## *Chapter 14*

# Behavioral responses – UVR avoidance and vision

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## Abstract

Light-mediated behaviors, such as visual foraging and migration, have been the focus of numerous studies spanning a wide variety of taxa; however, the role of UVR in these and other behaviors has generally been given less attention.

Recently, the effects of UVR on aquatic ecosystems have been examined more closely as a result of increasing UV-B radiation reaching the Earth's surface due to stratospheric ozone depletion. UVR is now known to penetrate deeply into many freshwater and marine systems, and organisms occupying all trophic levels are susceptible to damage or mortality from UVR exposure. Behavioral avoidance is one means by which organisms can reduce exposure to damaging radiation. Both laboratory and field experiments have demonstrated that many species are negatively phototactic to UV and shorter-wavelength visible light. In addition, UV photoreceptors have been reported in a variety of fish and invertebrates, suggesting that UV vision may be prominent in aquatic organisms. These UV photoreceptors are thought to be used for navigation, communication, enhanced foraging, and possibly UVR avoidance. Given the presence of negative phototactic behaviors as well as UV vision, UVR may be an important factor influencing migration and abundance patterns as well as predator–prey and intraspecific interactions.

## 14.1 Introduction

Behavioral responses to light have long been of interest to aquatic scientists, both freshwater and marine. Light-mediated behaviors such as mate recognition, visual foraging, and especially vertical migration are the focus of numerous studies spanning a wide diversity of taxa [1–3]. However, the role of UVR in these and other behaviors has only recently been more closely examined.

Until recent decades, UVR was not thought to be an important factor influencing aquatic ecosystems, as it was believed to rapidly attenuate through the water column. UVR is now known to penetrate deeply into many freshwater and marine systems, with dissolved organic carbon (DOC) as one of the primary factors regulating UV attenuation [4,5]. In addition, aquatic organisms occupying all trophic levels from viruses and phytoplankton to zooplankton and fish are susceptible to damage or mortality from UVR [6–9]. UVR may directly affect organisms via cellular and tissue damage, genetic mutation, or mortality; or it may indirectly affect organisms by constraining them to suboptimal habitats where temperature and food concentrations may be low and predation risk high. Tolerance to UVR differs among species [8–12] and therefore some species are more likely to respond behaviorally to damaging UVR than others. Consequently, UVR can alter species composition and trophodynamics within an ecosystem, possibly shifting communities towards more UV-tolerant species [13].

There are three means by which organisms can respond to potential UVR damage: (1) avoidance, (2) photoprotection, and (3) photorepair [14]. The extent to which organisms use each mechanism differs both within and among taxa. For example, among freshwater organisms, many species of the cladoceran *Daphnia* are capable of photorepair while copepods such as *Diaptomus oregonensis* and *Acanthodiaptomus denticornis* depend more on photoprotective compounds [15,16]. In the southern hemisphere, three species of the freshwater calanoid copepods within the genus *Boeckella* vary in their use of photoprotection versus photorepair [17]. Differences in photorepair and photoprotection are also seen among marine organisms. Photorepair in two closely related marine fish, the tautog *Tautog onitis* and the cunner *Tautogolabrus adspersus*, appears to be related to longevity, with the longer-lived tautog possessing greater photorepair capabilities than the shorter-lived cunner [18]. In Antarctica, where the ozone hole is the greatest, photoprotection by mycosporine-like amino acids is prevalent in several marine organisms from algae and invertebrates to fish [19]. Although our understanding of the photorepair and photoprotection capabilities of aquatic organisms is increasing, less is known about behavioral avoidance of UVR in nature.

While some wavelengths of UVR are damaging, others are potentially beneficial to aquatic organisms. For example, UV photoreceptors have been described in a variety of aquatic organisms from bacteria to fish [20]. The adaptive significance of these UV photoreceptors is not fully understood; however, research suggests that they may enhance navigation, communication, and foraging [20]. It is also possible that UV photoreceptors may help organisms to avoid depths at which damaging wavelengths are present.

This chapter first describes the underwater UV environment. The different types of phototactic responses, such as positive versus negative phototaxis, are then described and related to UV tolerance as well as UV vision. Finally, implications for behavioral responses to UVR are addressed, including the role of UVR in diel vertical migration (DVM) and predator–prey interactions.

## 14.2 The underwater UV environment

Solar radiation is both absorbed and scattered as it penetrates through water (see Chapter 3). As a result, downwelling irradiance decreases with depth, with shorter and longer wavelengths attenuating more rapidly than the wavelength of peak transmission (which is generally found from 470–550 nm). While particulates and the water itself contribute somewhat to the attenuation of UVR, absorption by DOC is one of the primary factors regulating variations in UV attenuation in aquatic ecosystems [4,5]. In systems with high DOC, UVR is attenuated rapidly while, in systems with low DOC, UVR can penetrate deeply into the water column. In 25% of lakes in several regions of North America, 1% attenuation depths (the depth to which 1% of surface irradiance penetrates) were estimated to be greater than 4 m for 320 nm and greater than 10 m for 380 nm [21]. In the clearest ocean waters, 1% attenuation depths are estimated to be 50 m for 320 nm and approximately 200 m for 380 nm (Figure 1) [22], and there is evidence that increased levels of UV-B are entering the oceans as stratospheric

