



Long-term changes in pigmentation of arctic *Daphnia* provide potential for reconstructing aquatic UV exposure



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ARTICLE INFO

Article history:

Received 23 March 2016

Received in revised form

17 May 2016

Accepted 17 May 2016

Keywords:

Arctic lakes
Fossil pigments
Paleolimnology
UV radiation
Zooplankton

ABSTRACT

Despite the biologically damaging impacts of solar ultraviolet radiation (UV) in nature, little is known about its natural variability, forcing mechanisms, and long-term effects on ecosystems and organisms. Arctic zooplankton, for example the aquatic keystone genus *Daphnia* (Crustacea, Cladocera) responds to biologically damaging UV by utilizing photoprotective strategies, including pigmentation. We examined the preservation and content of UV-screening pigments in fossil *Daphnia* remains (ephippia) in two arctic lake sediment cores from Cornwallis Island (Lake R1), Canada, and Spitsbergen (Lake Fugledammen), Svalbard. The aims were to document changes in the degree of UV-protective pigmentation throughout the past centuries, elucidate the adaptive responses of zooplankton to long-term variations in UV exposure, and estimate the potential of fossil zooplankton pigments in reconstructing aquatic UV regimes. The spectroscopic absorbance measurements of fossil *Daphnia* ephippia under UV (280–400 nm) and visible light (400–700 nm) spectral ranges indicated that melanin (absorbance maxima at UV wavebands 280–350 nm) and carotenoids (absorbance maxima at 400–450 nm) pigments were preserved in the ephippia in both sediment cores. Downcore measurements of the most important UV-protective pigment melanin (absorbance measured at 305 and 340 nm) showed marked long-term variations in the degree of melanisation. These variations likely represented long-term trends in aquatic UV exposure and were positively related with solar radiation intensity. The corresponding trends in melanisation and solar activity were disrupted at the turn of the 20th century in R1, but remained as strong in Fugledammen. The reversed trends in the R1 core were simultaneous with a significant aquatic community reorganization taking place in the lake, suggesting that recent environmental changes, likely related to climate warming had a local effect on pigmentation strategies. This time horizon is also concurrent with previously recorded major ecological shifts in circumpolar lakes when human induced changes in ecological processes of sensitive arctic ecosystems started to occur. The current centennial record of UV-induced melanisation of sedimentary *Daphnia* ephippia presents unique reference material for assessing UV impacts in arctic aquatic ecosystems before human influence and during the 20th century climate change and provides potential for assessing past aquatic UV regimes.

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1. Introduction

UV radiation (UV), the highly energetic waveband (280–400 nm) of solar irradiance, poses a significant threats to sensitive high latitude aquatic ecosystems, since it has many biologically deleterious effects. High underwater UV results in changes in productivity and species composition, and it ultimately alters

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ecosystem structure and functioning and biogeochemical cycles (Perin and Lean, 2004; Häder et al., 2015). Incident UV radiation is no longer increasing due to stratospheric ozone depletion, and a slow return to pre-1980 stratospheric ozone levels is expected in the coming decades. However, the exposure to UV in lakes continues to be altered by climate change, which will modify aquatic UV regimes (Williamson et al., 2014; Häder et al., 2015), as it generally results in longer ice-free season that consequently impacts primary production, lake-water transparency through dissolved organic carbon (DOC), and underwater UV exposure. Although increased UV is deemed as a serious environmental hazard and a threat to human health (ACIA, 2005), there are only a few paleolimnological records on natural UV fluctuations before human impact (Leavitt et al., 1997, 2003; Pienitz and Vincent, 2000; Hodgson et al., 2005; Verleyen et al., 2005). These previous studies have used sedimentary components related to phytoplankton and primary producers (i.e. diatoms and algal and cyanobacterial pigments) to infer lakes' UV exposure.

Cladocerans (Crustacea: Cladocera) of the genus *Daphnia* are an important group of zooplankton in arctic lakes and ponds, which are typically low-DOC systems and exhibit strong UV transparency. *Daphnia* are negatively affected by high intensities of underwater UV (Rautio and Korhola, 2002) but they possess multiple behavioral and physiological coping mechanisms against it (Rhode et al., 2001; Hansson et al., 2007). Among these, photoprotective pigmentation is of high significance in shallow and transparent arctic waters (Rautio et al., 2009; Rautio and Tartarotti, 2010) because the systems usually lack deep-water or vegetative UV refugia and are exposed to a long period of solar radiation during the polar summer. Most common UV protective pigments of arctic zooplankton include carotenoids, melanins, and scytonemin that induce red, brown, or black coloration (Hessen, 1996; Rautio et al., 2009). Of the zooplankton, cladocerans are able to synthesize melanin (Rautio and Korhola, 2002), whereas other photoprotectants are derived from phytoplankton or benthic food sources (Rautio et al., 2009). The photoprotective compounds increase the survival of zooplankton under intensive UV (Hebert and Emery, 1990; Hessen et al., 1999; Rautio and Korhola, 2002) but pigment synthesis is physiologically costly. There always occurs a tradeoff between the costs of pigmentation and threats of UV damage and fish predation as fish hunt the most pigmented individuals (Sægrov et al., 1996; Hansson, 2000).

