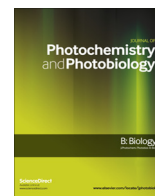




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Sex-dependent effects of ultraviolet radiation on the marine amphipod *Ampithoe valida* (Ampithoidae)



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ABSTRACT

The combined effects of solar radiation and diet on the marine amphipod *Ampithoe valida* were investigated exposing individuals to two solar radiation treatments: PAB (>280 nm, PAR + UV-A + UV-B) and P (>400 nm, only PAR), and three diets: poor (*Ulva rigida*) and rich (*Porphyra columbina*) in UV-absorbing compounds (UVAC), and mixed diet: (*U. rigida* + *P. columbina*). Females of *A. valida* showed higher food consumption rates when diets contained *P. columbina*, and preferred this macroalgae rather than *U. rigida*, resulting in a higher content of UVAC in their bodies. Moreover, the content of UVAC increased in the PAB treatment, thus suggesting the existence of a mechanism to accumulate these compounds under UVR. Although UVR affected the survival, the highest mortality rates were found in those females fed with poor-UVAC diets, which evidence that UVAC provided partial protection against UVR. Males preferred mixed diet, and did not show preference for any particular macroalgae. No differences in mortality were observed between radiation treatments, indicating that UVR did not affect the survival of males, independently if they accumulated UVAC or not. The vulnerability of females to UVR would be partially determined by the type of food consumed, which in turn would be closely related to the macroalgae composition of the intertidal they inhabiting. These effects could be even more pronounced under a global change scenario.

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1. Introduction

Since the discovery of ozone depletion and associated increases of ultraviolet radiation (UVR; mainly UV-B: 280–315 nm) reaching the Earth's surface [1–3] great number of publications focused on the potential role of UVR on aquatic ecosystems (e.g., [4–6]). Nowadays, it is widely demonstrated that individuals from phytoplankton to fish are negatively affected by UVR [7,6], with effects including DNA and protein damage, production of harmful reactive oxygen species, reduction in the survival and growth rates of organisms [8–10], and also changes in their behavior [11,12]. Beyond the individual level, UVR effects include changes in species composition and interactions, affecting ultimately the structure of communities, food web processes and ecosystem functions [13–15].

To cope with UVR (especially UV-B), aquatic organisms had developed a series of molecular, physiological and/or behavioral strategies such as chemical defenses like UV-absorbing compounds (UVAC; mainly mycosporine like amino acids – MAAs – [16,17]) or pigments like melanin and carotenoids [18]. UVAC absorb in the

range of 310–360 nm, and therefore are able to screen off or reduce harmful radiation before reaching important targets within the cells/organisms [19,17,20]. Although the protective role of UVAC have been demonstrated for many aquatic organisms [21–23], their ultimate protection ability is variable and species-specific. UVAC can be only synthesized by some primary producers (phytoplankton, macroalgae and some cyanobacteria; [24]) thus, the main way by which consumers can acquire them is through the diet [17,25,26]. Between primary producers, the amount of synthesized UVAC can be significantly different. While Rhodophyceae species synthesize high amount of these compounds, Chlorophyceae species synthesize very low concentrations of them [27,26]. Thus, dietary differences may result in varied adaptation/acclimation to the radiation climate which could affect, ultimately, individual's survival.

Marine mesoherbivores constitute a high percentage of the total epibenthic species [28] inhabiting intertidal areas [29,28], and play an important role in marine systems, being responsible for the transfer of energy to higher trophic levels [30]. They can be found often associated to living substrates such as macroalgae and sea-grasses, that provide them food and shelter, this latter against predators and environmental stress [28,30]. Although intertidal areas are one of the most studied environments in the Earth [31,32], relatively few studies considered the effects of ultraviolet

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radiation on mesoherbivores and even less on their trophic interactions (but see [33,34]). Taking into account their critical role as benthic secondary producers, any direct effect on them could indirectly affect the entire marine food web.

The aim of this study was to evaluate the trophic response of the marine amphipod *Ampithoe valida* Smith (1973) to solar UVR when fed on diets with different UVAC content. *A. valida* is a very abundant species in the South Atlantic coast of Argentina and constitutes an important prey in the diet of several commercial fish species of the region (mainly for artisanal fisheries), like the silver-sides *Odontesthes smitti* and *Odontesthes nigricans* [35]. We hypothesized that there is an interactive effect between exposure to UVR and the food-type consumed by *A. valida*, with organisms preferring diets rich in UVAC when exposed to UVR. This selection of diets will thus increase the survival of this amphipod species.

