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VULNERABILITY OF PATAGONIAN PLANKTONIC COPEPODS TO FLUCTUATIONS IN TEMPERATURE AND UV RADIATION

BY

PATRICIA ELIZABETH GARCIA[1]) and MARÍA C. DIEGUEZ
Laboratorio de Fotobiología, INIBIOMA-CONICET-UNComa, Quintral 1250,
8400 San Carlos de Bariloche, Rio Negro, Argentina

ABSTRACT

The aim of this investigation is to address the impact of fluctuations in temperature and ultraviolet radiation (UVR) on three species of South American copepods, *Boeckella antiqua*, *B. gracilis* and *B. brevicaudata*. These copepods are cold stenotherm and occur in high latitude lakes of South America and in mountain lakes in the Andes. The forecast scenarios for climate change in southern South America anticipate raising temperature and UVR levels. These changes may have the potential to impact high altitude and latitude ecosystems, including lakes and their cold adapted biota, such as those in Patagonia. Laboratory experiments, consisting of 10 day and 2 day incubations, were set up to analyse copepod mortality in relation with: (i) temperature, and (ii) the combined effect of temperature (5, 8, 12, 16, 20°C) and UV-B dose (61, 194 and 324 J m^{-2}). The results obtained showed up that temperature is a limiting factor for *B. brevicaudata* that did not survive above 12°C. *B. antiqua* and *B. gracilis* withstood the temperature range although their mortality was higher at 12-16°C. The survivorship of these copepod species to radiation was found to depend on the UV-B dose, resulting in higher mortality at the highest UV-B dose. Overall, at least one *Boeckella* species showed an acute sensitivity to increasing temperature, and the three species studied proved tolerant to the UV-B experimental exposure. The survivorship patterns observed in *Boeckella* species reflect clearly their adaptation to high solar radiation exposure and to temperate to cold environmental conditions.

RESUMEN

El objetivo de esta investigación es estudiar el impacto de las fluctuaciones de la temperatura y de la radiación ultravioleta (RUV) en tres especies de copépodos sudamericanos, *Boeckella antiqua*, *B. gracilis* y *B. brevicaudata*. La distribución geográfica de estas especies, restringida a latitudes altas de Sudamérica y a lagos de montaña en los Andes, indica su preferencia por ambientes templado-fríos. El aumento de temperatura y de los niveles de RUV a consecuencia del cambio climático impactarían particularmente a las especies estenotermas frías de lagos patagónicos. En este trabajo se realizaron incubaciones de laboratorio de 10 y 2 días para analizar la mortalidad de *Boeckella* spp. en relación con: (i) la temperatura y, (ii) combinaciones de niveles de temperatura (5, 8, 12, 16, 20°C) y dosis

[1]) Corresponding author; e-mail: blueameba@yahoo.com

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de UV-B (61, 194 y 324 J m^{-2}). Los experimentos evidenciaron que la temperatura es un factor limitante para *B. brevicaudata*, resultando los 12°C su límite de tolerancia. *B. antiqua* y *B. gracilis* resistieron el rango de temperaturas experimentales, sin embargo, presentaron mayor mortalidad a 12-16°C. La supervivencia de los copépodos a la exposición al UV-B resultó dependiente de la dosis. En general, al menos una especie de *Boeckella* presentó sensibilidad aguda al aumento de la temperatura, mientras que las tres especies resistieron la exposición experimental a la UV-B. Los patrones de tolerancia observados en *Boeckella* spp. reflejan su adaptación a ambientes templados y/o fríos expuestos a niveles elevados de radiación solar.

INTRODUCTION

Solar radiation is a major ecosystem modulator with a key role in regulating the primary production and the structure and dynamics of aquatic communities (Wetzel, 2003; Marinone et al., 2006; Häder et al., 2007). Increased levels of ultraviolet radiation (UVR; 280-400 nm) due to stratospheric ozone depletion (Farman et al., 1985; Solomon et al., 1986; Farman, 1988) can be an environmental threat with the potential to directly and indirectly affect biogeochemical processes, water properties, organisms and food webs (Häder et al., 2007). The impact of UVR on aquatic communities has been studied intensively during the last decades (Williamson, 1995; Grad et al., 2001; Williamson et al., 2001; MacFadyen et al., 2004; Marinone et al., 2006). UVR affects the motility, the reproduction and the survivorship of many planktonic organisms (Siebeck & Böhm, 1991; Zagarese et al., 1997; Grad et al., 2001; Rautio & Tartarotti, 2010; Williamson & Rose, 2010), and is a strong driving force in aquatic communities at high latitudes and altitudes (Williamson et al., 2002; Marinone et al., 2006; Rautio et al., 2011).

