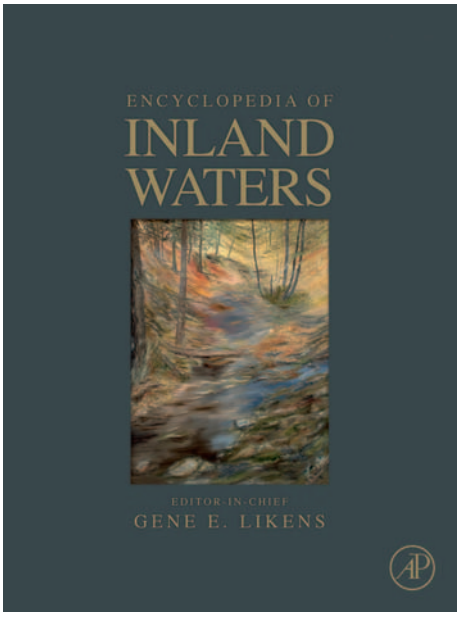

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Light, Biological Receptors

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Introduction

Most aquatic organisms possess photoreceptors that detect some portion of the visible spectrum (400–700 nm). However, some species also perceive UV radiation (UVR), particularly within the UV-A range (320–400 nm). UV photoreceptors have been detected in freshwater and marine organisms occupying multiple trophic levels, from bacteria to fish (Table 1), suggesting that UV vision is a prominent trait among aquatic organisms. Adaptive benefits vary among species and life-history stages and include enhanced visual communication, foraging, and possibly UVR avoidance. Nevertheless, UV vision is not without costs as exposure to shorter UV wavelengths can cause damage to the eye as well as image degradation. Given that UV sensitivity influences an organism's physiology and behavior, environmental stressors that alter the UV transparency of freshwaters are a potential concern. These include changes in atmospheric ozone, climatic patterns, and nutrient and sediment concentration. This article discusses (1) the underwater UV environment, (2) the structure and function of photoreceptors and the methods used to measure their spectral sensitivity, (3) the distribution of UV photoreceptors among freshwater organisms, (4) the adaptive significance of UV vision, and (5) potential effects of environmental stressors on UV vision.

Underwater Light Environment

Light is both absorbed and scattered as it penetrates through water. As a result, downwelling irradiance decreases with depth, with shorter and longer wavelengths attenuating more rapidly than the wavelength of peak transmission (generally between 470 and 550 nm). In clear, oceanic water, absorption by the water itself is the primary source of light attenuation. However, the absorption of light by dissolved organic carbon (DOC) is the dominant factor in freshwater ecosystems, particularly at UV wavelengths (300–400 nm). In systems with moderate-to-high DOC ($>3\,mg\,l^{-1}$), UV and blue wavelengths are attenuated rapidly, and the underwater light field is dominated by longer-wavelength yellow and red light (550 and 650 nm). In systems with low DOC ($<3\,mg\,l^{-1}$), shorter wavelength radiation penetrates farther, and UVR and blue light dominate. Although the average DOC concentration for freshwaters is approximately $10–13\,mg\,l^{-1}$, 25% of the lakes in North America were reported to have 1% attenuation depths (the depth to which 1% of surface irradiance remains) greater than 4 m for 320 nm UV-B and greater than 10 m for 380 nm UV-A. There is also evidence that levels of UV-B entering freshwaters are increasing at both temperate and high latitudes due to decreasing stratospheric ozone. Thus, biologically relevant UVR is present at considerable depths in many fresh waters.

In addition to DOC, other factors influence the depth to which various wavelengths of light penetrate, including solar elevation, cloud cover, turbidity, and the depth and reflectance of the bottom. Differences in light intensity as well as spectral composition create potential 'light niches.' For example, relative quantities of UV light can be greater during crepuscular periods (i.e., dawn and dusk) than daylight hours due to the increasing proportion of high-UV skylight in the total irradiance (Figure 1). These twilight hours may provide a temporal niche for predators with UV vision, enhancing target–background contrast and potentially silhouetting prey. In addition, clear waters near the surface may provide a spatial niche, with relatively more available UVR than at deeper depths (Figure 2). The relative abundance of UVR is highest in the horizontal and downward lines of sight, representing up to 40% of the total photons in clear surface waters. In both cases, UVR can serve as a short-range private communication channel for organisms with UV vision because it is absorbed and scattered more than most visible wavelengths.

Biological Photoreceptors

Structure and Function

Photoreceptors vary in structure across the animal kingdom, from simple clusters of cells that only detect the intensity of light to complex organs that form detailed images. All photoreceptors, however, possess photopigments (also referred to as visual pigments) that absorb light at specific wavelengths. These pigments are composed of a chromophore that is bound to and surrounded by a membrane protein. The peak absorbance of a photopigment is determined by the amino acid sequence of the surrounding protein,

Table 1 Survey of the distribution of UV photoreceptors among freshwater organisms