2. Materials and methods

2.1. Experimental procedure

Specimens were collected during Spring 2011 from Playa Bonita, located in the Patagonian coast (43° 22'S – 65° 03'W, Chubut, Argentina). Samples of green (*Ulva rigida*) and red (*Porphyra columbina*) macroalgae, and amphipods (*A. valida*) were collected in plastic containers and immediately taken to the laboratory (20 min away) where manual separation of organisms by sex was done. Adult males and females of similar sizes (length: 10 ± 1 mm, weight: 21 ± 3.5 mg) were left outdoors in the shadow in containers filled with filtered seawater, and maintained without food for 24 h before initiating the experiments. The amphipods were starved to avoid the influence of past diet on the feeding behavior (e.g., [36]).

For the experiments, individuals of *A. valida* were placed in 16 cm × 21 cm × 5 cm (wide × length × depth) containers, fed with three different diets and exposed to solar radiation (two treatments) in an experimental set up of 2 × 3 matrix, with radiation and diet as factors, respectively, as follows: (1) Radiation: (a) PAB treatment, amphipods receiving full solar radiation (PAR + UV-A + UV-B > 280 nm), containers covered with Ultraphan 290 film (in this case, the use of filters was only to avoid the evaporation of the sea water and the potential entrance of particles in the containers), and (b) P treatment (control), amphipods receiving Photosynthetic Active Radiation (PAR > 400 nm), containers covered with Ultraphan UV Opak Digefra film (see [37] for transmission spectral of these materials); (2) Diets: (a) only *U. rigida* (UI diet, poor in UVAC), (b) only *P. columbina* (Po diet, rich in UVAC), and (c) a mix of ca. equal parts of *U. rigida* and *P. columbina* (UI + Po diet). The experiments were performed simultaneously for males and females, to ensure that both sexes received the same solar radiation conditions.

All containers were placed in a big tank (3 m diameter, 0.22 m depth) that has a constant flow of water in order to maintain the temperature at 20 °C. We decided to use this temperature due to measurements performed in the field evidenced that during spring season, water in tide pools can reach temperatures of 23.5 °C when low tide is at noon, decreasing to 13 °C towards the afternoon-night. Thus, fixing the temperature at 20 °C we ensured that animals were within the thermal range that usually experience in their natural environment. The number of replicates per treatment was 5, with 50 individuals per container.

We used 50 amphipods in each replicate in order to have a good number of individuals until the end of the experiment to measure food consumption rates and UVAC content, considering the case of having high mortality rates. Even though amphipods could have aggressive behavior [38], we rarely observed this behavior in our

experiments. Nevertheless, and in order to evaluate if the high density of amphipod use in the experiments could promote the aggressive behavior between the individuals, and consequently affect the mortality rates, we performed a supplementary experiment to evaluate differences in mortality of *A. valida* depending on the density of individuals and on radiation. We did not find differences between treatments (two-way ANOVA, $F_{1,8} = 0.059$, $P = 0.814$), so we concluded that the results of mortality obtained in our experiments were not related to a possible aggressive behavior as a result of the high density of individuals in the containers.

Previous studies as well as an additional experiment we perform indicated that both *U. rigida* and *P. columbina* under P and PAB radiation treatments had significant differences in growth only after the third day of incubation (Repeated measures ANOVA, *U. rigida*: $F_{3,12} = 22.39$, $P < 0.05$, *P. columbina*: $F_{3,12} = 152.54$, $P < 0.05$). Based on these results, during the experiment we replaced the food in the containers daily (early in the morning), and no controls for autogenic changes were included as treatment.

2.2. Analysis and measurements

2.2.1. Food consumption rates (FCR) and food preferences

The diets for amphipods consisted on 10 small discs (diameter: 1.2 cm) of the corresponding macroalgae diet treatment. In the UI + Po diet, 5 discs of each macroalgae species were added. Each macroalgae disc was carefully dried on tissue paper and its wet weight recorded using a digital scale (Ohaus Pioneer™, precision: 0.1 mg) before been added to each container. The food discs were placed in the containers during the morning and left until the next morning, then the discs or the left overs were taken out, rinsed, gently dried and the wet weight was determined again. The same procedure was repeated during three consecutive days using new food each morning. There were no problems in recognizing the food from green or red macroalgae after the 24 h feeding; however, there were slight complications with small leftover parts in some treatments. Nevertheless, the uncertainty of these measurements was <2% of the ingested food.

The FCR was calculated as the difference between the initial and the final macroalgae wet weight, and expressed as mg macroalgae consumed per amphipod per day. There were no significant differences in the FCR among days for each corresponding treatment, so the average of the three days was used for statistical comparisons. In the mixed diet treatment we calculated the total FCR, and also the FCR separately for each macroalgae, to evaluate if amphipods preferred some specific food when they had the opportunity to choose between the two food options.

2.2.2. Mortality rates

Each morning, when replacing the food, the number of dead *A. valida* individuals was registered in each container (we considered as dead those individuals that did not have any type of movement). Mortality was estimated in each treatment as the relationship between the total dead individuals at the end of the experiment and the number of individuals added to each container at the beginning of it. Then, mortality in treatments exposed to PAR + UVR was normalized with the control samples exposed only to PAR with the aim to estimate the net effect of UVR on the amphipods.

