

Article

Lakes in a new light: indirect effects of ultraviolet radiation

Andrew J. Tucker^{1*} and Craig E. Williamson²

¹ 700 E High St, 212 Pearson Hall, Miami University, Oxford, OH 45056, USA. Email: tuckera2@muohio.edu

² Miami University, Oxford, OH 45056, USA. Email: craig.williamson@muohio.edu

* Corresponding author.

Received 15 November 2011; accepted 29 November 2011; published 19 December 2011

Abstract

Stratospheric ozone concentrations are not expected to recover to pre-ozone hole levels until the mid-21st century and, even after ozone recovery, climate and other anthropogenic changes will continue to alter ultraviolet radiation (UV) exposure regimes in aquatic ecosystems. Although our understanding of the ecology of UV continues to move towards a new paradigm that emphasises complex interactive and indirect effects of UV on communities of organisms, rather than simple direct negative effects on individuals, considerable uncertainty remains regarding the impacts of sustained or changing UV stress on aquatic ecosystems. In this synthesis we examine the importance of indirect UV effects for some key ecosystem level characteristics and processes in lakes. We draw particular attention to the implications of UV for disease dynamics, contaminant toxicity, biodiversity, and carbon cycling in lakes. Although UV has strong lethal mutagenic and chronic physiological effects on organisms, we suggest that indirect effect pathways, including UV effects on animal behaviour, food quality, and trophic interactions are likely to be important in lake ecosystem dynamics.

Keywords: Ultraviolet radiation; lakes; indirect effects; disease dynamics; contaminant toxicity; carbon cycling.

Introduction

Ultraviolet radiation (UV), high-energy solar radiation occurring at wavelengths between 280 and 400 nm in the Earth's atmosphere, is a potent and ubiquitous environmental stressor. While UV has long been recognised as an environmental driver, the discovery of the 'ozone hole' in the mid-1980s sparked greater interest in the important role of UV in the environment and marine studies in Antarctica focused attention on the implications

of increased UV exposure for aquatic ecosystems. From 1990 to 2000, the number of publications on UV and freshwater ecosystems in international scientific literature increased almost 300% (Bronmark & Hansson 2002). Many of these publications emphasised the detrimental effect of UV on aquatic ecosystems; some foretold ecological disaster, prompting swift action by the international community to limit the use of ozone depleting substances. International agreements to curb ozone depletion led to the Montreal Protocol which has been effective in reducing

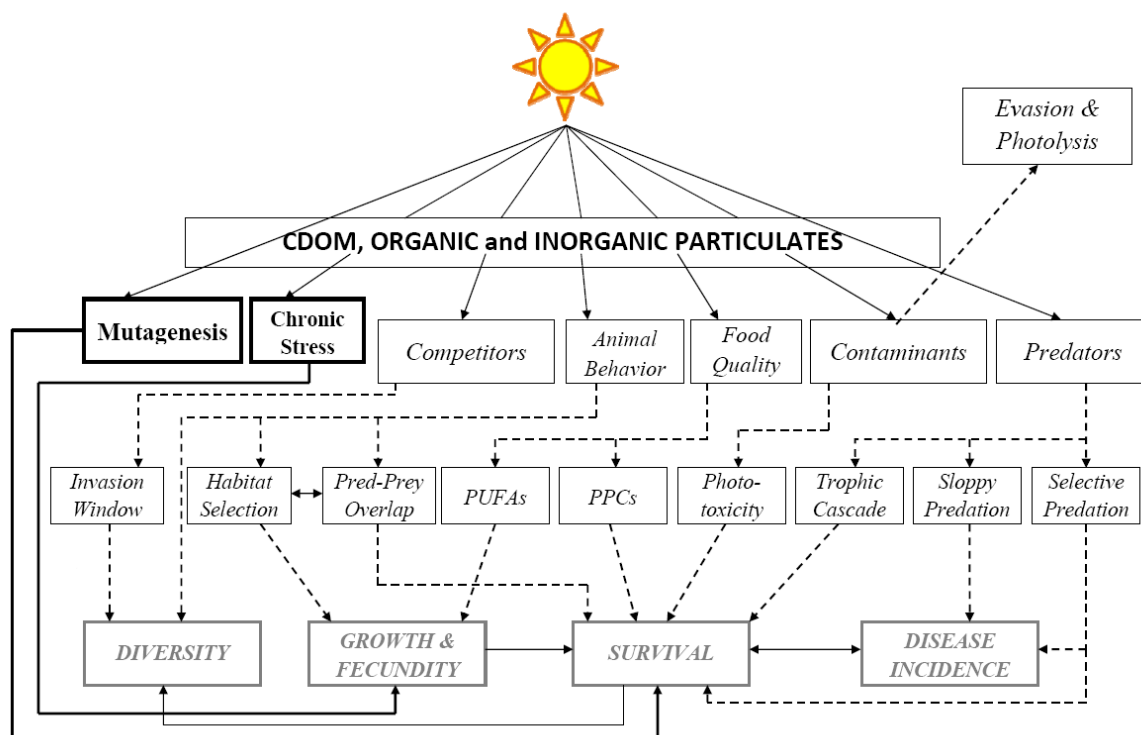


Fig. 1. Direct (bold text/solid lines) and indirect (italic text/dashed lines) effects of UV on the growth and survival of lake biota. Direct effects are only a small component of the many potential UV-mediated effects on lakes. Indirect effects mediate population and ecosystem level processes through any of a number of primary and secondary filters that result in either positive or negative effects on individual growth and survival. For example, UV effects on animal behaviour can influence habitat selection which can in turn induce trade-offs with predators, exposure to suboptimal temperatures, or other ecosystem components that may reduce growth and fecundity.

levels of anthropogenic ozone-depleting substances in the stratosphere (McKenzie et al., 2011). However ozone depletion continues and stratospheric ozone concentrations at mid-latitudes are not expected to recover to pre-1980 levels until the mid 21st century and perhaps even later in Polar Regions (Andrady et al., 2010; McKenzie et al., 2011).

Over the last decade we have developed a more nuanced understanding of the role that UV plays in aquatic systems, particularly in lakes. This new perspective recognises not only the detrimental effects of UV exposure but also the potential benefits of UV for individuals and whole lake ecosystems (Williamson et al., 2001a; Williamson & Rose, 2010). Advances in our understanding of the ecology of UV have also helped to explain some enigmatic patterns in lakes related to animal behaviour, phototoxicity and species diversity (Williamson & Rose, 2009).

Our goals in this synthesis are to highlight these more subtle indirect effects of UV on lakes and to draw attention to the implications of UV for disease dynamics, contaminant toxicity, biodiversity, and carbon cycling in lakes. We start by showing how indirect effect pathways can be as important as direct effects of UV on aquatic organisms in lakes (Fig. 1). We define indirect effects as pathways where UV interacts with some components of the environment (abiotic or biotic) to induce an effect on an individual or population that may or may not otherwise be directly exposed to or affected by UV. Examples include UV effects on predators, competitors, animal behaviour, or on organic and inorganic chemical compounds found in the water. In subsequent sections we describe UV effects on disease dynamics and contaminant toxicity in lakes as two specific examples that demonstrate the strong role that

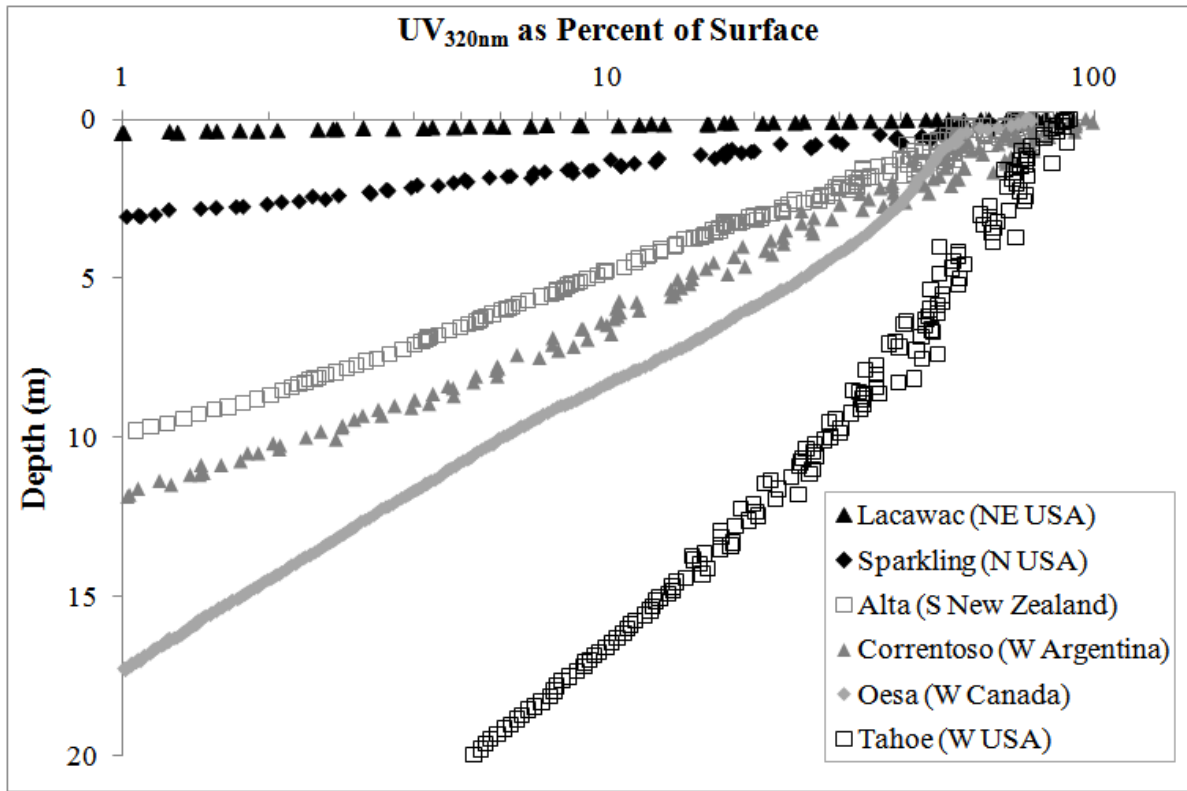


Fig. 2. Vertical profiles of UV vs. depth showing variation in summer UV transparency among lakes around the world. Intersection of lines with the vertical axis indicate the depth to which 1% of surface irradiance penetrates, an often-used convenient metric of UV transparency. The non-log linear trends evident in some profiles indicate that transparency can vary with depth, perhaps owing to differences in photobleaching and particulate concentrations through the water column.

indirect UV effects can play in regulating populations and communities of lake organisms. Finally, we discuss the role of UV in regulating species diversity and carbon cycling in lakes. We suggest that the strong direct and indirect effects of UV on these processes in individual lakes could have important implications for biodiversity and carbon balance on broader geographic scales. All of these UV-mediated effects are dependent upon levels of surface and underwater UV exposure in lakes. Therefore, we begin with a brief discussion of the factors that regulate UV exposure in lakes.

