

Effects of ultraviolet radiation on pigmentation, photoenzymatic repair, behavior, and community ecology of zooplankton†

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In this report, we provide a perspective on how zooplankton are able to respond to present and future levels of ultraviolet (UV) radiation, a threat that has been present throughout evolutionary time. To cope with this threat, zooplankton have evolved several adaptations including behavioral responses, repair systems, and accumulation of photoprotective compounds. Common photoprotective compounds include melanins and carotenoids, which are true pigments, but also mycosporine-like amino acids (MAAs) and several other substances, and different taxa use different blends of these compounds. It is not only the level of UV radiation, however, that determines the amount of photoprotective compounds incorporated by the zooplankton, but also other environmental factors, such as predation and supply rate of the compounds. Furthermore, compared to taxa that are less pigmented, those taxa with ample pigmentation are generally less likely to exhibit diel migration. The photoenzymatic repair of UV damages seems to be more efficient at intermediate temperature than at low and high temperatures, suggesting that it is less useful at high and low latitudes, where UV radiation is often extremely high. While predicted future increases in UV radiation are expected to substantially affect many processes, recent studies show that most zooplankton taxa are well adapted to cope with such increases, either by UV avoidance behavior or by incorporation of photoprotective compounds. Hence, we conclude that future increase in UV radiation will have only moderate direct effects on zooplankton biomass and community dynamics.

Introduction

In natural ecosystems, organisms are faced with fluctuations in several environmental threats such as ultraviolet (UV) radiation, and these vary both in temporal and spatial dimensions. The threat from UV has been present longer than any life on earth,

and radiation intensities were initially higher than at present.¹ As photosynthesizing organisms evolved, the ozone layer eventually developed; this layer screens out most of the UV, but some still enters the biosphere and affects life on earth. In response, a long series of evolutionary adaptations have coalesced into different strategies that allow organisms to cope with UV radiation. Due to recent stratospheric ozone reductions, the level of UV radiation has increased in many parts of the world and is likely to increase even further, at least during the forthcoming decades.² This raises concerns for increasing radiation damage to DNA and other cellular structures,^{3,4} as well as for biogeochemical processes.⁵

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UV radiation makes up only a small portion of the total solar radiation and attenuates rapidly in water; however, because of the considerable potential for UV-induced damage to many organisms, the observed increases are important also in aquatic ecosystems.^{6–8}

In this paper, we will focus on strategies that reduce UV damage, specifically among zooplankton. We include studies from both freshwater and marine systems and argue that the response of zooplankton to UV radiation is similar irrespective of salinity. Hence, we have not thematically separated these ecosystems. There is no doubt that UV is, and has always been, a strong selective force in ecological communities.⁹ Hence, in order to aid furthering the understanding of zooplankton community dynamics, it may be important to summarize the knowledge about how different taxa of zooplankton perceive and respond to UV. The UV threat may induce defences both in the form of behavioral responses, *e.g.* vertical migration,^{9,10} and in phenotypic responses, such as accumulation of photoprotective compounds.^{11–13} Such morphological protection may either be constitutive, *i.e.* present throughout the organism's lifetime, or induced when needed.^{14,15} In addition to synthesizing the knowledge regarding strategies to meet UV threats, we aim at disentangling how UV responses may alter the organism's performance on community and ecosystem levels.

An abundant literature exists about the effects of UV radiation, several overview papers have been written,^{3,6,8,16–21} and a search in the database Biosis on “UV OR ultraviolet AND zoopl*” gives more than 100 000 hits. Therefore, the main aim of this paper is not to cover all of the literature, but instead to summarize and synthesize the main paths of progress in the understanding of zooplankton responses to UV radiation. By this approach, we hope to provide a foundation for future hypotheses, studies, and understanding within this research area.

Biological damage caused by UV

Ultraviolet radiation is harmful to all life, and shorter wavelengths are more energetic and hence more reactive. UV-B, for example, is more harmful than UV-A²² and will, at high exposure, be directly fatal. There is no doubt that zooplankton are affected by UV, but their main food organisms—phytoplankton—are also affected.²⁰ Thus, UV may affect both phytoplankton (food) quantity and quality, and zooplankton ingestion and digestion rates.²³ Furthermore, reproduction by fish may also be affected, with resultant alterations in predation rate on zooplankton due to UV radiation.²⁰ Thus, there is a broad range of ways that UV can affect zooplankton, but we focus here on the direct effects from UV radiation that zooplankton experience and on the zooplankton response in terms of alterations in phenotypic expression, behavior, and community composition.

UV damages most biological macromolecules, including lipids, proteins, and nucleic acids, but the major concern is with DNA damage caused by UV-B radiation,²⁴ wherein, for example, cyclobutane pyrimidine dimers²⁵ are produced. These dimers are aberrant DNA that cause errors in transcription (and hence translation) and replication, affecting the functioning and existence of the individual and their reproductive success. The incidence of these dimers in the organism is linearly related to UV exposure.²⁴ UV-A, on the other hand, is absorbed mainly by

organic molecules other than DNA, such as proteins, lipids, and RNA. The dissipation of this absorbed energy generates several by-products, including hydroxyl radicals, hydrogen peroxide, and singlet-state oxygen, all of which cause oxidative damage to numerous cellular components.²⁶