It has been suggested that fossil UV-protective pigments (melanin) in sedimentary cladoceran remains provide a useful tool for estimating past UV regimes, since melanin can be preserved in ancient (up to 10,000 years old) cladoceran carapaces and ephippia and its abundance is likely attributable to past underwater UV regimes (Rautio and Nevalainen, 2013; Nevalainen and Rautio, 2014; Nevalainen et al., 2015a). In the current study, we determined the presence of UV-screening pigments and their long-term variation in fossil *Daphnia* ephippia extracted from two high arctic lake sediment sequences. The specific aims were to elucidate the adaptive responses of zooplankton to long-term variations in aquatic UV exposure, examine the usability of fossil zooplankton pigments in reconstructing past UV radiation regimes in UV sensitive arctic freshwater lakes, and evaluate the general long-term controls and impacts of natural UV fluctuations with respect to 20th century environmental changes. We hypothesize that the selected arctic study lakes, being small and shallow, are highly sensitive to UV and that their *Daphnia* populations are responsive to changes in underwater UV exposure allowing us to infer past underwater UV regimes. Many of the potential confounding factors that can de-couple the relationship between *Daphnia* pigmentation and UV, e.g. the presence of visual predators, are not operating in these study systems making them ideal to examine long-term

changes in underwater UV.

2. Material and methods

The study sites include two small and shallow lakes (R1 and Fugledammen) in the High Arctic (Fig. 1). Lake R1 is located in Resolute Bay of Cornwallis Island, Canada, and Lake Fugledammen is located in the Hornsund area of southern Spitsbergen in Svalbard, Norway. Limnological and geographical details of the lakes are provided in Table 1. A lacustrine sediment core from R1 was sampled with a Glew gravity corer from a small boat during summer 2003 and the retrieved sediment section (8.4 cm) was sectioned in situ at 0.2-cm intervals. A parallel 7.0 cm sediment core was also sampled from near the sampling point of the main core. A 100-cm core from Fugledammen was sampled with a Russian peat corer in summer 2013. The loose and undecomposed surface sediment was combined into a single subsample following 2-cm interval subsampling for the rest of the core.

The sediment cores were dated using ^{137}Cs and ^{210}Pb radiometric dating methods (Appleby, 2001) at the Radiochronology Laboratory of the Centre for Northern Studies (CEN), Laval University (Québec, Canada), with a High-Purity Germanium detector. Dates and sedimentation rates were obtained by unsupported ^{210}Pb (through decay of ^{222}Rn in the atmosphere), which represents the difference between total (measured) and supported (from ^{226}Ra decay) ^{210}Pb . The age-depth model for the R1 core was constructed based on CF-CS (constant flux and constant sedimentation) model. The activities were very low throughout the top section of the core (Fig. 2A), the age-depth model estimated that core depth 1.2 cm corresponds to ca. 1900 and 0.4 cm to 1965 CE (Fig. 2B). Below 1.4 cm, the activities were too low to be reliably used for age estimates. The selection of a simple CF-CS model was based on continuous but very slow rate of sedimentation in Lake R1 with only the uppermost ca. 1 cm having an elevated ^{210}Pb activity (Fig. 2). We believe that inconsistencies between different models are insignificant. Typical for arctic sediments, no terrestrial or aquatic macrofossils were found to provide ^{14}C dates from the lower parts of the core to approximate ages. Sedimentation rate in the top core varied between 0.010 and 0.016 cm yr^{-1} and accordingly, 0.01 cm yr^{-1} sedimentation rate was used to evaluate approximate ages for the pre-1900 CE sediment sections, resulting in an age estimate of 1200 CE for the core bottom. R1 basin is very small and shallow with a plain catchment relief and slow recent sedimentation rate (Fig. 2) and therefore we suspect it not to have

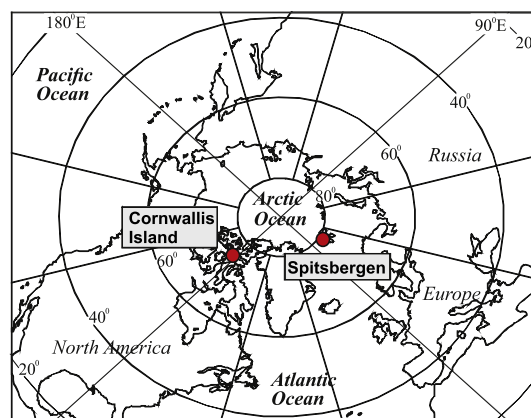


Fig. 1. Map of the study sites. Location of the study lakes R1 (Cornwallis Island, Canada) and Fugledammen (Spitsbergen, Norway) in the Arctic are marked with red dots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Study lakes and their geographical and limnological details. Attenuation coefficients (K_d) for UV wavelengths (280–400 nm) were calculated following Laurion et al. (1997), where dissolved organic carbon for Fugledammen was estimated to be 1 mg L^{-1} . Cumulative July surface UV irradiances (E0) were calculated using the FASTTRT model (Engelsen and Kylling, 2005) and underwater (i.e. mid water column at 1 m depth = Ez) UV doses were calculated with the formula $Ez = E0 \exp(-Kd \cdot z)$.

