Sentinel responses to droughts, wildfires, and floods: effects of UV radiation on lakes and their ecosystem services

Craig E Williamson[1*], Erin P Overholt[1], Jennifer A Brentrup[1], Rachel M Pilla[1], Taylor H Leach[1], S Geoffrey Schladow[2], Joseph D Warren[3], Samuel S Urmy[3], Steven Sadro[4], Sudeep Chandra[5], and Patrick J Neale[6]

Environmental drivers such as climate change are responsible for extreme events that are critically altering freshwater resources across the planet. In the continental US, these events range from increases in the frequency and duration of droughts and wildfires in the West, to increasing precipitation and floods that are turning lakes and reservoirs brown in the East. Such events transform and transport organic carbon in ways that affect the exposure of ecosystems to ultraviolet (UV) radiation and visible light, with important implications for ecosystem services. Organic matter dissolved in storm runoff or released as black carbon in smoke selectively reduces UV radiation exposure. In contrast, droughts generally increase water transparency, so that UV radiation and visible light penetrate to greater depths. These shifts in water transparency alter the potential for solar disinfection of waterborne parasites, the production of carcinogenic disinfection byproducts in drinking water, and the vertical distribution of zooplankton that are a critical link in aquatic food webs.

Front Ecol Environ 2016; 14(2): 102-109, doi:10.1002/fee.1228

Climate change is contributing to an increase in extreme weather events, ranging from heat waves and droughts to unusually heavy precipitation and record-breaking floods (Melillo *et al.* 2014). For example, much of the western US has experienced exceptional drought conditions accompanied by an increase in large wildfires (Figure 1, a and b). Wildfires burned on average over 2.6 million ha per year across the US from 2000 to 2010, with serious consequences for the landscape as well as for human health (Melillo *et al.* 2014). Large wildfires (> 405 ha) increased at a rate of seven fires per year in the western US from 1984 to 2011 (Dennison *et al.* 2014). In late August of 2015, over 70 large fires were burning simultaneously in 10 different states, covering much of the western US in smoke (NIFC nd); the predicted median increase in carbon emissions by the end of the century generated by California wildfires alone is 56% (Hurteau *et al.* 2014). In contrast, in the northeastern US, extreme precipitation events increased by 71% from 1958 to 2012 (Figure 2a), and many lakes and rivers are turning brown due to increases in the quantity and darker color of dissolved organic matter (DOM) as well as from increased turbidity (Figure 2b; Williamson *et al.* 2014a). These extreme events transform and transport organic carbon and particulate compounds across the planet in ways that alter exposure to solar ultraviolet (UV, ~295–400 nanometers [nm] for sunlight) radiation, with important consequences for freshwater ecosystems. Here we report on our recent research in lakes that are experiencing different extreme events, showing that drought, wildfire, and heavy precipitation can selectively alter exposure of aquatic ecosystems to UV radiation versus visible light (essentially photosynthetically active radiation [PAR], 400–700 nm) by producing smoke and by modifying terrestrially derived inputs of DOM (Panel 1).

Natural lakes and human-made reservoirs are effective sentinels of climate change. As low-elevation sites

In a nutshell:

- Extreme events related to climate change and other environmental drivers vary greatly among regions; for example, droughts and wildfires dominate in the western US, whereas heavy precipitation and floods are more common in the eastern US
- These extreme events transform and transport organic carbon and particulates in ways that alter exposure to ultraviolet (UV) radiation and visible light, with important implications for lakes and the ecosystem services they provide
- Interactions and feedbacks between climate change and UV radiation are altering terrestrial and aquatic ecosystems, making UV transparency a valuable indicator of how lakes, their watersheds, and their ecosystem services are being transformed by extreme events

[1]*Department of Biology, Miami University, Oxford, OH* [*]*(craig.williamson@miamiOH.edu);* [2]*Department of Civil and Environmental Engineering, University of California, Davis, Davis, CA;* [3]*School of Marine and Atmospheric Sciences, Stony Brook University, Southampton, NY;* [4]*Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA;* [5]*Department of Biology, University of Nevada, Reno, Reno, NV;* [6]*Smithsonian Environmental Research Center, Edgewater, MD*

