



Ultraviolet radiation studies upon phytoplankton from freshwater and marine ecosystems of Argentina

E. Walter Helbling* & Virginia E. Villafañe

With 4 figures

Abstract: Argentina, with its large latitudinal extent, has an important number of water bodies with different light scenarios therefore, variable responses to solar radiation are found. In this article we review the impact of UVR on phytoplankton from different aquatic ecosystems of Argentina, mostly focusing on targets such as the photosystem and the DNA molecule. Also, we present examples of different acclimation strategies that include, among others, the synthesis of UV-absorbing compounds and shifts in the community composition and structure as a result of UVR exposure. While we have obtained an important database about the effects and impacts of UVR on phytoplankton, especially from the Patagonia area, there are many points still to unveil, mainly those related to the interactive effects of climate change variables such as the increase in temperature and UVR levels, and how this would affect phytoplankton exposure and behaviour in different water bodies.

Keywords: Argentina, DNA, photosynthesis, phytoplankton, primary production, UVR

Introduction

The assessment of the impact of solar ultraviolet radiation (UVR, 280–400 nm) on marine and freshwater phytoplankton has been the focus of many investigations (see reviews of De Mora et al. 2000, Helbling & Zagarese 2003 & Häder et al. 2011) especially since the discovery of the Antarctic ozone “hole” and the associated increase in ultraviolet B radiation (UV-B, 280–315 nm) reaching the Earth’s surface (Farman et al. 1985). Nowadays, however, studies have demonstrated that not only enhanced UV-B, but also normal levels of UVR (both UV-B and UV-A – 315–400 nm) are harmful for aquatic organisms such as phytoplankton. Under some conditions, however, UVR can also result beneficial as its energy can be used in photoenzymatic repair and in photosynthesis (Buma et al. 2003, Helbling et al. 2003). In general, there is a high variability of responses to UVR exposure because the sensitivity and acclimation capacity towards these wavelengths are species-specific (Roy 2000,

Authors’ address:

Estación de Fotobiología Playa Unión (EFPU), Casilla de Correos N° 15 (9103) Rawson, Chubut, Argentina & Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

*Corresponding author: whelbling@efpu.org.ar

Vernet 2000, Häder et al. 2011). Environmental changes as occurring in the UVR climate (i.e., seasonal or produced by ozone depletion events) (Blumthaler & Webb 2003) as well as in other abiotic factors such as nutrient availability or temperature (Litchman et al. 2002, Sobrino & Neale 2007) also account for much of the observed variability in UVR responses of phytoplankton organisms.

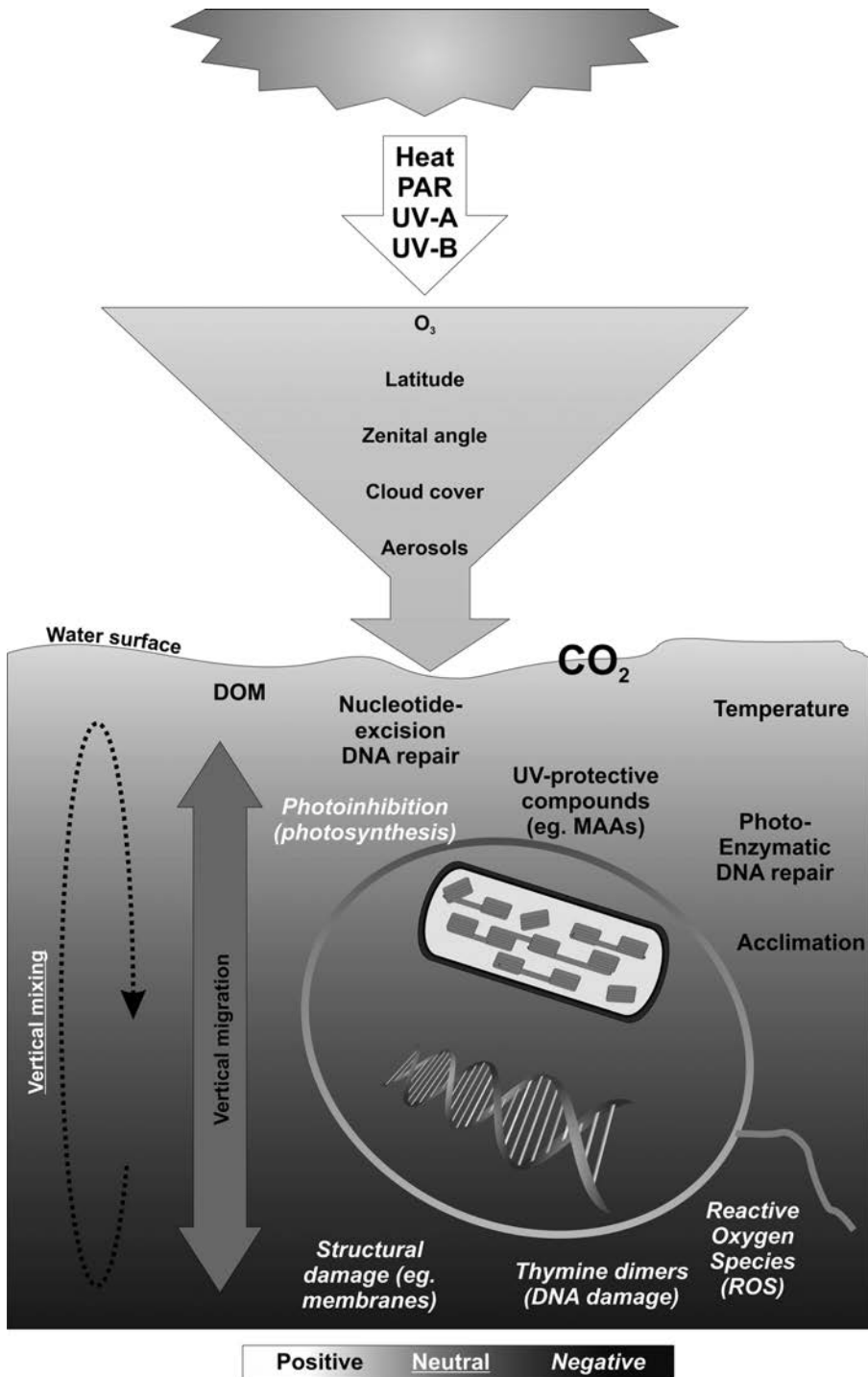
The dynamics of the UVR impact upon a cell or community is rather complex (Fig. 1). Firstly, solar UVR needs to reach the organism and then it has to be absorbed in order to cause a particular effect. This simple fact is not so easy to establish in phytoplankton, as cells are moving within the upper mixed layer (UML) or epilimnion at a certain rate that depends, in turn, on wind speed and duration and on the stability of the water column, among other factors (Helbling et al. 1994, Ferrero et al. 2006). After solar radiation had been absorbed by the cell, its impact will depend not only on the wavelength but also on the vulnerability of the target e.g., the DNA molecule, the photosynthetic apparatus or the cell membrane. However, and in spite of the negative effects caused by UVR, phytoplankton display a suite of mechanisms that allow them to minimize (or at least to reduce) the effect caused by deleterious wavelengths.

In this article we will analyze the radiation climate and its variability in the atmosphere. Then, and once solar radiation reached the water body, we will evaluate how it is modified until it impinges the phytoplankton cell (see also review by Gonçalves et al. 2010). Following that, we will review the impact of UVR on different cellular targets and the potential acclimation mechanisms towards these wavelengths, focusing on results obtained in marine and freshwater bodies of Argentina. Because the effects of UVR are frequently synergic or antagonistic with other variables (Dunne 2010) we will also consider the interaction of solar radiation with others such as mixing, nutrient addition and temperature.

The radiation climate

Solar UVR is modified in its way through the atmosphere due to the presence of several gases and pollutants; additionally, geographical (latitude and altitude) and seasonal factors are important at the time of determining the quantity and quality of solar radiation reaching a particular water body (Blumthaler & Webb 2003) (Fig. 1). In general, those sites in which important amounts of pollutants are present receive less radiation than their clean-air sites counterparts. In relation to the geographical factors, tropical latitudes receive higher radiation levels than polar sites, because of the short distance Earth to Sun and the low solar angles. Similarly, in high altitude locations higher radiation levels are received as compared to sea level sites (at comparable latitudes); in fact, the increase in solar UV-B can be as much as 10–20% every 1000 m (Blumthaler et al. 1992). The same rationale can be applied when comparing the radiation levels at different times of the year in a particular location: Solar radiation levels during the summer are generally higher than during the winter.