	R1	Fugledammen
Location	Cornwallis Island	Spitsbergen
Taxon	<i>D. middendorffiana</i>	<i>D. pulex</i> -gr.
Vegetation	Arctic desert	Arctic desert
Latitude	74°25' N	77°00' N
Longitude	95°00' W	15°52' E
Altitude (m a.s.l.)	10	10
Depth (m)	1.5	2.0
DOC (mg L^{-1})	1.7	<2.0
K_d (m^{-1})	3.46	2.16
Surface UV irradiance (mV m^{-2})	3323	7479
Underwater UV dose (mV m^{-2})	104	859

experienced any major changes in sedimentation patterns in the near past. However, our approximation of the past ages of the R1 core subsamples below the horizon of unsupported ^{210}Pb should be considered as cautious estimates. The age estimates for the Fugledammen core are based on a previously published age-depth model (Luoto et al., 2015).

Invertebrate community composition and diatom assemblages were analyzed to provide proxy data of the aquatic community structure in the R1 core. All encountered cladoceran exoskeletal body parts (ephippia, carapaces, headshields), head capsules of Chironomidae, and *Nostoc* balls (i.e. spherical cyanobacterial colonies of green-yellow color, evaluated as present or abundant) were handpicked from the sieved sediment-water solution under a binocular microscope. Diatom samples were prepared from the parallel core with standard methods (Battarbee et al., 2001). In the Fugledammen core, previously available data on *Daphnia* relative abundance was utilized (Luoto et al., 2015).

Fossil *Daphnia* ephippia were extracted from the lake sediment cores by washing the samples on a $100\text{-}\mu\text{m}$ mesh under running tap water. All encountered ephippia were hand-picked with fine forceps under a binocular microscope (R1 $N = 1\text{--}11$ and Fugledammen $N = 1\text{--}10$ in the samples where *Daphnia* occurred). The spectral

absorbance values were measured with a Shimadzu UV/VIS-2401PC dual-beam spectrophotometer (Shimadzu Corporation, Kyoto, Japan) following the carapace absorbance method (Nevalainen and Rautio, 2014) from randomly selected ephippia. The ephippia were attached individually to a specifically designed adapter and their absorbance was measured under the visible light and UV wavelengths between 700 and 280 nm (1-nm intervals). Depending on the visually observed pigmentations, i.e. how strong the black-brown coloration was, single (darker) or double (lighter) valves were measured. For stratigraphic downcore absorbance measurements, all available ephippia were extracted from the sediment subsections in cores R1 and Fugledammen. Ephippia were measured for their UV absorbance under 340 and 305 nm using the method described above (Nevalainen and Rautio, 2014). Mean absorbance values (with standard errors) were used when more than one ephippium was measured. All absorbance measurements were performed from corresponding points at the anterior-dorsal part of ephippia.

Long-term record of sunspot numbers as indicator for solar activity (Solanki et al., 2004) and UV intensity was used in comparison with the ephippia UV absorbance records. The sunspot data was obtained through the NOAA Paleoclimatology website (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data>). Relationships between UV absorbance and sunspots through time were tested with Pearson product-moment correlation coefficient (r) and the level of statistical significance (p).

3. Results and discussion

3.1. Photoprotective pigments in fossil ephippia

Spectral absorbance of fossil *Daphnia* remains from lakes R1 and Fugledammen showed highest absorbance values (up to maximum absorbance at 5 absorbance units) under UV wavelengths indicating the preservation of melanin pigment in the remains (Fig. 3A) that was also visually observable from the ephippia (Fig. 3B). The absorbance spectra were highly similar to previously published results of melanin in fossil cladoceran remains and to that of synthetic melanin (Rautio and Nevalainen, 2013; Nevalainen and Rautio, 2014) showing an absorbance maximum under the shortest UV wavelengths (<350 nm). The examined lakes are very

