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Differences in UV transparency and thermal structure between alpine and subalpine lakes: implications for organisms†

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Abstract

Ultraviolet (UV) radiation is a globally important abiotic factor influencing ecosystem structure and function in multiple ways. While UV radiation can be damaging to most organisms, several factors act to reduce UV exposure of organisms in aquatic ecosystems, the most important of which is dissolved organic carbon (DOC). In alpine lakes, very low concentrations of DOC and a thinner atmosphere lead to unusually high UV exposure levels. These high UV levels combine with low temperatures to provide a fundamentally different vertical structure to alpine lake ecosystems in comparison to most lowland lakes. Here, we discuss the importance of water temperature and UV transparency in structuring alpine lake ecosystems and the consequences for aquatic organisms that inhabit them. We present transparency data on a global data set of alpine lakes and nearby analogous subalpine lakes for comparison. We also present seasonal transparency data on a suite of alpine and subalpine lakes that demonstrate important differences in UV and photosynthetically active radiation (PAR, 400–700 nm) transparency patterns even within a single region. These data are used to explore factors regulating transparency in alpine lakes, to discuss implications of future environmental change on the structure and function of alpine lakes, and ways in which the UV transparency of these lakes can be used as a sentinel of environmental change.

Introduction

Mountains cover 25 percent of the Earth's land surface, host 12 percent of the human population, and supply fresh water to almost half of the world's population.¹ Despite the importance of alpine ecosystems, little is known about how the physical structure of alpine lakes differs from subalpine lakes and how this influences the biota within alpine lakes. While some clear progress has been made in understanding the role of UV in the ecology of alpine lakes (*e.g.* ref. 2–4), lowland lakes have received an inordinate amount of study in comparison to more remote and sensitive alpine lakes. The high elevation of alpine lakes gives them a fundamentally different physical structure from the lowland lakes on which our

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broader limnological knowledge is based. The differences in physical structure between alpine and lower elevation lakes may have important implications for the organisms that inhabit them.

Alpine lakes are physically harsh ecosystems that are sensitive to environmental change. Alpine lakes differ from lowland lakes in many fundamental ways. While lakes fall on a gradient of elevation, temperature, and watershed vegetation, “alpine” lakes are traditionally defined as those located above the treeline.² In this environment, levels of UV exposure, transparency, and highly contracted thermal structure are particularly harsh for the organisms that inhabit them (Fig. 1). Lake surface water temperatures may exhibit different responses to climate forcing based on elevation.⁵ Temperatures in alpine lakes are generally very low (mean annual air temperatures can be below 0 °C) influencing ice phenology; ice may cover alpine lakes 5–9 months of the year.⁶ For example, lakes above an elevation of 2500 m in the Beartooth Mountains of Montana and Wyoming, USA, often have ice cover well into July and ice may form again in October. This leads to much shorter ice-free “growing” seasons where sunlight is adequate to support primary production and water temperatures are above 4 °C. At lower elevations, lakes are exposed to longer periods of warmer temperatures⁵ and longer periods of sunlight that supports primary productivity. These lower elevation lakes are often much less transparent and surface temperatures much higher than in alpine lakes. In contrast, alpine lakes may stratify only briefly or not at all during the ice-free season (Fig. 1).

Cold alpine air temperatures also influence precipitation. Snowfall makes up a significant proportion of total annual precipitation in alpine environments. Low temperatures lead to thick ice accumulation on alpine lakes and slow melting in spring and summer.^{7,8} Thick ice and snow on alpine lakes may reduce under-ice solar irradiance (*e.g.* ref. 9). Snow melt may occur rapidly during the early summer, adding a pulse of allochthonous material and water into alpine lakes.¹⁰ In addition, cold temperatures mean that snowmelt is the dominant source of hydrologic event for many alpine lakes (*e.g.* ref. 11). Steep slopes in alpine watersheds may lead to rapid drainage. Alpine ecosystems also contain less terrestrial vegetation than lowland ecosystems as a consequence of their short growing season, high wind, and harsh climate. This combination of little or no terrestrial vegetation and steep slopes generates low DOC concentrations in alpine lakes and results in generally high transparency to both UV and PAR.^{2,12,13}

Alpine lakes usually receive higher UV exposure than lowland lakes. For example, in the European Alps, incident UV increases with elevation, up to 11% per 1000 m at 320 nm and 24% per 1000 m at 300 nm.¹⁴ A thinner atmosphere and lower aerosols contribute to high solar irradiance and higher levels of UV relative to longer wavelength photosynthetically active radiation (PAR, 400–700 nm). In lowland lakes, UV exposure is usually largely regulated by DOC concentration,^{13,15,16} though the chemical composition and optical properties of the DOC pool will largely determine the final K_d values¹⁸ and considerable variation in attenuation can be attributed to variation in optical properties of the DOC pool.^{13,19,20} In alpine lakes, chlorophyll measurements indicate that phytoplankton may play a role in regulating UV transparency.¹³

While these patterns are widely recognized, to date there has not been either a systematic or quantitative assessment of the differences in the physical structure of alpine *vs.* subalpine or other lower elevation lowland lakes, or the potential implications of these differences for the pelagic organisms that inhabit alpine lakes. Here we examine and compare the physical structure of alpine *vs.* subalpine lakes with an emphasis on differences in thermal structure and water transparency to both UV and PAR. The analysis includes a total of 22 alpine and 22 nearby subalpine lakes from several major temperate geographic regions of the world,

including the central and southern Rocky Mountains (USA), the Sierra Nevada Mountains (CA, USA), the Canadian Rocky Mountains, Patagonian Argentina, South Island of New Zealand, and the European Alps. We then discuss the implications of the differences between alpine and subalpine lakes in physical structure for the pelagic organisms that inhabit these lakes. We also present data on how transparency in a suite of alpine and subalpine lakes in the Beartooth Mountains (MT/WY, USA) changes seasonally as well as how physical characteristics of these sensitive ecosystems can be used as sentinels of environmental change over broader geographic regions from local to regional to global.

