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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

1 to which organisms use each mechanism differs both within and among taxa. For
2 example, among freshwater organisms, many species of the cladoceran *Daphnia*
3 are capable of photorepair while copepods such as *Diaptomus oregonensis* and
4 *Acanthodiaptomus denticornis* depend more on photoprotective compounds
5 [15,16]. In the southern hemisphere, three species of the freshwater calanoid
6 copepods within the genus *Boeckella* vary in their use of photoprotection versus
7 photorepair [17]. Differences in photorepair and photoprotection are also seen
8 among marine organisms. Photorepair in two closely related marine fish, the
9 tautog *Tautog onitis* and the cunner *Tautoglabrus adspersus*, appears to be
10 related to longevity, with the longer-lived tautog possessing greater photorepair
11 capabilities than the shorter-lived cunner [18]. In Antarctica, where the ozone
12 hole is the greatest, photoprotection by mycosporine-like amino acids is preva-
13 lent in several marine organisms from algae and invertebrates to fish [19].
14 Although our understanding of the photorepair and photoprotection capabili-
15 ties of aquatic organisms is increasing, less is known about behavioral avoidance
16 of UVR in nature.

17 While some wavelengths of UVR are damaging, others are potentially benefi-
18 cial to aquatic organisms. For example, UV photoreceptors have been described
19 in a variety of aquatic organisms from bacteria to fish [20]. The adaptive
20 significance of these UV photoreceptors is not fully understood; however, re-
21 search suggests that they may enhance navigation, communication, and foraging
22 [20]. It is also possible that UV photoreceptors may help organisms to avoid
23 depths at which damaging wavelengths are present.

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

31 14.2 The underwater UV environment

32
33 Solar radiation is both absorbed and scattered as it penetrates through water (see
34 Chapter 3). As a result, downwelling irradiance decreases with depth, with
35 shorter and longer wavelengths attenuating more rapidly than the wavelength of
36 peak transmission (which is generally found from 470–550 nm). While particu-
37 lates and the water itself contribute somewhat to the attenuation of UVR,
38 absorption by DOC is one of the primary factors regulating variations in UV
39 attenuation in aquatic ecosystems [4,5]. In systems with high DOC, UVR is
40 attenuated rapidly while, in systems with low DOC, UVR can penetrate deeply
41 into the water column. In 25% of lakes in several regions of North America, 1%
42 attenuation depths (the depth to which 1% of surface irradiance penetrates) were
43 estimated to be greater than 4 m for 320 nm and greater than 10 m for 380 nm
44 [21]. In the clearest ocean waters, 1% attenuation depths are estimated to be 50
45 m for 320 nm and approximately 200 m for 380 nm (Figure 1) [22], and there is
46 evidence that increased levels of UV-B are entering the oceans as stratospheric

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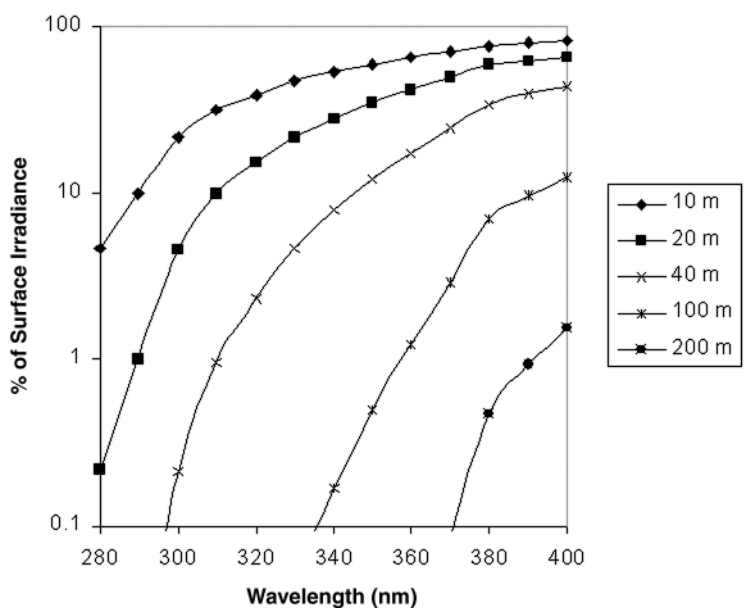


Figure 1. Percent of surface irradiance present at depth in the clearest ocean waters. Percent surface irradiance was determined using diffuse attenuation coefficients derived from Smith and Baker [22]. Measurements of irradiance were taken with a submersible spectroradiometer in the Sargasso Sea and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

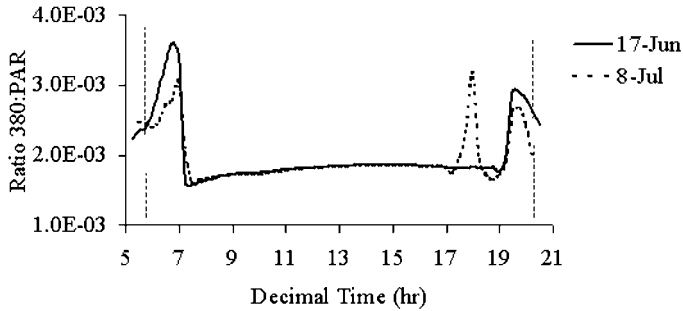


Figure 2. The ratio of UV-A (380 nm) to photosynthetically active radiation (PAR, 400–700 nm) in terms of W m^{-2} . Data were collected during the summer of 2001 with a UV radiometer (model Biospherical GUV-521) located at the Lacawac Sanctuary in the Pocono Mts., PA, USA (41.23 N, 75.21 W). Sunrise (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 is 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.

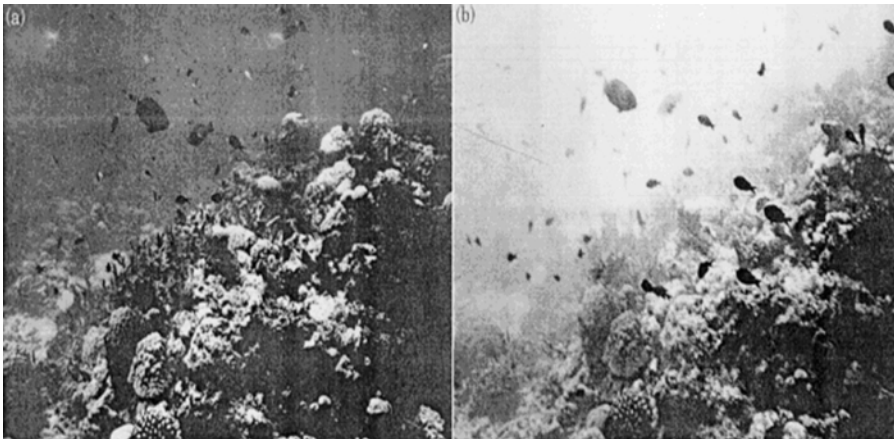


Figure 3. Simultaneous images taken at (a) green (490–560 nm) and (b) ultraviolet (350–380 nm) wavelengths. Note the bright background in the UV image that silhouettes fish strongly, even against the reef. [Taken from Losey et al. 27.]

