

UV radiation and freshwater zooplankton: damage, protection and recovery

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Abstract

While many laboratory and field studies show that zooplankton are negatively affected when exposed to high intensities of ultraviolet radiation (UVR), most studies also indicate that zooplankton are well adapted to cope with large variations in their UVR exposure in the pelagic zone of lakes. The response mechanisms of zooplankton are diverse and efficient and may explain the success and richness of freshwater zooplankton in optically variable waters. While no single behavioural or physiological protection mechanism seems to be superior, and while several unexplained and contradictory patterns exist in zooplankton UVR ecology, recent increases in our understanding are consistent with UVR playing an important role for zooplankton. This review examines the variability in freshwater zooplankton responses to UVR, with a focus on crustacean zooplankton (Cladocera and Copepoda). We present an overview of UVR-induced damages, and the protection and recovery mechanisms freshwater zooplankton use when exposed to UVR. We review the current knowledge of UVR impact on freshwater zooplankton at species and community levels, and discuss briefly how global change over the last three decades has influenced the UVR milieu in lakes.

Keywords: UV radiation; zooplankton; lakes; damage; protection; recovery.

Introduction

Solar ultraviolet radiation (UVR) has many deleterious effects on aquatic biota as a result of its highly energetic short wavelengths. UVR is the shortest wavelength band reaching the Earth's surface. It is arbitrarily divided into two wavebands: wavelengths from 280 nm to 320 nm

are referred as UV-B and those from 320 nm to 400 nm are referred to as UV-A. In most atmospheric situations, the UV-B range of the spectrum accounts for 0.1 %, UV-A 6 %, and the visible portion (400 nm to 700 nm) 50 % of the global radiation.

Zooplankton are present in the water column of most lakes throughout the world. In most lakes they occupy the

intermediate trophic position in the food web, channelling resources from primary producers and heterotrophic microorganisms to invertebrate predators and fish. Apart from this very general classification, the role and life of zooplankton can be very different in diverse lakes. Zooplankton inhabit lakes with varying temperature, depth, colour, and composition of other species. These environmental characteristics contribute to defining the exposure and the protective response of zooplankton to UVR. A mid-latitude *Daphnia* in a 20 m deep brown water lake may face only negligible levels of UVR (Kirk, 1994), while another *Daphnia*, in a shallow clear water tundra pond, may be exposed to nearly continuous UVR for all of its life during polar summer (Rautio & Korhola, 2002a). The habitat also defines which UVR protection strategies are available. Accumulation of red carotenoids or synthesis of black melanin are efficient and safe protection mechanisms in lakes where visually hunting fish are absent, while vertical migration and other means of less visible protection are more likely in the presence of fish (Hansson, 2000; Hylander et al., 2009a; Williamson & Rose, 2009). Hence, organisms are adapted to their habitat and cope with UVR differently which results in great species-specific variability in UVR protection (Zagarese et al., 1997a; Tartarotti et al., 1999; Leech & Williamson, 2001; Hylander & Hansson, 2010). Recently, the adaptations and abilities of species to respond to UVR have been challenged with increases in UVR that are beyond the natural range in the animal's habitat (ACIA, 2005). These increases have occurred mainly at high latitudes where the depletion of ozone in the stratosphere has caused greater intensities of UVR to reach the ground level.

Initially, the concern about UVR effects on aquatic ecosystems was directed particularly at Antarctic waters. The impact of the spring ozone hole on primary production and food chain processes in the marginal ice zone was predicted to range from negligible to catastrophic (Roberts, 1989). The first studies on the responses of marine and freshwater plankton to UVR dealt mainly with the survival of individual species and changes in photosynthesis (Siebeck, 1978; Lorenzen, 1979). These were soon followed by studies on different UVR protection

strategies (e.g. Hebert & Emery, 1990; Sommaruga & Garcia-Pichel, 1999). During the last decade, the focus has shifted from individual species' responses to ecosystem responses and changes in food webs and trophic cascades (Vinebrooke & Leavitt, 1998; Williamson et al., 1999; Wulff et al., 2000; Hylander & Hansson, 2010). Several studies have considered other global phenomena such as climate warming and acidification that can have a greater influence on the water column UVR regime (Schindler et al., 1996; Sommaruga et al., 1999; Williamson et al., 1999).

Research on solar ultraviolet radiation, and its ecological effects on zooplankton has expanded from few studies in the 1970s and earlier to several published papers per year in the first decade of the 21st century. We have chosen to include in this review papers that allow us to present a thorough overview of what is presently known about the responses of freshwater zooplankton to UV radiation and what is still unknown. Our aim is to give a holistic overview of the information published in research papers and reviews, which have either concentrated on a specific geographical region or on one or few aspects in UVR ecology, respectively. Most papers in this review relate to western alpine regions (reviewed by Zagarese et al., 2000; Sommaruga, 2001; Vinebrooke & Leavitt, 2005) and the Arctic (reviewed by Hessen, 2001; Perin & Lean, 2004) reflecting the geographical distribution of published UVR literature. Strict regulations on conduct of research and the lack of crustacean zooplankton in most lakes in the Antarctic (Rautio et al., 2008) reduce the UVR studies in this vast area that has been most influenced by ozone depletion and increases in UVR (but see Rocco et al., 2002). We address firstly the factors that define the geographical variability in the exposure of zooplankton to UVR, including the effects of climate change. We then review how to measure UVR-induced damage and what factors influence the damage. This is followed by the examination of types of protection and recovery mechanisms that are activated when freshwater zooplankton are exposed to UVR. Finally, we discuss UVR-induced changes at community level and comment on the state of understanding the ecology of UVR.

Geographical variability in freshwater zooplankton's exposure to UVR

The exposure of zooplankton to UVR varies largely depending on the lake that they inhabit. Alpine lakes (e.g. Alps, Andes, Himalayas, Rockies), with the exception of those fed by turbid glacier streams, are among the most UVR-transparent aquatic ecosystems in the world, with diffuse attenuation coefficients (K_d) similar to those found in ice-covered Antarctic lakes (Morris et al., 1995; Sommaruga, 2001). At the other end of the range are UVR-protected humic-rich lakes on wetlands (Arts et al., 2000), while the rate of change in UVR attenuation is greatest in arctic lakes that are influenced by global change. The variability in lake optics is determined by lake location, catchment soil type, and the exposure of the lake to global change (changes in ozone layer, precipitation). The importance of these factors is briefly presented below, while for more extensive reading, reviews on factors affecting surface UVR and biological UVR exposure in aquatic ecosystems are recommended (e.g. Weatherhead et al., 2005; Vincent et al. 2007).

Zenith angles and altitude

There is a large latitudinal variation in ground level UVR irradiances (Fig. 1). Most of this variation is caused by seasonal variation in the solar zenith. Zenith angles are small in low-latitude regions leading to UV irradiances that are higher than those at higher latitudes. However, when daily integrated doses are compared, the length of polar

summer days at high latitudes compensates for the effect of large solar zenith angles and the daily UVR doses approach those at the equator. UVR fluxes increase naturally with altitude, and have been measured to increase by 19 % per 1000 m in the Alps for the short wavelength UV-B radiation (Blumthaler et al., 1992). In a lake situated at 2000 m above sea level this can account for a substantial increase in the UVR exposure (Fig. 1). Small zenith angles and high elevation account for a great UVR exposure in mountain lakes at mid and low latitudes and zooplankton in these lakes are often observed to react strongly to UVR.

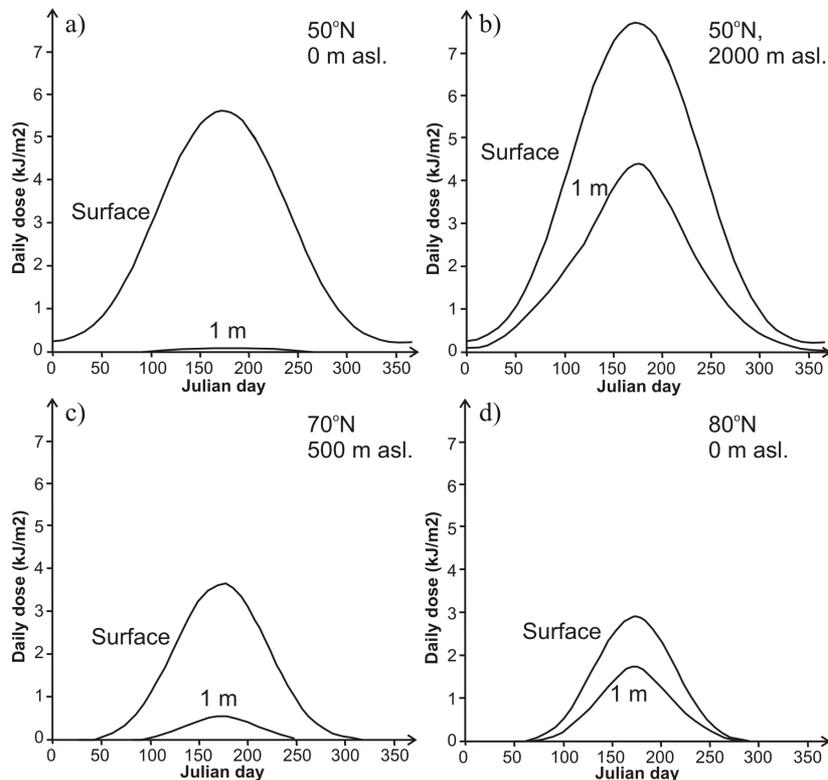


Fig. 1. UVR in the water column is defined by lake location (latitude and altitude) and water column transparency (K_d = attenuation coefficient). The figure shows the surface and 1 m depth daily theoretical erythemal UV radiation dose (kJ m^{-2}) for lakes in a) Great Plains at 50 °N and 0 m a.s.l. with average lake $K_{d,UVB} = 20 \text{ m}^{-1}$ (30 lakes), b) Tyrolian Alps at 50 °N and 2000 m a.s.l. with average lake $K_{d,UVB} = 0.56 \text{ m}^{-1}$ (11 lakes), c) Northern Finland at 70 °N and 500 m a.s.l. with average lake $K_{d,UVB} = 2 \text{ m}^{-1}$ (12 lakes), and d) Ellesmere Island at 80 °N and 0 m a.s.l. with average lake $K_{d,UVB} = 0.61 \text{ m}^{-1}$ (3 lakes). Ground level daily dose data from ACIA (2005), lake K_d data from Laurion et al. (2000), Arts et al. (2000), and Rautio, unpublished. 1 m UV radiation has been calculated using the equation $E_d(z) = E_d(0)e^{-K_d z}$ (Kirk, 1994), and assuming a 19 % increase in UVR per 1000 m (Blumthaler et al., 1992).