Organism	*Method*	*Wavelength of maximum response or absorption (nm)*	*Source*
Bacteria			
Mutant, *Escherichia coli*	Behavior	396–450	1
Purple eubacterium, *Ecotothiorhodospira halophila*	Behavior	N/A	2
Phytoplankton			
Cyanobacterium, *Chologloeopsis*	Physiology, MAA induction	310	3
Cyanobacterium, *Microcoleus chthonoplastes*	Behavior	310	4
Flagellate, *Euglena gracidis*	Behavior	360	5
Protozoans			
Ciliate, *Blepharisma japonicum*	Behavior	N/A	6
Crustaceans			
Cladoceran, *Daphnia magna*	Behavior	348	7
Cyclopid copepod, *Cyclops serrulatus*	Behavior	N/A	8
Ectoparasitic copepod, *Lepeophtheirus salmonis*	Behavior	352–400	9
Crayfish, *Procambarus clarkia*	MSP	440	10
Amphibians			
Tiger salamander, *Ambystoma tigrinum*	Electrophysiology	Below 400	11
Fishes			
Ostariophysi			
Minnow, *Phoxinus laevis*	Operant conditioning	Response down to 365	12
Roach, *Rutilus rutilus*	MSP	355–360	13
Goldfish, *Carassius auratus*	Heart-rate conditioning	365	14
Carp, *Cyprnus carpio*	MSP, behavior	377	15
Amarillo, *Girardinichthys multiradiatus*	Behavior	N/A	16
Danio, *Danio aequipinnatus*	Electophysiology	358	17
Eastern golden shiner, *Notemigonus crysoleucas*	MSP	355	18
Rudd, *Scardinius erythrophthalmus*	MSP	355–360	19
Japanese dace, *Tribolodon hakonensis*	MSP	350–370	20
Salmoniformes			
Rainbow trout, *Oncorhynchus mykiss*	Heart-rate conditioning	390	21
Brown trout, *Salmo trutta*	MSP	355	22
Atlantic salmon, *Salmo salar*	MSP	360	23
Sockeye salmon, *Oncorhynchus nerka*	MSP, Electrophysiology	N/A	24
Acanthopterygii			
Guppy, *Poecilia latipinna*	MSP	412	25
Guppy, *P. reticulata*	MSP	411	25
Three-spined sticklebacks, *Gasterosteus aculeatus*	MSP	365	26
Sunfish, *Lepomis* spp.	MSP	360–370	Personal communication
Yellow perch, *Perca flavescens*	MSP	385	27
Killifish, *Fundulus heteroclitus*	MSP	363	28
Killifish, *Lucania goodei*	MSP	359	29
Cichlid, *Metriaclima zebra*	MSP	368	30
African cichlids-Lk. Malawi	MSP		31
Cynotilapia afra		358	
Metriaclima barlowi		366	
M. benetos		379	
M. emmiltos		383	
M. livingstonii		364	
M. melabranchion		371	

Continued

Table 1 Continued

Organism	*Method*	*Wavelength of maximum response or absorption (nm)*	*Source*
Pseudotropheus t. pseudotropheus		371	
Reptiles			
Red-eared terrapin, *Pseudemys scripta elegans*	Electrophysiology	360	32
Caspian terrapin, *Mauremys caspica*	Electrophysiology	360	32

This list is not all-inclusive.

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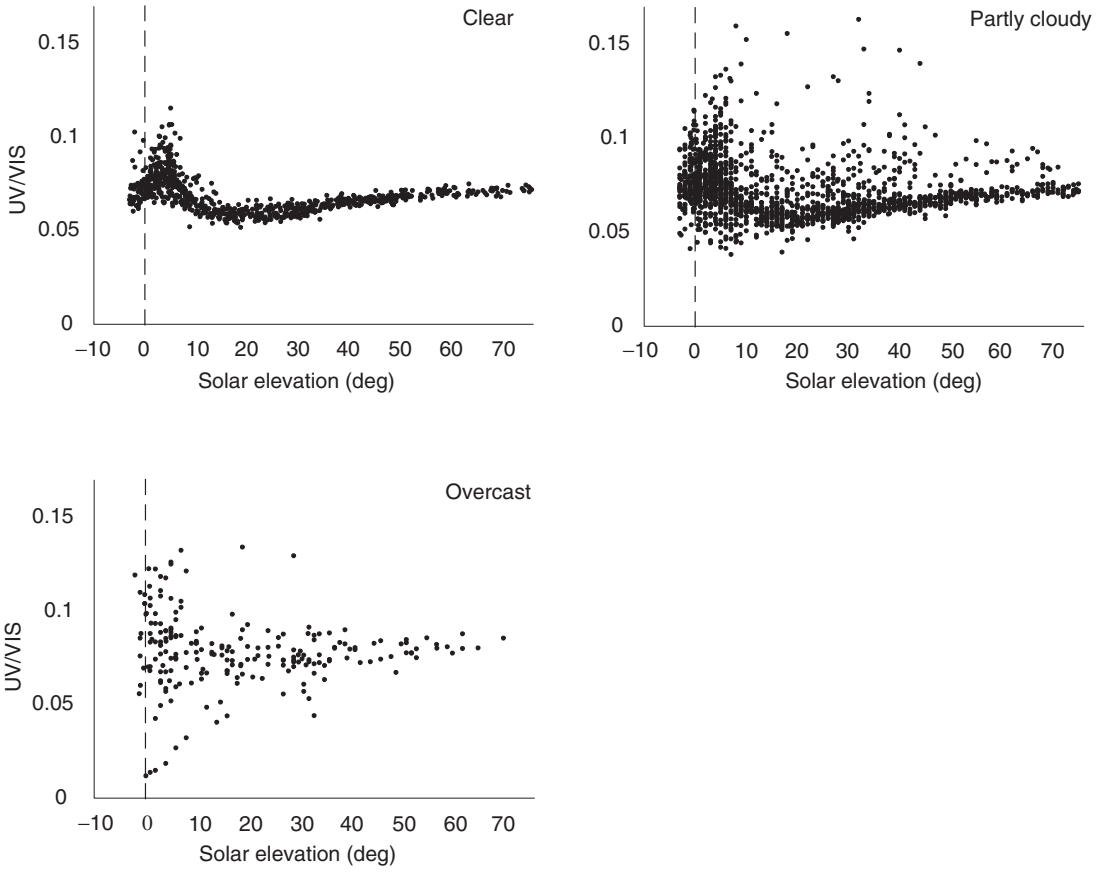