Current levels of UV radiation at temperate latitudes, which are generally below 20 and 0.2 W m⁻² for UV-A and UV-B, respectively, are associated with both behavioral responses and increased mortality in zooplankton.^{27–29} UV appears to also reduce fecundity, *e.g.* in the rotifer *Asplanchna*,³⁰ and in the cladocerans *Daphnia*³¹ and *Chydorus*.³² UV effects on freshwater copepod reproduction is less clear-cut, however—showing a decrease,^{16,26} an increase,³² as well as no effect at all³³ in different copepod species. Some zooplankton seem to be less affected by UV radiation; for example, the copepod species *Boeckella gibbosa* and *B. brevicaudata* showed no increased mortality upon exposure to UV.³⁴ After this brief introduction to these general and particular effects of UV, we now consider that, over evolutionary time, zooplankton have developed different strategies to handle the threat from UV radiation.^{6,35,36}

Strategies to handle UV problems

There are three basic ways for zooplankton to reduce damages caused by UV radiation. Avoidance *behavior*, such as diel vertical migration, and photoprotective compounds, such as *pigments*, may be categorized as preventive measures against UV damages. The third possibility for zooplankton is to *repair* damages;^{33,37} photoenzymatic repair requires light of longer wavelengths,³³ and nucleotide excision repair requires being active in darkness.³⁸ For an inducible preventive response to UV threat, a prerequisite is the ability to detect it. Many zooplankton species, *e.g.* *Daphnia*, have UV photoreceptors, with peak sensitivity at about 348 nm, and which are situated in the compound eye.³⁹ These allow them to show a negative phototaxis to wavelengths below about 360 nm, and a positive phototaxis to less harmful wavelengths.^{27,40} Overall, photoenzymatic repair and responses in pigmentation and behavior may function as complementary traits,^{41–43,58} and together they constitute a cocktail of tactics to reduce the threat from ultraviolet radiation. Below, we will first focus on photoenzymatic repair and then on preventive responses in behavior and phenotype (photoprotective compounds). Lastly, we provide a view of when, where, and how much different zooplankton use these responses when challenged with UV radiation.

Photoenzymatic repair

Many organisms can repair UV-damaged DNA through photoenzymatic repair. This process uses the enzyme photolyase in combination with photorepair wavelengths of UV-A or visible light to reverse the UV-B-induced production of, for example, cyclobutane pyrimidine dimers.^{24,25,31} The photolyase binds to cyclobutane pyrimidine dimers in the DNA, and after absorbing a near-UV or visible light photon, it splits the cyclobutane ring to restore the pyrimidines.³⁷ The rate of this process is strongly reduced at low temperatures, as illustrated in a study of Antarctic copepods exposed to UV radiation. This study found that the highly UV-resistant species *Boeckella poppei* relied mainly on photoprotection, rather than on photoenzymatic repair. Further,

it was postulated that photoenzymatic repair was not used because of inefficiency of the mechanism at low temperatures, especially close to 0 °C,³⁷ which has also been shown for several other taxa.⁴⁴ Recent studies also show that photoenzymatic repair rates for several species of *Daphnia* are greater at 10 °C than at higher temperatures (20 °C).⁴⁵ Thus, photoenzymatic repair is an adaptation that may be less useful in polar and tropical regions, where UV radiation levels, as well as the daily dose, are often very high.

The rate of the photoenzymatic repair reaction is relatively slow at high temperatures and may therefore be less efficient if the UV dose is high and given during a short period. On the other hand, if a similar dose of UV is given over a longer time period, the repair process may compensate for the damage, and the fitness reduction of the organisms may be relatively low.³¹ Even if the photoenzymatic repair processes are slow, very short periods (minutes) of photorecovery radiation (PRR; visible or near-UV radiation) can be efficient in increasing survival after exposure to UV radiation.^{33,46}

In a study of the cladoceran *Daphnia magna*, survival and reproductive output of 4 day old individuals were reduced by 25–75% at an UV exposure of 12 h, but both of these fitness variables improved if the animals were provided with photorecovery radiation after the UV exposure.⁴⁷ *Daphnia* is a genus that has been shown to rely heavily on photoenzymatic repair for its UV tolerance by some authors,³¹ but other studies conclude that only a minor portion (1–4%) of the protection is accounted for by repair systems.⁴⁸ However, since PRR (visible light or near-UV radiation) is generally always present in natural systems, the process of photoenzymatic repair may, despite its temperature dependence, be a very efficient and widespread adaptation to deal with UV damage.

Photoprotective compounds

Pigmentation in animals generally acts as sexual ornamentation to attract partners or camouflage to reduce the risk of predation. In zooplankton, however, pigments are frequently for photoprotection. Photoprotective compounds have been observed and quantified in copepods, cladocerans, rotifers, and ciliates.^{13,49–51} Serving in this role are carotenoids, melanin, and mycosporine-like amino acids (MAAs); note that MAAs are invisible in visible light and therefore not formally a pigment. These substances are quite different in structure and function: melanins and MAAs function mainly as sunscreens, dissipating the solar energy as heat.^{11,13} Carotenoids are strong antioxidants that function mainly as scavengers of photo-produced radicals.⁴⁹ All common photoprotective compounds in zooplankton are large, complex molecules, with a general chemical composition based on a large, but varying, number of carbon rings with oxygen and hydrogen attached. Some, for example many MAAs, also have nitrogen attached to their carbon rings.