UV attenuation in lakes

UV transparency varies substantially among lakes (Fig. 2). A useful tool for comparing UV transparency is the 1% attenuation depth ($Z_{1\%}$, the depth to which 1% of surface irradiance of a given wavelength penetrates)

for 320 nm UV. Although the 1% depth criterion has no particular ecological significance, it provides a convenient metric that is consistent with the 1% depth of photosynthetically active radiation (PAR; the compensation depth where photosynthesis equals respiration). The 320-nm wavelength is used because it is available on commonly used submersible radiometers and it is also within the wavelength range of maximum biological effect (Williamson et al., 2009). The $Z_{1\% 320nm}$ can vary between less than 1 m in some lakes but over 20 m in other lakes (Fig. 2).

Lake location, catchment features such as land use, soil type and slope, and atmospheric characteristics like precipitation levels and the ozone layer all influence UV exposure levels in lakes. Lakes at high latitudes tend to have lower incident UV exposure than equatorial lakes (Rautio & Tartarotti, 2010) although Polar Regions

have experienced the most substantial declines in ozone concentration and thus the greatest increase in UV exposure relative to baseline conditions (ACIA, 2005). UV exposure at the lake surface tends to increase with increasing elevation. For example, in the Central Alps UV-B flux increases by 19 % per 1000 m of elevation gain (Blumthaler et al., 1992). Below the lake surface dissolved and particulate substances determine the depth to which UV can penetrate. Coloured or chromophoric dissolved organic matter (CDOM), often measured as dissolved organic carbon concentration (DOC), is generally the most important determinant of UV transparency. Called the 'ozone of the underwater world' (Williamson & Rose, 2010), DOC concentrations are a good predictor of underwater UV levels (Morris et al., 1995; Rae et al., 2001). Two important exceptions to this are very low DOC lakes in alpine regions (Laurion et al., 2000; Sommaruga & Augustin, 2006), and relatively low DOC eutrophic lakes (Hodoki & Watanabe, 1998) where a wider variation in phytoplankton concentrations plays a more important role in regulating underwater UV exposure than DOC. In highly turbid reservoirs or glacial systems inorganic particulates are important UV transparency regulators (Belzile et al., 2002). The quality and quantity of UV regulating materials can vary seasonally as the physical and biological conditions in lakes change (Morris & Hargreaves, 1997; Hayakawa & Sugiyama, 2008). These changes can result in strong seasonal variation in UV transparency when combined with the variation in incident UV related to changes in the angle of the sun and ozone concentrations.

While stratospheric ozone concentrations are beginning to stabilise, moving atmospheric UV levels toward pre-ozone hole levels, the factors controlling UV attenuation in lakes remain highly variable. Many lakes in Europe and North America have shown increasing trends in DOC concentrations (Roulet & Moore, 2006). The magnitude of changes in DOC will vary with temperature and depend largely on precipitation levels (Pace & Cole, 2002), which vary regionally and have been shown to affect DOC concentrations in lakes at a continental scale (Zhang et al., 2010). Anthropogenic acidification can also have strong effects on DOC quality and quantity

and thus UV attenuation in lakes (Schindler et al., 1996; Williamson et al., 1996). In one lake, drought-induced acidification increased the estimated depth of UV-B penetration more than two-fold (Yan et al., 1996). There is some evidence that recovery of lakes from acidification can lead to a recovery in DOC concentration (Evans et al., 2006; Monteith et al., 2007). Elsewhere, decreasing DOC concentrations are still being reported (Striegl et al., 2005; Monteith et al., 2007) with likely corresponding increases in UV transparency and underwater exposure levels. Eutrophication driven changes in transparency to visible light have also been widely observed (Rast & Lee, 1978; Goldman, 1988). Seasonal and spatial changes in UV transparency are often more pronounced than changes in visible transparency in lakes (Rose et al., 2009). This suggests that anthropogenic eutrophication, particularly in low DOC lakes where phytoplankton play an important role in controlling UV attenuation, could also significantly reduce UV penetration in lakes.

Changes in underwater UV exposure in polar and alpine lakes can be especially strong due to the fact that some lakes at higher elevations and latitudes exist at the threshold where small changes in CDOM can heavily effect UV attenuation (Sommaruga et al., 1999; Pienitz & Vincent, 2000). These lakes are covered by snow and ice for much of the year, factors that substantially effect underwater UV levels. While ice can be highly transparent to UV as a result of CDOM exclusion during freeze-up (Belzile et al., 2002), overlying snow can significantly reduce underwater UV levels (Belzile et al., 2001). Thus, a trend toward earlier break-up of ice cover which has been documented for many lakes in northern latitudes (Duguay et al., 2006) is likely to have a significant effect on underwater UV levels.

Indirect effects of UV on lake organisms

Much of the initial information on the role of UV in lakes emphasised the direct negative impacts of short wavelength UV-B (280-315 nm) at the organism level. This approach made sense at the time, given the unknown effects of large increases in levels of this high energy radiation

in the atmosphere in the early days of ozone depletion and the evidence for strong chronic (physiological stress, depression of physiological processes) and lethal (mutagenesis) effects of UV-B in a variety of organisms. These strong negative direct effects led to the suggestion in some early reports that elevated UV could contribute to the collapse of entire aquatic food webs via direct effects on primary producers (El-Sayed, 1988). This concern was countered by awareness of the natural UV-protection mechanisms in marine and freshwater phytoplankton (e.g. Vincent & Roy, 1993). For some time now aquatic ecologists have recognised the potential for substantial, though more subtle and complex, impacts on lake ecosystems through indirect UV effects (e.g. Williamson, 1995). Research on the indirect effects of UV in lakes has generated important and surprising insights, even suggesting beneficial effects of UV, particularly longer wavelength UV-A (320–400 nm), on aquatic organisms (e.g. Williamson et al., 2001a; Cooke & Williamson, 2006). In this section we highlight some of the most important indirect effects of UV on phytoplankton, zooplankton, and fish in lakes.

Whereas UV can directly suppress primary production through photoinhibition by limiting the photosynthetic capacity of phytoplankton (Lorenzen, 1979; Olesen & Maberly, 2001; Leavitt et al., 2003), indirect trophic-mediated UV effects can, in some cases, increase primary production. For example, in a stream where benthic consumers were more sensitive to UV exposure than sympatric algae, chlorophyll concentrations actually increased under enhanced UV conditions (Bothwell et al., 1994). Assessments of UV effects based on changes in UV alone can also be misleading, thus it is important to consider the interaction of 'whole-ecosystem' processes such as mixing, temperature and nutrients when predicting the effect of UV on algal production. The effect of UV on algal production can be mediated by nutrient limitation. In general, algal sensitivity to UV increases with lake nutrient content but declines again as light becomes limiting at high algal biomass levels (Moeller, 1994; Xenopoulos et al., 2002). Furthermore, in light limiting conditions, increases in surface irradiance may stimulate phytoplankton growth in spite of increases

in UV exposure because light limitation can be more important than UV damage (Xenopoulos et al., 2009). UV can also interact with temperature to affect phytoplankton communities by altering zooplankton grazing rates which in turn change algal abundance levels (Williamson et al., 2010). Such UV and temperature mediated grazing effects are species-specific, suggesting that changes in UV and temperature may favour some algal species over others (Williamson et al., 2010). Moreover, thermal stratification can intensify the impact of UV on phytoplankton biomass and community composition (Xenopoulos et al., 2000).

In the case of zooplankton, the majority of studies on direct UV-induced damage report increased mortality (Zagarese et al., 2003; Rautio & Tartarotti, 2010). Some direct sub-lethal effects, including reduced growth rates and decreased fecundity (De Lange et al., 1999; Huebner et al., 2006), as well as increased respiration rates (Fischer et al., 2006) have also been reported. In some cases indirect effects may also negatively impact zooplankton demography. UV affects the morphology, biochemistry, and stoichiometry of phytoplankton (Hessen et al., 1997); thus, UV-irradiated algae can decrease zooplankton growth and fecundity through UV-induced changes in phytoplankton fatty acid composition (De Lange & Van Donk, 1997; De Lange & Van Reeuwijk, 2003). However, UV-induced changes in fatty acid composition and decreased C:P and N:P ratios in *Selenastrum* spp. had no significant effects on *Daphnia magna* (Straus, 1820) growth rate (Leu et al., 2006), suggesting that species-specific differences in phytoplankton response to UV (and therefore impacts on grazers) are important.

The extent to which zooplankton grazers are influenced by UV can depend heavily on ecological trade-offs. It has been demonstrated that in thermally stratified clear lakes the negative phototaxis of zooplankton in response to UV radiation can constrain them to suboptimal temperatures that may compromise fitness (Cooke et al., 2008). Other studies have shown that high-intensity UV may increase predator-prey overlap, increasing predation pressure on zooplankton (Alonso et al., 2004; Boeing et al., 2004). The role of photoprotective compounds (PPCs) in zooplankton survival provides a highly pertinent example of the kinds of UV-induced tradeoffs that exist

for zooplankton. Zooplankton accumulate PPCs, such as carotenoids or mycosporine amino-acids (MAAs), as protection against UV-induced DNA damage (Tartarotti et al., 2001; Persaud et al., 2007). Zooplankton do not appear to be able to synthesise PPCs, but acquire them directly from their food (Carefoot et al., 2000; Moeller et al., 2005). An important exception is the production of melanin in some zooplankton, particularly cladocerans (Hansson et al., 2007; Rautio et al., 2009), although this is an energetically expensive process and is an important trade-off in itself (Hessen, 1996). UV exposure regulates PPC levels in some phytoplankton (Riegger & Robinson, 1997). Thus UV effects on algal food quality, via changes in the concentration of PPCs, can increase UV-tolerance in zooplankton. However, the incorporation of algae rich in photoprotective carotenoids makes zooplankton more conspicuous to visual predators (Hansson, 2004).

Some recent studies suggest that zooplankton defence mechanisms may be optimized in order to minimise the potential cost of UV-induced trade-offs. For example, the transparency gradient hypothesis (TGH), based on data on zooplankton distribution in alpine and sub-alpine lakes and experimental tests of PPC concentration and UV tolerance, suggests that zooplankton respond to UV and predators in a way that reduces the overall threat of both stressors (Kessler et al., 2008). The TGH asserts that UV will drive vertical migration in high UV conditions but that fish predation is the most important driver of downward migration in low-UV lakes. A more recent in-depth review of the literature has led to the transparency regulator hypothesis (TRH), which emphasises the important role of water transparency and UV radiation in particular in regulating the diel vertical migration of zooplankton in more transparent lakes (Williamson et al., 2011). Another recent study, comparing population dynamics and reproduction of several zooplankton taxa in mesocosms, observed little difference in long-term zooplankton population dynamics under substantially different UV exposures (Hylander & Hansson, 2010). This study suggests that effective defence mechanisms might allow zooplankton population dynamics and community composition to persist relatively unchanged under changing UV

conditions. However, this experiment (conducted in small predator-free mesocosms) did not consider the full suite of UV-mediated indirect effects, such as UV-induced changes on the feeding efficiency of zooplankton predators or the implications of UV-induced migration into sub-optimal habitats. Although there is evidence that zooplankton can optimise their UV response to minimise both direct (e.g. by incorporating/synthesising PPCs) and indirect (e.g. optimised UV-avoidance strategies) UV effects (Hansson & Hylander, 2009), additional mechanistic studies that examine multiple UV-induced trade-offs simultaneously are needed to verify whether the net response to UV exposure in zooplankton is generally positive or negative.

