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Responses of plankton and fish from temperate zones to UVR and temperature in a context of global change

RODRIGO J. GONÇALVES [1,✉], MARÍA SOL SOUZA [2], JUANA AIGO [2], BEATRIZ MODENUTTI[2], ESTEBAN BALSEIRO [2], VIRGINIA E. VILLAFAÑE [1], VÍCTOR CUSSAC [2] & E. WALTER HELBLING [1]

[1] *Estación de Fotobiología Playa Unión & Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Chubut, Argentina.*

[2] *Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Universidad Nacional del Comahue - Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bariloche, Río Negro, Argentina*

ABSTRACT. In the last decades, both temperature and UVB (280-315 nm) radiation on the surface of the Earth increased at growing rates as a result of human activities. Many studies had evaluated the effects of temperature on aquatic ecosystems, but now the field broadens as the combination and variations of temperature and radiation gains especial importance. In this work we attempt to revisit some of our knowledge about the effects of UVR and temperature on marine and freshwater plankton and fish from temperate regions (defined here as latitudes between 30-60°), especially from the Patagonia area, due to the special characteristics found in these sites. UVR affects (often negatively) almost all processes, from carbon fixation to behavior; and certainly all trophic levels in plankton, from virus to fish larvae. The most prominent UVR danger is probably the mutagenic action of UVB, which will affect a number of processes such as photosynthesis, growth and cell division, among many others. In metazoans, UVR may cause stress upon survival or show sublethal effects such as those in behavior and feeding. It is difficult to extract a general pattern, even in a group of organisms, as responses to UVR appear to be species-specific and strongly influenced by local conditions (e.g., UVR penetration, PAR/UVR ratios, and acclimation). While in many cases significant effects have been determined, a number of mechanisms are available to avoid and / or minimize the damage produced by UVR. However, this may not hold true for global temperature changes. In the case of fishes for example, temperature appears as the main factor driving habitat distributions, so the biogeography must be taken into account to consider the potential outcomes of UVR and temperature changes. Even in the different scenarios predicted by climatic models (including ozone layer recovery and temperature rise over the next decades) more research combining UVR and temperature as factors will be needed to understand responses of aquatic ecosystems into the context of global change.

[Keywords: climate change, bacterioplankton, phytoplankton, zooplankton, fish, oxidative stress, upper mixed layer]

RESUMEN. **Respuestas del plancton y peces de zonas templadas a la RUV y la temperatura en un contexto de cambio global:**En las últimas décadas, tanto la temperatura como la radiación UVB (280-315 nm) en la superficie del planeta han aumentado a velocidades crecientes como resultado de las actividades humanas. Muchos estudios han evaluado ya los efectos de la temperatura en ecosistemas acuáticos, pero ahora el campo de estudio se amplía a medida que cobra importancia la combinación de dichos factores. En el presente estudio, intentamos rever una parte de lo que sabemos acerca de los efectos de la RUV y la temperatura en el plancton marino y dulceacuícola y

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✉ Estación de Fotobiología Playa Unión & Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Casilla de Correos 15, (9103) Rawson, Chubut, Argentina. rodrigo@efpu.org.ar

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peces de latitudes medias (definidas como aquellas comprendidas entre 30 y 60º), especialmente en la región Patagónica, debido a las características particulares de estas regiones. La RUV afecta (en general, negativamente) casi todos los procesos, desde la fijación de carbono hasta el comportamiento y ciertamente todos los niveles tróficos dentro del plancton, desde virus hasta larvas de peces. El mayor efecto negativo de la RUV es probablemente la acción mutagénica de la UVB, la cual afecta un número de procesos tales como fotosíntesis, crecimiento y división celular, entre muchos otros. En los metazoos, la RUV puede ser un factor de estrés que afecta la supervivencia, o bien puede mostrar efectos subletales tales como en el comportamiento y alimentación. Es difícil extraer un patrón general en cuanto a las respuestas, aun dentro de un grupo de organismos, ya que éstas son generalmente especie-específicas y están fuertemente influenciadas por condiciones locales (e.g., penetración de la RUV, relación PAR/RUV y aclimatación). A pesar de que en muchos casos se han determinado efectos significativos, muchos organismos también disponen de mecanismos para evitar o minimizar el daño producido por la RUV. Sin embargo, este puede no ser el caso si consideramos los cambios en la temperatura. En peces por ejemplo, la temperatura es probablemente el factor más importante que determina la distribución del hábitat, y por lo tanto la biogeografía debe ser considerada para considerar las posibles consecuencias de los cambios de temperatura y de la RUV. Aun en los diferentes escenarios predichos por los modelos climáticos (incluyendo la recuperación de la capa de ozono y el aumento de la temperatura durante las próximas décadas) serán necesarias más investigaciones combinando RUV y temperatura para entender las respuestas de los ecosistemas acuáticos en el contexto del cambio global.

[Palabras clave: cambio climático, bacterioplancton, fitoplancton, zooplancton, peces, estrés oxidativo, capa superficial de mezcla]

INTRODUCTION

More than half of the World's population lives in temperate zones (i.e., comprising latitudes between 30-60º S and N) and this implies a great impact of human activities on the environment. Temperate seas have the highest net primary productivity of the oceans (Geider et al. 2001), comparable to that of the most productive terrestrial biomes. From a climate point of view, temperate zones are characterized by seasonal changes with broad annual ranges of surface temperatures and radiation (Figure 1). Therefore, the first top meters of the water column will not only undergo marked periods of "cold" and "warm" conditions, but also of "low" and "high" solar radiation (PAR, 400-700 nm and UVR, 280-400 nm). These marked changes in temperature and solar radiation will induce, in turn, mixing in the water column, both in the sea and in many lakes, producing a fluctuating radiation regime that has important consequences for aquatic organisms.

Surface temperatures in mid latitudes are highly variable (Figure 2) with a mean winter-summer difference of ~3 and ~12 ºC for the Southern (SH) and Northern hemisphere (NH), respectively (Trenberth 2002). Northern temperate latitudes encompass relatively more land and thus have a higher thermal amplitude than their SH counterparts, which include mainly ocean waters. Ground-level solar radiation measurements (Figure 2) also indicate high UVR values at temperate latitudes. Furthermore, with many large lakes and rivers, temperate and high latitudes of NH are expected to have the largest temperature and precipitation increases in the next 100-200 yr due to increases in CO_2 and other greenhouse gases (Dai et al. 2001). On the other hand, climate in the SH may be affected in major ways by the stratospheric ozone (O_3) dynamics, more than previously predicted. In fact, according to recent model outputs, the westerly jet in the SH could be decelerated in summer (Son et al. 2008) with implications for surface temperatures, strength of wind-driven oceanic circulation, and the location and extent

