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Dietary Photoprotective Compounds Ameliorate UV Tolerance in Shrimp (*Pleoticus muelleri*) through Induction of Antioxidant Activity

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Abstract

The aim of this study was to determine the effects of ultraviolet radiation (UVR) on bioaccumulation of UV-absorbing compounds acquired through the diet, in larvae and postlarvae of *Pleoticus muelleri*, and to assess tissue antioxidant activity, survival, and development. Mysis stage I were exposed to two artificial radiation treatments: M-PAR (photosynthetically active radiation, range = 400–700 nm) and M-PAR + UVR (280–700 nm). The experimental larvae received a mixed dietary treatment of *Artemia persimilis* and the microalga *Pavlova lutheri*, reared under two radiation regimes: PAR (D-PAR) and PAR + UVR (D-PAR + UVR). Shrimp from all treatments reached 8 d postlarval stage (PL8), except those under M-PAR + UVR treatment fed the D-PAR-cultured algae, which had 0% survival. Larvae in M-PAR + UVR and M-PAR treatments fed with D-PAR + UVR diet presented the highest survival rates (70 and 75%, respectively), with 37 and 41% increase in PL size. UV-absorbing compounds were detected in microalgae and PL subject to PAR + UVR treatments. Antioxidant activity, quantified by measuring the free-radical 1,1-diphenyl-2-picrylhydrazyl in homogenates of PL8, decayed drastically under radiation treatment M-PAR + UVR fed with algae of the D-PAR + UVR treatment. It is concluded

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that the bioaccumulation of UV-absorbing compounds and the highest antioxidant activity in PL could improve the biochemical and photophysiological responses of shrimp under UVR stress.

KEYWORDS

antioxidant activity, climate change, live food, shrimp, UVR

Ultraviolet radiation (UVR, range = 280–400 nm) is a natural component of solar radiation; therefore the marine environment has always been exposed to different amounts of UVR, varying historically with the composition of the atmosphere (Tang et al. 2011). However, in recent years anthropogenic impacts such as stratospheric ozone depletion have caused an increase in the UVR flux to the Earth's surface (McKenzie et al. 2010). Because of this, studies on the effects of increased UVR on marine organisms are a relatively new development (Whitehead et al. 2000; Häder et al. 2011). There is some evidence that UV-B radiation (280–315 nm) and the shorter wavelengths of UV-A (315–400 nm) can significantly affect the biota in water depths up to 20 m (Häder et al. 2003). These can have adverse physiological effects on aquatic organisms such as the inhibition of photosynthesis, damage to the genetic material, and high mortality (Halac et al. 2011).

The response of microalgae to UVR varies depending on their sensitivity to this stressor (Neale et al. 1998). For example, it has been experimentally shown that the ecological succession of microalgae under UVR stress shifts in favor of species that are more UVR tolerant (Marcoval et al. 2008). UVR can also affect organisms indirectly by disrupting trophic-level interactions within aquatic ecosystems (Newman et al. 2000). Over the past two decades, many studies have focused on the impacts of environmental UVR on photosynthetic organisms and primary production, but in contrast, few studies have examined the effects of UVR on algal consumers such as zooplankton. This group of organisms is a key intermediary in trophic energy transfer and nutrient regeneration in aquatic food chains (Banse 1995). Moreover, early life stages of marine organisms, particularly planktonic eggs and larvae, have been regarded as being more vulnerable to solar UVR than later stages (Häder et al. 2011).

Recent studies point to the high sensitivity of marine phyto- and zooplankton to solar UVR and the different physiologic mechanisms through which they respond. DNA-damage repair (Buma et al. 2001; Mitchell et al. 2009) and activation of antioxidant systems (Moliné et al. 2010; Rastogi et al. 2010) are among some well-known mechanisms. The most extended photoprotective mechanism is the synthesis and accumulation of UV-absorbing compounds, such as mycosporine-like amino acids (MAAs) (Riegger and Robinson 1997). UV-absorbing compounds are geographically and taxonomically widespread among marine species and are particularly common in many classes of microalgae (Marcoval et al. 2007, 2008; Llewellyn and Airs 2010) and seaweeds (Kräbs et al. 2002), which have the biochemical pathways for *de novo* synthesis. Furthermore, there is evidence of MAA accumulation in marine invertebrates and vertebrates, derived from dietary accumulation (Helbling et al. 2002; Riemer et al. 2007; Hernández-Moresino and Helbling 2010), or via translocation from algal symbionts (Shick et al. 1999), as a means of acquiring protection against UVR (Whitehead et al. 2001). The UV physical screening function of MAAs lies in their photophysical characteristics (Shick et al. 2002), acting as passive screens dissipating the UV energy absorbed in a thermal form. Accumulation of MAAs is induced by both UVR (UVA and UVB) and by blue light in the photosynthetically active radiation (PAR) range of the electromagnetic spectrum (Karsten et al. 1998).