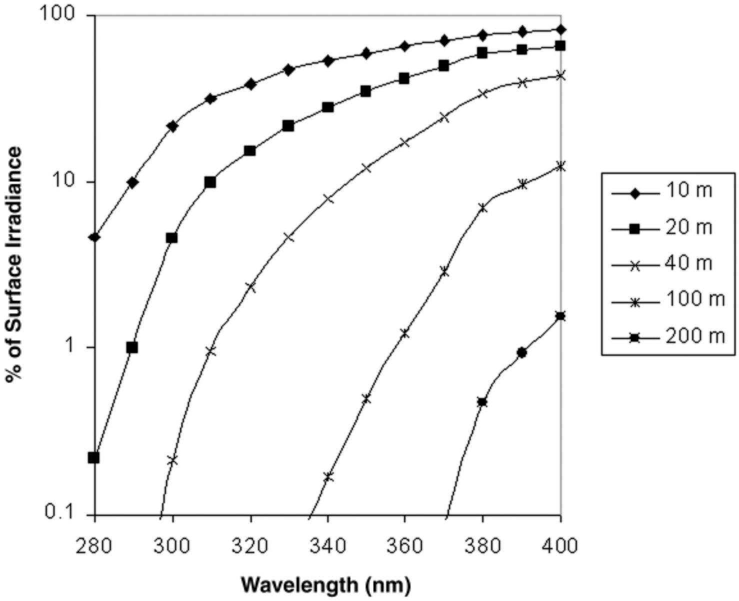

**Figure 1.** Percent of surface irradiance present at depth in the clearest ocean waters. Percent surface irradiance was determined using diffuse attenuation coeifficients derived from Smith and Baker [22]. Measurements of irradiance were taken with a submersible spectoradiometer in the Sargasso Sea and the Central Equatorial Pacific.

ozone decreases [23]. Thus, biologically relevant UVR is present at considerable depths in many freshwater and marine ecosystems. UV-sensitive organisms may avoid depths at which damaging wavelengths are present but may seek depths at which potentially beneficial wavelengths (i.e., used for photorepair and UV vision) are present.

In addition to DOC, other factors influence the depth to which UVR penetrates, including season, latitude, sea state, time of day, cloud cover, and turbidity (Chapters 2 and 3). Light intensity and spectral composition are both affected by each of these factors, creating potential “light niches”. For example, relative quantities of UVR are greater during crepuscular periods (i.e. dawn and dusk) than daylight hours (Figure 2) due to the increasing proportion of high-UV skylight in the total irradiance [24]. Many species of larval fish that possess UV vision feed primarily during crepuscular periods [24–26]. These twilight hours may provide an “optical foraging niche” for fish predators with UV vision, enhancing target-background contrast. Indeed, near the surface of the ocean, up to 40% of the UV-A is in the horizontal and downward directed lines of sight [27], potentially silhouetting prey (Figure 3).

## 14.3 Behavioral responses to UVR

Behavioral responses to radiation often vary with wavelength. Some

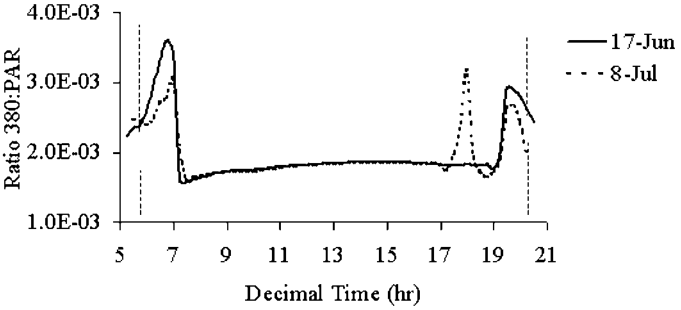

**Figure 2.** The ratio of UV-A (380 nm) to photosynthetically active radiation (PAR, 400–700 nm) in terms of W $m^{-2}$. Data were collected during the summer of 2001 with a UV radiometer (model Biospherical GUV–521) located at the Lacawac Sanctuary in the Pocono Mts., PA, USA (41.23 N, 75.21 W). Sunrise (5.27 h) and sunset (20.37 h) for 17 June 2001 are denoted by the vertical dashed lines. Sunrise and sunset on 8 July 2001 occurred at 5.36 h and 20.37 h, respectively. During crepuscular periods, there is more UV than PAR because the light field is mostly composed of skylight (see Section 14.1). As the sun's angle of incidence decreases, the amount of PAR increases and the light field in dominated by solar radiation. Note that a similar increase in UV-A-to-PAR occurs when patches of clouds pass over the sun. This is shown between 17.0–19.0 h on 8 July 2001.

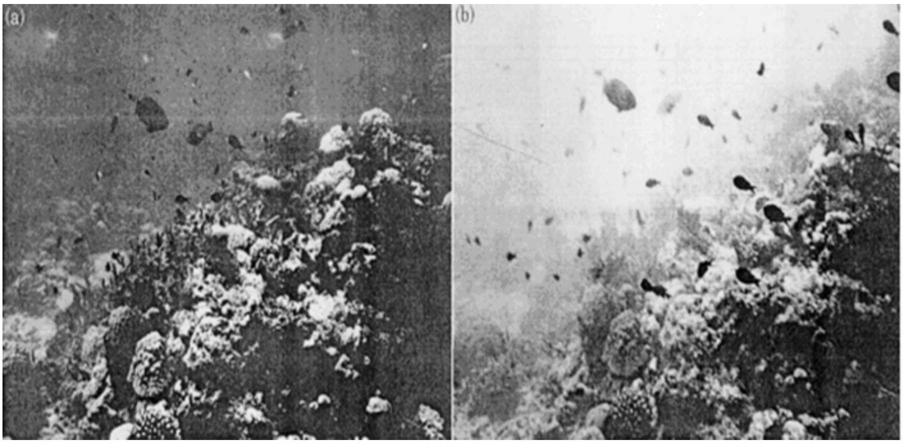

**Figure 3.** Simultaneous images taken at (a) green (490–560 nm) and (b) ultraviolet (350–380 nm) wavelengths. Note the bright background in the UV image that silhouettes fish strongly, even against the reef. [Taken from Losey et al. 27.]

wavelengths induce positive phototaxis or movement towards a light source while other wavelengths induce negative phototaxis or movement away from a light source. For many species, exposure to UVR (280–400 nm) and shorter-wavelength visible (i.e., blue light, 400–440 nm) light induces negative phototaxis. These negative phototactic or avoidance behaviors correspond to wavelengths that are also known to be potentially damaging or lethal [11,16]. In motile organisms, both vertical and horizontal movements have been observed in avoidance of exposure to damaging radiation [28–31], while in less motile organisms covering behaviors are exhibited [32]. Many organisms, such as sea anemones, sea urchins, and sea cucumbers, cover themselves with shells, rocks, and other materials during peak periods of irradiance. Hiding within burrows and among rocks and macrophyte beds, as seen in many amphibian and larval fish species, also helps organisms reduce exposure to damaging radiation.