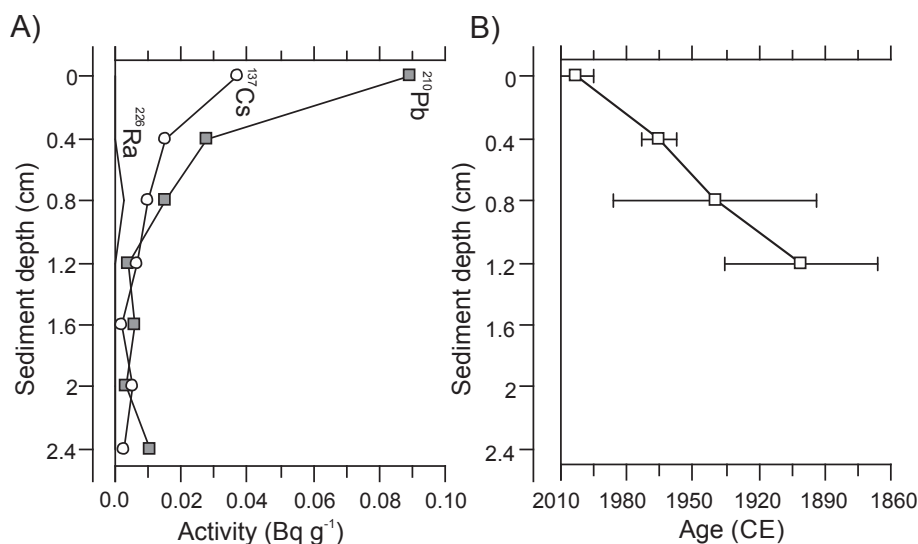


Fig. 2. Dating of the R1 core. A) Total specific activity of ^{210}Pb , ^{226}Ra , ^{137}Cs in the top most samples of the sediment core from R1 in Cornwallis Island, Canada. B) Age-depth model for the R1 core top based on CF-CS model of unsupported ^{210}Pb , where the solid black line indicates reliable age estimates.

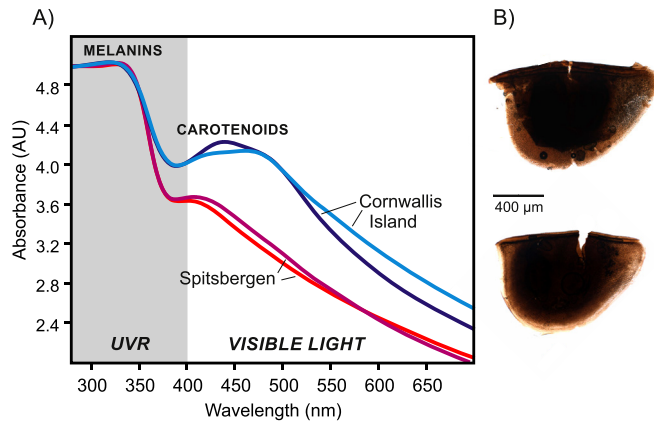


Fig. 3. Absorbance spectra and ephippia. A) *Daphnia* ephippia absorbance spectra (as relative absorbance units, AU) under wavebands 280–400 nm (UV) and 400–700 nm (visible light) in lakes R1 (Cornwallis Island) from sediment depth 0.2 and 1.4 cm and Fugledammen (Spitsbergen) from sediment depths 5 and 26 cm. Absorbance values are smoothed with smoothing spline models (1.5 and 1.0 for R1 and Fugledammen, respectively) and illustrated as double valve measurements for R1 and single valve measurements for Fugledammen to standardize the UV absorbance scale. B) Microphotographs of fossil *Daphnia* ephippia from R1 (top) and Fugledammen (bottom).

shallow (<1 m), lacking deep water or vegetative UV refugia, and low in UV-attenuating DOC (Table 1). Consequently, their water columns are highly transparent making the habitats vulnerable to high underwater UV doses (Table 1) that likely forces *Daphnia* to utilize melanisation as a photoprotective mechanism (Rautio and Korhola, 2002). The high degree of melanisation of the current *Daphnia* fossils (Fig. 3) is also consistent with the previous knowledge on *Daphnia* pigmentation in the Arctic (Hessen et al., 1999; Rautio and Korhola, 2002) and other UV-exposed regions, such as high latitude lakes (Sommaruga, 2010).

The examined *Daphnia* ephippia showed a consistent secondary minor absorbance maxima under 400–450 nm (Fig. 3A) corresponding to that of carotenoid pigments (Rowan, 1989). The absorbance spectra therefore suggest, for the first time, that carotenoids may be preserved in the remains. Carotenoids are important in photoprotection and they are accumulated into zooplankton from their variable planktonic and benthic food sources. Generally, carotenoids are common in northern cladoceran populations, but there is a significant geographical segregation in carotenoid composition between subarctic and high arctic regions (Rautio et al., 2009). Since carotenoids accumulate into the zooplankton from their food sources, they may give some indications on the feeding habits of zooplankton and autotrophic communities. Accordingly, measuring spectral absorbance of arctic cladoceran remains under carotenoid absorbance maxima (400–450 nm) can have significant implications for future paleolimnological studies on food web dynamics, but needs more detailed investigations in the future.

