irradiance at the surface (air scan). An analysis of variance (ANOVA) and Duncan's paired-grouping test were performed to detect differences in light intensity (spectral irradiance) among stations. Downwelling light extinction coefficients were calculated for each station using the formula (adapted from Tyler and Preisendorfer, 1962):

$$K[(<Z_1 + Z_2)>/2] = [1/(Z_2 - Z_1)]\ln[H(Z_1)/H(Z_2)]\,,$$

where, $K[(<Z_1 + Z_2)>/2]$ is the extinction coefficient for light travelling from depth Z_1 to depth Z_2 (in m^{-1}), and $H(Z_1)$ and $H(Z_2)$ are the downwelling irradiances at depths Z_1 and Z_2, respectively.

Quantum integrations over the ultraviolet (300–400 nm), short (401–470 nm), middle (471–570 nm) and long wavelength (571–765 nm) parts of the spectrum were carried out to show differences in relative intensities at particular times during the day. The ranges for each type of light correspond to the parts of the spectrum where the probability of quantal catch by each of the corresponding pigments (absorption) is highest (Fig. 3). Relative intensities were obtained by dividing the total amount of a certain type of light (e.g. ultraviolet) by the total spectrum (see Figs 7, 8, 9).

We used an eighth-order polynomial template for vertebrate cone absorption to correct the irradiance values measured for absorption of the four pigments found in juvenile salmonid retina (Bernard, 1987; personal communication). The polynomial template yielded normalized absorbance curves for each pigment as a function of the ratio of wavelength of maximum absorbance to wavelength (Fig. 3). Absorptance values were then generated using the equation:

$$\text{absorptance} = 1 - \text{transmission}\,,$$

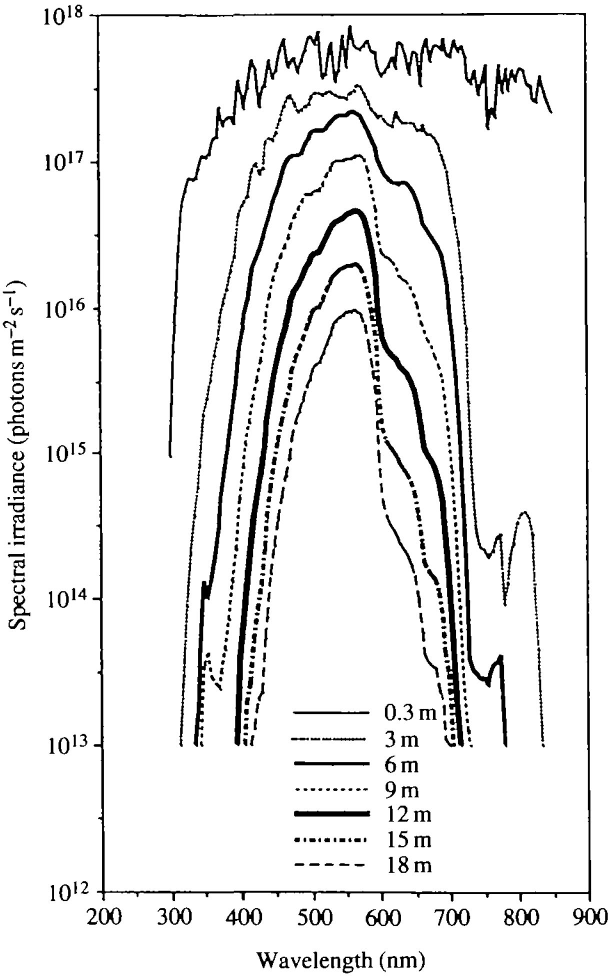

Fig. 2. Downwelling spectral irradiance, at different depths, from 18 m to the surface at location 1 (27th of June 1991, 10:00–10:40 h). Each curve corresponds to one spectral scan. The scans were taken under clear sky conditions [sun's altitude: 39° (start) to 52° (end)]. Mild winds created surface ripples, which are responsible for the peaks in the scan taken at 0.3 m. Similar trends with depth were also found under cloudy skies; however, in these cases the spectral irradiance values were lower and dependent on the thickness of cloud cover.

where $$\log_{10}(\text{transmission}) = -\text{absorbance}.$$

Thus, multiplication of the spectral irradiance values by these normalized absorptances corrected for the differential absorptance of each pigment over its active range. The resulting values, now corrected for pigment absorption, were multiplied by coefficients giving the percentage of light transmitted for each wavelength through the ocular media of small rainbow trout, *O. mykiss*