Carotenoids

Carotenoids are yellow, orange, or red substances that are synthesized by several taxa including bacteria, fungi, algae, and plants. However, other taxa, including zooplankton, must obtain carotenoids from their diet. Carotenoids have many functions

in nature, such as vitamin A precursors or as antioxidants that neutralize free radicals formed in cells when exposed to radiation.¹² Carotenoids have been observed and quantified in freshwater copepods (Fig. 1), cladocerans, and ciliates.^{49,52} With respect to rotifers, knowledge is scarce, but red pigmented forms have been anecdotally observed.³ Comparing pigment content in copepods and cladocerans reveals a striking difference, with sometimes as much as ten times more carotenoids in copepods than in cladocerans. This suggests that this pigment has different functions in the two taxa.^{3,52} Cladoceran carotenoid deposits are not evenly distributed in the body tissues and can in some cases be observed in only ovaries and eggs,³ and their protective role in cladocerans is suggested to be restricted mainly to the offspring.⁶

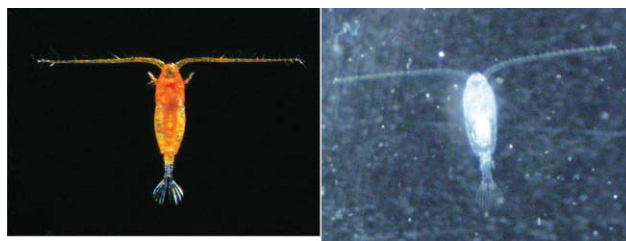


Fig. 1 Calanoid copepod with high (left) and low (right) levels of UV protective red carotenoids. Both specimens sampled during summer. (Photo: Hans Berggren and Samuel Hylander.)

Adaptive benefits of carotenoids. Since many copepod populations, in contrast to cladocerans, display strong carotenoid pigmentation, most of the research around carotenoids has focused on these organisms. Deeply-colored copepod populations are usually found in high latitude or altitude areas, but considerable pigmentation may also be observed in temperate regions.^{49,53–56} Early research showed that copepods with lower levels of protective pigmentation suffer from greater mortality when exposed to intense light.^{36,46,53,57} Furthermore, copepods accumulate more carotenoids when exposed to UV compared to when UV is reduced or absent^{19,54,55,58} (Fig. 1). Additionally, photoprotective carotenoids are transferred to eggs and, since copepod nauplii often reside in surface waters, this transfer is likely a way to reduce radiation mortality in offspring.³⁶ Several suggestions explaining the adaptive benefit of red carotenoid pigmentation have been put forward, including: metabolic benefit by heat absorption, association with lipid storage, and photoprotection from intense sunlight.^{49,53} In a series of studies, Hairston⁴⁹ concluded that photoprotection was the most probable hypothesis, based on its benefit. He rejected the lipid storage explanation because carotenoid and lipid contents were not correlated,⁵⁹ and heat absorbance was unlikely due to effective heat transfer in these small organisms.⁵⁷ The conclusion is also supported by the correlations between altitude and carotenoids, since UV exposure is known to increase with altitude both due to higher radiation and due to clearer waters.^{7,53}

Production and accumulation of carotenoids. Zooplankton are unable to produce carotenoids themselves, but have to incorporate them by consuming carotenoid-rich food, such as algae.^{12,60} Carotenoids are typically abundant in nature, and several studies from natural systems have confirmed that carotenoid concentrations in copepods are not entirely constrained by the availability

of carotenoids in the food.^{49,53} However, since zooplankton are dependent on the algal food for their carotenoid accumulation, it could be hypothesized that their content is merely a reflection of their food and that carotenoid accumulation does change when the diet is changed.^{19,58,60} This is not, however, the only factor, since copepods of the same species coming from two different lakes accumulated different amounts of carotenoids upon light exposure.⁴⁹ The species coming from the clearest lake had the highest accumulation efficiency; thus, this can be interpreted as an adaptation to high light environments.⁴⁹ In general then, carotenoid concentration in copepods may also be a function of variable selection pressures and consequent adaptations. Similar results were found in a marine copepod, *Calanus helgolandicus*, where the carotenoid (astaxanthin) content increased with high food availability, but the levels were further increased upon visible light exposure.⁶¹ However, since the copepods had high levels of astaxanthin also in darkness, the authors suggested that there must be additional reasons for pigment accumulation beyond protection against harmful radiation, although these reasons were not specified in the paper.⁶¹

The carotenoid concentration in copepods has also been shown to vary seasonally, with a peak in early spring and in some cases an additional peak in late fall.^{19,55,56,59} During summer, the concentrations are generally low, which has been interpreted as an adaptation to relatively higher UV threat in spring and more intense fish predation during summer^{44,55,56} (Fig. 2).

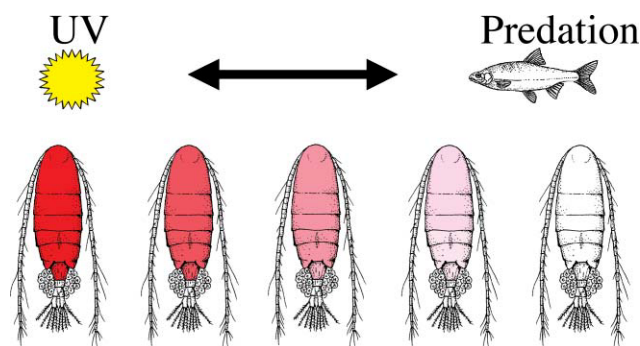


Fig. 2 A schematic illustration showing the trade-off in pigment level among copepod individuals between being pigmented and protected against UV radiation, but vulnerable to visual predators, such as fish. On the other hand the completely unpigmented individual has no protection against UV, but is less visible to the predator.