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

1 in avoidance of exposure to damaging radiation [28–31], while in less motile
2 organisms covering behaviors are exhibited [32]. Many organisms, such as sea
3 anemones, sea urchins, and sea cucumbers, cover themselves with shells, rocks,
4 and other materials during peak periods of irradiance. Hiding within burrows
5 and among rocks and macrophyte beds, as seen in many amphibian and larval
6 fish species, also helps organisms reduce exposure to damaging radiation.

9 14.3.1 Laboratory experiments

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

23 Laboratory experiments have clearly demonstrated that the wavelength of
24 incident radiation is an important behavioral cue for zooplankton. Certain
25 freshwater cladocerans become more agitated and negatively phototactic in the
26 presence of blue light but remain calm and positively phototactic to red light
27 [29]. These “color dances” of Cladocera were hypothesized to cue zooplankton
28 to high concentrations of algal food, which typically filters out short wavelengths
29 greater than longer wavelengths (i.e., “red-dance” keeps individual in place,
30 “blue-dance” promotes wandering). However, it was also suggested that the
31 patterns of the dances may explain patterns of diurnal vertical migration. More
32 recent studies with monochromatic radiation have demonstrated that *Daphnia*
33 *magna* are positively phototactic to visible light (421–600 nm) and negatively
34 phototactic to UVR (260–380 nm) with maximal sensitivity at 340 nm [34].
35 Copepods have also shown UV avoidance behavior in the laboratory. In small
36 experimental enclosures examining horizontal movements, the freshwater cyclo-
37 poid *Cyclops serrulatus* was found to avoid exposure to UV-B radiation
38 (280–320 nm) [10]. This study also noted that UV behavioral responses corre-
39 lated well with UV tolerance (i.e., UV-sensitive organisms avoid UV-B exposure,
40 see Section 14.3.4). UVR avoidance behaviors were also detected in the marine
41 echinoid larva *Dendroaster excentricus* exposed to an artificial UV-visible radi-
42 ation source (315–700 nm) [30].

43 Certain stream-dwelling organisms have been shown to be negatively photo-
44 tactic to UVR in laboratory microcosm experiments. Macroinvertebrates that
45 inhabit or feed on the tops or sides of rocks, such as larval stages of mayflies,
46

1 caddisflies, and blackflies, exhibited increased drift to more shaded areas when
2 exposed to increased UV-B radiation [31]. Drifting was 60–70% less in the
3 UV-B shielded controls.

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

9 For some organisms, short exposures to UVR inhibit movement altogether.
10 For example, following exposure to artificial UV-B, veligers and post-veligers of
11 the zebra mussel *Dreissena polymorpha* ceased all swimming and crawling
12 motions. However, exposure to UV-A and visible light had no effect on behavior
13 [36]. A similar delay in phototaxis was noted for the green algae *Volvox aureus*
14 exposed to both artificial and solar UV-B radiation [37].

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

28 29 30 *14.3.2 Field experiments*

31
32 Few field studies have examined behavioral responses of organisms to natural
33 solar radiation. One of the difficulties in these studies is determining whether a
34 behavior is in response to UVR or visible light. High UV systems are also high
35 visible light systems, both of which are known to be potentially damaging
36 [1,8,38]. In addition, many animals have a separate suite of responses to varying
37 levels of visible light. Typically, experimental enclosures are constructed of
38 materials that vary in UVR transmittance. Commonly used materials that
39 transmit full solar radiation include polyethylene, quartz, and acrylic plastics
40 such as OP-4 (CYRO Industries) and UVT (Spartech, Inc. formerly Town-
41 send/Glasflex), all of which can be expensive. UV-blocking materials include
42 Mylar® D and acrylic plastics such as OP-2 (CYRO Industries) and Plexiglas®.
43 While these materials vary in their UV transparency, they have similar transpar-
44 encies in the visible range. Therefore, using a combination of these materials,
45 behaviors and/or survival can be examined in the presence of full solar radiation,
46 in the absence of UV-B radiation, and in the absence of UV-B and UV-A

1 radiation. It is important to note that these experiments do not provide informa-
2 tion concerning responses to a single wavelength; instead, they examine the effect
3 of removing particular wavebands (i.e., UV-B or UV-B and UV-A). Because they
4 remove entire wavebands, the UV blocking materials also unavoidably change
5 the total irradiance, which can confound results. However, the difference in total
6 irradiance between the UV- transparent and UV-blocking materials is often less
7 than 10%. Finally, except for quartz, which is extremely expensive and hard to
8 fabricate, the usual UV-transparent materials tend to block a significant fraction
9 (25–50%) of UV-B.

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

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

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

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

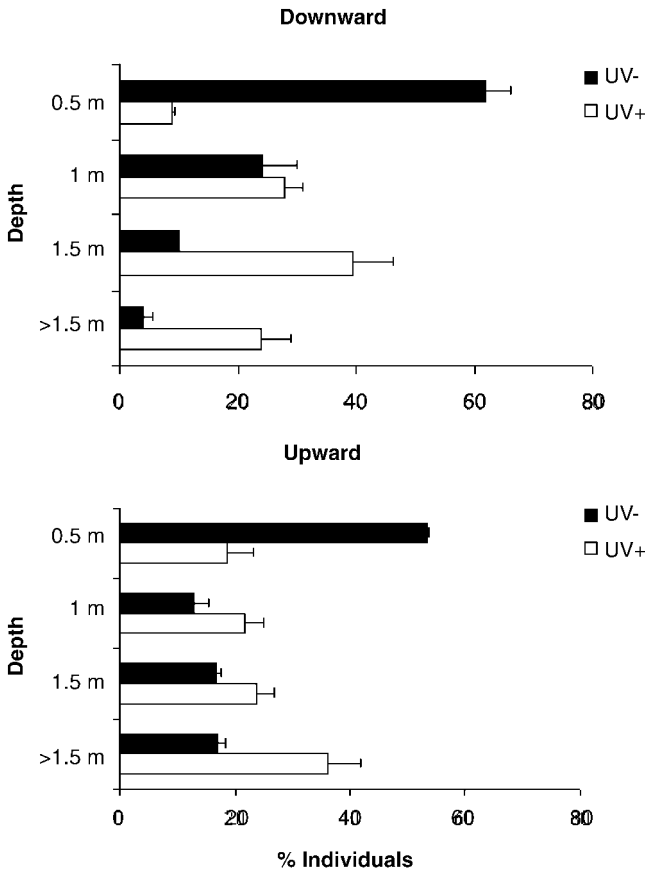


Figure 4. A comparison of the downward and upward migrations of *Daphnia catawba* in the presence and absence of UVR. There were three UV-transparent columns and three UV-opaque columns. Each column was suspended 10 cm below the surface of Lake Giles, a high-UV lake located in northeastern PA, USA. The 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

1 freely between the treatments and on average larval densities in the UV-shielded
2 channels were 161–168% greater than those in the UV-exposed channels.