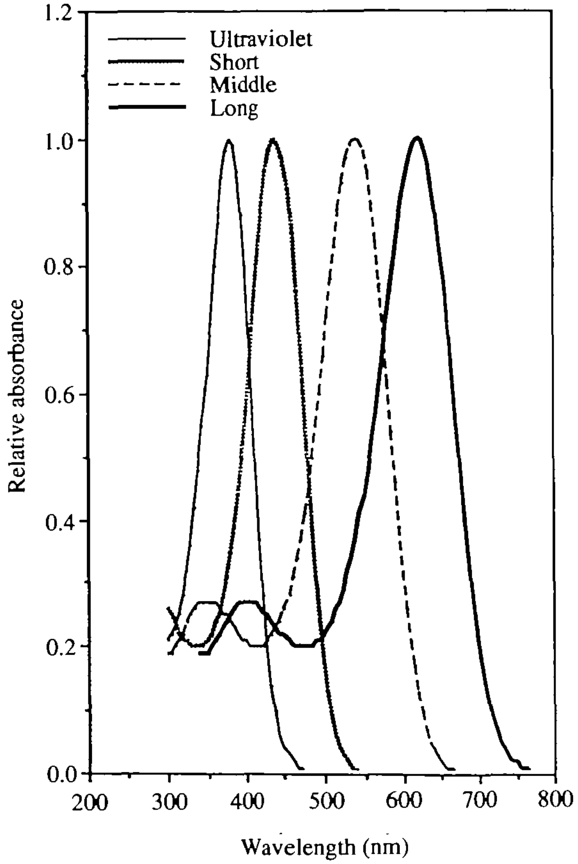

Fig. 3. A plot of the normalized absorbance spectra of each pigment in juvenile salmonid retina (rainbow trout) calculated from Bernard's (1987; personal communication) vertebrate cone template. Notice the ranges of maximum probability of quantal catch for the α absorption bands of each pigment (i.e. the range of wavelengths for which the main peak of a given pigment has the highest relative absorbance) and for the β absorption bands (the smaller peaks at shorter wavelengths) of the middle and long wavelength pigments. These ranges define the integration limits for the four types of light studied (ultraviolet, short, middle and long wavelengths).

(Hawryshyn *et al.* 1989). The modified irradiance values obtained after these two corrections represent the relative amounts of photons of each wavelength that are available to stimulate the cone photoreceptors in the fish retina. This, we denote, the 'available photon irradiance'. The values are relative because the actual absorption will depend, among other factors, on the relative numbers of each type of photoreceptor in the retinal region being illuminated. Quantum integrations over the full absorption spectrum of each pigment were then performed to obtain the total available photon irradiance from each type of light at each depth and in each direction.

Ultraviolet light is absorbed by the Schiff base linkage of the chromophores in salmonids (β absorption bands, Fig. 3). However, the sensitivity of the response to ultraviolet polarized light differs for these β absorption bands and ultraviolet cones (Hawryshyn and McFarland, 1987). Stimulation of the β bands of the middle and red cone mechanisms is an independent process from stimulation of the ultraviolet cone α band because these three types of cones are different physical entities in the retinal mosaic. Thus, neural processing of ultraviolet polarized light from two different cones may constitute a system for the discrimination of ultraviolet polarized light intensity and plane of polarization. Because of their potential role in orientation of young salmonids (Hawryshyn *et al.* 1990), further integrations were performed restricting the limits to the absorption ranges of these β bands (310–390 nm and 390–450 nm for the middle and long wavelength mechanisms respectively, see Fig. 3). The purpose of these integrations was to examine to what depths these secondary bands could be stimulated.

Water samples from different depths were collected at stations 1 and 2. These samples were treated for chlorophyll *a*, *b* and *c*. Pigment concentrations were obtained trichromatically using the procedure in Jeffrey and Humphrey (1975) for mixed phytoplankton communities. This procedure allowed the detection of possible relationships between phytoplankton concentrations at specific depths and changes in the spectral irradiance curves.

All the mathematical analyses were carried out using the LiCor spectroradiometer software and the SAS (version 5) statistical package.

Results

The light characteristics at most locations in Lake Cowichan were similar (Table 1), the differences arising to a great extent from the variable catchment areas (see footnote in Table 1). The light extinction coefficients show that ultraviolet is the type of light most attenuated (Table 2). With increasing depth, the light field exhibits its maximum in the mid-wavelength spectrum (around 560 nm, see Fig. 2). Owing to the small standard errors associated with the extinction coefficients, we are led to conclude that these trends in light transmission are representative of all the stations studied.

Analysis of water samples collected from stations 1 and 2 demonstrated chlorophyll *a* to be generally the most abundant pigment for all depths (Table 3). An abrupt rise in the concentration of this pigment occurs between 9 and 12 m in location 1.

The attenuation of downwelling irradiance with depth is shown in Fig. 2. Similar curve shapes were found at all the other locations for each orientation. Spectral irradiance values were usually observed to decrease in the following order: downwelling light, horizontal light (sun's direction), horizontal light (antisun's direction) and upwelling light (Fig. 4). In one special circumstance, deviations from these results were obtained (Fig. 5). It can be observed in this figure that the last scan (which was taken 1.5 m from the bottom) overlaps the previous one at

Table 1. *Light characteristics at locations on Lake Cowichan*

Station*	Mean	Grouping
5	0.25805	*A*
2	0.18010	*B*
6	0.13704	*C*
7	0.11251	*C*
4	0.10517	*C*
3	0.10374	*C*
1	0.05839	*D*

At each sampling location, the spectral irradiance values at 3 and 6 m were divided by the spectral irradiance at the surface. These values were then averaged to give the mean value at each station.

Values with the same letter grouping are not significantly different (Duncan's paired-grouping test). It can be observed that most stations share similar water characteristics.

*Station 2 is located in a pristine area and the current flowing is quite strong. Station 5 is located near the outflow of the lake. These two characteristics (unaltered catchment area and outflow point) may explain the high light transmission observed for these stations, if we consider the lake to be a sink of nutrients and particulates (Wetzel, 1975). Station 3 is a shallow lake (8.5 m depth) and the catchment area surrounding it has been extensively logged. Station 1 is bordered by resorts and the city's sewage pipe dumps its contents in these waters.

various wavelengths. The bottom, situated at 8.5 m, was composed of fine-grained sand which is a highly reflective material (Chen and Nagaraja Rao, 1968). Such a substratum is also important in terms of fish vision because it can produce up to 40 % polarized light when illuminated with diffuse light, and this may enhance target–background contrast (Loew and McFarland, 1990).

A mathematical analysis of the irradiance curves shows that light not only differs in intensity with direction, but also in spectral composition (Fig. 6). Near the surface, short wavelengths constitute a major part of the light in the horizontal antisun's direction. In the horizontal sun's and downwelling directions the light field peaks in the middle to long wavelengths. Upwelling light is composed primarily of middle wavelength photons, which is also the case in all directions with increasing depth.

