

Metabolic and behavioral responses of the reef fish *Patagonotothen cornucola* to ultraviolet radiation: Influence of the diet



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ABSTRACT

Most of the studies devoted to assess the effects of ultraviolet radiation (UVR) on fishes have been done with early life stages (i.e., eggs and larvae) as they are the most vulnerable to these wavelengths; however, the effects of UVR on juveniles or adults are less clear. This study evaluated the effects of UVR and diet (i.e., rich and poor in ultraviolet-absorbing compounds; UVAC) on the metabolic rates (respiratory frequency) and behavior (prey capture time) of juveniles of the reef fish *Patagonotothen cornucola*, a common species inhabiting the intertidal areas of the Patagonian coast. UVR was a significant stress factor for *P. cornucola* by increasing its respiratory frequency, which could be related to the costs of repairing any cellular components damaged during the exposure. Fish exposed to UVR took more time to detect and capture their prey, which could lead to a reduction in the prey capture rates, with the concomitant effects on growth. In addition, juveniles feeding on rich-UVAC diet had a significant lower respiratory frequency than those feeding on poor-UVAC diet. This differential response was not evident in the prey capture time. In their natural environment, *P. cornucola* could feed on a varied diet and could also partially avoid the exposure to UVR by hiding under the rocks or macroalgae. Future studies should consider the broad variety of diets that could be found in rocky intertidal areas, and how their qualities (in terms of UVAC content) could help to counteract the UVR effects on juvenile fish.

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1. Introduction

Solar ultraviolet radiation (UVR; 280–400 nm) has deleterious effects on aquatic organisms occupying all trophic levels (Cullen et al., 1992; Williamson, 1995; Häder et al., 2011). Some of the direct UVR effects on organisms are DNA, cellular and tissue damage, and even death (Dattilo et al., 2005; Fischer et al., 2006; Ban et al., 2007). The indirect effects include the use of sub-optimal habitats where UVR does not affect the organisms but also other abiotic factors that are critical for them, such as low food availability, and/or high predation risk (Häder et al., 2011). Since the tolerance to UVR is species-specific, some species are more likely to better cope with UVR damaging wavelengths than others (Siebeck and Bohm, 1994; Leech and Williamson, 2000). Despite these species-specific differences, there is consensus that the early life stages are the most susceptible to UVR damage (see review by Zagarese and Williamson, 2001; Bonaventura et al., 2006).

Abbreviations: UVR, ultraviolet radiation; UVAC, ultraviolet-absorbing compounds; RF, respiratory frequency; RRF, relative respiratory frequency; PCT, prey capture time.

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During evolution, aquatic organisms have developed different protective strategies to cope with UVR. These strategies include: (1) avoidance, such as moving away from the radiation source (i.e., vertical migration) or hiding under shaded places (Leech and Williamson, 2001; Holtby and Bothwell, 2008), (2) photoprotection, including chemical defenses such as the presence of UV-absorbing compounds (UVAC) to prevent damage (Helbling et al., 2002; Zamzow, 2007), and (3) repair of damage, either photorepair or dark enzymatic repair, after any damage has been done (Zagarese and Williamson, 2000). UVAC are the most common UV-screens in marine and freshwater organisms (Shick and Dunlap, 2002; Sommaruga et al., 2006). As UVAC can be only synthesized by photosynthetic organisms, animals obtain these compounds through the diet (Carroll and Shick, 1996; Carefoot et al., 1998; Riemer et al., 2007). Most of the studies about the role of UVAC in aquatic organisms have focused on their role in reducing mortality rates when organisms were exposed to UVR (Helbling et al., 2002; Moeller et al., 2005); however, much less is known about the role of these compounds to counteract the effects of UVR on behavior and feeding.

Intertidal rocky shores are important ecotones between terrestrial and aquatic systems, playing a key role as feeding and nursery areas for several fishes (Faria and Almada, 2006; Aburto-Oropeza et al., 2007) that use them during their first life stages, before migrating to open waters. As these environments are exposed to tidal regimes,

several fishes use these areas only during high tide, but some others remain during low tide in tidal pools. In this latter case, the exposure to UVR, mainly during high irradiance periods (noon time at spring–summer) could be critical for the organisms.