In Patagonia the incidence of UVR has been object of study and monitoring in the last decades due to the regional influence of the Antarctic ozone hole (Orce & Helbling, 1997; Villafañe et al., 2001; Diaz et al., 2006; Vernet et al., 2009). In this region the enhancement of UV-B from spring towards summer, when the greatest UV-B levels are recorded, is due to the combination of low solar zenith angles and the ozone depletion (Diaz et al., 1994). Concomitantly, the analysis of past temperature records points out an increment of about 1°C in Patagonia in the time lapse between 1961 and 2004 (Fundación Torcuato di Tella e Instituto Torcuato di Tella, 2006). This temperature raise has been involved in the explanation of the dramatic retreat of the largest temperate ice masses present in the Southern Hemisphere, located along the Argentinean and Chilean Patagonia (Rignot et al., 2003). At a smaller scale, a raise in water temperature may affect aquatic food webs through direct and indirect impacts on community structure and composition (Häder et al., 2007).

The aquatic communities of Patagonian lakes are unique and characterized by low diversity and high endemism. Most lakes of Patagonia are temperate to cold environments and the biota is adapted to low to moderate water temperature. Such environments are dominated by copepods of the genus *Boeckella* (cf. Bayly, 1992; Menu-Marque et al., 2000; Marinone et al., 2006), which are cold stenotherm (Gibson & Bayly, 2007; Adamowicz et al., 2010), and display combined strategies to cope with high ambient UV levels (Zagarese et al., 1997; Alonso et al., 2004; Tartarotti et al., 2004; Marinone et al., 2006; Tartarotti & Sommaruga, 2006). These strategies include diel vertical migration in lakes where depth can constitute a refuge; the acquisition of photo-protective compounds (mycosporine-like amino acids and carotenoids), and photo-enzymatic repair (Zagarese et al., 1997; Tartarotti et al., 1999; Alonso et al., 2004; Garcia et al., 2010; Perez et al., 2012). While these strategies provide photo-protection to the copepods, their occurrence appears to be balanced to a certain set of environmental variables, including the temperature regime. In copepods of the genus *Boeckella* the temperature has been found to affect not only their photo-protection but also the reproduction and survivorship (Jamieson & Burns, 1988; Hall & Burns, 2001; Garcia et al., 2008, 2010). Hall & Burns (2001) showed that temperatures below 10°C enhance the survivorship of *B. hamata*. Moreover, in several species of *Boeckella* the increase in temperature from 10 to 20°C causes changes in oxygen consumption which may be indicative of stress (Green, 1975; Green & Chapman, 1977). In addition, the acquisition of photo-protective compounds depends on temperature as it has been reported for *B. antiqua* and *B. gracilis* (Garcia et al., 2008, 2010). Further, temperature is known to limit the efficiency of the enzymatic photo-repair mechanism in *Boeckella* species (Rocco et al., 2002).

This investigation addresses the potential impact of temperature and UVR on the survivorship of three species of calanoid copepods of the genus *Boeckella*: *B. antiqua* Menu-Marque & Balseiro, 2000, *B. gracilis* (Daday, 1902) and *B. brevicaudata* (Brady, 1875). For this purpose, we first performed experimental incubations to study the effect of temperature on the survivorship of the different species of *Boeckella* applying a temperature gradient (5, 8, 12, 16, 20°C). Secondly, we studied the combined effect of temperature and UV-B in experiments exposing the three copepod species to different UV-B doses (61, 194 and 324 J m^{-2}) in a temperature range (5-20°C). Finally, we discussed the performance of the three species of *Boeckella* in the different UVR and temperature scenarios, their vulnerability to these variables and their potential to endure environmental changes in UVR and temperature.