MAAs

Mycosporine-like amino acids (MAAs) are a group of photoprotective compounds that are invisible in visible light and found in many organisms including algae, corals, and crustaceans.⁶² These substances have an absorption maximum between 310 and 360 nm,⁶³ and they function as sunscreens protecting against damage from harmful levels of UV radiation.¹¹ However, other functions have also been suggested, including antioxidant effects, easing of salt stress, and changes in internal nitrogen storage.⁶⁴ Zooplankton rich in MAAs do have higher survival than animals with low MAA content when exposed to UV.^{19,65} Like the carotenoids, MAAs can generally not be synthesized by animals but have to be ingested from the food,¹¹ although recent

studies indicate that some Cnidaria have pathways to potentially synthesize MAAs.⁶⁶

Among zooplankton, MAAs have been observed in copepods, rotifers, and ciliates;^{50,51,67} but in a study of 15 lakes, Tartarotti *et al.*⁵⁰ found no MAAs in cladocerans (*Daphnia*, *Bosmina*, *Chydorus*). This was confirmed by Persaud *et al.*⁵⁶ who also could not detect MAAs in cladocerans, even though these organisms came from the same systems as MAA-containing copepods and hence had the same food source. The reason for this is unknown, but it has been suggested that the cladocerans lack, or have inefficient, uptake systems for MAAs.⁵⁰ The low carotenoid and MAA levels observed in cladocerans may also contribute to the higher susceptibility to UV often observed in cladocerans.^{28,68} In contrast to cladocerans, copepods from tropical, temperate, and high latitude and altitude areas display a wide range of MAA concentrations.^{50,56,67,69} Additionally, life-stage-specific MAA concentrations have been shown for a cyclopoid copepod, with highest MAA concentrations in eggs, nauplii, and young copepodites, presumably providing a high level of photoprotection during early development.⁷⁰

MAA in phytoplankton. Knowledge about MAA concentrations in zooplankton food, *i.e.* in natural phytoplankton assemblages, is limited, but quantities seem to vary considerably among lakes and regions.^{58,69,71} MAAs in phytoplankton correlate positively with altitude, UV radiation, and the UV transparency of the water column.^{70,71} The strongest positive relationship, however, is between phytoplankton MAAs and temperature.⁷⁰ Furthermore, seston MAA concentrations are highest at the surface, compared with deep waters.^{67,70,71} When analyzing the instantaneous seston MAA content and correlating it to copepod content, it is not always obvious that they are related⁵⁰ even though other field surveys have confirmed such a relationship.⁵⁸ By adding a lag phase of about 3–4 weeks, the correlation between seston and copepod MAAs is stronger.⁷⁰

Uptake of MAAs in zooplankton. Accumulation efficiency of MAAs in zooplankton in both fresh and marine systems is linked to food availability and UV stress.^{19,43,58,72} For example, copepods exposed to only visible light accumulate about half the quantity of MAAs as those that are exposed to UV radiation,¹⁹ suggesting that UV radiation enhances the uptake of MAAs. This enhancement may be due to differences in MAA uptake rate in copepods and production in algae.^{19,72} Although MAAs are not produced by all algal species, the uptake by zooplankton living under high UV stress can be very efficient.^{11,19} Additionally, when MAAs are scarce in the food, copepods may increase the uptake of carotenoids as a compensatory action.⁵⁸ Since carotenoids are visible and MAAs are invisible in visible light, it has been hypothesized that these two substances could work as alternative photoprotective strategies.^{19,43,58} Giving support to this hypothesis, there is a seasonal variation in type of pigmentation, with high carotenoid concentrations during spring and high MAA concentrations in summer.^{19,55,56} This suggests that accumulation of carotenoids and MAAs can be regarded as alternative strategies when facing UV and predation threats of different strengths and blends.⁵⁸

Tartarotti *et al.*⁵⁰ found a close relationship between the MAA concentration in a copepod population and the ratio between 1% attenuation depth (320 nm) and the maximum depth, suggesting

that MAA concentrations are governed not only by UV exposure but also by the availability of deep water for escape. This relationship was also shown by Tartarotti *et al.* (2004)⁷³ and Persaud *et al.* (2007),⁵⁶ but they found that descriptive power was low, suggesting that other environmental factors may also play a role in determining the MAA concentration—factors such as unmeasured variability in dietary MAAs and possibly UV avoidance by the populations.

Melanin

Melanins are a group of black–brown or yellow–red–brown pigments that are derived from a complex series of chemical and biological transformations of tyrosine and related compounds.^{74,75} This biochemical machinery produces exoskeletal or cuticle pigmentation in many organisms including crustaceans (Fig. 3). The primary function of melanin in zooplankton is suggested to be as a radiation screener, just as in humans, yet some of its precursors may also act as scavengers of free radicals.^{13,74} Among zooplankton, melanin pigmentation has primarily been described in *Daphnia*^{13,76} (Fig. 3), but other cladoceran genera like *Scapholeberis*, *Polyphemus*, and *Bosmina* can also have melanin pigmentation.^{43,52}



Fig. 3 *Daphnia* sp. with low (upper) and high (lower) concentrations of the UV-protective pigment melanin. Both specimens sampled during summer. (Photo: Lars-Anders Hansson.)