Nototheniidae is an important family of reef fishes, playing a key role as predators, as they occupy most of the trophic niches available in the environment, feeding both on benthos and on plankton (Eastman, 1991; Eastman and McCune, 2000). Within this family, the genus *Patagonotothen* is one of the most important living in Patagonian coasts of Argentina (Galván et al., 2009). Most of the studies about this genus are descriptive (e.g., distribution and feeding habitats, Collins et al., 2007; reproduction, Brickle et al., 2006; Rae and Calvo, 1995), and much less information is available about their trophic behavior and metabolism (but see Agnisola et al., 1997; Fernández et al., 2002). Even more, the effect of variables associated to global change such as UVR on *Patagonotothen* spp. is, so far, virtually unknown. To fill this gap, the aim of this study was to evaluate the combined effects of UVR and diet on the metabolic rates (respiratory frequency) and behavior (prey capture time) in juveniles of the reef fish *Patagonotothen cornucola* (Richardson, 1844) from Patagonian coasts.

2. Methods

2.1. Study area, collection and maintenance of specimens

Juvenile specimens of *P. cornucola* were collected during the Austral Summer of 2013 from Playa Bonita (43° 21' 40" S, 65° 02' 55" W; Argentina) a rocky beach located 3 km away from the mouth of the Chubut River. Fish were caught from tide pools using a small hand net (1 cm mesh), stored in buckets and immediately transported to the laboratory at Estación de Fotobiología Playa Unión (EFPU, 20 min away from the sampling site). In the laboratory, individuals were placed in aquaria filled with seawater at 20 °C, with continuous aeration. Fish were maintained in the aquaria during three days before experimentation. During this period, individuals were fed on the amphipod *Ampithoe valida* (Smith, 1873) collected also from Playa Bonita.

2.2. Experimental procedure

To assess the combined effects of UVR and diet on fish respiratory frequency and prey capture time, individuals of *P. cornucola* were placed in 20 l plastic aquaria (1 fish per aquarium, $n = 12$), fed on 2 different diets and exposed to 2 artificial radiation conditions in an experimental set-up consisting of a 2×2 matrix, with radiation and diet as factors. The experimental conditions were as follows: a) Radiation: (1) PAB treatment, specimens receiving full radiation (PAR + UV-A + UV-B, >280 nm): 2 Phillips daylight fluorescence tubes for PAR and 2 tubes Q-Panel-UVA-340 for UVR, and (2) P treatment (control), specimens receiving only Photosynthetic Active Radiation (PAR: >400 nm): 2 Phillips daylight fluorescence tubes, and b) Diets: (1) poor in UVAC, amphipods fed on the green macroalgae *Ulva rigida* (C. Agardh, 1823), and (2) rich in UVAC, amphipods fed on the red macroalgae *Porphyra columbina* (Montagne, 1842). Three replicates per treatment were used. The duration of the experiment was of 9 days, with a 12 L:12D (light/dark) photoperiod. The irradiances received by the fish were 36.7 W m^{-2} in the P treatment, while in the PAB treatment organisms additionally received 9.87 W m^{-2} of UVR (UV-A + UV-B).

The amphipod *Ampithoe valida* was used as prey for the fish during the experiment. One week before the beginning of the experiment, individuals of *A. valida* were brought from the field, separated in 2 groups, and fed on 2 different diets: a) *U. rigida* (poor in UVAC) and, b) *P. columbina* (rich in UVAC). Previous experiments confirmed that *P. columbina* synthesized high amounts of UVAC (Helbling et al., 2004) while in *U. rigida* they were almost null. Amphipods accumulate these compounds in their bodies differentially (Valiñas and Helbling, 2015) thus it was possible to obtain amphipods rich and poor in UVAC as

food source for fish. Fish were provided with food ad libitum throughout the experiment by adding amphipods in all aquaria twice a day, in the morning and in the afternoon.