MATERIAL AND METHODS

Zooplankton sampling

The copepods used for this study were collected in two shallow ponds located inside the Nahuel Huapi National Park (North Patagonia, Argentina). The copepod

Boeckella antiqua was collected in Los Juncos Pond (41°03′38″S 71°00′38″W; 907 m.a.s.l; Z_{max} = 1.8 m). *B. gracilis* and *B. brevicaudata* were sampled in Teleférico Pond (41°07′S 71°22′W; 816 m.a.s.l; Z_{max} = 1.5 m). Zooplankton samples were obtained by horizontal tows using a 45 μm mesh dip net from early autumn to late winter.

The zooplankton samples were placed in 5-l polycarbonate carboys and transported to the laboratory. Adult copepods to be used in the experiments were sorted out using a Pasteur pipette and put into 2-l glass beakers filled with filtered (45 μm) lake water. These copepods were acclimated during 1 day at the temperature established for the experiment and in darkness. The pre-incubations and experimental assays were performed in a Sanyo test chamber (MLR5).

In addition, samples consisting in 200 individuals of each *Boeckella* species were separated from the zooplankton samples, put in Eppendorf vials (10 replicates for each species) and maintained at −20°C until the extraction of photoprotective compounds. Also, two replicates of 150 individuals of each of the three different species were sorted out to measure copepod dry weight (DW) according to Garcia et al. (2008).

Experimental design

Two series of experiments were designed to analyse: (i) the effect of temperature on the mortality of *Boeckella antiqua*, *B. gracilis* and *B. brevicaudata*, and (ii) the combined effect of temperature and UV-B (295-315 nm) on the mortality of these copepod species.

The first set of experiments consisted in incubations in batch cultures of the three copepod species initiated with 200 copepods, and incubated separately for 10 days at five temperatures (5, 8, 12, 16 and 20°C). Each temperature treatment was set up with three replicates, in acrylic containers (Plasmatic, Spain) filled with 2 l filtered (0.47 μm) natural lake water with the addition of the algae *Chamydomonas reinhardtii* (Dangeard) (4000 cells ml^{-1}) as food for the copepods. Half of the culture medium of each replicate (1 l) was replaced every 2 days. Radiation in the experimental set up was provided by 10 fluorescent lamps (Sanyo) and 2 Q-Panel 340 lamps, under a photoperiod of 12 h light : 12 h dark (3.5 W m^{-2} UV-A, 0.095 W m^{-2} UV-B plus 110 μmol quanta m^{-2} s^{-2} PAR). Although it is difficult to provide an accurate estimation of the natural UVR level to which copepods are effectively exposed in nature, all the experimental UVR levels applied are likely lower than those experienced by the copepods in their natural environments (i.e., Teleférico Pond: 6 W m^{-2}, Los Juncos Pond 5.8 W m^{-2}).

After the incubation period, live copepods were counted. The proportion of dead individuals (D) was calculated for each replicate at the different temperatures assayed as follows:

$$D = \left(\frac{I_{\text{ind}} - F_{\text{ind}}}{I_{\text{ind}}} \right)$$

where I_{ind} and F_{ind} are the number of copepods at the beginning and at the end of the experiment, respectively.

In the second experimental series, the three species of *Boeckella* were exposed separately to three UV-B doses, 61, 194 and 324 J m^{-2}, which were set using neutral density filters. These UV-B doses were purposely established below the natural levels of exposure to UV-B (5927 and 8647 J m^{-2} in Los Juncos and Teleférico ponds, respectively) because experimental conditions implied full exposure due to the lack of a depth refuge in the containers. Further, as we aimed to analyse the potential for an interactive effect of UV-B and temperature, the use of high UV-B levels could have masked the effect of temperature, or the interaction among temperature and UV-B. The experiments were run separately at different temperatures, 5, 8, 12, 16 and 20°C. UV-B radiation was provided by a Spectroline XX15-B lamp placed at 15 cm above the experimental vials and covered with a sheet of cellulose diacetate to remove the wavelengths shorter than 295 nm. This filter was renewed before each experiment. Replicates were set up in glass beakers (diameter 47 mm, depth 65 mm), filled with 50 ml of culture medium, containing 10 adult copepods and covered with quartz lids. A total of 24 experimental units (8 replicates for each of the 3 UV-B doses applied) were arranged on a turntable rotating at 2 rpm for each of the five temperatures. The copepods were exposed sequentially to 6 h UV-B + PAR, 8 h PAR and 10 h dark, for 2 consecutive days. The UV doses were measured using a spectroradiometer Ocean Optics 2000 USB, setting the light sensor at the same distance than the water surface inside the glass beaker for each of the specific filters applied. After the exposure, living and dead copepods were counted in each replicate and the proportion of dead individuals was calculated as described above.