Methods

Temperature and transparency data (320 and 380 nm UV and PAR) were collected using a Biospherical Instruments profiling UV-PAR radiometer (PUV 500, PUV 501B, specifications in ref. 16 or Biospherical Instruments Cosine [BIC] submersible radiometer²¹) on a series of alpine and subalpine lakes in Argentina, Colorado (USA), the Beartooth Mountains, the Canadian Rockies, the European Alps, the Sierra Nevada (CA, USA), and the Sierra Nevada (Spain). Mixed layer depths were calculated at the depth where temperature change exceeded 1 °C per metre. Diffuse attenuation coefficients (units: m⁻¹) were estimated according to Kirk:²²

$$K_d = -\frac{\ln\left(\frac{E_0}{E_z}\right)}{Z} \quad (1)$$

Optical data presented in Fig. 1 are based on the average epilimnetic K_d s among lakes. Irradiance at a given depth (E_z) is a function of the irradiance at the surface (E_0), the diffuse attenuation coefficient, and the depth interval (Z). We estimated the depth at which one percent of surface UV and PAR remained ($Z_{1\%}$, units: m) as:

$$Z_{1\%} = \frac{\ln(100)}{K_d} \quad (2)$$

In a subset of the study lakes, DOC and dissolved absorbance were measured with three replicates samples collected from within the epilimnion (2–3 m depth), filtered through Whatman GF/F filters, and stored in the cold and dark until analysis. DOC concentration was measured using a Shimadzu TOC-V_{CPH} Total Organic Carbon Analyzer and dissolved absorbance was measured using a Shimadzu UV/Visible UV-1650 PC spectrophotometer. DOC was measured in standard sensitivity mode, subtracting Milli-Q deionized water blanks (*ca.* 0.2 mg C L⁻¹) from standards and samples, and calibrating to dilutions of a certified DOC standard (Aqua Solutions, 50 mg L⁻¹ potassium biphthalate. Dissolved absorbance was corrected by subtracting Milli-Q water blanks and the average of absorbance at 775–800 nm. Dissolved absorption coefficients (units: m⁻¹) were calculated according to Kirk:²²

$$a_d = \frac{2.303 \times D}{r} \quad (3)$$

where D is the absorbance value obtained from the spectrophotometer reading and r (units: m) is the pathlength of the quartz cuvette. DOC-specific absorption coefficients (a_d : [DOC]) were calculated by dividing the dissolved absorption coefficient (a_d , m⁻¹) by the DOC concentration (mg L⁻¹).

In 2001–2008, transparency data in four alpine (Heart, Fossil, Emerald, and Glacier) and four subalpine (Beauty, Island, Beartooth, and Kersey) lakes in the Beartooth Mountains were collected during summer months. Transparency data for these lakes are presented as percent change in transparency relative to the earliest sampled ordinal day such that all years are compiled in one seasonal plot. Positive values or slopes indicate increasing transparency relative to the initial time point while negative values or slopes indicate decreasing transparency.

Student's *t*-tests were used to test if transparency to UV (320, and 380 nm) and PAR in alpine and subalpine lakes differed. Least squares linear regressions were used to relate the total winter snowfall measured in Red Lodge, MT, USA, during the winter before sampling summers to the residuals of the seasonal transparency model for the following summer. Residuals were calculated by subtracting the percent change in transparency predicted by the model from the actual percent change in transparency relative to the initial sampling date in each lake.

Least squares linear regression was used to relate DOC concentration to DOC-specific absorption coefficients in alpine and subalpine lakes, and to relate DOC absorption coefficients to diffuse attenuation coefficients in Beartooth Mountain lakes.

The physical structure of alpine and subalpine lakes

Alpine and subalpine lakes exhibited fundamental differences in their physical habitat structure (Fig. 1 and Table 1). UV transparency was significantly greater in alpine lakes than in subalpine lakes for all wavelengths ($p < 0.001$ for 320, and 380 nm UV and PAR). For example, the average depth of 1% at 320 nm (UV-B) was 8.1 m across alpine lakes, over four times deeper than the average 1% depth in subalpine lakes (1.9 m). PAR transparency was also greater in alpine lakes. The average 1% PAR depth was 20.2 m in alpine lakes, about 1.4 times deeper than subalpine lakes (14.2 m). The transparency ratio (the ratio of the 1% depth of 320 nm UV relative to the 1% depth of PAR) was consequently much greater in alpine lakes (34.4%) compared with subalpine lakes (12.6%). We documented transparency ratios above 50% in some alpine lakes, which is comparable with some of the most transparent lakes on Earth, such as the McMurdo Dry Valleys lakes,⁹ and in agreement with previous assessments of alpine lakes.¹³ Our results highlight important differences in physical structure between mountain lakes and lowland lakes. For example, Lake Lacawac, a lowland lake in eastern Pennsylvania, USA, had a 320 nm UV-B : PAR transparency ratio of about 3% in 2008, one tenth the mean in our survey of alpine lakes (Table 1).