Figure 1 Ratio of UV (300–380 nm) to visible light (380–780 nm) as a function of solar angle under clear, partly cloudy, and overcast conditions. A total of 2600 spectra were measured from the roof of the University of Granada's Science Faculty (Granada, Spain, 37°11′N 3°35′W, elevation 680 m) from February 1996 to February 1998 using a LI-1800 spectroradiometer (LI-COR Bioscience, Lincoln, NE, USA) fitted with a cosine-corrected receptor. Measurements were taken at all solar elevations greater than −4° and in all weather except for rain or snowfall. Data were collected at 5 nm intervals from 300 to 1100 nm. Data are courtesy of Dr. Javier Hernandez-Andres at the University of Granada in Spain.

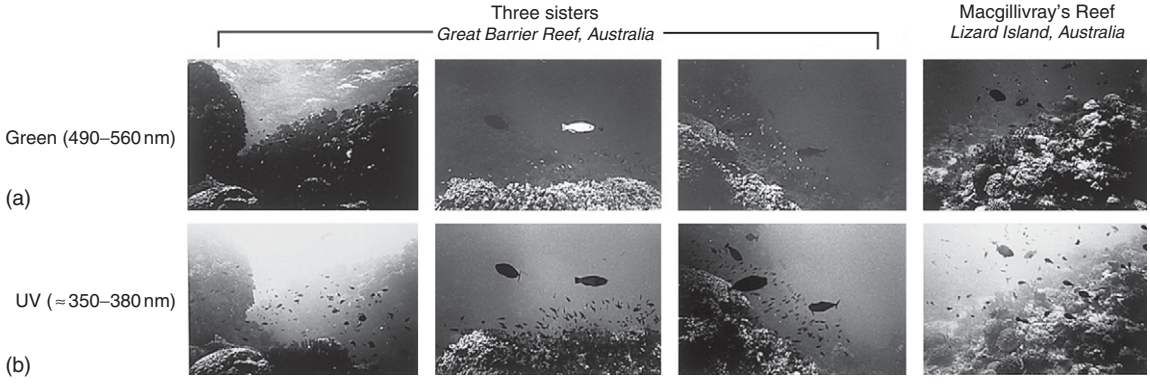

Figure 2 Simultaneous images taken at (a) green (490–560 nm) and (b) ultraviolet (350–380 nm) wavelengths. Note the bright background in the UV image that silhouettes fish strongly, even against the reef. Also note that distant items in the UV images have lower contrast than in the visible images. Images courtesy of Dr. Thomas Cronin at the University of Maryland, Baltimore Campus.

and the type of chromophore, which is typically a derivative of retinol (i.e., vitamin A). Interestingly, even single amino acid changes may cause 2–35 nm shifts in spectral sensitivity, depending on their location and proximity/interaction with the chromophore. Organisms often possess a number of visual pigments that allow them to measure and compare light intensity across a broader spectrum. For example,

there are typically five classes of proteins used for image formation in vertebrates, including rhodopsin RH and four cone opsins: SWS-1 (ultraviolet sensitive), SWS-2 (shortwave sensitive), MWS and LWS (mid- to long-wavelength sensitive).

Measurement of the Spectral Sensitivity of Vision

Spectral sensitivity is measured in three ways: (1) behavioral responses that provide action spectra of whole animals, (2) electroretinograms that determine the spectral sensitivity of whole eyes, and (3) microspectrophotometry (MSP) that measures the absorption spectra of the photopigments themselves. In behavioral experiments, measurements are made of changes in a specific behavior (e.g., swimming speed or direction) under exposure to varying wavelengths of light. Wavelengths that stimulate a maximum response represent peak spectral sensitivity. Electroretinograms use electrodes placed near the retina to monitor the electrophysiological responses of groups of photoreceptors to changes in wavelength and intensity. MSP determines the absorption characteristics of photopigments. Individual photoreceptor cells are isolated and exposed to a series of monochromatic lights to determine their specific absorbance spectra. Because photoreceptor cells generally only express one visual pigment, multiple cells must be isolated in order to determine the total number of visual pigments expressed by an organism. MSP does not include the transmission of the ocular media (including the cornea and lens), which must be considered to determine ultimate spectral sensitivity of the eye. For instance, retinal UV sensitivity is only possible if both UV photoreceptors are present and the ocular media are UV-transparent.

UV Photoreceptors in Freshwater Organisms

UV photoreceptors have been reported in diverse organisms, including arthropods, amphibians, reptiles, birds, and mammals. In freshwaters, UV photoreceptors have primarily been identified in fish. However, continuing research shows that UV photoreceptors are also present in freshwater bacteria, algae, and zooplankton (Table 1). Surveys of UV photoreceptors across both freshwater invertebrates and vertebrates show that organisms with UV vision typically inhabit high UV systems. However, variations are also seen with other environmental and physiological factors, such as water temperature, age, and behavior.