Several strong direct negative UV effects have been demonstrated in fish such as egg and larval mortality and 'sunburn,' which can initiate outbreaks of infectious disease (Zagarese & Williamson, 2001). However, as with zooplankton and phytoplankton, there are also some important indirect UV effects to consider. Many fish exhibit strong behavioural responses to UV. For example, larval whitefish (*Coregonus lavaretus*) avoid high UV conditions in the surface waters of transparent lakes on sunny days (Mönen et al., 2005). Spawning depths for yellow perch (*Perca flavescens*) and bluegill (*Lepomis macrochirus*) are greater in high UV lakes than in low UV lakes (Williamson et al., 1997; Gutierrez-Rodriguez & Williamson, 1999). While ambient UV levels can induce significant mortality for larval bluegill across the range of depths at which bluegill spawn, bluegill appear to select nest locations that limit UV exposure, and can even modify mean nest depth over a season to limit UV exposure (Gutierrez-Rodriguez & Williamson, 1999; Olson et al., 2008). For juvenile salmonids that can detect UV, there is also a tendency to increase shade-seeking behaviour in the presence of UV (Kelly & Bothwell, 2002; Holtby & Bothwell, 2008).

While these avoidance responses may alleviate the direct negative effects of UV on fish, there are some important implications of UV avoidance. For example, the tendency for juvenile salmon to seek shade under high UV conditions may increase visual isolation from neighbours. This will result in more fish occupying the same habitat, resulting in density-dependent decreases

in average size and reduced fitness (Holtby & Bothwell, 2008). Likewise, the tendency to select deeper nest depths under high UV conditions may impose thermal constraints, limiting reproductive success (Huff et al., 2004). UV-mediated habitat use (e.g. avoidance of surface waters by zooplankton) may also generate changes in predator-prey overlap (Alonso et al., 2004) that could alter food availability, thus affecting growth potential and reproductive capacity in planktivorous fish.

UV can influence disease dynamics in lakes

Pathogens, defined here as any infectious agent that causes disease to its host, have numerous impacts on lake structure and function. Pathogens can alter community composition by eliminating susceptible species from lakes (Scudder, 1983). Some bacterial parasites can reduce the population density of important plankton grazers in temperate lakes (Duffy & Hall, 2008). Parasites have even been known to induce changes in food chain length and increase omnivory in lake food webs (Amundsen et al., 2009). One of the most notorious pathogens, the chytrid fungus *Batrachochytrium dendrobatidis* has been implicated in the severe decline or extinction of nearly 200 species of frogs, presenting a very real threat to global biodiversity (Skerratt et al., 2007). How then, might UV interact with pathogens in lakes or alleviate or exacerbate pathogenic effects? Indirect UV-mediated trophic effects may be particularly influential with outcomes depending on 1) the relative susceptibility of host and pathogen to UV, 2) the interplay of host immune function and pathogen susceptibility to UV, 3) the effect of UV on available host types (susceptible hosts or less competent hosts, i.e. 'diluters'), and 4) the kind of predator community (visually selective predators or

non-selective, 'sloppy' predators that re-suspend infective spores while feeding) (Fig. 3).

UV exposure can directly reduce pathogen infectivity. Recent UV exposure experiments on *Cryptosporidium parvum*, a freshwater protozoan, showed that ambient levels of solar UV can rapidly inactivate oocysts and reduce infectivity (Connelly et al., 2007), although the effectiveness of UV disinfection in water varies with exposure time and water turbidity (Gomez-Couso et al., 2009). There is a paucity of studies that assess the interaction of UV-induced changes in pathogen infectivity and host susceptibility to pathogens under natural UV levels; however, one recent study has demonstrated that the fungal parasite *Metschnikowia bicuspidata* is notably less UV-tolerant than its host *Daphnia dentifera* (Overholt et al., in press). Field data from this study indicate that fungal epidemics are inversely correlated with variations in UV transparency among lakes and seasonal patterns of UV exposure. Some

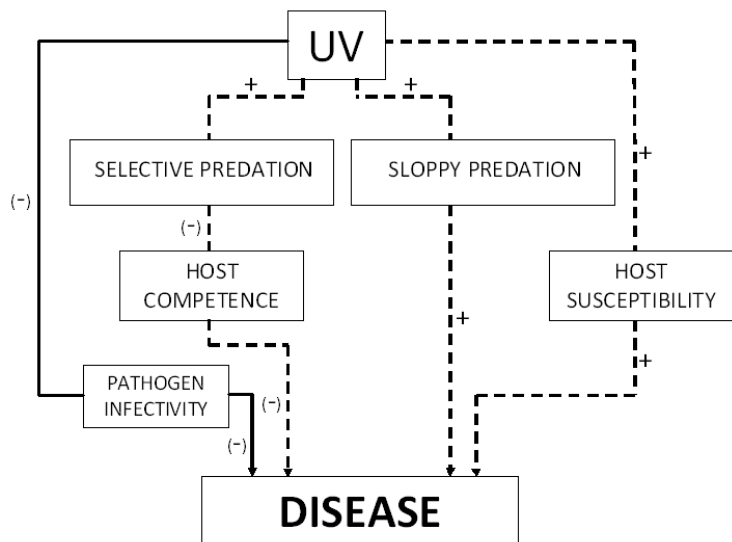


Fig. 3. Conceptual model of the role of UV in regulating pathogen effects in lakes. Arrows indicate effect pathways, (+) indicates an increase while (-) indicates a decrease from one box to the next. UV can affect disease incidence *directly*, by reducing pathogen infectivity, or *indirectly*. Indirect effects include UV-mediated changes in host susceptibility to pathogens or UV-mediated effects on predation intensity by either selective or sloppy predators. UV increases feeding efficiency by selective predators which will generally reduce host body size, the major determinant of host competence as measured by potential spore production. Sloppy predators re-suspend infective spores when feeding on infected hosts. Thus, UV-induced behavioural responses in hosts that increase their overlap with sloppy predators could increase disease incidence.

hosts are inherently more resistant to parasites than others. When parasite resistant hosts are present in large numbers, these so called 'diluters' can inhibit disease (Hall et al., 2009). We do not currently know if 'diluters' and susceptible hosts exhibit inherent differences in UV-tolerance, but UV-mediated shifts in host (i.e. zooplankton) community composition have been documented (e.g. Williamson et al., 2001b; Marinone et al., 2006) and changes in the relative abundance of susceptible versus resistant hosts could potentially influence disease dynamics in lakes.

UV-mediated trophic interactions have perhaps the greatest potential to either exacerbate or ameliorate epidemics. Many fish possess UV photoreceptors (Leech & Johnsen, 2003), which increase predation rates, foraging efficiency and enhance prey detection in fish from a variety of families, including centrarchids, percids and salmonids (Loew et al., 1993; Browman et al., 1994; Leech et al., 2009). In lakes, selective predation and increased predation intensity both stem epidemics, by culling infected hosts in the former case (Hall et al., 2005; Duffy et al., 2005) and reducing host body size (competence) in the latter case (Hall et al., 2007; Hall et al., 2010). Consequently, UV-enhanced fish predation on zooplankton hosts would appear to be a viable mechanism for inhibiting disease, although this hypothesis has not been tested. Nevertheless, results consistent with the idea that UV-mediated trophic interactions prevent disease have been reported. In a mesocosm experiment, yellow perch and bluegill introduced into low-DOC 'clearwater' mesocosms preferred *Daphnia* infected with chytrid over uninfected individuals. However, in mesocosms with high concentrations of DOC (suggesting lower UV conditions) fish did not show a preference for infected *Daphnia*. In the same study, a comparative survey showed that lakes supporting chytrid infections had higher DOC concentrations and lower light penetration (Johnson et al., 2006), suggesting a potential moderating influence of UV attenuation on disease incidence via two distinct mechanisms. One is that infected *Daphnia* tend to occur at greater densities in environments that conceal their visibility. The other is that UV has a stronger negative effect on the chytrid relative to its host, either due to lower UV

tolerance or the ability of *Daphnia* to behaviourally avoid UV damage by downward migration in the water column.

Whereas UV effects on selective vertebrate predators could inhibit disease outbreak in transparent lakes, UV transparent lakes with sizeable populations of 'sloppy' invertebrate predators could actually be more susceptible to parasite epidemics. While feeding, 'sloppy predators' such as *Chaoborus* often release spores contained in the prey they consume (e.g. infected *Daphnia*). The released spores, which are still infective, are thus re-suspended in the water column where they can be consumed by a new host. In the absence of 'sloppy predators' hosts dying of infection tend to sink to the lake bottom before releasing spores, which tend to become trapped in the bottom sediments. Consequently, 'sloppy predators' tend to facilitate epidemics in lakes (Caceres et al., 2009). High UV levels probably promote the downward migration of UV sensitive zooplankton to depths where invertebrate predators reside (Boeing et al., 2004), and may therefore promote the occurrence of epidemics by increasing 'sloppy predation'.

UV can influence contaminant toxicity in lakes

Organic and inorganic contaminants including polychlorinated biphenyls (PCBs), mercury (Hg), pesticides and polycyclic aromatic hydrocarbons (PAHs) are pervasive in lakes (Stahl et al., 2009), including remote 'pristine' systems (Landers et al., 2010). UV interacts with these contaminants in several ways. For example, UV can increase toxicity of contaminants to aquatic organisms through the induction of phototoxic effects. UV can also mitigate the toxicity of mercury, one of the most problematic aquatic contaminants. DOC plays a pivotal role in these relationships as it can both decrease UV transparency of lakes, and also mitigate contaminant toxicity.

The absorption of a UV photon by a photosensitising compound produces an excited state molecule that can react directly or indirectly with a biological substrate (e.g. DNA) to produce an adverse phototoxic effect (Kochevar, 1981). These phototoxic effects include covalent binding

of photoaddition products to DNA and the formation of active oxygen species that produce photooxidised molecules (Kochevar, 1981). These phototoxic effects ultimately impair cellular function. Phototoxicity is a rather common phenomenon for compounds in aquatic environments that are not otherwise acutely toxic (Arfsten et al., 1996; Diamond et al., 2000), normally amplifying the negative impacts of contaminant exposure for aquatic organisms. For example, UV enhances the toxicity of some pesticides by up to 10-fold (Zaga et al., 1998). For certain PAHs, UV increases toxicity by a thousand fold or more (Oris & Giesy, 1985). Others have observed UV-enhanced toxicity of selected antibiotics (Pandey et al., 2002), and there is evidence that some explosives that have been dumped in both lakes and oceans, are phototoxic (Dave et al., 2000). UV can also increase toxicity of heavy metals to a number of aquatic or semi-aquatic animals (Preston et al., 1999; Hansen et al., 2002; Baud & Beck, 2005). Sub-lethal effects have been documented for a few phototoxic compounds including a reduced ability to evade predators (Duesterloh et al., 2002), and depressed reproduction in zooplankton (Holst & Giesy, 1989).