2.2.3. Content of UVAC

The content of UVAC was measured in amphipods and macroalgae from their natural environment, and also in amphipods at the end of the feeding experiments. In the case of amphipods, before to start the analysis, organisms were left 24 h without food to empty their gut content. Specimens were carefully dried, weighted, and placed in 15 ml centrifuge tubes with 5 ml of absolute methanol.

The tissues of the macroalgae or the amphipods were initially broken with a glass rot followed by a sonication (i.e., 20 min at 25 °C), and extracted for at least 1 h. After extraction, the samples were centrifuged for 15 min at 1500 rpm and the spectral characteristics of the supernatants were measured from 280 to 750 nm using a scanning spectrophotometer (Hewlett Packard model HP-8453E). The amount of UVAC was estimated by peak analysis at 310–360 nm [39]. We are aware that other studies [40] used 20% methanol as the most effective solvent to extract MAAs; however, previous studies conducted in our laboratory did not find significant differences between 100% and 20% methanol. In addition, the use of 100% methanol allowed us to obtain whole spectral absorption characteristics within the UVR and PAR ranges for both algae and amphipods. Peak analysis was done using each obtained spectrum. The amount of UVAC in macroalgae was expressed as peak area per mg wet weight of tissue. For comparisons of the UVAC content between amphipods collected from the field (t_0) and amphipods from the experiments, UVAC content was expressed as peak area mg wet weight amphipod⁻¹. When comparisons in the UVAC content was performed only between amphipods from the experiments, under different radiation and diet treatments, the area was also normalized per the FCR (expressed as peak area mg amphipod⁻¹ mg of ingested macroalgae⁻¹). Before normalizing per FCR, the initial content of UVAC present in the amphipods (those which organisms brought from their natural environment) was subtracted from the total amount of UVAC measured at the end of the experiments, to have an estimation of the change in the amount of UVAC in males and females of *A. valida* during the experimental period.

2.2.4. Radiation data

Solar radiation was continuously monitored (every minute) during the whole experimental period using a broadband filter radiometer European Light dosimeter Network (ELDONET; Real Time Computers Inc., Mohrendorf Germany) that is permanently installed on the roof of the Estación de Fotobiología Playa Unión (EPPU). The radiometer has three channels for UV-B (280–315 nm), UV-A (315–400 nm) and PAR (400–700 nm) [41].

2.3. Statistical analysis

A two-way ANOVAs were used to evaluate differences in the FCR as a function of diet and radiation treatments, with subsequent LSD tests [42]. Food preferences were evaluated comparing differences in the FCR of *U. rigida* and *P. columbina* within the UI + Po diet.

One-way ANOVAs were performed to evaluate changes in the content of UVAC in males and females of *A. valida*, before and after being fed with *U. rigida*, *P. columbina* or a mix of *U. rigida* and *P. columbina* (at the end of the feeding experiments). Statistical comparisons were performed for each diet separately (i.e., t_0 vs. UI diet in PAB vs. UI diet in P). On the other hand, to evaluate differences in the UVAC content as a function of diet and radiation treatments, two-way ANOVAs were performed separately for males and females, with subsequent LSD tests [42]. Differences between mortality rates were also compared using two-way ANOVAs [42] with diet and radiation as factors.

For all statistical analysis, normality and homoscedasticity of the data set were tested using the Kolmogorov–Smirnov and Levene tests, respectively [42]. When necessary, data were transformed to fit parametric assumptions. In all cases, the comparisons were performed for males and females of *A. valida* separately.

3. Results

3.1. Radiation data

Mean daily solar irradiances received during the experimental period (Spring 2011) were 108.8, 15.7 and 0.41 W m⁻² for PAR, UV-A and UV-B, respectively, while mean daily doses were 4698.3, 679.7 and 18 kJ m⁻² for PAR, UV-A and UV-B, respectively. During the experiments total ozone column concentration (<http://ozoneaq.gsfc.nasa.gov>) varied between 298 and 324 Dobson units, values that were within the “normal” ozone column concentration for the area and do not correspond to a depleted ozone condition [43].