Determination of photo-protective compounds in *Boeckella* spp.

Sequential extractions of mycosporine-like amino acids (MAAs) and carotenoids were done in copepod samples from the different species of *Boeckella*. MAAs were extracted in 3 ml of 25% aqueous methanol according to Sommaruga & Garcia-Pichel (1999). After centrifugation for 5 min and filtration through glass fiber filters (GF/F, Whatman), the extracts were poured into a 1 cm pathlength quartz cuvette and scanned in a UV-Vis spectrophotometer (Hewlett-Packard 8453). The absorbance values obtained at the peak maximum (333-334 nm) were normalized to dry weight (DW) of the sample and expressed as AU (mg DW)$^{-1}$. The remaining pellet was suspended in 3 ml 96% ethanol for 24 h in darkness after centrifugation to extract the carotenoid pigments following Byron (1982). The extracts were scanned in the spectrophotometer. The concentration of carotenoids was calculated using the extinction coefficient of astaxanthin according to Hessen (1993) and expressed as μg (mg DW)$^{-1}$.

Statistical analysis

The effect of temperature in each of the three copepod species was analised in the first set of experiments by means of a one-way ANOVA, followed by post-hoc tests (Tukey). In order to compare the mortality of *B. antiqua*, *B. gracilis* and *B. brevicaudata* at the different temperatures, a two-way ANOVA was applied using temperature and species as main factors. This analysis was restricted to three temperatures, 5, 8 and 12°C, due the fact that *B. brevicaudata* could not be maintained in 10-day cultures above 12°C. Finally, experiments exposing copepods to UV-B at different temperatures were analysed using two-way ANOVA, with temperature (five levels) and UV-B dose (three levels) as main factors. The concentrations of photo-protective compounds, MAAs and carotenoids in the different species were compared using a one-way ANOVA. All the data from the experiments 1 and 2 and the concentrations of photoprotective compounds were tested for normality and homogeneity of variance before performing each of the statistical analyses (Zar, 1999). In order to fulfill the assumptions of ANOVA, the concentrations of photo-protective compounds were log-transformed.

RESULTS

Effects of temperature on *Boeckella* spp.

The laboratory experiments showed that temperature affected significantly the survivorship of the three species of *Boeckella*. All species had higher mortality at the higher end of the temperature range applied. In particular, *B. antiqua* exhibited the highest survivorship across the temperature range although its mortality was higher at 16 and 20°C ($F = 66.14$, $p<0.001$; fig. 1). *B. gracilis* presented the highest mortality at 16°C followed by 12°C ($F = 35.83$, $p<0.001$; fig. 1). Most interesting, *B. brevicaudata* could not be maintained in cultures above 12°C; showing an increasing mortality pattern from 5 to 12°C ($F = 61.74$, $p<0.001$; fig. 1).

The response to temperature of the three *Boeckella* species was studied by means of a two-way ANOVA, at 5, 8 and 12°C (the temperature levels tolerated by the three species). The results of this analysis showed a significant effect of temperature ($F = 50.05$, $p<0.001$), species ($F = 31.37$, $p<0.001$) and the

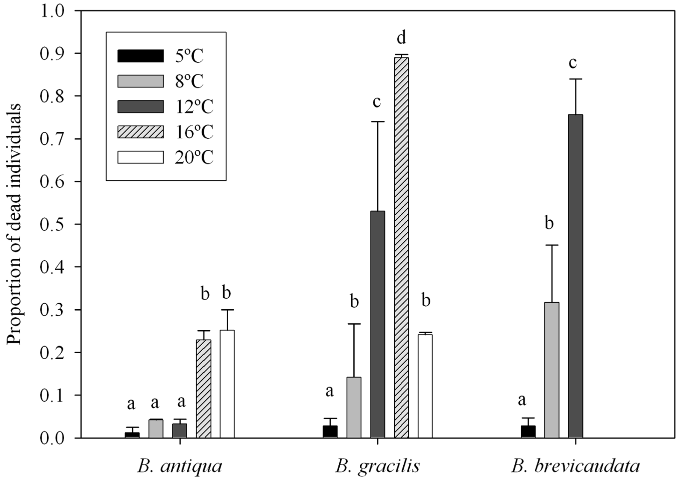

Fig. 1. Proportion of dead individuals at different temperatures in *Boeckella antiqua* Menu-Marque & Balseiro, 2000, *B. gracilis* (Daday, 1902) and *B. brevicaudata* (Brady 1875). The letters represent homogenous groups among temperatures for each *Boeckella* species.