Nevertheless, the UV photochemical transformation of compounds or elements could actually reduce the negative impacts of some contaminants, like mercury. Mercury (Hg) is a globally distributed, highly pervasive threat to lakes that is often transported in the atmosphere and then deposited far from emissions sources (Balcom et al., 2004). Coal combustion in electric power plants is the single largest source of atmospheric Hg emissions to the air, though industrial boilers and the burning of hazardous waste are also significant sources (Lindberg et al., 2007). The form of Hg that is present in lakes largely determines the potential effects. Methyl mercury (MeHg), the form that biomagnifies in food chains, is linked to immunological and reproductive dysfunction in top predators (Hammershmidt et al., 2002; Drevnik et al., 2008). MeHg is also 10 to 100 times more toxic than the inorganic form, Hg (II) (Boening, 2000). The negative effect of elemental mercury (Hg (0)) in lakes is limited since it is the major component of dissolved gaseous mercury and can therefore readily volatilise from lakes.

UV plays an important role in regulating Hg speciation processes. UV reduces soluble Hg (II) into Hg (0) and can therefore control evasion of Hg from lakes (Amyot et al., 1997). However, UV can also photooxidise volatile Hg (0) back to soluble Hg (II) (Lalonde et al., 2001). Consequently, the relative rates of UV-mediated photoredox reactions will ultimately control Hg concentrations in lakes. Photoredox rates and the transformation of Hg may be strongly influenced by DOC concentration. For example, DOC acts as a substrate that, when degraded, provides photoreactive intermediates that can reduce Hg (II) to volatile Hg (0) (Garcia et al., 2005). This suggests that high DOC concentrations in lakes would increase Hg evasion and reduce *in situ* Hg levels. However, high DOC concentrations can also increase mercury methylation (Weber, 1993), which could exacerbate the biological effect of Hg in high DOC lakes even if overall mercury concentrations are reduced. Other studies have suggested that DOC inhibits methylation, though the extent of methylation was dependent on both pH and salinity, with increased salinity and more neutral pH resulting in reduced rates of methylation (Barkay et al., 1997). A recent study in a relatively transparent lake showed that mercury flux, namely the reduction of Hg (II) to volatile elemental Hg (0), was driven primarily by UV exposure and that DOC quantity or quality had little or no effect (Peters et al., 2007). Clearly, more research is needed to resolve whether the interaction of UV and DOC ultimately increases or decreases Hg concentrations in lakes, and to elucidate to what extent pH, salinity and other abiotic factors influence Hg evasion and methylation from one lake to another. Nevertheless, it appears that UV alters the bioavailability and cycling of Hg.

UV can regulate biodiversity in lakes

High levels of UV generally reduce biodiversity in lakes; however, in some cases high UV levels might actually create conditions that promote or maintain biodiversity (Fig. 4). The effect of UV on biodiversity in lakes is largely dictated by interspecific differences in UV tolerance.

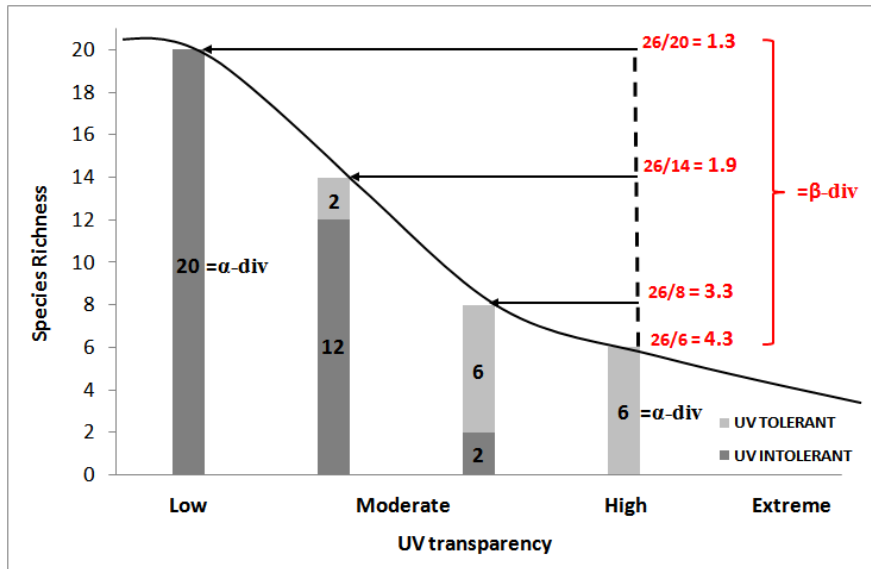


Fig. 4. Conceptual model showing species richness across a UV transparency gradient within a landscape. At the landscape level, species richness (i.e. γ -diversity) is 26 because there are 20 UV intolerant and 6 UV tolerant species. Within-lake richness (i.e. α -diversity) tends to decrease with increasing UV transparency as habitats become less suitable for otherwise competitively superior UV intolerant species. Along the UV transparency gradient the turnover in species composition among different lakes contributes additional diversity (i.e. β -diversity = γ/α) to the region so that the effective number of communities is greatest when all lake types are present on the landscape.

Zooplankton UV tolerance is strongly related to taxon and, to a lesser extent, body size. For example rotifers and copepods are usually more tolerant than cladocerans and smaller species tend to be more tolerant than larger species (Leech & Williamson, 2000). These differences in taxon-specific UV tolerance can potentially influence zooplankton community composition. A study of lakes with varying degrees of terrestrial succession in their catchments in Glacier Bay, Alaska, attributed differences in zooplankton species composition among lakes to the significant variation in UV attenuation from lake to lake (Williamson et al., 2001b). Likewise, in a survey of 53 temperate lakes situated along a UV exposure gradient, zooplankton species richness and Shannon-Wiener specific diversity were limited to minimum values when mean water column UV levels were high (i.e. average exposure levels were greater than 10 % of 320 nm surface irradiance) (Marinone et al., 2006). Similar results of depleted species richness and specific diversity with increasing UV exposure have been reported for artificial phytoplankton communities (Xenopoulos & Frost, 2003).

The examples above demonstrate the potential for UV to reduce species diversity by limiting the number of UV intolerant taxa that occur in high UV lakes. When taken in a different context, however, the exclusion of certain UV sensitive taxa from clear waters could actually help to maintain the integrity of communities of native species and thus promote higher levels of diversity. For example, in Lake Tahoe, introduced warm-water fish (in particular the bluegill and the largemouth bass) have virtually extinguished native minnow species in some littoral habitats. Experiments that isolated the effect of UV on survival of bluegill larvae demonstrated that high UV conditions may limit the susceptibility of littoral habitats to warm-water fish invasion by preventing the survival of this critical life stage (Tucker et al., 2010). In light of the documented negative impact of warm-water fish on fish species richness and cyprinid richness in particular (Jackson, 2002), the exclusion of warm-water fish invaders could help to maintain native biodiversity at least in more transparent lakes.

UV might also help to maintain species diversity in lakes through reproductive isolation. In Lake Victoria, decreases in UV exposure levels may help to explain the severe decline in cichlid diversity during anthropogenic eutrophication (Williamson & Rose, 2009; Williamson & Rose, 2010). Eutrophication in the lake has increased turbidity and seems to have interfered with visual cues for mate selection such as colouration and reflectance of the fish body, mechanisms that maintain reproductive isolation and thus species diversity for these cichlids (Seehausen et al., 2008). The role of UV in these declines

has not been explicitly tested but many cichlid species of Lake Malawi, one of the clearest African rift lakes, do have UV photoreceptors that may have some function in mate selection (Jordan et al., 2006) as is the case for other freshwater fish species (Smith et al., 2002; Rick et al., 2006).

Ultimately, any UV-mediated changes in community composition, and in species diversity in particular, will be scale-dependent and habitat- and taxon-specific. In some transparent high elevation lakes where increased nitrogen deposition and an advancing tree line indicate potential declines in current underwater UV exposure (Grabherr, 1994; Sommaruga et al., 1999), falling UV transparency could create a physical refuge for UV intolerant species that tend to thrive in 'disturbed' habitats. The replacement of highly UV tolerant endemic species with UV intolerant cosmopolitan species could subsequently reduce regional or even global diversity through biotic homogenisation (McKinney & Lockwood, 1999). In other lakes, like many in the northeastern USA, precipitation is expected to increase and recovery from acidification continues (Driscoll et al., 2007; Hayhoe et al., 2007). These trends are likely to shift lakes toward historical water clarity levels, decreasing underwater UV exposure and potentially increasing richness and/or diversity as UV sensitive species recolonise lakes in their native range. The extent to which UV-mediated behavioural or mate selection pathways may influence diversity is largely unexplored and could be a more general phenomenon with important implications for lake biodiversity worldwide.

UV can influence carbon dynamics in lakes

Exchange of carbon dioxide (CO₂) with the atmosphere in aquatic systems is a balance of uptake via photosynthesis and release through respiration or photodegradation of DOM into dissolved inorganic carbon. UV radiation can influence both of these processes. Because the UV-mediated effects on these processes often occur through photochemical transformation of organic material, UV will interact with DOM and may influence whether lakes are net sources or sinks of CO₂ (Fig. 5).

As discussed above, UV can depress algal photosynthetic capacity and overall primary production in lakes (e.g. Olesen & Maberly, 2001). Furthermore, UV is able to photobleach CDOM, which could increase underwater UV levels, potentially exacerbating photoinhibition of algal primary production (Helbling et al., 2001; Osburn et al., 2001). On the other hand, UV wavelengths are the most effective for photodegradation of dissolved organic matter (DOM) and the release of its nitrogen and phosphorus content in biologically available forms (Bushaw et al., 1996). In one study, UV transformed the pool of recalcitrant DOM into bioavailable forms at rates of 3 % per day for nitrogen and 17 % per day for phosphorus (Vahatalo et al., 2003). Thus, photochemical release of nutrients could appreciably enhance primary production in nutrient deficient systems. Moreover, some studies have shown that increased irradiance appears to increase the N:P ratio in phytoplankton and reduces herbivore efficiency (Dickman et al., 2006; Dickman et al., 2008). Although neither of these studies specifically assessed UV effects on phytoplankton stoichiometry or herbivore efficiency, the results are consistent with other studies demonstrating that UV can reduce P uptake in phytoplankton and reduce digestibility of algae for herbivores by increasing carbohydrate storage (Hessen et al., 1995; Van Donk & Hessen, 1995, though see Xenopoulos et al., 2002). Low P:C ratios have also been associated with decreased activity of the enzymes that protect *Daphnia* from UV damage (Balseiro et al., 2008), suggesting stoichiometric constraints increase the susceptibility of this important phytoplankton grazer to UV.