3.2. Food consumption rate

Mean values of FCR, expressed in mg of macroalgae ingested per amphipod per day under the different diet and radiation treatments are shown in Figs. 1 and 2. No significant interaction on the FCR between diets and radiation treatments was observed for *A. valida* (females: $F_{2,24} = 0.26$, $P > 0.05$; males: $F_{2,24} = 0.49$, $P > 0.05$; Fig. 1). The analysis of main factors revealed that the FCR did not differ between radiation treatments (females: $F_{1,24} = 0.82$, $P > 0.05$; males: $F_{2,24} = 0.029$, $P > 0.05$; Fig. 1), but it did between diets (females: $F_{2,24} = 5.72$, $P < 0.05$; males: $F_{2,24} = 100.62$, $P < 0.001$; Fig. 1). Females (Fig. 1A) consumed higher

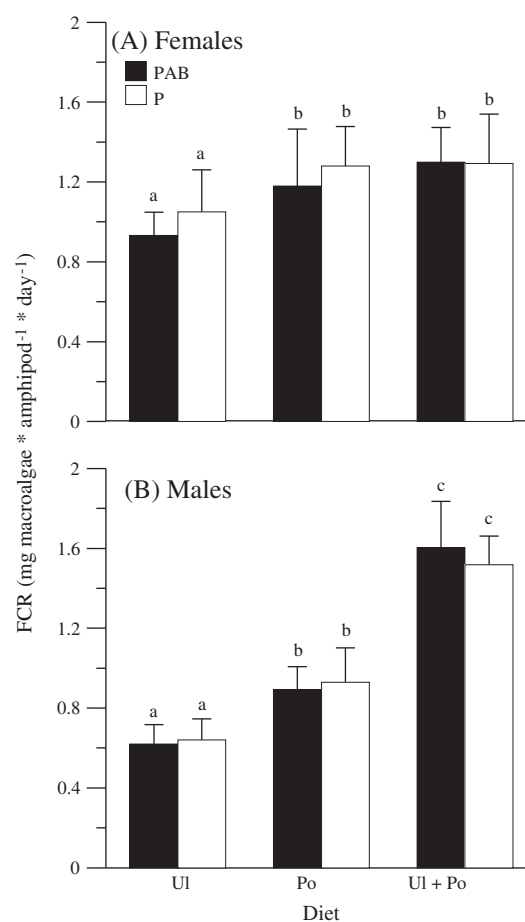


Fig. 1. Mean food consumption rates (FCR), in mg per day and per individual, of females (A) and males (B) of *A. valida* as a function of the radiation treatments and diets offered during the feeding experiments. The vertical lines indicate the standard deviation, while the different letters indicate significant differences between diets.

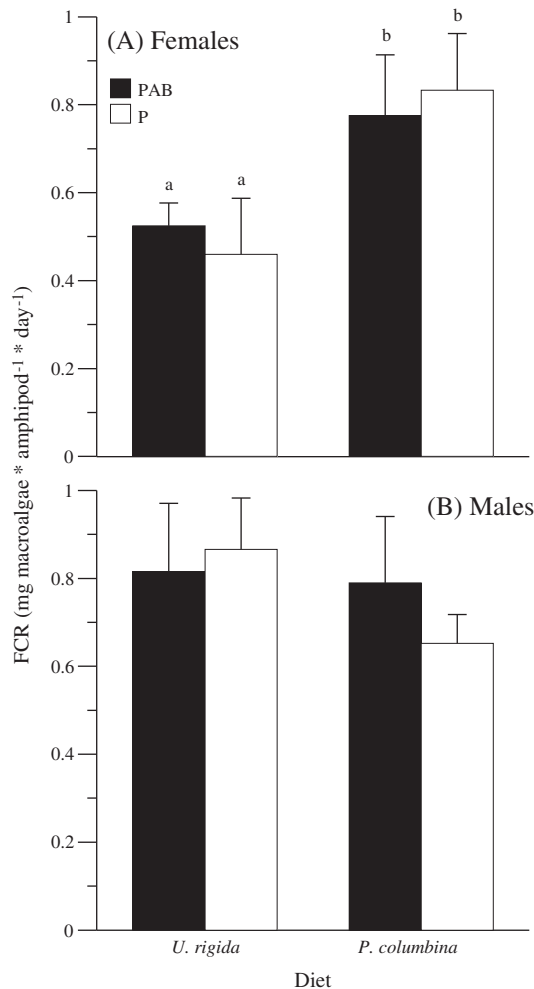


Fig. 2. Mean food consumption rates (FCR), in mg per day and per individual, of *U. rigida* and *P. columbina* within the UI + Po diet as a function of the radiation treatments. The vertical lines indicate the standard deviation, while the different letters indicate significant differences between diets.

proportions of food in the Po and UI + Po diets than in the UI diet (LSD test, $P < 0.05$). Males (Fig. 1B) had higher FCR in the UI + Po diet, followed by Po and UI diets, respectively (LSD test, $P < 0.05$).

No interaction effect was observed between diet and radiation treatments ($F_{1,16} = 1.36$, $P > 0.05$) when female amphipods (Fig. 2A) had the opportunity to choose between macroalgae species (UI + Po diet; Fig. 2). The FCR in females were not affected by solar radiation ($F_{1,16} = 0.004$, $P > 0.05$), but were significantly affected by the diet ($F_{1,16} = 35.72$, $P < 0.05$). When both macroalgae were offered simultaneously, females consumed significantly more *P. columbina* than *U. rigida* (Fig. 2A), evidencing the preference for the red macroalgae over the green one. In contrast to females, there were no significant differences in the FCR in *A. valida* males within the UI + Po diet (interactive effects: $F_{1,16} = 2.73$, $P > 0.05$; diet: $F_{1,16} = 4.42$, $P > 0.05$; radiation: $F_{1,16} = 0.58$, $P > 0.05$; Fig. 2B), suggesting no preference for a particular macroalgae.

