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Spectral absorbance of benthic cladoceran carapaces as a new method for inferring past UV exposure of aquatic biota

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ABSTRACT

We developed a method for measuring fossil cladoceran (Branchiopoda) carapace absorbance to infer past ultraviolet radiation (UV) exposure in lakes. This was done under the presumptions that cladocerans synthesize photoprotective compounds, of which melanin is the main UV-absorbing pigment, to their exoskeletons and melanin is preserved in sedimentary cladoceran remains. We extracted large-sized cladoceran (benthic *Alona* spp.) carapaces from subsections of sediment cores from two environmentally divergent lakes; a humic boreal forest lake in eastern Finland (past 1500 years) and a clear-water mountain lake in the Austrian Alps (past 300 years). We measured the absorbance of extracted carapaces with a spectrophotometer under visible light and UV wavelengths using an adapter, which was designed to hold the microfossils. When compared to the spectrum of synthetic melanin, the shapes of absorbance spectra at the 700–280 nm range suggested that the fossil carapaces contained melanin. The carapace absorbance under UV throughout the sediment cores was significantly higher in the clear-water alpine lake than in the humic boreal lake reflecting differences in the general underwater UV and optical environments between the sites. In addition, carapace absorbance was significantly higher during the Little Ice Age (LIA) than during pre- or post-LIA periods in both lakes. In the alpine lake, this was most likely a response to increased underwater UV induced by reduced primary production and more transparent water column during the cold summers of LIA, whereas reduced input of carbon compounds from the catchment through elongated permafrost and ice-cover periods likely induced higher water transparency in the boreal lake during this cold climate phase. We conclude that fossil melanin provides a good estimation of past underwater UV exposure in lakes with large cladoceran carapaces preserved in sediments and that the method introduced here is easy and cost- and time-efficient technique to be widely used in paleoaquatic UV inferences.

1. Introduction

Among the numerous environmental threats to climatically sensitive aquatic ecosystems, highly energetic ultraviolet radiation (UV) has many biologically deleterious effects and its increase results in changes in productivity and species composition, ultimately altering ecosystem structure, functioning and biogeochemical cycles (Perin and Lean, 2004; Häder et al., 2011). Exposure of aquatic organisms to UV is controlled by the inherent and extrinsic properties of a given water body. The most important inherent property is the concentration of dissolved organic carbon (DOC) (Schindler et al., 1996) although algal biomass also plays a role (Laurion et al., 2000). Both absorb UV before it penetrates deep in the water column. Extrinsic properties include the geographical location of the water body (latitude, altitude), seasons, and changes in the UV-protective ozone layer. While DOC and algal biomass vary naturally, e.g. due to lake succession in time (Williamson et al., 2001a), they are also highly influenced by anthropogenic effects such as catchment disturbance and the resultant changes in carbon export to lakes. Severe ozone depletion and increased UV since the 1970s are caused by manmade chlorofluorocarbons and halons, which interact with and destroy stratospheric ozone. Despite some recent global advances in reducing ozone-depleting chemicals, ozone depletion is expected to persist and worsen, resulting in significantly increased UV doses (Björn et al., 1998; ACIA, 2005; Manney et al., 2011). On the other hand, there are also signs that ozone layer has begun to recover regionally and will continue to

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recover in the coming decades (McKenzie et al., 2011; UNEP, 2012). Apart from changes in the ozone layer, climate warming that results in reduced ice-cover period and catchment-driven limnological changes will change underwater UV intensities in the future via direct increase in underwater exposure as well as through changes in water optical properties and UV attenuation (Vincent et al., 2008).

Aquatic microcrustaceans, such as cladocerans (Branchiopoda), are negatively affected by high intensities of UV (Williamson et al., 2001b; Rautio and Korhola, 2002a). However, these animals can also be well adapted to high UV, because they can synthesize and/or accumulate photoprotective compounds; melanin, carotenoid, scytonemin and mycosporine-like amino acids, repeatedly during their life (Hessen, 1996; Rautio et al., 2009). These compounds increase survival under intensive UV (Hairston, 1976; Hebert and Emery, 1990; Hessen et al., 1999), being adaptive responses to the underwater UV environment (Rhode et al., 2001). Pigment synthesis is considered to be energetically costly and there occurs a tradeoff between damage from UV exposure and the costs of pigmentation as well as increased predation from fish hunting the most visible prey, i.e. pigmented individuals (Hansson, 2000). Of the UV protective compounds, melanin pigment results in brown/black color of cladoceran carapace and if pigmentation is strong, it can be visually detected. Strongly melanic forms of cladoceran plankton and benthos have been observed from high latitude and altitude sites (Manca et al., 1998, 2006; Rautio and Korhola, 2002b; Sommaruga, 2010; Van Damme and Eggermont, 2011).