3.2. Long-term changes in melanisation

UV absorbance values, i.e. the degree of melanisation of *Daphnia* ephippia varied strongly throughout the investigated sediment cores. In R1 the absorbance trends indicate high melanisation of *Daphnia* around 1200, 1400, 1600 and 1900 CE and reduced melanisation in between these centuries and during the 20th century (Fig. 4A). The Fugledammen core showed higher melanisation during 1850 CE and late 20th century, whereas lower absorbance values were measured approximately between 1900 and 1950 CE and in the top sequence (Fig. 4B). Since melanisation of northern

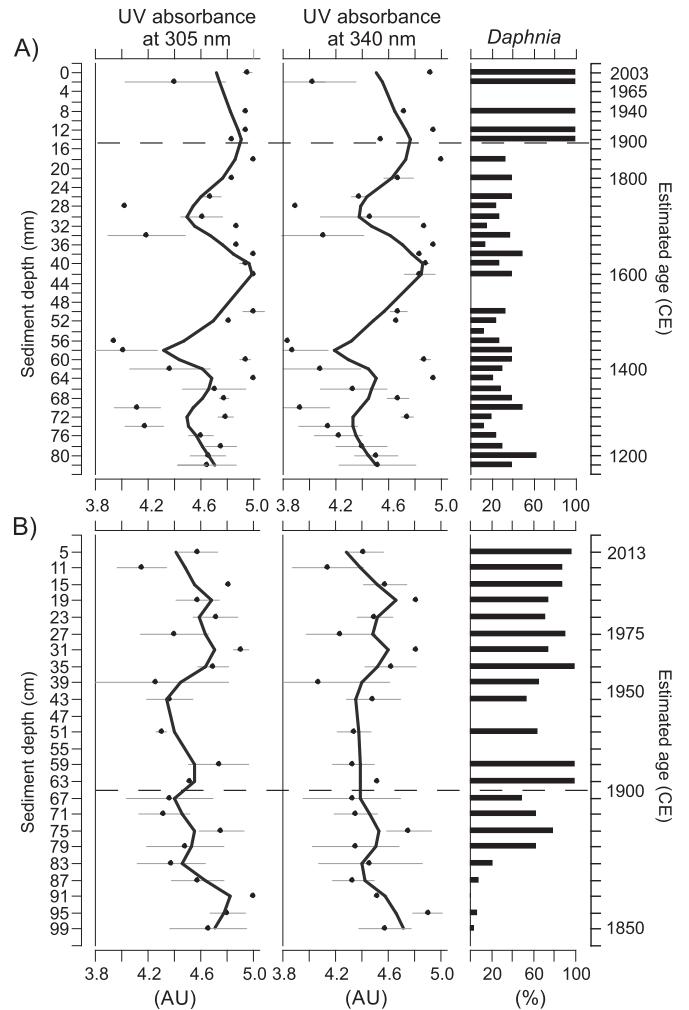


Fig. 4. Downcore UV absorbance measurements. Fossil *Daphnia* ephippia UV absorbance values (as relative absorbance units, AU) with standard deviations as horizontal gray lines and *Daphnia* relative abundance in cores A) R1 (Cornwallis Island) and B) Fugledammen (Spitsbergen). Solid black lines are smoothing curves for absorbance values (LOESS, span 0.25). UV absorbance is illustrated as double valve measurements for R1 and single valve measurements for Fugledammen to standardize the UV absorbance scale. The horizontal dashed line indicates the environmental change horizon 1900 CE.

cladoceran populations is usually related to the intensity of UV exposure of the habitat (Rautio and Korhola, 2002; Nevalainen et al., 2015b), periods of higher melanisation in the R1 and Fugledammen cores may indicate periods of higher UV exposure in the past. Previous melanin-based records from cladoceran genera *Alona* and *Chydorus* (Chydoridae) have suggested similar interpretations on the long-term relationship between melanisation and aquatic UV regimes (Nevalainen and Rautio, 2014; Nevalainen et al., 2015a).

However, there are plenty of confounding limnological and biological variables that may have impacted the pigmentation of *Daphnia* and its observed variations throughout the sediment cores in addition to direct UV effects (Fig. 4). For example, lake depth may have varied greatly in past impacting the UV penetration depth and the existence of depth refugia for *Daphnia*. The studied lakes are very shallow (<1 m) and located in plane areas, making them to be close to their theoretical maximum water depths. Therefore it is unlikely that altering lake depth and existence of deep water refugia has had major impact on the melanisation of *Daphnia* in the