3 Differences in the spawning depths of yellow perch, *Perca flavescens*, in a high-
4 versus a low-UV lake suggest that yellow perch also avoid UV exposure.
5 Spawning depth was reported to be deeper in a high-UV lake (median = 3.2 m)
6 compared to a low-UV lake (median = 0.4 m) [46]. In addition, yellow perch eggs
7 were incubated at the surface of each lake in a modified reciprocal transplant
8 experiment. Eggs were exposed to full solar radiation, shielded from UV-B, or
9 kept in the dark. In the high-UV lake, all eggs perished in all the light treatments,
10 but survival time was longer (2–4 days) for eggs in the UV-B shielded treatment.
11 Furthermore, those collected from the high-UV lake survived longer than those
12 collected from the low-UV lake. Most eggs (>96%) incubated in the light
13 treatments of the low UV lake as well as the dark controls of both lakes survived
14 to hatching. Comparable results, using a similar experimental design, were
15 reported for the bluegill *Lepomis macrochirus* in which the median nesting
16 depth was observed to be deeper in a high UV lake compared to a low UV lake
17 [47].

18 It is more difficult to perform behavioral experiments in the open ocean. The
19 approach has been to observe the distribution of organisms in relation to their
20 photic environment combined with laboratory experiments examining UV toler-
21 ance and phototaxis. Both ascidians and sea urchins were shown to exhibit UV
22 avoidance. The distribution of the solitary ascidian *Corella inflata* varied with
23 exposure to direct solar radiation, particularly UVR exposure, with populations
24 conspicuously absent from unshaded areas [48]. Laboratory experiments con-
25 firmed that UVR is lethal to all life history stages of *C. inflata*, with the younger
26 stages being most vulnerable. In addition, none of the life stages possessed
27 UV-absorbing photoprotective compounds. The sea urchins *Arbacia punctulata*
28 and *Lytechinus variegates* were shown to be negatively phototactic to bright
29 solar radiation but positively phototactic to white light [49]. These data are
30 consistent with the observation that echinoplutei migrate to deeper depths in the
31 water column during peak periods of irradiance [30,50], but this response could
32 also be related to other factors such as predator avoidance. The sea urchin
33 *Strongylocentrotus droebachiensis* shades or covers itself in response to UVR
34 exposure, particularly in response to UV-B or a combination of UV-B and UV-A
35 [32]. Covering behavior was also shown to increase with increasing intensity of
36 UVR exposure. In some sea urchin species, covering behavior has been observed
37 to vary diurnally, with the greatest response during peak irradiance [49,51].
38
39

40 14.3.3 Relation to UV tolerance, pigmentation, and photorepair

41 Behavioral responses to UVR appear to be related to UV tolerance (i.e., defined
42 as the sum of an organism's photoprotection (pigmentation) and photorepair
43 capabilities). For example, during periods of high UV, organisms occupying the
44 surface waters of Lake Giles, a high UV lake in the Pocono Mts., PA, USA, were
45 found to be more UV-tolerant than those inhabiting deeper waters during the
46

1 day [12]. Laboratory experiments with the ostracod *Cypris* sp. demonstrated
2 that this species is highly tolerant to UV-B exposure and actually showed a
3 behavioral preference or positive phototaxis towards UV-B irradiance [10]. In
4 the same study, the protozoan *Paramecium aurelia* was also shown to be highly
5 tolerant and positively phototactic to UV-B irradiance [10].

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

12 13 14 **14.4 UV vision and photoreception**

15
16 UV vision has been documented in a variety of terrestrial organisms including
17 insects, birds, amphibians, reptiles, and mammals [53–55]. It is therefore not
18 surprising that many aquatic organisms also perceive light in the UV spectrum.
19 Most UV photoreceptors in aquatic organisms have been described in fish
20 species; however, UV photoreceptors have also been reported in bacteria and
21 algae as well as some species of protozoans, annelids, cnidarians, and crustaceans
22 (Table 1).

23 24 25 *14.4.1 Relation to habitat and age*

26
27 Many UV photoreceptors have a maximum absorbance peak in the UV-A range
28 but UV-B photoreceptors have been documented in some species (Table 1). One
29 explanation for the rarity of UV-B vision is that UV-B radiation is potentially
30 more damaging to the eye. For instance, cataracts are reported to occur in
31 several fish species inhabiting shallow waters [56]. Seeing in the UV-A may
32 therefore be less detrimental to the eye; however, prolonged exposure to UV-A
33 radiation may also be potentially damaging, albeit less than UV-B. In addition,
34 since eyes are photon-, not energy-counters, seeing in the UV-A provides more
35 light than in the UV-B. However, visible light provides more photons than UV,
36 making UV vision a curious trait (See section 14.4.2).

37 Some authors have suggested that UV photoreceptors vary with habitat such
38 that peak absorbance correlates with wavelengths present in their photic envi-
39 ronment [57–59]. In some cases, species such as the rudd *Scardinius erythro-*
40 *thalmus* [60] and the brown trout, *Salmo trutta* [61], display seasonal changes in
41 spectral sensitivity that correspond to seasonal changes in the photic environ-
42 ment associated with daylength and temperature. Most of these shifts are in the
43 longer wavelengths with shorter wavelength sensitivity remaining the same [62].
44 Behavior shifts are also suggested to contribute to shifts in spectral sensitivity,
45 such as foraging at the surface during summer months and in deeper strata
46 during winter months [60].

1 UV photoreceptors in some fish species not only vary with habitat but with
2 age as well. Many fish species, such as *Lepomis gibbosus*, *Perca flavescens*, and
3 *Salmo* sp., possess UV photoreceptors as larvae but lose them with maturity
4 [63,64]. This loss of UV photoreception coincides with a habitat shift from the
5 surface waters to more demersal waters in addition to a change in diet from small
6 to larger zooplankton prey and/or fish [63–65]. In some species of salmonoids,
7 however, UV photoreceptors disappear during earlier life history stages and
8 reappear in adults. For example, ultraviolet cones and UV sensitivity in the
9 sockeye salmon, *Oncorhynchus nerka*, diminished during smoltification and re-
10 appeared at the late juvenile or adult stage [66]. The author also noted that the
11 arrangement of the UV cones in the retina of the adult sockeye salmon was
12 similar to those of saltwater salmon, *O. tshawytscha* and *O. keta*, collected while
13 migrating back to natal streams or spawning in streams. This suggests that UV
14 photoreceptors may assist in navigation during migrations. Goldfish and species
15 of cyprinids retain their UV photoreceptors as adults. These species experience
16 little to no change in habitat or diet and therefore a change in the spectral
17 sensitivity of their photoreceptors would not be expected. Ontogenetic changes
18 in spectral sensitivity among aquatic species other than fish are less well known.

