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Evidence That Ultraviolet Radiation may Depress Short-Term Photosynthetic Rates of Intertidal *Ulva lactuca* and Consumption by a Generalist Feeder (*Clibanarius vittatus*)

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This article considers the impact of ultraviolet radiation (UVR) on the photosynthesis and consumption of intertidal *Ulva lactuca*, an important producer and food resource in many coastal ecosystems. Algal fragments were exposed in the laboratory to either UVR and PAR (photosynthetically active radiation) simultaneously or PAR alone. The rates of photosynthesis and consumption by a generalist feeder, the stripped hermit crab (*Clibanarius vittatus*), were then compared between the two treatments. In both experiments, the biological weighted values for UVR in the laboratory indicate that the experimental set-up provided a level of UVR exposure that would occur in the field. The results show that UVR exposure depresses the photosynthetic rates of *U. lactuca* at light intensities between 1118 and 2206 μmol m^{-2} s^{-1}. UVR also reduced the grazing intensity of *C. vittatus* on *U. lactuca* with non-UVR-exposed algal pieces supporting about five times more consumption than exposed pieces. The relevance and implications of this study, however, are limited because the results have been obtained with short-term, simple experiments. Studies encompassing a longer time scale and the community of consumers (e.g. exposing both the algae and main consumers simultaneously to experimental UVR levels) are needed to elucidate whether the algae can offset UVR-deleterious effects through the induction of protective compounds and how these compounds and UVR exposure affects the activity of consumers.

Due mainly to the anthropogenic emission of chlorofluorocarbon gases, levels of stratospheric ozone have been decreasing over the past 20 yr (Madronich et al., 1995; Wardle et al., 1997). Substantial reductions have been detected in the Antarctic and the Arctic (Fergusson and Wardle, 1998; Goutail et al., 1999) and all over the globe because ozone depletion on the poles entails a further thinning of the layer around the planet (Björn et al., 1998; Goutail et al., 1999). As a consequence, the intensity of ultraviolet radiation (UVR) reaching the biosphere has been increasing over the past two decades (Madronich et al., 1995; Wardle et al., 1997).

This increase in UVR has generated abundant research on its effects on diverse marine organisms and populations. Most studies have focused on water-column organisms, such as phytoplankton, zooplankton, and bacteria (Smith and Cullen, 1995; Booth et al., 1997; Häder, 1997), with fewer studies addressing impacts on benthic organisms. In particular, the influence of UVR on the trophic interactions between benthic macroalgae and consumers is little known because most articles addressing the impact of UVR on macroalgae have been mainly concerned with the physiological consequences for the algae (Karentz, 1999). In addition, the few reports investigating the UVR effects on the grazing of macroalgae are limited to brown and red species (Cronin and Hay, 1996; Deal and Hay, 1996; Pavia et al., 1997).

The green macroalga *Ulva lactuca* is a cosmopolitan species, and it often contributes significantly to the total primary production of shallow coastal ecosystems (Valiela et al., 1997). Moreover, its tissues have high nutrient concentrations and low concentrations of deterrent compounds when compared with most marine macrophytes (Watson and Norton, 1983), thereby rendering the alga palatable. In fact, numerous grazers, such as snails, amphipods, isopods, and juvenile fish, feed intensively on *U. lactuca* (Geertz-Hansen et al., 1993; Sfriso and Marcomini, 1997). In addition, *U. lactuca* frequently occurs in the intertidal, where substantial exposure to UVR can occur (e.g., Henley et al., 1992). Thus, the study of the effects of UVR on *U. lactuca* photosynthesis and consumption is important for understanding how UVR presently affects the secondary production and food-web structure of coastal ecosystems where *U. lactuca* is dominant and how it might affect these ecosystems in the future if UVR increases.

In this study, we present evidence that UVR may decrease both the short-term photosynthetic rates of intertidal *U. lactuca* and the in-

tensity of consumption by a generalist feeder, such as the striped hermit crab (*Clibanarius vittatus*). We have done this by exposing algal fragments simultaneously to both UVR and photosynthetically active radiation (PAR) or to PAR alone in the laboratory and comparing the rates of photosynthesis and consumption between the two treatments. Levels of PAR and UVR measured in the laboratory were similar to those measured in the field.