UV-A versus UV-B Visual Sensitivity

Most UV photoreceptors have a maximum absorbance peak in the UV-A range but UV-B photoreceptors are found in some species (Table 1). One explanation for the rarity of UV-B vision is that UV-B radiation is potentially more damaging to the eye, causing corneal damage and cataract formation. Seeing in the UV-A may therefore be less detrimental. However, prolonged exposure to UV-A radiation may also cause damage, albeit less than UV-B. Eyes function by counting photons rather than measuring energy, thus another explanation is that seeing in the UV-A provides far more light than in the UV-B. In clear surface waters, approximately half the photons in horizontal and downward directions are UV-A, but a far lower proportion are UV-B. The ratio of UV-A to UV-B in water depends on many factors, but can easily reach several orders of magnitude.

Another disadvantage of UV vision is image degradation. Because the water and ocular media preferentially scatter UV light, image contrast is less at shorter wavelengths. In addition, short-wavelength light also focuses closer to the lens than does longer-wavelength light and therefore an image in focus for UV-sensitive photoreceptors will be out of focus for other photoreceptors.

Seasonal Differences in UV Sensitivity

Some species display seasonal changes in spectral sensitivity that correspond to changes in the photic environment associated with day length and temperature. With longer days and warmer temperatures, there is typically an increase in phytoplankton biomass, and thus chlorophyll concentration and suspended particles. This decreases light intensity and shifts the spectral composition of the underwater light to longer wavelengths, including the infrared. In fish, these changes are sometimes correlated with shifts in the wavelength of peak sensitivity of their long-wavelength, but not short-wavelength, pigments (Figure 3).

Seasonal shifts in spectral sensitivity are also associated with behavioral changes, such as feeding at the surface during summer months and in deeper strata during winter months. These shifts may be correlated with changes in the chromophore base related to water temperature. Vitamin A_1-based pigments are sensitive to shorter wavelengths of light than are A_2-based pigments, and studies show that some species of fish have a higher proportion of A_1-based pigments in the spring and summer than in the winter months. However, others show the opposite pattern or no change in chromophore base. Many argue that the

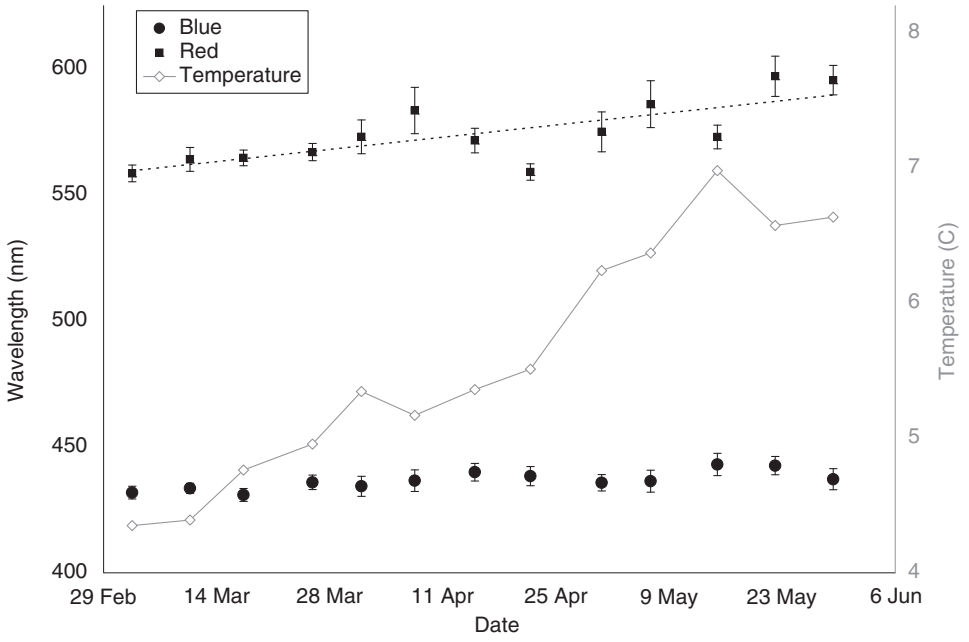

Figure 3 Changes in the peak absorbance of the blue and red pigments of smolt juvenile Coho salmon with changes in water temperature. Peak absorbance was determined using MSP. Note there is no change in the blue photopigment but the red pigment increases in peak absorbance with water temperature. Modified from Novales Flamarique I (2005) Temporal shifts in visual pigment absorbance in the retina of Pacific salmon. *Journal of Comparative Physiology A* 191: 37–49.

effects of temperature can be understood best by considering fluctuations in the hormonal regulation of photopigments (or chromophores). For instance, thyroid hormones, like thyroxine, have been demonstrated to regulate the ratio of A_1- to A_2-based pigments in the retina of several species of fish.