Fig. 1. Schematic diagram showing the main factors affecting the quantity and quality of UVR received by phytoplankton organisms. The negative effects caused by UVR are represented with white letters whereas counteracting mechanisms to reduce them are in black letters.



Due to its utmost importance for a broad range of disciplines (e.g., ecology, human health, agricultural purposes) different research groups/Institutions are currently monitoring solar radiation in several locations of Argentina (see review by Villafañe et al. 2001, Cede et al. 2002, Palancar & Toselli 2002, Vernet et al. 2009), but measurements are mainly concentrated in the Patagonia area, due to its proximity to the Antarctic ozone “hole” (Villafañe et al. 2001). As an example of these monitoring programs, solar radiation data collected in Playa Unión, on the Atlantic coast ($43^{\circ}18.7'S$; $65^{\circ}02.5'W$) are presented in Figure 2. It is evident the trend described above of high solar radiation levels during summer (i.e., as much

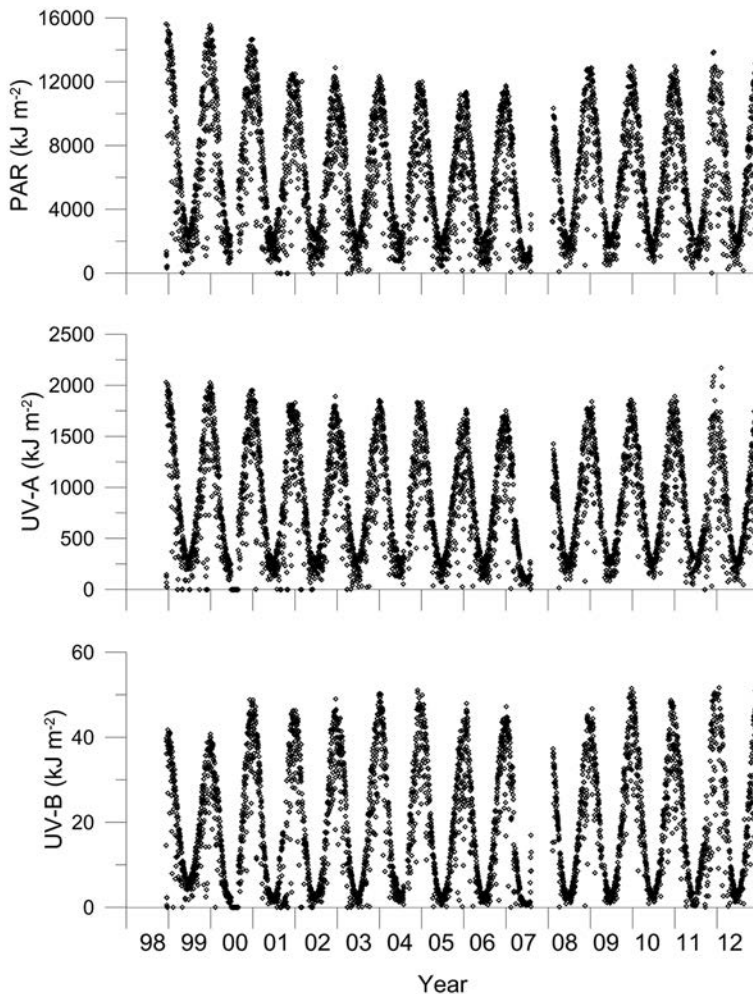


Fig. 2. Daily doses of solar radiation (in kJoules m⁻²) for PAR (400–700 nm), UV-A (315–400 nm) and UV-B (280–315 nm) for the period 1998–2012. The data were collected with an ELDONET filter radiometer permanently installed at EFPU ($43^{\circ}18.7'S$; $65^{\circ}02.5'W$) and represent the time-integrated values over a day of measurements collected every second and stored as mean minute average.

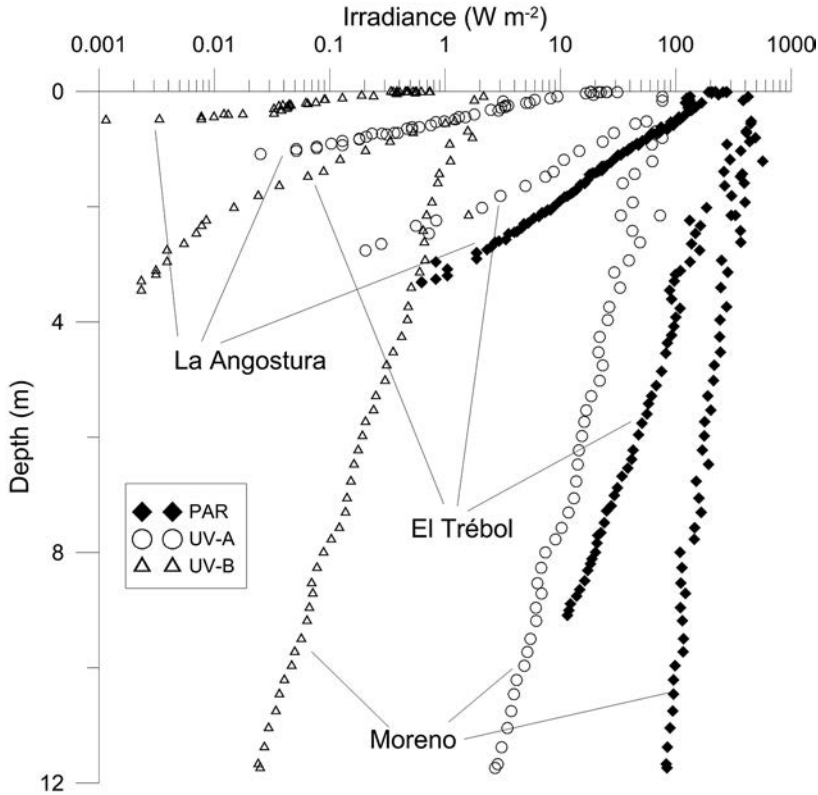


Fig. 3. Depth profiles of the penetration of solar radiation in the water column for PAR (400–700 nm), UV-A (315–400 nm) and UV-B (280–315 nm) in Lake Moreno (41°04.5'S, 71°30.3'W, 800 m a.s.l.) and Lake El Trébol (41°04.2'S, 71°29.4'W, 780 m a.s.l.) in the Andean region, and Lake La Angostura (26°45'S; 65°37'W, 1980 m a.s.l.) in the Peri-Pampean Sierras.

as 16000, 2000 and 50 kJoules m^{-2} for PAR, UV-A and UV-B, respectively) and low ones during winter. By monitoring solar radiation in different locations, latitudinal trends for UVR in Argentina have been established, with the ratio UV-B/UV-A decreasing from tropical latitudes towards the sub-polar region under “normal” ozone conditions (Orce & Helbling 1997, Diaz et al. 2006, Vernet et al. 2009). It has also been determined the presence of low-ozone air masses over Patagonia, either because the Antarctic polar vortex covers the tip of South America (Frederick et al. 1993, 1994, Díaz et al. 1994) or because ozone-depleted air masses detach from the polar vortex and circulate northwards (Atkinson et al. 1989, Kirchhoff et al. 1996). However, the dynamics of the polar vortex is such that these low-ozone air masses pass over Patagonia only a few days per year (Helbling et al. 2005). During ozone depletion events, the UV-B/UV-A ratio increases significantly and thus higher UVR levels, similar as those observed at or near the tropics, are registered (Orce & Helbling 1997). It should be noted that although ozone depletion events do affect normal radiation patterns, cloud cover, together with the solar zenith angle are much more important in explaining the variability of solar radiation reaching the Earth’s surface than any other variables (Helbling et al. 2005).