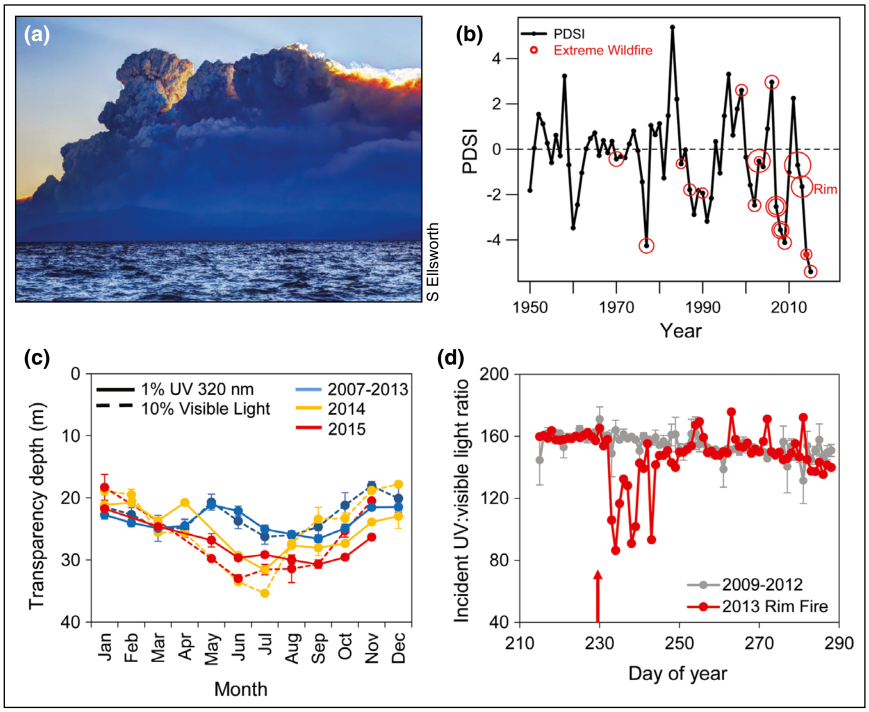


Figure 1. Drought and wildfire effects on UV radiation and visible light exposure. (a) Smoke plume from the 2014 King Fire over Lake Tahoe. (b) The Palmer Drought Severity Index (PDSI) for California, and 19 of the top 20 wildfires in the state's history (data from CAL FIRE 2015; NOAA nd). The size of the circle is proportional to the area burned; the red dot represents the 2014 King Fire, which was not among the top 20 largest fires. (c) Seasonal changes in water transparency as the depth to which 1% of subsurface UV radiation and 10% of subsurface visible sunlight penetrate (mean ± standard error) in Lake Tahoe 2007–2013 versus two exceptional drought years. (d) Selective decrease in incident UV radiation versus visible light reaching Lake Tahoe during the 2013 Rim Fire (red arrow is the time at which the fire started) compared to the average (± standard error) for the preceding 4 years.

within a given landscape, they serve as multi-proxy sensors. They provide sentinel responses, defined here as changes in the physics, chemistry, or biology of these systems, thereby informing scientists about how both terrestrial and aquatic ecosystems are being altered by varying (including extreme) environmental conditions across multiple time scales (Williamson *et al.* 2014a). Many of the sentinel responses of extreme events on lakes, such as changes in water levels or turbidity, are highly visible (Figure 2b). Other responses are more subtle, such as changes in the UV transparency of lakes, generally measured as the depth to which UV radiation penetrates. Exposure to UV radiation is mutagenic and potentially lethal to many aquatic organisms, especially the small, delicate, and often highly transparent eggs and larvae of various fish species (Zagarese and Williamson 2001; Tucker and Williamson 2014) as well as the plankton that make up the food webs of pelagic ecosystems (Rautio and Tartarotti 2010). Yet there is emerging evidence that UV radiation has many beneficial effects for aquatic ecosystems as well. Although damaging to DNA, solar UV radiation also serves as a key environmental cue for foraging and mating in fish, amphibians, and birds, and induces vitamin D production (Williamson *et al.* 2014b). UV radiation can also reduce the invasion success of certain fish (Tucker and Williamson 2014) and help to disinfect surface waters by killing parasites (Overholt *et al.* 2012). Here, we present evidence that extreme events, ranging from drought and wildfire to heavy precipitation and floods, alter UV radiation exposure in lakes. While we focus primarily on the less apparent effects of these extreme events on UV radiation, we also discuss some of the more apparent effects on visible light for comparison.

Droughts and wildfires

Extreme drought, especially when accompanied by high winds, can devastate landscapes. The Dustbowl of the 1930s in the Great Plains of the US is just one example: in that case, severe droughts led to continental-scale dust storms that eroded massive amounts of topsoil and transported it over long distances, with serious consequences for humans and natural ecosystems. Dust from arid desert regions can contribute enough DOM to reduce the UV transparency of highly transparent lakes, even at intercontinental scales (Mladenov *et al.* 2011). Yet under less extreme drought conditions or in less arid, more vegetated regions, droughts may reduce the inflow of water, DOM, and inorganic particulates to lakes, with consequent increases in water transparency to both UV radiation and visible light.

Located along the California–Nevada border in the western US, Lake Tahoe is one of the most transparent lakes in the world. One percent of the potentially damaging 320-nm ultraviolet-B (UV-B) radiation and 10% of both 380-nm ultraviolet-A (UV-A) radiation and visible light can penetrate up to 20–30 m below the lake's surface. We found that there is generally a strong seasonality to the transparency of Lake Tahoe, with UV and visible transparency being highest around March and August and lowest around May and November (blue line in Figure 1c). During 2014 and 2015, much of California, including the Lake Tahoe region, experienced an exceptional drought that led to an increase in UV-B penetration from the 20–25-m average observed in the previous 7 years to more than 30 m during the summer peak in inci-