Impact of the ozone layer and warmer climate

High latitude areas are most affected by ozone depletion and, therefore, experience the greatest increase in UVR, compared to the reference year 1979. The long-term trends in total column ozone obtained from satellite and ground-based data both indicate a latitudinal variation in the change of ozone concentration, with almost no change over the equator and substantial declines outside the 35 °S to 35 °N zone (ACIA, 2005). Although compounds such as chlorofluorocarbons and halons, which break down ozone and hence decrease the UVR absorption in the stratosphere, are mainly released from mid-latitudes, a combination of extreme cold and stratospheric circulation (the polar vortex) above the poles results in conditions that are favourable for ozone destruction (Anderson et al., 1991). In recent years, ozone loss rates in the Arctic region have reached values comparable to those recorded over the Antarctic although spring ozone levels over the Arctic often remain higher than those over the Antarctic (ACIA, 2005). Lower latitude zooplankton are not influenced by stratospheric ozone depletion in the same way as polar zooplankton, apart from some places in South America where evidence for Antarctic ozone 'hole' perturbation has been observed as far north as at 30 °S (Kirchhoff et al., 1996).

The increases in UVR irradiances occur primarily in spring, when ozone depletion reaches a maximum, and can result in spring UVR levels that are higher than those measured during the summer (ACIA, 2005). In the Scandinavian subarctic region, springtime irradiances of UV-B radiation reaching the surface of the Earth increased by 10–20 % between the late 1970s and 1995 (International Arctic Science Committee, 1995). Between 1979 and 2000, the trend in mean annual total column ozone over the Arctic was about -3 % per decade, while the trend in mean spring total column ozone was about -5 % per decade (ACIA, 2005). The observed changes in ozone depletion have not been symmetric around the North Pole. The greatest changes in ozone levels have been observed in the area between Siberia and Scandinavia where the climate

is more continental, thus enhancing the formation of cold stratospheric clouds that promote ozone (O₃) destruction.

Most polar lakes are still frozen at the time of elevated spring UVR irradiances and the zooplankton are therefore protected from solar damage. However, increases in CO₂ also account for warmer temperatures and a shorter period of ice cover (Livingstone, 1997; Rouse et al., 1997). A simulation study by Elo et al. (1998) suggested that doubling of CO₂ will lead to a 1–2 month earlier melting of the ice cover in Finnish lakes. Consequently, ice break-up in Finnish subarctic lakes would occur in May instead of late June, exposing the lake biota to the most intensive period of UVR. Historical observations of ice break-up times, including northern Lapland, and their comparison to present day measurements show that spring melting is occurring earlier (Magnuson et al., 2000). Alpine (Sommaruga-Wögrath et al., 1997) and Antarctic Peninsula regions (Quayle et al., 2002) are also being influenced by climate change-induced earlier melting of the ice, and subsequent increase in the underwater UVR exposure. Increased UV irradiance resulting from a combination of climatic warming and ozone depletion is likely to be lethal for zooplankton that are not able to adjust their protection against UVR.

Coloured dissolved organic matter (CDOM) and UV attenuation in water

The UVR regime in the water column differs from that reaching the ground. The penetration of UVR wavelengths into water is highly dependent on the colour of the water, which is defined by the amount of coloured dissolved organic matter (CDOM) in water and is estimated from the concentration of dissolved organic carbon (DOC). Typically, half of lake water DOC is composed of coloured compounds and DOC can therefore be used to predict UVR transparency, except in the lowest CDOM environments such as in some alpine lakes (Laurion et al., 1997; Sommaruga, 2001; Sommaruga & Augustin, 2006) where particles may also play a significant role in UVR attenuation, and in 'white DOC' lakes such as in Greenland where highly UVR-transparent lakes may

have very high concentrations of DOC ($> 100 \text{ mgC L}^{-1}$) (Anderson & Stedmon, 2007). The clearest lakes ($< 2 \text{ mgC L}^{-1}$) are usually found above the tree line (Morris et al., 1995; Vincent & Pienitz, 1996; Rautio & Korhola, 2002a) with UV-B penetration to several metres depth (Schindler et al., 1996), while some humic lakes can have DOC concentration $> 30 \text{ mgC L}^{-1}$ and the UVR is absorbed within the first few centimetres (Kirk, 1994) (Fig. 1). The darkest lakes can be considered well-protected from UVR, however UV-irradiated DOC may promote the formation of reactive oxygen species (ROS) that in turn are harmful to toxic to organisms including zooplankton (Souza et al., 2007). Along with changes in DOC concentrations, there may also occur significant qualitative changes in DOM composition (McKnight et al., 2001), which is reflected in the optical properties of this material. CDOM above the tree line has a bigger component of autochthonous compounds which absorb short wavelength radiation less than allochthonous carbon (McKnight et al., 1994).

Many lakes, especially northern lakes that have had a stable low DOC concentration and hence have been exposed to UVR in the same manner for decades and even centuries, are now changing in their optical properties due to climate change-induced melting of permafrost soils and the subsequent release of DOC into the downstream receiving waters (Rosén et al., 2009). This process will release the biota from UVR stress. The magnitude of new DOC pulses to the lakes is dependent on temperature but also on precipitation which varies regionally. In some areas, e.g. in Svalbard (80°N , 20°E), there has been a significant rise in precipitation from the 1960s to the 1990s (Hanssen-Bauer & Forland, 1998), however, other regions have shown little change or decreases in precipitation (Vincent et al., 2001). With decreasing precipitation the runoff and hence the amount of UV-absorbing organic material into the Canadian water bodies has decreased, making the water clearer and consequently more exposed to UVR (Schindler et al., 1996).

The intensity of UVR in water is also related to anthropogenic acidification (Schindler et al., 1996; Williamson & Rose, 2009). Acidification increases transparency as a result of coagulation

and removal of DOC by monomeric aluminium as well as by reduced productivity (Effler et al., 1985).

UVR impacts on zooplankton

UV radiation is likely to cause a variety of direct and indirect negative effects on zooplankton populations. The majority of studies concerning direct UV-induced damage on zooplankton have reported increased mortality rates (reviewed by Zagarese et al., 2003). In addition, there is a growing amount of literature on other negative UVR effects, including DNA damage (Malloy et al., 1997), reduced growth rates (de Lange et al., 1999), decreased fecundity (Williamson et al., 1994; Zellmer, 1996 & 1998; Huebner et al., 2006), increased UVR susceptibility in the presence of other environmental stressors (Hessen & Alstad Rukke, 2000; Cooke et al., 2006), and gut damage in zooplankton when fed with UVR pre-exposed algae (Zellmer et al., 2004). How and at what rate UVR influences zooplankton, however, varies greatly depending on the species in question, its physiological status, the environment it inhabits, and on its capability for UVR protection and recovery from damage.

Wavelength defines response

The negative effects of UVR on zooplankton, similar to all living organisms, are associated with the highly energetic short wavelengths. These UV wavelengths have low intensity at ground level but they can still cause the greatest biological damage due to the great energy content per photon (Frederik et al., 1989). The absorption maximum of DNA near 260 nm makes UV-B biologically the most dangerous waveband (Caldwell, 1979). However, the separation of solar radiation into UV-B and UV-A wavelengths is arbitrary, and full wavelength-dependent response curves need to be determined.

The effect or weight of a certain wavelength in solar damage can be quantified by biological weighting functions (BWF). BWFs are used to estimate the effects of different wavelengths on organisms by generating a function that provides a weighting coefficient for each individual

wavelength (Neale & Kieber, 2000; Williamson et al., 2001a). Depending on the morphology of an organism, and on the presence or absence of photo-protective pigments, different BWFs may result (Tartarotti et al., 2000). Pigmented and non-pigmented clones of the same zooplankton species are different in their UVR susceptibility (Hessen, 1996) which affects the relationship between the UVR dose and, for example, mortality. Furthermore, zooplankton may not respond in a similar way to a UVR dose that is received in a single sunny day as to a dose that is received over a period of several cloudy days (law of reciprocity).