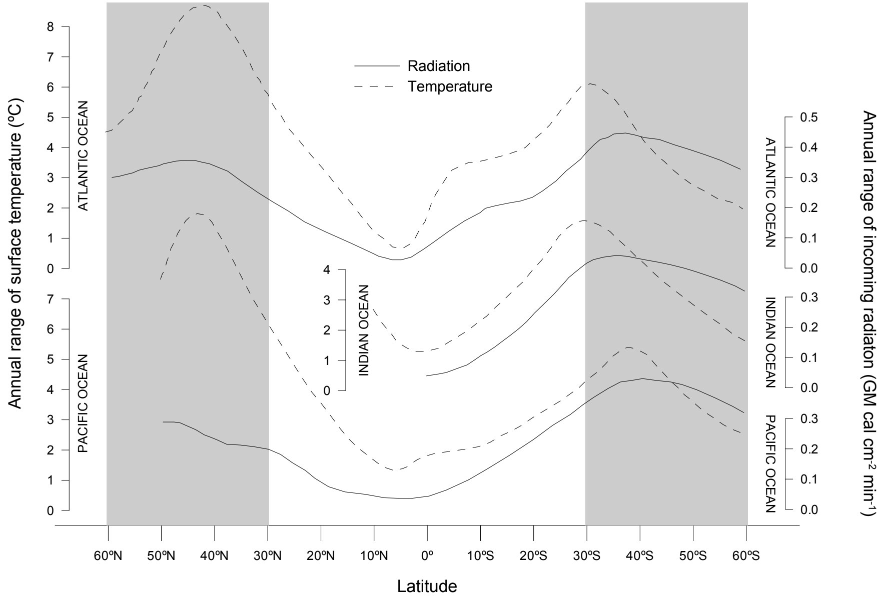

Figure 1. Ranges of temperature and solar radiaton over the oceans, highlighting those at mid-latitudes (gray areas). Note the broader ranges of temperature and radiation for Northern and Southern Hemisphere, respectively. Redrawn from Sverdrup et al. (1942).

of arid regions. This implies that the SH will suffer the impact of O_3 dynamics either way (i.e., whether it recovers at predicted rates or slower than expected).

Regarding the radiation climate, model outputs predict maximum daily-integrated irradiances at latitudes of about 40º (in spite of decreasing noontime irradiance from tropics to poles) due to a combination of low solar zenith angles and long daytime periods (Blumthaler & Webb 2003). For example, at coastal sites of Patagonia (Argentina) the records of irradiance (6 yr average) show annual ranges of 147-424, 18-65, and 0.3-1.9 W/m^2 for PAR, UVA (315-400 nm) and UVB (280-315 nm), respectively (Häder et al. 2007b). The relatively high radiation values during summer at this site, together with ~15 h-day lengths, result in daily doses comparable to those of tropical sites. For Patagonia also, surface daily doses show ranges of 1-14, 0.5-2 MJ/m^2, for PAR and UVA, respectively, and 4-45 kJ/m^2 for UVB (Helbling et al. 2005). In general, solar UVR shows a characteristic seasonal variability as well as the presence of O_3 depletion events in both hemispheres (Blumthaler & Webb 2003). These low O_3 air masses may extend to Southern and Northern mid latitudes (MacKenzie et al. 2007), thus enhanced UVB levels may reach the surface of the Earth. Because of the differences in the Earth´s geometry between both hemispheres, the radiation climate at comparable latitudes can be different; for example, erythemic doses over New Zealand can be twice as high as in Germany in the corresponding summer (Blumthaler & Webb 2003). In regard to the UVR climate in the aquatic environment, and although there is great variability, some of the natural waters with the deepest UVR penetration are found in temperate zones, as it is the case of Crater Lake, USA ($Z_{10\%, UVB}$=40 m) or the Atlantic Ocean [e.g., $Z_{10\%, UVB}$=23 m (Hargreaves 2003 and references therein)]. Contributing to this variability, "opaque" waters also occur frequently in temperate zones, as in coastal waters, lakes and rivers where land-derived material may be present and even show seasonal changes (Hargreaves 2003).

UVR and temperature are increasing, most likely due to human impact. In this text however, we will attempt to review some results of investigations not only about enhanced but also on natural, current levels of these variables. In doing so, we will attempt

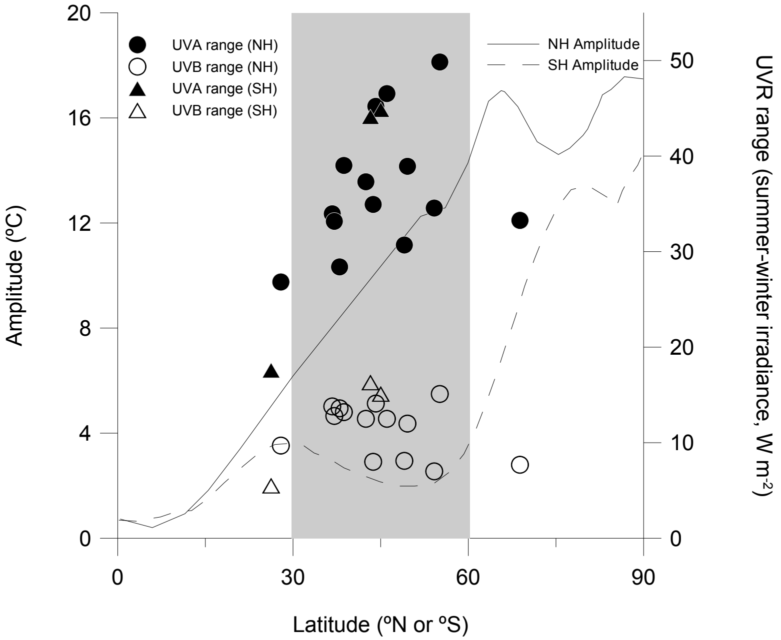

Figure 2. Modeled amplitude of mean surface temperatures (summer-winter) during the annual cycle in the Southern (SH) and Northern Hemisphere (NH). Redrawn from Trenberth (2002). Radiation data are actual ranges of UVR measured on ELDONET ground stations (from Häder et al. 2007b). UVB values are multiplied by 10 to fit the axis.

to link the current knowledge and potential changes of plankton and fishes in response to global change variations (i.e., a sustained increase of UVR and temperature in the water column). Given the importance on a global scale and the characteristics of temperate aquatic environments, we will focus on the effects of temperature and UVR on estuarine, freshwater and marine organisms from these latitudes; when data are available, studies from Patagonia are stressed. For plankton, we will address the effects of UVR on the genetic material, carbon dynamics, feeding, growth, reproduction and motility and we will present some examples of mechanisms to minimize the negative effects produced by UVR and temperature. Fish present a different situation as juvenile and adults can swim actively and choose their location in the water column (in relation to both UVR and temperature). This fact, and due to their body mass, frequently implies that UVR effects will be restricted to local effects on the body surface (however, this is not completely true for eggs and larvae, fish under culture conditions, or stream fish, see below). In addition, some fish may present migration not only vertically, but between habitats. In sum, the effects of global change, especially warming on fishes from Patagonia should be understood in the frame of their biogeographical history. Therefore, the section on responses to global change of fish will be treated here with a slightly different approach.