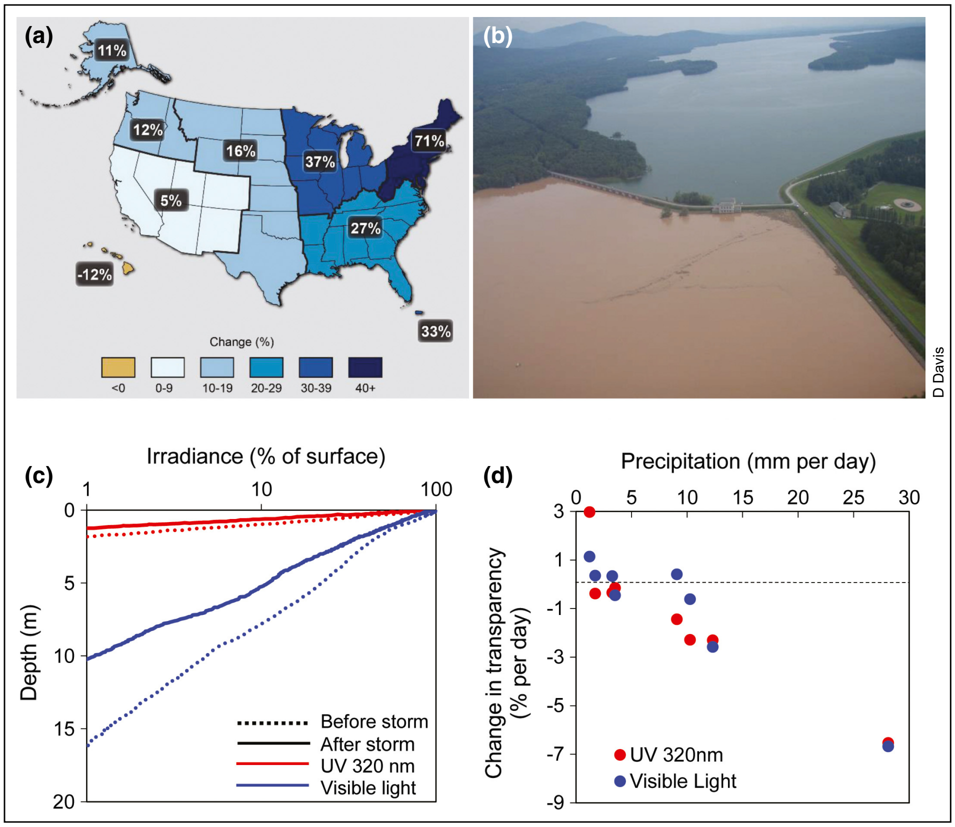


Figure 2. *Effects of heavy precipitation events on UV radiation and visible light in lakes. (a) Increase in extreme precipitation events (top 1%, 1958–2012; updated from Karl* et al. *2009 [Melillo* et al. *2014]). (b) A weir protects the east basin of New York City's Ashokan Reservoir from turbid water in the west basin induced by tropical storm Irene in 2011. (c) Profiles of UV radiation and visible light versus depth in Pennsylvania's Lake Giles before and after tropical storm Ivan in 2004. (d) Changes in transparency in Lake Giles as a function of precipitation during four storm events and four non-storm periods.*

dent solar UV radiation exposure (Figure 1c). Water transparency to visible light showed a similar drought-related increase (Figure 1c); this was more likely related to a reduction in fine particulates than to reductions in DOM, given that the former, including both inorganic sediments and phytoplankton, are the primary regulators of water transparency in Lake Tahoe (Swift *et al.* 2006). Fine particulates generally attenuate UV radiation and visible light to a more similar extent, whereas DOM, as with ozone in the atmosphere, selectively absorbs shorter UV wavelengths (Panel 1).

Severe drought conditions in California in recent years have resulted in an increase in the frequency of large wildfires (Figure 1b). Wildfires fundamentally transform terrestrial landscapes, burning much of the vegetation and converting fixed organic carbon to gaseous and particulate carbon. Wildfires also lead to massive erosion through the burning of terrestrial vegetation, which destabilizes soils; as a result, when wildfires burn a large portion of a vegetated lake catchment, the concentration of DOM in the lake can increase (Allen *et al.* 2003). Large fires also produce vast smoke plumes that can transport organic carbon and other combustion byproducts at continental to global scales (Figure 4). Data on the UV absorbing capacity of wildfire smoke plumes are very sparse, although the organic matter in smoke may selectively reduce exposure to incident solar UV radiation versus visible light through both scattering and absorption (Kalashnikova *et al.* 2007).

Our studies, based on multi-year records of water transparency in Lake Tahoe before and during the Rim Fire in 2013 and the King Fire in 2014 (both in California), showed no changes in UV or visible transparency of the water from smoke or ash deposition, likely due to the long distance (Rim Fire) or wind direction (King Fire) (Williamson *et al.* unpublished data). Neither fire was located within the Lake Tahoe catchment, thus eliminating any potential fire-induced increases in erosion. The UV and visible transparency of Lake Tahoe may have been reduced by the Angora Fire that burned within the lake's catchment in 2007 (Rose *et al.* 2009). Despite a lack of evidence that smoke/ash deposition from the Rim and King fires affected water transparency in Lake Tahoe, the fires' smoke plumes did alter incident exposure to UV radiation. For example, when the smoke plume from the distant Rim Fire (120 km south of Lake Tahoe) traversed the lake in 2013 (Figure 4a), incident solar UV radiation relative to visible light was reduced (Figure 1d). Over a period of about 10 days, the UV-to-visible light ratio remained lower than usual, albeit with high variability due to changes in wind direction and the thickness of the smoke plume. Nonetheless, at times, the UV-to-visible light ratio was reduced by almost 50% as compared with normal non-smoke levels for that time of year (Figure 1d). This demonstrates the presence of teleconnections (connections between environmental events occurring great distances apart) wherein smoke plumes can selectively reduce UV exposure levels even in lakes that are located at considerable distances from the wildfire.