Ontogenetic Differences in UV Sensitivity

UV sensitivity can also vary with age. For example, species of *Lepomis*, *Perca*, and *Salmo* possess UV photoreceptors as larvae but lose them with maturity. Loss of UV photoreception coincides with a shift from foraging at the surface to more demersal waters and a change in diet from smaller to larger zooplankton and/or fish. In some species of salmonids, UV photoreceptors disappear during earlier life-history stages and reappear in adults. For example, ultraviolet cone density and UV sensitivity in sockeye salmon (*Oncorhynchus nerka*) and other salmonids diminish during smolting and reappear at the late juvenile or adult stage. In contrast, goldfish and other species of cyprinids retain their UV photoreceptors throughout their lives. As these species experience little to no change in habitat or diet, a change in the spectral sensitivity of their photoreceptors is not to be expected. Ontogenetic changes in spectral sensitivity among aquatic species other than fish are less well known.

Habitat and Gene Regulation of UV Sensitivity

Using molecular techniques, scientists have recently shown that some organisms possess visual pigment genes that are not expressed. When seen, variable gene expression is correlated with habitat and behavioral characteristics. For example, African cichlids inhabiting Lake Malawi possess genes for proteins representing each of the five classes of vertebrate photopigments. However, photopigment expression differs among species depending on body color and habitat (i.e., sand-dwellers versus rock-dwellers). Similar results have been noted for bluefin killifish (*Lucania goodie*) inhabiting clear versus humic-stained ponds. Relatively more UV- and blue-sensitive photopigments are expressed in clear ponds versus longer wavelength red- and yellow-sensitive photopigments in humic ponds. More investigation is needed, however, to determine if the unused genes are expressed at different life-history stages.

In some cases, UV-sensitive photopigments are expressed in waters with low UV transparency. However, the ratio of UV to longer-wavelength photoreceptors decreases. For example, the relative number of UV-sensitive cells in the retinae of Atlantic mollies (*Poecilia* spp.) was greater in populations and species inhabiting clear waters versus murkier waters and dark caves. In addition, peak absorbance of the UV photoreceptors shifted to longer wavelengths (i.e., $\lambda_{max} = 349–373$ nm) in organisms inhabiting darker or less UV-transparent waters.

Behavioral Adaptations of UV Vision

For some species, UV vision aids in color discrimination and/or contrast enhancement against background illumination, improving visual communication as well as foraging. In others, UV photoreceptors are also polarization-sensitive and are used for orientation and navigation. UV vision may also be used to avoid the shallower depths at which damaging UVR is present. Most of these tests of function, however, have been conducted in the laboratory, with fish.

Mate Choice

UV-mediated mate choice has been demonstrated in several fish species, including guppies (*Poecilia reticulata*) and swordtails (*Xiphophorus nigrensis*). Experiments show that females often exhibit a preference for males viewed under artificial UVR compared with those viewed in the absence of UV, perhaps due to UV-reflective patterns on the males (Figure 4). Similar results were shown for three-spined sticklebacks (*Gasterosteus aculeatus*), in which females spent more time courting males viewed through UV-transparent filters than UV-blocking. Control experiments with neutral density filters suggest that UV vision is used more for color discrimination instead of detecting differences in brightness. In outdoor experiments using natural sunlight, female Amarillo (*Girardinichthys multiradiatus*) preferred males viewed under full spectrum irradiance than those viewed without UVR.

One confounding variable in these experiments is fluorescence, in which short-wavelength UVR is absorbed and then reemitted at visible wavelengths. Recent experiments have shown that many shallow-water animals exhibit fluorescence that brightens body coloration in the visible spectrum. Thus, future research needs to examine this variable more closely.

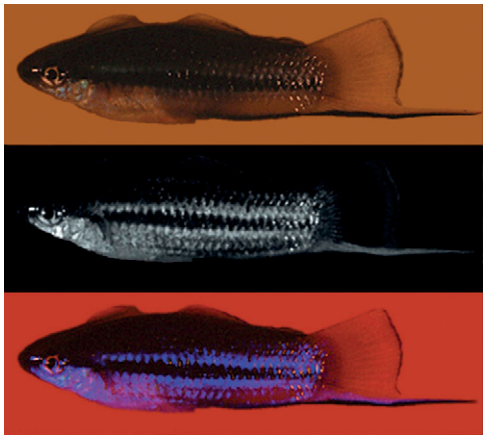

Figure 4 UV reflectance of swordtails. Top) image under visible light. Middle) image under UV light alone. Bottom) combined UV and visible image. UV portion is colored violet. Modified from Cummings ME, Rosenthal GC, and Ryan MJ (2003) A private ultraviolet channel in visual communication. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 897–904, with permission from the Royal Society of London.

Foraging

UV photoreceptors are also thought to enhance prey contrast for visual foragers. Zooplankton prey, such as *Daphnia* and *Diaptomus*, often contain compounds that absorb UV-A and short-wavelength blue light (e.g., carotenoids, melanin, and mycosporine-like amino acids (MAAs)). While these compounds block UVR, they may also make zooplanktors appear darker than the background. In addition, zooplankton also scatter light and may appear lighter or darker depending on the direction of illumination as well as the organism's shape and refractive index. Scattering of UVR is higher than that of longer-wavelength visible light, giving predators with UV vision a particular advantage.

In laboratory experiments, larval fish within the genera *Lepomis*, *Perca*, and *Oncorhynchus* caught more prey and had longer pursuit distances in the presence of UVR. In some cases, fish fed better under UV-A alone than under visible light at the same energy. Predation rates of African cichlids feeding on *Artemia* spp. were greater for species with UV sensitivity than those without, suggesting that UV vision does provide an adaptive advantage. In field experiments with juvenile bass (*Micropterus salmoides*), animals preyed more heavily on calanoid copepods in the presence of UVR (Figure 5). These copepods are known to possess UV-absorbing compounds, which may increase their visibility to predators with UV vision.