### *14.3.1 Laboratory experiments*

Thus far, behavioral responses to damaging light have primarily been examined in the laboratory using artificial UV radiation sources. Experiments have been conducted on a variety of organisms from both freshwater and marine systems occupying all trophic levels. At the lower trophic levels, both phytoplankton and protozoa have been shown to exhibit negative phototaxis to UVR. For example, individual cells within mats of the filamentous marine cyanobacteria *Microcoleus chthonoplastes* were shown to migrate to greater depths in response to increased UV-B exposure [28]. The red-colored freshwater ciliate *Blepharisma japonicum* responded with backward swimming when exposed to wavelengths within the UV-B range but began swimming forward when exposed to visible light at 580 nm [33]. It is important to investigate the behavior of organisms at these lower trophic levels as their response to UVR may directly or indirectly influence responses of those at higher trophic levels.

Laboratory experiments have clearly demonstrated that the wavelength of incident radiation is an important behavioral cue for zooplankton. Certain freshwater cladocerans become more agitated and negatively phototactic in the presence of blue light but remain calm and positively phototactic to red light [29]. These “color dances” of Cladocera were hypothesized to cue zooplankton to high concentrations of algal food, which typically filters out short wavelengths greater than longer wavelengths (i.e., “red-dance” keeps individual in place, “blue-dance” promotes wandering). However, it was also suggested that the patterns of the dances may explain patterns of diurnal vertical migration. More recent studies with monochromatic radiation 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 [34]. Copepods have also shown UV avoidance behavior in the laboratory. In small experimental enclosures examining horizontal movements, the freshwater cyclopoid *Cyclops serrulatus* was found to avoid exposure to UV-B radiation (280–320 nm) [10]. This study also noted that UV behavioral responses correlated well with UV tolerance (i.e., UV-sensitive organisms avoid UV-B exposure, see Section 14.3.4). UVR avoidance behaviors were also detected in the marine echinoid larva *Dendraster excentricus* exposed to an artificial UV–visible radiation source (315–700 nm) [30].

Certain stream-dwelling organisms have been shown to be negatively phototactic to UVR in laboratory microcosm experiments. Macroinvertebrates that inhabit or feed on the tops or sides of rocks, such as larval stages of mayflies, caddisflies, and blackflies, exhibited increased drift to more shaded areas when exposed to increased UV-B radiation [31]. Drifting was 60–70% less in the UV-B shielded controls.

Interestingly, deep-sea crustaceans also respond behaviorally to UVR. Tethered individuals of the oplophorid shrimp *Systellaspis debilis* respond to changes in ambient UVR by pitching, changing swimming speed, and moving their feeding appendages [35]. Possible explanations for behavioral responses to UV in deep-sea crustaceans are discussed in Section 14.4.2.

For some organisms, short exposures to UVR inhibit movement altogether. For example, following exposure to artificial UV-B, veligers and post-veligers of the zebra mussel *Dreissena polymorpha* ceased all swimming and crawling motions. However, exposure to UV-A and visible light had no effect on behavior [36]. A similar delay in phototaxis was noted for the green algae *Volvox aureus* exposed to both artificial and solar UV-B radiation [37].

Although these studies provide valuable information regarding organismal responses to varying wavelengths of radiation (i.e., action spectra), they do not tell us how animals respond to natural levels of solar radiation. Artificial lamps generally do not exactly replicate the solar spectrum. UV-B lamps often have greater output in the UV-B range compared to the solar spectrum. In order to supplement UV-A and visible light, UV-A and cool white lamps are used in laboratory setups, and these lamps often have less output in the UV-A and visible range than solar radiation. The total intensity of these lamps in terms of energy or quanta may be similar to solar radiation, but the spectral composition varies greatly (i.e., skewed towards the shorter wavelengths). Solar simulators come the closest to replicating both the intensity and spectral output of the sun; however, these instruments are very expensive, only irradiate a small area, and are only used by a handful of laboratories.

### *14.3.2 Field experiments*

Few field studies have examined behavioral responses of organisms to natural solar radiation. One of the difficulties in these studies is determining whether a behavior is in response to UVR or visible light. High UV systems are also high visible light systems, both of which are known to be potentially damaging [1,8,38]. In addition, many animals have a separate suite of responses to varying levels of visible light. Typically, experimental enclosures are constructed of materials that vary in UVR transmittance. Commonly used materials that transmit full solar radiation include polyethylene, quartz, and acrylic plastics such as OP-4 (CYRO Industries) and UVT (Spartech, Inc. formerly Townsend/Glasflex), all of which can be expensive. UV-blocking materials include Mylar® D and acrylic plastics such as OP-2 (CYRO Industries) and Plexiglas®. While these materials vary in their UV transparency, they have similar transparencies in the visible range. Therefore, using a combination of these materials, behaviors and/or survival can be examined in the presence of full solar radiation, in the absence of UV-B radiation, and in the absence of UV-B and UV-A radiation. It is important to note that these experiments do not provide information concerning responses to a single wavelength; instead, they examine the effect of removing particular wavebands (i.e., UV-B or UV-B and UV-A). Because they remove entire wavebands, the UV blocking materials also unavoidably change the total irradiance, which can confound results. However, the difference in total irradiance between the UV- transparent and UV-blocking materials is often less than 10%. Finally, except for quartz, which is extremely expensive and hard to fabricate, the usual UV-transparent materials tend to block a significant fraction (25–50%) of UV-B.

In the field, solar UV-B has been demonstrated to inhibit motility and oriented movement in phytoplankton such as eukaryotic flagellates, blue–green algae or cyanobacteria, and gliding green algae [39]. When motility is compromised, phytoplankton are at risk of being exposed to greater light intensities, which may result in a bleaching of pigments; or they may be exposed to reduced light intensities, which may result in a reduction in photosynthetic rates. Exposure to increased or decreased irradiances also depends on mixing processes as well as the buoyancy of the individual cells (see also Chapter 4).