The spectral characteristics of Lake Cowichan during crepuscular periods exhibit an increase towards shorter wavelengths. The relative intensities of ultraviolet and blue light peak prior to sunrise and immediately after sunset (Fig. 7). The opposite trend was observed for the long wavelengths. The middle wavelength part of the spectrum is stable for most of the day but exhibits relative intensity peaks of short duration during crepuscular periods. These peaks are the result of wavelengths from 470 to 500 nm, which form the short wavelength part of the middle wavelength pigment integration spectrum. We examined the spectral characteristics at dawn with higher temporal resolution (Fig. 8). Although the curves follow previously mentioned trends, it can be further observed that the long wavelength part of the spectrum exhibits a local peak between approximately 4.6

Table 2. *Light extinction coefficients for the downwelling ultraviolet and short, middle and long wavelength parts of the spectrum and for total spectral irradiance*

Depth (m)	Light	Extinction coefficient (m^{-1})	S.E. (m^{-1})
1.5	Ultraviolet	1.147	0.078
	Short	0.492	0.057
	Middle	0.276	0.068
	Long	0.537	0.095
	Total	0.487	0.077
4.5	Ultraviolet	0.914	0.040
	Short	0.457	0.027
	Middle	0.238	0.036
	Long	0.356	0.032
	Total	0.306	0.032
7.5	Ultraviolet	0.996	0.053
	Short	0.474	0.025
	Middle	0.309	0.026
	Long	0.376	0.029
	Total	0.339	0.027
10.5	Ultraviolet	1.143	0.019
	Short	0.466	0.009
	Middle	0.281	0.016
	Long	0.364	0.047
	Total	0.297	0.023
13.5	Ultraviolet	0.653	0.009
	Short	0.427	0.017
	Middle	0.234	0.033
	Long	0.326	0.015
	Total	0.306	0.038
16.5	Ultraviolet	–	–
	Short	0.347	0.044
	Middle	0.186	0.026
	Long	0.272	0.018
	Total	0.203	0.032

The values, calculated for the various depths studied, represent averages from the seven stations.

A dash indicates that the values could not be computed as the orginal irradiance data were within the noise band of the spectroradiometer (only irradiance values equal to or bigger than 10^{12} photons $m^{-2} s^{-1}$ were considered).

and 6 h. The peaks in ultraviolet light during crepuscular periods can be observed more accurately by plotting the relative intensity of this type of light independently (Fig. 9).

Correction of the irradiance values for ocular media transmission and pigment

Table 3. *Chlorophyll values (in mg ml^{-1}) and standard errors for stations 1 and 2*

Depth (m)	Station	Chlorophyll *a*	Chlorophyll *b*	Chlorophyll *c*
3	1	0.326±0.097	0.043±0.019	0.395±0.227
3	2	0.335±0.129	0.773±0.302	0.491±0.849
6	1	0.816±0.225	0.048±0.024	0
6	2	0.501±0.254	0.846±0.324	0.064±0.796
9	1	12.9±3.04	1.46±0.553	0.756±0.621
12	1	14.1±1.56	0	0
15	1	3.98±0.396	1.87±0.151	2.35±0.024
18	1	11.2±5.03	0.743±0.927	0.708±1.20

Values are mean±S.E. obtained from averages of two samples.

absorption of rainbow trout results in the bar graphs shown in Fig. 10. In laboratory experiments, fish are presented with light stimuli of specific wavelengths and the responses are assessed electrophysiologically (e.g. Beaudet *et al.* 1991) or behaviourally (e.g. Hawryshyn *et al.* 1989). After a period of background adaptation that isolates the sensitivity of the ultraviolet photoreceptor mechanism, salmonids have been shown to respond to light stimuli of the order of 10^{13} photons m^{-2} s^{-1} (using 380 nm stimulus, Beaudet *et al.* 1991; Hawryshyn *et al.* 1989). The middle and long wavelength photoreceptor mechanisms are the least sensitive and may require up to 100 times the previous intensities to be stimulated (Hawryshyn, 1991). Nevertheless, Fig. 10 shows that, in Lake Cowichan, there is enough downwelling light to stimulate all the photoreceptor mechanisms at all depths studied. However, as is the case for the ultraviolet mechanism (Fig. 10), the β band of the mid-wavelength mechanism appears to have a stimulation threshold depth at 18 m (Fig. 11). These conclusions were reinforced by calculating the available light at 19 m, given an ultraviolet extinction coefficient of 0.65 m^{-1} (Table 2; 13.5 m depth), and finding it insufficient in both cases. Ultraviolet photoreceptor stimulation by upwelling light is restricted to depths less than 9 m (the value at 15 m is questionable because of the high standard error associated with it), whereas reception from sidewelling light is restricted to depths smaller than 18 m. At all depths, the middle and long wavelength receptors are the most likely to be stimulated. It is important to realize that these and previous conclusions are based on results from statistical tests using pool data from different locations. Analysis of specific locations alone may yield significant results at greater depths.