3.3. Accumulation of UVAC

The absorption characteristics of the specimens used in the experiments as well as the content of UVAC throughout the experiments are shown in Fig. 3. Both males and females of *A. valida* collected from the field (Fig. 3A) exhibited UVAC in their bodies, which were evidenced by the presence of peaks between 310 and 360 nm,

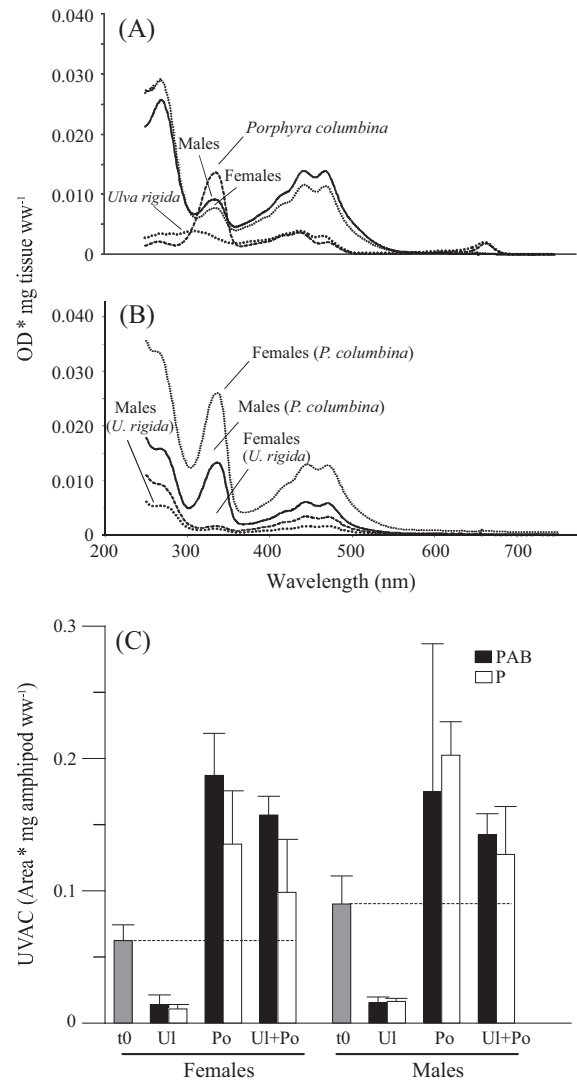


Fig. 3. Optical density (OD) per mg (wet weight) of tissue (amphipods or macroalgae) as a function of the wavelength. Representative scans (250–750 nm) for (A) males and females of *A. valida* and for the two macroalgae (*U. rigida* and *P. columbina*) used as amphipod diet, collected from their natural environment and (B) males and females of *A. valida* at the end of the feeding experiments (C) Mean UVAC per mg (wet weight) in amphipod males and females, at the beginning (t_0) and at the end of the feeding experiments.

corresponding to these compounds. In the case of the macroalgae, a significant peak was detected in the UV region for *P. columbina*, while a small “shoulder” was detected for *U. rigida*. Both amphipods and macroalgae had peaks in the PAR range that correspond to chlorophyll and carotenoids. There were significant differences in the amount of UVAC that amphipods had in their bodies at the end of the experiments as compared to the amount that individuals brought from their natural environment, as seen from the peak analysis (Fig. 3B and C). Both males and females showed higher UVAC content when fed on Po diet (females: $F_{2,12} = 19.37$, $P < 0.0001$; males $F_{2,12} = 5.39$, $P < 0.05$) and on UI + Po diet (females: $F_{2,12} = 17.54$, $P < 0.0001$; males $F_{2,12} = 5.46$, $P < 0.05$) as compared to the ambient values (t_0 ; Fig. 3C). At the end of the experiment, the amount of UVAC in females fed on *P. columbina* were higher than at the beginning of the experiment by 200% and 117% in the PAB and P radiation treatments, respectively, while in females fed on UI + Po diet, the abundances of UVAC were also higher than at the beginning by 152% and 58% in PAB and in P, respectively. In contrast, the UVAC content in females fed on *U.*

rigida (UI diet) decreased as they lost 82% of the compounds that they brought from the environment ($F_{2,12} = 40.41$, $P < 0.001$; Fig. 3C). In the case of males, the content of UVAC in amphipods fed on *P. columbina* at the end of the experiment was 94% and 125% higher than the initial value in the PAB and P radiation treatments respectively, while in males fed on UI + Po diet, the content of UVAC was higher than at the beginning by 58% and 42% in PAB and P radiation treatments, respectively. As seen with females, males lost UVAC when fed on *U. rigida* (UI diet) by as much as 82% of the value at t_0 .