2.3. Analyses and measurements

2.3.1. UV-absorbing compounds analysis

The content of UVAC in both macroalgae and in the amphipods used as food for fish was measured to verify that the food provided to the amphipods had different UVAC content, and that the amphipods used as food for fish accumulated different amounts of UVAC. The UVAC measurements in the amphipods were done at the initial time (t_0), to determine the amount of compounds that individuals brought from their natural environment, and after the 7-days feeding period. Previous to the analysis of UVAC, the amphipods were left for 24 h without any food to empty their gut content. As a general procedure (for both, amphipods and macroalgae), the tissues were weighted (wet weight), placed in 15 mL centrifuge tubes, broken with a glass rot, and extracted in absolute methanol (Holm-Hansen and Riemann, 1978). After the extraction period, a scan between 250 and 750 nm was done using a spectrophotometer (Hewlett Packard, model HP 8453E). The amount of UVAC was estimated by peak analysis in the range 310–360 nm (Helbling et al., 1996). For comparisons, the UVAC content was expressed as the peak area per wet weight of amphipod or macroalgae.

2.3.2. Respiratory frequency (RF)

The number of times that individuals opened and closed their operculum was registered during 1 min, and this was used as an indirect estimation of their degree of stress. The observations started after the individuals stayed at least 2 min motionless, so that the RF was not affected by any recent fish swimming activity. Measurements were performed at t_0 and then once a day from the third to the ninth day of the experiment. The mean RF obtained at t_0 was subtracted to the RF values obtained for the different treatments, thus the relative respiratory frequency (RRF) was used for statistical comparisons. All measurements were performed 2 h before the end of the light period. The observations of the individuals were done behind a dark curtain to avoid disturbing the fish.

2.3.3. Prey capture time (PCT)

This term refers to the time (in sec), measured with a chronometer, since the prey was thrown into the aquarium chamber until the fish caught it. To standardize the procedure, the measurements started when the fish were located in the left corner of the aquarium, throwing the prey at the opposite corner. Thus, in all measurements, the distance that fish swam to capture their prey and the visual angle from which prey appeared was the same. The PCT was measured on the last day of the experiment, 2 h before the end of the light period. Three amphipods, one at a time, were thrown to each aquarium, and the mean PCT for each replicate was calculated. A high PCT means that fish took longer to capture their prey than those with low PCT. As for RF, all the measurements were done behind a dark curtain.

3. Statistical and data analysis

To evaluate differences in the abundance of UVAC of both macroalgae species used as food for fish, a t-test was performed (Zar, 1999). Differences between the initial content of UVAC in the amphipod' bodies (UVAC that individuals accumulated in the field), and the content of these compounds after individuals were fed on *U. rigida* or *P. columbina* were analyzed using a one-way ANOVA (Zar, 1999). For RRF, and because no statistical differences were detected between days, the data from the different days were pooled and the mean RRF was compared between radiation and diet treatments using a two-way ANOVA (Zar, 1999). The same statistical analysis was used to determine differences in PCT. In all cases, Tukey's tests were performed if the

ANOVA revealed significant interactions or differences in the main factors (Zar, 1999). For all statistical analyses, normality and homoscedasticity of the data set were tested using the Kolmogorov–Smirnov and Cochran tests, respectively. When necessary, data were transformed to fit parametric assumptions.

4. Results

4.1. UV-absorbing compounds

Both macroalgae (*U. rigida* and *P. columbina*) (Fig. 1) had UVAC in their tissues, evidenced by the peaks between 310 to 360 nm. In the case of *P. columbina*, a significant peak was detected in the UV region, while a small “shoulder” was detected in *U. rigida* (Fig. 1A). The amount of UVAC in *P. columbina* was significantly higher than that in *U. rigida* ($t = -12.63$, $df = 4$, $P < 0.01$; Fig. 1A). In amphipods used as food for fish (Fig. 1B), there was differential accumulation of UVAC in the individuals depending on the diet provided (ANOVA, $F = 19.43$, $df = 2$, $P < 0.01$; Fig. 1B): Amphipods fed on *U. rigida* did not accumulate UVAC, and had a similar amount of compounds than individuals at t_0 . Amphipods fed on *P. columbina*, however, accumulated UVAC, increasing their content more than three times in relation to the amount present in the individuals at t_0 , or that those fed on *U. rigida* (Tukey test, $P < 0.05$; Fig. 1B). These results confirmed that during the experiment, fish effectively fed on diets containing different amounts of UVAC.