Despite the detrimental impacts of UV in nature, little is known about its natural variability or long-term effects on ecosystems and individual organisms since meteorological and biological monitoring does not extend longer than 1970's to record past changes (Rozema et al., 2002). Natural variability in UV attenuation in lakes is strongly related to long-term climatic variation in temperature and precipitation patterns via catchment characters, water depth, productivity, and ice-cover period. For example, permafrost and surface runoff resilience impacts in releasing or holding DOC (Schindler et al., 1996; Rosén et al., 2009b), developed soils or vegetation and catchment characters act as sources of DOC (Pienitz and Vincent, 2000; Saulnier-Talbot et al., 2003; Schmidt et al., 2008), water depth affects the size of UV-free refugia in the water column (Leavitt et al., 2003), and persistent snow and ice-cover effectively attenuates UV (Vincent et al., 2007; Lami et al., 2010).

Previously, UV absorbing pigments in benthic and planktonic algae and in cyanobacteria, extracted from lake sediments, have been used as aquatic biological proxies in inferring historical patterns in UV (Leavitt et al., 1997, 1999, 2003; Verleyen et al., 2005; Lami et al., 2010). Furthermore, fossil diatom assemblages combined with bio-optical models have been used in assessing past variation in underwater light regime, and accordingly, magnitude of UV (Pienitz and Vincent, 2000; Saulnier-Talbot et al., 2003). UV absorbing compounds in plants (phenolic acids in pollen, spores, cuticles, seed coats, and wood) have proven to retain potential as a proxy for UV inferences in terrestrial and lacustrine cores (Rozema et al., 2001, 2009). However, the existing UV reconstructions are scarce and far from straightforward; it is extremely difficult to completely isolate the effects of UV, especially in aquatic ecosystems where DOC and water depth play a significant role in the range and magnitude of UV penetration (Leavitt et al., 2003, 2009; Verleyen et al., 2005). Accordingly, new supplementary approaches for long-term UV inferences are needed.

The degree of melanin pigmentation in cladocerans is related to the UV exposure of a given water body (Rautio and Korhola, 2002b; Tollrian and Heibl, 2004). Melanin is also chemically inert in chitinous sedimentary cladoceran remains after death or molting of the organism (Rautio, 2007) and it has been suggested that fossil melanin in cladoceran remains can be a valuable indicator of past underwater light regimes (Jeppesen et al., 2001; Rautio, 2007). However, no down-core studies have tested this yet. Although there exists standardized protocols for measuring extracted melanin content from modern zooplankton (e.g. Hebert and Emery, 1990), they are not optimum for sedimentary cladoceran remains, since it would be too time consuming to extract enough remains from lake sediments for the analysis due to the small size and weight of the remains. To overcome this problem, we report here a new method for evaluating past fluctuations of UV protective phenotypic features (melanin pigment) in sedimentary cladoceran remains. Our aim is to develop an easy and cost-efficient method for paleoaquatic inferences of past underwater UV and to apply and test this method for disentangling fluctuations in pigmentation, and hence in the UV exposure, in limnologically and geographically divergent (alpine versus boreal) lakes. We hypothesize that melanin is preserved in fossil cladoceran remains in centuries old lake sediment deposits and can be inferred via spectrophotometric carapace absorbance measurements. Furthermore, we presume that the UV absorbance of cladoceran carapaces would be more pronounced in the clear-water alpine site than in the boreal humic lake.

2. Regional setting

The cladoceran carapaces, which are used for developing and testing the new method for paleoaquatic UV inferences, originate from sediment cores from lakes Pieni-Kauro and Oberer Landschitzsee. Pieni-Kauro is a north boreal forest lake in eastern Finland with slightly acidic and mesohumic lake-water (Table 1). The Pieni-Kauro basin is open, connected to other lakes via streams, and its catchment consists mainly of boreal coniferous forests and mires. The Pieni-Kauro core (35 cm) was investigated for the current study at 2-cm intervals, resulting in 18 samples. The time span of the core is from *ca* 1500 yr BP to present. The details of core collection and dating of the Pieni-Kauro core are available in Luoto and Helama (2010) and environmental settings in Luoto (2010). The general cladoceran community development of the Pieni-Kauro core is previously presented and discussed in Nevalainen et al. (2013). Oberer Landschitzsee is located in the Austrian Alps above the present-day tree line and it is a clear-water and slightly alkaline mountain lake (Table 1). Oberer Landschitzsee is an enclosed basin and its catchment consists of alpine meadows with grasses and scattered dwarf pines. The core from Oberer Lanschitzsee (17 cm) was investigated with 1-cm intervals (17 samples) and the temporal range of the core is from *ca* 300 yr BP to present. Detailed environmental characteristics and coring and dating details for Oberer Landschitzsee are given by Nevalainen and Luoto (2012), who also depict and discuss the general cladoceran community succession.

Table 1
General geographical and limnological features of the study sites in Finland (Pieni-Kauro) and Austria (Oberer Landschitzsee).

	Pieni-Kauro	Oberer Landschitzsee
Location	64°17′ N, 30°07′ E	47°15′ N, 13°52′ E
Altitude	188 m a.s.l.	2076 m a.s.l.
Biome	Boreal forest	Alpine tundra
Water color	Darkbrown	Clear
Trophic status	Oligo-dystrophic	Ultra-oligotrophic
pH	Acidic-circumneutral	Alkaline-circumneutral
Maximum depth	7.9 m	13.6 m
Hydrology	Open basin	Enclosed basin