In the present study, the Argentine red shrimp, *Pleoticus muelleri*, has been used as an experimental model organism for marine crustaceans. This species is a commercially important coastal decapod distributed in the Southwest Atlantic, from Southern Brazil to Patagonia (23–50°S),

which is also the subject of experimental aquaculture practices. The aim of this study was to determine the effects of UVR on bioaccumulation of UV-absorbing compounds acquired through the diet, in larvae and postlarvae (PL) of *P. muelleri*, and to assess tissue antioxidant activity, survival, and development.

Materials and Methods

Source of Experimental P. muelleri *Mysis (M)*

Ovigerous females of *P. muelleri* (25–35 mm carapace length, $n = 7$) were collected from coastal waters of Argentina (38°02′ S, 57°30′W), and placed in individual 75-L cylindrical fiberglass spawning tanks at J.J. Nágera Coastal Station, National University at Mar del Plata. Nauplii (N) were transferred to 10-L upwelling tanks at a density of 100 larvae per liter under controlled conditions (22°C, S‰ = 33, pH = 7.5) and fed the haptophyte microalaga, *Pavlova lutheri* (4.6 ± 0.32 µm ESD = equivalent spherical diameter), at concentrations of 100,000 cell/mL d, until larvae reached the mysis stage I (M I).

Experimental Design and Setup

The experimental design consisted of a 2 × 2 design comprising two radiation and two feeding treatments. M I were reared at 50 larvae per liter density in 10-L upwelling tanks under controlled conditions (22°C, S‰ = 33, pH = 7.5). M I were exposed by triplicate to two radiation treatments: (a) tanks covered with Ultraphan film (opaque to UVR, Digefra, 50% transmission at 395 nm) received only PAR (400–700 nm; namely M-PAR, hereafter) and (b) uncovered tanks received the total radiation spectrum (280–700 nm; namely M-PAR + UVR, hereafter). Light sources were 40 W cool-white fluorescent bulbs (Philips) for PAR and Q-Panel UVA-340 bulbs placed 20 cm from the water surface for UVR. The light regime was set at a 12 : 12 h light: dark cycle, with an average irradiance of 65.4 W/m^2 for PAR (Lutron Lx. 107) and 20 W/m^2 for UVR (Lutron UVA 340). These are realistic radiation doses, corresponding to local noontime solar radiation of mid-summer sunny days (Marcoval et al. 2016).

The diet of larvae and PL consisted of two food items: nauplii of the branchiopod, *Artemia persimilis*, and the haptophyte *P. lutheri*, known to produce UV-absorbing compounds when cultured under UVR (Jeffrey et al. 1999; Carreto and Carignan 2011; Häder et al. 2011). Accordingly, two feeding treatments were considered: (a) *A. persimilis* nauplii supplemented with *P. lutheri*, both cultured under a PAR + UVR radiation regime in order to promote UV-absorbing compounds synthesis and accumulation in the haptophyte (D-PAR + UVR, hereafter) and (b) *A. persimilis* and *P. lutheri* cultured under a PAR regime (namely D-PAR, hereafter). *P. lutheri* and *A. persimilis* have a high nutritional value and therefore are of common use in aquaculture practices (Lavens and Sorgeloos 1996; Støttrup et al. 1999; Mallo and Fenucci 2004; Cohen 2012); in addition, *P. lutheri* was chosen as a diet item for being a component of the plankton community, sympatric with the distribution of the shrimp.

In summary, each experiment comprised four dietary and radiation treatments: M-PAR/D-PAR (considered as the control), M-PAR/D-PAR + UVR (Treatment 1), M-PAR + UVR/D-PAR (Treatment 2), and M-PAR + UVR/D-PAR + UVR (Treatment 3).