Discussion

The average extinction coefficients found for the various parts of the visual spectrum are at least five times those published for blue waters of the open ocean (Lenoble, 1954; Morel, 1965). Similarly, the extinction coefficients for total

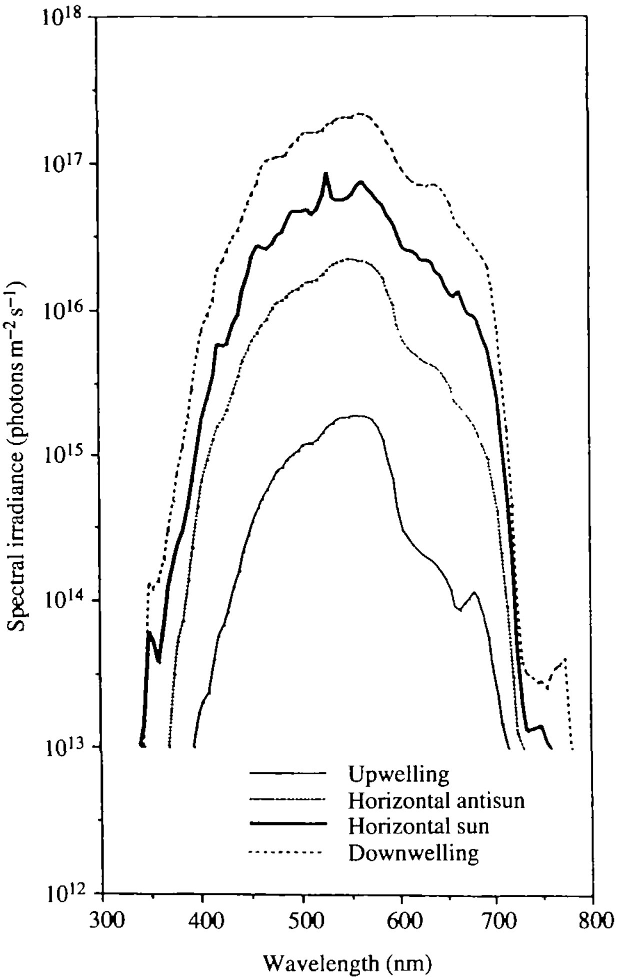

Fig. 4. Differences in light intensity with direction for location 1 at 6 m depth. Atmospheric conditions were the same as those in Fig. 2. The same trends were detectable at all depths studied. However, with increasing depth, the differences became smaller and the light more monochromatic (see Fig. 6).

irradiance are much higher than those calculated for ultraoligotrophic lakes (Table 2; Smith *et al.* 1973). Lake Cowichan would be classified as a mesotrophic lake (Wetzel, 1975) or as having waters of type 1 (Jerlov, 1976). These discrepancies between Lake Cowichan and blue waters of oligotrophic systems are essentially due to the higher concentrations of phytoplankton, DOM, organic and inorganic particulates in Lake Cowichan (see Heinerman and Ali, 1988, for lignin effects in mesotrophic lakes).

The tight link between phytoplankton populations and available light is exemplified by the high ultraviolet and blue extinction coefficients found at 10.5 m

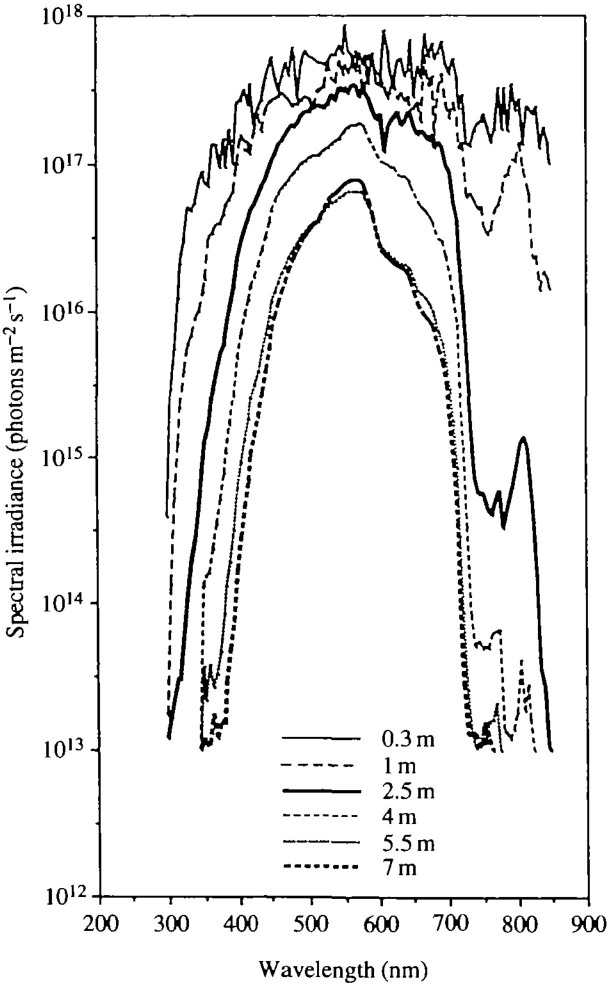

Fig. 5. Downwelling spectral irradiance at station 3 (19th of June 1991, 11:04 h). The scans were taken under clear sky conditions. Notice the increase in irradiance at 7 m due to reflected light from the bottom of the lake.

Fig. 6. Average spectral irradiance and associated standard errors for each type of light from all stations. UP, upwelling light; HA, horizontal antisun; HS, horizontal sun; DO, downwelling light. Each depth plot is divided into these four orientations and, within each orientation, bar graphs show the amounts of ultraviolet, short, middle and long wavelengths present in the water column. In surface waters, light in the horizontal antisun direction contains a large quantity of scattered short-wavelength photons. However, downwelling and horizontal sunlight is composed mostly of middle to long wavelength radiation. Upwelling light peaks in the middle wavelengths, which is also the case in every direction with increasing depth.