interaction of both factors ($F = 12.62$, $p<0.001$). At 5°C, all species had similarly low mortality values. At 8°C, *B. gracilis* and *B. brevicaudata* showed similar mortalities which were higher than in *B. antiqua*. At 12°C, *B. brevicaudata* showed the highest mortality, followed by *B. gracilis* and finally by *B. antiqua* (fig. 1).

Overall, these experiments indicated that *B. brevicaudata* is a sensitive cold stenotherm species. Whereas, *B. gracilis* and *B. antiqua* can tolerate a comparatively broader temperature range, even though temperatures lower than 12°C favoured their survivorship.

Effect of temperature and UV-B radiation on *Boeckella* spp.

The mortality of the three *Boeckella* species was highest at the higher UV-B dose assayed (table I). In *B. gracilis* and *B. brevicaudata*, mortality increased at the higher temperatures of the range, whereas in *B. antiqua* the temperature did not significantly influence the survivorship. The interactive effect of temperature and UV-B dose was not significant in any of the three species analysed (table I).

In the case of *B. antiqua* only the UV-B dose affected significantly the mortality, and the largest proportion of dead copepods was found at the highest UV-B dose (324 J m^{-2}) ($p<0.001$), while the remaining doses resulted in similarly lower proportions of dead copepods (fig. 2a). In *B. gracilis* and *B. brevicaudata* the mortality was affected both by temperature and UV-B (table I); with higher mortalities recorded at the highest UV-B dose and at 20°C ($p<0.01$). The major effect of temperature and UV-B on copepod mortality was found in *B. brevicaudata* (fig. 2b and c, respectively).

TABLE I

Results of the two-way ANOVA applied to study the effect of temperature (5 levels) and UV-B dose (three levels) in *Boeckella antiqua* Menu-Marque & Balseiro, 2000, *B. gracilis* (Daday, 1902) and *B. brevicaudata* (Brady, 1875)

Species	Factor	df	*F*	*p*
B. antiqua	Temperature	4	0.453	0.770
	UV-B dose	2	24.061	<0.001
	Temperature × UV-B dose	8	0.574	0.797
B. gracilis	Temperature	4	8.879	<0.001
	UV-B dose	2	6.091	0.003
	Temperature × UV-B dose	8	0.420	0.907
B. brevicaudata	Temperature	4	35.040	<0.001
	UV-B dose	2	4.442	0.014
	Temperature × UV-B dose	8	0.768	0.632

Overall these results indicate that the three *Boeckella* species studied have a remarkable tolerance to UV-B and that vulnerability to UVR increased at higher temperature.

The concentration of photo-protective compounds, particularly of the total MAAs, varied among the three species studied. The highest MAAs concentrations were recorded in *B. gracilis* followed by *B. brevicaudata* and *B. antiqua* ($F = 63.07$, $p < 0.001$). The three species had similar concentrations of carotenoids ($F = 0.017$, $p = 0.98$; table II). Remarkably, although the concentration of carotenoids was similar among species, the color of each species was distinctive. *B. antiqua* varied between burgundy and blue, *B. gracilis* was always bright orange to red and *B. brevicaudata* was dark blue.

DISCUSSION

Our results showed clearly that the three species of *Boeckella* had higher survivorship at temperatures below 8°C, suggesting their cold stenotherm condition (i.e., adaptation). Although *B. antiqua* and *B. gracilis* withstood the full thermal gradient applied, higher mortalities were found at temperatures above 12°C. In the case of *B. brevicaudata*, temperature acted as a limiting factor strongly affecting its survivorship. This species could not be cultured above 12°C, thus indicating its sensitivity to moderate to high water temperatures. The different responses to temperature recorded could reflect species-specific adaptations. South American species of *Boeckella* are mostly distributed in lakes and ponds of Patagonia which are temperate or cold environments (Menu-Marque et al., 2000; Gibson & Bayly, 2007; Persaud et al., 2007; Adamowicz et al., 2010). In particular, the cold stenotherm condition of *B. brevicaudata* can also be inferred from its restricted spatial and/or temporal distribution. This species has been recorded in a few lakes