There were also important temperature differences between alpine and subalpine lakes (Fig. 1 and Table 1). The average epilimnetic water temperature of subalpine lakes was 15.5 °C while in alpine lakes it was 9.4 °C. Average depth of the mixed layer was essentially the same in both subalpine lakes (5.2 m) and in alpine lakes (5.1 m). The effect of lake size and fetch on mixing depth may be much greater than the effect of elevation or transparency.^{23,24} In alpine lakes, the average 1% depth of 320 nm UV, the wavelength generally considered most biologically damaging, was deeper than the mixed layer. Furthermore, the average 1% 380 nm UV-A was 3 times deeper than the mixed layer. In subalpine lakes, by contrast, all UV wavelengths attenuated much more rapidly and only the 1% depth of PAR was below the mixed layer.

The high UV : PAR in alpine lakes may reflect both low DOC concentration and the increased role of phytoplankton in UV attenuation.²⁵ In most lakes, DOC concentration is usually the most important factor regulating UV and PAR transparency.¹⁵⁻¹⁷ Elevation gradients in DOC concentrations in lakes mean that high elevation alpine lakes often have very low DOC.^{26,27} Because DOC strongly absorbs shorter wavelength UV relative to

PAR, decreases in DOC concentration increase the UV : PAR ratio. DOC quality can also be very important to water transparency and consequently to UV : PAR ratios.^{20,28} Despite the pattern of decreasing DOC with elevation, some alpine lakes contain very high concentrations of DOC and the lakes we sampled were only from temperate regions. For example, the DOC concentration for two alpine lakes in northern Chile was relatively very high. The DOC concentration of Laguna Simbad, an alpine lake located at 5870 m was 3.5 mg L⁻¹ and Laguna Aguas Calientes, located at 4600 m had a DOC concentration of 5.4 mg L⁻¹. The higher DOC concentration of these lakes may be due to long residence time of the lakes. Despite the high DOC concentration, DOC-specific absorption was very low and zooplankton found in Aguas Calientes were highly pigmented (Rose, personal observation).

The high UV transparency in alpine lakes may reflect a highly autochthonous DOC source. While variation in transparency has been linked to variation in DOC concentration, changes in the optical properties of the DOC pool along elevation gradients are also thought to play a role in the high UV transparency of alpine lakes.²⁷ When the 1% depths at 320 nm (UV-B), 380 nm (UV-A), and PAR are plotted vs. DOC concentration (Fig. 2a, data from ref. 16) all increase much more rapidly at low concentrations of DOC. This rapid change in transparency may reflect a fundamental change in DOC optical quality as terrestrial DOC inputs are reduced at high elevations. When the diffuse attenuation coefficients (K_d) are plotted vs. DOC concentration (Fig. 2b), the relationship is much more linear, reflecting the fact that the 1% depth vs. DOC concentration relationship is largely a simple product of the inverse transformation from K_d to 1% depth (eqn (2) above). However, the relationship between DOC-specific absorption coefficients and DOC concentration in alpine lakes indicates that part of this relationship is also due to changes in DOC optical quality at the very low DOC concentrations found in alpine lakes (Fig. 3). Alpine lakes showed a significant relationship between the 305 nm and 320 nm DOC-specific absorption coefficients and DOC concentrations (305 nm $R^2 = 0.33$, $p = 0.025$, 320 nm $R^2 = 0.31$, $p = 0.030$, Fig. 3). This relationship was not significant for 380 nm UV ($R^2 = 0.25$, $p = 0.058$), 440 nm visible light ($R^2 = 0.25$, $p = 0.151$) or PAR ($R^2 = 0.08$, $p = 0.307$). In subalpine lakes, there was considerable variation in DOC-specific absorption, but no significant relationship with DOC concentration (Fig. 3). In the alpine lakes, the relationships with 305 nm and 320 nm were consistent with the fact that shorter wavelengths are more responsive to variation in DOC optical properties and may be a better indicator of DOC properties than longer wavelengths.²⁹ An important implication of these relationships is that, at low DOC concentrations (<~0.7 mg L⁻¹), very small changes in DOC concentration or in the dominant source of this material (autochthonous vs. allochthonous) could lead to important changes in the depth to which UV penetrates in alpine lakes (Fig. 3).

Several factors may play a role in reducing DOC-specific absorbance at low DOC concentrations. These include a shift in the dominant DOC source from more allochthonous to more autochthonous input, increased photobleaching, or changes in lake chemistry. Sparse terrestrial vegetation in alpine watersheds may reduce the input of highly chromophoric allochthonous DOC.¹³ The DOC pool of some alpine lakes is derived more from algal productivity within the lake, which is generally much less light absorbing than terrestrially derived material.^{11,25,30} Previous studies indicate that DOC-specific absorption in the UV range increases with increasing percent forest in the watershed.³¹ Recently, bacterial activity has also been linked to the generation of chromophoric dissolved organic matter (CDOM) in alpine lakes of the Sierra Nevada, Spain.³² Several studies have suggested that changes in the character of DOC with increasing DOC concentrations reflect a change in the source of the organic material.^{15,19}

Low DOC-specific absorption in alpine lakes may also be driven by high rates of photobleaching. As incident UV generally increases and DOC concentrations decrease along

an elevation gradient, photobleaching may reduce DOC-specific absorption more in alpine lakes relative to subalpine lakes. Lake morphology and water residence time may regulate DOC-specific absorbance because photobleaching of DOM may be greater in lakes with longer residence times. Across lakes of the USA and Canada, lake color has been negatively related to watershed slope, mean lake depth, and lake area.³³ Lake morphometry and catchment characteristics are generally related to elevation, where higher elevation lakes tend to be shallower with smaller surface areas.³⁴ The residence time of alpine lake Gossenköllesee was estimated at 52 days,³⁵ however little is known about the residence time of alpine lakes in general. The water residence time was not measured in most lakes of this study and we observed no obvious morphometric patterns among or between the alpine and subalpine lakes.