(Table 2), and the presence of a bloom at this depth in location 1 (Table 3). Although a full spectrum of chlorophyll concentrations with depth is only available for location 1, we believe these results to be representative of the entire lake for

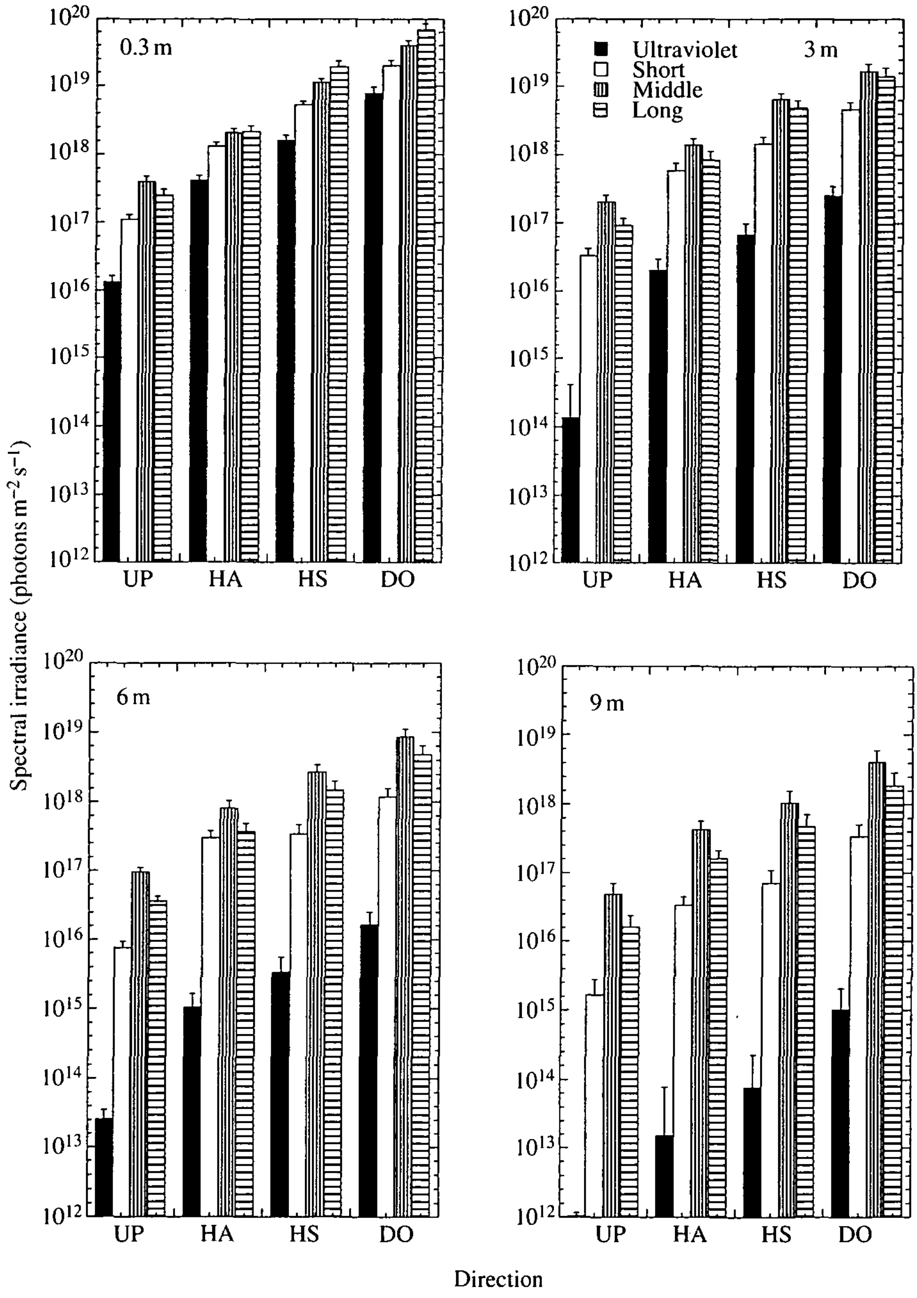

Fig. 6

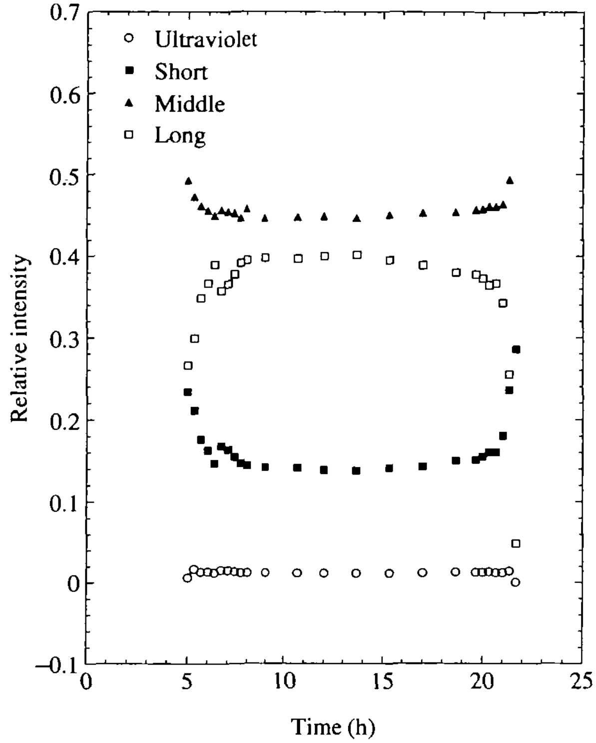

Fig. 7. Relative intensity (irradiance) of each type of light to the total spectrum (300–850 nm) (20th of June 1991). The downwelling scans from which the points derive were taken with the spectroradiometer lying at 3 m depth facing the surface in station 1. The atmospheric conditions were complete overcast with irregular periods of rainfall. Shorter (ultraviolet and short) and middle wavelengths exhibit peaks during crepuscular periods and decrease in relative intensity during the day; the opposite trend can be observed for the long wavelength part of the spectrum. Long wavelength light exhibits local maxima at dawn and to a lesser extent at dusk. Sunrise and sunset occurred at 05:11 and 21:19 h, Pacific Standard Time (Meteorological Information Center, Sidney, BC).