Recent field studies have also reported that zooplankton exhibit UVR avoidance in nature. The first evidence of a vertical avoidance response of *Daphnia* to solar UVR was recently published [40]. In the presence of full solar radiation, *D. pulicaria* rapidly descended from the surface waters (1.5 m) of a high-UV lake. In the absence of UV-B and shorter wavelength UV-A radiation ($<380$ nm), the majority of *D. pulicaria* remained in the surface waters. Thus, a stronger negative phototactic response was detected in the presence of UVR than in the absence of UVR. Negative phototactic behaviors have also been observed in a population of *D. catawba* inhabiting a high-UV lake located in the Pocono Mts., PA, USA (Figure 4) [41]. Experiments conducted in this study demonstrated that, in some cases, *D. catawba* actually swim towards the surface waters in the absence of UVR in spite of the probable presence of fish kairomones (Figure 4). These field results for *Daphnia* are supported by smaller scale experiments conducted in the laboratory [42,43].

Although *Daphnia* often displayed a preference for the surface waters in the absence of UVR, the response was variable, with mean depths of *Daphnia* increasing in the absence of UVR [41]. The reason for this variability is unknown. One explanation is that irradiance differed among experiments. Although the experiments in this study were not designed to specifically test zooplankton responses to irradiance, preliminary observations suggest that as irradiance increased, *Daphnia* responded with increased negative phototaxis. Because the acrylic used to construct the UV-blocking columns did transmit some longer wavelength UV-A (50% transmittance at 384 nm), this may be an avoidance response to either longer wavelength UV-A light or visible light [40]. Other species, such as the freshwater copepod *Diaptomus nevadensis*, the marine copepod *Acartia tonsa*, the cladoceran *Daphnia magna*, and the hydromedusan *Polyorchis penicillatus* also become negatively phototactic in response to increasing irradiance, both in the UV and visible range [1,38].

The harpacticoid copepod *Tigriopus californicus*, which lives in shallow tide

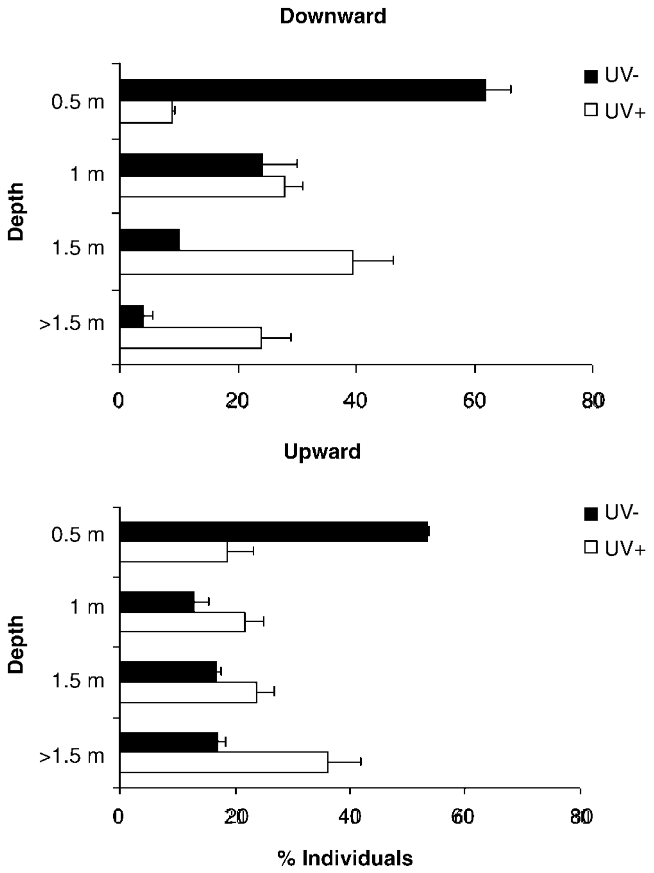

**Figure 4.** A comparison of the downward and upward migrations of *Daphnia catawba* in the presence and absence of UVR. There were three UV-transparent columns and three UV-opaque columns. Each column was suspended 10 cm below the surface of Lake Giles, a high-UV lake located in northeastern PA, USA. The downward experiment was conducted on 14 July 2000 and the upward on 2 August 2000. Mean solar irradiance was measured with a LICOR model LI–200SA pyranometer near solar noon (1300 h) when the experiments were conducted. Mean solar irradiance equaled 659 $Wm^{-2}$ on 14 July 2000 and 694 $Wm^{-2}$ on 2 August 2000.

pools, was found to aggregate in shaded regions of pools at midday but show no preference at dawn and dusk [44]. These same authors used lab experiments to demonstrate that *T. californicus* responds more to UV-B than to visible radiation and suggest that they may possess UV photoreceptors.

Small stream invertebrates have also been noted to respond negatively to UVR in nature. Blackfly larvae appear to exhibit a diurnal emigration, or migration out of UV-exposed stream channels, during periods of peak irradiance but return to UV-exposed regions as irradiance levels decrease [45]. In streams that were experimentally shielded from UVR exposure, however, larvae remained in the stream channels throughout the day. Larvae were allowed to move freely between the treatments and on average larval densities in the UV-shielded channels were 161–168% greater than those in the UV-exposed channels.

Differences in the spawning depths of yellow perch, *Perca flavescens*, in a high- versus a low-UV lake suggest that yellow perch also avoid UV exposure. Spawning depth was reported to be deeper in a high-UV lake (median = 3.2 m) compared to a low-UV lake (median = 0.4 m) [46]. In addition, yellow perch eggs were incubated at the surface of each lake in a modified reciprocal transplant experiment. Eggs were exposed to full solar radiation, shielded from UV-B, or kept in the dark. In the high-UV lake, all eggs perished in all the light treatments, but survival time was longer (2–4 days) for eggs in the UV-B shielded treatment. Furthermore, those collected from the high-UV lake survived longer than those collected from the low-UV lake. Most eggs (>96%) incubated in the light treatments of the low UV lake as well as the dark controls of both lakes survived to hatching. Comparable results, using a similar experimental design, were reported for the bluegill *Lepomis machrochirus* in which the median nesting depth was observed to be deeper in a high UV lake compared to a low UV lake [47].