The existing zooplankton BWFs generally indicate the same result: the shortest wavelength UV-B radiation is in the order of a thousand times more damaging than is the longest wavelength UV-A (Kouwenberg et al., 1999; Tartarotti et al., 2000; Williamson et al., 2001a). Williamson et al. (2001a) showed that the most biologically damaging radiation for *Daphnia pulex* was in the 305 nm to 322 nm range. The contribution of UV-B to the mortality of *D. pulex* was 64 % while UV-A contributed 36 %. Other studies have also demonstrated that while UV-B causes the greatest damage, UV-A also induces mortality in zooplankton, including both copepods and cladocerans (Zellmer, 1998; Tartarotti et al., 2000; Rautio & Korhola, 2002a). The shape of the BWF curve of zooplankton closely resembles the action spectra for UV-induced erythema in human skin with the highest damage in the shortest UV-B wavelengths but some damage also occurring in the UV-A range (Tartarotti et al., 2000; Williamson et al., 2001a) (Fig. 2).

Defining BWFs for zooplankton is laborious; hence, they have been used in only a small number of studies. Most studies have instead used a broad band (e.g. full sunlight, UV-B, UV-A) or single wavelength response of zooplankton to natural solar or artificial radiation sources. One of the first such studies is from Siebeck (1978) who demonstrated that *Daphnia pulex*, *D. galeata* and *D. longispina* survival increased when UVR was blocked out with a glass filter. More than 20 years later, Rautio & Korhola (2002a) performed a similar experiment with *D. pulex*, *D. longispina* and the copepod *Eudiaptomus graciloides* using

four filters that block solar radiation differently. The three zooplankton species showed a similar ranking of response. Mortality of each species was highest in the full sunlight treatment and decreased with declining UV intensity, while not only the presence of UV-B but also UV-A resulted in high and rapid mortality. Similarly, Zagarese et al. (1994) showed how the intensity of UVR affects zooplankton survival. Significant in situ mortality of *Daphnia* was observed after two days of exposure at and above 73 % of surface radiation at 320 nm but not at 63 %.

Variability in damage

The vast number of studies conducted on zooplankton UVR tolerance clearly demonstrates that different species (Siebeck & Böhm, 1994; Hurtubise et al., 1998; Tartarotti et al., 1999; Leech & Williamson, 2000; Rautio & Korhola, 2002a), species from the same genus (Zagarese et al., 1997a; Rocco et al., 2002), or even the same species but during different seasons or from different lakes (Stutzman, 1999; Tartarotti et al., 1999), respond differently to UVR. This makes defining accurate UVR tolerance limits difficult if not impossible. Some general conclusions can, however, be drawn.

Most studies that have included age as a variable in UVR response have shown that adults tolerate UVR better than juvenile stages (Leech & Williamson, 2000; Vega & Pizarro, 2000; Ramos-Jiliberto et al., 2004; Huebner et al., 2006). One of the few documented exceptions from this pattern is the

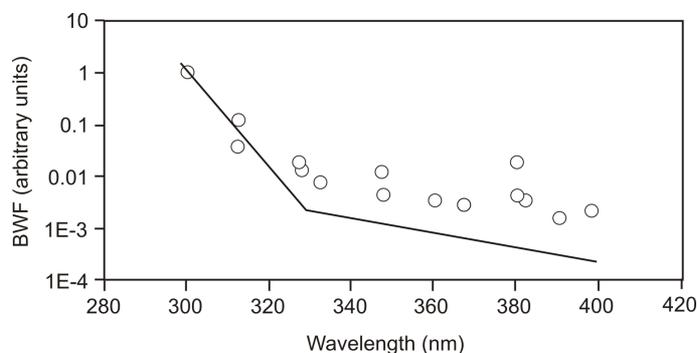


Fig. 2. Biological weighting function for the mortality of the copepod *Boeckella gracilipes* (open circles) and action spectra for erythema in human skin (continuous line). Redrawn from Tartarotti et al. (2000).

higher adult mortality in the rotifer *Asplanchna girodi* in comparison to its juveniles (Grad et al., 2003). Using four species of copepods (*Diaptomus minutus*, *D. spatulocrenatus*, *Mesocyclops edax* and *Cyclops scutifer*), Leech & Williamson (2000) showed that adults had up to 34 % higher LD₅₀ UVR values than nauplii. Huebner et al. (2006) reported a similar age-dependent survival in *Daphnia magna*: after 12 h of UV-B exposure nearly 80 % of the oldest (4 days old) individuals were alive whereas less than 10 % of the 2 day olds survived and none of the one day olds did. Similarly, Ramos-Jiliberto et al. (2004) showed that *Ceriodaphnia dubia* less than 48 h of age were significantly more sensitive to UVR than adults of the same species. Most likely due to their greater sensitivity to UVR, photo-protective defences are also strongest among the young. Very high concentrations of UV-absorbing compounds (mycosporine-like amino acids, MAAs) have been measured in *C. abyssorum taticus* populations from a UV-transparent high mountain lake, with eggs, nauplii, and young copepodid life stages having the highest contents (Tartarotti et al., 2001; Tartarotti & Sommaruga, 2006). Similar to MAAs, ontogenetic differences were found between nauplii and adult life stages of copepods, the former containing 3–10 times higher carotenoid concentrations (Hairston, 1978).

Previous exposure to UVR, i.e. experience of and acclimation to UVR, is an important factor determining the tolerance of zooplankton to UVR (Siebeck, 1978; Stutzman, 1999; Rautio & Korhola, 2002a; Zellmer et al., 2004). *Daphnia pulex obtusa* from a transparent mountain pond tolerated higher radiation doses than *D. galeata* and *D. longispina* which inhabit darker lowland lakes (Siebeck, 1978). In another study, *D. pulex* that originated from a clear pond were more UV-tolerant than *D. longispina* from a moderately humic and *D. longispina* from a very humic pond (Zellmer et al., 2004). These two studies compared different species of *Daphnia* which could explain the different tolerances to UVR. Other evidence, however, suggests that the same pattern also occurs within one species. Stutzman (1999) showed that populations of *Diaptomus minutus* routinely experiencing high levels of UVR in their natural environment were more tolerant to UVR than those that routinely experience low levels of UVR.

The study of Stutzman (1999) demonstrated that the UVR tolerance of the same population varies seasonally. Because of the high spatial and temporal variability within one species, only results from one lake and from one time can be compared when ranking species-specific UVR tolerances (as in Leech & Williamson, 2000). Studies that have made comparisons between species from different lakes are still valuable but rather than providing data for accurate ranking (as the species are most likely to have different previous UVR acclimation and protection strategies) they show the tremendous plasticity of zooplankton to cope with UVR under different environmental scenarios. Results from a 3-day in situ incubation in ultra-oligotrophic Lake Toncek, Argentina, showed that *Boeckella gracilipes* was highly vulnerable to UV-B and UV-A radiation (Zagarese et al., 1997b). In contrast, in another clear lake, Laguna Negra in the Chilean Andes, *B. gracilipes* was much more UV-tolerant and showed mortality only when exposed for 70 h to UVR (Tartarotti et al., 1999). Other species from this same genus (*B. gibbosa*, *B. antique*, *B. poppei*) have been reported to be highly UV-tolerant (Zagarese et al., 1997a; Rocco et al., 2002). The following conclusion made by Rocco et al. (2002) can be modified to include all zooplankton species: plasticity in UVR tolerance has probably been key to zooplankton success at colonising a great variety of UV environments, ranging from large oligotrophic lakes to ephemeral pools, and from sea level to high-elevation habitats.

Interactive effects of UVR and other environmental variables also modify the response of zooplankton to UVR. Dissolved organic carbon is the most studied variable in association with UVR and its influence is most often positive, arising from the efficient absorbance of UVR. Rautio & Korhola (2002a) showed that zooplankton survival increased > 50 % when DOC doubled from 5 mgC L⁻¹ to 11 mgC L⁻¹. Zagarese et al. (1994) reported a similar reduction in mortality for *Daphnia* populations, as did Cooke et al. (2006) for the fecundity of the copepod *Leptodiatomus ashlandi* when DOC increased (Fig. 3). Food stimulation is another positive effect from the DOC-UV interaction. UVR breaks larger macromolecules into smaller units which are then more readily usable for

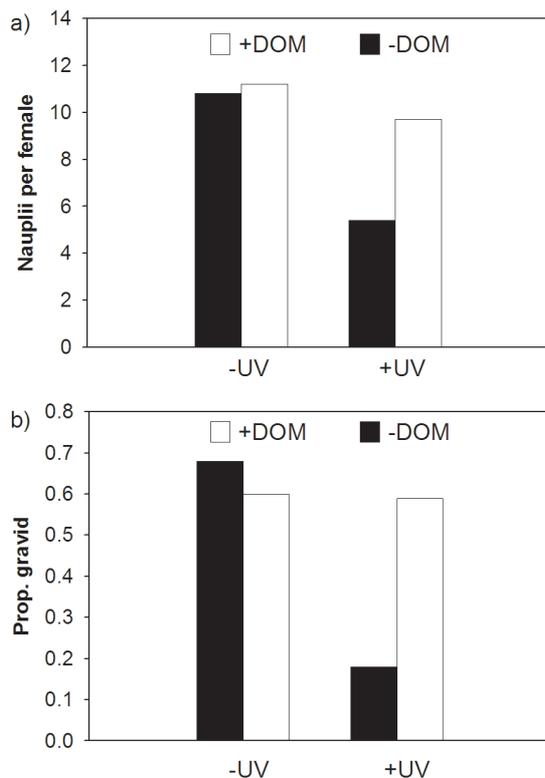


Fig. 3. (a) Mean number of nauplii produced per female *Leptodiatomus ashlandi* and (b) mean proportion of surviving females in the gravid state in +UVR and -UVR treatments with low levels of dissolved organic matter (DOM) (1.0 mg L⁻¹, white bars) and when DOM was added (10.3 mg L⁻¹, black bars). From Cooke et al., 2006.

microorganisms that metabolise DOC. They in turn can be an important nutritional source for zooplankton (Salonen & Hammer, 1986; de Lange et al., 2003). However, UV-irradiated DOC also promotes the formation of ROS that are harmful to zooplankton (Souza et al., 2007). Although no measurements exist for ROS in the zooplankton body, it is generally accepted that zooplankton are exposed to UV-induced ROS, formed either in surface waters of high-DOC lakes (Cooper et al., 1994) or inside the animals' bodies by interaction between sensitive molecules and photons. Activation of photo-reactivation mechanisms, such as increased activity of antioxidant enzymes and the presence of carotenoid pigments, are considered as indices for the presence of ROS (Hessen, 1994; Borgeraas & Hessen, 2002a).