21 14.4.2 Adaptive significance

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

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

46 Laboratory experiments have demonstrated that larval fish do feed better in

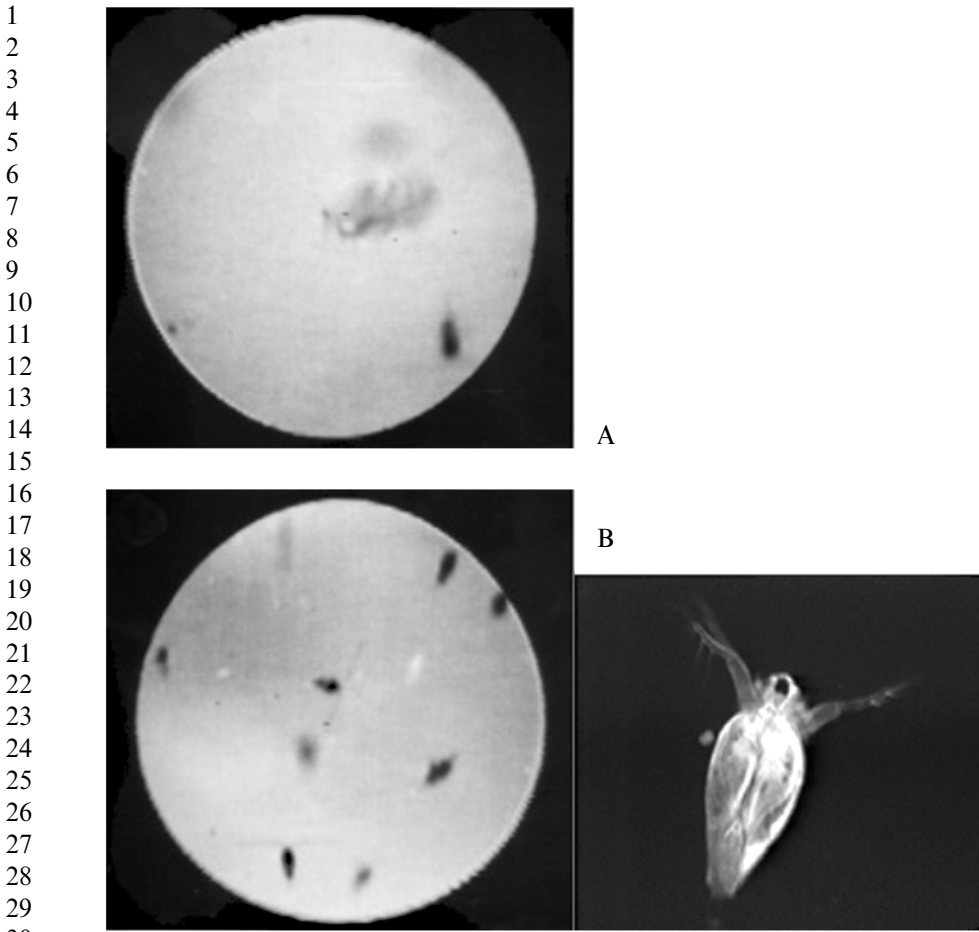
Table 1. Survey of the distribution of UV photoreceptors among aquatic organisms. (This list is not all-inclusive) microspectrophotometry is abbreviated as MSP

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

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Table 1. (cont.)

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



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

37 the presence of UV-A wavelengths [63,64] and can feed under monochromatic
 38 UV-A [63]. However, recent experiments with trout suggest that UV photo-
 39 receptors do not enhance foraging under natural levels of solar radiation [73]. In
 40 field experiments conducted in Patagonia, Argentina (41°08'S, 71°25'W) with
 41 rainbow trout, *Oncorhynchus mykiss*, the removal of UV wavelengths from solar
 42 radiation had no effect on the number of prey eaten or on prey preference. These
 43 experiments were run outdoors between 1000–1300 h local time. It is not known
 44 if a difference would have been noticed during crepuscular periods when relative
 45 UV levels are higher and planktivory is more challenging.

46 It has been suggested that increased absorbance in prey species in the UV

1 range due to photoprotective pigments increases visibility to predators, especial-
2 ly in transparent organisms. Transparent organisms occupying the epipelagic
3 zone in the Northwest Atlantic Ocean were found to be more UV absorbent than
4 those occupying the deeper mesopelagic zone, while visible transparency was
5 similar for organisms inhabiting both regions [74]. However, absorbance was
6 greatest in the UV-B range not in the UV-A range where UV vision occurs. In
7 addition, species with high UV-absorption tended to be less transparent in the
8 visible range. For both these reasons, the effects of UV absorption on UV
9 visibility were predicted to be slight in comparison to potential photoprotection.

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

14 The presence of both UV photoreception and negative phototaxis in some
15 species suggest that UV photoreceptors may help animals to avoid depths at
16 which levels of damaging solar radiation are high. Indeed, it is not known if
17 organisms can sense the UV damage they are incurring and respond appropri-
18 ately without the aid of UV photoreceptors. In the cyanobacterium *Cholog-
19 loeopsis*, a UV-B photoreceptor is linked to the production of the photoprotec-
20 tive compound shinorine, a mycosporine-like amino acid [76]. Induction
21 efficiency of shinorine was greatest when organisms are exposed to UV-B at
22 310 nm.

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

37 38 39 **14.5 Implications for behavioral responses to UVR**

40
41 The distribution and abundance of organisms can have a profound effect on an
42 ecosystem's structure and function. Nutrient cycling, predator-prey interactions,
43 and community structure may all be influenced by distribution patterns. As such,
44 numerous studies have been conducted to understand factors influencing vertical
45 and horizontal distribution and abundance [2,78]. However, UVR has histor-
46 ically received less attention. Implications of behavioral responses to UVR in diel

1 vertical migration and predator–prey interactions are discussed further below.

2 3 4 *14.5.1 Diel vertical migration*

5
6 One of the most interesting behavioral responses to solar radiation is the
7 phenomenon of zooplankton diel vertical migration (DVM). Large zooplankton
8 often exhibit strong migrations during the day to deeper, darker depths in the
9 water column. Smaller zooplankton, in turn, remain in the surface waters during
10 daylight and migrate to the deeper waters at night to avoid predation or
11 interference by larger zooplankton [52,79,80]. Many hypotheses have been
12 proposed to explain these patterns. Some of the earliest works on DVM demon-
13 strated that solar radiation was a potentially important proximate as well as an
14 ultimate factor inducing migrations [81–83]. These experiments, however, were
15 conducted in the laboratory and no field studies were conducted to demonstrate
16 a clear link between damaging solar radiation and zooplankton migration
17 patterns in nature. Consequently, other factors such as temperature, food, and
18 especially predation have typically been more widely studied and identified as
19 the primary factors inducing DVM [78].

20 In spite of the importance of predators inducing migrations, predation alone
21 does not explain the variety of DVM patterns observed in nature [84,85]. For
22 example, vertical migrations have been detected in organisms inhabiting fishless
23 systems [52]. Most of these systems tend to be high alpine or desert lakes in
24 which damaging solar radiation can be intense. Several experiments have shown
25 that ambient levels of UVR can lead to a decrease in survival as well as a decrease
26 in growth and reproduction in both freshwater and marine organisms
27 [6,8,14,86], and negative phototactic behavior has been demonstrated in the
28 laboratory and field [28–38,40–51]. Given these recent findings, UVR may be
29 more important than previously thought in influencing the vertical migration
30 and distribution of organisms [34,84], serving as both a proximate and an
31 ultimate cause of DVM.

32 Indeed, zooplankton often migrate deeper than the depths to which damaging
33 UV-B radiation penetrates, in both freshwater and marine systems. While
34 damaging UV-B may not be present, UV-A radiation continues to penetrate
35 through the water column. For example, in the open ocean, the 1% level of 375
36 nm is four times as deep as the 1% level of 310 nm (Jerlov type II oceanic water)
37 [87], and in freshwater lakes, UV-A penetration can be two times or greater [21].
38 Given that many fish species use UV-A light to forage, zooplankton may migrate
39 to deeper depths in order to avoid visually feeding predators with UV-A photo-
40 receptors. Many freshwater and marine species, however, continue to migrate to
41 even deeper depths, suggesting that other factors besides UVR, such as tempera-
42 ture and predation, are inducing migrations.