Melanin is deposited mainly in the parts of the carapace directed toward the surface and in the head shield and antennae,⁷⁷ indicating its importance in light interception (Fig. 3). At each molt, the *Daphnia* individual has to synthesize new melanin since the melanin is stored in the discarded carapace.^{13,78,79} In the absence of blue light and UV, *Daphnia* do not restore a melanized carapace after molting, indicating that short-wavelength light is the cue for melanin synthesis.⁸⁰

Melanized clones of *Daphnia* occur in Arctic or high-altitude environments but are generally absent in the temperate, low-altitude areas.¹³ Most of the colored clones are found in the clearest ponds without depth refugia,^{6,79} though melanized forms

at high altitude can be found also in lakes deeper than 20 m.⁸¹ Less-pigmented clones occur mainly in more turbid, colored (dissolved humics), or vegetated waters.¹³ This trend is illustrated in other ways by an inverse relationship between melanin content and dissolved organic carbon (DOC) concentration and by the relationship between UV transparency and the presence of melanized vs. non-melanized clones.^{13,78} Melanized *Daphnia* are most abundant in lakes with a DOC concentration below 2 mg L⁻¹.⁸² Melanized clones of *Daphnia* have a higher tolerance to UV radiation compared to animals without melanin pigment.⁷⁹ Studies involving extraction of the pigment indicate that melanin levels in melanized clones are around 0.03% of the body weight but still can prevent 90% of the UV transmission.¹³ In contrast to these studies, melanized *Daphnia middendorffiana* was not better protected against DNA damage than three non-melanized species.⁴⁵

Other UV protective compounds

The black pigment stentorin, which is used by, for example, the ciliate *Stentor araucanus*, has been suggested to be a protection against UV radiation.⁸³ This ciliate is highly resistant to UV (Table 1) and is one of the few organisms that forms population maxima in surface waters of clear-water lakes (*e.g.* in the Andes, Argentina) where the UV radiation is extremely high.⁸³

There are also several antioxidants often used in combination with pigments, *e.g.* in combination with melanin among *Daphnia*.⁸⁴ These antioxidants are enzymes, such as catalase (CAT) and superoxide dismutase (SOD), which detoxify UV-induced reactive oxygen species, such as singlet oxygen, hydrogen peroxides and superoxides. Glutathione transferase (GST) is a more multifunctional enzyme involved in several detoxifying processes, *e.g.* taking care of toxic substances produced during lipid peroxidation. The concentration of such antioxidant enzymes may be expected to be higher in non-pigmented zooplankton than in pigmented.⁸⁴ Borgeraas and Hessen (2002), in developing this hypothesis, showed that two of the antioxidants (GST and SOD) occurred in higher concentrations among hyaline (non-pigmented) *Daphnia longispina* than in melanized individuals. It has also been shown that activity of these enzymes (when challenged with UV) decrease with lowered food quality, thereby inhibiting this defense system in highly oligotrophic, clear-water lakes.⁸⁵

Another, more direct, protection is to have a physical shield such as the carapace of ostracods⁸⁶ (Table 1) offering more or less complete protection against UV radiation. Moreover, marine corals are known to cover themselves with a surface microlayer of mucus and bacteria, which has been suggested to partly function as a photoprotective mechanism.⁸⁷

Behavior

Among herbivorous zooplankton, competition for food is often intense and usually the highest quantity (but not necessarily the highest quality⁸⁸) of algal food is close to the surface where UV intensities are highest. Thus, zooplankton are faced with a trade-off situation where the best area for feeding is also the most dangerous with respect to UV radiation. Accordingly, zooplankton also employ behavioral responses to UV.^{9,10,89} Since colored or chromophoric dissolved organic matter attenuates UV

Table 1 Resistance to UV among different zooplankton taxa. Note that all studies were performed under different conditions and that the degree of resistance is a relative and very rough estimate that is aimed at providing only a general view of UV resistance among different groups of zooplankton. The level of resistance was suggested by each respective author, but for clarity, we have transformed the suggestions to numbers: 1 = very low, 2 = low, 3 = moderate, 4 = high, 5 = very high resistance. N.D. = not determined; ^ = the organisms use migration in natural systems, but were not able to migrate in the study