Other environmental variables that have been studied in relation to zooplankton UVR tolerance include temperature, oxygen, nutrients, water hardness, and pH (Borgeraas & Hessen, 2000; Hessen & Alstad Rukke, 2000; Williamson et al., 2001a; Cooke et al., 2006). It has been suggested that UVR is a more important stressor to zooplankton at colder temperatures than at warmer temperatures because enzymatic processes like UVR repair mechanisms (e.g. DNA repair) and detoxification of ROS are slower at colder temperatures (Hessen, 1996; Buma et al., 2001). Some experimental evidence supports this: for example, at colder temperatures, in comparison with warmer temperatures, copepods produced fewer nauplii in the presence of UVR than when UVR was excluded (Cooke et al., 2006). Other studies, however, have shown a different pattern. *Leptodiatomus ashlandi* adult survival was higher in the presence than in the absence of UVR in the cold treatment (Persaud & Williamson, 2005), and survival tests of Borgeraas & Hessen (2000) at different temperatures showed that reduced temperatures significantly increased *Daphnia magna* survival in the presence of UVR. Interactions involving temperature are complex, influencing not only UVR repair mechanisms but also life span, generation time, metabolic activity and indirect influence from the food web. The acclimation of organisms to a certain temperature range is also likely to be a key factor that determines how zooplankton will react to the combination of different UV-temperature interactions. *Daphnia longispina* survival in the +UVR treatment was highest when exposing them to temperatures between 12 °C and 17 °C corresponding to the temperature in their natural habitat. At 6 °C as well as at 20 °C survival was significantly reduced with the highest mortality at 20 °C (Zellmer, personal communication).

Zooplankton UVR tolerance has been reported to be almost unaffected by ambient oxygen (Borgeraas & Hessen, 2000) and nutrient concentrations (Cooke et al., 2006) despite their potential role in ROS stress and in food availability through stimulation of the phytoplankton community. Water hardness, however, may be a major determinant for zooplankton UVR susceptibility among calcium (Ca) demanding zooplankton (Hessen & Alstad Rukke, 2000). Survival of *Daphnia magna*

and *D. tenebrosa* under UVR exposure was strongly reduced at low Ca concentrations commonly found in soft-water localities in Canadian Shield lakes and major parts of Scandinavia (Hessen & Alstad Rukke, 2000). Anthropogenic acidification may also have many adverse effects on zooplankton UVR tolerance. DOC declines with lake acidification and consequently increases UVR penetration (Schindler et al., 1996; Williamson et al., 1996).

UVR damage may also occur via trophic interactions. UVR has been reported to have negative effects on phytoplankton, some species of which provide a source of food to zooplankton, hence alterations in food quantity and quality may suppress zooplankton survival, growth and reproduction (Hessen et al., 1997). Some of the negative algal responses to UVR may, however, be beneficial for zooplankton. Leu et al. (2006) showed that in order to compensate for UVR stress, the chlorophyte *Selenastrum capricornutum* synthesised more polyunsaturated fatty acids (PUFAs) which are essential for zooplankton growth. The algae also increased phosphorus uptake which resulted in more favourable C:P and N:P ratios for zooplankton. Despite these positive UV-induced changes in nutritional quality of *S. capricornutum*, however, no significant effects on zooplankton growth or reproduction were detected (Leu et al., 2006). Other studies have reported negative effects on zooplankton that have been feeding on UV-exposed algae. A decline in growth rate and fecundity in *Daphnia* sp. feeding on UV-irradiated algae has been observed by Scott et al. (1999) and de Lange & van Reeuwijk (2003). Huebner

et al. (2006) recently showed that this decline carries across two *Daphnia* generations. Both phytoplankton quality and quantity influence zooplankton UVR tolerance (Schönberger & Zellmer, 1994; Zellmer, 1996; Zellmer et al., 2004). Increasing food levels improved *Daphnia* survival rates and UV-B pretreatment of the algae enhanced the negative effects in *Daphnia* (Zellmer et al., 2004) (Fig. 4).

Protection mechanisms

Much of the variability in zooplankton responses to UVR is due to the extent the species or the population is able to use protection strategies against UVR (see Hansson & Hylander, 2009a for a review). Zooplankton have several defence mechanisms against UV damage including avoidance, screening, quenching and repair.

Physically moving away from damaging fluxes of UVR by undergoing vertical migration (VM) or staying deep in the water column during the day is a very

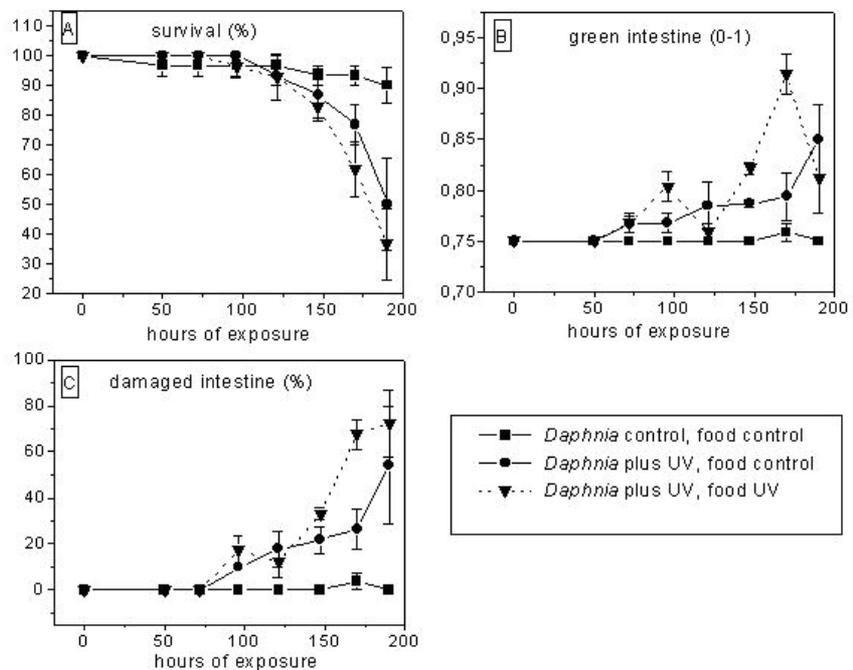


Fig. 4. *Daphnia pulex* a) survival in different UV exposures when fed with and without UVR-pretreated algae, b) proportion of gut that appeared green in color (0 = no green, 1 = entire gut is green), and c) prevalence of damaged intestine (% of live animals). From Zellmer et al. (2004). Copyright regents of the University of Colorado.

effective strategy to minimise UVR exposure. Vertical migration of zooplankton is commonly explained as a strategy to avoid visual predators like fish (Zaret & Suffern, 1976; Stich & Lampert, 1981; Ringelberg, 1991); however, several authors have proposed that VM is a natural response of zooplankton to UVR (e.g. Damkaer, 1982; Hessen, 1993; 1994). Evidence of the important role of UVR in zooplankton vertical distribution was found in the migratory behaviour of zooplankton in habitats devoid of vertebrate predators (Hessen, 1993; Williamson et al., 2001b; Rautio et al., 2003; Aguilera et al., 2006; Kessler et al., 2008). Both laboratory and field experiments demonstrated that downward migration is a common UVR avoidance strategy in cladocerans like *Daphnia* (Storz & Paul, 1998; Leech & Williamson, 2001; Rhode et al., 2001; Leech et al., 2005a, b; Fischer et al., 2006; Hansson et al., 2007; Hansson & Hylander, 2009b). Active UVR avoidance, for example, was experimentally induced in several *Daphnia* clones (Hessen, 1994). UV-B radiation, however, is unlikely to be responsible for the deep vertical distribution during the day, as the main daytime distribution of most zooplankton is close to or below the 10 % attenuation depth of UV-B radiation (Zagarese et al., 1997b). Nevertheless, in transparent subalpine and alpine lakes with few or no fish, UVR has been suggested to be the primary driver in explaining the vertical distribution of zooplankton (Kessler et al., 2008). Those findings and others support the transparency-gradient hypothesis, indicating that UVR is more important than fish predation in determining the vertical distribution of zooplankton in clear lakes (Leech et al., 2005a; Kessler et al., 2008). Several studies have assessed zooplankton response to simultaneous UVR and predator threats (Ringelberg, 1999; Hansson, 2000; Leech & Williamson, 2001; Rautio et al., 2003; Hansson, 2004; Hansson, et al., 2007; Hylander et al., 2009a). A conflicting selective pressure for zooplankton vertical distribution, for instance, was found when exposing *Daphnia* simultaneously to the invertebrate predator *Chaoborus* and UVR (Boeing et al., 2004). Although *Chaoborus* itself does not respond to UVR (detection and/or avoidance) (Persaud et al., 2003), it modified the depth distribution of *Daphnia* relative to UVR (Boeing et al., 2004). A recent experimental