43 44 *14.5.2 Predator–prey interactions*

45
46 While both UV-B and UV-A can be damaging, UV-B is generally more damag-

1 ing than UV-A radiation per photon. The UV photoreceptors in many species
2 peak in the UV-A range (see Table 1). If animals are cueing to UV-A wavelengths
3 that penetrate more deeply into the water column, they would be protected from
4 potentially more damaging UV-B found closer to the surface. These alterations
5 in depth to prevent UVR exposure may in turn influence the overlap of predator
6 and prey in both time and space. For example, UV-tolerant zooplankton may
7 find refuge from larval fish predators, which are susceptible to UV damage
8 [46,86], in the surface waters of high UV systems.

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

16 17 **14.6 Future directions** 18

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

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

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

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References

1. R.B. Forward (1988). Diel vertical migration: zooplankton photobiology and behavior. *Oceanogr. Mar. Biol. Ann. Rev.*, **26**, 361–393.
2. W. Lampert (1989). The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.*, **3**, 21–27.
3. I. Huse, J.C. Holm (1993). Vertical distribution of Atlantic salmon (*Salmo salar*) as a function of illumination. *J. Fish Biol.*, **43**, 147–156.
4. J.T.O. Kirk, B.R. Hargreaves, D.P. Morris, R.B. Coffin, B. David, D. Fredrickson, D. Karentz, D.R.S. Lean, M.P. Lesser, S. Madronich, J.H. Morrow, N.B. Nelson, N.M. Scully (1994). Measurements of UV-B radiation in two freshwater lakes: an instrument comparison. *Arch. Hydrobiol. Ergebn. Limnol.*, **43**, 71–99.
5. D.P. Morris, H. Zagarese, C.E. Williamson, E.G. Balseiro, B.R. Hargreaves, B. Modenutti, R.E. Moeller, C. Queimalinos (1995). The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.*, **40**, 1381–1391.
6. J.J. Karanas, H. van Dyke, R.C. Worrest (1979). Midultraviolet (UV-B) sensitivity of *Acartia clausii* Giesbrecht (Copepoda). *Limnol. Oceanogr.*, **24**, 1104–1116.
7. J.J. Cullen, P.J. Neale, M.P. Lesser (1992). Biological weighting functions for the inhibition of phytoplankton photosynthesis by ultraviolet radiation. *Science*, **258**, 646–650.
8. O. Siebeck, T. Vail, C.E. Williamson, R. Vetter, D. Hessen, H. Zagarese, E. Little, E. Balseiro, B. Modenutti, J. Seva, A. Shumate (1994). Impact of UV-B radiation on zooplankton and fish in pelagic freshwater ecosystems. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 101–114.
9. C.E. Williamson (1995). What role does UV-B radiation play in freshwater ecosystems?. *Limnol. Oceanogr.*, **40**, 386–392.
10. J.A. Barcelo, J. Calkins (1978). Positioning of aquatic microorganisms in response to visible light and simulated solar UV-B irradiation. *Photochem. Photobiol.*, **29**, 75–83.
11. R.C. Worrest (1982). Review of literature concerning the impact of UV-B radiation upon marine organisms. In: J. Calkins (Ed.), *The Role of Solar Ultraviolet Radiation in Marine Ecosystems* (pp. 429–457). Plenum, New York.
12. D.M. Leech, C.E. Williamson (2000). Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency?. *Ecol. Appl.*, **10**, 1530–1540.
13. M.L. Bothwell, D.M.J. Sherbot, C.M. Pollock (1994). Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. *Science*, **265**, 97–100.
14. H.E. Zagarese, C.E. Williamson (1994). Modeling the impacts of UV-B radiation on ecological interactions in freshwater and marine ecosystems. In: R.H. Biggs, M.B.E. Joyner (Eds), *Stratospheric Ozone Depletion/UV-B Radiation in the Biosphere* (pp. 315–328). Springer-Verlag, New York.
15. J. Ringelberg, A.L. Keyser, B.J.G. Flik (1984). The mortality effect of ultraviolet radiation in a red morph of *Acanthodiaptomus denticornis* (Crustacea: Copepoda) and

- 1 its possible ecological relevance. *Hydrobiologia*, **112**, 217–222.
- 2 16. O. Siebeck, U. Bohm (1991). UV-B effects on aquatic animals. *Ver. Int. Verein. Theor.*
3 *Angew. Limnol.*, **24**, 2773–2777.
- 4 17. H.E. Zagarese, M. Feldman, C.E. Williamson (1997). UV-B induced damage and
5 photoreactivation in three species of *Boeckella* (Copepoda, Calanoida). *J. Plankton*
6 *Res.*, **19**, 357–367.
- 7 18. J.D. Regan,, W.L. Carrier, C. Samet, B.L. Olla (1982). Photoreactivation in two
8 closely related marine fishes having different longevities. *Mech. Aging Develop.*, **18**,
9 59–66.
- 10 19. D. Karentz, F.S. McEuen, M.C. Land, W.C. Dunlap (1991). Survey of mycosporine-
11 like amino acid compounds in Antarctic marine organisms: potential protection from
12 ultraviolet exposure. *Mar. Biol.*, **108**, 157–166.
- 13 20. N. Shashar (1994). UV vision by marine animals: mainly questions. In: D. Gulko, P.L.
14 Jokiel (Eds), *Ultraviolet Radiation and Coral Reefs* (HIMB Tech. Report #41, pp.
15 201–206). UNIH-Sea Grant-CR-95-03.
- 16 21. C.E. Williamson, R.S. Stemberger, D.P. Morris, T.M. Frost, S.G. Paulsen (1996).
17 Ultraviolet radiation in North American lakes: attenuation estimates from DOC
18 measurements and implications for plankton communities. *Limnol. Oceanogr.*, **41**,
19 1024–1034.
- 20 22. R.C. Smith, K.S. Baker (1981). Optical properties of the clearest natural waters
21 (200–800 nm). *Appl. Opt.*, **20**, 177–184.
- 22 23. J.B. Kerr, C.T. McElroy (1993). Evidence for large upward trends of ultraviolet-B
23 radiation linked to ozone depletion. *Science*, **262**, 1032–1034.
- 24 24. I. Navales-Flamarique, A. Hendry, C.W. Hawryshyn (1992). The photic environment
25 of a salmonid nursery lake. *Exp. Biol.*, **169**, 121–141.
- 26 25. J.F. Haney (1989). Diel patterns of zooplankton behavior. *Bull. Mar. Sci.*, **43**, 583–603.
- 27 26. L.J. Shoeneck, C.E. Williamson, M.E. Stoeckel (1990). Diel periodicity and selectivity
28 in the feeding rate of the predatory copepod *Mesocyclops edax*. *J. Plankton Res.*, **12**,
29 29–40.
- 30 27. G.S. Losey, T.W. Cronin, T.H. Goldsmith, D. Hyde, N.J. Marshall, W.N. McFarland
31 (1999). The UV visual world of fishes: a review. *J. Fish Biol.*, **54**, 921–943.
- 32 28. B.M. Bebout, F. Garcia-Pichel (1995). UV-B induced vertical migrations of cyanobacteria
33 in a microbial mat. *Appl. Environm. Microbiol.*, **61**, 4215–4222.
- 34 29. F.E. Smith, E.R. Baylor (1953). Color responses in the cladocera and their ecological
35 significance. *Am. Nat.*, **87**, 49–55.
- 36 30. J.T. Pennington, R.B. Emler (1986). Ontogenetic and diel vertical migration of a
37 planktonic echinoid larva, *Dendraster excentricus* (Eschscholtz): occurrence, causes,
38 and probable consequences. *J. Exper. Mar. Biol. Ecol.*, **104**, 69–95.
- 39 31. P.M. Kiffney, E.E. Little, W.H. Clements (1997). Influence of ultraviolet-B radiation
40 on the drift response of stream invertebrates. *Freshwat. Biol.*, **37**, 485–492.
- 41 32. N.L. Adams (2001). UV radiation evokes negative phototaxis and covering behavior
42 in the sea urchin *Strongylocentrotus droebachiensis*. *Mar. Ecol. Progr. Ser.*, **213**,
43 87–95.
- 44 33. F. Lenci, G. Checcucci, F. Ghetti, D. Gioffre, A. Sgarbossa (1997). Sensory perception
45 and transduction of UV-B radiation by the ciliate *Blepharisma japonicum*. *Biochim.*
46 *Biophys. Acta*, **1336**, 23–27.
34. U.C. Storz, R.J. Paul (1998). Phototaxis in water fleas (*Daphnia magna*) is different-
ly influenced by visible and UV light. *J. Comp. Physiol. A*, **183**, 709–717.
35. T.M. Frank, E.A. Widder (1994). Evidence for behavioral sensitivity to near-UV light
in the deep sea crustacean *Systellaspis debilis*. *Mar. Biol.*, **118**, 279–284.