Taxa	Resistance	Protection	Source
Copepods			
<i>Boeckella gibbosa</i>	5	Carotenoids, photo-repair	Zagarese <i>et al.</i> (1997) ³³
<i>Boeckella brevicaudata</i>	4	Pigment, photo-repair	Zagarese <i>et al.</i> (1997)
<i>Boeckella gracilipes</i>	1	Migration [^]	Zagarese <i>et al.</i> (1997)
<i>Boeckella gracilipes</i>	5	Migration, pigment, photo-repair	Cabrera <i>et al.</i> (1997) ³²
<i>Boeckella poppei</i>	5	MAA	Rocco <i>et al.</i> (2002) ³⁷
<i>Boeckella antiqua</i>	4	Photo-repair	Rocco <i>et al.</i> (2002)
<i>Cyclops scutifer</i>	4-5	N.D.	Leech & Williamson (2000) ⁶⁸
<i>Mesocyclops edax</i>	5	N.D.	Leech & Williamson (2000)
Cladocerans			
<i>Ceriodaphnia quadrangula</i>	2	N.D.	Williamson <i>et al.</i> (2001) ⁹
<i>Ceriodaphnia reticulata</i>	3	N.D.	Hurtubise <i>et al.</i> (1998) ⁸⁶
<i>Scapholeberis kingii</i>	2	N.D.	Hurtubise <i>et al.</i> (1998)
<i>Daphnia magna</i>	3	N.D.	Hurtubise <i>et al.</i> (1998)
<i>Daphnia catawba</i>	2	N.D.	Leech & Williamson (2000) ⁶⁸
<i>Daphnia pulicaria</i>	3	N.D.	Leech & Williamson (2000)
<i>Daphnia galeata</i>	1	Photo-repair, migration [^]	Siebeck & Böhm (1994) ⁴
<i>Daphnia pulex obtusa</i>	3	Photo-repair	Siebeck & Böhm (1994)
<i>Bosmina longirostris</i>	2	N.D.	Williamson <i>et al.</i> (2001) ⁹
<i>Chydorus sphericus</i>	2	N.D.	Cabrera <i>et al.</i> (1997) ³²
Ostracods			
<i>Cyprinotus incongruens</i>	5	Carapace	Hurtubise <i>et al.</i> (1998) ⁸⁶
Heterotrophic nanoflagellates			
<i>Bodo saltans</i>	1	N.D.	Sommaruga <i>et al.</i> (1996) ¹¹⁰
<i>Bodo</i> sp.	3	N.D.	Mostajir <i>et al.</i> (1999) ¹¹⁶
<i>Monosiga marina</i>	3	N.D.	Mostajir <i>et al.</i> (1999)
Rotifers			
<i>Keratella taurocephala</i>	5	N.D.	Leech & Williamson (2000) ⁶⁸
<i>Keratella cochlearis</i>	4	N.D.	Leech & Williamson (2000)
<i>Lepadella ovalis</i>	2	N.D.	Cabrera <i>et al.</i> (1997) ³²
<i>Asplanchna</i> sp.	3	N.D.	Cabrera <i>et al.</i> (1997)
<i>Asplanchna priodonta</i>	1	N.D.	Williamson <i>et al.</i> (2001) ⁹
<i>Polyarthra dolichoptera</i>	5	MAA	Obertegger <i>et al.</i> (2008) ¹²⁵
Ciliates			
<i>Stentor araucanus</i>	5	Stentorin	Modenutti <i>et al.</i> (2005) ⁸³
<i>Strobilidium</i> spp.	1	N.D.	Mostajir <i>et al.</i> (1999) ¹¹⁶
<i>Askenasia</i> sp.	1	N.D.	Mostajir <i>et al.</i> (1999)
<i>Uronema marinum</i>	1	N.D.	Mostajir <i>et al.</i> (1999)
<i>Laboe</i> sp.	1	N.D.	Mostajir <i>et al.</i> (1999)
Insect larvae			
<i>Chaoborus</i> (instar II–IV)	4	N.D.	Leech & Williamson (2000) ⁶⁸
<i>Chaoborus obscuripes</i>	5	MAA	Nagiller & Sommaruga (2009) ¹²⁶
<i>Chaoborus pallidus</i>	2	N.D.	Nagiller & Sommaruga (2009)
Corals			
<i>Montastrea faveolata</i>	2	Mucus microlayer	Lyons <i>et al.</i> (1998) ⁸⁷
<i>Colpophyllia natans</i>	2	Mucus microlayer	Lyons <i>et al.</i> (1998)

radiation efficiently,⁷ depth can often serve as a refuge from UV radiation. On the other hand, individuals with protective pigmentation, *e.g.* copepods with carotenoids (Fig. 1), may utilize surface waters more than less pigmented individuals or taxa.⁹⁰ Such depth separation among taxa was ably illustrated in the highly UV transparent Lake Giles, USA, where most rotifers (*Keratella taurocephala*) and generally also copepods (*Diaptomus minutus*) occurred in surface waters, whereas the more UV-sensitive cladoceran *Daphnia catawba* rarely spent time close

to the surface.⁶⁸ Although the earliest studies on zooplankton vertical migration suggested sunlight as the driving force,⁹¹ diel vertical migration has traditionally been seen as a predator response.^{92–94} However, diel vertical migration has also been reported in lakes lacking predators, and the magnitude of *Daphnia* vertical migration is often strongest in very transparent lakes,⁹⁵ suggesting that UV may be a prompt for vertical migration.⁹ *Daphnia* are also known to respond with strong negative phototaxis, “light dances”, in response to UV-wavelengths

(260 and 380 nm), whereas they are positively phototactic to visible light (420–600 nm).⁴⁰ Furthermore, diel migrations are more accentuated when differences between day and night light regimes are stronger, such as in southern Europe, than at higher latitudes where the sun is constantly above the horizon during summer.⁹⁶ This may be interpreted as if zooplankton diel migration is induced by a combination of light, UV and predation. In support, an experimental study found that UV strongly affected the depth distribution of all size classes of *Daphnia longispina*, whereas predation risk in combination with visible light (UV screened out) affected depth distribution of larger, but not smaller, size classes.⁹⁷ The reason why small size classes (length less than 0.9 mm) remained in surface waters during daytime was likely that small individuals are less vulnerable to predation than larger ones.⁹⁷ Such size-class separations may also lead to competitive advantages for smaller sized animals, since they can continue feeding closer to the surface compared to larger ones.⁹⁷

In both laboratory and field studies, diel vertical migration in response to UV radiation has been repeatedly demonstrated in *Daphnia*,^{10,27,40,98} but with respect to copepods reports on behavioral responses are few and contradictory.^{55,99,100} Among the few, the vertical distribution of the marine calanoid copepod *Tortanus dextrilobatus* was considerably altered in the presence of UV radiation.¹⁰¹ Similar results were experimentally found by Cooke *et al.* (2008),¹⁰² wherein *Daphnia catawba* migrated downwards in the presence of UV, but showed no migratory behavior when UV was screened out. In this study, migration was also exhibited by the copepod *Leptodiatomus minutus*, but less so than the *Daphnia*. Similarly, in a Swedish study, copepods were found to respond to UV, but their response was weak, suggesting that copepods may rely mainly on pigments when challenged with UV.⁶⁹