The changing UV radiation environment in transparent lakes like Lake Tahoe – in response to drought and wildfires – may have important ecological conse-

Panel 1. Effects of three important environmental substances on attenuation of the different wavelengths of sunlight in terrestrial and aquatic ecosystems

Atmospheric ozone, 90% of which is located in the lower stratosphere, and smoke resulting from wildfires and the burning of biomass, attenuate sunlight before it reaches terrestrial and aquatic ecosystems (Figure 3). Dissolved organic matter (DOM), although derived primarily from terrestrial ecosystems, attenuates sunlight primarily in aquatic ecosystems (Figure 3). Attenuation of UV radiation by ozone is much more restricted to the shorter wavelengths of UV-B, whereas both DOM and especially smoke attenuate UV-A radiation and visible light in addition to UV-B. These three ubiquitous environmental substances (ozone, DOM, and smoke) are therefore critical in regulating UV-to-visible light ratios in the environment, which influence important processes ranging from DNA damage and vitamin D production (both of which show maximum response to very short wavelengths of UV-B) to the direction of migration of zooplankton in the water column. For example, the common freshwater crustacean *Daphnia* is attracted to longer wavelength visible light but avoids UV radiation. Wavelength-specific attenuation by particulates is not shown here as it depends on size and chemical composition of the particulate material.

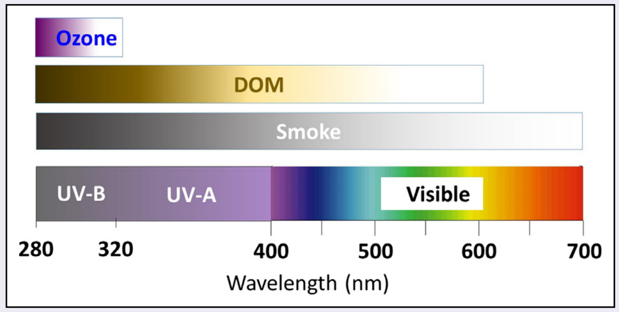
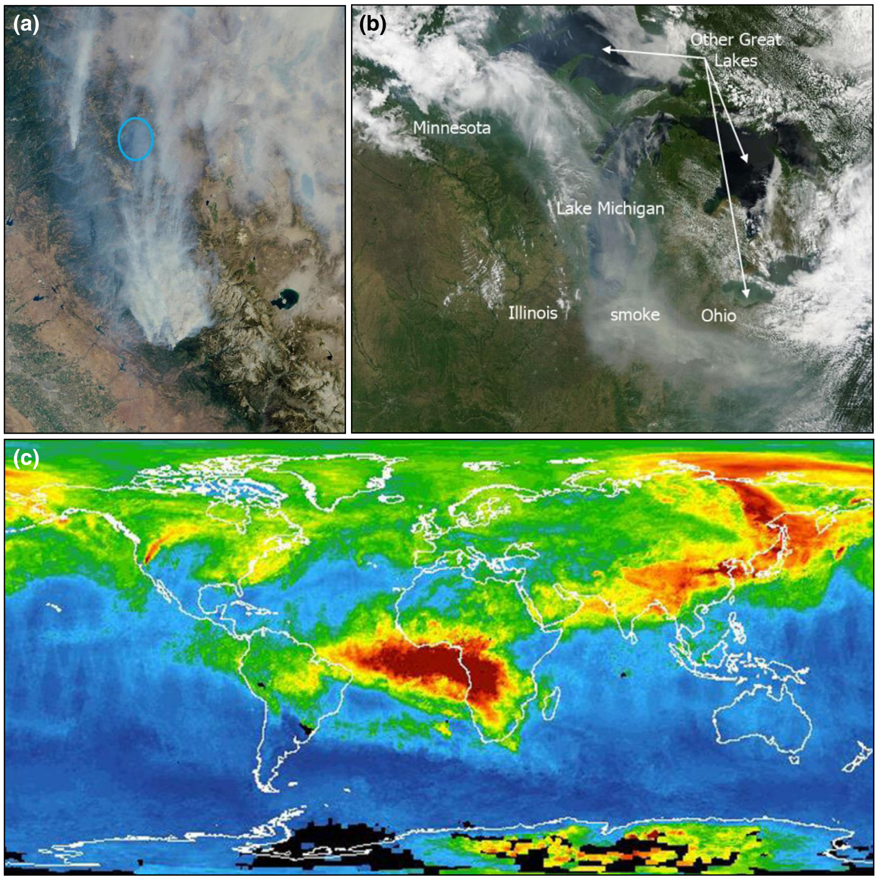