Alkalinity and pH may also affect photobleaching rates, but previous studies present conflicting results. Reche *et al.* (1999) report that photobleaching is more rapid in lakes with a high acid neutralizing capacity,³⁶ however, other studies show that photo-oxidation may occur faster in more acidic environments.³⁷⁻³⁹ Lakes at high latitudes and high elevations may be especially sensitive to changes in pH⁴⁰ due to their poor buffering capacity. While chemical composition and optical properties of the DOC pool will largely determine the final K_d values,¹⁸ more research is needed to understand what is driving this relationship.

Seasonal changes of UV and PAR transparency in alpine and subalpine lakes

Seasonal changes of both UV and PAR transparency have been well documented in lowland lakes where transparency generally increases during the summer months. Zooplankton grazing has been implicated in stimulating this “clear water phase” period that is usually measured by Secchi depth.^{41,42} While photobleaching of DOC accounts for a majority of the seasonal changes in UV transparency,²⁰ zooplankton grazing may also contribute to a lesser extent.⁴³ In alpine lakes, DOC concentration and optical quality is generally low, however biomass of zooplankton grazers is often very low.^{21,44} Interestingly, Sommaruga and Augustin²⁵ found that seasonal changes in UV transparency for the alpine lake Gossenköllesee in Austria were related to changes in phytoplankton biomass and not to changes in DOC absorbance.

In our analysis of lakes in the Beartooth Mountains, we found that transparency generally increased throughout the open water season in both alpine lakes (Heart, Fossil, Emerald, and Glacier) and subalpine lakes (Beauty, Beartooth, Island, and Kersey). However, lakes varied considerably in the degree of transparency change and the wavelengths that changed the most (Fig. 4). For example, transparency increased up to 170% for 380 nm UV-A in Heart Lake, while in Kersey Lake, 380 nm UV-A increased only up to 30%. In Beartooth and Beauty Lakes, UV transparency increased dramatically throughout the open water period. The 380 nm UV-A increased up to 124% in Beauty Lake and 106% in Beartooth Lake, while 320 nm UV-B increased 128% in Beauty Lake and 86% in Beartooth Lake. In both lakes, PAR increased considerably less, 59% in Beauty Lake and 28% in Beartooth Lake. In other lakes, 320 nm UV-B, 380 nm UV-A, and PAR exhibited a similar seasonal pattern suggesting that the same processes are driving changes in both UV and PAR transparency in these systems.

While prior studies suggest that changes in chromophoric dissolved organic matter (CDOM) were not clearly linked to seasonal changes in transparency in Gossenköllesee in the Austrian Alps,²⁵ changes in the dissolved absorption coefficient are highly predictive of the diffuse attenuation coefficient in the Beartooth Mountains, both early season (soon after ice out) and in late summer (late August) (Fig. 5). The relatively high DOC concentration in

Beartooth Mountain Lakes ($0.45\text{--}3.10\text{ mg L}^{-1}$) compared with that in Gossenköllesee ($0.12\text{--}0.65\text{ mg L}^{-1}$) may explain this difference. In Beartooth Mountain lakes, the relationship between dissolved absorbance and K_d was stronger for UV wavelengths than for PAR (Table 2). This suggests that changes in DOC absorbance may control seasonal changes in transparency in lakes in the Beartooth Mountains.

Patterns of seasonal transparency change in Beartooth Mountain lakes differ considerably even among this geographically proximate group of lakes. Local climate in specific mountain areas is often different from regional average conditions because of the presence of orographic barriers to movement of air masses and precipitation.⁴⁵ Even though lakes may be similar topographically, geographically, and morphologically, they may exhibit very little temporal coherence because of the orographic influence on regional climate⁴⁶ and variation in terrestrial features such as vegetation cover that can strongly influence alpine lake characteristics.^{12,47} However, other studies have shown that some alpine lake characteristics such as water temperature respond coherently to climate forcing.⁴⁸ In lowland lakes, research has shown that temporal coherence between lakes is greater for limnological variables directly influenced by climatic factors than for variables either indirectly affected by climate or complexly influenced by other types of factors.⁴⁹ Thus transparency in alpine lakes, which is primarily controlled by DOC and phytoplankton biomass, may be less temporally coherent due to local climate conditions and in-lake processes.

Implications for organisms

The high UV irradiance, high UV transparency, and cold temperatures associated with alpine lakes may have important implications for the survival, growth, and reproduction of their biota. For example, zooplankton species richness and diversity decrease in lakes with high estimated UV exposure.⁵⁰ However, few *in situ* studies have demonstrated detrimental effects of UV on biological communities and related ecological processes (*e.g.* production and grazing rates).³ In stratified alpine lakes, UV-sensitive organisms that can detect and avoid UV may be faced with tradeoffs between warmer surface water where there is high UV exposure and cold hypolimnetic water where there is low UV exposure (Fig. 1). In lowland or subalpine lakes, UV attenuates more rapidly and almost all damaging UV is removed within the mixed layer. Therefore, UV sensitive organisms can remain in warmer surface waters while still avoiding high UV at the surface.

Alpine lakes often develop a deep chlorophyll maximum (DCM).^{6,51} It has been suggested that the DCM forms in response to UV avoidance by phytoplankton,⁵² however, research shows that greater nutrients below the thermocline are more predictive of DCM formation in alpine lakes of the central US Rocky Mountains.⁵¹ Zooplankton avoidance of high UV irradiance in alpine lake surface waters may stimulate some zooplankton taxa to graze deeper in the water column where temperatures are lower but phytoplankton biomass and food quality may be higher.