Exposure to UVR of plankton organisms further depends on the intrinsic characteristics of the water body. In the water column, solar radiation decreases exponentially with depth, although the attenuation depends on the wavelength considered, being the shorter ones (i.e., UVR) those that attenuates faster as compared to PAR. Attenuation of solar radiation also depends on the amount of chromophoric dissolved organic material (CDOM) and inorganic (sediments), and organic particles (plankton) present in the water (see review by Hargreaves 2003). In particular, it has been found a significant correlation between the amount of dissolved organic carbon (DOC) and the attenuation of UV-B (Morris et al. 1995); moreover, studies carried out by Bastidas Navarro & Modenutti (2010) in Andean lakes demonstrated that UVR plays a substantial role on optical features and phosphorous release of DOM from lake water and macrophyte leachates. Although it is difficult to generalize for the whole country, Argentina present two contrasting scenarios in relation to the underwater radiation characteristics of its water bodies: In general, shallow and turbid lakes characterize the Chaco-Pampa Plain (Allende et al. 2009) whereas deep, clear lakes are found in the Andean Mountains region (Pérez et al. 2007). Still, there are exceptions of this general rule, as lakes in stable state with low phytoplankton biomass (and hence, relatively clear) (Scheffer et al. 1993) are also found in the Chaco-Pampa Plain (Quirós et al. 2002) whereas shallow lakes in the Andean region can contain high amounts of CDOM thus being rather turbid (Villafañe et al. 2004b). A typical example of the attenuation of solar radiation for different water bodies of Argentina is shown in Figure 3. In the case of Lake Moreno (in the Andean region) the attenuation coefficients (k_d) were 0.15, 0.28, and 0.37 m^{-1} , for PAR, UV-A, and UV-B, respectively whereas in Lake El Trébol, also in the Andean region, k_d were higher, with values of 0.4, 2.39 and 2.54 m^{-1} , for PAR, UV-A, and UV-B, respectively (Villafañe et al. 2004b). Further attenuation of solar radiation was observed in Lake La Angostura in the Peri-Pampean Sierras, with k_d values of 1.73, 5.69, and 9.1 m^{-1} , for PAR, UV-A, and UV-B, respectively. Additionally, variability in the light climate can be determined within a particular water body, due for example, to the differential input of particulate materials such as those from glacial origin (Modenutti et al. 1998) or transported by rain (Medina et al. 2010). Recent studies (Modenutti et al. 2013 a, b) have also determined the effects of ash and pumice loads on the light climate of Andean lakes after the eruption of the Puyehue volcano; post-eruption data showed that k_{PAR} increased 1.5- to 2.5-fold after the eruption in lakes Espejo, Correntoso, and Nahuel Huapi, being k_{PAR} the primary variable that was associated with variations in chlorophyll in these lakes.

Mixing conditions and the depth of the UML/epilimnion also affect the exposure of organisms to UVR by conditioning the time that cells spend in the photoactive zone – close or at the surface receiving high solar irradiances (Helbling et al. 1994, Neale et al. 2003). For phytoplankton this is especially important, as mixing causes that these cells – that move passively in the water column, circulate within the UML while being exposed to fluctuating radiation regimes. Moreover, if other conditions are the same, phytoplankton circulating within a deep UML will be exposed to a lower mean irradiance as compared to conditions of shallow UML (Helbling et al. 1994). An interesting example constitutes the yearly study carried out throughout tidal cycles in the Chubut River estuary (Patagonia) where a maximum k_{PAR} value of $\sim 4.5 m^{-1}$ was determined during mixed conditions (i.e., the period high tide-ebb-low tide) whereas during strong stratification (i.e., flood) k_{PAR} dropped to values of $\sim 0.5 m^{-1}$ (Helbling et al. 2010). It should be noted that in temperate and sub-polar and polar

latitudes wind not only strongly conditions the depth of the UML/epilimnion but also it is important in re-suspending particulate material, thus further increasing the attenuation of solar radiation in the water column.

Effects of UVR on phytoplankton

Phytoplanktons are key aquatic primary producers that contribute for a substantial share of CO₂ fixation in both marine and freshwater ecosystems. In the euphotic zone (i.e., the area where solar radiation reaches 1% of the incident value at the surface) however, cells are exposed not only to photosynthetically active radiation (PAR – 400–700 nm) but also to UVR. While PAR is the most important waveband involved in the photosynthetic process, UVR is a stressor that may damage important cellular components such as the DNA molecule or proteins (Buma et al. 2003, Bouchard et al. 2006) or affect physiological processes, such as photosynthesis and growth (Villafañe et al. 2003), nutrient uptake (Aubriot et al. 2004) or fatty acids composition and hence food quality (Arts & Rai 1997, Leu et al. 2006), among others. On the other hand, beneficial effects of this waveband, particularly UV-A, have also been reported (see below).

When addressing the impact of UVR on phytoplankton it is important to consider the time scale of experimentation, i.e., short (less than one day) or long-term (several days). Both types of experimentation provide complementary information to obtain a broad view of the effects of solar radiation on a particular organism or ecosystem. In general, short-term experiments provide insights on how fast mechanisms respond to this particular stressor, such as the electron transport rates within the photosystem II (PSII), daily primary production or dissipation of excess energy, among others. On the other hand, long-term experiments are useful to assess the acclimation mechanisms of phytoplankton and processes that occur over longer time spans, such as growth rates, changes in species composition or synthesis of protective compounds (see below).

In the following paragraphs we will present results of studies aiming to determine the impact of UVR on phytoplankton from aquatic systems of Argentina i.e., mainly those related to photoinhibition and DNA damage (short-term effects) and those occurring over long-term scales of experimentation, as those involved in potential acclimation mechanisms studied in phytoplankton species/communities.

a) Effects of UVR on photosynthesis: One of the best known effects of solar radiation upon the photosynthesis process is the photoinhibition – i.e., the reduction of photosynthetic rates (Osmond 1994). This effect is mostly caused by high PAR irradiances, but UVR also contributes for a variable share, depending on the quality and quantity (irradiance or dose) received by the cells, their specific sensitivity and acclimation potential, among other factors. Photoinhibition due to UVR is clearly observed during in situ incubations, with surface samples generally having lower photosynthetic rates than those incubated at depth, where radiation levels are lower. An example of inhibition caused by UVR and UV-A during short-term in situ incubations (i.e., as assessed through measurements of carbon incorporation) is presented in Figure 4. Because of the differential depth distribution of cells among the lakes, comparisons are made using the optical depth (Villafañe et al. 2001). The general pattern is of higher inhibition due to UV-A as compared to that due to UV-B, as seen in many

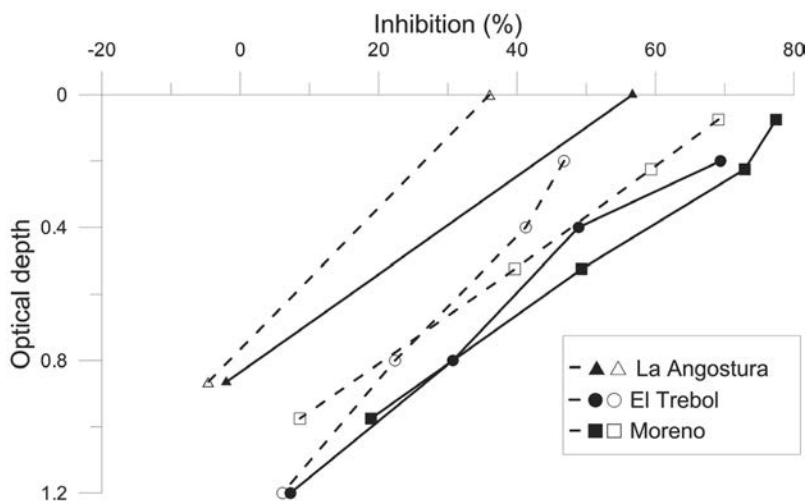


Fig. 4. Inhibition of photosynthesis due to UVR (280–400 nm, black symbols) and UV-A (315–400 nm, open symbols) as a function of the optical depth (i.e., $k_d \cdot z$) for: Lake Moreno (41°04.5'S, 71°30.3'W, 800 m a.s.l.) and Lake El Trébol (41°04.2'S, 71°29.4'W, 780 m a.s.l.) in the Andean region, and Lake La Angostura (26°45'S; 65°37'W, 1980 m a.s.l.) in the Peri-Pampean Sierras.

environments of the world (see review by Villafañe et al. 2003). In this particular example, the highest photosynthetic inhibition in surface waters was determined in the clear Lake Moreno, whereas the lowest values were determined in Lake La Angostura. Some studies have also determined a latitudinal trend, with tropical species being more resistant to UVR than those from polar environments (Helbling et al. 1992) due to their evolutionary light history of naturally high radiation levels. Moreover, tropical phytoplankton had a higher irradiance threshold for photosynthesis inhibition (Helbling et al. 2001c) than polar species (Helbling et al. 1992, Helbling & Villafañe 2002) thus providing further evidence of their higher resistance to high UVR levels. However, and due to the scattered data currently available, it has not been possible yet to establish such a latitudinal trend along Argentina.