current records. Presence and changes in visually predating fish could also easily change melanisation patterns of *Daphnia*, since fish tend to prey on the pigmented individuals (Hansson, 2000). *Daphnia middendoffiana*, adapted to the arctic fish free habitats, does not respond to presence of fish by altered pigmentation, but *Daphnia pulex* reduces melanisation under fish predation (Tollrian and Heibl, 2004). Due to the shallowness of the current basins (Table 1), freezing to the bottom during winter times, these habitats are fish-free. In addition, clonal shifts may account for the variation in melanisation (Gerrish and Cáceres, 2003; Bellati et al., 2014). Furthermore, even small changes in DOC concentrations of low-DOC lakes, such as the current study lakes (Table 1), may alter underwater UV environment significantly as UV penetration changes exponentially at the 1–2 mg C L⁻¹ threshold (Williamson et al., 1996). This will necessitate UV-protective pigmentation around this threshold (Rautio and Korhola, 2002; Nevalainen et al., 2015b). The terrestrial DOC pool of lakes R1 and Fugledammen is poor, since they are located in barren arctic landscapes, but changes in lakes' DOC concentrations could have been driven by e.g. permafrost thawing (activation of soil carbon) and bird impact (fertilization from bird guano). These confounding factors should be taken carefully into account when assessing if *Daphnia* melanisation is as a direct response to UV and inferring past UV regimes with fossil melanin, although their specific roles cannot be reliably estimated in paleolimnological investigations.

The downcore absorbance measurements may be partly hampered by the fact that ephippia were mostly very scarce in the examined sediments, as a mean of ~3–4 ephippia were found in the samples where *Daphnia* occurred. The low number of ephippia measured may increase the risk that ephippia do not reflect an average melanisation of the active season's population but rather seasonal and individual variability. Previously, a wider set of absorbance measurements (N = 10) has been used (Nevalainen and Rautio, 2014; Nevalainen et al., 2015a, 2015b). A higher number of measurements, most preferably >10 per sediment section, should be used whenever possible for reliable estimations on populations' melanisation patterns through time. However, since arctic *Daphnia* are highly responsive to UV by melanisation (Hessen et al., 1999), their local populations are likely genetically homogeneous (Weider et al., 1999), and the active season is extremely short producing only a few generations due to short open-water season (Ebert, 2005), the lower number of measurements may still provide a reliable estimation on populations' melanisation degree.

Lake biota, and especially zooplankton, only respond directly to UV when lakes are shallow without depth refugia, without visually feeding predators, and extremely depleted in UV-attenuating organic molecules (e.g. DOC), as is the case in lakes R1 and Fugledammen (Table 1). Accordingly, based on the current records of *Daphnia* melanisation, it is likely that aquatic UV varied significantly throughout the cores and high UV exposure (inferred from high melanisation) occurred in cycles (Figs. 4–5). UV exposure of arctic freshwaters depends not only on the thickness of ozone layer but also on climate change impacts altering ice-cover duration and in-lake productivity (Vincent et al., 2007; Häder et al., 2015). In addition, changes in catchment properties, such as in vegetation cover and soils, can have a strong impact on UV exposure through DOC in tree line lakes (Pienitz and Vincent, 2000; Saulnier-Talbot et al., 2003). In high arctic lakes, where primary production is usually very low and catchments consist of barren landscape, solar activity may be linked to aquatic UV-regimes (Nevalainen et al., 2015a). The long-term trends in *Daphnia* melanisation in lakes R1 and Fugledammen, that were probably related to the lakes' UV exposure, seemed to coincide with solar activity during the past centuries (Fig. 5). The trends agreed in a way that during sunspot maxima in approximately every 100–200 years *Daphnia*

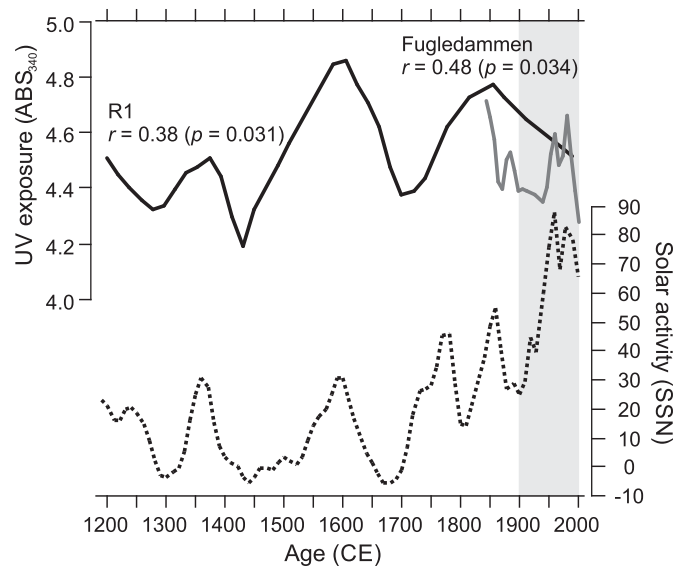


Fig. 5. UV reconstruction in relation to sunspots. Long-term trends of underwater UV exposure as inferred from fossil *Daphnia* UV absorbance at 340 nm (ABS_{340} , LOESS smooth 0.25) in lakes R1 (black) and Fugledammen (gray) following solar activity trends as sunspot numbers (SSN). The relationships between the two variables throughout the cores are indicated by Pearson's correlations (r) and the levels of statistical significance (p), where no periodicities (autocorrelation) were detected. The gray band between 1900 and 2000 CE indicates the environmental change horizon, when the correlations changed to negative in R1 ($r = -0.97$, $p = 0.036$) but remained positive in Fugledammen ($r = 0.88$, $p = 0.001$). Ephippia absorbance values are illustrated as double valve measurements for R1 and single valve measurements for Fugledammen to standardize the UV absorbance scale.