However, other studies have detected no effect of UVR on foraging, including laboratory experiments with the guppy *P. reticulata* and juvenile bluegill *Lepomis macrochirus*. In field experiments conducted in Patagonia, Argentina (41°08′ S, 71°25′ W), with rainbow trout (*Oncorhynchus mykiss*), the removal of UV wavelengths from solar radiation had no effect on the number of prey eaten or on prey preference. These experiments were run outdoors between 10.00 a.m. and 1.00 p.m. local time, so it is not known if a difference would have been detected during crepuscular periods when relative UV levels are higher and planktivory is more challenging.

Avoidance of Damaging UV Radiation

Algae Exposure of phytoplankton to high intensities of sunlight may result in a bleaching of pigments

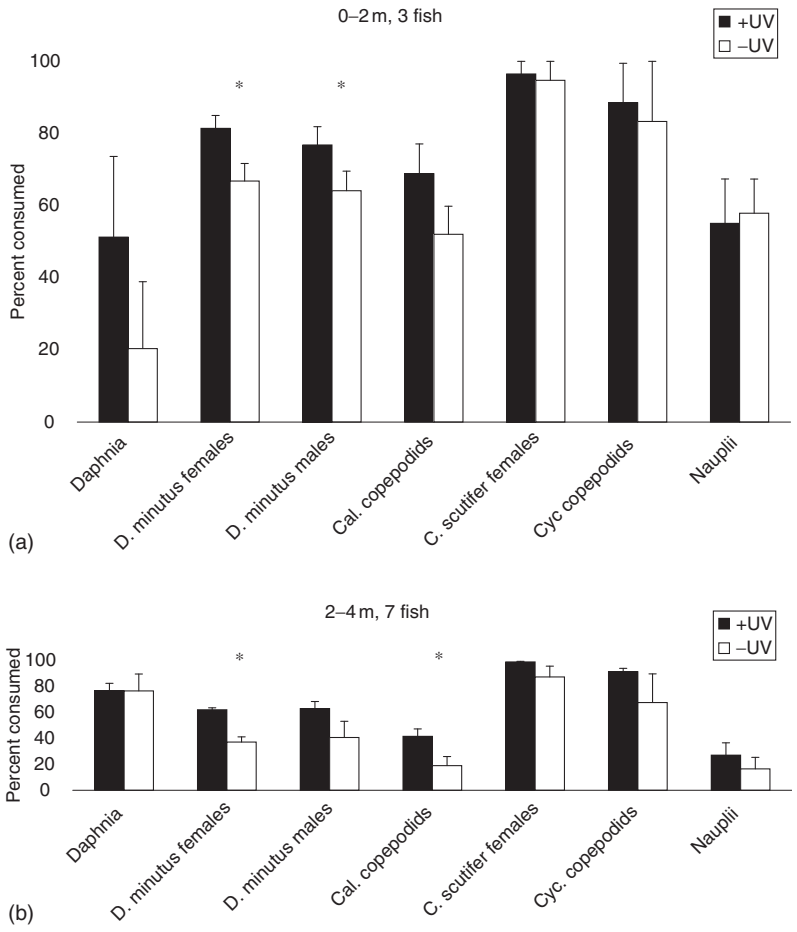

Figure 5 Zooplankton species consumed by juvenile largemouth bass (*Micropterus salmoides*) in the presence and absence of UV radiation at 0–2 m (A) and 2–4 m (B). Error bars represent standard errors. Experiments were conducted in 2.2 m long acrylic columns (shown in **Figure 6**) that were either UV-transparent or UV-blocking and suspended in the surface waters of high UV Lake Giles, Pocono Mountains, PA, USA.

critical to photosynthesis. Thus, avoidance of UVR is beneficial to maintaining photosynthetic rates and growth. Negative phototactic responses to UVR have been detected in the red-colored freshwater ciliate *Blepharisma japonicum*, which swims away from wavelengths of UV-B but swims towards yellow light (580 nm). Within filamentous cyanobacterial mats, individual cells of *Microcoleus chthonoplastes* were shown to migrate to greater depths in response to increased UV-B exposure.

Zooplankton Behavioral responses to UVR are also seen in zooplankton. Recent studies with monochromatic light have demonstrated that *Daphnia magna* are positively phototactic to visible light (421–600 nm) and negatively phototactic to UVR (260–380 nm) with maximal sensitivity at 340 nm. In addition, field experiments have demonstrated a strong negative phototactic response to UVR in *Daphnia* inhabiting high-UV lakes (**Figure 6**). Copepods avoid UVR both in the laboratory and field (**Figure 6**). For example, in small horizontal enclosures, the UV-sensitive freshwater cyclopoid *Cyclops serrulatus* selectively avoided exposure to UV-B (280–320 nm).