In other studies describing UVR-induced photoinhibition responses of phytoplankton from Patagonian marine coastal waters (Bahía Engaño, Chubut) Villafañe et al. (2004a) performed a time series throughout the year and found that most of the observed variability in UVR effects was inter-seasonal, although small intra-seasonal fluctuations were also determined. It was also found that although absolute values of photosynthesis inhibition were lower during the bloom (during winter time) this assemblage was more sensitive to UVR (especially in the UV-B region) than those of the pre- and post-bloom periods, as assessed through biological weighting functions – BWFs (i.e., inhibition per unit energy). Seasonal variations of UVR effects throughout the year were also determined in the turbid Lake Chascomús in the Pampa Plain, where the photoinhibition index (i.e., UV_{50} – the UV-A irradiance required to reduce primary productivity by 50%) increased with irradiance, clearly hinting for an acclimation strategy towards high radiation levels (Torremorell et al. 2009).

It has also been noticed that not only climatologically and geographical factors are key in determining the response of species towards UVR exposure but also taxonomic compo-

sition plays an important role. This was clearly seen in a detailed time series study carried out during the summer also in Bahía Engaño (Villafañe et al. 2008): While throughout the study period picoplankton cells ($< 2 \mu\text{m}$ in effective diameter) dominated in terms of abundance, the community showed varied proportions of diatoms, chlorophytes and cyanobacteria; UVR-induced photoinhibition varied accordingly, with high values when diatoms dominated, whereas low ones were determined when chlorophytes dominated. In studies assessing the P-E (photosynthesis versus irradiance) relationships of marine assemblages of Bahía Nueva and Bahía Camarones in the Chubut Province, Villafañe et al. (2004c) also determined the key role of the taxonomic composition on UVR-induced effects on photosynthesis: UVR significantly reduced P_{max} (i.e., the maximum rate of carbon fixation) during the pre-bloom, but not during the post-bloom period in Bahía Nueva samples. Additionally, UVR significantly affected E_k (i.e., the light saturation parameter of the P vs E curve) in all Bahía Camarones samples, but only in some of Bahía Nueva. Besides the species-specific sensitivity, cell size also seems to influence UVR responses, so that when addressing photosynthetic inhibition small cells are generally more resistant than large ones. It is suggested that this occurs because small cells can acclimate faster to changes in solar radiation, as determined in a comparative study carried out with winter phytoplankton communities from Andean lakes, where the larger cells of Lake Moreno displayed higher photosynthetic inhibition as compared to the smaller-sized from Lake Morenito (Helbling et al. 2001b). The importance of cell size was also highlighted in studies carried out in large oligotrophic Andean lakes, where it was found that picoplankton cells were particularly well adapted to these environments as a consequence of their high phosphorous assimilation capacity and light harvesting efficiency (Callieri et al. 2007). In an apparent contrast with these previous findings, experiments carried out with dinoflagellates differing in their size showed that the smallest species (i.e., *Gymnodinium chlorophorum*) was the most sensitive towards UVR (as compared to the large *Prorocentrum micans*) but this study further highlighted for the importance of considering the mixing conditions as well as the acclimation via the synthesis of UV-absorbing compounds at the time to interpret the results obtained (Helbling et al. 2008).

Indeed, mixing can also contribute to the variability in photosynthetic responses to UVR, as a result of fluctuations in the underwater radiation field under which cells are exposed. Particularly, and for polar waters, it was found that fluctuating radiation regimes due to vertical mixing were more important in affecting phytoplankton photosynthesis than the variations of irradiance due to ozone levels (Helbling et al. 1994, Neale et al. 1998). In studies carried out with marine phytoplankton assemblages from Patagonia Barbieri et al. (2002) found that UVR effects were highly dependent on the portion of the euphotic zone that was mixed: When the UML encompassed a small portion of the euphotic zone ($Z_{\text{UML}}/Z_{\text{Eu}} < 0.5$) the inhibition of photosynthesis was high. However, when mixing was deep ($Z_{\text{UML}}/Z_{\text{Eu}} > 0.7$) (and thus mean PAR levels were low) phytoplankton were able to use UV-A as source of energy for photosynthesis, as also seen for tropical phytoplankton of southern China, under conditions of fast mixing (Helbling et al. 2003). The importance of mixing in determining UVR-induced photoinhibition was assessed in studies carried out during tidal cycles in the Chubut river estuary where Helbling et al. (2010) found significant inhibition of photosynthesis of nanoplankton cells during the flood, while microplankton sank out and thus, were less inhibited. Mixing conditions during the ebb, together with relatively high concentration of DOM and particulate material, resulted in partial protection for phytoplankton against

solar radiation stress. In other studies carried out with phytoplankton species from Patagonia Barbieri et al. (2006) found that even though the different radiation treatments did not affect oxygen evolution, mixing, and particularly the different pathways that cells performed within the water column (i.e., from the surface downwards or viceversa) was extremely important at the time to assess primary productivity in areas exposed to changing meteorological conditions throughout the year.

Besides carbon fixation or oxygen evolution, photosynthesis can be estimated through measurements of pulsed amplitude modulated fluorescence (PAM) which is a non-invasive technique that evaluates changes in the electron transport rates (see Villafañe et al. 2014). The UVR impact on the photochemical quantum yield (Y) was assessed for marine phytoplankton species and natural communities of the Patagonian coast (Marcoval et al. 2007, 2008). During daily cycles, Y displayed a characteristic pattern of relatively high values early in the morning with a sharp decrease at noon; recovery was observed late in the afternoon, when solar radiation levels decreased. Still, there was a clear component of species-specific sensitivity. In these experiments it was also seen that nutrient addition played a significant role by reducing UVR-induced inhibitory effects; additionally, they were reduced with time due to the presence of photoacclimation mechanisms (see below). UVR-induced photoinhibition was also found to be affected by the antagonistic effect of high temperature which benefited photosynthetic performance of some phytoplankton species (Halac et al. 2010); however, in recent studies carried out with natural communities of Bahía Engaño, Villafañe et al. (2013) determined diverse responses in relation to the combination of UVR and temperature: Increasing temperatures had little effect on pre-bloom communities but helped to counteract the magnitude of the yield decrease during the bloom onset. However, during the bloom and in the spring, temperature and UVR acted synergistically, increasing the overall photochemical inhibition.

Finally, seasonal changes in UVR-induced photoinhibition of Y were determined in the eutrophic Lake Chiquichano in the Chubut Province. In this study, Gonçalves et al. (2011) suggested that the ecological succession of phytoplankton was dependent on zooplankton abundance and solar radiation, so that their temporal variations in turn influenced photosynthetic responses. Fiorda Giordanino et al. (unpubl. data) carried out experiments during the different seasons aimed to determine the joint effects of UVR and increased temperature over the course of several days of natural populations of this lake, and found that temperature had larger (beneficial) effects on Y than UVR, especially in winter and in spring. Similar studies performed in the Lake Don Tomás in La Pampa Province; however, increased temperature seemed to be detrimental in spring and summer populations, therefore increasing negative effects of UVR on Y .

b) Effects of UVR on the DNA molecule: Another target of UVR is the DNA molecule, being UV-B responsible of the formation of cyclobutane pyrimidine dimers (CPDs) such as TT, CC and TC dimers (Buma et al. 2003). CPDs may hinder cell cycle progress and replication inhibition, because they obstruct *de novo* synthesis of cellular components and substances required for growth and cell maintenance; as a consequence, population growth is reduced. This type of damage accounts for about 80–90% of photoproducts formed (Buma et al. 2003) but other UVR-induced photoproducts such as pyrimidine (6–4) pyrimidone photoproducts [(6–4) PDs],

although induced in lower proportion, can be as 300 times more effective in blocking DNA polymerase, being therefore more cytotoxic than CPDs (Mitchell & Nairn 1989).