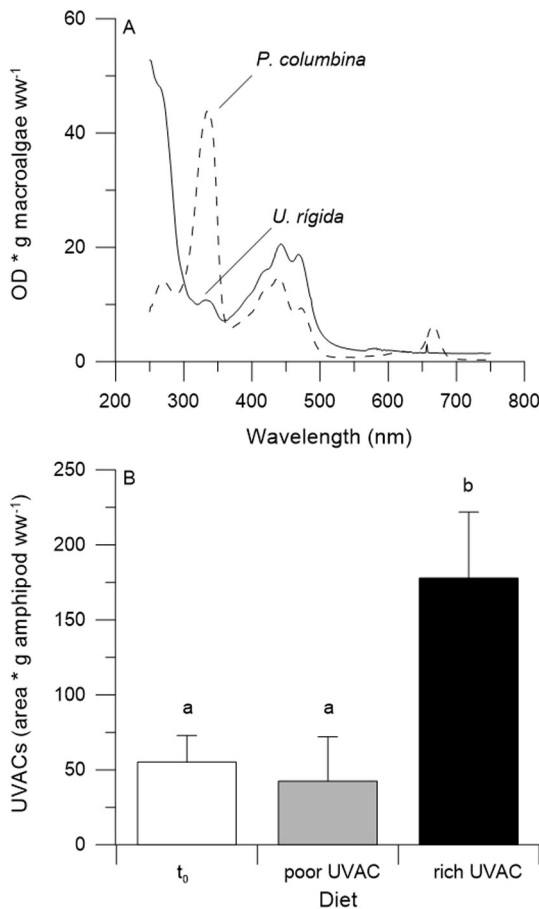


Fig. 1. (A) Optical density (OD) per g (wet weight) of macroalgae (used as food for amphipods) as a function of wavelength. Representative scans (250–750 nm) of *U. rigida* (solid line) and *P. columbina* (dashed line). (B) Mean UVAC per g (wet weight) of amphipod depending on the diet provided. The different letters indicate significant differences between diets.

4.2. Respiratory frequency

The mean RF of individuals at t_0 was 49.61 (± 21.60) operculum movements per min. No interaction effects between radiation and diet treatments were observed in the RRF ($F_{1,32} = 0.187$, $P = 0.667$; Fig. 2). A significant effect of UVR ($F_{1,32} = 4.827$, $P < 0.05$) was observed, with organisms having higher RRF in the PAB as compared to the P treatment (Fig. 2). In addition, significant differences in the RRF as a function of the diet ($F_{1,32} = 21.375$, $P < 0.001$) were observed, with fish fed on a diet poor in UVAC having higher RRF than those ones fed on a diet rich in UVAC (Fig. 2).

4.3. Prey capture time

No interaction effects between diet and radiation treatments were observed ($F_{1,8} = 0.228$, $P = 0.647$) in regard to the PCT of *P. cornucola* (Fig. 3). The analysis of the main factors revealed that the PCT was not affected by the diet ($F_{1,8} = 0.855$, $P = 0.386$), but it did by radiation ($F_{1,8} = 33.675$, $P < 0.05$). Fish exposed to UVR (PAB treatment) took longer time to capture their prey than those exposed only to PAR (Fig. 3).

5. Discussion

The effects of UVR on fishes had been widely studied in the last decades (Zagarese and Williamson, 2001; Holtby and Bothwell, 2008; Zamzow et al., 2013). Most of these studies had been performed on early life stages (eggs and larvae) because they are more vulnerable to UVR (Fukunishi et al., 2006; Olson et al., 2006), but much less is known about the effects of UVR on juveniles or adults. In the following paragraphs the effects of UVR on the metabolism and the behavior of juveniles of *P. cornucola* will be discussed, addressing also the potential role of UVAC as a photoprotective mechanism to reduce/counteract the negative effects of this waveband.