Photochemical transformation of the DOM pool can also affect bacterial biovolume and overall microbial respiration. For example, although UV increases the bioavailability of nutrients for photosynthesisers, bacterial biovolume may increase by 70 % at the same time (Vahatalo et al., 2003). Bioassays showed that bacterial respiration increased in UV exposed (relative to non-exposed) treatments which is consistent with other studies that show how photochemically induced increases in DOM bioavailability often enhance microbial respiration (De Lange et al., 2003; Daniel et al., 2006). Thus, even if UV increases nutrient availability and subsequently

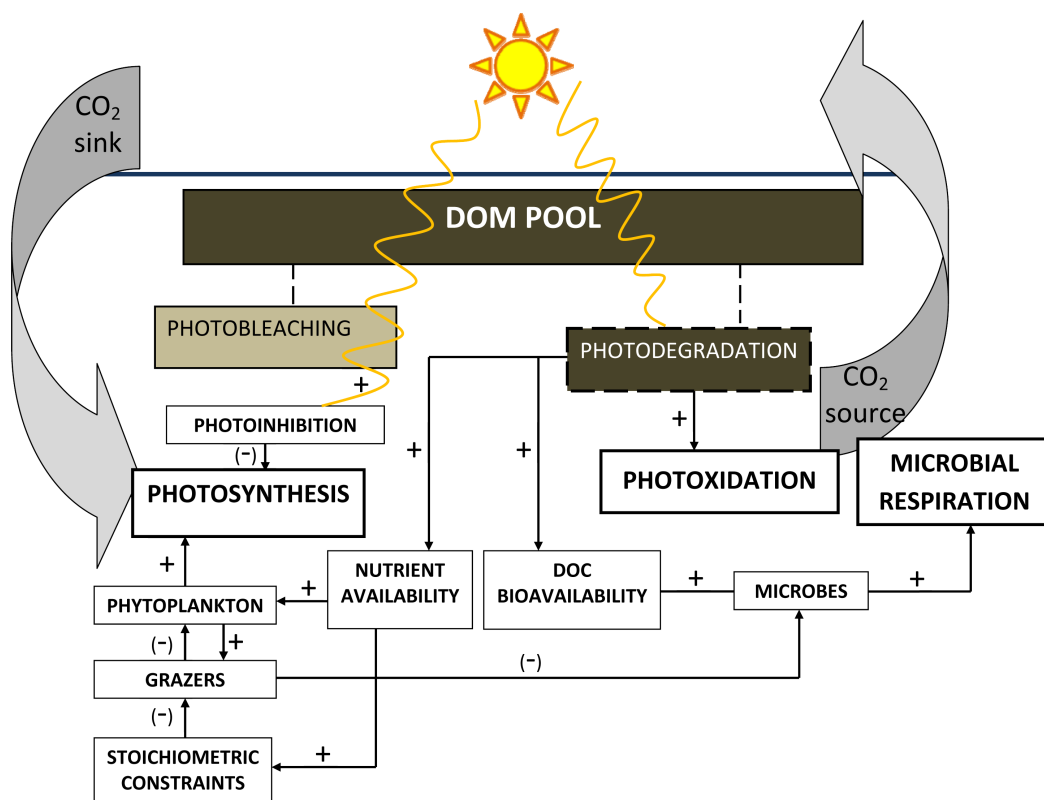


Fig. 5. Conceptual model of possible effects of UV on carbon cycling in lakes. Arrows indicate effect pathways, (+) indicates an increase while (-) indicates a decrease from one box to the next (e.g. photobleaching of DOM increases photoinhibition, which in turn decreases photosynthesis). UV effects on carbon cycling are largely regulated by the DOM pool in lakes.

enhances primary production, coincident increases in microbial respiration could still result in net carbon loss from lakes. However this may depend strongly on the source of DOM in lakes because UV-induced increases in bacterial production have been observed in lakes with more recalcitrant forms of DOM (i.e. allochthonous forms/humic lakes), but not in lakes with primarily autochthonous DOM (Tranvik & Bertilsson, 2001).

UV can also convert carbon to CO_2 through direct photochemical mineralisation of DOM, though on a global scale this is not a significant source of carbon flux from aquatic systems (Moran & Zepp, 1997). In a humic lake, UV was found to mineralise approximately 22 % of DOC to CO_2 in one week (Vahatalo, 1999). However, DOC quality and quantity are also important for photomineralisation. Less recalcitrant forms of DOC (i.e. autochthonous) appear to be less photoreactive and therefore less likely

to be mineralized to CO_2 (Obenosterer & Benner, 2004). Furthermore, UV photodegradation and the retention of carbon in lakes (i.e. storage in sediments or evasion to atmosphere) are most pronounced in low DOC systems ($< 4 \text{ mg L}^{-1}$; Molot & Dillon, 1997). Whether carbon is stored in sediments or lost to the atmosphere is also strongly related to lake pH. In acidified lakes more carbon is evaded than stored (Dillon & Molot, 1997; Reche et al., 1999; Gennings et al., 2001; Anesio & Graneli, 2004), presumably because of oxidation with hydroxyl (OH) radicals via the iron mediated photo-Fenton pathway (Voelker et al., 1997). In alkaline lakes it appears that non-OH mechanisms operating in the longer wavelength UV-A region might be most important for the photo-oxidation of DOC (Molot et al., 2005).

Given the myriad complex interactions of UV and DOM, long-term field experiments that measure carbon flux under different light and DOM regimes (and that also

consider additional factors like pH and the underlying mechanisms for photodegradation of DOM) could help to resolve whether UV exposure tends to promote the loss or storage of carbon in lakes. These are important questions because changes in lake carbon dynamics have the potential to influence the global carbon budget. Although they represent only a small portion of the Earth's continental land surface area (~3%, Downing et al., 2006, but see Seekell & Pace, 2011) lakes appear to play an important role in carbon cycling. Freshwater aquatic systems receive 2.9 Pg C y⁻¹ from the terrestrial environment (Tranvik et al., 2009). Though seemingly insignificant in comparison to gross carbon fluxes for the terrestrial biosphere or oceans, the emissions of inland waters (1.4 Pg C y⁻¹) are the same order of magnitude as carbon emissions caused by deforestation (1.6 Pg C y⁻¹) and carbon uptake by oceans (2.6 Pg C y⁻¹) (Burgermeister, 2007). Lakes are also a substantial source of methane, one of the most potent greenhouse gases, and as such offset 25 % of the estimated land carbon sink (Bastviken et al., 2011). Clearly increases or decreases in export or storage rates of carbon in fresh water could represent a significant sink for anthropogenic carbon (Cole et al., 2007).

Conclusions

Ecology is rarely as simple as understanding the direct effect of one organism or factor on another. It should come as no surprise then that some of the most interesting and important effects of UV on lakes are not directly attributable to exposure of individuals or groups of organisms to UV. Nor are UV effects limited to the direct negative effects on biota with which UV is so often associated. Rather, UV effects in lakes are often realised through indirect effect pathways and can induce a range of beneficial or detrimental impacts on lakes and the organisms therein. The role that UV plays in regulating animal behaviour, contaminant toxicity, or food quality subsequently affects habitat selection, predator-prey interactions, disease incidence, and habitat invasibility among other things. Ultimately, these UV-mediated effects influence the survival of organisms and the structure of

lake communities. In some cases the interactions initiated by UV will impact biodiversity or carbon cycling, which could have important implications for these dynamics at broader scales.

Even with 'normal' levels of atmospheric UV (e.g. after recovery of stratospheric ozone depletion) there are still likely to be many fascinating interactive effects of UV on lakes and the organisms that reside in them. In fact, differences in the community composition of alpine and sub-alpine lakes and seasonal patterns in carbon retention in lakes are just two examples that suggest that many of these intriguing effects are already apparent across the strong environmental gradients of UV in space and time. Climate change and other stressors are altering UV environments in lakes. For example, climate-induced changes in DOC-export to lakes and the eutrophication of once oligotrophic lakes by atmospherically deposited nutrients threaten substantially to alter underwater UV levels in lakes. These reductions in UV transparency may enhance invasion by warm-water species in cold clear lakes, especially in rapidly warming alpine and subalpine zones. Reductions in UV transparency may also have the potential to contribute to an increase in pathogens, like *Cryptosporidium*, that are sensitive to UV and yet are not removed from municipal water supplies by traditional chemical water treatment methods such as chlorination. It is therefore imperative that we continue to pursue an understanding of the important direct and especially indirect effects of UV on lake ecosystems. Our ability to effectively forecast and mitigate the environmental impacts of climate change and other stressors on lakes depends on our efforts.

References

- ACIA (2005). Arctic climate impact assessment. Cambridge University Press, Cambridge. 1042 pp.
- Alonso, C., Rocco, V., Barriga, J.P., Battini, M.A. & Zagarese, H. (2004). Surface avoidance by freshwater zooplankton: field evidence on the role of ultraviolet radiation. *Limnology and Oceanography* **49**, 225-232.
- Amundsen, P.A., Lafferty, K.D., Knudsen, R., Primicerio, R., Klemetsen, A. & Kuris, A.M. (2009). Food web topology and

- parasites in the pelagic zone of a subarctic lake. *Journal of Animal Ecology* **78**, 563-572.
- Amyot, M., Lean, D. & Mierle, G. (1997). Photochemical formation of volatile mercury in high Arctic lakes. *Environmental Toxicology and Chemistry* **16**, 2054-2063.
- Andrady, A., et al. (2010). Environmental effects of ozone depletion and its interactions with climate change: progress report, 2009. *Photochemical and Photobiological Sciences* **9**, 275-294.
- Anesio, A.M. & Graneli, W. (2004). Photochemical mineralization of dissolved organic carbon in lakes of differing pH and humic content. *Archiv Fur Hydrobiologie* **160**, 105-116.
- Arfsten, D.P., Schaeffer, D.J. & Mulveny, D.C. (1996). The effects of near ultraviolet radiation on the toxic effects of polycyclic aromatic hydrocarbons in animals and plants: a review. *Ecotoxicology and Environmental Safety* **33**, 1-24.
- Barkay, T., Gillman, M. & Turner, R.R. (1997). Effects of dissolved organic carbon and salinity on bioavailability of mercury. *Applied and Environmental Microbiology* **63**, 4267-4271.
- Baud, D.R. & Beck, M.L. (2005). Interactive Effects of UV-B and Copper on Spring Peeper Tadpoles (*Pseudacris crucifer*). *Southeastern Naturalist* **4**, 15-22.
- Balcom, P.H., Fitzgerald, W.F., Vandal, G.M., Lamborg, C.H., Rolffhus, K.R., Langer, C.S. & Hammerschmidt, C.R. (2004). Mercury sources and cycling in the Connecticut River and Long Island Sound. *Marine Chemistry* **90**, 53-74.
- Balseiro, E., Souza, M.S., Modenutti, B. & Reissig, M. (2008). Living in transparent lakes: low food P:C ratio decreases antioxidant response to ultraviolet radiation in *Daphnia*. *Limnology and Oceanography* **53**, 2383-2390.
- Bastviken, D., Tranvik, L.J., Downing, J.A., Crill, P.M. & Enrich-Prast, A. (2011). Freshwater methane emissions offset the continental carbon sink. *Science* **331**, 50.
- Belzile, C., Gibson, J.A.E. & Vincent, W.F. (2002). Colored dissolved organic matter and dissolved organic carbon exclusion from lake ice: implications for irradiance transmission and carbon cycling. *Limnology and Oceanography* **47**, 1283-1293.
- Belzile, C., Vincent, W.F. & Kumagai, M. (2002). Contribution of absorption and scattering to the attenuation of UV and photosynthetically available radiation in Lake Biwa. *Limnology and Oceanography* **47**, 95-107.
- Belzile, C., Vincent, W.F., Gibson, J.A.E. & Van Hove, P. (2001). Bio-optical characteristics of the snow, ice and water column of a perennially ice-covered lake in the high Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 2405-2418.
- Blumthaler, M., Ambach, W. & Rehwald, W. (1992). Solar UV-A and UV-B radiation fluxes at two alpine stations at different altitudes. *Theoretical Applied Climatology* **46**, 39-44.
- Boening, D.W. (2000). Ecological effects, transport, and fate of mercury: a general review. *Chemosphere* **40**, 1335-1351.
- Boeing, W.J., Leech, D.M., Williamson, C.E., Cooke, S.L. & Torres, L. (2004). Damaging UV radiation and invertebrate predation: conflicting selective pressures for zooplankton vertical distribution in the water column of low DOC lakes. *Oecologia* **138**, 603-612.
- Bothwell, M.L., Sherbot, D.M.J. & Pollock, C.M. (1994). Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. *Science* **265**, 97-100.
- Bronmark, C. & Hansson, L. (2002). Environmental issues in lakes and ponds: current state and perspectives. *Environmental Conservation* **29**, 290-306.
- Browman, H.I., Novales-Flamarique, I. & Hawryshyn, C.W. (1994). Ultraviolet photoreception contributes to prey search behaviour in two species of zooplanktivorous fishes. *Journal of Experimental Biology* **186**, 187-198.
- Burgermeister, J. (2007). Missing carbon mystery: case solved? *Nature Reports* **3**, 36-37.
- Bushaw, K.L., Zepp, R.G., Tarr, M.A., Schulz-Jander, D., Bourbonniere, R.A., Hodson, R.E., Miller, W.L., Bronk, D.A., Moran, M.A. (1996). Photochemical release of biologically available nitrogen from aquatic dissolved organic matter. *Nature* **381**, 404-407.
- Caceres, C.E., Knight, C.J. & Hall, S.R. (2009). Predator-spreaders: Predation can enhance parasite success in a planktonic host-parasite system. *Ecology* **90**, 2850-2858.
- Carefoot, T.H., Karentz, D., Pennings, S.C. & Young, C.L. (2000). Distribution of mycosporine-like amino acids in the sea hare *Aplysia dactylomela*: effect of diet on amounts and types sequestered over time in tissues and spawn. *Comparative Biochemistry and Physiology* **126**, 91-104.
- Cole, J., Prairie, Y., Caraco, N., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J. & Melack, J. (2007). Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems* **10**, 171-184.
- Connelly, S.J., Wolyniak, E.A., Williamson, C.E. & Jellison, K.L. (2007). Artificial UV-B and solar radiation reduce in vitro infectivity of the human pathogen *Cryptosporidium parvum*. *Environmental Science and Technology* **41**, 7101-7106.
- Cooke, S.L. & Williamson, C.E. (2006). Positive effects of UV radiation on a calanoid copepod in a UV transparent lake: do competition, predation, or food availability play a role? *Journal of Plankton Research* **28**, 171-179.
- Cooke, S.L., Williamson, C.E., Leech, D.M., Boeing, W.J. & Torres, L. (2008). Effects of temperature and ultraviolet radiation on diel vertical migration of freshwater crustacean zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1144-1152.
- Daniel, C., Graneli, W., Kritzbeg, E.S. & Anesio, A.M. (2006). Stimulation of metazooplankton by photochemically modified