Relatively few studies related to the UVR effects on the DNA molecule of phytoplankton organisms have been carried out in Argentina. In Patagonian marine ecosystems Helbling et al. (2001a) found significant DNA damage i.e., about 600 TT dimers per megabase in picophytoplankton incubated at surface waters; in another set of experiments Buma et al. (2001) further corroborated the vulnerability of this group towards UVR, as seen in the accumulation of DNA damage late in the afternoon, as a consequence of a rather limited photoreactivation (see below). In a study carried out in the Lake Cacique Chiquichano, Klisch et al. (2005) found comparatively much lower CPDs formation in surface waters, hinting for a higher tolerance of this community (mostly dominated by chlorophytes and cyanophytes) as compared with marine ones. In Patagonian Andean lakes, Villafañe et al. (2004b) carried out a comparative study to assess the vulnerability of phytoplankton characteristic from different light environments. In this study it was determined significantly higher UV-B-induced damage in “opaque” lakes (i.e., Lake Morenito) as compared to the “clear” Lake Moreno that presented lower CPDs accumulation rates. Thus in these lakes the previous light history (together with taxonomic composition) seems to play an important role at the time to evaluate the impact of UVR. Finally, in a study carried out in the Peri-Pampean Sierras (Lake La Angostura), Helbling et al. (2006) found little DNA damage – < 30 CPDs per megabase between 0 and 4 m depth. In these experiments mixing favoured phytoplankton by allowing cells to be transported to depths where active repair could take place. This mechanism to reduce UVR-induced DNA damage was therefore of great advantage for these assemblages dominated by small cyanobacteria and chlorophytes where UV-absorbing compounds that could act as sunscreens are virtually absent (see below).

c) Long term effects: Studies to evaluate the long-term effects of UVR were carried out with marine communities characterizing the seasonal succession off Bahía Nueva in the Chubut Province (Marcoval et al. 2008). In these experiments, the effects of solar UVR were assessed together with those produced by nutrient addition. It was found that cultures in which nutrients were added had significantly higher growth rates (μ) than that non-enriched cultures; additionally, μ depended on the radiation treatment so that those samples that received UVR had lower μ than those exposed only to PAR, as also seen in studies carried out by Hernando & San Román (1999) and Hernando et al. (2005) with phytoplankton species / communities from the Beagle Channel, and those carried out by Pérez et al. (2003) with freshwater communities from the Andean region. In these type of experiments performed with natural communities, it was generally observed a shift in the taxonomic composition towards more tolerant / less sensitive species (Helbling et al. 2005, Hernando et al. 2006, Marcoval et al. 2008). However, in studies carried out by Halac et al. (2011) with summer natural phytoplankton communities of Bahía Engaño it was found that although after one week a shift in species composition occurred this was mainly conditioned by the initial composition rather than by exposure to solar UVR. In studies performed with cyanobacteria species, Fiorda Giordanino et al. (2011) found morphological changes that were associated to the joint effects of increased temperature and exposure to UVR: Higher temperature was associated to an increase in the chain area of *Anabaena* sp., and to bigger trichomes in *A. platensis*; how-

ever, no morphological effects were observed in *Microcystis* sp. In addition, in *Nostoc* sp. the increase in temperature counteracted the UVR impact on the reduction of the chain area.

Mechanisms to minimize UVR-induced negative effects

Phytoplankton display a suite of mechanisms that allow them to counteract (or at least minimize) the deleterious effects of short wavelengths. One of such strategies is to rely on UVR-absorbing compounds, namely mycosporine like amino acids (MAAs, maximum absorption between 310–360 nm) which protect the cells by absorbing UVR and thus avoiding damage in vital targets of the cell (Banaszak 2003). Among the different taxonomic groups of phytoplankton, MAAs have been detected in cyanobacteria, diatoms and dinoflagellates, but only traces of them were found in green algae (Banaszak 2003). Besides this taxonomic variability, a size dependence of MAAs synthesis was determined, so that MAAs are mainly present in large cells, as in small ones it would be energetically too costly (Garcia-Pichel 1994). Studies carried out in different aquatic bodies of Argentina did not determine significant amounts of MAAs in natural communities, either in marine (Villafañe et al. 2004a, 2008) or in freshwater environments (Helbling et al. 2001b, Villafañe et al. 2004b, Klisch et al. 2005, Gonçalves et al. 2002, 2011). Still, in experiments performed with monospecific cultures it was observed that some species were able to synthesize them: Important amounts of MAAs after one week of exposure to solar UVR were detected in the dinoflagellate *Prorocentrum micans*, and relatively less in the diatoms *Chaetoceros gracilis* and *Thalassiosira fluviatilis*; on the other hand, MAAs were virtually absent in the dinoflagellate *Heterocapsa triquetra* (Marcoval et al. 2007). The presence of MAAs in turn, was related to a better photosynthetic performance, especially in *P. micans* (Marcoval et al. 2007, Helbling et al. 2008, Richter et al. 2011), as also observed in other experiments designed to evaluate the combined effects of UVR and mixing speed in dinoflagellates (Helbling et al. 2008). Another strategy to cope with UVR-induced damage includes the presence of xanthophylls compounds, which provided at least a partial protection against UVR stress in phytoplankton communities from Patagonia (Villafañe et al. 2008) as also seen in the diatom *Thalassiosira weissflogii* and in the chlorophyte *Dunaliella tertiolecta* (Buma et al. 2009, Van de Poll et al. 2010). Finally, in studies performed also with the diatom *T. weissflogii* it was determined that an increase in temperature due to climate change partially counteracted the negative effects of UVR by increasing the response of metabolic pathways, such as those involved in RUBISCO (Helbling et al. 2011).

UVR also causes oxidative stress through the generation of reactive oxygen species (ROS) which are highly cytotoxic and are also associated with induction of cell death i.e., apoptosis (Martindale & Holbrook 2002). Thus, cells have developed a variety of antioxidant mechanisms for defence, including non-enzymatic molecules like reduced glutathione and carotenoids as well as enzymatic scavengers (Monaghan et al. 2009). In studies carried out with *Chlorella vulgaris* Malanga et al. (1995) determined ca. 300% increase in oxygen radical generation and ca. 150% in lipid peroxidation in UV-B-irradiated cells, and antioxidant activities and content increased accordingly. In the flagellate *Asteromonas* sp., isolated from the Beagle Channel, lipid oxidative damage induced by UVR was observed and, consequently, significant antioxidant activity (i.e., estimated through the concentrations of α -tocopherol and β -carotene) was determined (Hernando et al. 2005). On the other hand, in

Thalassiosira weissflogii and *Dunaliella tertiolecta* exposed to solar radiation under different mixing regimes, antioxidants played a minor role in conferring extra resistance to UVR stress (Janknegt et al. 2009).

Other mechanisms to reduce UVR-induced damage have been studied in phytoplankton from different water bodies of Argentina. Active DNA repair (i.e., photoreactivation, either favoured by PAR or UV-A) is an ubiquitous mechanism determined in phytoplankton (Buma et al. 2003). However, in natural communities of Patagonia, photoreactivation was of minor importance as high CPDs levels remained unaffected in all radiation treatments (Buma et al. 2001). In organisms from Andean lakes, low photoreactivation was also determined; indeed, it was suggested that dark repair might be of importance, especially for phytoplankton from the clear Lake Moreno (Villafañe et al. 2004b). Finally, another mechanism to reduce negative effects produced by UVR includes the escape towards deeper waters, which is present in organisms having flagella that allow them to migrate vertically (Roy 2000). In studies carried out in the Patagonian region, Richter et al. (2007) found significant inter-specific responses: *Tetraselmis suecica* was insensitive to UVR under high radiation levels while *Dunaliella salina* was very sensitive, as assessed through its ability to migrate deep in the water column avoiding UVR stress. On the other hand, the dinoflagellate *Gymnodinium chlorophorum* had an intermediate behaviour, being distributed more or less homogeneously within the water column.

Concluding remarks

The proximity of Argentina to the Antarctic ozone “hole” during the austral spring has motivated the establishment of various networks for monitoring solar radiation (Villafañe et al. 2001). However, relatively much less energy and resources were put to obtain information on the potential impacts of solar radiation not only on phytoplankton but also in other trophic levels of the aquatic food web. This is particularly important, considering the continuing increase of atmospheric temperature and acidification of the aquatic systems due to climate change, because the equilibrium damage/repair in different UVR targets of phytoplankton would be altered under these conditions. Moreover, the relatively few existing data on interactive effects of climate change variables (e.g., temperature, UV-B and CO₂) points out that the responses of organisms towards them are clearly species-specific which preclude the generalizations and extrapolations. Future studies are needed to emphasize multiple stressors responses of phytoplankton in order to better understand how climate change would, in turn, affect aquatic bodies.