field study by Hansson & Hylander (2009b) confirmed that UV was the major force behind the depth distribution of the zooplankton population (*Daphnia*), while there was no statistically significant effect of fish or interactions between fish and UVR. These responses, however, incur a physiological cost (Stich & Lampert, 1984; Dawidowicz & Loose, 1992) or increase the risk of predatory losses (Stich & Lampert, 1981; Gliwicz, 1986). Zooplankton may use PAR (photosynthetically active radiation) as a proxy for UVR to initiate downward migration, or they may detect changes directly in the UV irradiance. Photoreceptors specific to UV-B have not been described until now, but the cladoceran *Daphnia magna* has a photoreceptor with peak sensitivity in the UV-A wavelength range (348 nm) (Smith & Macagno, 1990). Visual UVR photosensitivity of the compound eye of *Daphnia* was already suggested in the early studies of Koehler (1924) and Merker (1930) as cited in Smith & Macagno (1990). Copepods, however, have often been reported to be less responsive to UVR (Leech & Williamson, 2001; Hansson, 2004; Leech et al., 2005a, b; Fischer et al., 2006), although avoidance of surface waters with higher UVR irradiance has been observed (Alonso et al., 2004). Recent studies show that copepods invest mainly in photo-protective pigmentation and less in VM when exposed to UVR (Hansson et al., 2007; Hylander et al., 2009b). In shallow, highly transparent water bodies, UVR avoidance may not be feasible. Moreover, wind-induced turbulence can result in strong vertical mixing of the water column which is an additional factor that may lower the effectiveness of the avoidance strategy (Zagarese et al., 1998). Thus, organisms living in UV-exposed systems with a small depth refuge need other strategies to receive substantial protection against UVR.

One important UVR defence strategy in zooplankton is the synthesis or accumulation of photo-protective compounds (Fig. 5) acting either as sunscreens or as antioxidants. Among the coloured sunscreens known in zooplankton is melanin, a tan-brown to black cuticular pigment, which is typically found in high-latitude and high-altitude cladocerans such as in *Daphnia* and *Scapholeberis* (Hebert & Emery, 1990; Hessen & Sørensen, 1990; Hobaek & Wolf, 1991; Rautio & Korhola, 2002b;

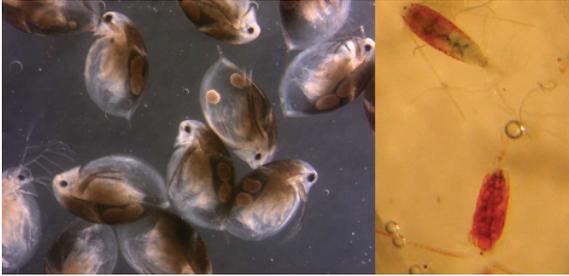


Fig. 5. Pigmented zooplankton. Melanised *Daphnia umbra* (left) and *Eudiaptomus graciloides* with red carotenoids (right) from Kilpisjärvi, Finnish Lapland. Photographs Paavo Junntila and M.R.

Hansson et al., 2007; Rautio et al., 2009). Only recently, melanin was detected in Arctic fairy shrimps (*Artemiopsis stefanssoni* and *Branchinecta paludosa*), although both species lacked the typically characteristic dark coloration (Rautio et al., 2009). In *Daphnia pulex*, for example, melanin concentrations were genetically determined within populations and correlated to UVR sensitivity; pigmented animals survived better than pale individuals (Hessen, 1996). Several studies showed that melanised *Daphnia* have higher UVR tolerance as compared to non-melanised relatives (Luecke & O'Brien, 1983; Hebert & Emery, 1990; Zellmer, 1995; Hessen, 1996; Hessen et al., 1999; Rhode et al., 2001) and that melanisation is reduced when the UVR threat is removed (Luecke & O'Brien, 1983; Hessen, 1996; Hansson et al., 2007; Rautio, 2007). The only deviation from these observations is the recent finding of Connelly et al. (2009) whose *D. middendorffiana* population remained pigmented when kept in the laboratory for six months under PAR only, and was not better protected from UVR than hyaline species. Pigmentation is assumed to be metabolically costly. Melanised *Daphnia* show delayed age at first reproduction and smaller clutch size, resulting in an overall lower growth rate of pigmented individuals compared to non-melanised conspecifics (Weider, 1987; Hessen, 1996). Moreover, after each moult *Daphnia* has to synthesise new melanin since the pigment is shed with the carapace (Hebert & Emery, 1990). This probably explains the failure of melanised clones to compete with transparent ones in less clear waters lacking predators (Hebert & Emery, 1990; Hessen, 1996; Rautio & Korhola, 2002b). Strong seasonal patterns in melanin contents were found

in *Daphnia*. The subarctic cladoceran *D. umbra* synthesised pigments only during the summer months, starting directly after ice out (Rautio & Korhala, 2002b) (Fig. 6). In summary, melanin seems to be synthesised to increase survival of aquatic organisms under harmful UVR despite being energetically costly and increasing vulnerability to visual predators (Hessen, 1996; Hansson, 2000).

A family of intracellular colourless UV-absorbing compounds, mycosporine-like amino acids (MAAs; absorption maxima between 309 nm and 360 nm), has been reported for several hundred species of marine organisms with their distribution ranging from the tropics to polar latitudes (see Karentz, 2001 and Shick & Dunlap, 2002 for reviews). Over the last years, these compounds have been described for several freshwater taxa including copepods, fairy shrimps, *Chaoborus* larvae, rotifers and ciliates (Sommaruga & Garcia-Pichel, 1999; Tartarotti et al., 2001; Gonçalves et al., 2002; Helbling et al., 2002; Rocco et al., 2002; Tartarotti et al., 2004; Moeller et al., 2005; Hansson et al., 2007; Persaud et al., 2007; Sonntag et al., 2007; Obertegger et al., 2008; Nagiller & Sommaruga, 2009; Rautio et al., 2009). Accumulation of MAAs does not seem to be a photo-protective strategy utilised by *Daphnia* or other cladocerans as they lack these compounds or show only trace amounts (Tartarotti et al., 2001; Gonçalves et al., 2002; Tartarotti et al., 2004; Hansson et al., 2007; Persaud et al., 2007). However, UV-absorbing compounds with properties similar to MAAs have been reported for Arctic *Daphnia middendorffiana* (Rautio et al., 2009). Variation in the qualitative and quantitative composition of MAAs in different copepod species has been found in lakes located across an altitude gradient (Central Alps, Austria) (Tartarotti et al., 2001). Apart from altitude, the variability in the MAA concentration of *Cyclops* populations was also strongly correlated with the lake transparency and the depth refuge. Although similar altitude and depth refuge relationships were observed in copepods from a set of Patagonian (Argentina) water bodies, lake transparency explained a lower percentage of the MAA variability compared with that found in Alpine lakes (Tartarotti et al., 2004). In a study by Persaud et al. (2007), copepods from higher UVR lakes located in Argentina, New Zealand

and the USA tended to have higher MAA contents. Similar to melanin in cladocerans, MAA contents in copepods have been shown to vary seasonally in some lakes (Fig. 6). Concentrations of MAAs in *C. abyssorum tatricus* were on average three times higher in the summer compared to ice-cover periods (Tartarotti & Sommaruga, 2006). From these studies it is apparent that MAAs play an important role in UVR protection, and direct evidence of increased UVR tolerance was demonstrated for copepods (*Leptodiatomus minutus*) rich in MAAs (Moeller et al., 2005). Since metazoans seem to lack the putative shikimate acid pathway needed to synthesise MAAs (Bentley, 1990), the UV-absorbing compounds found in zooplankton are thought to have a dietary origin. However, some recent evidence (García et al., 2008) shows that copepods are also able to accumulate these compounds even when maintained on a MAA-free diet. The source of MAAs in these copepods is likely to be the prokaryotic organisms that live on or in the animals (García et al., 2010). Laboratory experiments confirmed the dietary acquisition of MAAs by a freshwater zooplankter, *L. minutus* (Moeller et al., 2005). This experimental work is supported by a field survey showing that MAA concentrations

in late copepodid to adult life stages of *C. abyssorum tatricus* were significantly correlated to those in phytoplankton when considering a time lag of 3–4 weeks between the synthesis and subsequent accumulation of these compounds (Tartarotti & Sommaruga, 2006). However, in laboratory conditions zooplankton MAA accumulation from food has been noted to occur at rates as fast as 3–4 days (Hylander & Jephson, 2010).