two reasons: light penetration at the various locations is similar (Table 1) and the lake was stratified at the time of the study. The attenuation of middle wavelength radiation peaks around 7.5 m is probably the result of reflection from the first phytoplankton layer (located somewhere between 6 and 9 m) (Davies-Colley *et al.* 1988). However, once in the phytoplankton layer (depth 10.5 m), this type of light is the least attenuated. A possible explanation is that multiple scattering by phytoplankton cells is concentrating middle wavelength light in the downwelling direction (Mie theory, Van de Hulst, 1957).

The differences in light transmission for the various parts of the spectrum can also be explained in terms of scattering theory (Jerlov, 1976). Small particles scatter most strongly the ultraviolet and short wavelengths, while water molecules

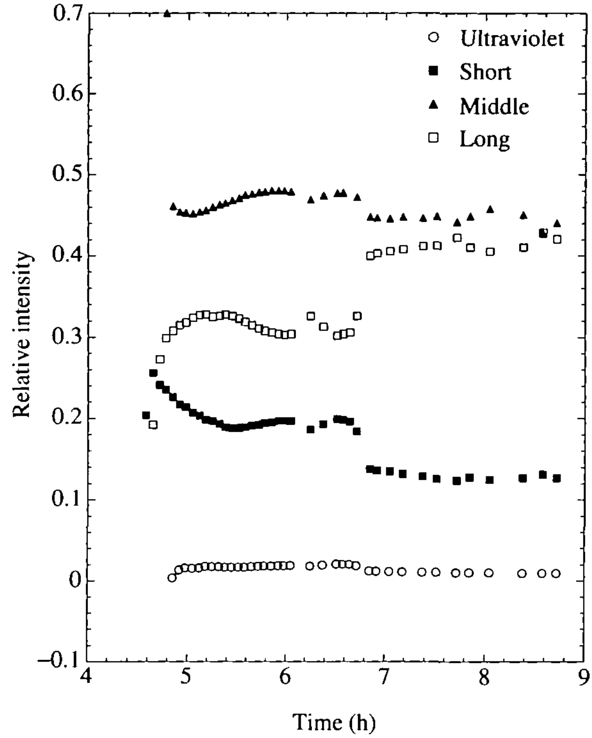

Fig. 8. Spectral irradiance ratios of each type of light to the total spectrum at dawn (28th of June 1991). Same collecting set-up as in Fig. 7. Sunrise was predicted at 05:13 h Pacific Standard Time (Meteorological Information Center, Sidney, BC). However, local topography may have impeded the appearance of the sun until 6.6 h, explaining the rapid changes in slope observed in the curves at this time. The weather conditions were clear skies for the entire period. A local maximum in long wavelengths parallels the peaks from ultraviolet, short and middle wavelengths. This local peak is slightly displaced in time with respect to the shorter wavelength maxima, as would be expected from the gradual change in pathlength of incoming solar radiation.

have absorption bands in the ultraviolet and long wavelength parts of the spectrum (Hecht and Zajac, 1974). Furthermore, any DOM present will absorb ultraviolet light extensively. Thus, in accordance with published results for the open ocean, the ultraviolet region of the spectrum was the most attenuated in our study. Attenuation of the short and long wavelength parts of the spectrum can be accredited mostly to absorption by the various chlorophylls (Wetzel, 1975).

Further analysis of the irradiance results shows that the light transmitted varies in magnitude and spectral composition depending on the direction, the depth of observation and the time of day (see Jerlov, 1976; McFarland and Munz, 1975). Ultraviolet and short wavelengths are preferentially scattered by small particles and water molecules (Rayleigh, 1889). However, ultraviolet light is also absorbed more extensively than short wavelengths in the atmosphere and in the water

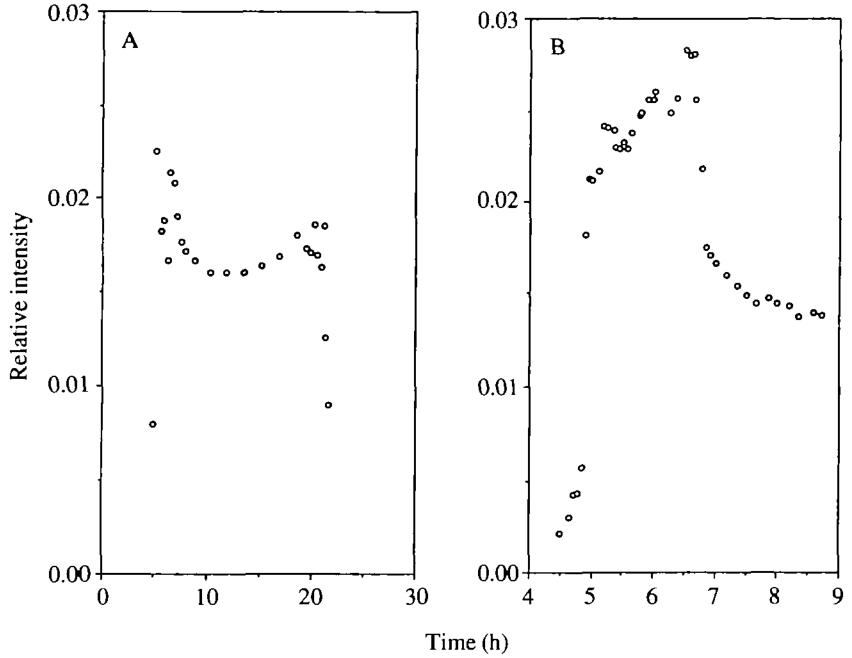

Fig. 9. (A) Relative intensity of ultraviolet light for an entire day and (B) at dawn. Replotted from Figs 7 and 8.

column. As a result, the amount of ultraviolet light in the horizontal antisun direction is smaller than the amount of short wavelength light (Fig. 6). Downwelling light and horizontal light in the sun's direction exhibit maxima in the middle to long wavelength range. This is due to sunlight impinging directly on the cosine collector, longer wavelengths being scattered the least through the atmosphere. Upwelling light is maximal in the middle wavelengths as a result of scattering from phytoplankton and algal substrates.