Acknowledgments

We thank R. Gonçalves for his help with computer drawings. This work was supported by Agencia Nacional de Promoción Científica y Tecnológica (PICT2007-18-01651, Argentina), Consejo Nacional de Investigaciones Científicas y Técnicas (Argentina) – Deutsche Forschungsgemeinschaft (Germany) (CONICET-DFG-2009), Ministerio de Ciencia, Tecnología e Innovación Productiva (Argentina) – Consejo Nacional de Ciencia y Tecnología (Mexico) (Project N° MX/09/13) and Fundación Playa Unión, Argentina. This is Contribution No. 119 of Estación de Fotobiología Playa Unión.

References

- Allende, L., Tell, G., Zagarese, H., Torremorell, A., Pérez, G., Bustingorry, J., Escaray, R. & Izaguirre, I. (2009): Phytoplankton and primary production in clear-vegetated, inorganic-turbid, and algal-turbid shallow lakes from the pampa plain (Argentina). – *Hydrobiologia* **624**: 45–60.
- Arts, M. T. & Rai, H. (1997): Effects of enhanced ultraviolet-B radiation on the production of lipid, polysaccharide and protein in three freshwater algal species. – *Freshwat. Biol.* **38**: 597–610.
- Atkinson, R. J., Matthews, W. A., Newman P. A. & Plumb, R. A. (1989): Evidence of the mid-latitude impact of Antarctic ozone depletion. – *Nature* **340**: 290–294.
- Aubriot, L., Conde, D., Bonilla, S. & Sommaruga, R. (2004): Phosphate uptake behavior of natural phytoplankton during exposure to solar ultraviolet radiation in a shallow coastal lagoon. – *Mar. Biol.* **144**: 623–631.
- Banaszak, A. T. (2003): Photoprotective physiological and biochemical responses of aquatic organisms. – In: Helbling, E. W. & Zagarese, H. E. (eds.): *UV effects in aquatic organisms and ecosystems*. – The Royal Society of Chemistry, Cambridge, pp. 329–356.
- Barbieri, E. S., Villafañe, V. E. & Helbling, E. W. (2002): Experimental assessment of UV effects upon temperate marine phytoplankton when exposed to variable radiation regimes. – *Limnol. Oceanogr.* **47**: 1648–1655.
- Barbieri, E. S., Villafañe, V. E. & Helbling, E. W. (2006): Dynamics of oxygen production/consumption in *Dunaliella salina*, *Thalassiosira weissflogii* and *Heterocapsa triquetra* circulating within a simulated upper mixed layer. – *Invest. Mar.* **24**: 97–108.
- Bastidas Navarro, M. & Modenutti, B. (2010): UVR induce optical changes and phosphorous release of lake water and macrophyte leachates in shallow Andean lakes. – *J. Limnol.* **69**: 112–119.
- Blumthaler, M., Ambach, W. & Rehwald, W. (1992): Solar UV-A and UV-B radiation fluxes at two alpine stations at different altitudes. – *Theor. Appl. Climatol.* **46**: 39–44.
- Blumthaler, M. & Webb, A. R. (2003): UVR climatology. – In: Helbling, E. W. & Zagarese, H. E. (eds.): *UV effects in aquatic organisms and ecosystems*. – The Royal Society of Chemistry, Cambridge, pp. 21–58.
- Bouchard, J. N., Roy, S. & Campbell, D. A. (2006): UVB effects on the photosystem II-D1 protein of phytoplankton and natural phytoplankton communities. – *Photochem. Photobiol.* **82**: 936–951.
- Buma, A. G. J., Boelen, P. & Jeffrey, W. H. (2003): UVR-induced DNA damage in aquatic organisms. – In: Helbling, E. W. & Zagarese, H. E. (eds.): *UV effects in aquatic organisms and ecosystems*. – The Royal Society of Chemistry, Cambridge, pp. 291–327.
- Buma, A. G. J., Helbling, E. W., De Boer, M. K. & Villafañe, V. E. (2001): Patterns of DNA damage and photoinhibition in temperate South-Atlantic picophytoplankton exposed to solar ultraviolet radiation. – *J. Photochem. Photobiol. B Biol.* **62**: 9–18.
- Buma, A. G. J., Visser, R. J., Van De Poll, W., Villafañe, V. E., Janknegt, P. J. & Helbling, E. W. (2009): Wavelength-dependent xanthophyll cycle activity in marine microalgae exposed to natural ultraviolet radiation. – *Eur. J. Phycol.* **44**: 515–524.
- Callieri, C., Modenutti, B., Queimaliños, C., Bertoni, R. & Balseiro, E. (2007): Production and biomass of picophytoplankton and larger autotrophs in Andean ultraoligotrophic lakes: differences in light harvesting efficiency in deep layers. – *Aquat. Ecol.* **41**: 511–523.
- Cede, A., Luccini, E., Nuñez, L., Piacentini, R. D. & Blumthaler, M. (2002): Monitoring of erythral irradiance in the Argentine ultraviolet network. – *J. Geophys. Res.* **107**(D13): AAC 1-1–AAC 1-10.
- De Mora, S., Demers, S. & Vernet, M. (2000): *The effect of UV radiation in the marine environment*. Cambridge Univ. Press, Cambridge.
- Díaz, S., Camilión, C., Deferrari, G., Fuenzalida, H., Armstrong, R., Booth, C., Paladini, A., Cabrera, S., Casiccia, C., Lovengreen, C., Pedroni, J., Rosales, A., Zagarese, H. & Vernet, M. (2006): Ozone and UV radiation over Southern South America: Climatology and anomalies. – *Photochem. Photobiol.* **82**: 834–843.
- Díaz, S. B., Booth, C. R., Lucas, T. & Smolskaia, I. (1994): Effects of ozone depletion on irradiances and biological doses over Ushuaia. – *Arch. Hydrobiol.* **43**: 115–122.

- Dunne, R. P. (2010): Synergy or antagonism—interactions between stressors on coral reefs. – *Coral Reefs* **29**: 145–152.
- Farman, J. C., Gardiner, B. G. & Shanklin, J. D. (1985): Large losses of total ozone in Antarctica reveal seasonal ClOx/NOx interaction. – *Nature* **315**: 207–210.
- Ferrero, E., Eöry, M., Ferreyra, G., Schloss, I., Zagarese, H., Vernet, M. & Momo, F. (2006): Vertical mixing and ecological effects of ultraviolet radiation in planktonic communities. – *Photochem. Photobiol.* **82**: 898–902.
- Fiorda Giordanino, M. V., Strauch, S. M., Villafañe, V. E. & Helbling, E. W. (2011): Influence of temperature and UVR on photosynthesis and morphology in four species of cyanobacteria. – *J. Photochem. Photobiol. B* **103**: 68–77.
- Frederick, J. E., Diaz, S. B., Smolskaia, I., Esposito, W., Lucas, T. & Booth, C. R. (1994): Ultraviolet solar radiation in the high latitudes of South America. – *Photochem. Photobiol.* **60**: 356–362.
- Frederick, J. E., Soulen, P. F., Diaz, S. B., Smolskaia, I., Booth, C. R., Lucas, T. & Neuschuler, D. (1993): Solar ultraviolet irradiance observed from Southern Argentina: September 1990 to March 1991. – *J. Geophys. Res.* **98**(D5): 8891–8897.
- García-Pichel, F. (1994): A model for internal self-shading in planktonic organisms and its implications for the usefulness of ultraviolet sunscreens. – *Limnol. Oceanogr.* **39**: 1704–1717.
- Gonçalves, R. J., Souza, M. S., Aigo, J., Modenutti, B., Balseiro, E., Villafañe, V. E., Cussac, V. & Helbling, E. W. (2010): Responses of plankton and fish from temperate zones to UVR and temperature in a context of global change. – *Ecol. Austral* **20**: 129–153.
- Gonçalves, R. J., Villafañe, V. E. & Helbling, E. W. (2002): Photorepair activity and protective compounds in two freshwater zooplankton species (*Daphnia menucoensis* and *Metacyclops mendocinus*) from Patagonia, Argentina. – *Photochem. Photobiol. Sci.* **1**: 996–1000.
- Gonçalves, R. J., Villafañe, V. E., Medina, C. D., Barbieri, E. S. & Helbling, E. W. (2011): Plankton dynamics and photosynthesis responses in a eutrophic lake of Patagonia (Argentina): Influence of grazing and UVR. – *Latin. Amer. J. Aquat. Res.* **39**: 117–130.
- Häder, D. P., Helbling, E. W., Williamson, C. E. & Worrest, R. C. (2011): Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. – *Photochem. Photobiol. Sci.* **10**: 242–260.
- Halac, S., Villafañe, V. E. & Helbling, E. W. (2010): Temperature benefits the photosynthetic performance of the diatoms *Chaetoceros gracilis* and *Thalassiosira weissflogii* when exposed to UVR. – *J. Photochem. Photobiol. B* **101**: 196–205.
- Halac, S. R., Villafañe, V. E., Gonçalves, R. J. & Helbling, E. W. (2011): Long term UVR effects upon phytoplankton natural communities of Patagonian coastal waters. – In: Atazadeh, I. (ed.): Remote sensing of biomass: Principles and applications. Book 2. – Intech Open Access Publishers, pp. 229–248.
- Hargreaves, B. R. (2003): Water column optics and penetration of UVR. – In: Helbling, E. W. & Zagarese, H. E. (eds.): UV effects in aquatic organisms and ecosystems. – The Royal Society of Chemistry, Cambridge, pp. 59–105.
- Helbling, E. W., Barbieri, E. S., Marcoval, M. A., Gonçalves, R. J. & Villafañe, V. E. (2005): Impact of solar ultraviolet radiation on marine phytoplankton of Patagonia, Argentina. – *Photochem. Photobiol.* **81**: 807–818.
- Helbling, E. W., Buma, A. G. J., Boelen, P., Van Der Strate, H. J., Fiorda Giordanino, M. V. & Villafañe, V. E. (2011): Increase in Rubisco activity and gene expression, due to elevated temperature, partially counteracts UVR-induced photoinhibition in the marine diatom *Thalassiosira weissflogii*. – *Limnol. Oceanogr.* **56**: 1330–1342.
- Helbling, E. W., Buma, A. G. J., De Boer, M. K. & Villafañe, V. E. (2001a): In situ impact of solar ultraviolet radiation on photosynthesis and DNA in temperate marine phytoplankton. – *Mar. Ecol. Prog. Ser.* **211**: 43–49.
- Helbling, E. W., Buma, A. G. J., Van De Poll, W., Fernández Zenoff, M. V. & Villafañe, V. E. (2008): UVR-induced photosynthetic inhibition dominates over DNA damage in marine dinoflagellates exposed to fluctuating solar radiation regimes. – *J. Exp. Mar. Biol. Ecol.* **365**: 96–102.