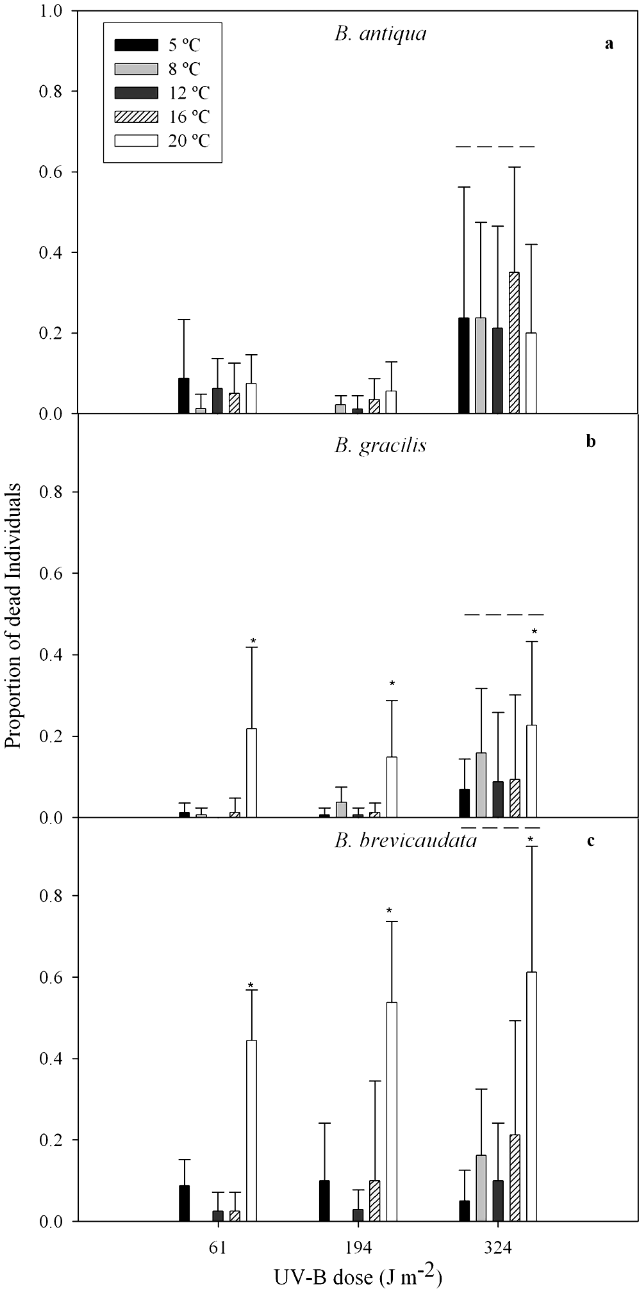

Fig. 2. Proportion of dead individuals (mean ± SD) in three species of the genus *Boeckella* exposed to different UV-B doses at 5, 8, 12, 16 and 20°C. a, *Boeckella antiqua* Menu-Marque & Balseiro, 2000 from Los Juncos pond; b, *B. gracilis* (Daday, 1902); and c, *B. brevicaudata* (Brady, 1875), both from Teleférico Pond. The asterisk (*) indicates significant differences among temperature levels and the dashed line (---) indicates significant differences among the UV-B doses applied.

TABLE II

Concentrations of photo-protective compounds, MAAs and carotenoids (mean ± 1SD), in *Boeckella antiqua* Menu-Marque & Balseiro, 2000, *B. gracilis* (Daday, 1902) and *B. brevicaudata* (Brady, 1875)

Species	MAAs (AU (mg DW)$^{-1}$)	Carotenoids (μg (mg DW)$^{-1}$)
B. antiqua	0.0129 ± 0.004	1.438 ± 0.333
B. gracilis	0.119 ± 0.082	1.274 ± 0.711
B. brevicaudata	0.0167 ± 0.004	1.244 ± 0.592

of Antarctica and in shallow ponds of Patagonia during winter (Menu-Marque et al., 2000; Garcia, 2010; Laspoumaderes et al., 2010). In contrast, *B. antiqua* was the species with highest tolerance along the whole temperature range applied. This species is restricted to a few ponds in extra-Andean Patagonia. In the shallow pond Los Juncos, *B. antiqua* endures a wide range of thermal conditions, ranging from 4 to 22°C (Garcia et al., 2008). Furthermore, this species is exposed to fluctuating temperature on a daily basis due to the low thermal resilience of shallow ponds and the high thermal amplitude between day and night, typical of the extra-Andean Patagonia.