The amplitude of vertical migration has been shown to increase with transparency.⁵³ Some species of zooplankton have the ability to detect UV, and UV wavelengths stimulate a negative phototaxis.^{54,55} Further, studies suggest that some species of zooplankton may perform diel vertical migration (DVM) to reduce UV exposure^{56,57} and, within the water column, more sensitive zooplankton are found in lower UV environments in alpine and subalpine lakes.²² In stratified alpine lakes where, on average, the 1% depth of 380 nm UV penetrates to 3 times deeper than the mixed layer, UV-induced DVM may bring zooplankton well below the mean mixed layer into cold hypolimnetic water (but closer to the DCM). In the hypolimnion, UV may be reduced, but there may be important tradeoffs as the lower

temperature reduces growth and reproduction. For example, diel vertical migration of *Daphnia* out of warmer epilimnetic water into the hypolimnion in response to predation reduced growth rates of *Daphnia* by 36%.⁵⁸ This contrasts with subalpine lakes, where the average 1% depths of all UV wavelengths attenuate rapidly within the mixed layer and low UV conditions can be found within the warmer epilimnion. In alpine or other lakes with a DCM, the tradeoff with food availability may not be as severe because food resources increase near the DCM.⁵⁹

High UV transparency and cold temperatures in alpine lakes may also have important implications for predator–prey interactions. The vertical distribution of zooplankton in alpine and subalpine lakes may be influenced by UV exposure^{21,57,60} and/or temperature.⁶¹ In lakes containing visual predators such as fish, high UV : PAR may stimulate zooplankton to migrate deeper into the water column to lower levels of PAR compared with subalpine and lowland lakes, thereby reducing predation risk. In some lakes, however, predators may be able to take advantage of high light levels to utilize hypolimnetic and benthic productivity. For example, research has shown that young of year fish predation on zooplankton is higher in the presence of UV.⁶² In this case, high hypolimnetic light levels in alpine lakes may increase predation risk. Additional research is necessary to understand how high UV and low temperature in alpine lakes alter predator–prey interactions.

Many alpine lakes are naturally fishless; however, when cold water fish such as trout are introduced to alpine lakes, they initiate dramatic changes throughout food webs⁶³ with implications for the UV tolerance of zooplankton.⁶⁴ For example, highly pigmented zooplankton may be especially vulnerable to fish predation.^{64–66} Synthesis or accumulation of photoprotective compounds such as carotenoids may protect many taxa from UV damage,⁶⁷ however these compounds may make prey more visible to fish. Alpine zooplankton may also have mycosporine-like amino acids that only absorb UV wavelengths⁶⁸ and could be preferentially accumulated in the presence of fish. Fish may also be sensitive to the high UV conditions found in alpine lakes. Studies have shown that high UV may reduce survival of sensitive life stages of some fish species, including yellow perch (*Perca flavescens*⁶⁹) and bluegill sunfish (*Lepomis macrochirus*^{70,71}) and the high UV irradiance and cold temperatures in alpine lakes may reduce the reproductive success of fish (e.g. ref. 69 and 71).

In addition to zooplankton and fish, the UV and temperature environment in alpine lakes may have important implications for phytoplankton. Sunlight exposure can control the abundance and species distribution of algae.⁷² While some species are adapted to high light environments, others are limited to exposure that may amount to a few percent of surface irradiance. High UV may be harmful to phytoplankton and phytobenthos. For example, in the Canadian Rockies, abundance of rock-attached algae was negatively correlated with elevation and positively correlated with DOC.⁷³ Others have noted that benthic mats exposed to high UV contain high concentrations of photoprotective compounds.^{9,68}

Seasonally-late ice off in alpine lakes implies that light conditions may change rapidly from low levels under ice conditions to high solar exposure during the longest days of the year. We found that the mean surface water temperature differed by 6 °C between alpine lakes (9.4 °C) and subalpine lakes (15.5 °C). In a series of experiments incubated at two different temperatures (6 °C and 14 °C), Doyle *et al.*⁷⁴ found that while UV exposure depressed growth rates at 6 °C, when nutrient additions were excluded UV did not have a negative effect at 14 °C. This suggests that UV and temperature may interact in complex ways with other limiting growth factors such as nutrients to influence the behavior, growth, survival, and reproduction of alpine species.

Nutrient conditions in alpine lakes may play a role in mediating UV and temperature tolerances of phytoplankton and zooplankton that inhabit alpine lakes. Interactive effects of UV, DOC, and inorganic nutrients on algal community composition and productivity depend on the chemical conditions in mountain lakes.^{74,75} Doyle *et al.*⁷⁴ found that when nutrients were added to phytoplankton assemblages, UV depressed growth rates of some species at both 6 °C and 14 °C. UV radiation and phosphorus (P) may also affect phytoplankton abundance, biomass, and species composition in alpine lakes. For example, both UV and P may have direct effects on phytoplankton communities where UV inhibited growth and P stimulates growth.⁷⁶ Low nutrients and consequent low food quality in alpine lakes may also influence the ability of zooplankton to repair UV-induced damage. Balseiro *et al.*⁷⁷ found that low nutrients may place stoichiometric constraints on zooplankton which may reduce the function of enzymes to repair UV-induced damage.