Materials and Methods

Thalli of *U. lactuca* were collected from the intertidal zone off boat ramps and jetties located at the eastern end of Dauphin Island, AL (30°15.02'N 88°04.76'W), in June 2000. They were immediately transported to the laboratory in coolers filled with water from the collection site (in situ water). In the laboratory, an experiment to examine the effect of UVR on short-term algal photosynthetic rates (photosynthesis experiment) and another to investigate the effects on algal consumption by *C. vittatus* (grazing experiment) were performed. All experiments started less than 1 hr after collection.

Photosynthesis experiment.—Fragments similar in size (ca. 0.5 cm^2) were gently sectioned from the thalli while submerged in the coolers. Four fragments were then transferred to a 10-ml vial filled with GF/C-filtered in situ seawater. To rule out any possible carbon limitation during photosynthesis, we added 0.04 g of sodium bicarbonate to the vial (Levavasseur et al., 1991). Subsequently, we exposed the algal fragments to each of the six levels of PAR (390, 755, 1,118, 1,481, 1,843, and 2,206 $\mu mol\ m^{-2}\ s^{-1}$) either without (control) or with (treatment) simultaneous exposure to 24.9 $W\ m^{-2}$ of UVR-A and 4.9 $W\ m^{-2}$ of UVR-B. The ordering of the six levels of PAR was random for each trial, and the irradiances encompassed the typical PAR range recorded at the intertidal collection site in June 2000. The experimental UVR levels applied also corresponded to the mean values recorded at the collection site in June 2000. We changed PAR by adjusting the distance between the vial and a 24-W General Electric (GE) halogen bulb. Four UVA-340 lamps (Q-Panel Lab Products, Cleveland, OH), which emit both UV-A (315–400 nm) and UV-B (280–315 nm) radiation, were used as the UVR source. Intensity of PAR was measured with an LI-192SA underwater quantum sensor attached to an LI-1000 data logger (LICOR, Lincoln, NE) and UV-A and UV-B irradiance with a hand-held PMA 2100 photometer coupled to a PMA 2110 UVR-A or a PMA 2106 UVR-B detector, respectively (Solar Light Co., Philadelphia, PA).

We measured the algal photosynthetic rate using a YSI oxygen meter specially adapted for small-volume samples (YSI-Model 5300 Biological Oxygen Monitor, YSI, Marion, MA). To do so, we secured the 10-ml vial with a ring clamp, sealed the oxygen probe, and measured the increase in oxygen concentration over a 3-min period under PAR or under PAR and UVR exposure after a period of acclimation to each new PAR level. Usually, the rate of oxygen production at the new PAR level became constant in less than 1 min. The photosynthetic rate at each PAR intensity was then calculated and expressed in micromoles of oxygen per gram fresh weight per minute. We replaced 75% of the water in the vial with fresh filtered water after each 3-min period to prevent oxygen saturation, and less than 5 min elapsed between each measurement of oxygen production. The ring clamp and attached vial were placed above a magnetic stirring table and the vial contents stirred throughout exposure to all PAR intensities. Moreover, water temperature in the vials was maintained close to the in situ value (25 C) throughout the experiment. After exposing the vial to all PAR intensities either without or with exposure to UVR, the algal fragments were removed from the vial and pressed firmly between folded paper towels, and the fresh weight (FW) was measured. In addition, we ran a number of blanks (vials containing no algae) and did not observe any measurable change in oxygen concentration in the absence of algal fragments. For each PAR intensity, we ran a total of eight control replicates (exposed only to PAR) and eight treatment replicates (exposed to both PAR and UVR).

To ensure that the UV irradiance in our laboratory experiments was similar to the UV irradiance of sunlight at our algal collection site, we compared the spectral irradiance of our UVR light source with the spectral UV irradiance of sunlight. We obtained the spectral irradiance of the UVA-340 lamps directly from Q-Panel Lab Products, and we modeled the spectral irradiance of sunlight at our collection site on 15 June 2000 at solar noon using the software STARsci version 2.1/2001 (Ruggaber et al., 1994). These spectra, along with scaling coefficients from the literature, were then used to calculate biologically weighted measures of UV irradiance for our laboratory experiments and the sunlight model. To account for attenuation by the vial during the photosynthesis experiment, a Spectronic Genesys2 UV/VIS spec-

trophotometer (Thermo Spectronic, Rochester, NY) was used to determine the amount of light passing through one side of the vial at each wavelength. This was accomplished by placing a piece from the side of the vial across the light path of the spectrophotometer and by measuring the percent transmittance at each wavelength from 200 to 400 nm. These percent transmittance data were then multiplied by the irradiance emitted at each wavelength by our UVR source to calculate the UV irradiance that was reaching the center of the vial at each wavelength. This measure of irradiance was then used when calculating the biologically weighted measures of UV irradiance for the photosynthesis experiment. In the grazing experiment, the algae had only a thin layer of water separating them from the UVR source, so it was not necessary to make a similar adjustment when calculating the biologically weighted UV irradiances for the grazing experiment.