The changes of UVAC during the experiment, as a function of the different radiation and diet treatments, were also observed when the amounts of UVAC were normalized by the amounts of algae consumed during the feeding experiments (Fig. 4). The amount of UVAC decreased from the initial content in both males and females when fed with *U. rigida*, and this is why their values in Fig. 4 are negative. Significant differences between radiation ($F_{1,24} = 6.92$, $P < 0.05$) and also between diet treatments ($F_{2,24} = 71.13$, $P < 0.0001$) were observed for females (Fig. 4A). The content of UVAC in females fed with *P. columbina* or with a mixed diet was higher than the ones fed with *U. rigida* (LSD test, $P < 0.05$; Fig. 4A), and also higher in PAB than in P radiation treatment (LSD test, $P < 0.05$; Fig. 4A). We calculated the amount of UVAC incorporated by the females in relation to the UVAC content of the macroalgae and the amount of food ingested by the individuals, and we observed that in diets containing *P. columbina* (Po or UI + Po diets) females incorporated 19% and 11% of the total amount of compounds ingested, respectively.

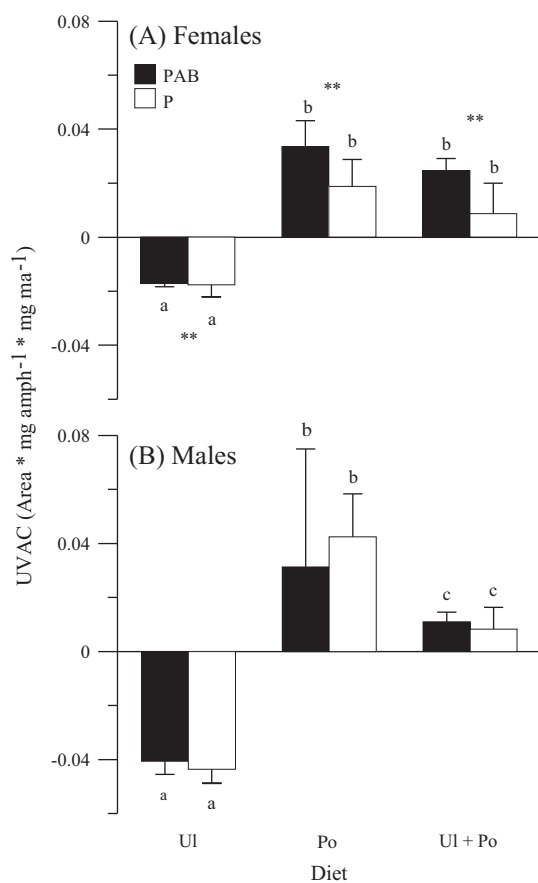


Fig. 4. Mean changes in the content of UVAC (area) per mg (wet weight) of amphipod and per mg (wet weight) of macroalgae ingested during the experiments, as a function of the radiation and diets received (A) by females and (B) males of *A. valida*. The vertical lines indicate the standard deviation, the different letters indicate significant differences between diet treatments, and the asterisks indicate significant differences between radiation treatments.

In the case of males (Fig. 4B), the amount of UVAC differed between diets ($F_{2,24} = 18.66$, $P < 0.001$), being higher in the Po diet followed by UI + Po and UI diets, respectively (LSD test, $P < 0.05$; Fig. 4B). Contrary to what was observed for females, no differences were found in UVAC content between radiation treatments ($F_{1,24} = 0.13$, $P > 0.05$). The amount of UVAC acquired by males, accounted for 24 and 3.7% of the amounts of UVAC ingested, for the Po and UI + Po diets, respectively.

3.4. Potential role of UVAC acquired through the diet

The effects of UVR on mortality of amphipod females are shown in Fig. 5. Mortality was higher in PAB than in P radiation treatment ($F_{1,24} = 8.04$, $P < 0.05$), evidencing a negative effect of the UVR on females of *A. valida*. Moreover, mortality in this sex differed between diets ($F_{2,24} = 15.76$, $P < 0.05$; Fig. 5). Higher mortality was observed in females fed on UI diet than in those fed on Po or on UI + Po diets (LSD test, $P < 0.05$; Fig. 5). The overall mean mortality of females due to PAR was 11%. In the case of *A. valida* males, there were no significant differences between the PAB and P radiation treatments ($F_{1,24} = 0.079$, $P > 0.05$), indicating that there were no mortality due to UVR. The overall mean mortality of males due to PAR was 14%; there were slight but significant differences among diets ($F_{2,24} = 15.37$, $P < 0.05$), with higher percentage of dead individuals in the UI and in the Po diets than in the mixed diet treatment.