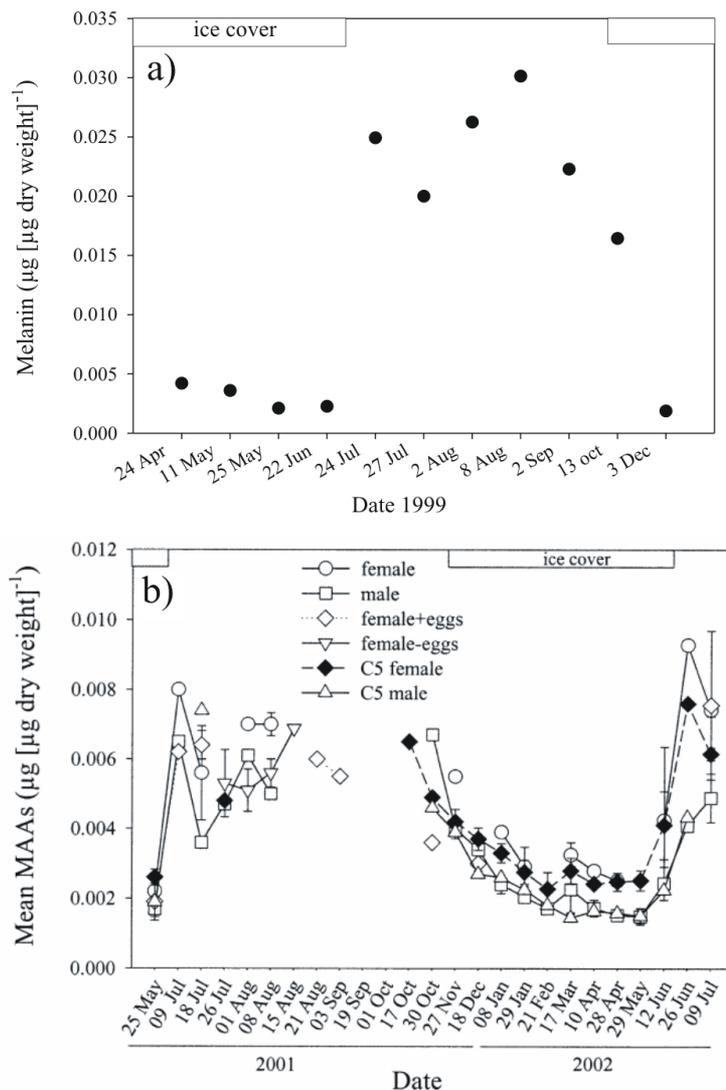


Fig. 6. Seasonal variation of a) melanin in subarctic *Daphnia umbra* and b) mycosporine-like amino acids (MAAs) in alpine *Cyclops abyssorum*. From Rautio & Korhola (2002b) and Tartarotti & Sommaruga (2006). Copyright (2002, 2006) by the American Society of Limnology, Inc.

Another defence mechanism of many organisms against UVR is the possession of antioxidants like carotenoids, which quench photo-oxidative reactions, or enzymes such as superoxide dismutase that can counteract the oxidative nature of peroxides and other radicals. The strikingly red pigmentation of alpine and highly UV-exposed organisms has been known since the early work of Brehm (1938) and Gilchrist & Green (1962). Carotenoids (primarily free or esterified astaxanthin and

canthaxanthin) have been found in several zooplankton taxa like copepods, cladocerans, fairy shrimps, and ciliates (Hairston, 1976; Byron, 1982; Ringelberg et al., 1984; Mostajir et al., 1998; Rautio et al., 2009), however with a greatly variable quantitative and qualitative composition. High carotenoid levels have been reported for copepod species from diverse alpine aquatic systems (Hairston, 1978; Hessen & Sørensen, 1990; Hessen, 1993; Tartarotti et al., 1999; Persaud et al., 2007; Sommaruga, 2010). Although to a much lesser extent, carotenoids are found in cladocerans, particularly in their ovaries and eggs (Siebeck et al., 1994). This discrepancy in carotenoid levels suggests that these compounds have different function in these taxa (Hessen & Sørensen, 1990; Siebeck et al., 1994). Since carotenoids can not be synthesised *de novo* by zooplankton, they are incorporated in the animals' bodies by consumption of algal food (Andersson et al., 2003; Moeller et al., 2005). It has long been known that pigmented copepods are less UV-sensitive when exposed to UVR than unpigmented ones (Byron, 1982; Ringelberg et al., 1984). Furthermore, the content of carotenoids in these animals has been shown to increase with altitude and decrease with lake depth (Byron, 1982). All these findings support the physiological role of carotenoids as photoprotectants, although other functions were proposed such as metabolic benefit or the role as nutritional deposit (Ringelberg & Hallegraeff, 1976; Hairston, 1979; Byron, 1982). Further, observations of carotenoid-rich copepods under the ice in darkness also suggest that carotenoids have multiple roles in zooplankton (Hairston, 1976, 1981). In laboratory experiments, UVR did cause the copepod *Leptodiatomus minutus* to accumulate carotenoids, but only if the diet lacked MAAs, which

they otherwise accumulated instead of carotenoids (Moeller et al., 2005). Exposure to UVR, however, did not result in accumulation of carotenoids in cladocerans; their protective function seems to be restricted to the offspring (Hessen, 1994). High carotenoid levels do not necessarily imply high MAA contents as was shown in red pigmented calanoid copepods from North American lakes (Persaud et al., 2007). Comparable results have been observed in copepods from high altitude Himalayan lakes, concentrations of carotenoids were among the highest reported while content and diversity of MAAs were low (Sommaruga, 2010). Recent studies propose that MAAs and carotenoids are complementary photo-protective compounds in copepods, i.e. one is high when the other is low (Hylander et al., 2009b) (Fig. 7). Both cladocerans and copepods are able to increase or reduce pigmentation (i.e. melanin, carotenoids, and/or MAAs) in response to changed UVR and in response to predators (Hansson, 2000; Hansson, 2004; Tollrian & Heibl, 2004). Moreover, the size of the carotenoid reserves seems to be a plastic trait (van

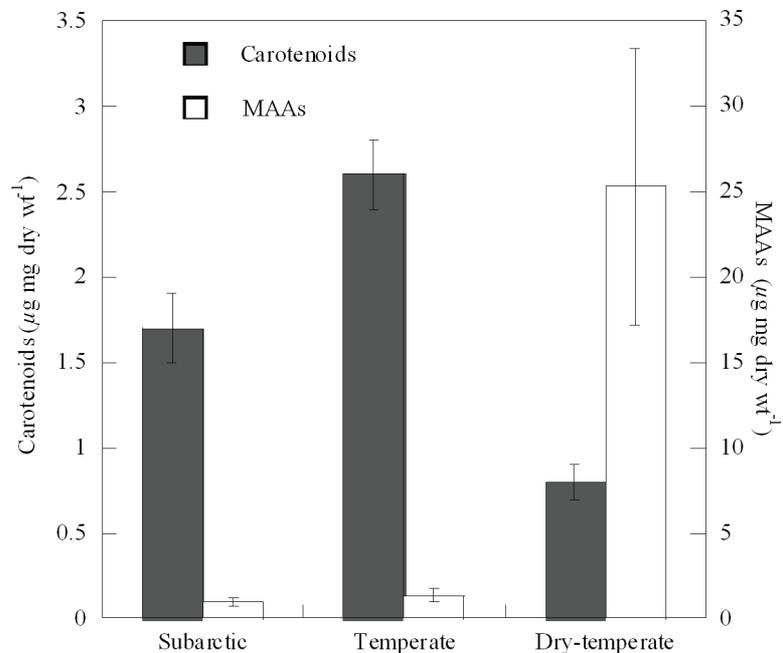


Fig. 7. Concentrations (± 1 SD) of carotenoids ($\mu\text{g mg}^{-1}$ dry wt) and MAAs ($\mu\text{g mg}^{-1}$ dry wt) in subarctic, temperate, and dry-temperate copepods ($n = 13, 12,$ and $12,$ respectively). From Hylander et al. (2009b). Copyright (2009) by the American Society of Limnology, Inc.

der Veen, 2005). A prominent seasonal pattern of higher carotenoid/low MAA content in spring, changing to low carotenoid/higher MAA content in summer, was found in calanoid copepods from relatively UV-transparent lakes (Moeller et al., 2005; Persaud et al., 2007). No clear seasonal pattern of photo-protective compounds (carotenoids and MAAs), however, was observed in the calanoid copepod *Boeckella antiqua* from a fishless shallow pond with low UV transparency (García et al., 2008). High contents of melanin, MAAs, and/or carotenoids probably provide zooplankton with substantial UV protection; however, there are other means that are useful for evading UV damage.

Only recently, scytonemin, an extracellular UV-screening pigment (in vivo absorption maximum at 370 nm) of cyanobacterial origin was detected in two crustacean species, *Daphnia middendorffiana* and the fairy shrimp *Branchinecta paludosa*, from Arctic (Canada, Alaska) freshwater bodies (Rautio et al., 2009). This yellow-brown pigment, which occurs in all sheathed cyanobacterial groups and increases the UVR tolerance of these species (García-Pichel & Castenholz, 1991), has not been previously described in zooplankton. In the same study, four types of UVR protectants (carotenoids, melanins, scytonemin and MAAs) were studied simultaneously. Photoprotectants were detected in all Arctic crustacean species investigated and most populations had multiple pigments, suggesting a combination of defences in these organisms, including broadband screening of UVR and carotenoid quenching of ROS.