Alpine lakes as sentinels of environmental change

Lakes are sentinels of broader scale processes throughout their watersheds.^{78,79} Lying in the lowest point in a landscape, lakes integrate changes throughout their watershed. Environmental changes that alter DOC, UV, or temperature may dramatically alter the ecology of alpine lakes.^{78,79} Alpine lakes may not respond to the same drivers that modify lowland ecosystems⁴⁵ and small changes in energy, water chemistry, and precipitation in alpine ecosystems may result in large changes in the physical structure, ecosystem dynamics, and water quality of alpine lakes^{11,80,81} as many ecological processes are regulated by the cold temperatures.⁸² Ecosystem responses to climate change are complex and depend on a series of interacting factors like climate, geology, and topography.⁸³ As lakes drain larger landscapes, they may integrate these changes and subtle terrestrial changes may be magnified in alpine lakes. Like Arctic and Antarctic lakes,^{4,9} alpine lakes may serve as sensitive indicators of environmental change.^{40,47,84,85}

As a class, alpine lakes may respond differently to environmental changes depending on lake depth and volume because of their physical and biological differences inherent among lakes. For example, shallow alpine lakes (maximum depth < 10–15 m) may not have a refuge for biota from high UV exposure which may regulate what species can survive. Research suggests that this depth threshold may regulate the biological community⁴⁷ and hence may alter how a particular lake responds to environmental change.

Environmental changes, such as variation in snowfall, that partially control the timing and magnitude of allochthonous inputs into alpine lakes may affect transparency in alpine lakes. Snowfall records in Red Lodge, MT (adjacent to the Beartooth Mountains), reveal that there has been a long term increase in snowfall precipitation over the period 1903–2008 ($R^2 = 0.15$, $p < 0.001$) (Fig. 6). However, there has also been a significant decline in snowfall since 1975 ($R^2 = 0.49$, $p < 0.001$). Throughout the twentieth century, the central US Rockies have experienced an increase in total annual precipitation and mean minimum temperature.⁸⁶ We found that annual snowfall records in Red Lodge, MT, USA were related to seasonal changes in transparency in four of our eight study lakes in the region (Table 3). Variation in transparency between years was related to total snowfall in the previous winter, where following high snowfall winters lakes were less transparent. This result contrasts to other research indicating that similar lakes in the Canadian Rockies were clearer following high snowfall and cold winters.⁸⁵ In the Canadian Rocky lakes, high snowfall years were followed by warm dry summers which may have offset any changes in DOC induced by high snowfall.

Linking seasonal changes in transparency to snowfall effectively shows that transparency is a sentinel of climate patterns. Regular monitoring of the physical and biological structure of

alpine lakes should provide a particularly sensitive system for detecting biogeochemical responses of high mountain catchments to climate change.

Alpine lakes may also be sentinels of many other types of environmental changes^{40,84,87-92} For example, in areas of the southern Rocky Mountains of Colorado (USA), anthropogenic deposition of nitrogen (N) has stimulated changes in high elevation productivity, and many lakes are now N saturated⁹³ These N changes have been driven by small changes in atmospheric deposition and have the potential to result in large changes in ecosystem dynamics and water quality.⁴⁵ In the Colorado Front Range and the Beartooth Mountains, changes in diatom community structure over the last century have occurred due to enhanced atmospheric nitrogen deposition;^{94,95} some of these community changes in the Beartooth Mountains may be driven by changes in climate.⁹⁶ Sediment records in alpine lakes also reveal past climate signals. For example, Leavitt *et al.*⁹⁷ found that fossil pigments in lake sediments could be used to reconstruct the past UV environment, and measurements of total organic carbon in lakes sediments can be used to infer changes in tree line.⁹⁸

Alpine regions around the world are projected to increase in temperature more than lower elevation regions as a result of anthropogenically induced climate change⁹⁹ Climate warming may have important implications for the physical structure and consequently for the biology of alpine ecosystems; it may alter terrestrial vegetation in alpine environments as terrestrial biomass increases and tree line advances in response to longer growing seasons and warmer temperatures.^{10,11,100} Long term changes in DOC, both increases and decreases, have been recorded in many different regions of the northern hemisphere. While research suggests that changes in many areas are not climate-related,¹⁰¹ other studies suggest that recent reductions in arctic DOC export may be a product of climate change.¹⁰² Changes in DOC optical quality and quantity as a result of changes in alpine vegetation may induce consequent changes in transparency.^{19,103} Changes in treeline associated with climate warming may dramatically alter transparency of alpine lakes¹⁰⁴ and lakes close to but above treeline may experience dramatic reductions in UV transparency due to climate change.³ UV transparency, therefore, may serve not only as an important abiotic force structuring the ecology of alpine lakes, but also as a sensitive sentinel of environmental changes in alpine ecosystems.

Conclusions

High UV irradiance and transparency, coupled with low temperature in alpine lakes regulate the physical structure of alpine lakes and have important implications for the organisms that inhabit these systems and their vertical distribution within the water column.

High UV transparency in alpine lakes is largely a product of low DOC concentrations but also low DOC-specific absorbance. Future changes in DOC induced by climate warming may increase both DOC concentration and DOC-specific absorbance. These changes may reduce the UV transparency and alter the physical structure of alpine lakes.

Seasonal changes in transparency of alpine and subalpine lakes appear to differ from lowland lakes and may be driven by climate conditions. Future changes in snowfall and allochthonous inputs may alter the transparency of alpine lakes.

Just as Arctic lakes can be effective optical indicators of environmental change,^{4,9} alpine lakes also serve as particularly sensitive indicators of environmental changes. As such, alpine lakes have an important role to play in understanding how complex environmental changes are influencing natural ecosystems.

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Craig Williamson received his PhD from Dartmouth College and was a professor at Lehigh University before moving to Miami University in 2005. He spent two summers at marine labs: in Woods Hole, MA, USA, and at University of Washington's Friday Harbor lab. His early research was on trophic interactions involving zooplankton, but in the past 16 years his work has focused on the ecology of UV in alpine lakes worldwide. Since 2001 he has led a large NSF IRCEB project on UV effects on pelagic freshwater ecosystems. His more recent work is on UV as a component of climate change.