P. lutheri *Cultures*

Microalgae were grown in semi-continuous, batch cultures (Hoff and Snell 2001) in 1-L UV-transparent polycarbonate containers (Plexiglas UVT, GS 2458, Röhm and Haas, Darmstadt, Germany). Cultures were grown in f/2 medium (Guillard and Ryther 1962) prepared with autoclaved, 0.22 µm filtered seawater (S‰ = 33) at 22°C. As previously stated, cultures were subject to the two radiation treatments used in the experimental setup: (a) PAR and (b) PAR + UVR. Microalgae were harvested at the stationary phase for the feeding of *P. muelleri* M I and PL; the stationary stage of any algal culture has the highest content of accumulated UV-absorbing compounds (Helbling et al. 1996; Neale et al. 1998; Zudaire and Roy 2001).

Artemia persimilis *Culture*

Branchiopod cysts were disinfected and decapsulated prior to incubation in a hypochlorite solution. Cysts were hatched in 10-L tanks under controlled conditions (25–28°C, S ‰ = 15–35, minimum pH = 7.5) and near-saturation oxygen levels, at maximum cyst densities of 2 g/L, and strong PAR irradiation of 300 µmol/quanta/m^2/s (Lavens and Sorgeloos 1996). Just-hatched *A. persimilis* instar I were offered to M and PL of *P. muelleri* at concentrations of 6 nauplii/mL (Mallo 2005).

Determination of UV-Absorbing Compounds

Microalgae (20–100 mL, depending on culture density) were concentrated onto Whatman GF/F glass fiber membranes (25-mm diameter), from which photosynthetic pigments and UV-absorbing compounds were extracted with 7 mL of absolute methanol during 8 h. For *P. muelleri* the whole body of animals was placed in 15-mL centrifuge tubes with 5 mL of absolute methanol for at least 4 h (Hernández-Moresino and Helbling 2010), after which all samples were centrifuged at 800*g* for 15 min. The concentration of UV-absorbing compounds was estimated with a diode array spectrophotometer (Shimadzu UV-2102 PC, UV–visible Scanning Spectrophotometer), scanning the extracts between 250–750 nm. Contents of photosynthetic pigments (420–440 nm and 665 nm) and UV-absorbing compounds (310–360 nm) (Hernández-Moresino and Helbling 2010) were calculated from absorbance peak heights. For phytoplankton, the content was expressed as a function of cell density in the culture at the moment of sampling. For *P. muelleri*, the concentration of UV-absorbing compounds was normalized per gram of dry tissue weight, which was determined by drying subsamples in an oven at 40°C until constant weight.

Growth of P. muelleri *Larvae and Postlarvae*

Every 24 h, three to five individuals were taken from each treatment and preserved in 70% ethanol for subsequent individual growth assessment. Individual length was measured from the rostrum to the telson under a stereomicroscope. Individual growth and development was determined according to Johnson and Olson (1948).

Survival

Live organisms were counted at the end of the feeding experiments, considering as dead those individuals with total absence of motility in their locomotor appendages.

Antioxidant Activity

The potential antioxidant activity of postlarval extracts was determined on the basis of the scavenging activity of the stable 1,1-diphenyl-2-picryhydrazyl (DPPH) free radical, using Electron Paramagnetic Resonance (EPR) with a Bruker ELEXSYS E500T spectrometer. Amplitude signals were transformed into free radical concentrations by comparing the area under the EPR absorption spectrum of the sample to that of a chloroform solution of the concentration standard, DPPH (Díaz et al. 2014). Approximately 25 mg of lyophilized tissue from individuals sampled from each treatment were mixed with 1 mL of chloroform under an argon atmosphere. Each reaction mixture contained 50 µL of the tissue solution and 50 µL of DPPH 3.02×10^{-5} M. Each data-acquisition event was performed with the following settings: 13 mW microwave power; 9.751 GHz microwave frequency; 100 kHz modulation frequency; 12 dB attenuation; 2 Gpp modulation amplitude; magnetic field center at 347 mT; sweep width = 20 mT; sweep time = 60 s for $n = 5$ scans (Díaz et al. 2013). Measurements were repeated at least three times to minimize random errors. The standard plotting program, Origin Pro, was used to fit all sets of points whenever necessary.

Statistical Analysis

A two-way ANOVA was performed on individual growth data to detect significant differences among treatments. Survival rate data were transformed to arcsine before performing ANOVA on this data set. Analysis of covariance (ANCOVA) was performed on the DPPH

scavenging capacity data between treatments and the control. Statistical differences were determined with the statistical package Vassar Stats (v. 2013). In cases of statistically significant differences, mean values were compared with Tukey's multiple range test (Zar 1999). All analyses were performed with the Statistical Package Statistix 8 (v. 2000), at a significance level of $P < 0.05$.