- dissolved organic matter. *Limnology and Oceanography* **51**, 101-108.
- Dave, G., Nilsson, E. & Wernersson, A-S. (2000). Sediment and water phase toxicity and UV-activation of six chemicals used in military explosives. *Aquatic Ecosystem Health & Management* **3**, 291-299.
- De Lange, H.J. & Van Donk, E. (1997). Effects of UV-B irradiated algae on life history traits of *Daphnia pulex*. *Freshwater Biology* **38**, 711-720.
- De Lange, H.J., Verschoor, A.M., Gylstra, R., Cuppen, J.G.M. & Van Donk E. (1999). Effects of artificial ultraviolet-B radiation on experimental aquatic microcosms. *Freshwater Biology* **42**, 545-560.
- De Lange, H.J. & Van Reeuwijk, P.L. (2003). Negative effects of UVB-irradiated phytoplankton on life history traits and fitness of *Daphnia magna*. *Freshwater Biology* **48**, 678-686.
- De Lange, H.J., Morris, D.P. & Williamson, C.E. (2003). Solar ultraviolet photodegradation of DOC may stimulate freshwater food webs. *Journal of Plankton Research* **25**, 111-117.
- Diamond, S.A., Mount, D.R., Burkhard, L.P. & Ankley, G.T. (2000). Effect of irradiance spectra on the photoinduced toxicity of three polycyclic aromatic hydrocarbons. *Environmental Toxicology and Chemistry* **19**, 1389-1396.
- Dickman, E.M., Vanni, M.J. & Horgan, M.J. (2006). Interactive effects of light and nutrients on phytoplankton. *Oecologia* **149**, 676-689.
- Dickman, E.M., Newell, J.M., González, M.J. & Vanni, M.J. (2008). Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. *Proceedings of the National Academy of Sciences of the USA* **105**, 18408-18412.
- Dillon, P.J. & Molot, L.A. (1997). Dissolved organic and inorganic carbon mass balances in central Ontario lakes. *Biogeochemistry* **36**, 29-42.
- Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M. & Middelburg, J.J. (2006). The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography* **51**, 2388-2397.
- Drevnik, P.E., Roberts, A.P., Otter, R.R., Hammerschmidt, C.R., Klaper, R. & Oris, J.T. (2008). Mercury toxicity in livers of northern pike (*Esox lucius*) from Isle Royal, USA. *Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology* **147**, 331-338.
- Driscoll, C.T., Driscoll, K.M., Roy, K.M. & Dukett, J. (2007). Changes in the chemistry of lakes in the Adirondack region of New York following declines in acidic deposition. *Applied Geochemistry* **22**, 1181-1188.
- Duesterloh, S., Short, J.W. & Barron, M.G. (2002). Photoenhanced toxicity of weathered Alaska north slope crude oil to the calanoid copepods *Calanus marshallae* and *Metridia okhotensis*. *Environmental Science and Technology* **36**, 3953-3959.
- Duffy, M.A. & Hall, S.R. (2008). Selective predation and rapid evolution can jointly dampen effects of virulent parasites on *Daphnia* populations. *The American Naturalist* **171**, 499-510.
- Duffy, M.A., Hall, S.R., Tessier, A.J. & Huebner, M. (2005). Selective predators and their parasitized prey: are epidemics in zooplankton under top-down control? *Limnology and Oceanography* **50**, 412-420.
- Duguay, C.R., Prowse, T.D., Bonsal, B.R., Brown, R.D., Lacroix, M. & Menard, P. (2005). Recent trends in Canadian lake ice covers. *Hydrological Processes* **20**, 781-801.
- Edmondson, W.T. (1991). The uses of ecology: Lake Washington and beyond. University of Washington Press. 329 pp.
- El-Sayed, S.Z. (1988). Fragile life under the ozone hole. *Natural History* **97**, 72-81.
- Evans, C.D., Chapman, P.J., Clark, J.M., Monteith, D.T. & Cresser, M.S. (2006). Alternative explanations for rising dissolved organic carbon export from organic soils. *Global Change Biology* **12**, 2044-2053.
- Fischer, J.M., Fields, P.A., Pryzbylkowski, P.G., Nicolai, J.L. & Neale, P.J. (2006). Sublethal exposure to UV radiation affects respiration rates of the freshwater cladoceran *Daphnia catawba*. *Photochemistry and Photobiology* **82**, 547-550.
- Garcia, E., Amyot, M. & Ariya, P.A. (2005). Relationship between DOC photochemistry and mercury redox transformations in temperate lakes and wetlands. *Geochemistry et Cosmochemistry Acta* **69**, 1917-1924.
- Gennings, C., Molot, L.A. & Dillon, P.J. (2001). Enhanced photochemical loss of organic carbon in acidic waters. *Biogeochemistry* **52**, 339-354.
- Goldman, C.R. (1988). Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. *Limnology and Oceanography* **33**, 1321-1333.
- Gomez-Couso, H., Fontan-Sainz, M., McGuigan, K.G. & Ares-Mazas, E. (2009). Effect of the radiation intensity, water turbidity and exposure time on the survival of *Cryptosporidium* during simulated solar disinfection of drinking water. *Acta Tropica* **112**, 43-48.
- Grabherr, G., Gottfried, M. & Pauli, H. (1994). Climate effects on mountain plants. *Nature* **369**, 448.
- Gutierrez-Rodriguez, C. & Williamson, C.E. (1999). Influence of solar ultraviolet radiation on early life-history stages of the bluegill sunfish, *Lepomis macrochirus*. *Environmental Biology of Fishes* **55**, 307-319.
- Hall, S.R., Duffy, M.A. & Caceres, C.E. (2005). Selective predation