It is more difficult to perform behavioral experiments in the open ocean. The approach has been to observe the distribution of organisms in relation to their photic environment combined with laboratory experiments examining UV tolerance and phototaxis. Both ascidians and sea urchins were shown to exhibit UV avoidance. The distribution of the solitary ascidian *Corella inflata* varied with exposure to direct solar radiation, particularly UVR exposure, with populations conspicuously absent from unshaded areas [48]. Laboratory experiments confirmed that UVR is lethal to all life history stages of *C. inflata*, with the younger stages being most vulnerable. In addition, none of the life stages possessed UV-absorbing photoprotective compounds. The sea urchins *Arbacia punctulata* and *Lytechinus variegates* were shown to be negatively phototactic to bright solar radiation but positively phototactic to white light [49]. These data are consistent with the observation that echinoplutei migrate to deeper depths in the water column during peak periods of irradiance [30,50], but this response could also be related to other factors such as predator avoidance. The sea urchin *Strongylocentrotus droebachiensis* shades or covers itself in response to UVR exposure, particularly in response to UV-B or a combination of UV-B and UV-A [32]. Covering behavior was also shown to increase with increasing intensity of UVR exposure. In some sea urchin species, covering behavior has been observed to vary diurnally, with the greatest response during peak irradiance [49,51].

### *14.3.3 Relation to UV tolerance, pigmentation, and photorepair*

Behavioral responses to UVR appear to be related to UV tolerance (i.e., defined as the sum of an organism's photoprotection (pigmentation) and photorepair capabilities). For example, during periods of high UV, organisms occupying the surface waters of Lake Giles, a high UV lake in the Pocono Mts., PA, USA, were found to be more UV-tolerant than those inhabiting deeper waters during the day [12]. Laboratory experiments with the ostracod *Cypris* sp. demonstrated that this species is highly tolerant to UV-B exposure and actually showed a behavioral preference or positive phototaxis towards UV-B irradiance [10]. In the same study, the protozoan *Paramecium aurelia* was also shown to be highly tolerant and positively phototactic to UV-B irradiance [10].

The action spectrum of phototaxis in copepods has been demonstrated to depend on pigmentation. Within the visible light spectrum, *Diaptomis nevadensis* swimming speeds were faster in blue light compared to red light [38]. In addition, less pigmented individuals were more responsive to changes in wavelength than pigmented individuals [52]. Similar results have been reported for melanized *Daphnia* within the UV spectrum [43].

## 14.4 UV vision and photoreception

UV vision has been documented in a variety of terrestrial organisms including insects, birds, amphibians, reptiles, and mammals [53–55]. It is therefore not surprising that many aquatic organisms also perceive light in the UV spectrum. Most UV photoreceptors in aquatic organisms have been described in fish species; however, UV photoreceptors have also been reported in bacteria and algae as well as some species of protozoans, annelids, cnidarians, and crustaceans (Table 1).

### *14.4.1 Relation to habitat and age*

Many UV photoreceptors have a maximum absorbance peak in the UV-A range but UV-B photoreceptors have been documented 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. For instance, cataracts are reported to occur in several fish species inhabiting shallow waters [56]. Seeing in the UV-A may therefore be less detrimental to the eye; however, prolonged exposure to UV-A radiation may also be potentially damaging, albeit less than UV-B. In addition, since eyes are photon-, not energy-counters, seeing in the UV-A provides more light than in the UV-B. However, visible light provides more photons than UV, making UV vision a curious trait (See section 14.4.2).

Some authors have suggested that UV photoreceptors vary with habitat such that peak absorbance correlates with wavelengths present in their photic environment [57–59]. In some cases, species such as the rudd *Scardinius erythrophthalmus* [60] and the brown trout, *Salmo trutta* [61], display seasonal changes in spectral sensitivity that correspond to seasonal changes in the photic environment associated with daylength and temperature. Most of these shifts are in the longer wavelengths with shorter wavelength sensitivity remaining the same [62]. Behavior shifts are also suggested to contribute to shifts in spectral sensitivity, such as foraging at the surface during summer months and in deeper strata during winter months [60].

UV photoreceptors in some fish species not only vary with habitat but with age as well. Many fish species, such as *Lepomis gibbosus*, *Perca flavescens*, and *Salmo* sp., possess UV photoreceptors as larvae but lose them with maturity [63,64]. This loss of UV photoreception coincides with a habitat shift from the surface waters to more demersal waters in addition to a change in diet from small to larger zooplankton prey and/or fish [63–65]. In some species of salmonoids, however, UV photoreceptors disappear during earlier life history stages and reappear in adults. For example, ultraviolet cones and UV sensitivity in the sockeye salmon, *Oncorhynchus nerka*, diminished during smoltification and reappeared at the late juvenile or adult stage [66]. The author also noted that the arrangement of the UV cones in the retina of the adult sockeye salmon was similar to those of saltwater salmon, *O. tshawytsha* and *O. keta*, collected while migrating back to natal streams or spawning in streams. This suggests that UV photoreceptors may assist in navigation during migrations. Goldfish and species of cyprinids retain their UV photoreceptors as adults. These species experience little to no change in habitat or diet and therefore a change in the spectral sensitivity of their photoreceptors would not be expected. Ontogenetic changes in spectral sensitivity among aquatic species other than fish are less well known.

### *14.4.2 Adaptive significance*

The adaptive role of UV vision is not completely understood. In some organisms, UV photoreceptors assist in navigation and orientation, associated with the e-vector of the polarized light field [67,68], while in others they have been demonstrated to enhance color discrimination [55,69]. Recognition and communication between conspecifics and mates at UV wavelengths has been speculated in species of coral reef fish [20,27]. Recently, the epithelial mucus of several marine fish species was found to contain UV-absorbing compounds, which may be seen by fish with UV vision [70]. Consequently, it is suggested that one fish may see another as “tanned” or “untanned”, potentially playing an important role in visual communication.