melanisation was strongest and *vice versa* (Fig. 5). This long-term positive relationship appears to suggest that high solar activity has increased aquatic UV exposure in arctic lakes in the past, although further UV reconstructions and adequately dated sediment records are needed to verify this connection.

High solar activity should in general reduce biologically damaging UV-B radiation in Earth's surface by thickening ozone layer through intensive UV-C radiation (Rozema et al., 2002), inducing lower UV exposure during the periods of high solar activity. In agreement with the negative relationship of UV and solar activity (Rozema et al., 2002), an Antarctic UV reconstruction based on algal pigments showed that periods of solar minima coincide with UV maxima (Verleyen et al., 2005) contradicting our results (Fig. 5). The solar-atmospheric-terrestrial processes in relationships between sun activity, ozone production and transport, and UV radiation are highly complex (Reid, 1999) and even more complex in aquatic ecosystems, where DOC plays a significant role (Williamson et al., 1996). Intense solar radiation causes increased photochemical degradation of DOC in aquatic systems leading to oxidation or breakage of the UV-absorbing molecules (Cory et al., 2013; Porcal et al., 2014) and increasing aquatic UV exposure. Accordingly, higher photodegradation of UV-attenuating DOC during sunspot maxima may have indirectly been responsible of the observed relationship between *Daphnia* melanisation and habitats' UV exposure and solar activity (Fig. 5). However, factors related to the chronological control of the R1 core, i.e. lack of ¹⁴C datable terrestrial material and low ¹³⁷Cs and ²¹⁰Pb activities (Fig. 2) that are typical for arctic lake sediments, may also cause uncertainty to the interpretations.

3.3. The 20th century environmental change

At the turn of the 20th century, the long-term positive

correlation between solar activity and UV exposure was disrupted in R1, as *Daphnia ephippia* UV absorbance trend declined despite increased sunspot numbers (Fig. 5). Yet, the corresponding trends remained in the Fugledammen core and became even stronger (Fig. 5). During this time horizon, matching approximately with 1900 CE, there occurred a distinct change in aquatic communities of R1 (Fig. 6). Of the invertebrates *Chydorus* (Cladocera, Chydoridae) disappeared and chironomid remains increased (Fig. 6). Simultaneously, diatoms appeared to the stratigraphy and were found abundantly and with diverse communities in the top section of the core together with abundant *Nostoc* colonies (Fig. 6). This episode of pronounced change within the biological assemblages coincided with the major shift seen in several other diatom records from the circumpolar Arctic that have been explained by rapidly increasing temperatures lengthening the open-water season and causing limnological regime shifts (Smol et al., 2005; Antoniadou et al., 2007). Since Lake R1 is located in a very remote location in High Arctic Canada (Fig. 1) far from any direct human influence, it is possible that the reason for the major biotic changes was of atmospheric origin and related to warming temperatures. It is also possible that the change horizon in the biostratigraphy of R1 at 1900 CE (Fig. 6) is at least partly hampered, since the absence of diatoms in the early record may also have been caused by dissolution of the siliceous diatom valves due to some limnological factor, e.g. ionic concentrations (Ryves et al., 2006). However, since invertebrates also seem to respond at the change horizon simultaneously (Fig. 6), it seems likely that some significant environmental change took place at that time.

Over the past century, the Arctic has been subjected to more extensive environmental change than in the preceding centuries, including ozone depletion and warming temperatures (ACIA, 2005; Manney et al., 2011; Kaufman et al., 2009) that influence aquatic UV exposure via direct changes in atmospheric UV absorbance and indirectly through altering ice-cover duration, lake productivity, and catchment processes (Pienitz and Vincent, 2000; Häder et al., 2015). Since the long-term positive relationship between UV exposure and solar activity turned to negative in R1 (Fig. 5) but remained strongly positive in Fugledammen, it is possible that *Daphnia* melanisation was recording regional UV signals that differ significantly between the study sites. For example, cloudiness has increased over the Arctic Canadian Archipelago during the late 20th century due to reduced summertime sea ice (Kahru et al., 2010; Zhang et al., 2013) and may have induced lower UV irradiance