- and productivity jointly drive complex behavior in host-parasite systems. *The American Naturalist* **165**, 70-81.
- Hall, S.R., Sivars-Becker, L., Becker, C., Duffy, M.A., Tessier, A.J. & Caçeres, C.E. (2007). Eating yourself sick: transmission of disease as a function of foraging ecology. *Ecology Letters* **10**, 207-218.
- Hall, S.R., Becker, C.R., Simonis, J.L., Duffy, M.A., Tessier, A.J. & Caçeres, C.E. (2009). Friendly competition: evidence for a dilution effect among competitors in a planktonic host-parasite system. *Ecology* **90**, 791-801.
- Hall, S.R., Smyth, R., Becker, C.R. et al. (2010). Why Are *Daphnia* in Some Lakes Sicker? Disease Ecology, Habitat Structure, and the Plankton. *BioScience* **60**, 363-375.
- Hammerschmidt, C.R., Sandheinrich, M.B., Wiener, J.G. & Rada, R.G. (2002). Effects of dietary methylmercury on reproduction of fathead minnows. *Environmental Science and Technology* **36**, 877-883.
- Hansen, L.J., Whitehead, J.A. & Anderson, S.L. (2002). Solar UV Radiation enhances the toxicity of arsenic to *Ceriodaphnia dubia*. *Ecotoxicology* **11**, 279-287.
- Hansson, L.-A. (2004). Plasticity in pigmentation induced by conflicting threats from predation and UV radiation. *Ecology* **85**, 1005-1016.
- Hansson, L.-A. & Hylander, S. (2009). Effects of ultraviolet radiation on pigmentation, photoenzymatic repair, behavior, and community ecology of zooplankton. *Photochemical and Photobiological Sciences* **8**, 1266-1275.
- Hansson, L.-A., Hylander, S. & Sommaruga, R. (2007). Escape from UV threats in zooplankton: A cocktail of behavior and protective pigmentation. *Ecology* **88**, 1932-1939.
- Hayakawa, K. & Sugiyama, Y. (2008). Spatial and seasonal variations in attenuation of solar ultraviolet radiation in Lake Biwa, Japan. *Journal of Photochemistry and Photobiology B: Biology* **90**, 121-133.
- Hayhoe, K., Wake, C.P., Huntington, T.G., Luo, L., Schwartz, M.D., Sheffield, J., Wood, E., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T.J. & Wolfe, D. (2007). Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynamics* **28**, 381-407.
- Helbling, E.W., Villafane, V.E., Buma, A.G.J., Andrade, M. & Zaratti, F. (2001). DNA damage and photosynthetic inhibition induced by solar ultraviolet radiation in tropical phytoplankton (Lake Titicaca, Bolivia). *European Journal of Phycology* **36**, 157-166.
- Hessen, D.O. (1996). Competitive trade-off strategies in Arctic *Daphnia* linked to melanism and UV-B stress. *Polar Biology* **16**, 573-579.
- Hessen, D.O., Van Donk, E. & Andersen, T. (1995). Growth responses, P-uptake and loss of flagellae in *Chlamydomonas reinhardtii* exposed to UV-B. *Journal of Plankton Research* **17**, 17-27.
- Hessen, D.O., De Lange, H.J. & Van Donk, E. (1997). UV-induced changes in phytoplankton cells and its effects on grazers. *Freshwater Biology* **38**, 513-524.
- Hodoki, Y. & Watanabe, Y. (1998). Attenuation of solar ultraviolet radiation in eutrophic freshwater lakes and ponds. *Japanese Journal of Limnology* **59**, 27-37.
- Holst, L.L. & Giesy, J.P. (1989). Chronic Effects of the photoenhanced toxicity of anthracene on *Daphnia magna* reproduction. *Environmental Toxicology and Chemistry* **8**, 933-942.
- Holtby, L.B. & Bothwell, M.L. (2008). Effects of solar ultraviolet radiation on the behaviour of juvenile coho salmon (*Oncorhynchus kisutch*): avoidance, feeding, and agonistic interactions. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 701-711.
- Huebner, J.D., Young, D., Loadman, N.L., Lentz, V.J. & Wiegand, M.D. (2006). Age-dependent survival, reproduction and photorepair activity in *Daphnia magna* (Straus, 1820) after exposure to artificial ultraviolet radiation. *Photochemistry and Photobiology* **82**, 1656-1661.
- Huff, D.D., Grad, G. & Williamson, C.E. (2004). Environmental constraints on spawning depth of yellow perch: the roles of low temperatures and high solar ultraviolet radiation. *Transactions of the American Fisheries Society* **133**, 718-726.
- Hylander, S. & Hansson, L.-A. (2010). Vertical migration mitigates UV effects on zooplankton community composition. *Journal of Plankton Research* **32**, 971-980.
- Jackson, D.A. (2002). Ecological effects of *Micropterus* introductions: the dark side of black bass. *American Fisheries Society Symposium* **31**, 221-233.
- Johnson, P.T.J., Stanton, D.E., Preu, E.R., Foshay, K.J. & Carpenter, S.R. (2006). Dining on disease: how interactions between infection and environment affect predation risk. *Ecology* **87**, 1973-1980.
- Jordan, R., Kellogg, K., Howe, D., Juanes, F., Stauffer, J. & Loew, E. (2006). Photopigment spectral absorbance of Lake Malawi cichlids. *Journal of Fish Biology* **68**, 1291-1299.
- Kelly, D.J. & Bothwell, M.L. (2002). Avoidance of solar ultraviolet radiation by juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 474-482.
- Kessler, K., Lockwood, R.S., Williamson, C.E. & Saros, J.E. (2008). Vertical distribution of zooplankton in subalpine and alpine lakes: ultraviolet radiation, fish predation, and the transparency-gradient hypothesis. *Limnology and Oceanography* **53**, 2374-2382.
- Kochevar, I.E. (1981). Phototoxicity mechanisms: chloropromazine photosensitized damage to DNA and cell membranes. *Journal of Investigative Dermatology* **77**, 59-64.
- Lalonde, J.D., Amyot, M., Kraepiel, A.M.L. & Morel, F.M.M. (2001). Photooxidation of Hg(0) in artificial and natural waters. *Environmental Science and Technology* **35**, 1367-1372.

- Landers, D.H., Simonich, S.M., Jaffe, D., Geiser, L., Campbell, D.H., Schwindt, A., Schreck, C., Kent, M., Hafner, W., Taylor, H.E., Hageman, K., Usenko, S., Ackerman, L., Schrlau, J., Rose, N., Blett, T. & Morrison Erway, M. (2010). The western airborne contaminant assessment project (WACAP): an interdisciplinary evaluation of the impacts of airborne contaminants in western US national parks. *Environmental Science and Technology* **44**, 855-859.
- Laurion, I., Ventura, M., Catalan, J., Psenner, R. & Sommaruga, R. (2000). Attenuation of ultraviolet radiation in mountain lakes: factors controlling the among- and within-lake variability. *Limnology and Oceanography* **45**, 1274-1288.
- Leavitt, P.R., Cumming, B.F., Smol, J.P., Reasoner, M., Pienitz, R. & Hodgson, D.A. (2003). Climatic control of ultraviolet radiation effects on lakes. *Limnology and Oceanography* **48**, 2062-2069.
- Leech, D.M. & Johnsen, S. (2003). Behavioral responses – UVR avoidance and vision. In: *UV effects in aquatic organisms and ecosystems* (eds E.W. Helbling & H.E. Zagarese), Royal Society of Chemistry, Cambridge pp. 455-475.
- Leech, D.M. & Williamson, C.E. (2000). Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? *Ecological Applications* **10**, 1530-1540.
- Leech, D.M., Boeing, W.J., Cooke, S.L., Williamson, C.E. & Torres, L. (2009). UV-enhanced fish predation and the differential migration of zooplankton in response to UV radiation and fish. *Limnology and Oceanography* **54**, 1152-1161.
- Leu, E., Faerovig, P.J. & Hessen, D.O. (2006). UV effects on stoichiometry and PUFAs of *Selenastrum capricornutum* and their consequences for the grazer *Daphnia magna*. *Freshwater Biology* **51**, 2296-2308.
- Lindberg, S., Bullock, R., Ebinghaus, R., Engstrom, D., Feng, X., Fitzgerald, W., Pirrone, N., Prestbo, E. & Seigneur, C. (2007). A synthesis of progress and uncertainties in attributing the sources of mercury in deposition. *Ambio* **36**, 19-33.
- Loew, E.R., Mcfarland, W.N., Mills, E.L. & Hunter, D. (1993). A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. *Canadian Journal of Zoology* **71**, 384-386.
- Lorenzen, C.J. (1979). Ultraviolet radiation and phytoplankton photosynthesis. *Limnology and Oceanography* **24**, 1117-1120.
- Marinone, M.C., Marque, S.M., Suárez, D.A., del Carmen Diéguez, M., Pérez, P., De Los Ríos, P., Soto, D. & Zagarese, H.E. (2006). UV radiation as a potential driving force for zooplankton community structure in Patagonian lakes. *Photochemistry and Photobiology* **82**, 962-971.
- McKenzie, R.L., Aucamp, P.J., Bais, A.F., Bjorn, L.O., Ilyas, M. & Madronich, S. (2011). Ozone depletion and climate change: impacts on UV radiation. *Photochemical and Photobiological Sciences* **10**, 182-198.
- McKinney, M.L. & Lockwood, J.L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**, 450-453.
- Moeller, R.E. (1994). Contribution of ultraviolet radiation (UV-A, UV-B) to photoinhibition of epilimnetic phytoplankton in lakes of differing UV transparency. *Archiv für Hydrobiologie Beihefte Ergebnisse der Limnologie* **43**, 157-170.
- Moeller, R.E., Gilroy, S., Williamson, C.E., Grad, G. & Sommaruga, R. (2005). Dietary acquisition of photoprotective compounds (mycosporine-like amino acids, carotenoids) and acclimation to ultraviolet radiation in a freshwater copepod. *Limnology and Oceanography* **50**, 427-439.
- Molot, L.A. & Dillon, P.J. (1997). Photolytic regulation of dissolved organic carbon in northern lakes. *Global Biogeochemical Cycles* **11**, 357-365.
- Molot, L.A., Hudson, J.J., Dillon, P.J. & Miller, S.A. (2005). Effect of pH on photo-oxidation of dissolved organic carbon radicals in a coloured, softwater stream. *Aquatic Sciences* **67**, 189-195.
- Monteith, D.T., Stoddard, J.L., Evans, C.D. et al. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* **450**, 537-541.
- Moran, M.A. & Zepp, R.G. (1997). Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter. *Limnology and Oceanography* **42**, 1307-1316.
- Morris, D.P. & Hargreaves, B.R. (1997). The role of photochemical degradation of dissolved organic carbon in regulating the UV transparency of three lakes on the Pocono Plateau. *Limnology and Oceanography* **42**, 239-249.
- Morris, D.P., Zagarese, H., Williamson, C.E., Balseiro, E.G., Hargreaves, B.R., Modenutti, B., Moeller, R. & Queimalinos, C. (1995). The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography* **40**, 1381-1391.
- Obernosterer, I. & Benner, R. (2004). Competition between biological and photochemical processes in the mineralization of dissolved organic carbon. *Limnology and Oceanography* **49**, 117-124.
- Olesen, B. & Maberly, S.C. (2001). The effect of high levels of visible and ultra-violet radiation on the photosynthesis of phytoplankton from a freshwater lake. *Archiv für Hydrobiologie* **51**, 301-315.
- Olson, M.H., Adams-Deutsch, T., Cassels, K.J., Oliver, A.E. & Mitchell, D.L. (2008). Patterns of Ultraviolet Radiation Exposure in Bluegill Nests over the Course of the Spawning Season. *Transactions of the American Fisheries Society* **137**, 1446-1454.
- Oris, J.T. & Giesy, J.P. (1985). The photoenhanced toxicity of anthracene to juvenile sunfish (*Lepomis* spp). *Aquatic Toxicology* **6**, 133-146.
- Osburn, C.L., Zagarese, H.E., Morris, D.P., Hargreaves, B.R.