UV photoreceptors are also thought to help in the detection of prey during visual foraging by enhancing prey contrast [20,63,64]. Planktonic prey, such as *Daphnia* and *Diaptomus*, absorb solar radiation in the near-UV [71]. Because of this, these zooplanktors may appear darker than their surrounding background. In addition, planktonic prey also scatter light and may appear lighter or darker depending on the direction of illumination, shape, and refractive index differences (Figure 5) [71]. Larvae of the phantom midge *Chaoborus trivittatus* reflect blue light greater than longer wavelength red light and it is predicted that the reflectance curve will shift towards shorter wavelengths as the angle of incidence increases [72]. These differences in reflectance were hypothesized to reduce visibility to visual feeding fish and therefore reduce mortality. This would be true for fish without UV photoreceptors, but increased reflectance at shorter wavelengths may increase visibility to foragers with UV vision.

Laboratory experiments have demonstrated that larval fish do feed better in

**Table 1.** Survey of the distribution of UV photoreceptors among aquatic organisms. (This list is not all-inclusive) microspectrophotometry is abbreviated as MSP

| Organism | Method | Wavelength of maximum response or absoption (nm) | Reference |
|---|---|---|---|
| **Bacteria** | | | |
| Mutant, *Escherichia coli* | behavior | 396–450 | [89] |
| Purple eubacterium, *Ecotothiorhodospira halophila* | behavior | N/A | [90] |
| Saltwater bacterium, *Halobacterium halbium* | behavior | 280, 370 | [91] |
| **Phytoplankton** | | | |
| Cyanobacterium, *Chologloeopsis* | physiology, MAAs induction | 310 | [76] |
| Green alga rhizoid, *Bryopsis plumosa* | physiology, MAAs induction | 260, 310 | [92] |
| **Protozoans** | | | |
| Ciliates | | | |
| *Chlamydodon mnemosyne* | behavior | 360 | [93] |
| *Blepharisma japonicum* | behavior | N/A | [33] |
| **Annelids** | | | |
| Alciopid worm, *Torrea candida* | electrophysiology | 400 | [77] |
| **Cnidarians** | | | |
| Sea anemone, *Anthopleura xanthogrammica* | behavior | 360 | [91] |
| **Molluscs** | | | |
| Giant clam, *Tridacna* sp. | electrophysiology | 360 | [94] |
| **Crustaceans** | | | |
| Cladoceran, *Daphnia magna* | behavior | 348 | [75] |
| Harpacticoid copepod, *Tigriopus californicus* | behavior | N/A | [44] |
| Ectoparasitic copepod, *Lepeophtheirus salmonis* | behavior | 352–400 | [95] |
| Crayfish, *Procambarus clarkia* | MSP | 440 | [53] |
| Mantis Shrimp, *Pseudosquilla ciliate* | MSP | 400 | [96] |
| Deep sea oplophroid shrimp | | | |
| *Systellaspis debilis* | behavior | 410 | [35] |
| *Janicella spinacauda* | electrophysiology | 370 | [97] |

| | | | |
|---|---|---|---|
| *Oplophorus spinosus* | electrophysiology | 400 | [97] |
| *Oplophorus gracilirostris* | electrophysiology | 400 | [97] |
| Estuarine intertidal crabs | | | |
| *Sesarma reticulatum* | behavior | 360 | [98] |
| *S. cinereum* | behavior | 360 | [98] |
| *Pinnotheres ostreum* | behavior | 360 | [98] |
| Prawn, *Palaemonetes vulgaris* | electrophysiology | 390 | [99] |
| Spiny lobster, *Panulirus argus* | MSP, electrophysiology | 370 | [100] |
| Horseshoe crab, *Limulus polyphemus* | electrophysiology | 360 | [101] |
| **Fishes** | | | |
| **Clupeomorpha** | | | |
| Northern anchovy, *Engraulis mordax* | MSP | 358, 365 | [102] |
| Ostariophysi | | | |
| Minnow, *Phoxinus laevis* | operant conditioning | response down to 365 | [103] |
| Roach, *Rutilus rutilus* | MSP | 355–360 | [104] |
| Goldfish, *Carassius auratus* | heart-rate conditioning | 365 | [105] |
| Carp, *Cyprnus carpio* | MSP, behavior | 377 | [106] |
| Danio, *Danio aequipinnatus* | electophysiology | 358 | [107] |
| Eastern Golden Shiner, *Notemigonus crysoleucas* | MSP | 355 | [27] |
| Rudd, *Scardinius erythrophthalmus* | MSP | 355–360 | [108] |
| Japanese dace, *Tribolodon hakonensis* | MSP | 350–370 | [109] |
| Salmoniformes | | | |
| Rainbow trout, *Oncorhynchus mykiss* | heart-rate conditioning | 390 | [110] |
| Brown trout, *Salmo trutta* | MSP | 355 | [65] |
| Atlantic salmon, *Salmo salar* | MSP | 360 | [111] |
| Sockeye salmon, *Oncorhynchus nerka* | MSP, electrophysiology | N/A | [66] |
| Acanthopterygii | | | |
| Guppy, *Poecilia latipinna* | MSP | 412 | [112] |
| Guppy, *P. reticulata* | MSP | 411 | [112] |
| Sunfish, *Lepomis* spp. | MSP | 360–370 | E. Loew, (personal commun.) |
| Yellow perch, *Perca flavescens* | MSP | 385 | [113] |
| Atlantic Silverside, *Menidia menidia* | MSP | 365 | [114] |
| Killifish, *Fundulus heteroclitus* | MSP | 363 | 115] |
| California topsmelt, *Atherinops affinis* | MSP | 355 | [116] |