PLANKTON

Exposure of organisms to UVR

Plankton organisms offer a unique opportunity to study the effects of UVR on aquatic ecosystems due to their short generation times and their utmost importance within aquatic food webs. Some organisms are exposed to UVR during their whole life cycle, whereas others will be only during the larvae/ juvenile stages. Several factors influence the UVR exposure of organisms, such as presence of atmospheric gases, cloud cover, dissolved organic matter (DOM) or mixing regime

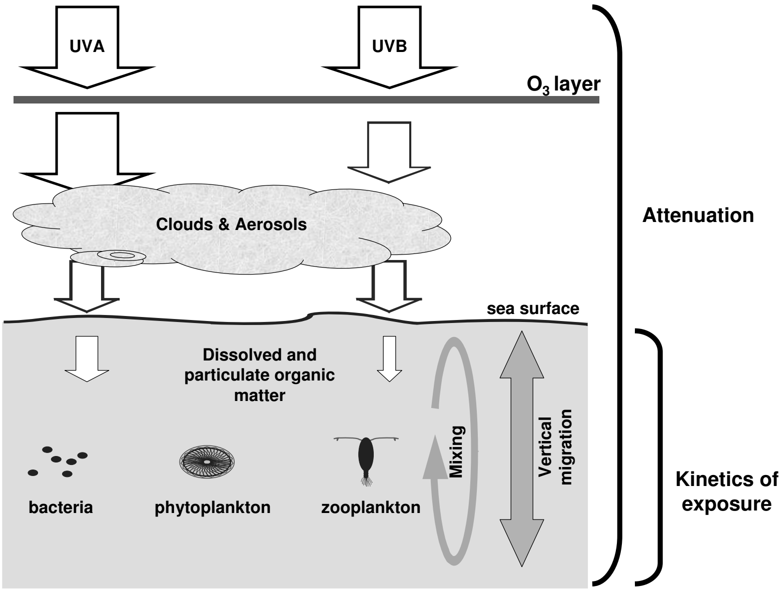

Figure 3. Main factors affecting the quantity and quality of UVR received by plankton organisms. Note the relative differences between UVA and UVB due to absorption by atmospheric ozone.

(Blumthaler & Webb 2003; Hargreaves 2003). A simplified diagram showing how solar UVR is modified until it reaches a cell is presented in Figure 3. The first filter for UVR is the atmosphere, in which stratospheric O_3 plays a very important role, absorbing UVB. Clouds and aerosols account for most of the absorption (PAR, UVA and UVB in different ratios) in the rest of the downwelling path of solar radiation through the atmosphere, until it reaches the water surface. Radiation is further weakened through the water column as its energy is partially absorbed or scattered by water molecules and dissolved and particulate matter (plankton included). For a "fixed point" exposure, such as a non-motile phytoplankton cell in a strongly-stratified water column, the radiation received is basically a function of the attenuation through the atmosphere and the hydrosphere down to its position (given a certain latitude, time, date and zenith angle). However, it is rare to find such "fixed points", so that the "kinetics of exposure" (i.e., the potential displacement / speed through vertical movements that change the distance between the surface and the biological target) needs to be considered. Moreover, the kinetics of exposure is important in terms of acclimation and adaptation: In a shallow upper mixed layer (UML) the average amount of solar radiation is higher than in a deep UML. In addition, mixing speed will determine how fast the exposure varies between maximum (surface) and minimum (bottom of the UML) irradiance. It has been shown that in temperate zones, the average UML is deeper than in tropical waters (Sverdrup et al. 1942) due to the presence of strong winds and, in particular, mixing in temperate Southern latitudes is further enhanced by the strongest time-averaged oceanic winds in the World: the "roaring forties" (i.e., the westerly winds between 40 and 60º S). Since the depth of the UML varies with wind strength, plankton is likely to be subjected to seasonal changes of exposure to solar radiation, including those produced during "ozone hole" events. Overall, exposure to UVR at temperate zones is probably more variable than in other latitudes, a condition that arises not only from seasonal changes in the radiation intensity, but also from changes of kinetics exposure. Finally, the marked seasonality of chromophoric dissolved organic matter (CDOM) which greatly affects light penetration (Osburn & Morris 2003) should be considered. Exposure of CDOM itself to UVR complicates its attenuation capacity, since its efficiency as UVR-absorbent may be reduced by photodegradation (Hargraves 2003). Collectively, changes in mixing regime and CDOM content of waters may be more important than stratospheric O_3 depletion in conditioning the underwater UVR climate (Pienitz & Vincent 2000).

Considering both the increase of UVB and temperature in the Earth's surface in a context of global change, interesting speculations can be made: For example, a significant warming of the upper water column may enhance stratification processes or extend the stratification period (Winder & Hunter 2008) which could translate into a decrease of UML depths or modification of mixing regimes. Therefore, if the organism has the ability to vertically migrate as some zooplankton species do, or if they follow the circulation into the UML (e.g., non-motile phytoplankton) their exposure to UVR may be increased i.e., due to a combination of enhanced solar UVB and shallower UML, spending thus more time exposed to solar radiation. In addition, enhanced stratification and longer residence time in the UML will lead to less exchange between the UML and deeper waters, thus affecting nutrient and CDOM concentration and their cycling within the UML.

Effects of UVR on plankton – Generalities

Solar radiation can interact with different chemical bonds / structures of biomolecules to generate structural and functional changes as it happens in photosynthesis. Similarly, UVR (and most notably UVB) may affect some biomolecules, such as DNA and proteins. In plankton organisms for example, UVR is known to produce mutations in the genetic material (Buma et al. 2003) and alterations in other cell components such as membranes, proteins and pigments (Borgeraas & Hessen 2002; Bouchard et al. 2005; Rijstenbil 2002; Sobrino et al. 2004). In surface waters, UVR may also induce chemically reactive intermediates [i.e., superoxides, hydrogen peroxides, hydroxide radicals and carbon monoxide (Buma et al. 2003; Choudhury & Panda 2005) that resemble a xenobiotic redox imbalance that could be more damaging than direct UVR exposure (Hessen et al. 2002; Perin & Lean 2004)].

There is not a uniform pattern of plankton responses to UVR, but the overall effect appears to be mostly negative. Some studies reported a slight latitudinal trend for UVR effects upon the DNA molecule, with temperate species being more sensitive than those from the tropics (Helbling et al. 2001a, 2001b) but others either have found no clear pattern (Buma et al. 2003; Meador et al. 2009) or even opposite responses: For example, Wong et al. (2007) found that a temperate *Chlamydomonas* (Ehrenberg 1834) strain was more sensitive to UVB stress than its tropical and Antarctic counterparts. Additionally, it has been found that, when considered separately, the effects of UVR may differ from those obtained in combination with other environmental variables. This is the case, for example, of two coexisting species of ciliates that had great differences in sensitivity, but one of them showing temperature-dependent photorepair rates (Sanders et al. 2005). Other studies found an increased sensitivity of dinoflagellates towards UVR in nutrient depleted cultures (Litchman et al. 2002) as also determined by Marcoval et al. (2008) in natural populations of Patagonia. In other studies it was also determined that some organisms may be more affected by UVR in a mixed than in a stationary (or less mixed) environment (Helbling et al. 1994; Zagarese et al. 1998a, 1998b); however, other well protected species have shown no differences in epilimnetic static or moving incubations (Modenutti et al. 2005). In other studies carried out with zooplankton, it was shown that static incubations increased the chances of survival (up to 80%) of embryos of the marine copepod *Calanus finmarchicus* (Kuhn et al. 2000) but the freshwater copepod *Boeckella gracilipes* showed higher mortality in rotating incubations at the same average depths. In regard to the speed of mixing, slow rather than fast mixing in combination with UVR affected nutrient uptake, species composition, and other variables of estuarine phytoplankton (Fouilland et al. 2003). Overall, the responses seem to have an important component of species-specificity.