- & Cravero, W.E. (2001). Calculation of spectral weighting functions for the solar photobleaching of chromophoric dissolved organic matter in temperate lakes. *Limnology and Oceanography* **46**, 1455-1467.
- Overholt, E.P., Hall, S.P., Williamson, C.E., Meikle, C.E., Duffy, M.A. & Cáceres C.E. (in press). Solar radiation decreases parasitism in *Daphnia*. *Ecology Letters*.
- Pace, M.L. & Cole, J.J. (2002). Synchronous variation of dissolved organic carbon and color in lakes. *Limnology and Oceanography* **47**, 333-342.
- Pandey, R., Mehrotra, S., Ray, R.S., Joshi, P.C. & Hans, R.K. (2002). Evaluation of UV-Radiation induced singlet oxygen generation potential of selected drugs. *Drug and Chemical Toxicology* **25**, 215-225.
- Persaud, A.D., Moeller, R.E., Williamson, C.E. & Burns, C.W. (2007). Photoprotective compounds in weakly and strongly pigmented copepods and co-occurring cladocerans. *Freshwater Biology* **52**, 2121-2133.
- Peters, S.C., Wollenberg, J.L., Morris, D.P. & Porter, J.A. (2007). Mercury emission to the atmosphere from experimental manipulation of DOC and UVR in mesoscale field chambers in a freshwater lake. *Environmental Science and Technology* **41**, 7356-7362.
- Pienitz, R. & Vincent, W.F. (2000). Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. *Nature* **404**, 484-487.
- Preston, B.L., Snell, T.W. & Kneisel, R. (1999). UV-B exposure increases acute toxicity of pentachlorophenol and mercury to the rotifer *Brachionus calyciflorus*. *Environmental Pollution* **106**, 23-31.
- Rae, R., Howard-Williams, C., Hawes, I., Schwarz, A-M. & Vincent, W.F. (2001). Penetration of solar ultraviolet radiation into New Zealand lakes: influence of dissolved organic carbon and catchment vegetation. *Limnology (Japanese Society of Limnology)* **2**, 79-89.
- Rast, W. & Lee, G.F. (1978). Summary analysis of the North American (US Portion) OECD eutrophication project: nutrient loading, lake response relationships, and trophic state indices. US EPA, EPA-600/3-78-008. Corvallis Environmental Research Laboratory, Corvallis, Oregon. 454 pp.
- Rautio, M. & Tartarotti, B. (2010). UV radiation and freshwater zooplankton: damage, protection and recovery. *Freshwater Reviews* **3**, 105-131.
- Rautio, M., Bonilla, S. & Vincent, W.F. (2009). UV photoprotectants in arctic zooplankton. *Aquatic Biology* **7**, 93-105.
- Reche, I., Pace, M.L. & Cole, J.J. (1999). Relationship of trophic and chemical conditions to photobleaching of dissolved organic matter in lake ecosystems. *Biogeochemistry* **44**, 259-280.
- Rick, I.P., Modarressie, R. & Bakker, T.C.M. (2006). UV wavelengths affect female mate choice in three-spined sticklebacks. *Animal Behavior* **71**, 307-313.
- Riegger, L. & Robinson, D. (1997). Photoinduction of UV-absorbing compounds in Antarctic diatoms and *Phaeocystis antarctica*. *Marine Ecology Progress Series* **160**, 13-25.
- Rose, K.C., Williamson, C.E., Schladow, S.G., Winder, M. & Oris, J.T. (2009). Patterns of spatial and temporal variability of UV transparency in Lake Tahoe, California-Nevada. *Journal of Geophysical Research-Biogeosciences* **114** 9 pp.
- Roulet, N. & Moore, T.R. (2006). Environmental chemistry - Browning the waters. *Nature* **444**, 283-284.
- Schindler, D.W., Curtis, P.J., Parker, B.R. & Stainton, M.P. (1996). Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature* **379**, 705-708.
- Scudder, G.G.E. (1983). A review of factors governing the distribution of two closely related corixids in the saline lakes of British Columbia. *Hydrobiologia* **105**, 143-154.
- Seehausen, O., Terai, Y., Magalhaes, I.S., Carleton, K.L., Mrosso, H.D.J., Miyagi, R., van der Sluijs, I., Schneider, M.V., Maan, M.E., Tachida, H., Imai, H. & Okada, N. (2008). Speciation through sensory drive in cichlid fish. *Nature* **455**, 620-623.
- Seekell, D.A. & Pace, M.L. (2011). Does the Pareto distribution adequately describe the size-distribution of lakes? *Limnology and Oceanography* **56**, 350-356.
- Skerratt, L.F., Berger, L., Speare, R., Cashins, S., McDonald, K.R., Phillott, A.D., Hines, H.B. & Kenyon, N. (2007). Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *Ecohealth* **4**, 125-134.
- Smith, E.J., Partridge, J.C., Parsons, K.N., White, E.M., Cuthill, I.C., Bennett, A.T.D. & Church, S.C. (2002). Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*). *Behavioral Ecology* **13**, 11-19.
- Sommaruga, R. & Augustin, G. (2006). Seasonality in UV transparency of an alpine lake is associated to changes in phytoplankton biomass. *Aquatic Sciences* **68**, 129-141.
- Sommaruga, R., Psenner, R., Schafferer, E., Koinig, K.A. & Sommaruga-Wogratz, S. (1999). Dissolved organic carbon concentration and phytoplankton biomass in high-mountain lakes of the Austrian Alps: potential effect of climatic warming on UV underwater attenuation. *Arctic Antarctic and Alpine Research* **31**, 247-253.
- Stahl, L.L., Snyder, B.D., Olsen, A.R. & Pitt, J.L. (2009). Contaminants in fish tissue from US lakes and reservoirs: a national probabilistic study. *Environmental Monitoring and Assessment* **150**, 3-19.
- Striegl, R.G., Aiken, G.R., Domblaser, M.M., Raymond, P.A. & Wickland, K.P. (2005). A decrease in discharge-normalized DOC export by the Yukon River during summer through

- autumn. *Geophysical Research Letters* **32**, L21413.
- Tartarotti, B., Laurion, I. & Sommaruga, R. (2001). Large variability in the concentration of mycosporine-like amino acids among zooplankton from lakes located across an altitude gradient. *Limnology and Oceanography* **46**, 1546-1552.
- Trankvik, L.J. & Bertilsson, S. (2001). Contrasting effects of solar UV radiation on dissolved organic sources for bacterial growth. *Ecology Letters* **4**, 458-463.
- Tranvik, L.J., et al. (2009). Lakes and reservoirs as regulators of carbon cycling and climate. *Limnology and Oceanography* **54**, 2298-2314.
- Tucker, A.J., Williamson, C.E., Rose, K.C., Oris, J.T., Connelly, S.J., Olson, M.H. & Mitchell, D.L. (2010). Ultraviolet radiation affects invasibility of lake ecosystems by warmwater fish. *Ecology* **91**, 882-890.
- Vahatalo, A.V., Salonen, K., Salkinoja-Salonen, M. & Hatakka, A. (1999). Photochemical mineralization of synthetic lignin in lake water indicates enhanced turnover of aromatic organic matter under solar radiation. *Biodegradation* **10**, 415-420.
- Vahatalo, A.V., Salonen, K., Munster, U., Jarvinen, M. & Wetzel, R.G. (2003). Photochemical transformation of allochthonous organic matter provides bioavailable nutrients in a humic lake. *Archiv Fur Hydrobiologie* **156**, 287-314.
- Van Donk, E. & Hessen, D.O. (1995). Reduced digestibility of UV-B stressed and nutrient-limited algae by *Daphnia magna*. *Hydrobiologia* **307**, 147-151.
- Vincent, W.F. & Roy, S. (1993). Solar ultraviolet-B radiation and aquatic primary production: damage, protection, and recovery. *Environmental Reviews* **1**, 1-12.
- Voelker, B.M., Morel, F.M.M. & Sulzberger, B. (1997). Iron redox cycling in surface waters: Effects of humic substances and light. *Environmental Science and Technology* **31**, 1004-1011.
- Weber, J.H. (1993). Review of possible paths for abiotic methylation of mercury (II) in the aquatic environment. *Chemosphere* **26**, 2063-2077.
- Williamson, C.E. (1995). What role does UV-B radiation play in freshwater ecosystems? *Limnology and Oceanography* **40**, 386-392.
- Williamson, C.E. & Rose, K.C. (2009). Ultraviolet insights: attempting to resolve enigmatic patterns in pelagic freshwaters - the historical context and a view to the future. *International Review of Hydrobiology* **94**, 129-142.
- Williamson, C.E. & Rose, K.C. (2010). When UV meets freshwater. *Science* **329**, 637-639.
- Williamson, C.E., Stemberger, R.S., Morris, D.P., Frost, T.M. & Paulsen, S.G. (1996). Ultraviolet radiation in North American lakes: attenuation estimates from DOC measurements and implications for plankton communities. *Limnology and Oceanography* **41**, 1024-1034.
- Williamson, C.E., Metzgar, S.L., Lovera, P.A. & Moeller, R.E. (1997). Solar ultraviolet radiation and the spawning habitat of yellow perch, *Perca flavescens*. *Ecological Applications* **7**, 1017-1023.
- Williamson, C.E., Neale, P.J., Grad, G., De Lange, H.J. & Hargreaves, B.R. (2001a). Beneficial and detrimental effects of UV on aquatic organisms: implications of spectral variation. *Ecological Applications* **11**, 1843-1857.
- Williamson, C.E., Olson, O.G., Lott, S.E., Walker, N.D., Engstrom, D.R. & Hargreaves, B.R. (2001b). Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. *Ecology* **82**, 1748-1760.
- Williamson, C.E., Neale, P.J. & Likens, G.E. (2009). Ultraviolet Light. In: *Encyclopedia of Inland Waters*. Elsevier, Oxford. 6492 pp.
- Williamson, C.E., Salm, C., Cooke, S.L. & Saros, J.E. (2010). How do UV radiation, temperature, and zooplankton influence the dynamics of alpine phytoplankton communities? *Hydrobiologia* **648**, 73-81.
- Williamson, C.E., Fischer, J.M., Bollens, S.M., Overholt, E.P. & Breckenridge, J.K. (2011). Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnology and Oceanography* **56**, 1603-1623.
- Xenopoulos, M.A. & Frost, P.C. (2003). UV radiation, phosphorus, and their combined effects on the taxonomic composition of phytoplankton in a boreal lake. *Journal of Phycology* **39**, 291-302.
- Xenopoulos, M.A., Prairie, Y.T. & Bird, D.F. (2000). Influence of ultraviolet-B radiation, stratospheric ozone variability, and thermal stratification on the phytoplankton biomass dynamics in a mesohumic lake. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 600-609.
- Xenopoulos, M.A., Frost, P.C. & Elser, J.J. (2002). Joint effects of UV radiation and phosphorus supply on algal growth rate and elemental composition. *Ecology* **83**, 423-435.
- Xenopoulos, M.A., Leavitt, P.R. & Schindler, D.W. (2009). Ecosystem-level regulation of boreal lake phytoplankton by ultraviolet radiation. *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 2002-2010.
- Yan, N.D., Keller, W., Scully, N.M., Lean, D.R.S. & Dillon, P.J. (1996). Increased UV-B penetration in a lake owing to drought-induced acidification. *Nature* **381**, 141-143.
- Yönonen, O., Huuskonen, H. & Karjalainen, J. (2005). Effects of UV radiation on the vertical distribution of vendace [*Coregonus albula* (L.)] larvae in Finnish lakes. *Ecology of Freshwater Fish* **14**, 161-167.
- Zaga, A., Little, E.E., Rabeni, C.F. & Ellersieck, M.R. (1998). Photoenhanced toxicity of a carbamate insecticide to early life stage anuran amphibians. *Environmental Toxicology and Chemistry* **17**, 2543-2553.

- Zagarese, H.E. & Williamson, C.E. (2001). The implications of solar UV radiation exposure for fish and fisheries. *Fish and Fisheries* 2, 250-260.
- Zagarese, H.E., Tartarotti, B. & Añón Suárez, A. (2003). The significance of ultraviolet radiation for aquatic organisms. In: *Modern Trends in Applied Aquatic Ecology* (eds R.S. Ambast & N.K. Ambast), pp. 173-200. KluwerAcademic/Plenum Press, New York, USA.
- Zhang, J., Hudson, J., Neal, R., Sereda, J., Clair, T., Turner, M., Jeffries, D., Dillon, P., Molot, L., Somers, K. & Hesslein, R. (2010). Long-term patterns of dissolved organic carbon in lakes across eastern Canada: evidence of a pronounced climate effect. *Limnology and Oceanography* 55, 30-42.

Author Profile

Andrew Tucker is a postdoctoral fellow at Miami University where he also received his PhD under the advisement of Dr. Craig Williamson. Andrew's research interests include the ecology of UV radiation, invasion ecology, and ecotoxicology.

Craig Williamson received his PhD from Dartmouth College and was a professor at Lehigh University before moving to Miami University in 2005. 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. As part of his service to the scientific and global community, Craig serves on the United Nations Environment Programme Environmental Effects Assessment Panel on ozone depletion.