Figure 3. *Relative strength of attenuation of UV radiation and visible light in solar radiation by ozone, terrestrially derived, dissolved organic matter, and smoke from wildfires and biomass burning. The darker colors in each bar represent greater attenuation at the corresponding wavelength.*

quences. Differential tolerance of UV and visible solar radiation for eukaryotic versus prokaryotic picophytoplankton has been experimentally demonstrated in Lake Tahoe, and this tolerance may have contributed to vertical niche partitioning between these two major groups (Winder 2009). Furthermore, the vertical distribution of the copepod-dominated zooplankton in the lake was 3 m shallower when the edge of the smoke plume from the King Fire reduced exposure to incident UV radiation by 9% with no measureable changes in visible light on two sequential days (Urmy *et al.* unpublished data). Upon exposing copepods – inhabiting 15 lakes across North and South America – to sunlight from which UV wavelengths had been experimentally removed, Overholt *et al.* (2016) detected strong and statistically significant behavioral responses in eight of nine copepod species and in 12 of 15 copepod populations, including populations from Lake Tahoe. In addition to influencing copepod behavior, UV radiation has a wide variety of other effects on many zooplankton species (Rautio and Tartarotti 2010). Exposure to different UV-to-PAR ratios in lakes may be particularly important in zooplankton species, such as *Daphnia*, that have both UV radiation and visible light receptors and are attracted to visible light but avoid UV radiation (Storz and Paul 1998). Elevated levels of UV radiation in the surface waters of Lake Tahoe have the potential to reduce the reproductive success of invasive warm-water fish species (Tucker and Williamson 2014), and UV radiation and even visible light transparency may also enhance the solar disinfection of parasites of *Daphnia* in lakes that are much less transparent than Lake Tahoe (Overholt *et al.* 2012).

Extreme precipitation and floods

Heavy precipitation and flood events are becoming more frequent, especially in the northeastern US (Figure 2a), and are increasing the transport of dissolved and particulate matter into lakes and reservoirs, turning them brown (Figure 2b). Increases in the concentration and in the dark color of terrestrially derived DOM lead to reductions in UV transparency, and can be observed on scales ranging from single storm events to interdecadal trends of increasing precipitation (Williamson *et al.* 2014a). During extreme precipitation events, increases in particulates may similarly reduce water transparency to visible light. During tropical storm Ivan, for instance, which generated 16.6 cm of rain in a single day, water transparency to UV radiation and visible light in Lake Giles, a seepage lake with essentially no stream inputs in Pennsylvania, was reduced by one-third (Figure 2c). To examine this further, we collated data for this lake from four events for which UV radiation and visible light transparency measurements before and after a storm were available, as well as during four non-storm periods. The storms included tropical storms Floyd (17 September 1999), Ivan (18 September 2004), Irene, and Lee (28 August and 7 September 2011; these two events were combined in our analysis), and an unnamed storm (26 June 2006; see Rose *et al.* 2012). This analysis revealed a strong decrease in UV radiation and visible light transparency with increasing strength of the precipitation event (Figure 2d). Transparency to UV radiation and visible light were higher during the non-storm periods with very low precipitation (Figure 2d), results that



(a), (b), and (c) NASA

Figure 4. *Images of the far-reaching effects of smoke plumes on UV radiation and photosynthetically active radiation (PAR) exposure in aquatic ecosystems, including smoke from (a) the California Rim Fire on 27 August 2013 drifting up across Lake Tahoe (blue oval) 120 km away, (b) smoke from Canadian wildfires drifting down across the Laurentian Great Lakes on 9 June 2015, and (c) an image from 24 August 2013 showing global smoke plumes (yellow to red) that stretch across oceans. Note the small size of the Rim Fire (third largest in California's history) as compared with smoke from biomass burning.*

were consistent with our observations of increased transparency related to extreme droughts in Lake Tahoe (Figure 1c).

The ecological consequences of precipitation-induced reductions in the transparency of lakes include shallower and warmer surface mixed waters, along with shallower chlorophyll maxima (the depth at which the maximum chlorophyll concentration is observed) and greater oxygen depletion in deeper waters. Shallower daytime depth distributions of important zooplankton grazers, such as *Daphnia*, have also been observed in response to single extreme precipitation events (Rose *et al.* 2012). The ability of *Daphnia* to detect and respond differently to UV radiation and visible light enable it to regulate its position in the water column and avoid exposure to potentially damaging UV in surface waters. Thus, selective changes in water transparency to UV radiation relative to visible light resulting from contrasting climate-driven extreme events can modify the vertical habitat gradients and depth distribution of zooplankton. This has the potential to change the vertical overlap between zooplankton and their food resources, as well as in relation to their planktivorous fish predators, with concomitant implications for trophic interactions and the flow of nutrients and energy through aquatic ecosystems.