**Table 1.** (*cont.*)

| Organism | Method | Wavelength of maximum response or absoption (nm) | Reference |
|---|---|---|---|
| Grunion, *Leuresthes tenuis* | MSP | 355 | [116] |
| Kelp greenling, *Hexagrammos decagrammus* | MSP | 350, 358 | [102] |
| White spotted greenling, *H. steilen* | MSP | 364 | [102] |
| Lingcod, *Ophiodon elongates* | MSP | 359 | [102] |
| Puget Sound sculpin, *Artedius meanyi* | MSP | 363, 375 | [102] |
| Cabezon, *Scorpaenichthys marmorutus* | MSP | 364 | [102] |
| Rock prickleback, *Xiphister mucosus* | MSP | 364 | [102] |
| Dwarf wrymouth, *Lyconectes aleutensis* | MSP | 355 | [102] |
| Wolf-eel, *Anarrhichthys oceliatus* | MSP | 378 | [102] |
| Pacific sandfish, *Trichodon trichodon* | MSP | 359 | [102] |
| Atlantic halibut, *Hippoglossus hippoglossus* | in situ hybridization | N/A | [117] |
| Cichlid, *Metriaclima zebra* | MSP | 368 | [118] |
| Damselfish, *Dascyllus albisella* | MSP | $>400$ | [119] |
| Pomacentridae, | | | |
| *Dascyllus trimaculatus* | | | |
| *Pomacentrus coelestris* | | | |
| *Chromis punctipinnis* | MSP | 360 | [120] |
| **Reptiles** | | | |
| Red-eared terrapin, *Pseudemys scripta elegans* | electrophysiology | 360 | [121] |
| Caspian terrapin, *Mauremys caspica* | electrophysiology | 360 | [121] |

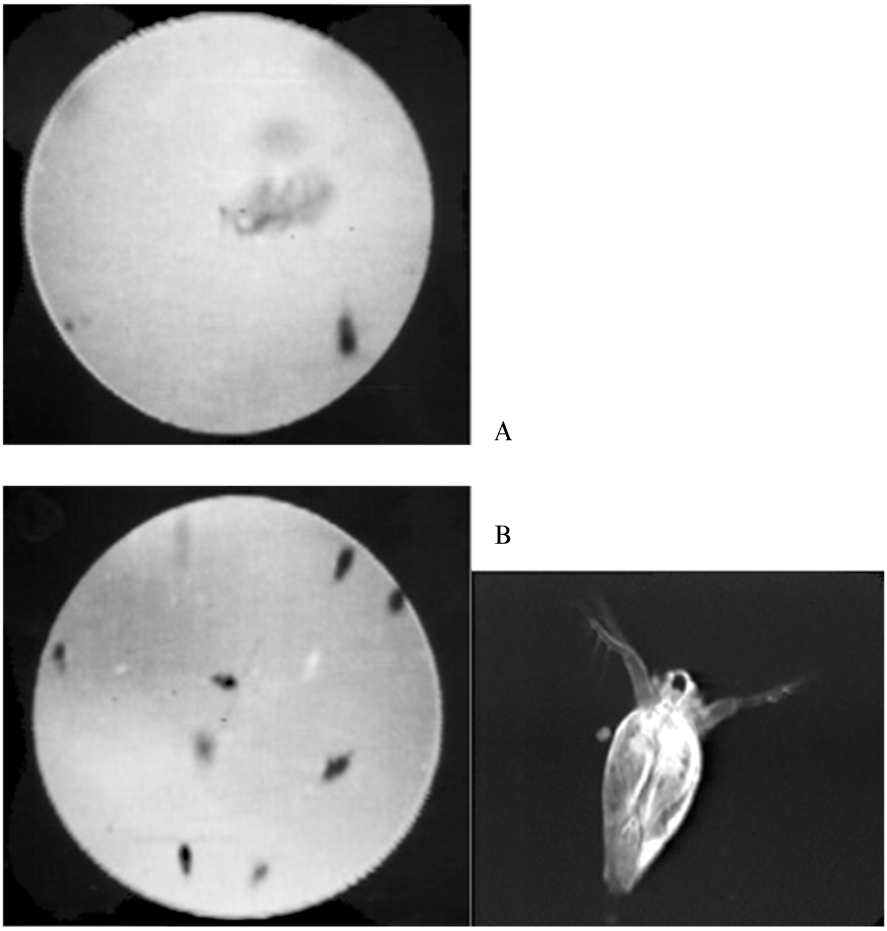

**Figure 5.** UV images taken with a UV video camera sensitive between 320 nm and 410 nm. (A) Image taken in Oneida Lake, NY, USA showing *Daphnia* sp. in silhouette against the brighter skylight. Freshwater copepods *Diaptomus siscilis* are also shown and appear darker because they contain a dense, UV-absorbing (orange) pigment. (B) Image of *Daphnia* sp. showing UV scatter 90° from the direction of artificial UV illumination from a xenon light source. [Photos provided by E.R. Loew and W.N. McFarland.]

the presence of UV-A wavelengths [63,64] and can feed under monochromatic UV-A [63]. However, recent experiments with trout suggest that UV photoreceptors do not enhance foraging under natural levels of solar radiation [73]. 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 1000–1300 h local time. It is not known if a difference would have been noticed during crepusclular periods when relative UV levels are higher and planktivory is more challenging.

It has been suggested that increased absorbance in prey species in the UV range due to photoprotective pigments increases visibility to predators, especially in transparent organisms. Transparent organisms occupying the epipelagic zone in the Northwest Atlantic Ocean were found to be more UV absorbent than those occupying the deeper mesopelagic zone, while visible transparency was similar for organisms inhabiting both regions [74]. However, absorbance was greatest in the UV-B range not in the UV-A range where UV vision occurs. In addition, species with high UV-absorption tended to be less transparent in the visible range. For both these reasons, the effects of UV absorption on UV visibility were predicted to be slight in comparison to potential photoprotection.

UV photoreceptors have also been identified in several zooplankton prey, such as the cladoceran *Daphnia magna* [75]. It is possible that these UV photoreceptors may also serve a means of predator avoidance. However, this hypothesis has yet to be fully tested.