The presence of backgrounds differing in hue with direction of observation has important consequences for the perception and tracking of objects in the water column. For instance, detection of dark objects is usually favoured against a bright background. Thus, a fish's position that would maximize illuminance in the direction of observation (i.e. towards the sun) would be most beneficial. However, the conspicuousness of lighter objects is often increased on a dark background, in which case vision in the antisun direction would be more effective. Furthermore, it has been suggested that reflected polarized light from fish scales may also be used by other fish to detect targets on dark backgrounds (a diffusing background producing less polarized light; Denton and Nicol, 1965). These different scenarios suggest that an ideal orientation for maximal perception of light cues in surface waters is dependent on visual task. Fish may compromise between the previous advantages by travelling in the direction of the sun. In this case spectral irradiance in the forward direction is high, yet some of the photons originating from sideways

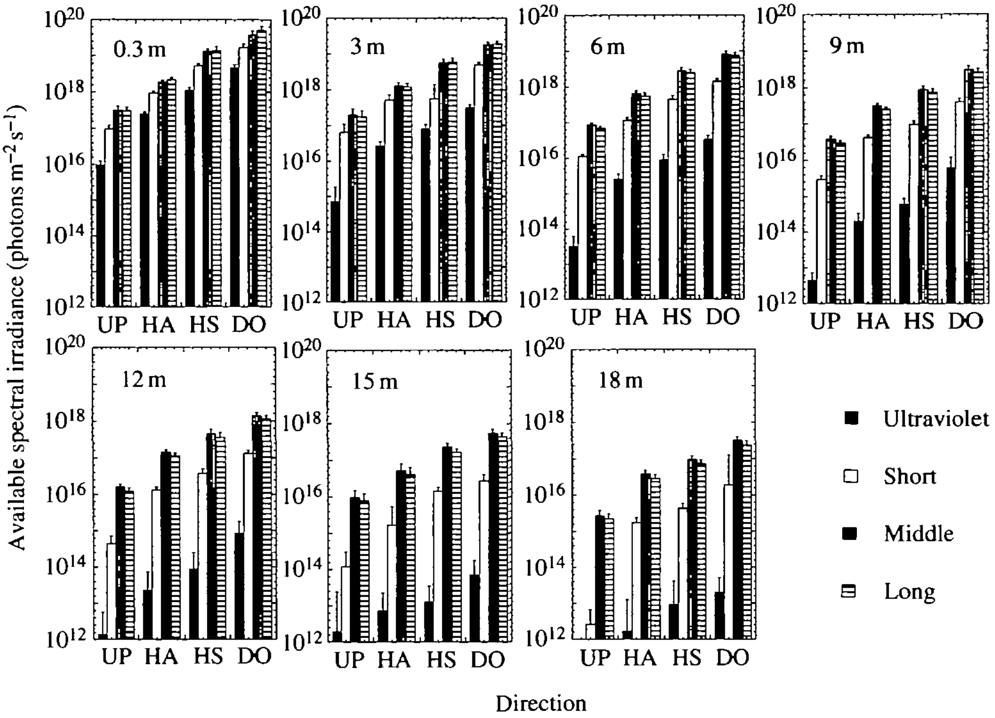

Fig. 10. Average spectral irradiance values corrected for salmonid pigment absorption and ocular media transmission of small rainbow trout. Standard errors are indicated on the bar graphs. Presentation of data is the same as that in Fig. 6. This series of bar graphs represents a map of available light for activation of the different photoreceptor mechanisms with depth and direction.

particle scattering would be polarized (and this, importantly, as the background becomes dimmer). Whether fish prefer to swim in directions related to background light cues is yet to be examined.

The gradient of light attenuation from surface to deeper waters also implies adaptability of the retina to varying spectral backgrounds (Singarajah and Harosi, 1992). As the fish travels down the water column, perception of a silhouette on a bright background becomes increasingly difficult (Le Grand, 1939). In deep waters, a point is reached when the light field is homogeneous (Jerlov, 1976) and the retinal sensitivity no longer varies with direction of observation. A highly reflective bottom in shallow waters creates an effect opposite to the attenuation mechanism just described. Because of reflection, upwelling light near the bottom can be more or nearly as intense as that at lower depths (Fig. 5). Bottom predators may take advantage of the additional background illuminance and possible creation of polarized light (Chen and Nagaraja Rao, 1968) for target detection. This is perhaps another reason why darker animals may not be found near sandy bottoms, even at considerable depths.