Regional variability

Extreme events show strong regional variation (Melillo *et al.* 2014). In the US, the effects of wildfire are not limited to lakes in the western states, nor are the effects of heavy precipitation limited to lakes in the Northeast. However, in spite of this regional variability, the sentinel responses remain similar. For example, smoke plumes from wildfires in Canada frequently reach far south into the US, often traversing the Laurentian Great Lakes (Figure 4b). In 2002, a series of these Canadian wildfires caused pollution and concerns about human health as far south as the Baltimore–Washington, DC region (Melillo *et al.* 2014), a distance of over 1500 km. Our data revealed that these 2002 fires reduced daily total solar irradiance in the Baltimore–Washington, DC region by up to 60% and incident 320-nm UV-B by up to 93%. In the western US, a single storm event that generated 18.5 cm of rain in one day increased particulates and nearly doubled DOM concentrations in Emerald Lake, an alpine lake in California, cutting the depth of visible light penetration by one-half and shifting the lake from net autotrophy to net heterotrophy (Sadro and Melack 2012). Heavy rainfall in Florida related to the Atlantic Multidecadal Oscillation has similarly reduced visible light penetration (measured as Secchi depth, the depth at which a 20-cm white, or white and black, disk can be observed underwater) in subtropical Lake Annie from 4–8 m to 0.1–3 m on a cyclical multiannual basis (Gaiser *et al.* 2009). Many other types of extreme events may have similar effects. For example, an avalanche in the watershed of alpine Lake Oesa in the Canadian Rocky Mountains reduced UV transparency (1% of 320-nm subsurface levels) from the 12–21-m depths generally observed in July to only 4.5–7.8 m (Brentrup *et al.* unpublished data). The 1% visible light transparency in Lake Oesa was reduced to less than half of the mean depth of 32.6 m.

On a global scale, dust storms contribute substantial amounts of DOM and thus alter UV radiation exposure even in remote alpine lakes (Mladenov *et al.* 2011). Smoke from large-scale biomass-burning incidents extends not only across lakes in terrestrial landscapes but also over much of the world's oceans (Figure 4c). Climate teleconnections, including the El Niño–Southern Oscillation and North Atlantic Oscillation, are also related to oscillations in atmospheric ozone concentrations, and thus UV radiation exposure in lakes across North America (Petropavlovskikh *et al.* 2015).

Interactions with climate change

There are some potentially important interactions and feedbacks between climate, extreme events (including fires), and exposure to UV radiation and visible light. Climate change is projected to increase lightning strike frequency, a source of ignition for wildfires (Romps *et al.* 2014). The char produced by incomplete combustion of carbon by wildfires is highly resistant to biodegradation, but exposure to UV radiation increases the biodegradability of DOM leachates from char in soils from burn sites, thereby accelerating the conversion of fixed carbon to greenhouse gases (Olefeldt *et al.* 2013). Black carbon produced from the burning of massive amounts of biomass (Figure 4c) decreases albedo, thereby increasing air temperatures and accelerating snow and ice melt; this will in turn alter downstream lakes and coastal marine systems, as well as the frequency and severity of regional droughts (Hadley and Kirchstetter 2012), and consequently the UV and visible transparency of these ecosystems. The warming of coastal waters increases water vapor in the atmosphere, which is linked to the severity of extreme precipitation events (eg the large-scale flooding that caused the deaths of 170 people in Krymsk, Russia, in 2012; Meredith *et al.* 2015). These extreme precipitation events can provide positive feedback by transporting DOM to coastal waters, which leads to increased absorption of sunlight by surface waters. In consequence, surface water temperatures rise and evaporative loss of water to the atmosphere increases, creating the potential for further extreme rain events. The increase in extreme rain events and transport of DOM to coastal (and inland) waters will in turn decrease underwater UV radiation exposure in these aquatic ecosystems. Interactions such as these are clearly evident in the Arctic, where climate warming is creating a positive feedback by melting organic-carbon-rich permafrost that releases DOM to aquatic ecosystems. The DOM absorbs more sunlight, further warming and decreasing the UV transparency of these surface waters. This DOM is mineralized, largely by UV radiation, and releases greenhouse gases to the atmosphere, which will promote further warming. Sunlight (and UV radiation exposure in particular) may account for between 70% and 95% of the processing of DOM in Arctic streams, lakes, and rivers (Cory *et al.* 2014). On a global scale, stratospheric ozone depletion not only increases exposure to damaging UV-B radiation but also modifies weather patterns and oceanic circulation in the Southern Hemisphere. This in turn alters patterns of flooding, droughts, and wildfires, increasing the salinity of, and decreasing biodiversity in, Antarctic lakes (Robinson and Erickson 2015). These transitions from drought to flood conditions (and the reverse) will change the UV transparency of both coastal and inland waters through the mechanisms described above, but at present we lack the UV data to assess the consequences of these modifications.