Grazing experiment.—Thalli of *U. lactuca* were transferred to two tanks filled with GF/C-filtered in situ water. Using the same light sources as in the photosynthesis experiment, we exposed one tank to 1,500 μmol m^{-2} s^{-1} PAR, 24.9 W m^{-2} UVR-A, and 4.9 W m^{-2} UVR-B for 4 hr and the other tank to only 1,500 μmol m^{-2} s^{-1} PAR for the same period of time. Both tanks were aerated and kept at in situ temperature and salinity for 4 hr. Subsequently, the thalli were sectioned into smaller pieces of similar size (ca. 5 cm^2), pressed firmly between folded paper towels, and weighed to the nearest 10^{-4} g. A small portion of each piece was then sandwiched between two glass slides, the edges of the slides wrapped with parafilm, and the pieces introduced into a 40-liter aquaria filled with seawater. This approach helped keep the pieces at the bottom of the aquaria floating upright throughout the duration of the experiment. Three UVR-exposed and three non–UVR-exposed pieces were randomly located in each aquarium.

Hermit crabs of similar size were collected at the docks 1 d before the grazing experiment. The crabs were starved for 24 hr in tanks filled with filtered in situ water and maintained at in situ temperature. One crab was introduced into each of 32 aquaria immediately after the algal pieces, whereas 22 aquaria were left with no crab to serve as controls. The crabs were then allowed to feed for 24 hr under 16 hr of 20 μmol m^{-2} s^{-1} PAR and 8 hr of darkness. The water also was bubbled with air to ensure mixing and to prevent hypoxia. In situ temperature and salinity conditions were maintained throughout the 24-hr grazing experiment.

After 24 hr, the algal pieces were removed from the aquaria, pressed firmly between folded paper towels, and weighed again. To standardize the variability in the initial weight of the algal pieces in each aquarium, we calculated the total percent weight change for the non–UVR-exposed or UVR-exposed pieces by dividing the difference between the sum of the final weights and the sum of the initial weights by the sum of the initial weights of the three non–UVR-exposed or UVR-exposed pieces, respectively, and by multiplying the quotient by 100 (Eq. 1).

$$\left[\frac{\Sigma(\text{final weights}) - \Sigma(\text{initial weights})}{\Sigma(\text{initial weights})}\right] \times 100 = \text{total \% weight change} \quad (1)$$

Finally, we derived grazing intensity on non–UVR-exposed or UVR-exposed *U. lactuca* as the difference between the average total percent weight change in the control (nongrazing) aquaria and the average total percent weight change in the grazing aquaria for the non–UVR-exposed or UVR-exposed algal pieces, respectively (Eq. 2).

$$\text{average total \% weight change (nongrazing aquaria)} - \text{average total \% weight change (grazing aquaria)} = \text{grazing intensity} \quad (2)$$

Results and Discussion

The spectral irradiances of our laboratory UVR source and sunlight model were similar in the UVR-B and for the shorter wavelengths of UVR-A but differed for the longer wavelengths of UVR-A, with considerably less irradiance generated in the laboratory (Fig. 1). However, relatively longer-wavelength UV-A radiation often has low biological activity when compared with shorter-wavelength and highly effective UV-B radiation (Cullen and Neale, 1994; Neale, 2000). Biological weighting functions take into account this change in effectiveness with wavelength and make it possible to quantitatively compare two different UVR sources (Cullen and Neale, 1994; Neale, 2000). A search of the literature found no published biological weighting functions for *Ulva* sp. or macroalgal photosynthesis, so we chose to use