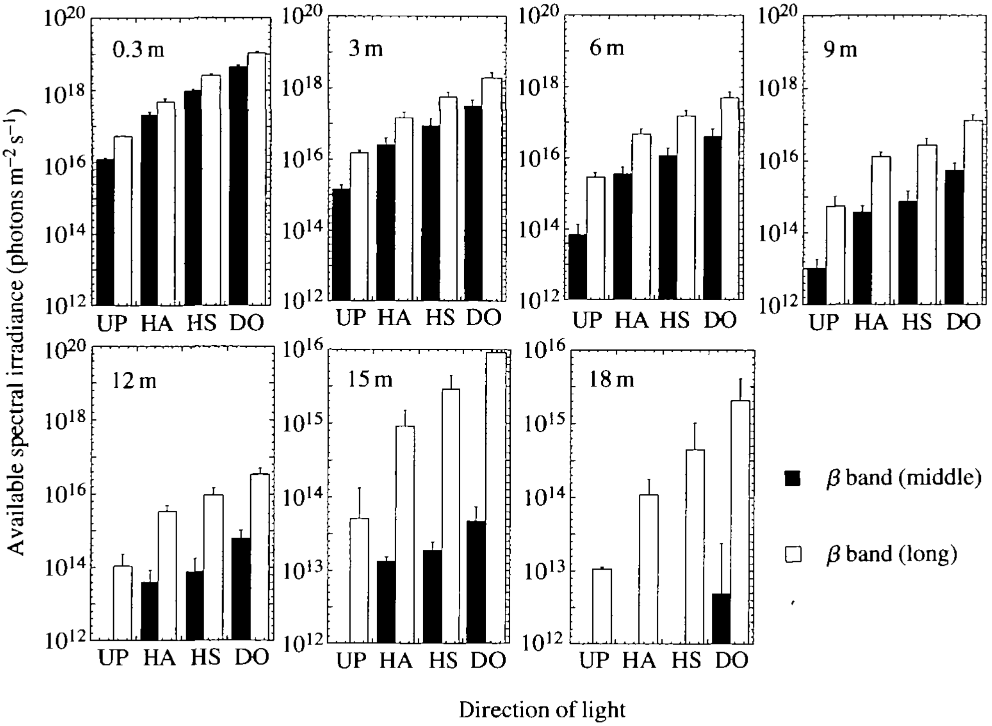

Fig. 11. Average spectral irradiance values corrected for the β band pigment absorption curves of the middle and long wavelength cone mechanisms. Values were also corrected for ocular media transmission of small rainbow trout. Data presentation as in Fig. 10. Where columns for the β band of middle wavelength light have been omitted, the values were less than 10^{13} photons m^{-2} s^{-1}.

Although the spectral composition at twilight has been examined by McFarland and Munz (1975), these authors did not examine the ultraviolet part of the spectrum. Furthermore, a rigorous mathematical analysis of the various parts of the spectrum through a 24 h period is not available. Our results for Lake Cowichan for this period show opposite trends for the ultraviolet, short and middle wavelengths *versus* the long wavelength part of the spectrum (Figs 8 and 9). Relative quantities of ultraviolet, short and middle wavelengths are most abundant during crepuscular periods, while relative amounts of long wavelengths increase during daylight hours. The long wavelength part of the spectrum also exhibits a local peak during crepuscular periods (Fig. 8). Some of these changes have been observed previously for the spectrum from 400 to 700 nm (McFarland and Munz, 1975). They are due to preferential scattering of shorter wavelengths in the atmosphere by Rayleigh-size particles and increased scattering of longer wavelengths at particular pathlengths of incoming solar radiation (Lythgoe, 1979).

The relative increase in ultraviolet light during crepuscular periods may be important for salmonid navigation since these fish have been found to orient to the

E-vector of polarized ultraviolet light (Hawryshyn *et al.* 1990). Given the relationship between the sun's position and the most intense band of polarized light (approximately 90° separation; Waterman, 1954), salmonids could potentially be using polarized light vision as an orientation mechanism during migration (Groot, 1965; Dill, 1971; Quinn, 1980). Interestingly, various authors have reported that migratory episodes occur during crepuscular periods (Johnson and Groot, 1963; Groot, 1965). Furthermore, the fish are observed to travel near the surface where stimulation of the ultraviolet cones is possible (Fig. 10).

The light patterns at dawn and dusk may also play a role in foraging if, indeed, ultraviolet vision enhances target–background contrast. Our results for Lake Cowichan suggest that predators and prey with ultraviolet vision would be the most effective at obtaining food and lowering the risks of being captured, respectively. In the case of juvenile salmonids, ultraviolet vision may be used to detect zooplankton as these organisms absorb high quantities of ultraviolet light (Bowmaker and Kunz, 1987).

Another characteristic of the light field during crepuscular periods is its rapid changes in spectral composition. Two peaks of ultraviolet and short wavelength light occur before and at the moment when the sun rises over the horizon (Figs 8 and 9B). These peaks are accompanied by local maxima in middle and long wavelength light, although these trends vary in time as well (Fig. 8, 5.0–7.0 h). Camouflage of any sort could be very difficult in such a varying light field and this may be the cause for the observed high predation during crepuscular periods (Hobson, 1972). To counter these rapid changes in illumination, some coral reef fishes have developed combinations of pigments whose maximum absorptions approximate the peak wavelengths found in the environment during these periods (Munz and McFarland, 1973).

Our results demonstrate that ultraviolet-mediated visual behaviour is possible at all depths studied (Fig. 10). However, 18 m was found to be the threshold depth for ultraviolet cone stimulation (Fig. 10). Such a depth restriction would force the fish to rise in the water column in order to profit from ultraviolet light cues for purposes of orientation. Surfacing, however, involves higher risks of predator detection from below and from outside the water column. A compromise could then be reached by swimming in a sinusoidal pattern, surfacing at regular intervals. Such a swimming pattern has been observed during salmonid migratory episodes (Groot, 1972; Westerberg, 1982; Ruggerone *et al.* 1990).

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