Economic implications and conclusions

There are major financial costs associated with the consequences of environmental extremes affecting DOM and water resources more broadly. On the west coast of North America, for instance, exceptional drought conditions prompted the US Federal Government to allocate over $4 billion for drought-related economic losses, and the White House budgeted $110 million in 2015 alone just to fight wildfires (Showstack 2015). With their estimated current costs of $6 billion per year expected to increase as much as tenfold by 2050 (Hallegatte *et al.* 2013), floods present similar economic challenges to major cities in North America. Only recently have the more complex effects of UV radiation and its interactions with climate change been recognized as an information-rich emerging frontier (Mladenov *et al.* 2011; Fichot *et al.* 2013; Williamson *et al.* 2014b). The cost of flood-related increases in DOM and decreases in UV transparency has not been assessed but is likely to be substantial in terms of their effects on water quality, human health, and the provision of ecosystem services. In 2011, increases in DOM due to heavy precipitation from tropical storms Irene and Lee led to the production of carcinogenic disinfection byproducts during chlorination that exceeded drinking water standards in New York City reservoirs (Mukundan and Van Dreason 2014). The marked increases in extreme precipitation events in the northeastern US and other regions of the world make the creation of carcinogenic disinfection byproducts a widespread concern for providing clean and contaminant-free drinking water. Solar UV radiation provides a valuable ecosystem service by breaking down DOM (Cory *et al.* 2014), which can reduce the potential for production of toxic disinfection byproducts, although the prevalence of this effect at temperate latitudes is still a subject of active investigation.

Other UV-radiation-related ecosystem services include the removal of important parasites and pathogens, and the exclusion of invasive warm-water fish species from cold, clear-water lakes. These fish nest in warmer surface waters but successful reproduction is prevented when the delicate larvae are killed by damaging UV radiation if the waters remain clear. Reductions in UV transparency due to storm-related DOM inputs to lakes can provide a refuge for less UV-radiation-tolerant invasive species (Tucker and Williamson 2014). Parasites that are inactivated by solar UV radiation include the human intestinal parasite *Cryptosporidium* (King *et al.* 2008), the chytrid fungus responsible for global declines in amphibians (Ortiz-Santaliestra *et al.* 2011), and lethal fungal parasites of important zooplankton grazers (Overholt *et al.* 2012).

Extreme weather events and their ecological and economic impacts on water resources are by no means limited to the US and represent a global problem that is most severe in developing countries that do not have sufficient financial resources to undertake mitigation programs. Changes in the UV environment, although invisible to the human eye, serve as valuable sentinel responses of changes driven by extreme events. Advances in UV-radiation-based optical metrics and remote-sensing approaches now enable researchers to image terrestrial DOM inputs into large and diverse ecosystems, ranging from the Gulf of Mexico (Fichot *et al.* 2014) to the Arctic Ocean (Fichot *et al.* 2013), as well as in high-elevation subalpine and alpine lakes (Rose *et al.* 2009; Mladenov *et al.* 2011). Elucidating the role of UV radiation and the information that it provides on how aquatic ecosystem services are being transformed by extreme events will better inform scientists, managers, and policy makers about how best to invest limited financial resources to more effectively manage the world's critical freshwater resources.

Acknowledgements

We thank B Allen, K Webb, and the staff of the UC Davis Tahoe Environmental Research Center for critical assistance in the field at Lake Tahoe, and the Blooming Grove Club for access to Lake Giles. This work was supported by NSF-DEB #1360066.

References

Allen EW, Prepas EE, Gabos S, *et al.* 2003. Surface water chemistry of burned and undisturbed watersheds on the Boreal Plain: an ecoregion approach. *J Environ Eng Sci* **2**: S73–86.

CAL FIRE (California Department of Forestry and Fire Protection). 2015. Top 20 largest California wildfires. Sacramento, CA: Department of Forestry and Fire Protection. www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Acres.pdf. Viewed 27 Dec 2015.

Cory RM, Ward CP, Crump BC, *et al.* 2014. Sunlight controls water column processing of carbon in arctic fresh waters. *Science* **345**: 925–28.

Dennison PE, Brewer SC, Arnold JD, *et al.* 2014. Large wildfire trends in the western United States, 1984–2011. *Geophys Res Lett* **41**: 2928–33.

Fichot CG, Kaiser K, Hooker SB, *et al.* 2013. Pan-Arctic distributions of continental runoff in the Arctic Ocean. *Scientific Reports* **3**: 1–6.

Fichot CG, Lohrenz SE, and Benner R. 2014. Pulsed, cross-shelf export of terrigenous dissolved organic carbon to the Gulf of Mexico. *J Geophys Res-Oceans* **119**: 1176–94.

Gaiser EE, Deyrup ND, Bachmann RW, *et al.* 2009. Multidecadal climate oscillations detected in a transparency record from a subtropical Florida lake. *Limnol Oceanogr* **54**: 2228–32.

Hadley OL and Kirchstetter TW. 2012. Black-carbon reduction of snow albedo. *Nature Clim Change* **2**: 437–40.

Hallegatte S, Green C, Nicholls RJ, *et al.* 2013. Future flood losses in major coastal cities. *Nature Clim Change* **3**: 802–06.

Hurteau MD, Westerling AL, Wiedinmyer C, *et al.* 2014. Projected effects of climate and development on California wildfire emissions through 2100. *Environ Sci Technol* **48**: 2298–304.

Kalashnikova OV, Mills FP, Eldering A, *et al.* 2007. Application of satellite and ground-based data to investigate the UV radiative effects of Australian aerosols. *Remote Sens Environ* **107**: 65–80.

Karl TR, Melillo JM, and Peterson TC (Eds). 2009. Global climate change impacts in the United States. New York, NY: Cambridge University Press.