Results

The preliminary spectrophotometry scanning of *P. lutheri* cultures showed that the haptophyte had UV-absorbing compounds and that these were putatively induced upon exposure to the PAR + UVR radiation treatment. UV-absorbing compounds reached a maximum concentration of 5×10^{-6} OD/(cell mL), and this differed significantly from cultures that were not exposed to UVR (maximum concentration = 1.5×10^{-6} OD/(cell mL); ANOVA, $P < 0.01$ (Fig. 1).

Pleoticus muelleri larvae reached the postlarvae 8 (PL8) stage in most treatments except Treatment 2 (i.e., M-PAR + UVR/D-PAR), for which mortality was 100% at the transition from mysis (MIII) to postlarvae (PL1) (Fig. 2). For all other treatments, survival rates were around 75%, not presenting significant differences among them.

Larvae showed exponential growth under most radiation treatments, except in Treatment 2. No significant differences in growth were detected between the control and Treatment 1, but significant differences were found between these two treatments and Treatment 3 (ANOVA,

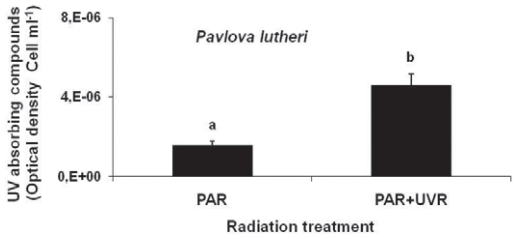

FIGURE 1. *UV-absorbing compounds content in the microalga* Pavlova lutheri *under two radiation treatments, (a) photosynthetically active radiation (PAR) and (b) PAR + ultraviolet radiation (UVR).*

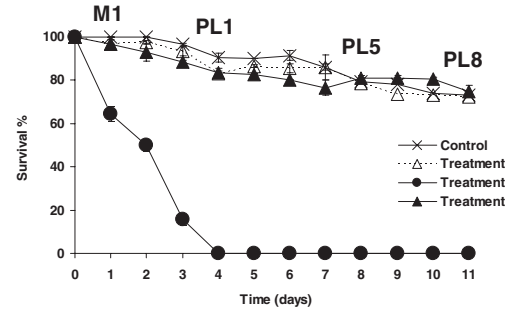

FIGURE 2. *Survival (%) of* Pleoticus muelleri *larvae, fed* Pavlova lutheri *and* Artemia persimilis*, from mysis stage I to postlarvae stage 8. Control: M-PAR/D-PAR; Treatment 1: M-PAR/D-PAR + UVR; Treatment 2: M-PAR + UVR/D-PAR; Treatment 3: M-PAR + UVR/D-PAR + UVR.*

$P < 0.001$) until reaching PL5 (Fig. 3). No significant differences in PL8 growth were detected among the three remaining treatments after 11 d of feeding trials.

The synthesis of UV-absorbing compounds was detected not only in the food but also in *P. muelleri* larvae that were subject to UVR radiation stress. The concentration of UV-absorbing compounds grew exponentially in mysis and PL of *P. muelleri*, either indirectly through the food (Treatment 1) or directly on both larvae and food (Treatment 3). UV-absorbing compound contents were 12.70 ± 0.14 and 13.40 ± 0.28 OD g/dry weight on PL8, for Treatments 1 and 3, respectively (Fig. 4).

Antioxidant capacity was observed in tissue homogenates of surviving larvae from all treatments, although there were significant differences among them (ANCOVA; $P = 0.004$) (Fig. 5). The DPPH radical signal decayed drastically in Treatment 3 within 3 min (65%) and after 1 h the DPPH remnant was about 20%. Treatment 1 (50% decay) and the control (30% decay) showed similar kinetic curves, with the lowest activity being registered in the control treatment.