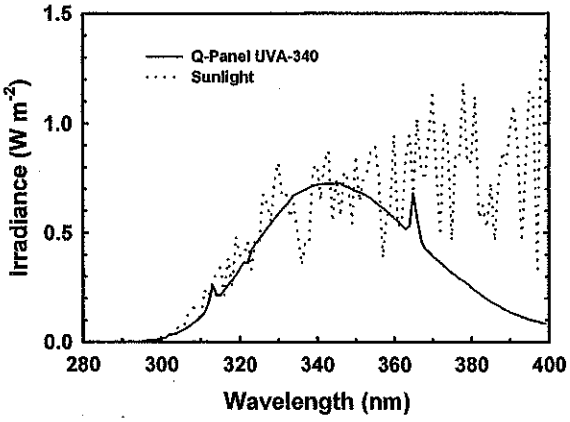

Fig. 1. Ultraviolet radiation irradiance (280–400 nm) in the laboratory UVR treatment (Q-Panel UVA-340) and sunlight at the algal collection site on 15 June 2000 at solar noon (18:00 UTC) modeled using the software STARsci version 2.1/2001 (Ruggaber et al., 1994) [Model parameters: uv-1nm.wvl (wavelength field), 30° latitude, 272° longitude, const3.alb(spectral albedo), 0.0 km above sea level, summer.o3 (O_3 profile), 300 DU (O_3 amount), no SO_2, no NO_2, 1015.0 hPa (pressure at ground), summer temperature (temperature profile), summer humidity (relative humidity profile), 0.38 (aerosol optical depth at 550 nm), background (stratospheric conditions), depth 3.0 km (boundary layer), maritime clean (aerosol type), no clouds, slit function gaussian 1.0 nm FWHM (site and instrument properties)].

biological weighting functions derived from work on phytoplankton photosynthesis. Although the nonweighted UV irradiances of our laboratory experiments and sunlight model differ substantially, when these irradiances are biologically weighted the differences between the photosynthesis experiment and the sunlight model are generally less than 40% and the differences between the grazing experiment and the sunlight model are generally less then 30% (Table 1). The differences between the two experiments are due to the attenuation of light by the vial, which held the algae during the photosynthesis experiment. In both experiments, the biological weighted values are not unreasonable for *U. lactuca* that is partially submerged or exposed at times other than the solar noon time. Overall, our laboratory UVR source and the experimental conditions likely provide a level of UVR exposure that occurs in the field.

The UV irradiance for sunlight on June 15 at solar noon with no cloud cover (our sunlight model) likely reflects the upper extreme of UVR exposure at our collection site. A solar position other than solar noon, cloud cover, or increasing algal submergence would reduce the amount of UV irradiance reaching the *U. lactuca* growing at the collection site. It is important to note that the sum of the UVR-A (24.9 W m^{-2}) and UVR-B (4.9 W m^{-2}) values measured for the laboratory treatment using the PMA 2100 photometer is less then the nonweighted value of 39.138 W m^{-2} calculated from the data provided by Q-Panel Lab Products for the grazing experiment. This difference is likely because of the range of our UVR-A and UVR-B detectors. The detectors are non-

TABLE 1. Nonweighted (W m^{-2}) and biologically weighted UV (280–400 nm) irradiance (unitless) for the laboratory UV treatment (Q-Panel UVA-340) during the photosynthesis and grazing experiments and natural sunlight at solar noon (18:00 coordinated universal time) on 15 June 2000, with no cloud cover derived from the model STARsci version 2.1/2001 (Ruggaber et al., 1994) (see Fig. 1 for model parameters). Values in parentheses are the percentage of weighted UVR irradiance produced by the Q-Panel UVA-340 lamps relative to the sunlight model.

Weighting function	Q-Panel UVA-340		Sunlight
	Photosynthesis experiment	Grazing experiment	
Nonweighted UVR	35.007 (55.2%)	39.138 (61.7%)	63.429
Photoinhibition (*Pocillipora damicornis*)[a]	1.981 (63.7%)	2.276 (73.1%)	3.112
Photoinhibition[b]			
Phaeodactylum sp. (marine diatom)	1.137 (71.3%)	1.314 (82.4%)	1.594
Prorocentrum micans (dinoflagellate)	1.072 (76.3%)	1.260 (89.7%)	1.405
Inhibition of primary production (phytoplankton in southern ocean)[c]	4.519 (69.2%)	5.655 (86.7%)	6.526
Photoinhibition (phytoplankton in subarctic oligotrophic lake)[d]	7.340 (66.6%)	8.253 (74.9%)	11.017

[a] Lesser and Lewis (1996).
[b] Cullen et al. (1992).
[c] Boucher and Prézelin (1996).
[d] Milot-Roy and Vincent (1994).

weighted and do not detect irradiance equally across their range. The UVR-A detector has a peak absorbance at 365 nm and detects 80% or more of the UVR at each wavelength between 340 and 385 nm, whereas the UVR-B detector has a peak absorbance at 312 nm and detects 80% or more of the UVR at each wavelength between 291 and 324 nm. As a result, these broadband sensors tend to underestimate irradiance. However, using the spectral response of each detector and the spectral irradiance of the UVR source, it is possible to predict the UVR-A and UVR-B levels that should be measured by the detectors (Neale et al., 2001). The predicted UVR-A (25.9 W m^{-2}) and UVR-B (5.3 W m^{-2}) values are similar to the actual UVR-A and UVR-B values measured by the detectors, 24.9 and 4.9 W m^{-2}, respectively, indicating that the UVR source was emitting an irradiance spectrum similar to the spectrum described by the manufacturer and plotted in Figure 1.