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Fig. 1. Mean percent irradiance for 320 nm, 380 nm UV, and PAR and temperature data for subalpine (left, A) and alpine (right, B) lakes plotted vs. depth show that physical structure of subalpine, and alpine lakes differ in important ways. Transparency data are based on average epilimnetic diffuse attenuation coefficients and temperature data are based on surface temperatures, mixing depths, and hypolimnetic temperatures of lakes in Table 1.

Fig. 2.

One percent (of surface irradiance) depths and diffuse attenuation coefficients (K_d) plotted as a function of DOC concentration. The more rapid change in 1% depths with small changes in DOC lakes in alpine *versus* lowland lakes (A) are expected based on a simple inverse transformation of the linear relationship between diffuse attenuation coefficients and DOC concentrations (B). While the rapid increase in transparency at low DOC concentrations results largely from the exponential relationship between light and depth, there is also evidence for changes in the optical quality of the DOC at very low concentrations (see Fig. 4). Data from Morris *et al.* (1995).¹⁶

Fig. 3.

DOC-specific absorption coefficients ($a_d:[DOC]$) plotted as a function of DOC concentration (mg L^{-1}) show that DOC-specific absorbance increases with DOC concentration in alpine lakes. In subalpine lakes, there was no relationship between DOC-specific absorption coefficient and DOC concentration for any wavelengths (left graph). In alpine lakes, variation in DOC concentration was significantly related to the DOC-specific absorption coefficient for 305 nm UV ($R^2 = 0.33$, $p = 0.0247$) and 320 nm UV ($R^2 = 0.31$, $p = 0.0297$), but not for 380 nm UV ($R^2 = 0.25$, $p = 0.0577$), 440 nm ($R^2 = 0.25$, $p = 0.1508$) and PAR ($R^2 = 0.08$, $p = 0.3073$) in alpine lakes (right graph). Several factors such as allochthony, photobleaching, or lake chemistry could explain these patterns in alpine lakes.

Fig. 4.

Seasonal transparency data for four alpine (Heart, Fossil, Emerald, and Glacier) and four subalpine (Beauty, Island, Beartooth, and Kersey) lakes in the Beartooth Mountains, WY/MT, USA. Data plotted are from multiple years (2001–2008) and presented as percent change relative to the profile collected earliest in the year for 320 and 380 nm UV and PAR. Seasonally, most lakes increased in transparency. In two lakes, Beartooth and Beauty, there was a strong difference in the seasonal patterns of change of UV (320 and 380 nm) relative to PAR.

Fig. 5.

Absorption coefficients for 305, 320, and 380 nm UV, and PAR *vs.* diffuse attenuation coefficients (K_d) of 305, 320, and 380 nm UV and PAR from both alpine and subalpine study lakes in the Beartooth Mountains in 2007. The tight linear relationship shows that variations in dissolved absorbance alone can account for the majority of variation in water transparency among lakes and seasonally. Ten lakes were sampled soon after ice out in 2007 (early July) and eight of these were sampled again in late August (end of summer) 2007. See also Table 2.

Fig. 6. Snowfall records (cm of snow) in Red Lodge, MT, USA, for the period 1903–2008. Note that there has been a long term increase in snowfall precipitation over the entire period (solid line, $R^2 = 0.15$, $p < 0.001$), yet there has also been a significant decline in snowfall since 1975 (dashed line, $R^2 = 0.49$, $p < 0.001$).

Mixed layer depths and depths to which one percent of surface irradiance at different wavelengths ($Z_{1\%}$, 320 and 380 nm UV and PAR, 400–700 nm) penetrates in a series of alpine lakes from diverse geographic regions in comparison to nearby sub-alpine lakes. 320 : PAR represents the 320 nm $Z_{1\%}$ depth as a percent of the PAR $Z_{1\%}$ depth. Surface temperatures were measured at 0.5 m depth. Mixed layer depths were calculated at the depth where temperature change exceeded 1 °C per metre and (B) indicates that the lake was mixed to the maximum depth sampled (either the bottom of the lake or the maximum length of the radiometer cable)

Table 1

Alpine lakes									
Region	Lake	Mixed layer/m	$Z_{1\%}(320)/m$	$Z_{1\%}(380)/m$	$Z_{1\%}(PAR)/m$	320 : PAR (%)	Surface T/°C		
New Zealand (S. Island)	Alta	21.8 (B)	11.1	21.0	34.9	31.8	6.6		
Beartooths (MT/WY, USA)	Little Heart	1.8	1.9	3.7	10.7	17.7	7.4		
Beartooths (MT/WY, USA)	Heart	4.8	2.5	4.4	10.8	23.1	8.9		
Beartooths (MT/WY, USA)	Emerald	5.4	4.3	7.7	15.3	28.1	5.6		
Beartooths (MT/WY, USA)	Fossil	8.1	2.9	5.5	15.6	18.6	10.3		
Beartooths (MT/WY, USA)	Glacier	13.8 (B)	3.7	6.9	18.4	20.1	7.0		
Beartooths (MT/WY, USA)	Dewey	1.4	2.9	6.1	12.4	23.5	9.7		
Beartooths (MT/WY, USA)	Fizzle	7.3	3.4	7.0	12.1	28.1	12.1		
Colorado (USA)	Forest #2	1.1 (B)	1.0	1.4	3.4	29.5	10.4		
Colorado (USA)	Green #4	4.5 (B)	2.4	4.5	10.4	23.2	12.4		
Canadian Rockies	Amiskwi	9.6	8.0	13.0	17.1	47.0	10.5		
Canadian Rockies	Eifel	7.7	30.9	78.1	59.8	51.7	9.0		
Canadian Rockies	Hamilton	2.1	3.7	4.4	7.7	48.5	9.5		
Canadian Rockies	Oesa	4.5	11.1	14.9	21.8	51.0	6.6		
Canadian Rockies	Opabin	1.8	3.7	5.1	9.8	37.4	6.5		
Canadian Rockies	Sunlite	21.9 (B)	8.5	13.5	20.0	42.7	3.5		
Austrian Alps	Faselfadsee	12.4 (B)	37.1	63.8	55.1	67.4	9.3		
Austrian Alps	Gossenköllesee	9.0 (B)	15.0	27.5	31.3	47.9	13.4		
Argentina	Toncek	9.4 (B)	7.3	14.3	27.1	26.9	11.0		
Sierra Nevadas (CA, USA)	Lower Treasure	5.6 (B)	8.2	14.6	20.6	40.0	13.0		
Sierra Nevadas (Spain)	La Caldera	8.2 (B)	6.7	9.8	17.9	37.4	10.0		
Switzerland Alps	Cadagno	7.0	1.8	3.8	11.5	15.7	15.0		
Mean		5.1	8.1	15.0	20.2	34.4	9.4		
Standard error		0.8	2.0	4.1	3.0	2.9	0.6		