4. Discussion

It is broadly accepted that high quality food enhance fitness and is selectively consumed by organisms when available (reviewed by [44,45]). Thus, herbivores can optimize their diet by preferential consumption of macroalgae of high nutritional quality (e.g., [46–48]). Previous studies suggested that in general, green macroalgae are of better quality as food source than red ones [49]. Nevertheless, we measured the C/N/P ratio in both macroalgae species used as food in our experiment and the ratios were 10.1/1.2/1 for *U. rigida* and 7/0.93/1 for *P. columbina*, indicating that *P. columbina* had slightly higher nutritional quality (i.e., more nitrogen and phosphorus per carbon unit) than *U. rigida*. Thus, the low FCR in amphipods, both males and females (Fig. 1), fed with UI diet could be not only related with the low amount of UVAC offered by this macroalgae, but also with their lower nutritional quality.

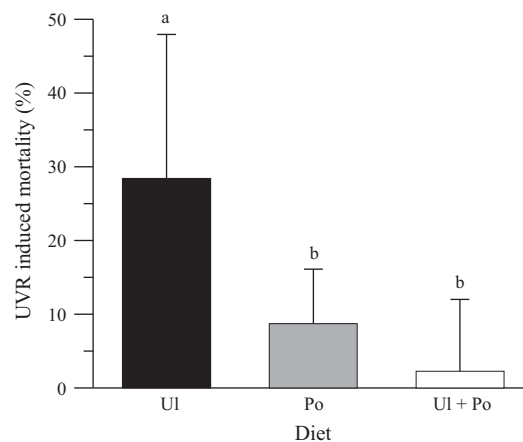


Fig. 5. Mean percentage of total UVR induced mortality of *A. valida* females, after being normalized by the mortality in the P radiation treatment. No data for males are shown because there was no mortality due to UVR for this sex. The vertical lines indicate the standard deviation and the different letters indicate differences between diet treatments.

Females had higher FCR when diets contained *P. columbina* (both Po and UI + Po diets), and preferred this macroalgae rather than *U. rigida*, when they were offered together. Although we could not separate if the preference for *P. columbina* was related to their higher nutritional quality, or to their higher UVAC content, or both of them, the benefit by selecting the red macroalgae would be greater than by selecting the green one, in terms of food quality and potential photoprotection. In the case of *A. valida* males the higher FCR in UI + Po diet (Fig. 2B), and the lack of preference for a particular macroalgae species (Fig. 3B) would indicate that males prefer mixed diets over single ones. Dietary mixing has been well documented for a variety of marine, freshwater, and terrestrial herbivores [50,36,51], as a way to obtain adequate nourishment from low quality, or nutritionally unbalanced food [36,45,52]. Positive effects of mixed diets on fitness associated variables had been observed in cladocerans [53], gastropods [54,36], fish [55], and insects [56].

The absorption characteristics of the macroalgae offered to the amphipods, agree with previous studies showing that Rhodophyceae species contain higher amounts of UVAC as compared to Chlorophyceae species [27,22,57]. In particular, studies conducted in the Patagonian coast, determined that *P. columbina* is one of the Rhodophyceae species with the highest amount of UVAC, with two mycosporine like amino acids being the responsible for the absorption characteristics of this species, Shinorine and Porphyra-334 [58]. In our study, the amount of UVAC found in *U. rigida* was almost depreciable as compared with the amount found in *P. columbina*. Thus, for amphipods inhabiting these intertidal areas, if UVAC has an effective photoprotective role, the food-type consumed would play a critical role in their survival, mainly during low tide of spring-summer seasons when organisms are exposed to high UVR levels.

Considering the ecological role of UVAC as photoprotective compounds, relatively few studies have focused on their transfer from primary producers and posterior bioaccumulation in higher trophic levels of the aquatic food web [59,60]. Moreover, that a diet is rich in UVAC does not necessarily mean that the UVAC will be accumulated by the grazer, and that these compounds will protect the individuals against UVR. In fact, most studies showed that the photoprotective capacity of these compounds is species-dependent [21–23]. If transfer and bioaccumulation of UVAC occur, it would be expected that the concentration in higher trophic levels would depend mostly on their diet as found, for example, in studies carried out with sea urchins [59], copepods [61,62], ciliates [63], and rotifers [64]. In this study, both males and females of *A. valida* collected from the field showed absorbance peaks in the range corresponding to UVAC, confirming the results obtained in previous studies, about the ability of *A. valida* to accumulate these compounds [22]. Nevertheless, due to the fact that amphipods can consume a range of plants, animals, and detrital foods in their natural environment [65,66], they may have acquired these compounds from various sources and, at this point, we cannot know whether the compounds derived from the macroalgae, or from other food source, or from both.