Discussion

The results presented here demonstrate that early life stages of *P. muelleri* are highly vulnerable to UVR, but this can also be differentially

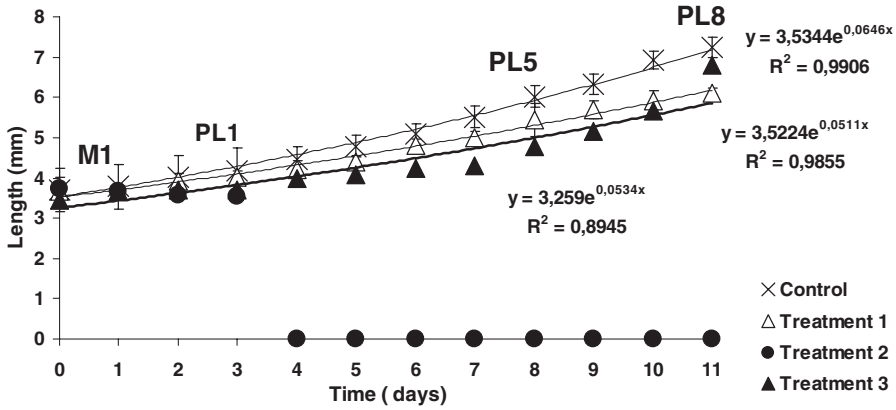

FIGURE 3. *Growth by total body length (mm) of* Pleoticus muelleri *larvae–fed* Pavlova lutheri *and* Artemia persimilis*, from mysis stage I to postlarvae stage 8. Control: M-PAR/D-PAR; Treatment 1: M-PAR/D-PAR + UVR; Treatment 2: M-PAR + UVR/D-PAR; Treatment 3: M-PAR + UVR/D-PAR + UVR.*

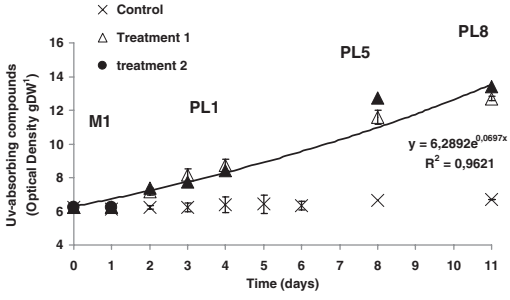

FIGURE 4. *Progression of bioaccumulation of UV-absorbing compounds of* Pleoticus muelleri *larvae–fed* Pavlova lutheri *and* Artemia persimilis *from mysis stage I to post larvae stage 8. Control: M-PAR/D-PAR; Treatment 1: M-PAR/D-PAR + UVR; Treatment 2: M-PAR + UVR/D-PAR; Treatment 3: M-PAR + UVR/D-PAR + UVR.*

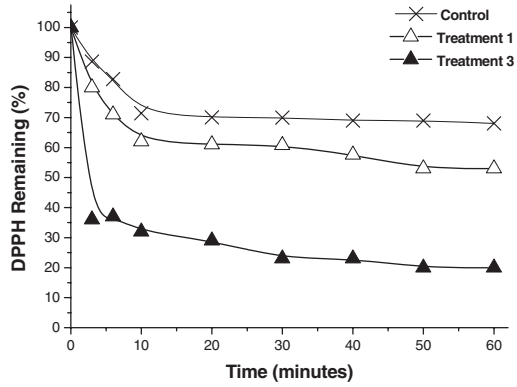

FIGURE 5. *Free-radical 1,1-diphenyl-2-picrylhydrazyl (DPPH) reaction kinetics estimated in tissue homogenates of* Pleoticus muelleri *larvae (PL8). Control: M-PAR/D-PAR; Treatment 1: M-PAR/D-PAR + UVR; Treatment 3: M-PAR + UVR/D-PAR + UVR.*

modulated depending on the quality and previous conditioning of their diet. When the food had low content of UV-absorbing compounds, the exposure of mysis to UVR resulted in 100% mortality rate (Treatment 2), failing to molt to the PL1 stage. Conversely, larvae-fed food rich in UV-absorbing compounds had survival rates of around 90% in the transition from MI to PL1, which was in the same range as in the control. This indicates that the bioaccumulation of UV-absorbing compounds from the diet contributes to a photoprotective effect under UVR stress.

The lack of significant differences in growth among controls and Treatments 1 and 3 suggests that subjecting food items to UVR irradiation during their rearing would not affect the nutritional quality. Similar findings have been cited for crab larvae (Hernández-Moresino and Helbling 2010; Hernández-Moresino et al. 2014), and copepods (Moeller et al. 2005), but little is known about the larval growth of marine penaeoids reared under UVR stress. For krill, *Euphausia superba*, exposed to UVR, Newman et al. (2000) found a positive relationship between ingestion and the amount of MAAs in the diet, which led to an increased postlarval growth.