Body pigmentation also influences zooplankton behavioral responses to light. Many zooplankton accumulate compounds, such as carotenoids, melanin, and MAAs, through their diet, which serve as a sunscreen against damaging radiation. With increased pigmentation, organisms are often less responsive to shorter-wavelength radiation. Interestingly, in the cyanobacterium *Chologloeopsis*, a UV-B photoreceptor is linked to the production of the MAA compound shinorine. Production was greatest when organisms are exposed to UV-B light at 310 nm. In the copepod *Diaptomis nevadensis*, the ratio of swimming speeds under blue versus red light was higher in nonpigmented versus pigmented individuals. Similar results have been reported for melanized *Daphnia* within the UV spectrum, with a greater downward migration in less-pigmented individuals in the presence of full solar radiation.

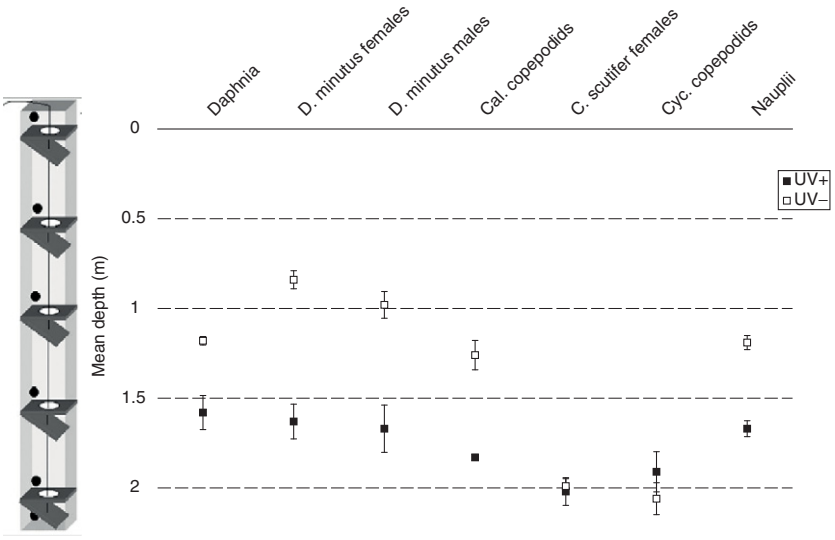

Figure 6 Mean depths of zooplankton in the presence and absence of UVR at the surface of Lake Giles, Pocono Mountains, PA, USA. Error bars represent standard errors. Zooplankton were placed in 2.2 m long acrylic columns that were either UV-transparent or UV-blocking columns (shown to the left). Columns were suspended from 0–2 m between 9:00 p.m. on 20 June to 10.30 a.m. on 21 June 2001. At the end of the experiment, the trap doors were closed and the number of species in each section was counted. Species included the cladoceran *Daphnia catawba*, the calanoid copepod *Diaptomus minutus*, and the cyclopoid copepod *Cyclops scutifer*. Copepod naupllii represent both calanoids and cyclopids. Note the deeper distribution of the *Daphnia* and calanoid copepods in the presence of UVR. *C. scutifer* is a cold water species that typically inhabits the deeper waters of Lake Giles during both the day and night. Therefore, their deep distribution in both the UV+ and UV− treatments is expected.

Macroinvertebrates Some stream invertebrates also avoid UVR in nature. Blackfly larvae (Diptera: Simuliidae) appear to migrate out of UV-exposed channels during periods of peak irradiance but return to UV-exposed regions as irradiance levels decrease. In streams that were experimentally shielded from UVR (290–400 nm), however, larvae remained in the stream channels throughout the day, with densities 161–168% greater than those in UV-exposed channels.

Fish Differences in the spawning depths of yellow perch (*Perca flavescens*) in a high- versus a low-UV lake suggest that they also avoid UV exposure. Spawning depth was 2.8 m deeper in a high-UV lake (median = 3.2 m) than in a low-UV lake (median = 0.4 m). The eggs of *P. flavescens* incubated at the surface of the high-UV lake under full solar radiation all perished after 6 days, but survived for 8–10 days in UV-B shielded treatments. Most eggs (>96%) incubated in the light treatments of the low-UV lake or in the dark controls of both lakes survived to hatching (14 days). Comparable results using a similar experimental design were reported for the bluegill *L. macrochirus* in which the median nesting depth was deeper in a high-UV lake than in a low UV-lake.

Avoidance of damaging UVR is also suggested in larval vendace (*Coregonus albula*). The percentage of individuals occupying the surface waters of clear Finnish lakes decreased on sunny days than on cloudy days. However, no differences between sunny and cloudy days were observed in lakes with higher DOC concentration. This may also be a response to visual predators although sufficient visible light was available in the surface waters for predators on both sunny and cloudy days.

Schooling

Schooling animals are continually evaluating whether to join, stay, or a leave a group. While living in groups reduces predation risk, it does have certain costs, such as increased competition for food as well as susceptibility to disease. Selecting a group to join is therefore an important decision for an individual. Only one study has quantitatively examined the use of UV vision in the schooling of freshwater fish. Laboratory experiments with three-spined sticklebacks (*G. aculeatus*) demonstrated that animals prefer to join schools seen under UV+ conditions.

Navigation

In some species of salmonids (i.e., *Oncorhynchus nerka*, *O. tshawytsha*, and *O. keta*), UV photoreceptors are arranged in the retina such that animals can detect the polarization pattern of skylight. This is

believed to assist salmonids in navigating to their natal streams for spawning. As mentioned above, UV photoreceptors are expressed in larvae and early juveniles but disappear from the retina during a metamorphosis that prepares fish for deeper, marine waters. Subsequently, UV photoreceptors reappear 5–6 years later, with the onset of sexual maturation and the initiation of their return migration. Experiments have shown that polarized light is only detected in the UV range, with remarkable discrimination between small differences in the angle of the e-vector of skylight.