Effects of UVR on the genetic material

UVB-induced structural changes in DNA are probably the most important deleterious consequences of UVR (Buma et al. 2003). The results of these mutations are typically cyclobutane pyrimidine dimers (CPDs) such as thymine dimers (TD) and (6-4) pyrimidone photoproducts (PP). A high proportion of CPDs produced in eukaryotic microorganisms at temperate zones appear to be TD, but a latitudinal study in the Central Pacific Ocean found PP only in tropical sites (Meador et al. 2009). These mutations may be responsible for reductions in growth and photosynthetic rates (Buma et al. 2003) and a general decrease in performance (Zagarese et al. 1997; Helbling et al. 2001a; Visser et al. 2002; Connelly et al. 2009). In Patagonian waters, post-bloom piconanoplankton had high amounts of CPDs (i.e., 500 CPD MB^{-1} accumulated at the end of afternoon) when incubated at surface; however, this amount decreased significantly at depth suggesting an active repair (Buma et al. 2001; Helbling et al. 2001a). In Andean lakes significant amounts of CPDs were determined in "opaque" waters whereas they were lower in "clear" ones, hinting for a differential acclimation as a function of CDOM (Villafañe et al. 2004a). Interestingly, in studies evaluating the combined impact of UVR and mixing revealed that photosynthesis, rather than DNA, was the main target in dinoflagellates during ozone depletion events in early spring in Patagonia (Helbling et al. 2008).

Studies have also provided information about the vulnerability towards UVR of different life stages of zooplankton: About 30 CPDs MB^{-1} have been reported in laboratory studies carried out with eggs of *Calanus finmarchicus* while nauplii showed >45 CPDs MB^{-1} when incubated at the same wavelengths (Browman et al. 2000, 2003a, 2003b; Browman 2003). For freshwater ciliates such as *Glaucoma* and *Cyclidium*, DNA damage can be relatively similar [e.g., 29 and 18 CPDs MB^{-1}, respectively (Sanders et al. 2005)], while for the cladoceran *Daphnia pulicaria* it was difficult to detect measurable levels of DNA damage even with high-sensitivity assays (MacFadyen et al. 2004). In regard to bacterioplankton off the upwelling region of Chile, relatively low values (up to 60 CPDs MB^{-1}) were detected, even during high irradiance periods (Hernández et al. 2007). Finally, the combined effects of mixing and UVR on the genetic material of bacterioplankton from the Gulf of Mexico was studied by Jeffrey et al. (1996) and they found that DNA damage was greatest in "calm seas", but undetectable during moderate mixing conditions.

Overall, and although UVB seems to be responsible for a significant portion of damage to the genetic material in temperate zones of both hemispheres there is widespread evidence of active DNA-repair activity (Buma et al. 2001; Helbling et al. 2001a; Hernández et al. 2007; Villafañe et al. 2004a). However, in a context of global change, it could be argued that a continuous increase in UVB together with shallower UMLs may result in a higher impact on the DNA of plankton. As PAR (i.e., "repair radiation") levels are not expected to change, relatively less repair capacity (due to a higher damage / repair ratio) may be expected. On the other hand, an increase in temperature would benefit repair by enhancing enzymatic processes. This contrasting potential increase of repair capability would be especially significant for SH species that currently experience relatively low temperature amplitude (Figure 2).

Phytoplankton and bacterioplankton production

From the trophodynamics point of view, the first step for the production of "new" organic matter in nature is carbon fixation through photosynthesis, which is carried out by autotrophic organisms. The deleterious effects of UVR on phytoplankton production can be due to direct damage to the photosynthetic machinery (Bouchard et al. 2005) or as an indirect result of DNA damage (Buma et al. 2001). Other components and functions of the cell can be affected as well [i.e., lipids, protein and polysaccharides synthesis, and antioxidant activity (Malanga & Puntarulo 1995; Rijstenbil 2002; Häder et al 2007a)] thus contributing to the overall reduction of carbon fixation. Carbon fixation may also be affected if its concentration mechanism [e.g., bicarbonate uptake system (Sobrino et al. 2005a; Wu & Gao 2009)] is a target for UVR.

There is extensive literature about the impact of UVR on photosynthesis and primary production (see review by Villafañe et al. 2003 and references therein) but specifically for temperate marine waters, it has been observed that in general is negative. However, some temperate phytoplankton species showed higher photosynthetic rates when exposed to UVR+PAR than those exposed only to PAR, therefore hinting for a beneficial use of UVR, especially under low PAR irradiance (Barbieri et al. 2002). In general, UVR effects on carbon fixation show a high component of specificity, as evidenced in a temperate estuarine system from Patagonia, being higher in bloom communities than in those characterizing the pre- and post-bloom (Villafañe et al 2004b). In addition, the underwater climate also conditions the responses of organisms when exposed to UVR. In general, it is considered that waters with high CDOM content can provide more "protection" against UVR, compared to more transparent waters (Zagarese et al. 1997) but it has been also observed that natural phytoplankton from "clear" lakes may show a relatively higher tolerance against UVR than that from "opaque" lakes, due to their previous acclimation to the underwater radiation climate (Villafañe et al. 2004a). Still, there is not a uniform pattern in regard to the previous acclimation, as determined by Litchman & Neale (2005) who documented that, after being grown under high PAR conditions, *Cryptomonas* sp. was more photoinhibited by UVB than the diatom *Thalassiosira pseudonana*. On the other hand, and after a week-long exposure to moderate UVR, the sensitivity of *Cryptomonas* declined, while that of *T. pseudonana* did not change. Finally, it should be noted that the observed responses of plankton to solar UVR may display a size-dependence with small nanoplankton cells having less photosynthetic inhibition than microplankton (Helbling et al. 2001a); interestingly, the opposite may occur when evaluating DNA damage (Buma et al. 2001; Helbling et al. 2001a). Effects of UVR on photosynthetic efficiency of phytoplankton have been determined by pulse amplitude modulated (PAM) fluorescence techniques in diverse temperate environments. Typically, photosynthetic efficiency is depressed when exposed to moderate / high levels of solar radiation (e.g., at noon) (Villafañe et al. 2003). Towards the afternoon, however, there is a recovery of yield which is variable according to the acclimation capacity of the species / community, as well on the radiation levels impinging the organism (Häder et al. 2007a). For temperate marine systems of Argentina, it has been shown that environmental conditions (i.e., light history, nutrient concentration) together with the physiological status of the cells play a very important role at the time to assess the combined effect of nutrient addition and solar radiation (Marcoval et al. 2008) on photosynthetic efficiency. In addition, it has been show that tidal dynamics together with physical forcing are key factors to determine the distribution, dynamics, and photoinhibition of phytoplankton in the Chubut river estuary (Helbling et al. 2010).

It is noteworthy to mention the effects of UVR on some microorganisms that have a non-feeding dependence on primary production, such as mixotrophic ciliates. An example is that of *Stentor araucanus* from Andean Argentinean Patagonia. This ciliate lives autotrophically with endosymbiotic *Chlorella*-type algae, and it has been determined that primary production is relatively unchanged by UVR, even considering that *S. araucanus* lives in oligotrophic, UVR-transparent lakes around 41° S (Modenutti et al. 2005). On the other hand, other mixotrophic ciliate from the same region (*Ophrydium naumanni* Pejler) may exhibit a reduced primary production (up to 80%) when exposed to full solar radiation (Modenutti et al. 2004).