- Helbling, E. W., Farías, M. E., Fernández Zenoff, M. V. & Villafañe, V. E. (2006): In situ responses of phytoplankton from the subtropical Lake La Angostura (Tucumán, Argentina) in relation to solar ultraviolet radiation exposure and mixing conditions. – *Hydrobiologia* **559**: 123–134.
- Helbling, E. W., Gao, K., Gonçalves, R. J., Wu, H. & Villafañe, V. E. (2003): Utilization of solar UV radiation by coastal phytoplankton assemblages off SE China when exposed to fast mixing. – *Mar. Ecol. Prog. Ser.* **259**: 59–66.
- Helbling, E. W., Pérez, D. E., Medina, C. D., Lagunas, M. G. & Villafañe, V. E. (2010): Phytoplankton distribution and photosynthesis dynamics in the Chubut River estuary (Patagonia, Argentina) throughout tidal cycles. – *Limnol. Oceanogr.* **55**: 55–65.
- Helbling, E. W. & Villafañe, V. E. (2002): UVR effects on phytoplankton primary production: A comparison between Arctic and Antarctic marine ecosystems. – In: Hessen, D. (ed.): *UV Radiation and Arctic Ecosystems*. – Springer-Verlag, Berlin, Heidelberg, pp. 203–226.
- Helbling, E. W., Villafañe, V. E. & Barbieri, E. S. (2001b): Sensitivity of winter phytoplankton communities from Andean lakes to ultraviolet-B radiation. – *Rev. Chil. Hist. Nat.* **74**: 273–282.
- Helbling, E. W., Villafañe, V. E., Buma, A. G. J., Andrade, M. & Zaratti, F. (2001c): DNA damage and photosynthetic inhibition induced by solar UVR in tropical phytoplankton (Lake Titicaca, Bolivia). – *Eur. J. Phycol.* **36**: 157–166.
- Helbling, E. W., Villafañe, V. E., Ferrario, M. E. & Holm-Hansen, O. (1992): Impact of natural ultraviolet radiation on rates of photosynthesis and on specific marine phytoplankton species. – *Mar. Ecol. Prog. Ser.* **80**: 89–100.
- Helbling, E. W., Villafañe, V. E. & Holm-Hansen, O. (1994): Effects of ultraviolet radiation on Antarctic marine phytoplankton photosynthesis with particular attention to the influence of mixing. – In: Weiler, C. S. & Penhale, P. A. (eds.): *Ultraviolet Radiation in Antarctica: Measurements and Biological Effects*. – American Geophysical Union, Washington, D.C, pp. 207–227.
- Helbling, E. W. & Zagarese, H. E. (2003): *UV effects in aquatic organisms and ecosystems*. The Royal Society of Chemistry, Cambridge.
- Hernando, M. P. & San Román, N. (1999): Preliminary data on chronic effects of ultraviolet radiation on the growth of some phytoplankton species of the Beagle Channel, Argentina. – *Sci. Mar.* **63**: 81–88.
- Hernando, M. P., Schloss, I., Roy, S. & Ferreyra, G. (2006): Photoacclimation to long-term ultraviolet radiation exposure of natural sub-Antarctic phytoplankton communities: Fixed surface incubations versus mixed mesocosms. – *Photochem. Photobiol.* **82**: 923–935.
- Hernando, M. P., Malanga, G. & Ferreyra, G. A. (2005): Oxidative stress and antioxidant defenses generated by solar UV in a sub-Antarctic marine phytoflagellate. – *Sci. Mar.* **68**: 287–295.
- Janknegt, P. J., De Graaff, M., Van De Poll, W., Visser, R. J., Helbling, E. W. & Buma, A. G. J. (2009): Antioxidative responses of two marine microalgae during acclimation to static and fluctuating natural UV radiation. – *Photochem. Photobiol.* **85**: 1336–1345.
- Kirchhoff, V. W. J. H., Schuch, N. J., Pinheiro, D. K. & Harris, J. M. (1996): Evidence for an ozone hole perturbation at 30° south. – *Atmos. Environ.* **30**: 1481–1488.
- Klisch, M., Sinha, R. P., Helbling, E. W. & Häder, D. P. (2005): Induction of thymine dimers by solar radiation in natural freshwater phytoplankton assemblages in Patagonia, Argentina. – *Aquat. Sci.* **67**: 72–78.
- Leu, E., Færøvig, P. J. & Hessen, D. O. (2006): UV effects on stoichiometry and PUFAs of *Selenastrum capricornutum* and their consequences for the grazer *Daphnia magna*. – *Freshwat. Biol.* **51**: 2296–2308.
- Litchman, E., Neale, P. J. & Banaszak, A. T. (2002): Increased sensitivity to ultraviolet radiation in nitrogen-limited dinoflagellates: Photoprotection and repair. – *Limnol. Oceanogr.* **47**: 86–94.
- Malanga, G. & Puntarulo, S. (1995): Oxidative stress and antioxidant content in *Chlorella vulgaris* after exposure to ultraviolet-B radiation. – *Physiol. Plant.* **94**: 672–679.
- Marcovall, M. A., Villafañe, V. E. & Helbling, E. W. (2007): Interactive effects of ultraviolet radiation and nutrient addition on growth and photosynthesis performance of four species of marine phytoplankton. – *J. Photochem. Photobiol. B Biol.* **89**: 78–87.