B. gracilis showed an idiosyncratic pattern with temperature, although its mortality increased from 5°C to 16°C and decreased at 20°C. This species endures temperatures up to 23°C during summer in a similar temporary pond in the area (Garcia, 2010), which is an indication of its broad tolerance to fluctuating temperature.

The exposure to UV-B in the temperature range assayed resulted in differences in the survivorship of *Boeckella antiqua*, *B. gracilis* and *B. brevicaudata*. The three species showed a remarkable survivorship at the highest UV-B dose. This notable tolerance to UV-B exposure may stand from their adaptation to high solar radiation exposure in their natural environments. For example, considering solar radiation measurements in the surface layer (10 cm), *B. gracilis* and *B. brevicaudata* may experience natural UV-B levels around 28 000 J m^{-2} in Teleférico Pond, while *B. antiqua* may resist levels around 17 000 J m^{-2} in Los Juncos Pond (García, 2012).

Although the interaction between UV-B exposure and temperature resulted not significant, mortality was particularly high at 20°C in *B. gracilis* and *B. brevicaudata*, while *B. antiqua* was affected by the higher dose of UV-B regardless of the temperature. The increased mortality of *Boeckella* exposed to UVR may reflect DNA damage, the negative effect of cellular photochemical reactions, and also the indirect impact of photoproducts (reactive oxygen species) in the culture medium (Lesser, 1996; Borgeraas & Hessen, 2002; Souza et al., 2007, 2010). In fact, the production of reactive oxygen species as a consequence of molecular photodegradation is known to be enhanced at high temperatures (Borgeraas & Hessen, 2000).

In our experiments the impact of the exposure to UV-B on the three copepod species was found to be dose-dependent. Remarkably, the negative effect of the UV-B exposure was more evident in *B. antiqua* and *B. brevicaudata* than in *B. gracilis*. These differences in vulnerability may be due to the fact that the three species bear different levels of photo-protection, particularly of MAAs (table II). MAAs provide comprehensive photo-protection since they act as sunscreens filtering out the damaging UV wavelengths and dissipating the energy as heat (Shick & Dunlap, 2002). Moreover, in the genus *Boeckella* (i.e., *B. titicacae* Harding, 1955) there is a direct relationship between MAAs concentration and UVR tolerance (Helbling et al., 2002). In our experiments, *B. gracilis*, the species with the highest level of MAAs, was the most tolerant to UVR exposure. Carotenoid concentrations were similar in the three copepod species and, therefore, these pigments cannot be recalled to explain the differences in tolerance to UV-B. In addition, in our experiments we provided photosynthetic active radiation, light fraction that is necessary for the photoreactivation. Thus, we cannot rule out the incidence of photo-reactivation in the copepods. This process could also account to explain the differences in the tolerance observed among copepod species. *B. antiqua* is known to take advantage of the combination of photo-protection and photo-repair (Zagarese et al., 1997; Rocco et al., 2002) but there is no evidence of this mechanism in *B. brevicaudata* and *B. gracilis*.

On the whole, the evidence recorded in this investigation suggests the existence of species-specific tolerance to UVR and temperature in copepods of the genus *Boeckella* which may stand from their adaptation to local light and temperature climates. In fact, tolerant species such as *B. antiqua* and *B. gracilis* dwell in shallow ponds and lakes from winter throughout summer, experiencing highly variable UVR and temperature levels. Whereas, *B. brevicaudata* develops in comparatively more stable environmental conditions such as those occurring in shallow ponds during winter. In contrast, *B. brevicaudata* has a life cycle restricted to a few weeks during winter when endures low temperatures and low ambient levels of UVR (Garcia, 2010; Laspoumaderes et al., 2010).

The differences in the vulnerability of the three species of *Boeckella* to UV-B and temperature found could account to infer their potential to endure fluctuations in these variables. In *B. brevicaudata*, abrupt changes in temperature alone would represent a bottleneck for its survivorship in natural environments. In contrast, *B. antiqua* and *B. gracilis*, may better endure wider fluctuations in natural levels of radiation and temperature.

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