One important member of the cellular defence system against oxidative stress is the enzyme catalase (CAT) (Barata et al., 2005). This enzyme mainly assists in detoxifying hydrogen peroxide (H_2O_2) to oxygen and water. Glutathione transferase (GST) is assumed to work primarily at the intracellular level, neutralising peroxidised macromolecules and detoxifying breakdown products after lipid peroxidations (Hiratsuka et al., 1999), while the antioxidant enzyme superoxide-dismutase (SOD) is recognised to eliminate the superoxide radical. Antioxidant enzymes play a significant role in the UVR tolerance of microorganisms, plants, mammalian cells and skin tissues (Murali et al., 1988; Wang & Schellhorn, 1995; Bertling et al.,

1996; Kerb et al., 1997). Relatively little is known about the protective function of these enzymes in pelagic freshwater organisms. In the cladoceran *Daphnia magna*, CAT activity was not affected by UVR, while GST activity was slightly influenced (Borgeraas & Hessen, 2000). Conversely, Vega & Pizarro (2000) found UV-B-increased CAT activity in another *Daphnia* species (*D. longispina*), suggesting an increased response to oxidative stress. Interestingly, no major differences in the concentrations of several enzymes (CAT, GST and SOD) were found between melanised and hyaline organisms in different species and populations of the cladoceran *Daphnia* (Borgeraas & Hessen, 2002b). Among the alpine populations of *D. longispina* examined, however, a significant positive relationship between absorbance (300 nm) of the pond water and CAT activity was found, which in turn could be related to ambient levels of photo-induced H_2O_2 production in these small water bodies (Borgeraas & Hessen, 2002b). A field study by Borgeraas & Hessen (2002a) showed a clear diel cycle in antioxidant enzyme activities in highly UV-exposed alpine *Daphnia*. In the hyaline morph, maxima in CAT and SOD concentrations were found at midday, while there was no elevated activity in the melanic morph at midday; on the contrary, it rather showed a midday minimum in GST contents. The higher enzyme activity in the hyaline *Daphnia* was explained by the need for photoprotection in these individuals compared to the more UV-protected pigmented animals (Borgeraas & Hessen, 2002a). A difference in antioxidant enzyme activity was found between copepods and cladocerans from Andean (Argentina) lakes (Souza et al., 2007). The CAT activity was significantly higher (4–5-fold) in the cladoceran *Ceriodaphnia dubia* than in the copepod *Boeckella gracilipes*, suggesting a differential importance of this mechanism probably associated with the absence of MAAs in cladocerans. The GST activity was similar in both crustacean groups; this enzyme detoxifies reactive species from different origins, this also including those not necessarily associated with UVR exposure. A comparison of enzyme activity in *B. gracilipes* populations from lakes of varying DOC levels showed variation in GST but not in CAT activity. The authors speculate that high GST activity was driven by both high (toxic-

derived photoproducts) and low (increases in H₂O₂) DOC concentrations (Souza et al., 2007). Contrasting enzyme patterns were found in Arctic *Daphnia* along gradients of DOC and UVR exposure (Hessen et al., 2002). Activities of CAT were lower at low DOC, while the contrary was observed for GST. A negative relationship between CAT and solar radiation was found for the different DOC contents, indicating inhibition or inactivation of this enzyme by UVR, whereas there were no such effects in GST activities. Balseiro et al. (2008) found that low food quality (low P:C ratio) decreased the antioxidant response to UVR in *Daphnia*. The activities of GST and CAT were significantly affected by low food quality with strongly decreased enzyme activity in response to UVR for both enzymes.

Highly conserved polypeptides known as stress or heat shock proteins (Hsps) (see Sanders, 1993 and Feder & Hofmann, 1999 for reviews) may have physiological functions related to UVR protection. These proteins play an important role in maintaining protein homeostasis, and they act as molecular chaperones to stabilise and refold denatured proteins (Feder & Hofmann, 1999). Furthermore, the rapid up-regulation of heat shock proteins after a sublethal event can induce stress tolerance and protection against a subsequent stress. The most abundant and widely studied group of these chaperones is the 70 kDa heat shock protein family including constitutive (Hsc70) and stress-inducible forms (Hsp70). Induction of Hsps has been described in response to a variety of stresses including heat, hypoxia, toxins and UVR. While in mammalian cells the up-regulation of Hsps has been recognised as part of an adaptive cellular UV-protective mechanism (Trautinger et al., 1996), studies on the role of UVR in the synthesis of Hsps in aquatic organisms are limited. Induction of Hsps by UVR was found in UV-sensitive (but not in UV-tolerant) marine diatoms (Dohler et al., 1995), and in sea urchin embryos (Bonaventura et al., 2005, 2006), while responses in fish appear to be species-specific (Vehniäinen et al., 2003; Häkkinen et al., 2004). In the marine copepod *Acartia tonsa*, general protein synthesis was suppressed by high UVR intensities, while levels of constitutively expressed 70 kDa heat-shock proteins increased (Tartarotti & Torres, 2009). High incident solar radiation increased the

levels of Hsp70 in adult females of the freshwater copepod *Cyclops abyssorum taticus* (Tartarotti et al., unpublished data). Although this copepod species is very UV-resistant in terms of mortality (Tartarotti et al., 1999), at a sublethal molecular level female copepods seem to be more responsive than younger life stages. The rapid increase (within hours) in stress protein levels might be part of the suite of molecular and biochemical processes that can promote survival in highly UV-exposed aquatic organisms.

Recovery

When protective measures are not sufficient, zooplankton can repair UV-induced damage to some extent. Organisms generally have some kind of DNA repair system. In zooplankton there are primarily two repair processes: nucleotide excision repair (NER, dark repair) and photo-enzymatic repair (PER, light repair). Nucleotide excision repair is an energetically costly complex multi-protein, multi-step pathway, and is found in almost all taxa without being specific to UV-induced DNA damage (Mitchell & Karentz, 1993; Sancar, 1994a; Sinha & Häder, 2002), while PER uses the enzyme photolyase in the presence of longer wavelength UV-A and PAR (UV-A and PAR = photorepair radiation). This mechanism can reverse pyrimidine dimers (Sutherland, 1981; Mitchell & Karentz, 1993), and since it is a single-enzymatic process driven by photorepair radiation, it is less costly to the cell than is NER (MacFadyen et al., 2004). Although PER is specific to UV-induced DNA damage, it is not present in all taxa (Sancar, 1994b). The studies focusing on repair mechanisms in zooplankton show differences among taxa, species, and life stages (Siebeck & Böhm, 1991; Zagarese et al., 1997a; Grad et al., 2001, 2003; Gonçalves et al., 2002; Rocco et al., 2002; MacFadyen et al., 2004; Ramos-Jiliberto et al., 2004; Connelly et al., 2009). Survival of UV-stressed *Daphnia* increased in the presence of photo-repair radiation (Siebeck & Böhm, 1991; Grad et al., 2001; Williamson et al., 2001a, 2002; Huebner et al., 2006); this light-induced repair was assumed to rely on PER of DNA damage (Fig. 8). A study by MacFadyen et al. (2004) provided evidence of enzymatic photorepair in *Daphnia* at the molecular level.

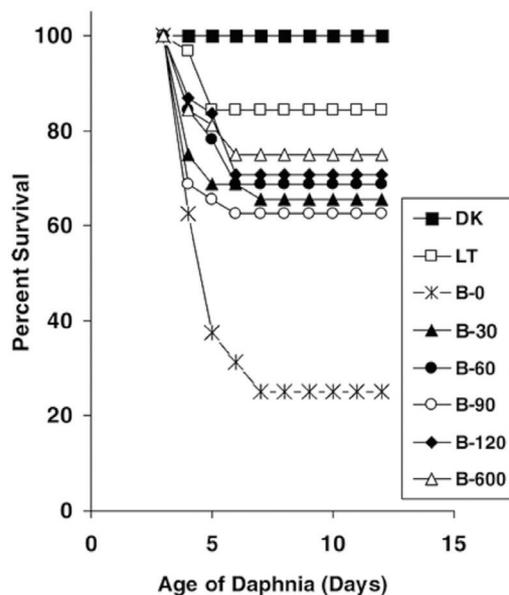


Fig. 8. Mortality of *Daphnia magna* after a 6 h UV-B exposure followed by variable durations of photorepair radiation (UV-A and PAR). DK, LT: dark and light controls. B-0 B-600: UV-B exposure followed by 0–600 min of photorepair radiation. From Huebner et al. (2006).

PER enhanced the repair of cytotoxic photoproducts (cyclobutane pyrimidine dimers, CPDs, and pyrimidine (6–4) pyrimidone photoproducts, (6–4)PDs), and was likely to be responsible for increases in *Daphnia* survival following UV-B exposure. Other zooplankters such as the rotifer *Asplanchna girodi* seem to utilise dark repair and have little to no PER (Sawada & Enesco, 1984; Grad et al., 2001). In juvenile *A. girodi*, however, evidence of photoreactivation has been found (Williamson et al., 2002; Grad et al., 2003). The importance of repair processes in copepods is not well understood. Zagarese et al. (1997a) found that photorepair accounted for the relatively high UV-B tolerance in red *Boeckella gibbosa*, while little evidence of PER was found in *Boeckella gracilipes* (Zagarese et al., 1997a; Tartarotti et al., 2000). Both the cyclopoid copepod *Metacyclops mendocinus* and the calanoid copepod *Leptodiaptomus minutus* showed high efficiency for photorepairing UV-B-induced DNA damage (Gonçalves et al., 2002; Williamson et al., 2002). PER and NER are temperature-dependent mechanisms (i.e. greater repair at higher temperatures), thus zooplankton such as *Daphnia* that rely heavily on DNA

repair may be less able to survive high UVR intensities in low temperature environments (Williamson et al., 2002; MacFadyen et al., 2004). Surprisingly, when exposing four different *Daphnia* species to a single acute UV-B dose, higher survival and repair rates were found for the lower experimental temperature (10 °C compared to 20 °C), indicating that the enhanced rate of PER at the lower temperature contributed significantly to the recovery of these organisms (Connelly et al., 2009). The same authors confirm that photorepair is the primary mechanism to remove DNA lesions in *Daphnia*.