Carbon fixation by bacteria may be also affected by solar radiation as seen in studies carried out in the upwelling off the coast of Chile, where a significant reduction of bacterial production was due to UVR exposure, although it was determined that the highest impact was due to PAR (Hernández et al. 2006, 2007). Other studies have determined variability in UVR-induced inhibition of bacterial production, according to the local conditions and methods used: For example, in studies carried out at Santa Rosa Sound, thymine and leucine incorporation were inhibited by UVR (by 44% and 25%, respectively) but in the Gulf of Mexico the inhibition of thymine incorporation was twice as much as that of leucine incorporation (Aas et al. 1996).

Feeding

Organisms not able to synthesize the starting "blocks" of organic matter may obtain them as simple forms (e.g., zooplankton). UVR can produce different effects on the processes by which zooplankton obtain, ingest, digest, and assimilate their food. In general, it has been found that the effects are species-specific for both prey and predator. When algae is exposed to UVB and used as food source for zooplankton, ingestion and incorporation rates can increase or decrease (in a short-term basis) for different predators, depending on prey also (De Lange & Lürling 2003). The number of cells ingested can increase if algae were exposed to UVB, but overall biomass may not be significantly higher (Germ et al. 2004). Even if an organism such as *Daphnia* (Müller 1785) does not show a grazing response to UVB, a species within the genus may show negative effects on several reproduction and life history traits, which would indicate a constraint in the quality of UVB-exposed algae as food (De Lange & van Reeuwijk 2003) even if prey cells show "normal" contents of lipids, proteins and non-structural carbohydrates (Scott et al. 1999). An example from the marine environment is the copepod *Calanus helgolandicus*, which showed reduced reproductive output when fed with UVB-cultivated cells of the diatom *Skeletonema costatum* (Kouwenberg et al. 1999). Digestibility can also be lowered (e.g., due to changes in cell wall) which may be interpreted as a defense mechanism of UVB-stressed algae against grazing (Van Donk & Hessen 1995). Feeding can also be negatively affected when the predator is exposed to high UVB doses (Lacuna & Uye 2001). It has been observed in laboratory studies that two heterotrophic nanoflagellates reduced grazing on autotrophic picoplankton (*Synechococcus* Nägeli) when exposed to UVR, to a degree directly related to irradiance (Ochs 1997). In another study it was found that UVR can inhibit grazing rates of heterotrophic nanoflagellates, which could be mediated by changes in cell morphology and motility (Sommaruga 2003) thus favoring bacterial proliferation due to reduced bacterivory. The effects on grazing can be even stronger if both prey and predators are exposed to UVR, and non-lethal damage of the intestinal system may precede individual's death in such a way that the predator may experience a "starvation-like" condition (Zellmer et al. 2006). In systems in which both consumer and food are exposed, UVR effects may be more important in one of them, thus leading to "non-expected" results or "trade-off" strategies (Bothwell et al. 1994; Hansson 2000).

Growth and reproduction

One of the most evident effects of UVR on plankton organisms is the reduction of growth rates, considered both for populations and individuals of sensitive species. Differences in growth and reproduction of some species over others often result in changes in the taxonomic composition of the community, which may shift towards small-sized cell dominated populations (Villafañe et al. 1995). For temperate areas, important changes in taxonomic composition after UVR exposure have been found, not only in marine (Santas et al. 1997; Helbling et al. 2005) but also in freshwater systems (Cabrera et al. 1997) although in some lakes no significant changes in species composition were reported (Halac et al. 1997). It should be noted that, in general, changes in species composition and community structure due to UVR exposure may be more important than those occurring in phytoplankton biomass (Roy et al. 2006).

Some algae species can grow at lower rates or not grow at all after exposure to UVR (Andreasson & Wängberg 2007; Sobrino et al. 2005b) or show a recovery after an initial decrease (Scott et al. 1999), as seen also in marine systems of the Patagonia region, with species characterizing different periods of the annual succession having reduced growth rates under UVR exposure, or having no effect at all (Marcoval et al. 2008). In another example of marine coastal waters of Argentina, the pennate diatom *Navicula* showed no changes on growth whereas a cryptophyte species of the same community had lower growth rates when exposed to UVB (Hernando & San Román 1999). At a northern mid-latitude site it was determined 2-61% inhibition of specific growth rates and biomass after UVR exposure in the diatom *Phaeodactylum tricornutum* when nutrients were not limiting (Behrenfeld et al. 1994). It was also found that phytoplankton cells grow larger than normal under UVR (Sobrino et al. 2005b) most probably due to the malfunctioning of cell-division mechanisms driven by DNA (i.e., another target for UVB); this failure of cell division may result in reduced population growth but enlarged cell size (Buma et al. 1996). Finally, phytoplankton growth can be affected by a combination of nutrient availability and UVR (Marcoval et al. 2008; Xenopoulos et al. 2002) although other factors such as species composition and their position within the mixed layer (Xenopoulos & Schindler 2003), short- versus long-term exposure and presence of consumers will contribute as well (Bothwell et al. 1994).

For bacterioplankton, similar results and variations are also found in regard to the effects of UVR on growth. In Canada lakes, biomass and production of near-surface bacterioplankton was reduced after 4 h-exposure to UVR but increased after 48 h, so it seems that the negative effects are not ubiquitous and they may be dependant on community assemblage (Xenopoulos & Schindler 2003). In a study carried out in Lake Caldera (Spain) UVR and P limitation appeared as relevant factors on the structure and functioning of the ecosystem: full solar radiation did not affect bacterial growth but it did enhance the bacterial dependence on the algae-released photosynthetic carbon (Carrillo et al. 2006). Additionally, there is evidence that bacterial growth can be even stimulated under UVR, whether due to less bacterivory or more organic carbon availability resulting from the photobleaching of CDOM (Sommaruga 2003; Pérez et al. 2003) and sometimes causing a shift towards a microbial-dominated community (Mostajir et al. 1999). For example, natural UVB is known to produce photolysis of humic substances in plant-derived DOC which may result in large increases of fatty acids, readily metabolized by natural bacteria, thus stimulating and sustaining their growth (Wetzel et al. 1995). Moreover, UVR also can enhance the excretion of organic carbon by phytoplankton, thus increasing the DOC available for co-existing bacteria (Carrillo et al. 2002). In other cases, however, it has been found that the degree of aromatization of the UVR-exposed organic matter could in fact reduce the availability of carbon and thus its uptake by bacteria (Bastidas Navarro et al. 2009).

For zooplankton, and at the individual level, *Daphnia* species may show a decreased growth rate when fed with UVB-exposed algae, even when the algae recovered their growth (Scott et al. 1999), indicating that UVR effects (or the lack of them) determined at lower levels of the food web can not be readily extrapolated to higher trophic levels (Sommaruga 2003). Other studies carried out with different species of ciliates exposed to UVB also determined decreased growth rates, in which temperature also played a role in enhancing photoenzymatic repair (Sanders et al. 2005). Early stages of some organisms (i.e., eggs, embryo, and larvae) are often more sensitive to UVR than adults (Lacuna & Uye 2001; Browman 2003; Browman et al. 2003a, 2003b). In fact, in several species, reproduction variables (e.g., egg per female, number of juveniles, hatching success, etc.) have also been observed to be negatively affected by UVR (Saito & Taguchi 2003) and temperature appears as an interacting factor conditioning responses (Persaud & Williamson 2005).