- Marcovál, M. A., Villafañe, V. E. & Helbling, E. W. (2008): Combined effects of solar ultraviolet radiation and nutrients addition on growth, biomass and taxonomic composition of coastal marine phytoplankton communities of Patagonia. – *Photochem. J. Photobiol. B Biol.* **91**: 157–166.
- Martindale, J. L. & Holbrook, N. J. (2002): Cellular response to oxidative stress: Signaling for suicide and survival. – *J. Cell. Physiol.* **192**: 1–15.
- Medina, C. D., Tracanna, B. C., Hilal, M., González, J. A. & Prado, F. E. (2010): Effect of solar UV-B exclusion on the phytoplankton community in a sub-tropical mountain reservoir: A mesocosm study. – *Lakes. Reserv. Res. Manage.* **15**: 237–253.
- Mitchell, D. L. & Nairn, R. S. (1989): The biology of the (6-4) photoproduct. – *Photochem. Photobiol.* **49**: 805–819.
- Modenutti, B. E., Balseiro, E., Diéguez, M. C., Queimaliños, C. & Albariño, R. (1998): Heterogeneity of fresh-water Patagonian ecosystems. – *Ecol. Austral* **8**: 155–165.
- Modenutti, B. E., Balseiro, E. G., Bastidas Navarro, M., Laspoumaderes, C., Souza, M. S. & Cuassolo, F. (2013a): Environmental changes affecting light climate in oligotrophic mountain lakes: the deep chlorophyll maxima as a sensitive variable. – *Aquat. Sci.* **75**: 361–371.
- Modenutti, B. E., Balseiro, E. G., Elser, J., Bastidas Navarro, M., Cuassolo, F., Laspoumaderes, C., Souza, M. S. & Díaz Villanueva, V. (2013b): Effect of volcanic eruption on nutrients, light, and phytoplankton in oligotrophic lakes. – *Limnol. Oceanogr.* **58**: 1165–1175.
- Monaghan, P., Metcalfe, N. B. & Torres, R. (2009): Oxidative stress as a mediator of life history trade-offs: mechanisms, measurements and interpretation. – *Ecol. Lett.* **12**: 75–92.
- Morris, D. P., Zagarese, H. E., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B. E., Moeller, R. & Quemaliños, C. P. (1995): The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. – *Limnol. Oceanogr.* **40**: 1381–1391.
- Neale, P. J., Davis, R. F. & Cullen, J. J. (1998): Interactive effects of ozone depletion and vertical mixing on photosynthesis of Antarctic phytoplankton. – *Nature* **392**: 585–589.
- Neale, P. J., Helbling, E. W. & Zagarese, H. E. (2003): Modulation of UVR exposure and effects by vertical mixing and advection. – In: Helbling, E. W. & Zagarese, H. E. (eds.): UV effects in aquatic organisms and ecosystems. – The Royal Society of Chemistry, Cambridge, pp. 108–134.
- Orce, V. L. & Helbling, E. W. (1997): Latitudinal UVR-PAR measurements in Argentina: Extent of the “ozone hole”. – *Global Planet Change* **15**: 113–121.
- Osmond, C. B. (1994): What is photoinhibition? Some insights from comparisons of shade and sun plants. – In: Baker, N. R. & Bowyer, J. R. (eds.): Photoinhibition of photosynthesis, from molecular mechanisms to the field. – Bios Sci. Publ., Oxford, pp. 1–24.
- Palancar, G. G. & Toselli, B. M. (2002): Erythematous ultraviolet irradiance in Córdoba, Argentina. – *Atmos. Environ.* **36**: 287–292.
- Pérez, A. P., Diaz, M. M., Ferraro, M. A., Cuminsky, G. C. & Zagarese, H. E. (2003): Replicated mesocosm study on the role of natural ultraviolet radiation in high CDOM, shallow lakes. – *Photochem. Photobiol. Sci.* **2**: 118–123.
- Pérez, G., Queimaliños, C., Balseiro E. & Modenutti, B. (2007): Phytoplankton absorption spectra along the water column in deep North Patagonian Andean lakes (Argentina). – *Limnologica* **37**: 3–16.
- Quirós, R., Rennella, A. M., Boveri, M. B., Rosso, J. J. & Sosnovsky, A. (2002): Factores que afectan la estructura y el funcionamiento de las lagunas pampeanas. – *Ecol. Austral* **12**: 175–185.
- Richter, P. R., Häder, D. P., Gonçalves, R. J., Marcovál, M. A., Villafañe, V. E. & Helbling, E. W. (2007): Vertical migration and motility responses in three marine phytoplankton species exposed to solar radiation. – *Photochem. Photobiol.* **83**: 810–817.
- Richter, P., Helbling, E. W., Villafañe, V. E. & Häder, D.-P. (2011): Action spectrum of mycosporine-like amino acid (MAA) induction in *Prorocentrum micans* under solar radiation. – In: Sinha, R. P., Sharma, N. K. & Rai, A. K. (eds.): Advances in life sciences. – I. K. Internat. Publ. House Pvt. Ltd., pp. 441–449.
- Roy, S. (2000): Strategies for the minimization of UV-induced damage. – In: De Mora, S. J., Demers, S. & Vernet, M. (eds.): The effects of UV radiation in the marine environment. – Cambridge Univ. Press, Cambridge, pp. 177–205.

- Scheffer, M., Hosper, S. H., Meijer, M. L., Moss, B. & Jeppesen, E. (1993): Alternative equilibria in shallow lakes. – *Trends Ecol. Evol.* **8**: 275–279.
- Sobrino, C. & Neale, P. J. (2007): Short-term and long-term effects of temperature on photosynthesis in the diatom *Thalassiosira pseudonana* under UVR exposures. – *J. Phycol.* **43**: 426–436.
- Torremorell, A., Llamas, M. E., Pérez, G. L., Escaray, R., Bustingorry, J. & Zagarese, H. (2009): Annual patterns of phytoplankton density and primary production in a large, shallow lake: the central role of light. – *Freshwat. Biol.* **54**: 437–449.
- Van De Poll, W., Buma, A. G. J., Visser, R. J., Janknegt, P. J., Villafañe, V. E. & Helbling, E. W. (2010): Xanthophyll cycle activity and photosynthesis of *Dunaliella tertiolecta* (Chlorophyceae) and *Thalassiosira weissflogii* (Bacillariophyceae) during fluctuating solar radiation. – *Phycologia* **49**: 249–259.
- Vernet, M. (2000): Effects of UV radiation on the physiology and ecology of marine phytoplankton. – In: De Mora, S. J., Demers, S. & Vernet, M. (eds.): *The effects of UV radiation in the marine environment*. – Cambridge Univ. Press, Cambridge, pp. 237–278.
- Vernet, M., Diaz, S. B., Fuenzalida, H. A., Camilion, C., Booth, C. R., Cabrera, S., Casiccica, C., Deferrari, G., Lovengreen, C., Paladini, A., Pedroni, J., Rosales A. & Zagarese, H. (2009): Quality of UVR exposure for different biological systems along a latitudinal gradient. – *Photochem. Photobiol. Sci.* **8**: 1329–1345.
- Villafañe, V. E., Banaszak, A. T., Guendulain-García, S. D., Strauch, S. M., Halac, S. R. & Helbling, E. W. (2013): Influence of seasonal variables associated with climate change on photochemical diurnal cycles of marine phytoplankton from Patagonia (Argentina). – *Limnol. Oceanogr.* **58**: 203–214.
- Villafañe, V. E., Barbieri, E. S. & Helbling, E. W. (2004a): Annual patterns of ultraviolet radiation effects on temperate marine phytoplankton off Patagonia, Argentina. – *J. Plankton Res.* **26**: 167–174.
- Villafañe, V. E., Buma, A. G. J., Boelen, P. & Helbling, E. W. (2004b): Solar UVR-induced DNA damage and inhibition of photosynthesis in phytoplankton from Andean lakes of Argentina. – *Arch. Hydrobiol.* **161**: 245–266.
- Villafañe, V. E., Helbling, E. W. & Zagarese, H. G. (2001): Solar ultraviolet radiation and its impact on aquatic systems of Patagonia, South America. – *Ambio* **30**: 112–117.
- Villafañe, V. E., Janknegt, P. J., De Graaff, M., Visser, R. J. W., Van De Poll, W. H., Buma, A. G. J. & Helbling, E. W. (2008): UVR-induced photoinhibition of summer marine phytoplankton communities from Patagonia. – *Mar. Biol.* **154**: 1021–1029.
- Villafañe, V. E., Marcoval, M. A. & Helbling, E. W. (2004c): Photosynthesis versus irradiance characteristics in phytoplankton assemblages of Patagonia (Argentina): Temporal variability and solar UVR effects. – *Mar. Ecol. Prog. Ser.* **284**: 23–34.
- Villafañe, V. E., Sundbäck, K., Figueroa, F. L. & Helbling, E. W. (2003): Photosynthesis in the aquatic environment as affected by UVR. – In: Helbling, E. W. & Zagarese, H. E. (eds.): *UV effects in aquatic organisms and ecosystems*. – The Royal Society of Chemistry, pp. 357–397.
- Villafañe, V. E., Fiorda Giordanino, M. V. & Helbling, E. W. (2014): Phytoplankton primary production in freshwater environments of Argentina. – *Adv. Limnol.* **65**: 393–407.