The differences in the amount of UVAC in *P. columbina* and *U. rigida* were reflected in their differential accumulation in the amphipod bodies. Previous studies have demonstrated that in general, red macroalgae synthesize higher amounts of UVAC than green macroalgae (Karsten et al., 1998; Helbling et al., 2004); even this pattern was confirmed in a previous study which compared the amounts of UVAC in *P. columbina* and *U. rigida* (Valiñas and Helbling, 2015). Moreover, the

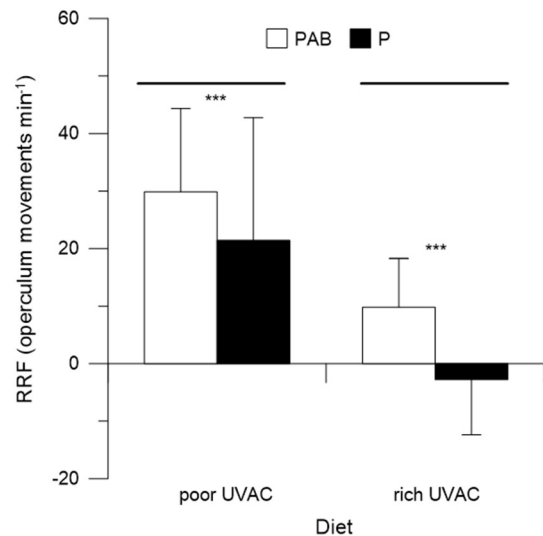


Fig. 2. Relative respiratory frequency (RRF, number of operculum movements per min) of *P. cornucola* as a function of the diet and radiation treatments. The vertical lines indicate the standard deviation. The lines on top of the panel indicate significant differences between diets, and the asterisks indicate significant differences between radiation treatments.

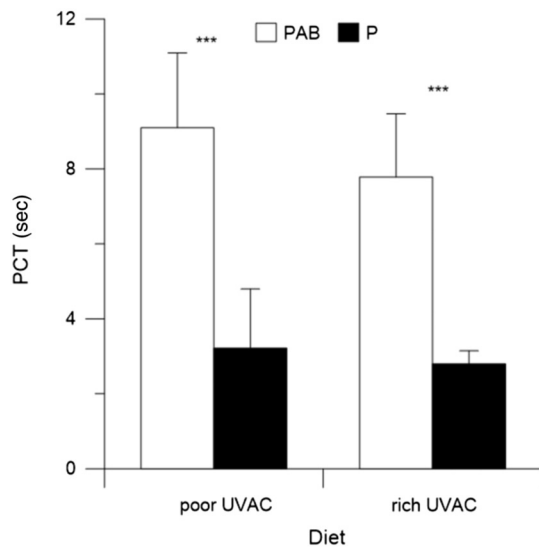


Fig. 3. Prey capture time (PCT; in seconds) of *P. cornucola* as a function of the diet and radiation treatments. The lines on top of the bars indicate the standard deviation. The asterisks indicate significant differences between radiation treatments.

ability to accumulate UVAC through the diet has been previously reported for several aquatic organisms like cladocerans (Gonçalves et al., 2002), crab larvae (Hernández Moresino and Helbling, 2010), and even in *A. valida* (Helbling et al., 2002; Valiñas and Helbling, 2015). Nevertheless, it has been demonstrated that the amount of UVAC in primary producers show a strong seasonal pattern (Tartarotti and Sommaruga, 2006; Riemer et al., 2007) and that can change throughout the day (Yakovleva and Hidaka, 2004). Thus, the analysis of the UVAC content in the macroalgae and in the amphipods was necessary to confirm that the prey offered to the fish had different content of these compounds.