Intraspecific differentiation of UV and predation effects on diel migration in zooplankton was also shown in a study performed in high-latitude lakes where UV radiation is generally high. Diel vertical migration in *Daphnia longispina* was induced by UV radiation during sunny days, but on overcast days predatory threat from the phantom midge (*Chaoborus obscurpis*) was a better predictor of *Daphnia* depth distribution.⁹⁴

Dual threats: UV and predation

An important component of environmental variability is predation. The number of studies examining consumer strategies and prey escape adaptations is substantial and constitutes fundamental parts of several concepts in biology. Studies in terrestrial, as well as in aquatic ecosystems, have shown that many prey organisms gather information from their environment by being receptive to chemicals exuded by predators,^{14,103} and they also use this information to induce defenses against the predator. Such inducible defenses may be especially beneficial in situations where several threats act simultaneously. A striking example of how an adaptation can be beneficial against one threat, but simultaneously disastrous against another, is the bright red pigmentation of carotenoids (Fig. 1), which effectively protects the animal from being harmed by UV radiation.^{36,58} However, being intensely colored increases the risk of mortality through predation from visual hunters such as fish, as shown for pigmented *versus*

transparent copepods^{49,104,105} (Fig. 2). The explanation generally presented as to why copepods are less pigmented in the presence of predators than in their absence is that pigmented morphs are selectively preyed upon. Hence, in Antarctic and sub-Antarctic lakes, where UV radiation is intense but fish predation is absent due to biogeographical isolation,¹⁰⁶ copepods are bright red. On the other hand, in temperate lakes, fish predation is generally high and UV radiation is moderate; accordingly, copepods here tend to have low concentrations of pigments.

Daphnia clones with melanin pigments have delayed age of first reproduction, smaller clutch size but larger offspring size, and, thus, lowered intrinsic growth rate compared with non-melanized clones;^{79,107} this suggests a cost associated with melanin production. A trade-off between the metabolic tax paid for melanin synthesis and its UV protection abilities is hence suggested.^{52,76} Lower growth capacity, however, may also be caused by polyploidy, as has been demonstrated, and some melanized clones have indeed been shown to be polyploid.¹⁰⁸ The differential competitiveness of transparent *versus* melanized clones is probably why most authors report that melanized clones seldom co-occur with transparent clones in low-UV environments.^{13,78,79} Studies addressing seasonal changes in melanin content are scarce. In one study involving sub-Arctic areas, melanin synthesis was low during winter and peaked immediately after ice breakup, which was also the time for maximum underwater UV intensity.⁷⁸ This seasonal pattern is similar to the one found for carotenoids in copepods.⁵⁵ Predation pressure on melanized clones is also suggested to be high, and most melanized clones are found in lakes devoid of fish, although this is not always the case.^{13,81} Since the melanin provides photoprotection but at the same time increases visibility, the amount of melanin in *Daphnia* is suggested to be a plastic trait for organisms that are adapted to environments with contrasting or variable selection pressures.¹⁵ Furthermore, there is also a relationship between melanin occurrence and vertical position in the water column. During the daytime, melanized *Daphnia* may utilize the water column, but transparent forms are close to the bottom.^{13,109} Melanized clones were shown to decrease their pigmentation when released from UV radiation, but upon reintroduction of UV exposure, started to migrate vertically instead. This suggests a trait compensation between pigmentation and behavior.⁴³

Both, predation and UV vary spatially and temporally and it may therefore be predicted that zooplankton pigmentation would be highest in those locations where UV penetration is high and predation pressure is low. Similarly, within each lake, pigmentation level may be predicted to be highest during times when UV penetration is high, that is when turbidity in the water of eutrophic lakes is low, and when feeding efficiency by fish is low. Hence, from the hypothesis that copepods adjust their pigmentation level according to the relative threats from UV and predation (Fig. 2), we arrive at the somewhat counter-intuitive prediction that pigmentation level should be highest during spring and fall, when UV penetration through the water is high and lower temperature reduces fish feeding rate. This pattern was shown in a long-term study of six lakes in southern Sweden, where copepods temporally adjusted their pigmentation levels up or down depending on which was the most pronounced threat,⁵⁵ UV or predation. Similarly, *Daphnia* may adjust their pigmentation in environments with variable selection pressures.¹⁵

Species differences in response to UV damage

Different taxa have different strategies to handle the threat from UV radiation, and some are very well protected by different morphological adaptations, while others rely mainly on behavioral escape from high doses of radiation. With respect to general differences in resistance to UV radiation, copepods seem to be better equipped than cladocerans (Table 1; ref. 32). There may even be considerable differences within the same genus as illustrated by three Patagonian copepod species.³³ Two of the species, *Boeckella gibbosa* and *B. brevicaudata*, show high resistance to UV due to strong pigmentation, as well as photoenzymatic repair, whereas the third species (*B. gracilipes*) has low levels of protective pigmentation and shows no photoreactivation (Table 1). As a result, this latter species is restricted to deep, dark waters, or to turbid lakes, whereas the other two have access also to more UV-exposed habitats.³³ In a laboratory study, an ostracod species was shown to be less sensitive to UV than cladocerans (Table 1), mainly due to its covering carapace.⁸⁶ Some rotifers, such as several *Keratella* species, seem to have high UV tolerance, whereas others, such as *Asplanchna* spp., may show weak tolerance (Table 1). The heterotrophic nanoflagellate *Bodo saltans* is very sensitive to UV radiation and responds by changing its morphology into a spherical form as well as by reducing its feeding rate on bacteria (Table 1).¹¹⁰

Hence, there is a considerable variation in UV resistance among species and, in addition, some species have photoreceptors allowing them to adjust their position in the water. For example, the photoreceptors in the compound eye of *Daphnia* do not have their peak sensitivity in the most harmful UV-B range, but well within the less dangerous UV-A part of the spectrum (348 nm). This may be interpreted as a precautionary strategy: because UV-A reaches deeper into the water than UV-B, the animal uses UV-A as a warning signal and stays at a depth where UV-A is detected. On the other hand, many fish predators perceive radiation within the UV-A range (350–370 nm), which has been suggested to aid the predator in finding zooplankton prey.¹¹¹ Hence, since *Daphnia* is able to “see” UV-A radiation, it “knows” that it is also visible for the predator and presumably responds, e.g. by descending deeper. However, the knowledge regarding interactions between photoreceptors and behavior is still very scarce and further research is needed.