Effects of Environmental Stressors on UV Vision

Shifts in water transparency and thus the spectral composition of underwater light may result from a variety of abiotic and biotic stressors. For instance, changes in global climate are likely to influence inputs of dissolved and particulate organic matter to freshwaters, leading to a potential decrease in UV transparency. Eutrophication can also decrease water transparency as well as filter out shorter wavelengths of light. In contrast, increases in acid rain and the concomitant breakdown of DOC have been shown to increase the UV transparency of freshwaters. As mentioned earlier, changes in water temperature can affect spectral tuning by altering the hormonal regulation of the peak absorbance of visual pigments (e.g., thyroxine control on the ratio of vitamin A_1- to vitamin A_2-based chromophores). These alterations in the underwater photic environment may, in turn, affect the overall structure and function of freshwaters.

Community Structure and Biodiversity

With a change in photic environment comes a possible shift in species composition. For example, as water transparency decreases, there can be a shift from visual predators (e.g., planktivorous fish) to tactile predators (e.g., chironomids). Decreases in water clarity can interfere with mate choice as is seen in African cichlids inhabiting Lake Victoria. Fishes were unable to clearly recognize their own species, due to turbidity associated with eutrophication. This led to increased interbreeding and an overall loss in diversity. Increased turbidity is also a major problem in coastal waters, and anadromous fishes using UV vision as a means of polarization-mediated navigation may find it increasingly difficult to return to their spawning streams with decreases in UV water transparency.

Increases in water transparency can also affect species composition. Surveys of freshwaters indicate that species inhabiting high-UV waters tend to be more UV-tolerant, having evolved mechanisms to cope with UV stress (i.e., photoprotective pigmentation, photorepair, and behavioral avoidance). Typically, rotifers and copepods tend to be more UV-tolerant than cladocerans and are proportionally more abundant in the surface waters of high-UV systems during the day.

Predator–Prey Interactions

Alterations in spectral composition may also affect organisms using UV vision to forage. While increases in the UV transparency of freshwaters may benefit visual predators, decreases in light availability, related to increases in DOC concentration and/or turbidity, may decrease a predator's ability to detect potential prey. This may be a particular problem for planktivorous larval fish, which require substantial nourishment during a critical stage in development.

Distribution and Migration Patterns

The distribution of organisms in the water column during the day versus night may also change with water transparency and spectral composition. One of the most interesting behavioral responses to sunlight is the phenomenon of zooplankton diel vertical migration (DVM). Large zooplankton often exhibit strong migrations during the day to deeper, darker depths in the water column. Smaller zooplankton, in turn, remain in the surface waters during daylight and migrate to the deeper waters at night to avoid predation or competition with larger zooplankton. Many factors, including temperature and food availability, have been proposed to explain these patterns; however, predation by visually feeding fish is typically identified as the primary factor inducing DVM. Recent experiments, however, have shown the UVR may also induce downward, negative phototaxis in zooplankton in high-UV systems (**Figure 6**). Alterations in species depth distribution, associated with changes in freshwater UV transparency, may affect predator–prey overlap, competition for resources, and nutrient cycling.

Conclusions

In recent decades, UV photoreceptors have been detected in many species of freshwater organisms, particularly in those inhabiting high-UV systems.

Although its adaptive significance remains speculative, research suggests that UV vision enhances visual communication, navigation, foraging, and avoidance of damaging UVR. Thus, changes in the UV transparency of freshwaters, associated with natural and anthropogenic stressors, may have adverse affects on species physiology and behavior.

Knowledge Gaps

Studies identifying UV photoreceptors in species other than fish are needed: As noted in this article, most studies examining UV photoreceptors and their adaptive significance are centered on fish. More investigation is needed to identify photoreceptors in other species as well as their functional significance. For example, prey species may have evolved UV photoreceptors to use as a private communication channel between conspecifics or possibly to avoid depths to which damaging UVR penetrates.

Studies conducted under natural irradiance are needed: Although laboratory experiments using artificial illumination are informative, they do not replicate the solar spectrum. UV lamps typically emit disproportionately more UV-B compared to natural sunlight. Thus, more studies need to be conducted under natural conditions in order to better understand the functional significance of UV vision as well as to predict organismal responses to changes in the underwater UV environment.

Studies examining the interaction between UV vision and environmental stressors are needed: UV vision is also likely to interact with abiotic and biotic stressors (i.e., temperature, food availability, and predation), influencing the vertical and seasonal abundance and distribution of aquatic organisms. For example, high UV-B levels in the surface waters of low DOC systems may force animals into deeper waters where habitats are suboptimal due to lower temperatures, food availability, or greater risk of predation.

See also: Color of Aquatic Ecosystems; Diel Vertical Migration; Effects of Climate Change on Lakes; Optical Properties of Water; Ultraviolet Light.

Further Reading

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Relevant Websites

The following websites are the home pages of prominent researches in the field of vision ecology, including UV vision and its adaptive significance.

www.biology.duke.edu/johnsenlab/.
www.vet.cornell.edu/BioSci/Faculty/Loew/.
www.umbc.edu/biosci/Faculty/cronin.
www.hawaii.edu/zoology/faculty/losey.