- 1 36. L. Chalker-Scott, J. Scott, J. Titus (1994). Brief exposure to ultraviolet radiation
2 inhibits locomotion of veligers and juvenile *D. polymorpha*. In: *37th Conference of the*
3 *International association for Great Lakes research and Estuarine Research Federation:*
4 *Program and Abstracts* (pp. 166). IAGLR, Buffalo, NY.
- 5 37. M.K. Blakefield, J. Calkins (1992). Inhibition of phototaxis in *Volvox aureus* by
6 natural and simulated solar ultraviolet light. *Photochem. Photobiol.*, **55**, 867–872.
- 7 38. N.G. Hairston Jr. (1976). Photoprotection by carotenoid pigments in the copepod
8 *Diaptomus nevadensis*. *Proc. Nat. Acad. Sci. U.S.A.*, **73**, 971–974.
- 9 39. D.-P. Häder (1993). Effects of enhanced solar ultraviolet radiation on aquatic ecosys-
10 tems. In: M. Tevini (Ed.), *UV-B Radiation and Ozone depletion: Effects on Humans,*
11 *Animals, Plants, Microorganisms and Materials* (pp. 155–192). Lewis Publishers.
- 12 40. D.M. Leech, C.E. Williamson (2001). In situ exposure to solar UV radiation alters the
13 depth distribution of *Daphnia*. *Limnol. Oceanogr.*, **46**, 416–420.
- 14 41. D.M. Leech, A.T. Padeletti, C.E. Williamson. Behavioral responses to UV radiation
15 vary across zooplankton taxa. *Limnol. Oceanogr.*, submitted.
- 16 42. D.O. Hessen (1994). *Daphnia* responses to UV-light. *Arch. Hydrobiol. Beih. Ergebn.*
17 *Limnol.*, **43**, 185–195.
- 18 43. S. Rhode, M. Pawlowski, R. Tollrian (2001). The impact of ultraviolet radiation on
19 the vertical distribution of zooplankton genus *Daphnia*. *Nature*, **412**, 69–72.
- 20 44. G.G. Martin, C. Speckmann, S. Beidler (2000). Photobehavior of the harpacticoid
21 copepod *Tigriopus californicus* and the fine structure of its nauplius eye. *Inv. Biol.*, **119**,
22 110–124.
- 23 45. W.F. Donahue, D.W. Schindler (1998). Diel emigration and colonization responses of
24 blackfly larvae (Diptera: Simuliidae) to ultraviolet radiation. *Freshwat. Biol.*, **40**,
25 357–365.
- 26 46. C.E. Williamson, S.L. Metzgar, P.A. Lovera, R.E. Moller (1997). Solar ultraviolet
27 radiation and the spawning habitat of yellow perch, *Perca flavescens*. *Ecol. Appl.*, **7**,
28 1017–1023.
- 29 47. C. Gutierrez-Rodriguez, C.E. Williamson (1999). Influence of solar radiation on early
30 life-history stages of the bluegill sunfish, *Lepomis machrochirus*. *Environ. Biol. Fishes*,
31 **55**, 307–319.
- 32 48. B.L. Bingham, N.B. Reynolds (1999). Ultraviolet radiation and distribution of the
33 solitary ascidian *Corella inflata*. *Biol. Bull.*, **196**, 94–104.
- 34 49. D.T. Sharp, I.E. Gray (1962). Studies on factors affecting the local distribution of two
35 sea urchins, *Arbacia punctulata* and *Lytechinus variegates*. *Ecology*, **43**, 309–313.
- 36 50. J.L.J. Eastwood (1972). *The Development and Photic Behavior of Lytechinus Varie-*
37 *gates Echinoplutei Larvae* (Ph.D. thesis). Lehigh University, Bethlehem, PA, USA.
- 38 51. N. Millot (1975). The photosensitivity of echinoids. In: F.S. Russell, M. Yonge (Eds),
39 *Advances in marine biology* (pp. 1–52). Academic Press, New York.
- 40 52. N.G. Hairston (1980). The vertical distribution of diaptomid copepods in relation to
41 body pigmentation. In: W.C. Kerfoot (Ed.), *Evolution and Ecology of Zooplankton*
42 *Communities* (pp. 98–110). University Press, Hanover, New Hampshire.
- 43 53. M.J. Tovee (1995). Ultra-Violet photoreceptors in the animal kingdom: their distribu-
44 tion and function. *TREE*, **10**, 455–459.
- 45 54. T.H. Goldsmith, G.D. Bernard (1985). Visual pigments in invertebrates. *Photochem.*
46 *Photobiol.*, **42**, 805–809.
55. G.H. Jacobs (1992). Ultraviolet vision in vertebrates. *Am. Zool.*, **32**, 544–554.
56. A.P. Cullen, C.A. Monteith-McMaster (1993). Damage to rainbow trout (*Oncorhyn-*
chus mykiss) lens following acute dose of UV-B. *Curr. Eye Res.*, **14**, 359–377.
57. J.N. Lythgoe (1984). Visual pigments and environmental light. *Vision Res.*, **24**,