For species having planktonic larvae, UVR supposes a potential stress on the population, which includes not only mortality but also malformations and impaired fertilization (Lu & Wu 2005; Bonaventura et al. 2006; Dong et al. 2007). Additionally, changes in body size have been detected due to UVR exposure, but temperature played a role as well, as seen in studies carried out with *Daphnia* (Williamson et al. 2002).

Motility and behavior

Within the pelagic realm, plankton organisms have free movement within certain limits (e.g., within the euphotic layer, the mixed layer or close to their food source) provided they can adjust their vertical distribution. When exposed to UVR, motile cells of some phytoplankton species can undergo vertical migration which is more noticeable than under PAR, showing also lower swimming speed and percentage of motile cells at high irradiances (Richter et al. 2007). This vertical migration to avoid surface UVR has also been documented for several crustacean zooplankton species (Hessen 2003 and references therein). By migrating deeper into the water column, some zooplankton species may find a protective layer given by the absorption of UVR by DOC and chlorophyll (de los Ríos & Soto 2005). Conflicting pressures may arise if predators exist, which could limit the vertical distribution (Job & Bellwood 2000; Johnsen & Widder 2001). This response however, is not universal, and several other factors (such as DOC content, predation or food availability) may play a role in the behavioral responses to UVR (Leech et al. 2005; Gonçalves et al. 2007; Cooke et al. 2008). In subarctic ponds, for example, Rautio et al. (2003) found that on sunny days, the vertical distribution of *Daphnia longispina* was strongly related to UVR, whereas on overcast days predators were the main factor modifying the vertical position of both juvenile and adults *Daphnia*. Some benthic species may suffer important consequences for their population if settling of their planktonic larvae is negatively affected by UVR (Chiang et al. 2003, 2007). Other effects of UVR on motility processes include those observed in the heterotrophic nanoflagellate *Paraphysomonas bandaiensis* that turned their movement into slow circle-shaped movements as compared to rapid and random direction movements of non-UVR irradiated cells (Ochs 1997). In contrast, *P. imperforata* did not show evident changes, again stressing the species-specific responses pattern.

Mechanisms to minimize UVR-induced effects on plankton

One of the "internal filtering" 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 strongly and stably absorbing the energy of incident radiation. MAAs have been extensively studied and recorded from many different organisms (Banaszak 2003) and studies have shown that those having higher concentrations of MAAs may have increased tolerance to UVR stress, whether they are freshwater copepods, dinoflagellates, freshwater *Chlorella*-ciliate symbiosis, coastal phytoplankton, or cyanobacteria. Phytoplankton and cyanobacteria can synthesize these compounds, but not zooplankton and invertebrates, which need to obtain them from their diet (Banaszak 2003). One example is the freshwater calanoid copepod *Leptodiaptomus minutus* from Lake Giles (~41° N). When exposed to UVR this species was capable of acquiring twice as much MAAs from its diet than it did when growing under non-UVR conditions therefore increasing its overall tolerance to this stress factor (Moeller et al. 2005). Pérez et al. (2006) found that two freshwater copepods were able to adjust their tissue concentration of MAAs in response to environmental signals. In the northern hemisphere, Hylander et al (2009) found that some copepods may be able to adjust their levels of MAAs and carotenoids in order to cope with UVR and predators. Another strategy to cope with UVR-induced damage includes the presence of xantophylls, which provide al least partial protection against UVB in phytoplankton from temperate environments (Villafañe et al. 2008). Active DNA repair is another ubiquitous mechanism determined both in phytoplankton (Buma et al. 2003) and zooplankton (Gonçalves et al. 2002; Persaud et al. 2007). Additionally, escape towards deeper waters is also an option if the organism is able to migrate vertically (see previous section).

It is known that UVR causes oxidative stress through the generation reactive oxygen species (ROS), which are highly cytotoxic and are also associated with induction of programmed cell death called apoptosis (Martindale & Holbrook 2002). Thus, cells have developed a variety of defense mechanisms including the presence of non-enzymatic molecules like reduced glutathione (GSH) and carotenoids as well as enzymatic scavengers (Monaghan et al. 2009). Among these, catalase (CAT) is an important member of the cellular defense system (Monaghan et al. 2009) and glutathione S-transferase (GST) also acts as a detoxifying enzyme (Atkins et al. 1993). In addition, non-enzymatic molecules contribute to the maintenance of redox homeostasis, as GSH that is oxidized, and afterwards reduced by glutathione reductase (GR) (Hanzel et al. 2005). In studies carried out with *Chlorella vulgaris* Beijerinck, it was seen that UVB-irradiated cells in exponential growth showed ca. 300% increase in oxygen radical generation and ca. 150% in lipid peroxidation, and the antioxidant activities and content increased accordingly (Malanga & Puntarulo 1995). Similar patterns were found for the diatom *Thalassiosira pseudonana* which showed elevated malonaldehyde concentration and activities of superoxide dismutase (SOD) and GR after being exposed to UVB for 4 h (Rijstenbil 2002). On the other hand, in *Thalassiosira weissflogii* and *Dunaliella tertiolecta* exposed to solar radiation under static and fluctuating radiation regimes, antioxidants played a minor role in conferring extra resistance to these algae (Janknegt et al. 2009).

Dimethylsulphoniopropionate (DMSP) of marine algae can also increase its concentration when cells are subjected to oxidative stressors (not only UVR but CO_2 limitation, Fe limitation, excessive H_2O_2) suggesting that DMSP may play a role as antioxidant (Sunda et al. 2002). Other potential antioxidants are polysaccharide molecules, which could "scavenge" free radicals (produced by exposure to high radiation) from the cell and transport them to the medium (Tannin-Spitz et al. 2005). In the cladoceran *Daphnia longispina* for example, it has been found that the absorbance of the pond water in the UVB region was positively correlated with the antioxidant CAT, suggesting that oxidative stress may play a role in their habitat (Borgeraas & Hessen 2002). When compared to cladocerans, some copepods show almost null activities of CAT but similar activity of the other antioxidant (i.e., GST), therefore suggesting that each species may rely on different mechanisms even when having available more than one (Souza et al. 2007). Recently, in *Daphnia commutata* from Andean lakes, it has been demonstrated that food quality (phosphorus [P]: carbon [C] ratio) affected the response of antioxidant enzymes to UVR (Balseiro et al. 2008). Enzyme activities in the organisms exposed to or protected from UVR showed a direct relationship with food P:C ratio that fit exponential models. Although GST and CAT differed slightly in their response to UVR, both enzymes were significantly affected by food quality: In low P:C treatments, there was significantly lower enzyme activity in response to UVR for both enzymes. Low food quality (less P for biosynthesis) may also impose a weaker antioxidant response on the organisms, a response of considerable ecological relevance in transparent Andean lakes which combine high UVR intensities with low seston P:C ratios (Balseiro et al. 2008).