Alterations in community composition due to UV radiation

Since some zooplankton taxa are less sensitive to UV radiation than others are, they may be expected to dominate at elevated UV levels. Although generalizations are difficult to make, copepods are viewed as more resistant to UV radiation than cladocerans^{18,112} (Table 1), and copepods may therefore be expected to dominate over cladocerans in places such as close to the equator and in polar regions. One reason for this possible difference is that cladocerans require more energy for photoprotection than copepods,¹¹³ a concept strengthened by the observation of improved performance by *Daphnia pulicaria* under UV stress when provided with high, rather than with low, food availability.¹¹²

High levels of ultraviolet radiation may considerably affect zooplankton species composition, as shown in a large set of Arctic

lakes where one rotifer species (*Asplanchna priodonta*) and two cladocerans (*Bosmina longirostris* and *Ceriodaphnia quadrangula*) were absent from the clearest lakes.⁹ Although the absence may have been due to reasons other than UV radiation, experimental tests showed that these species perished within days when exposed to the UV radiation levels of these clear-water lakes.⁹ Additionally, in a survey of Patagonian lakes, the diversity of zooplankton species was negatively correlated with UV penetration through the water column.¹¹⁴ However, in a long-term experiment comparing zooplankton community composition at low and elevated UV levels (37% above ambient radiation), no alterations in community composition or abundances were found to be attributed to UV radiation. Instead, it was suggested that other factors such as nutrient availability, competition, and predation override the UV effects.¹¹⁵

On the other hand, marine ciliates were shown to be more sensitive to UV radiation than their prey, such as flagellates and phytoplankton, which resulted in a strong increase in abundances of prey organisms at elevated UV radiation.¹¹⁶ Since ciliates comprise an important feeding link between the microbial community and higher trophic levels, such taxa-specific differences in UV sensitivity may have a dramatic influence on food web dynamics in aquatic systems.¹¹⁶

Perspectives and suggestions for future studies

It is clear that UV radiation has had a major effect on zooplankton over evolutionary time. They have been forced to evolve sophisticated defense strategies such as pigmentation, migratory behavior, and repair systems to cope with the UV threat. A major conclusion from this review is that “the ghost of past UVR” (*sensu* Hessen (2008))¹ may be enough preparation for zooplankton to meet predicted future increases in UV radiation. However, some of the genotypic diversity may have been lost during later evolution due to selection against UV protection, which may restrict the potential for future adaptations to changing conditions, such as increases in UV radiation. In spite of this possibility, UV may not be the most severe environmental threat that zooplankton communities face, and no zooplankton species is known to be in danger of becoming extinct due to predicted increases in UV radiation in the forthcoming decades. This fortunate situation is partly due to adaptations already employed by zooplankton to cope with the radiation and partly due to the efficient attenuation of short-waved radiation by the water column. In addition, the ozone levels are within the coming decades predicted to return to levels recorded before the ozone thinning started.¹¹⁷ Therefore, even though most papers that address UV effects start from the perspective of thinning of the ozone layer and widening of the ozone hole, it may be of importance to clearly state that other factors—such as predation, changes in DOC input, cloud cover, and the organism’s position in the water column—will likely be more important than alterations in UV due to reduced stratospheric ozone.^{26,88,118,119} Hence, a more fruitful perspective would be to view UV as one among several everyday threats that zooplankters have had to contend with throughout evolutionary time in order to improve their fitness, and that future studies should be directed toward the understanding of UV effects on ecosystems and individuals, instead of treating UV as a “new” environmental hazard for zooplankton.

An interesting aspect of zooplankton–UV interactions is that zooplankton, as they feed on phytoplankton, reduce the amount of particles (algal cells) in the water, but simultaneously increase the amount of dissolved substances through excretion from the zooplankton;^{120–123} this causes a shift in the light transmission properties of the water toward more UV-absorbing substances. This ameliorating effect from zooplankton grazing has been shown in the laboratory for both fresh¹²³ and marine waters,¹²⁴ and it illustrates a potentially important indirect way by which UV damage is reduced.

As indicated in Table 1, the efficiency of different photoprotective compounds, and the relative level of UV protection employed by different taxa, are largely unknown and still controversial. Hence, studies simultaneously addressing these aspects of photoprotection within different zooplankton communities are needed.

Other future directions that have the potential to advance the research field include studies on interactions between photoreceptors and behavior in zooplankton; these may be expected to show why, when, and how zooplankton migrate. Further studies addressing biogeographical differences among taxa with regard to UV risk have the potential to improve our understanding of zooplankton distribution, dominance patterns, and community ecology. During recent years, more photoprotective compounds have been discovered, and it is likely that there are several UV protective compounds still to be identified. Traditionally, there have been few interactions between UV radiation researchers and ecologists, and this has slowed the pace of research. Meshing of these research lines has the potential to create synergies and deeper understanding of UV effects on organisms.

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