Although UV irradiance in the laboratory resembles what *U. lactuca* encounters in the field, our experimental PAR source and the ratio of UVR to PAR differs to some extent from natural sunlight. Irradiation from halogen bulbs, similar to our 24 W GE halogen bulb, is comparable to that of sunlight at wavelengths between 590 and 750 nm (yellow to red). However, these bulbs generate less irradiance from 400 to 500 nm (violet to blue). This difference is potentially important because some plants can moderate and even eliminate damage by UVR-B when PAR levels are above a certain threshold (Teramura et al., 1980; Warner and Caldwell, 1983; Caldwell et al., 1994). Yet, although our laboratory PAR source may have slightly less photosynthetically usable radiation (PUR) when compared with sunlight, UVR repair and UVR protection mechanisms that require PUR tend to act over time scales considerably longer than our short-term assessment of photosynthesis. For example, the accumulation of UVR-absorbing compounds such as mycosporine-like amino acids often occurs over days rather than minutes or hours (Helbling et al., 1996; Reigger and Robinson, 1997; Pérez-Rodríduez et al., 1998; Franklin et al., 2001). Photoreactivation, which can act over shorter time scales, may be the exception (Pakker et al., 2000), but it acts to repair deoxyribonucleic acid damage and not damage to photosynthetic pathways. Therefore, even if photosynthetic activity would have been higher with a PAR source whose spectra was closer to sunlight, it is unlikely that the short-term effects of UVR we observed on photosynthetic activity would have been substantially different. The ratio of UVR to PAR is a different subject and merits further discussion. Because our experimental design varied PAR while keeping UVR constant and at a level comparable to the UVR in full sunlight (PAR > 2,000 μmol m^{-2} s^{-1}), the ratio of UVR to PAR at the lower PAR intensities is not natural. Fiscus and Booker (1995) have pointed out the dangers of such an approach, which tends to overestimate the effectiveness of the UVR. As a result, we have chosen to restrict our analysis and discussion of the photosynthesis experiment to those intensities where the ratio of UVR to PAR is closer to the ratio in sunlight (PAR > 1,100 μmol m^{-2} s^{-1}).

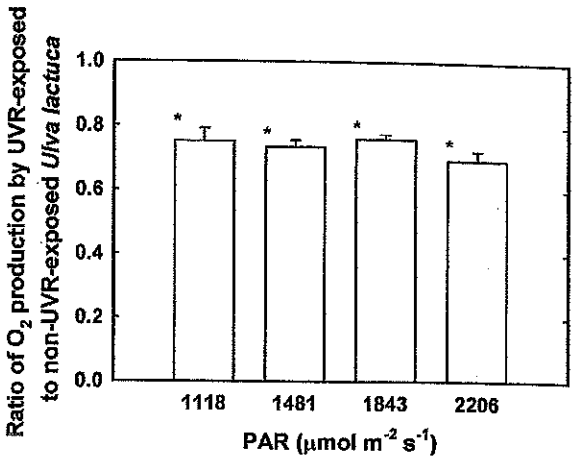

Fig. 2. The ratio of photosynthetic oxygen production by UVR-exposed *Ulva lactuca* to that by non–UVR-exposed *U. lactuca* at four PAR intensities. Bars are mean ± standard error and "*" indicates a mean significantly different than 1 (one-sample t-test, $P < 0.001$).

To best represent the effect of UVR on algal photosynthetic rates, we calculated the ratio between the average rate of UVR-exposed fragments and that of non–UVR-exposed fragments for each PAR intensity examined (Fig. 2). The results show that UVR exposure depresses the photosynthetic rates of *U. lactuca* at the light intensities between 1,118 and 2,206 μmol m^{-2} s^{-1}. At these four light intensities, the ratio of oxygen production by UVR-exposed to non–UVR-exposed fragments is significantly less than one (one-sample t-test, $P < 0.001$). The ratios vary little over the range of light intensities, with the highest ratio (0.76 ± 0.02) found at 1,843 μmol m^{-2} s^{-1} and the lowest (0.69 ± 0.03) at 2,206 μmol m^{-2} s^{-1}.