FISH

UVR effects

A vast literature is currently available about cascade effects of UVR on fish populations (Alonso et al. 2004; Holtby & Bothwell 2008; Leech et al. 2009). Direct effects of UVR have been studied for example in the viability of embryos from the plaice *Pleuronectes platessa*, Linneaus 1758. In this species, embryos can be impaired, either by relatively low UVB doses during early development or by higher UVB doses during late development (Steeger et al. 1999). The exposure to natural UVR also causes egg mortality in *Galaxias maculatus* (Jenyns 1842) in Patagonian lakes, depending on water transpareny and incubation depth (Battini et al. 2000). Additionally, damage produced by UVB can be linked (Armstrong et al. 2002) with CPDs formation, photorepair capability and pigmentation in larval *Oryzias latipes* (Temminck & Schlegel 1846). Field experiments with pike suggest that a minor increase of ambient UVB might cause sub-lethal effects to larval fish (Häkkinen & Oikari 2004). Similarly, larval stages of *Solea solea* (Linnaeus 1758) demonstrated skin lesions at elevated levels of UVB, characteristic of sunburn damage, with a reduction in the size of mucus-secreting cells and an increased epidermal thickening (McFadzen et al. 2000). Sunburn caused by UVR is also known for farmed *Oncorhynchus mykiss* (Walbaum 1792) at high elevations like in Lake Titicaca (3810 m.a.s.l.) (Sommaruga 2001). Epidermal ulceration has been reported in *P. platessa* exposed to UVB and in Atlantic salmon and rainbow trout exposed to UVA and dietary photosensitizing compounds (Fletcher 1981). In addition, the number of goblet cells (mucus-secreting cells) in the dorsal epidermis of two cyprinids [*Phoxinus phoxinus* (Linnaeus 1758) and *Alburnus calcoides* (Güldenstädt 1772)] and two salmonids [*O. mykiss* and *Salvelinus alpinus* (Linnaeus 1758)] was significantly reduced by both artificial and solar UVB radiation (Kaweewat & Hofer 1997).

UVA also affects metabolic rates in *Amatitlania nigrofasciata* (Günther 1867) (Winckler & Fidhiany 1996). Both UVA and UVB irradiations suppress transiently mitogen-stimulated proliferation of blood lymphocytes. Exposure to UVA decreases hematocrit, plasma protein, and plasma immunoglobulin levels and increases the proportions of unidentified leukocytes, possibly UVA-damaged lymphocytes. Also, UVB alters the functioning of head kidney and blood phagocytes, induces granulocytosis and lymphocytopenia in the blood and increases plasma cortisol concentration. These results imply that both UVA and UVB are potent modulators of the immune defence of fish (Salo et al. 2000).

Temperature effects

Present and potential effects of global change on freshwater biodiversity (Dudgeon et al. 2006), marine, estuarine (Roessig et al. 2004) and freshwater fishes and fisheries (Shuter & Post 1990; Jansen & Hesslein 2004) have been exhaustively analyzed in the NH. In addition to model predictions indicating that global climate change will continue even if greenhouse gas emissions decrease or cease, proactive management strategies such as removing other stressors from natural systems were emphasized in order to sustain freshwater fisheries (Ficke et al. 2007).

The metabolic rate of ectothermic organisms depends on temperature and body size, particularly the aquatic organisms due to the large thermal capacity of the water (Clarke & Johnston 1999). Temperature gradients produced by latitudinal or altitudinal changes create scenarios for geographic variations in metabolic rate (Conover & Schultz 1995). The greater latitudinal representation of SH temperate freshwaters occurs in Southern South America, thus some reviews on this area deserve to be mentioned (Lauenroth et al. 2004; Barros et al. 2006; Volpedo & Fernández Reyes 2008). Temperature affects the viability of populations either through constraints to body size imposed by winter starvation conditions (Shuter & Post 1990) or directly by lethality (Fry 1971; Elliot 1981) provoked by low or high temperatures. The mismatch between the demand for oxygen and the capacity of the oxygen system to supply tissues will be the primary mechanism that restricts an animal's tolerance to thermal extremes (Pörtner & Knust 2007). Finally, thermal habitat quality has been recently quantified for rainbow trout by means of heat shock protein 70 and whole body lipid levels (Feldhaus 2006).

Climate trends regarding southern South

America provide some relevant data. One is the 2 ºC increase in the mean annual air temperature over the last century in the South Orcadas Islands (60º45´ S, 44º43´ W, Servicio Meteorológico Nacional, www.meteonet.com.ar). The other are the climatic scenarios developed by high-resolution model MM5/CIMA for the 21st century, where the main expected changes are : a) strong decreasing trends of precipitation in the Andean western stripe from approximately 45° S to the North, b) moderate positive trends of precipitation in the North of Río Negro Province and North of the provinces of La Pampa and Buenos Aires (Argentina) and, c) a warming of ~0.5 °C for the 2020 decade and of 2 °C for the 2080 one, in all the Patagonia and North of the provinces of La Pampa and Buenos Aires (Fundación Torcuato Di Tella & Instituto Torcuato Di Tella 2006). Valuable tools in order to consider fish exposure to temperature are the estimation of lake bottom water temperature by annual mean air temperature observed from data of Quirós & Drago (1985) and Quirós (1991), the estimation of surface lake water summer temperatures by summer mean air temperatures (Livingstone & Lotter 1998) and the simulation model for daily lake water temperature profiles of Stefan et al. (1998).

Precipitation changes already have generated modifications in the biogeography of southern South American fishes. Dyer (2000) noted that the Atacama Desert area of northern Chile and southern Perú between the rivers Loa and Rimac, previously considered ''empty'' (Ringuelet 1975; Arratia et al. 1983; Arratia 1997) is at present inhabited by the Atherinopsidae *Basilichthys semotilus* (Cope 1874) and the Trichomycteridae *Trichomycterus punctulatus* (Valenciennes 1846). During 2000, new wetlands with nine species of Brazilian fishes were recorded in the formerly called ''pampeana'' dry zone (Canevari et al. 1998). These new locations were the consequence of an increase in average annual rainfall and the construction of new artificial drainage channels, allowing for the rapid dispersion of fish into an ecophysiologically suitable range (Gómez et al. 2004a, 2004b; Gómez & Menni 2005).

The effects of global warming on the fishes of Patagonia should be understood in the frame of their biogeographical history (Cussac et al. 2009). The latitudinal development of Patagonia generates a major thermal gradient for freshwater fishes and this is the historic consequence of Gondwanaland fragmentation, the opening of the Drake Passage, and the establishment of the Antarctic Polar Front ca. 30 million years ago (Cione et al. 2007). In the SH, we should distinguish between the species limited in their southward distribution by low temperatures and those limited in their northward distribution by high temperatures. The first one is the situation of the Neotropical fish fauna present in Patagonia. Southern extensions of Neotropical biota were present under the warmer climatic conditions registered during the Tertiary (Arratia et al. 1983; Cione 1986; Cione et al. 2005; Cione & Báez 2007) and at the present, this presence is exemplified by extant fishes like the characins *Gymnocharacinus bergii* (Steindachner 1903) (Menni & Gómez 1995; Ortubay et al. 1997) and *Cheirodon australe* (Eigenmann 1928) (Campos et al. 1996; Dyer 2000), and the catfishes of the genus *Nematogenys*, *Trichomycterus*, *Hatcheria*, and *Diplomystes* (Gómez 1990; Azpelicueta 1994; Dyer 2000; Unmack et al. 2009). Lower , lethal thermal levels correlate with the southern limit of the geographical distribution of several Neotropical species (Gómez 1996). At the same time, southward decrease of fish diversity correlates with water temperature (Menni & Gómez 1995). In the last years, new localities for Neotropical species in the Andean and Patagonian Provinces (''sensu'' López et al. 2008) have been noted. The new records were *Astyanax eigenmanniorum* (Cope 1894), *Cheirodon interruptus* (Jenyns 1842), *Oligosarcus jenynsii* (Günther 1864), *Corydoras paleatus* (Jenyns 1842), *Rhamdia quelen* (Quoy & Gaimard 1824), *Cnesterodon decemmaculatus (Jenyns 1842), and Odontesthes bonariensis* (Valenciennes 1835). Some of the new records reveal established populations with a high number of individuals captured, such is the case of *A. eigenmanniorum* and *O. jenynsii* (Almirón et al. 1997; Aigo et al. 2008).