The results presented here indicate that UVR acted as a stress factor in *P. cornucola* by increasing their respiratory frequency, and that a diet rich in UVAC helped to counteract this effect. The negative effect of UVR on respiration has been previously reported in juveniles of the rainbow trout (*Oncorhynchus mykiss*) exposed to UV-B (Alemanni et al., 2003) and in juveniles of the cichlid fish, *Cichlasoma nigrofasciatum* exposed to UV-A (Winckler and Fidhiany, 1996). However, UVR effects are strongly species-specific, as other studies demonstrated that the white fish *Coregonus lavaretus* and the vendace *Coregonus albula* were not affected when exposed to UV-B (Häkkinen et al., 2002). To cope with UVR (especially UV-B), aquatic organisms had developed molecular, physiological and/or behavioral responses (Williamson et al., 1997; Leech et al., 2009; Manek et al., 2012). All these strategies require metabolic energy in the form of ATP (Sinha and Häder, 2002), and could explain the increase in the respiration rates observed in *P. cornucola*.

Independently of the quality of radiation, individuals of *P. cornucola* fed on a diet poor in UVAC showed higher RRF than those fed on a diet rich in UVAC. A recent study performed in the Patagonian coast demonstrated that *P. columbina* had a higher nutritional quality than *U. rigida* (Valiñas and Helbling, 2015). Thus, the nutritional quality of amphipods fed on *P. columbina* could be probably higher than those fed on *U. rigida*; this in turn would be consequently traduced in food of different nutritional qualities for *P. cornucola*. Organisms can compensate the low nutritional quality of food by increasing the amount ingested, thereby offsetting quality by quantity (Graça et al., 1993; Cruz-Rivera and Hay, 2000). An increase in the food consumption rates implies a higher metabolic activity of organisms, which results, for example, in increased RF. This might also explain the higher RRF found in *P. cornucola* fed on amphipods of low nutritional quality.

It is widely accepted that UV vision is used primarily to enhance the detection of planktonic prey, and some investigations have shown

that the presence of UVR improves the search behavior of certain UV-sensitive zooplanktivorous fishes (Zagarese and Williamson, 2001) by increasing fish foraging efficiency (Browman et al., 1994; but see Leech and Johnsen, 2006; Holtby and Bothwell, 2008). For benthivorous fishes such as *P. cornucola*, the information is less clear. Although previous studies suggested that several notothenioid fish species use UV-vision during swimming activity and probably in prey encounters (Miyazaki et al., 2001; Miyazaki et al., 2002) there are no experimental studies that actually demonstrate that their prey capture efficiency increases under UVR. In fact, in this study, PCT was higher when fish were exposed to UVR, suggesting that the UVR effect was particularly negative for detecting and locating prey in juveniles of *P. cornucola*. Even if the damage induced by UVR is no lethal, fish can be weakened by UVR exposure, which might lead to reduced performance as predators. Hunter et al. (1979) found that a 4-day period of exposure to sub-lethal levels of UV-B induced lesions in the eyes of larvae of the northern anchovy *Engraulis mordax*. In this study, the eyes of juveniles of *P. cornucola* were not observed, so the possibility that UVR induced any eye damage (thus reducing the ability of juvenile fish to recognize their prey, leading to significantly lower successful captures) cannot be ruled out. Holtby and Bothwell (2008) found that juveniles of the coho salmon *Oncorhynchus kisutch* made fewer feeding strikes in the presence of UVR. Also, a reduction in prey consumption under UVR had been reported in larvae of the Atlantic cod *Gadus morhua* (Fukunishi et al., 2013, but see Browman et al., 1994; Holtby and Bothwell, 2008). Thus, the fact that fish needed more time to capture their prey could be translated in a reduction of the prey capture rates, with the consequent effects on growth as shown for the anchovy *Engraulis mordax* (Hunter et al., 1979) and for juveniles of the Atlantic salmon *Salmo salar* (Jokinen et al., 2008).

The present study shows the negative effects of UVR on juveniles of *P. cornucola* in terms of respiration rates and predator-prey interactions. At the same time it provides evidence that life stages other than eggs and larvae are also susceptible to UVR exposure. In their natural environment, *P. cornucola* feeds on varied diets and could partially avoid the exposure to UVR by hiding under the rocks or macroalgae. Future studies should consider a broad variety of diets available in rocky intertidal areas, and how their qualities (in terms of UVAC content) could help to counteract the net effects of UVR on juvenile fish.

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