King BJ, Hoefel D, Daminato DP, *et al.* 2008. Solar UV reduces *Cryptosporidium parvum* oocyst infectivity in environmental waters. *J Appl Microbiol* **104**: 1311–23.

Melillo J, Richmond TC, and Yohe GW (Eds). 2014. Climate change impacts in the United States: the third national climate assessment. Washington, DC: US Global Change Research Program; doi:10.7930/J0Z31WJ2.

Meredith EP, Semenov VA, Maraun D, *et al.* 2015. Crucial role of Black Sea warming in amplifying the 2012 Krymsk precipitation extreme. *Nat Geosci* **8**: 615–19.

Mladenov N, Sommaruga R, Morales-Baquero R, *et al.* 2011. Dust inputs and bacteria influence dissolved organic matter in clear alpine lakes. *Nat Commun* **2**; doi:10.1038/ncomms1411.

Mukundan R and Van Dreason R. 2014. Predicting trihalomethanes in the New York City water supply. *J Environ Qual* **43**: 611–16.

NIFC (National Interagency Fire Center). nd. National Interagency Fire Center. Boise, ID: NIFC. www.nifc.gov. Viewed 21 Aug 2015.

NOAA (National Oceanic and Atmospheric Administration). nd. www.ncdc.noaa.gov. Silver Spring, MD: NOAA. Viewed 19 Jun 2015.

Olefeldt D, Turetsky MR, and Blodau C. 2013. Altered composition and microbial versus UV-mediated degradation of dissolved organic matter in boreal soils following wildfire. *Ecosystems* **16**: 1396–412.

Ortiz-Santaliestra ME, Fisher MC, Fernandez-Beaskoetxea S, *et al.* 2011. Ambient ultraviolet B radiation and prevalence of infection by *Batrachochytrium dendrobatidis* in two amphibian species. *Conserv Biol* **25**: 975–82.

Overholt EP, Hall SH, Williamson CE, *et al.* 2012. Solar radiation decreases parasitism in *Daphnia*. *Ecol Lett* **15**: 47–54.

Overholt EP, Rose KC, Williamson CE, *et al.* 2016. Behavioral responses of freshwater calanoid copepods to the presence of ultraviolet radiation: avoidance and attraction. *J Plankton Res*; doi:10.1093/plankt/fbv113.

Petropavlovskikh I, Evans R, McConville G, *et al.* 2015. The influence of the North Atlantic Oscillation and El Nino-Southern

Oscillation on mean and extreme values of column ozone over the United States. *Atmos Chem Phys* **15**: 1585–98.

Rautio M and Tartarotti B. 2010. UV radiation and freshwater zooplankton: damage, protection and recovery. *Freshw Rev* **3**: 105–31.

Robinson SA and Erickson DJ. 2015. Not just about sunburn – the ozone hole's profound effect on climate has significant implications for Southern Hemisphere ecosystems. *Glob Change Biol* **21**: 515–27.

Romps DM, Seeley JT, Vollaro D, *et al.* 2014. Projected increase in lightning strikes in the United States due to global warming. *Science* **346**: 851–54.

Rose KC, Williamson CE, Fischer JM, *et al.* 2012. The role of UV and fish in regulating the vertical distribution of *Daphnia*. *Limnol Oceanogr* **57**: 1867–76.

Rose KC, Williamson CE, Schladow SG, *et al.* 2009. Patterns of spatial and temporal variability of UV transparency in Lake Tahoe, California–Nevada. *J Geophys Res-Biogeo* **114**: G00D03; doi:10.1029/2008jg000816.

Sadro S and Melack J. 2012. The effect of an extreme rain event on the biogeochemistry and ecosystem metabolism of an oligotrophic high-elevation lake. *Arct Antarct Alp Res* **44**: 222–31.

Showstack R. 2015. White House focuses on drought and wildfire threats. *EOS* **96**; doi:10.1029/2015EO031727.

Storz UC and Paul RJ. 1998. Phototaxis in water fleas (*Daphnia magna*) is differently influenced by visible and UV light. *J Comp Physiol A* **183**: 709–17.

Swift TJ, Perez-Losada J, Schladow SG, *et al.* 2006. Water clarity modeling in Lake Tahoe: linking suspended matter characteristics to Secchi depth. *Aquat Sci* **68**: 1–15.

Tucker AJ and Williamson CE. 2014. The invasion window for warmwater fish in clearwater lakes: the role of ultraviolet radiation and temperature. *Divers Distrib* **20**: 181–92.

Williamson CE, Brentrup JA, Zhang J, *et al.* 2014a. Lakes as sensors in the landscape: optical metrics as scalable sentinel responses to climate change. *Limnol Oceanogr* **59**: 840–50.

Williamson CE, Zepp RE, Lucas RM, *et al.* 2014b. Solar ultraviolet radiation in a changing climate. *Nature Clim Change* **4**: 434–41.

Winder M. 2009. Photosynthetic picoplankton dynamics in Lake Tahoe: temporal and spatial niche partitioning among prokaryotic and eukaryotic cells. *J Plankton Res* **31**: 1307–20.

Zagarese HE and Williamson CE. 2001. The implications of solar UV radiation exposure for fish and fisheries. *Fish Fish* **2**: 250–60.