Subalpine lakes									
Region	Lake	Mixed layer/m	Z _{1%} (320)/m	Z _{1%} (380)/m	Z _{1%} (PAR)/m	320 : PAR (%)	Surface T/°C		
New Zealand (S. Island)	Hayes	0.7	1.7	4.0	10.8	15.9	19.0		
	Beartooths (MT/WY, USA)	3.9	0.5	1.4	10.4	4.8	16.2		
	Beartooths (MT/WY, USA)	4.9	1.1	2.8	12.5	9.1	14.8		
	Beartooth (MT/WY, USA)	4.5	1.4	3.1	11.2	12.1	14.1		
	Beartooths (MT/WY, USA)	1.6	0.6	1.4	7.4	8.1	13.8		
	Beartooths (MT/WY, USA)	4.8	2.5	6.1	18.7	13.4	13.1		
	Beartooths (MT/WY, USA)	6.3	0.8	1.9	9.2	8.8	13.0		
	Beartooths (MT/WY, USA)	5.8	2.3	5.6	16.4	14.0	14.6		
	Colorado (USA)	Unknown	1.2	2.7	7.9	15.7	Unknown		
	Colorado (USA)	Unknown	0.1	0.3	1.5	8.3	Unknown		
Canadian Rockies	Duchesnay	1.6 (B)	1.7	4.2	11.3	15.2	16.4		
	Hungabee	1.8 (B)	3.8	10.5	35.4	10.6	13.4		
	Sink	0.8 (B)	2.2	5.2	12.9	17.0	17.3		
	Summit	0.6 (B)	1.0	2.3	7.5	13.6	17.4		
	Mary	3.1 (B)	4.7	10.2	26.4	17.8	14.1		
	Achensee	14.8 (B)	2.6	6.1	15.3	17.0	19.3		
	Tovel	1.5	4.6	11.8	27.3	16.8	12.9		
	Mondsee	Unknown	1.8	4.9	10.6	17.0	Unknown		
	Piburgersee	10.1	1.4	3.7	17.7	7.9	10.9		
	Trebol	7.9	1.4	2.9	12.0	11.7	19.5		
Sierra Nevadas (CA, USA)	Escondido	5.4	0.6	1.5	10.0	6.0	20.0		
	Rock Creek	9.7	2.9	6.6	19.2	15.3	14.5		
	Mean	5.2	1.9	4.5	14.2	12.6	15.5		
	Standard Error	0.8	0.3	0.7	1.6	0.9	0.6		

Table 2

Results of least squares linear regression to test whether dissolved absorption coefficients were related to diffuse attenuation coefficients for early season and late season samples from Beartooth Mountain lakes. The high R^2 values for UV wavelengths in particular indicate that dissolved absorbance accounts for the majority of variation in transparency among lakes and seasonally. See also Fig. 5

	Early season				Late season			
	305 nm	320 nm	380 nm	PAR	305 nm	320 nm	380 nm	PAR
R^2	0.99	0.98	0.97	0.61	1.00	1.00	0.99	0.86
p	<0.001	<0.001	<0.001	0.008	<0.001	<0.001	<0.001	<0.001
Slope	1.12	1.12	1.12	0.68	1.12	1.14	1.23	0.84
Intercept	0.38	0.32	0.26	0.26	0.29	0.22	0.1502	0.2312

Table 3

Results of least squares linear regression to test if total annual snowfall from the previous winter was related to seasonal changes in transparency. In four of eight lakes there were significant relationships (bold text). In all other lakes except for Heart Lake, a trend was present but was not significant. These data reveal that seasonal changes in transparency are a sensitive indicator of snowfall in some high mountain lakes

Lake	320 nm		380 nm		PAR	
	<i>R</i> ²	<i>p</i>	<i>R</i> ²	<i>p</i>	<i>R</i> ²	<i>p</i>
Heart	0.07	0.480	0.01	0.812	0.01	0.811
Fossil	0.49	0.082	0.46	0.095	0.15	0.392
Emerald	0.30	0.042	0.25	0.070	0.19	0.117
Glacier	0.37	0.063	0.25	0.143	0.10	0.377
Beauty	0.24	0.106	0.36	0.038	0.00	0.986
Beartooth	0.49	0.008	0.41	0.019	0.27	0.067
Island	0.35	0.057	0.23	0.138	0.00	0.967
Kersey	0.61	0.023	0.69	0.010	0.10	0.440