- 1 1539–1550.
- 2 58. J.S. Levine, E.F. MacNichol (1979). Visual pigments in telost fishes: Effects of habitat,
3 microhabitat and behavior on visual system evolution. *Sensory Proc.*, **3**, 95–131.
- 4 59. J.K. Bowmaker (1990). Visual pigments of fishes. In: R.H. Douglas, M.B.A. Djamgoz
5 (Eds), *The Visual System of Fish* (pp. 81–108). Chapman and Hall Press, London.
- 6 60. W.B.A. Muntz, A.W. Wainwright (1978). Annual cycles in the light environments and
7 visual mechanisms of fishes. In: J.E. Thorpe (Ed.), *Rhythmic Activity of Fishes* (pp.
8 105–129). Academic Press, London.
- 9 61. W.B.A. Muntz, G.S.V. Mouat (1984). Annual variations in the visual pigments of
10 brown trout inhabiting lochs providing different light environments. *Vision Res.*, **24**,
11 1575–1580.
- 12 62. A.V. Whitmore (1988). *The Visual Pigments and Action Spectra of Five Types of Cone*
13 *in the Retina of the Rudd, Scardinius erythrophthalmus*, (PhD. Thesis). University of
14 London.
- 15 63. E.H. Loew, W.N. McFarland, E.L. Mills, D. Hunter (1993). A chromatic action
16 spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. *Can. J.*
17 *Zool.*, **71**, 384–386.
- 18 64. H.I. Browman, I. Novales-Flamarique, C. Hawryshyn (1993). Ultraviolet photorecep-
19 tion contributes to prey search behavior in two species of zooplanktivorous fishes. *J.*
20 *Exp. Biol.*, **186**, 187–198.
- 21 65. J.K. Bowmaker, Y.W. Kuntz (1987). Ultraviolet receptors, tetrachromatic color vi-
22 sion and retinal mosaics in the brown trout (*Salmo trutta*): age-dependent changes.
23 *Vision Res.*, **27**, 2101–2108.
- 24 66. I. Novales Flamarique (2000). The ontogeny of ultraviolet sensitivity, cone disappear-
25 ance and regeneration in the sockeye salmon *Oncorhynchus nerka*. *J. Exp. Biol.*, **203**,
26 1161–1172.
- 27 67. C.W. Hawryshyn (1992). Polarization vision in fish. *Am. Sci.*, **80**, 164–175.
- 28 68. D.C. Parkyn, C.W. Hawryshyn (1993). Polarized light sensitivity in the rainbow trout
29 (*Oncorhynchus mykiss*): characterization from multiunit responses in the optic nerve.
30 *J. Comp. Physiol.*, **172**, 493–500.
- 31 69. D. Coughlin, C.W. Hawryshyn (1994). The contribution of ultraviolet and short-
32 wavelength sensitive cone mechanisms to color vision in rainbow trout. *Brain Behav-*
33 *ior. Evol.*, **43**, 219–232.
- 34 70. J.P. Zamzow, G.S. Losey. Ultraviolet radiation absorbance by coral reef fish mucus:
35 photo-protection and visual communication. *Environ. Biol. Fish.* in press.
- 36 71. E.R. Loew, W.N. McFarland (1990). The underwater visual environment. In: R.H.
37 Douglas, M.B.A. Djamgoz (Eds), *The Visual System of Fish* (pp. 1–44). Chapman and
38 Hall Press, London.
- 39 72. L.A. Giguere, R.L. Dunbrack (1990). Thin layer interference may reduce the visibility
40 of transparent phantom midge (*Chaoborus trivittatus*) to predators. *Can. J. Fish.*
41 *Aquat. Sci.*, **47**, 1043–1046.
- 42 73. V. Rocco, J.P. Barriga, H. Zagarese, M. Lozada (2002). How much does ultraviolet
43 radiation contribute to the feeding performance of rainbow trout, *Oncorhynchus*
44 *mykiss*, juveniles under natural illumination?. *Environ. Biol. Fish.*, **63**, 223–228.
- 45 74. S. Johnsen, E.A. Widder (2001). Ultraviolet absorption in transparent zooplankton
46 and its implications for depth distribution and visual predation. *Mar. Biol.*, **138**,
717–730.
75. K.C. Smith, E.R. Macagno (1990). UV photoreceptors in the compound eye of
Daphnia magna (Crustacea, Branchiopoda): A fourth spectral class in single om-
matidia. *J. Comp. Physiol. A*, **166**, 597–606.

- 1 76. A. Portwich, F. Garcia-Pichel (2000). A novel prokaryotic UVB photoreceptor in the
2 cyanobacterium *Chlorogloeopsis* PCC6912, *Photochem. Photobiol.*, **71**, 493–498.
- 3 77. G. Wald, S. Rayport (1977). Vision in annelid worms. *Science*, **196**, 1434–1439.
- 4 78. W.E. Neill (1990). Induced vertical migration in copepods as a defense against
5 invertebrate predation. *Nature*, **345**, 524–526.
- 6 79. M.D. Ohman (1990). The demographic benefits of diel vertical migration by zooplan-
7 kton. *Ecol. Monogr.*, **60**, 257–281.
- 8 80. A.G. Huntsman (1924). Limiting factors for marine animals. I. The lethal effect of
9 sunlight. *Contr. Can. Biol.*, **2**, 82–88.
- 10 81. A.B. Klugh (1930). The effect of the ultraviolet component of the sun's radiation upon
11 some aquatic organisms. *Can. J. Res.*, **2**, 312–317.
- 12 82. A.R. Moore (1912). Concerning negative phototropism in *Daphnia pulex*. *J. Exp.*
13 *Zool.*, **13**, 573–575.
- 14 83. W.C. Kerfoot (1985). Adaptive value of vertical migration: comments on the pred-
15 ation hypothesis and some alternatives. *Contr. Mar. Sci.*, **27**, 91–113.
- 16 84. J. Ringelberg (1999). The photobehavior of *Daphnia* spp. as a model to explain diel
17 vertical migration in zooplankton. *Biol. Rev.*, **74**, 397–423.
- 18 85. C. Loose, E. von Elert, P. Dawidowicz (1993). Chemically-induced diel vertical
19 migration in *Daphnia*: a new bioassay for kairomones exuded by fish. *Arch. Hy-*
20 *drobiol.*, **126**, 329–337.
- 21 86. C.E. Williamson, H.E. Zagarese, P.C. Schulze, B.R. Hargreaves, J. Seva (1994). The
22 impact of short-term exposure to UV-B radiation on zooplankton communities in
23 north temperate lakes. *J. Plankton Res.*, **16**, 205–218.
- 24 87. N.G. Jerlov (1976). *Optical Oceanography*, Elsevier Publishing Company, Amster-
25 dam.
- 26 88. S. Madronich (1994). Increase in biologically damaging UV-B radiation due to
27 stratospheric ozone reductions: a brief review. *Arch. Hydrobiol. Ergebn. Limnol.*, **43**,
28 17–30.
- 29 89. H. Yang, H. Inokuchi, J. Adler (1995). Phototaxis away from blue light by an
30 *Escherichia coli* mutant accumulating protoporphyrin IX. *Proc. Nat. Acad. Sci.*
31 *U.S.A.*, **92**, 7332–7336.
- 32 90. W. Sprenger, W.D. Hoff, J.P. Armitage, K. Hellingwerf (1993). The eubacterium
33 *Ectothiorhodospira halophila* is negatively phototactic, with a wavelength dependence
34 that fits the absorption spectrum of the photoactive yellow protein. *J. Bacteriol.*, **175**,
35 3096–3105.
- 36 91. R. Menzel (1979). Spectral sensitivity and color vision in invertebrates. In: H. Hutrum
37 (Ed.), *Comparative Physiology and Evolution in Invertebrates* (pp. 503–580). Springer-
38 Verlag, New York.
- 39 92. M. Iseki, S. Wada (1995). Action spectrum in the ultraviolet region for phototropism
40 of *Bryopsis* rhizoids. *Plant Cell. Physiol.*, **36**, 1033–1040.
- 41 93. M. Selbach, H.W. Kuhlmann (1999). Structure, fluorescent properties and proposed
42 function in phototaxis of the stigma apparatus in the ciliate *Chlamydomonadopsis*.
43 *J. Exp. Biol.*, **202**, 919–928.
- 44 94. L.A. Wilkens (1984). Ultraviolet sensitivity in hyperpolarizing photoreceptors of the
45 giant clam *Tridacna*. *Nature*, **309**, 446–448.
- 46 95. I. Novales Flamarique, H.I. Browman, M. Belanger, K. Boxaspen (2000). Ontogenetic
changes in visual sensitivity of the parasitic salmon louse *Lepeophtheirus salmonis*. *J.*
Exp. Biol., **203**, 1649–1659.
96. T.W. Cronin, N.J. Marshall (1989). A retina with at least ten spectral types of
photoreceptors in a stomatopod crustacean. *Nature*, **339**, 137–140.