The fishes limited northward by high temperatures include the marine-related species that colonize temperate, mainly post glacial open niches, like Galaxiidae, Atherinopsidae, Percichthyidae and the man-introduced salmonid fishes (Pascual et al. 2007). It must be noted the low abundances of *G. maculatus* observed by Alvear et al. (2007) in the Negro River, in the northern limit of its distribution (Cussac et al. 2004). Salmonid abundance shows negative relationships with climatic changes (Bryant 2009) and particularly with increasing temperature in the NH (Nakano et al. 1996; Boylan & Adams 2006; Reist et al. 2006a, 2006b; Graham & Harrod 2009). Ficke et al. (2007) considered increased temperature and decreased dissolved oxygen, among the main mechanism provoking changes in fish habitat, restricting the use of water column due to increased solar radiation on the epilimnion and decreasing concentration of dissolved oxygen in the hipolimnion. One of the main studied effects of global warming is the exclusion of salmonid fishes from the littoral zone of the lakes due to an increase in water temperature at lake shores (Jansen & Hesslein 2004). This have been shown to benefit native *Percichthys trucha* (Valenciennes 1833) and adversely affect exotic salmonids in Patagonia (Aigo et al. 2008) at least regarding relative abundances in littoral captures and in agreement with data on thermal tolerances and preferences of *P. trucha* and *O. mykiss* (J. Aigo personal communication) and the data of Quirós (1991), Quirós & Drago (1985) and Quirós et al. (1986). Similarly to global aquaculture (Handisyde et al. 2006) and as a related consequence to the effect of warming on salmonid populations, an alteration of the conditions for salmonid aquaculture is currently being observed in Patagonia (Báez VH, personal communication).

Thermal niche constraints applied on temperate fishes in the lapse of few decades preclude the possibility of long term evolutionary responses and limits the menu to acclimation and adaptation. Making accurate predictions of the evolutionary trajectories of salmonid fishes is currently a difficult task (Carlson & Seamons 2008; Crozier et al. 2008). In this sense the situation of *Percichthys* (Dyer 2000; Ruzzante et al. 2006) is particularly interesting. Natural distribution of *P. trucha* encompasses almost all the Andean and Patagonian Provinces from San Juan (32º S) to Santa Cruz (50º S) (Liotta 2006). In the last years, and at the same time that salmonid relative abundance declined, the relative abundance of *P. trucha* increased (Aigo et al. 2008). The main reason for this situation seems to be the acclimation abilities of the thermal preferences of *P. trucha* (J. Aigo, personal observation) and the abilities for using trophic and spatial benthic resources (Cussac et al. 1998; Ruzzante et al. 1998, 2003; Logan et al. 2000). Also through geological history, *P. trucha* has shown a strong adaptability in relation to climatic changes (Ruzzante et al. 2008). However, it must be noted that in the northern area of distribution (Andean Province), *P. trucha* was almost completely replaced by the exotic *Cyprinus carpio* (Linnaeus 1758) (Cussac V., unpublished data), probably due to a better tolerance to benthic low oxygen availabilities.

Another thermal-related effect is the relationship between landlocked and diadromous/anadromous life histories of galaxiid and salmonid fishes and latitude. The causes that favored these alternative life patterns seem to rely on the different thermal inertia of freshwater bodies and oceans. Consequently, temperature has differential effects on freshwater and marine aquatic primary production and the opportunities for planktonic feeding, thereby favoring landlocked life at low latitudes and diadromy and anadromy southward (Gross et al. 1988). McDowall (1980) proposed that the adaptive value of diadromy was the escape from the cold Pleistocene winters. It should not be expected that winter temperatures imply the same constraint for lacustrine (landlocked) or marine (diadromous/anadromous) larvae or juveniles. The ability of the South American species of Galaxiidae to display diadromous or landlocked life history patterns along large latitudinal and altitudinal ranges (McDowall 1971; Cussac et al. 2004; Barriga et al. 2007; Boy et al. 2007; Lattuca et al. 2007) is paralleled by the pattern followed by the salmonid species introduced into Patagonia (Pascual & Ciancio 2007), with a "spontaneous" establishment of anadromous populations of *O. mykiss* and

Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) in southern Patagonia (Pascual et al. 2001; Ciancio et al. 2005; Soto et al. 2007).

Temperature constraints the viability of populations through minimum body size imposed by conditions of winter starvation (Shuter & Post 1990). This implies an acute selection pressure applied on life history and reproductive traits of the species. One step forward, the "pejerrey" *O. bonariensis*, a species stocked in Patagonian and Andean lakes and reservoirs, has replaced almost completely the *Odontesthes hatcheri* (Eigenmann 1909) populations in their northern area of distribution (Andean Province) (Liotta 2006; C. Conte-Grand et al. personal communication). However, *O. bonariensis* could not overlap all of the distribution range of *O. hatcheri* due to its different degree of temperature dependent sex determination (TSD) (Strüssmann et al. 1997). TSD could represent a differential constraint for both species, within the biogeographical range established by thermal tolerance and body size during the first winter. Reported values of TSD show high agreement with the summer water temperatures in the distribution areas of each of the species (Liotta 2006; Cussac et al. 2009).

CONCLUDING REMARKS

When considering "climate change" in aquatic environments one must bear in mind that it may include a) more UVB reaching (at least) the top of the water column, b) increased UVR if mixing is weakened/stratification is strengthened, c) temperature rise and, d) modification of some related variables such as precipitation. The effects of these variations on aquatic organisms encompass a vast and complex range, from damage to the genetic material and physiological alterations at cellular and organism level, to changes in habitat use and geographical distribution. Probably, one of the goals of the broad picture as presented here is to confirm the occurrence of the effects previously enunciated as potential and showing, at least in part, the magnitude reached by these effects at very different levels.

There is no doubt that our knowledge about the effects of UVR and temperature on plankton has advanced. There are proven facts (i.e., the increment of UVB and temperature) that need to be addressed, therefore more research will help to understand how plankton may be globally affected by the current and potential future scenarios. However, many studies are still not readily translated to field conditions, due to the complexity and changing nature of the natural environment. Temperature appears as a more important factor for fish populations. However, due to the interactive nature of the atmospheric circulation, temperature patterns and ozone changes, there is not yet a consensus in the scientific community about some predictions (or there is an incomplete understanding of some phenomena). For example, it is not clear how much time would it take until the ozone layer recovers, even assuming global compliance with the international agreements such as the Montreal Protocol (Li et al. 2009; Ravishankara et al. 2009). In sum, we consider that more research is needed about the combined effects of temperature and UVR on plankton, and under these sometimes uncertain predictions, we should encourage the multi-factorial approach when possible. Regarding fish studies, more research on the physiological effects of combined UVR and temperature would constitute a valuable complement to the biogeographical data in this global change context.

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