Females fed with diets containing *P. columbina* (Po or UI + Po diets), and exposed to PAB radiation treatment showed the highest levels of UVAC in their bodies. It is interesting, though, that this difference between radiation treatments was not observed in the FCR (Figs. 1 and 2). On the other hand, one can speculate about the potential increase of UVAC in *P. columbina* during the exposure to UVR, and thus resulting in higher content in the PAB radiation treatment. Nevertheless, previous studies performed with this macroalgae [58] demonstrated a high variability in the amount of UVAC during the day, but very little variation between samples exposed to PAB or P radiation treatment. Thus, the differential accumulation of UVAC between radiation treatments seems more related to a stimulation of *A. valida* females to accumulate UVAC

when exposed to UVR, a mechanisms that had been reported in other aquatic invertebrates like the freshwater copepod *Boeckella antiqua* [67,68], and the calanoid copepod *Leptodiaptomus minutus* [69]. For example, Hylander et al. [70] found that copepods can upregulate their UVAC content when UVR threat was increasing. If not, they instead compensated with higher carotenoid accumulation, being able to adjust the blend of different UVR protective compounds to optimize their defenses to the prevalent threats of UVR and predation.

A. valida males accumulated more UVAC in Po and UI + Po diets respectively than in UI diet, but contrary to what was observed for females, no differential accumulation of these compounds was observed between radiation treatments. The fact that only females accumulated higher amounts of UVAC when they were exposed to UVR could be a reproductive strategy to protect their progeny. Photoprotection of offspring had been observed in studies performed with several aquatic organisms, which in turn evidenced the positive effects of UVAC on different aspects of the fitness of the progeny [17,71,72]. For example, Adams and Shick [17] demonstrated that embryos of sea urchins with high amounts of UVAC were better protected from UVR damage than embryos in which the amounts of UVAC were lower. On the other hand, Wraith et al. [72] showed that the survivorship of the embryos of the intertidal gastropod *Bembicium nanum* was positively correlated with the amount of UVAC accumulated in their body.

Although it is well established that UVAC function as sunscreens protecting against damage from harmful levels of UVR [73,74,61], as we previously mentioned, the ultimate protection ability of these compounds is species-specific [24,75]. In the present study, even the UVR affected the mortality of females in all diet treatments, the highest mortality rates were registered in those individuals fed with poor-UVAC diet (UI diet), which seems to indicate that, in diets containing *P. columbina* (Po or UI + Po diets) UVAC did, in fact, protect females against UVR, but did not provide them a full photoprotection. In the case of males, UVR did not affect the mortality of individuals, even in those fed on UI diets, suggesting that males were more resistant than females to UVR, independently if they accumulate UVAC or not. Previous studies performed with *A. valida* evidenced that the presence of UVAC might represent an effective protection against high levels of UV-B, due to the fact that no significant UV-B-induced mortality was observed when the concentration of UVAC was high, but survival decreased significantly when the diet was poor in these compounds [22]. In contrast to the previous study, in our work the amphipods were exposed not only to UV-B if also to UV-A. Negative effects of solar UV-B radiation on bacterioplankton, phytoplankton and macrophytic algae, zooplankton, and ichthyoplankton have all been documented (see reviews by [76,77,6]), while the role of UV-A radiation is not as clearly defined, although it appears to be involved in the photorepair of UV-B-induced damage [78–80]. However, several studies have demonstrated its deleterious effects on aquatic organisms [13,81,82]. It has been observed that UV-A radiation inhibits photosynthesis in marine phytoplankton, and in freshwater algae [83,13], decrease the hatching success in cladocerans, as well as increase mortality in eggs of copepods and fish [81,84]. Thus, the difference between the full and partial protection observed in both studies performed with *A. valida* could be attributable to the effects of UV-A, evidencing their detrimental effects on this amphipod species.

This work provides evidences about the differential trophic response of males and females of *A. valida* to the combined effect of diet and solar UVR, as well as the role of UVAC in providing partial photoprotection against UVR, this latest for amphipod females. In intertidal areas dominated by macroalgae with low amount of UVAC, as in our study, dietary scarcity of UVAC could constrain this partial protection against UVR. Moreover, if individuals have

reduced mobility, the chance to make movements to find other type of food is scarce, and the situation is even more complicated. This would be the case of *A. valida*, which is considered a sedentary amphipod species, thus limiting their foraging range [85,86]. Nevertheless, for this epibenthic species, part of the protection could be achieved by avoiding UVR when hiding behind the macroalgae. Thus, the macroalgae taxonomic composition of the intertidal could have strong effects in the population dynamics of *A. valida*, particularly for females in which UVAC constitute an important source of photoprotection against UVR. This same scenario might also be applied to other sedentary organisms that inhabit the intertidal regions over the world.

5. Abbreviations

UVAC	UV-absorbing compounds
UVR	ultraviolet radiation
FCR	food consumption rates

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