It is known that UV-B radiation is absorbed by molecules such as nucleic acids and proteins and may cause cellular damage by altering enzymes and membrane lipids, generating free radicals that interfere with the mitotic cycle and promote changes in DNA structure (Hansson and Hylander 2009). In that sense, developing a mechanism to quench DPPH radicals in organisms that are subject to UVR becomes of paramount importance. Interestingly, this study found significant differences in the capacity of postlarval tissue homogenates to quench free radicals among the assayed treatments. Greater antioxidant activity was observed in PL8 under the M-PAR + UVR/D-PAR + UVR treatment, indicating that the UV-absorbing compounds acquired through the diet provide a beneficial effect to the photophysiology of larval shrimp exposed to UVR. Furthermore, in the control treatment in which both the dietary items and the larval shrimp were solely exposed to PAR showed the lowest activity, which suggests that the photoprotective activity is increased in shrimp exposed to UVR, promoting an increment in detoxification mechanisms.

In UVR-acclimated *Leptodiaptomus minutus*, the resistance to UVR increased 2.5-fold for MAAs-rich animals but only 1.5-fold for carotenoid-rich animals (Moeller et al. 2005). These authors suggested that UVR-stressed animals switched from carotenoid accumulation to MAAs accumulation when dietary MAAs were made available. It has been previously documented that MAAs as well as carotenoids can help organisms to cope with excessive radiation (Hernández-Moresino et al. 2014); MAAs absorbing radiation in the UV wavelength range and directly protecting organisms by absorbing and dissipating UVR energy, while carotenoids are involved in antioxidant activities, counteracting the effect of free-radical products generated by UV-B exposure (Hernández-Moresino and Helbling 2010). On the other hand, mycosporine glycine (MG), a representative of MAAs, was found in *Escherichia coli* to be an effective suppressor of various detrimental effects of the type-II photosensitization in biological systems, such as inactivation of mitochondrial electron transport, lipid peroxidation of microsomes, and growth inhibition. The $^{-1}O_2$ quenching experiments conducted by Suh et al. (2003) with MAAs preparations from various marine organisms, demonstrated that at least three more members of the MAAs group besides MG can also quench $^{-1}O_2$ to some extent. Therefore, it would not be unreasonable to assume that MAAs act as scavengers of photodynamically generated reactive oxygen species in marine organisms as proposed by Suh et al. (2003). In connection to that, our data support the hypothesis that in *P. muelleri*, UV-absorbing compounds acquired through the diet represent a group of secondary metabolites that provide protection against free radicals produced by certain endogenous photosensitizers.

In a previous work, Díaz et al. (2013) determined the relationship between tissue concentrations of carotenoids and free-radical-scavenging properties of different larval and postlarval stages of *P. muelleri*. It was demonstrated that postlarval stages with higher carotenoid concentration exhibited high percentage of DPPH decay over time, because radicals are consumed in the tissue at a speed that depends on the amount of protective substances. In this study, the lowest scavenging capacity of DPPH was observed in the mysis stages, in congruence with low levels of UV-absorbing compounds in this stage; while on the other hand PL exhibited high levels of UV-absorbing compounds and high antioxidant activity. The drastic decay in DPPH observed in Treatment 3 could be attributed to the highest accumulation of UV-absorbing compounds (13.4 OD g/dry weight) which most likely provides protection against the oxidative stress caused by radiation.

As previously mentioned, *P. muelleri* is an important target species for aquaculture in the Southwest Atlantic, and the results presented in this work provide an explanation for the higher survival rate of early life stages under stressful light conditions when fed diets rich in UV-absorbing compounds. Moreover, the protective capacity that the endogenous antioxidant system of *P. muelleri* has shown in the neutralization of DPPH radicals provides a useful index in order to measure the relative susceptibility of tissue damage caused by free radicals.

When PL are grown in shallow ponds (1–3 m deep) in aquaculture practices, they become subject to fluctuating environmental conditions, determined by solar radiation, air temperature, wind speed, atmospheric humidity, water turbidity, and basin morphometry (Daw et al. 2012). The projections of global climate change indicate that these factors can have a negative impact on marine organisms. From a productive aquaculture perspective, nutritional strategies may be appropriate for mitigating this environmental concern (Kumar et al. 2016), and in this regard, the results of this study emphasize the importance that UV-absorbing compounds acquire when they become incorporated by higher trophic levels and ameliorate the impact of increased UVR levels that these may be subject to.

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