Net community impact imposed by UV

At the species level, the net UV stress and damage imposed by UV is defined by the combination of photochemical degradation and the energetic costs of photoprotection (Vincent & Neale, 2000). The studies focusing on community responses show that with more interactions between species the responses to UVR become less clear (reviewed by Sommaruga, 2003).

De Lange et al. (1999) were not able to detect any changes in the abundance, species composition or biovolume of the phytoplankton or zooplankton communities, nor in the periphyton or macroinvertebrate community during an eight-week microcosm experiment. Cabrera et al. (1997) studied phytoplankton and zooplankton responses to UVR in a high-altitude Andean lake for a 30-day period in three different years. They showed different responses to different species ranging from positive, no effects, to negative effects. They concluded that although different species had different tolerances to UVR, the population fluctuations were most dependent on life cycles and the period of time the organisms were exposed to UVR. Vinebrooke & Leavitt (1999) studied littoral communities during a one-month period and showed that zoobenthos and zooplankton biomass were unaffected by UVR but species composition changed. The 4-month mesocosm study by Hylander & Hansson (2010) concluded that zooplankton communities were well buffered in response to UVR changes, due to efficient defence mechanisms, suggesting that future potential increases

in UVR may have only a small impact on zooplankton population dynamics and community composition.

The above studies have extended the UV impact studies from single species to communities, and the study period to weeks and months from the more common day to week duration of an experiment. However, even a month scale is still a short period in terms of ecosystem dynamics, and precludes the detection of potential UV effects on the reproductive success of copepods, many of which require more than one year to complete a life cycle (Elgmork & Eie, 1989). Vinebrooke & Leavitt (2005) discuss how extrapolation of UVR results from small-scale laboratory and field experiments to larger spatial and temporal scales is a challenge. Damages in cell structures and avoidance response may take only hours to detect, but changes in zooplankton community composition and functioning may be seen only after months or years, while changes in optical properties of lakes may take decades.

There exist, however, some field data on zooplankton distribution in relation to UVR which indicate that zooplankton communities in lakes differ according to the presence of UVR in the water. A dataset that includes the above mentioned longer time-scales comes from Williamson et al. (2001b). They investigated changes in UVR attenuation and zooplankton community structure in a deglaciation chronosequence in Alaska. Terrestrial succession in the catchment area had resulted in increasing lake DOC content over time and decreases in UV attenuation depth. This attenuation depth (1 % of surface irradiance at 320 nm) was at 14 m in the youngest lake (10 years old), but only 0.6 m in the oldest (90 years old). Zooplankton community structure also changed across lakes of different ages. The pelagic cladocerans *Ceriodaphnia quadrangula* and *Bosmina longirostris* and the rotifer *Asplanchna priodonta* were absent from the clearest lakes, and it was shown that this was due to higher UVR in these lakes.

Further evidence of UVR effects on zooplankton community structure comes from a study of shallow ponds (<0.5 m) in Finnish Lapland (Rautio & Korhola, 2002b) and from Patagonian lakes (Marinone et al., 2006). *Daphnia* in Finnish ponds were absent when DOC was < 5 mgC L⁻¹, most likely because the ponds were too shallow to provide

refuge from UVR. In Patagonia, zooplankton species richness and diversity decreased with high water column irradiance in lakes. Molot et al. (2004) also studied the distribution of zooplankton (*Daphnia*) in lakes in relation to UVR. They, however, showed that in >250 Canadian lakes *Daphnia* distribution was not restricted by UV-B but their lake set did not include many very clear and shallow systems.

Most UVR studies to date have been done using a small number of species. Only about 50 crustacean zooplankton species have been studied for their UVR tolerance and 16 of these are from the genus *Daphnia* (data from papers referred in this review). More than half of all freshwater zooplankton UVR studies have been conducted with the genus *Daphnia*. Most studied species, including *Daphnia*, are also pelagic which skews the results. The vast number of littoral and benthic zooplankton, mostly belonging to Cladocera, in lakes with abundant littoral vegetation may experience a more sheltered and therefore more UV-protected environment than the pelagic zooplankton. Their need to respond to UVR is likely to be different and smaller than that of pelagic species. The few published results of the response of littoral communities to UVR are, however, contradictory. Vinebrooke & Leavitt (1999) showed that responses were taxon- and habitat-specific. UVR did not adversely affect motile taxa that could seek refuge in sediments but rotifers were significantly suppressed in UVR treatments. In another study (Cabrera et al., 1997), a common littoral cladoceran *Chydorus sphaericus* and the rotifer *Lepadella* were strongly inhibited by UV-B. However, in this study the zooplankton was kept in mesocosms near the surface and the species were not able to seek the shelter they would have in their natural environment.

Conclusions

Laboratory and short-term mesocosm experiments have convincingly shown that most species do better when UVR is excluded from the environment; however, the increased system complexity at the community level may compensate for some of the negative UVR effects observed at species level, or completely reverse species success. A UV-tolerant species can be excluded when the habitat

becomes shielded from UVR if its superior competitor is released from UVR control (Jokiel, 1980). Furthermore, some longer-term mesocosm experiments and field observations have indicated no or very little zooplankton community response to UVR. However, some systems may be strongly controlled by UVR, showing that interactions at community level may vary greatly among systems. Vinebrooke & Leavitt (1999) have suggested that the importance of UVR for lake organisms is influenced by the system productivity and presence of other stressors. UVR effects may be more pronounced in extreme (i.e. alpine and polar) and anthropogenically-stressed (i.e. acidified) lakes in which abiotic regulation of communities is common. In more productive systems, increased biotic regulation of food-web structure may reduce the importance of direct UVR effects. Some evidence for this can be seen when studies in productive Dutch lakes (de Lange et al., 1999) were compared with studies in oligotrophic Andean lakes (Cabrera et al., 1997), with the latter community changing more in the UVR treatment.

The variability in zooplankton UVR responses may also result from the seasonally and ontogenetically changing inherent properties of different species, and create inconsistency among results. The physiological and developmental state of an organism and its prior history with UVR, as well as other environmental factors such as temperature, set limits or opportunities for the induction of different UV protections. For instance, although it is generally accepted that compounds such as MAAs and various pigments (e.g. melanin, carotenoids) have photo-protective roles, and should be synthesised or accumulated in zooplankton in the presence of UVR, it is also known that these compounds sometimes occur in the absence of UVR under the ice in winter (Hairston, 1979; Tartarotti & Sommaruga, 2006). Maybe they have been accumulated in advance to provide photoprotection at the time of ice break-up but it is likely that many mechanisms that have UV-protective effects are also induced for other ecological reasons. Carotenoids may have an important function in display and as they are bound to lipids they are likely to play a role in zooplankton energy metabolism, especially in low food winter conditions. Vertical migration is

a well-known behavioural response induced by fish, perhaps more often than by UVR. Furthermore, many photo-protective strategies may also be complementary (Hylander et al., 2009b) and, hence, cannot be detected in all UVR situations. Lack of vertical migration in copepods in the absence of visually hunting predators may, for example, be explained by their high concentration of MAAs that allows an efficient enough shield from UVR for the copepods to stay in surface waters. Zooplankton may also use a broad band strategy to cope with UVR (Rautio et al., 2009). Species that accumulate multiple photo-protective pigments may have a lower concentration of a certain pigment for a given irradiance than its conspecific that uses a single protective strategy. All above examples create inconsistency in UVR responses and without measuring multiple photo-protective strategies may underestimate the UVR impact on zooplankton.

Inconsistencies are also found when studying the effect of temperature on zooplankton UVR tolerance. Many papers have stated that cold lake water has an effect on the efficiency of species recovery from UVR damage because with lower temperatures enzymatic reactions should slow down, including the repair rate of photochemical damage. Some recent studies, however, have shown that in some systems enzyme activities are higher in the cold (Connelly et al., 2009) and species survival when exposed to UVR is also better in colder water (Borgeraas & Hessen, 2000). Some of these variations can be explained by scale differences. In some studies the temperature range tested has been 15 °C to 25 °C while in others it has been 5 °C to 15 °C. It is also very likely that the temperature in the species' natural habitat has an influence. As the natural distribution of *Daphnia middendorffiana* is restricted to lakes with temperature < 15 °C (Patalas, 1990), it should not be a surprise that it tolerates UVR better in + 10 °C than in + 20 °C (Connelly et al., 2009).

To summarise, the relationship between UVR and the response of zooplankton is well documented for many damage (decreased survival and fecundity, reduced growth rates and offspring production) and protection (vertical migration, pigments, antioxidant enzymes) mechanisms, and there occurs a general consensus that

UVR induces important behavioural or physiological responses in zooplankton. However, the accurate quantification of responses is more demanding given the range of variability in responses at species level, and especially the system complexity in natural communities which may either amplify or reduce direct UVR effects. The recent discoveries about the potential importance of heat shock proteins and scytonemin in zooplankton UVR protection, and the evidence that MAAs in zooplankton are not only accumulated from food but come also from associated bacteria, suggest that we do not yet know everything about the UV–zooplankton relationship. More studies are needed on both species and ecosystem levels to better understand the drivers that determine the multiple interactions in ecosystem responses to UVR, and to better predict how zooplankton respond to increases in UVR from climate change. Given the presence of UVR on the Earth since the beginning of life, and first in substantially higher intensities than presently, we predict that the diverse protection strategies observed in zooplankton may be enough to allow broad species distributions in future even in the clearest, most UV-exposed sites.

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