The presence of both UV photoreception and negative phototaxis in some species suggest that UV photoreceptors may help animals to avoid depths at which levels of damaging solar radiation are high. Indeed, it is not known if organisms can sense the UV damage they are incurring and respond appropriately without the aid of UV photoreceptors. In the cyanobacterium *Chlogloeopsis*, a UV-B photoreceptor is linked to the production of the photoprotective compound shinorine, a mycosporine-like amino acid [76]. Induction efficiency of shinorine was greatest when organisms are exposed to UV-B at 310 nm.

Curiously, UV vision is also noted in some mesopelagic and benthic organisms where little to no UVR is present. One explanation for UV vision at these depths is that many deep-sea fishes and some crustaceans possess photophores, light emitting organs with maximum emission in the blue, that may be used to communicate information between conspecifics and/or predators and prey. UV photoreceptors in these species have significant blue sensitivity, and the emissions of the photophores correlate well with the maximum transmission of the water as well as with the maximum sensitivity of the visual pigments [59]. These organisms are also known to be vertical migrators and it is suggested that UV photoreceptors may be used to detect varying ratios of shorter to longer wavelengths that would occur at sunrise and sunset, which could trigger the organisms to ascend and descend if enough solar radiation were available [35]. In the alciopid worm, *Torrea candida*, it is suggested that UV photoreceptors are used as a depth gauge [77].

## 14.5 Implications for behavioral responses to UVR

The distribution and abundance of organisms can have a profound effect on an ecosystem's structure and function. Nutrient cycling, predator–prey interactions, and community structure may all be influenced by distribution patterns. As such, numerous studies have been conducted to understand factors influencing vertical and horizontal distribution and abundance [2,78]. However, UVR has historically received less attention. Implications of behavioral responses to UVR in diel vertical migration and predator–prey interactions are discussed further below.

### *14.5.1 Diel vertical migration*

One of the most interesting behavioral responses to solar radiation 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 interference by larger zooplankton [52,79,80]. Many hypotheses have been proposed to explain these patterns. Some of the earliest works on DVM demonstrated that solar radiation was a potentially important proximate as well as an ultimate factor inducing migrations [81–83]. These experiments, however, were conducted in the laboratory and no field studies were conducted to demonstrate a clear link between damaging solar radiation and zooplankton migration patterns in nature. Consequently, other factors such as temperature, food, and especially predation have typically been more widely studied and identified as the primary factors inducing DVM [78].

In spite of the importance of predators inducing migrations, predation alone does not explain the variety of DVM patterns observed in nature [84,85]. For example, vertical migrations have been detected in organisms inhabiting fishless systems [52]. Most of these systems tend to be high alpine or desert lakes in which damaging solar radiation can be intense. Several experiments have shown that ambient levels of UVR can lead to a decrease in survival as well as a decrease in growth and reproduction in both freshwater and marine organisms [6,8,14,86], and negative phototactic behavior has been demonstrated in the laboratory and field [28–38,40–51]. Given these recent findings, UVR may be more important than previously thought in influencing the vertical migration and distribution of organisms [34,84], serving as both a proximate and an ultimate cause of DVM.

Indeed, zooplankton often migrate deeper than the depths to which damaging UV-B radiation penetrates, in both freshwater and marine systems. While damaging UV-B may not be present, UV-A radiation continues to penetrate through the water column. For example, in the open ocean, the 1% level of 375 nm is four times as deep as the 1% level of 310 nm (Jerlov type II oceanic water) [87], and in freshwater lakes, UV-A penetration can be two times or greater [21]. Given that many fish species use UV-A light to forage, zooplankton may migrate to deeper depths in order to avoid visually feeding predators with UV-A photoreceptors. Many freshwater and marine species, however, continue to migrate to even deeper depths, suggesting that other factors besides UVR, such as temperature and predation, are inducing migrations.

### *14.5.2 Predator–prey interactions*

While both UV-B and UV-A can be damaging, UV-B is generally more damaging than UV-A radiation per photon. The UV photoreceptors in many species peak in the UV-A range (see Table 1). If animals are cueing to UV-A wavelengths that penetrate more deeply into the water column, they would be protected from potentially more damaging UV-B found closer to the surface. These alterations in depth to prevent UVR exposure may in turn influence the overlap of predator and prey in both time and space. For example, UV-tolerant zooplankton may find refuge from larval fish predators, which are susceptible to UV damage [46,86], in the surface waters of high UV systems.

Many species of larval fish have retinal cones that perceive UV-A (350–370 nm) and these are thought to help larvae locate and capture their prey [63,64]. However, some prey species also have UV-A photoreceptors. Responses to UV-A wavelengths in these organisms may therefore also be a means of predator avoidance in the surface waters. In this case, predation may be the ultimate cause of DVM but UV-A light would be the proximate cue. Further investigation is needed to test these types of hypotheses.

## 14.6 Future directions

As levels of stratospheric ozone continue to decrease, future increases in UVR reaching the Earth's surface are predicted [88]. UVR has been shown to be damaging to many aquatic organisms from bacteria to fish [6–9], and UV avoidance behavior has been observed in several species [28–51]. Yet responses to future changes in the underwater UVR environment are largely unknown.

The presence of UV photoreceptors in such a wide variety of freshwater and marine organisms suggests that UV vision is prominent in aquatic ecosystems. Further experimentation is needed to identify potential UV photoreceptors as well as action spectra for behavioral responses to varying wavelengths of light. In addition, field experiments are needed to understand responses to natural solar radiation. As seen in the feeding experiments with rainbow trout [73], laboratory results may not always match those reported in the field. Interpreting responses of organisms to solar radiation may require an integration of scientists working in the fields of vision ecology, behavioral ecology, as well as bio-optics.

UVR is only one of many potential stressors acting on aquatic communities. Other stressors such as pH, temperature, competition, predation, and food limitation can also influence the vertical and seasonal abundance and distribution of aquatic organisms. UVR is likely to interact with these stressors through a variety of mechanisms. For example, high UVR levels in the surface waters of low DOC systems may force animals into deeper waters where habitats are suboptimal due to lower temperatures or greater risk of predation. Further investigation is needed to understand how UVR interacts with these other important abiotic and biotic stressors.

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