and consequently reduced melanisation in the R1 core. It is also possible that the post-1900 CE UV exposure of R1 has remained in connection with solar activity in a similar manner as in Fugledammen but was not recorded in *Daphnia* melanisation. For example, altered photoprotective strategies of *Daphnia* or a change in UV transparency of the water column may have interfered with the melanisation signal in R1. The ecosystem functioning of R1 clearly changed at around 1900 CE when indicators of primary production (diatoms and cyanobacteria) increased in the sediment record (Fig. 6) suggesting that benthic microbial mats were established (Bonilla et al., 2009; Lionard et al., 2012). Such changes were not observed in Fugledammen core where primary production has been of planktonic origin recently (Luoto et al., 2015). Following the functional reorganization of R1 food web, photoprotective strategies of *Daphnia* may have changed when they have started to utilize UV-absorbing compounds originating from benthic microbial substratum. The current UV-protection of *Daphnia* individuals in R1 includes a significant utilization of algal pigments from benthic microbial mats in addition to synthesized melanins (Rautio et al., 2009). Alternatively, DOC pool of the lake may have been changed due to warming climate (e.g. thawing permafrost) since UV attenuation of low DOC lakes ($1\text{--}2\text{ mg L}^{-1}$) may be highly susceptible to even slight changes in DOC (Williamson et al., 1996).

4. Conclusions

Our paleolimnological analyses suggest that UV-protective melanin pigments, in addition to carotenoids, are preserved in fossil zooplankton remains and that the long-term variation in the degree of melanisation is likely related to underwater UV exposure. The melanin-based UV records coincided with past trends in solar activity and suggest that solar forcing is a major contributor to long-term UV exposure of high arctic aquatic ecosystems. With this respect, our long-term UV records of melanisation provide important reference data for assessing the impacts of the recent environmental changes, including ozone depletion and climate warming, on arctic aquatic ecosystems and organisms. The current records provide indications that zooplankton are able to adapt to long-term changes in aquatic UV exposure by melanin-derived photoprotection. The recent climate-induced shifts in arctic limnology can however overrule the mechanisms that induce melanisation by significant reorganizations in ecosystem structure and functioning, and affect the success of aquatic organisms in the

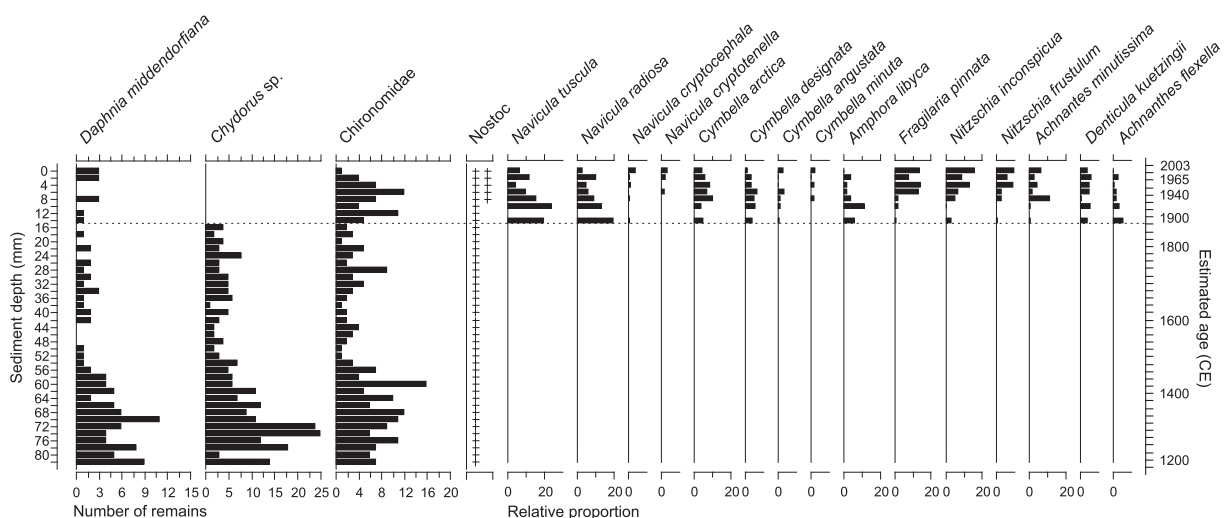


Fig. 6. Biostratigraphy of the R1 core. Aquatic invertebrate remains, *Nostoc* (+present, ++ abundant), and diatom assemblages (most common taxa) in the R1 core, where the horizontal dashed line indicates time horizon 1900 CE.

rapidly changing arctic lakes.

Acknowledgements

This study was funded by the Academy of Finland projects #287547 (VIOLET) and #259343 (QUAL) and the Doctoral Program in Geosciences of the University of Helsinki. Constructive comments by professors Roger Jones, Lars-Anders Hansson, Dermot Antoniadis, Murray Hay, and an anonymous reviewer are sincerely acknowledged.

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