- 1 97. T.M. Frank, J.F. Case (1988). Visual spectral sensitivities of bioluminescent deep-sea
2 crustaceans. *Biol. Bull.*, **175**, 261–273.
- 3 98. R. Forward, T.W. Cronin (1979). Spectral sensitivity of larvae from intertidal crusta-
4 ceans. *J. Comp. Physiol.*, **133**, 311–315.
- 5 99. G. Wald, E.B. Seldin (1968). Spectral sensitivity of the common prawn *Palaemonetes*
6 *vulgaris*. *J. Gen. Physiol.*, **51**, 694–700.
- 7 100. D.R. Cummins, D.M. Chen, T.H. Goldsmith (1984). Spectral sensitivity of the spiny
8 lobster *Panulirus argus*. *Biol. Bull.*, **166**, 269–276.
- 9 101. G. Wald, J.M. Krainin (1963). The median eye of *Limulus*: an ultraviolet receptor.
10 *Proc. Nat. Acad. Sci. U.S.A.*, **50**, 1011–1017.
- 11 102. L.L. Britt, E.R. Loew W.N. McFarland (2001). Visual pigments of PNW fish larvae.
12 *J. Exp. Biol.*, **204**, 2581–2587.
- 13 103. F. Schiemanz (1924). Über den Farbensinn der Fische. *Z. Vergl. Physiol.*, **1**, 175–200.
- 14 104. J.A. Avery, J.K. Bowmaker, M.B.A. Djamgoz, J.E.G. Downing (1983). Ultraviolet
15 sensitive receptors in a freshwater fish. *J. Physiol., London*, **334**, 23P.
- 16 105. C.W. Hawrynszyn, R. Beauchamp (1985). Ultraviolet photosensitivity in goldfish:
17 an independent UV retinal mechanism. *Vision Res.*, **25**, 11–20.
- 18 106. C.W. Hawrynszyn, F.I. Harosi (1991). Ultraviolet photoreception in carp: MSP and
19 behaviorally determined action spectra. *Vision Res.*, **31**, 567–576.
- 20 107. A.G. Palacios, T.H. Goldsmith, G.D. Bernard (1996). Sensitivity of cones from a
21 cyprinid fish (*Danio aequipinnatus*) to ultraviolet and visible light. *Vision Neurosci.*,
22 **13**, 411–21.
- 23 108. A.V. Whitmore, J.K. Bowmaker (1989). Seasonal variation in cone sensitivity and
24 short-wave absorbing visual pigments in the rudd. *J. Comp. Physiol.*, **166**, 103–115.
- 25 109. F.I. Harosi, Y. Hashimoto (1983). Ultraviolet visual pigment in a vertebrate: a
26 tetrachromatic cone system in the dace. *Science*, **222**, 1021–1023.
- 27 110. C.W. Hawrynszyn, M.G. Arnold, D.J. Chaisson, P.C. Martin (1987). Developmental
28 changes in ultraviolet photosensitivity in rainbow trout. *Social Neurosci. Abs.*, **13**,
29 1298.
- 30 111. Y.W. Kunz (1987). Tracts of putative ultraviolet receptors in the retina of the two
31 year old brown trout and the Atlantic salmon. *Experientia*, **43**, 1202–1204.
- 32 112. J.S. Levine, E.F. MacNichol (1982). Color vision in fishes. *Sci. Am.*, **246**, 140–149.
- 33 113. E.R. Loew, C.M. Wahl (1991). A short wavelength sensitive cone mechanism in
34 juvenile yellow perch, *Perca flavescens*. *Vision Res.*, **31**, 353–360.
- 35 114. I. Novales Flamarique, F.I. Harosi (1999). Photoreceptor pigments of the Blueback
36 Herring (*Alosa aestivalis*, Clupeidae) and the Atlantic Silverside (*Menidia menidia*,
37 Atherinidae). *Biol. Bull.*, **197**, 235–236.
- 38 115. I. Novales Flamarique, F.I. Harosi (2000). Photoreceptors, visual pigments, and
39 ellipsosomes in the killifish, *Fundulus heteroclitus*: A microspectrophotometric and
40 histological study. *Visual Neurosci.*, **17**, 403–420.
- 41 116. E.R. Loew, R.A. McAlary, W.N. McFarland (1996). Ultraviolet visual sensitivity in
42 the larvae of two species of marine atherinid fishes. In: P.H., Lenz, D.K. Hartline, J.E.
43 Purcell, D.L. Macmillan (Eds), *Zooplankton: Sensory Ecology and Physiology* (pp.
44 195–210). Gordon and Breach Publishers, Amsterdam.
- 45 117. J.V. Helvik, O. Drivenes, T. Harboe, H.-C. Seo (2001). Photoreceptor cells in
46 Atlantic halibut retina. *J. Exp. Biol.*, **204**, 2553–2559.
118. K.L. Carlton, F.I. Harosi, T.D. Kocher (2000). Visual pigments of African cichlid
fishes: evidence for ultraviolet vision from microspectrophotometry and DNA se-
quences. *Vision Res.*, **40**, 879–890.
119. G.S. Losey, P.A. Nelson, J.P. Zamzow (2000). Ontogeny of spectral transmission in

- 1 the eye of the tropical damselfish and possible effects on UV vision. *Environ. Biol.*
2 *Fishes*, **59**, 21–28.
- 3 120. W.N. McFarland, E.R. Loew (1994). Ultraviolet visual pigments in marine fishes of
4 the family Pomacentridae. *Vision Res.*, **34**, 1393–1396.
- 5 121. J. Ammermuller, A. Itzhaki, R. Weiler, I. Perlman (1998). UV-sensitive input to
6 horizontal cells in the turtle retina. *Eur. J. Neurosci.*, **10**, 1544–1552.

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