Because intertidal populations of *U. lactuca* in the northern Gulf of Mexico are often ex-

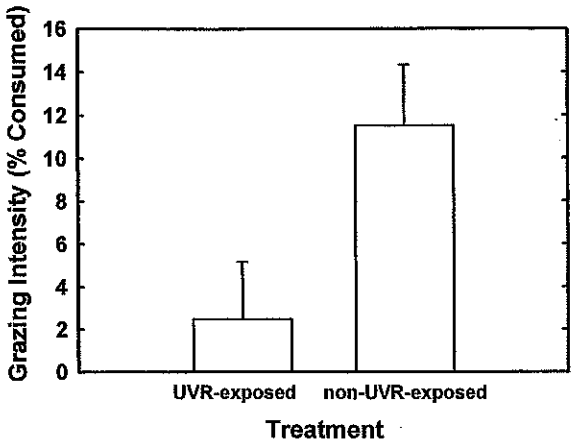

Fig. 3. Average grazing intensity of *Clibanarius vittatus* on UVR-exposed and non–UVR-exposed *Ulva lactuca*. Bars represent standard error calculated with techniques of error propagation (Tsokos, 1972).

posed to PAR intensities higher than 1,000 μmol m^{-2} s^{-1} (Lartigue, unpubl. data), our findings suggest that UVR may be a significant depressor of short-term photosynthetic oxygen production in those populations. However, there is evidence that some species of the genus *Ulva* may synthesize UVR-absorbing compounds and offset detrimental physiological effects imposed by the radiation. For instance, Altamirano et al. (2000b), working with an intertidal population of *U. rigida*, found that pigment content (chlorophyll *a* and *b* and carotenoids) increased after exposure to UVR, suggesting an efficient protective pigment mechanism. Altamirano et al. (2000b) also found that the initial negative effect of UVR on algal growth disappeared after 20 d of exposure. Gómez et al. (1998) found further evidence of a possible photoprotective mechanism in another species of green algae, *Dasycladus vermicularis*. Whether intertidal *U. lactuca* is capable of a similar response is not known. Further studies are needed to establish the overall significance of UVR effects on the physiology and growth of intertidal *U. lactuca*.

Ultraviolet radiation also reduced the grazing intensity of *C. vittatus* on *U. lactuca*. On average, non–UVR-exposed algal pieces supported about five times more consumption than did exposed pieces, despite substantial within-treatment variability (Fig. 3, two-sample t-test, $P < 0.01$). This result contrasts with the few reports that have addressed UVR effects on macroalgae–grazer interactions. Cronin and Hay (1996) and Deal and Hay (1996) found that exposure to UVR may reduce the levels of chemical defense in the algae *Dictyota ciliolata* and *Fucus vesiculosus*, which, in turn, may enhance their susceptibility to herbivores. Meanwhile, Pavia et al. (1997) showed that in the tissues of *Ascophyllum nodosum*, increased UV irradiance promoted the concentration of phlorotannins, a group of structurally related compounds, some of which can function as herbivore deterrents. However, the specific phlorotannins that were concentrated in the tissues of *A. nodosum* did not decrease algal palatability for the isopod *Idotea granulose* (Pavia et al., 1997). Unfortunately, we did not make any effort to measure the palatability (i.e., concentration of nutrients and deterrent compounds) of our control and UVR-exposed *U. lactuca*. Hence, our interpretation of the reduced grazing observed on the exposed thalli can only be speculative, and we point to some possibilities below. At any rate, the little information so far available shows that the impact of UVR on macroalgal consumption by grazers can differ widely, depending on the type of algae and the type of grazer (i.e., generalist or specialist feeder).

One possible explanation for the depressed grazing observed on our UVR-exposed *U. lactuca* is the induction of UVR-absorbing compounds, which also happen to decrease the palatability of the algae. However, neither did we test for the induction of UVR-absorbing compounds in this study nor were we able to find any examples of UVR-absorbing compounds deterring the consumption of *U. lactuca* in the literature. Another possibility is that the lower photosynthetic rates of the exposed thalli may have contributed to these differences. Depressing photosynthesis may reduce the synthesis of low–molecular weight carbohydrates and amino acids (Lobban and Harrison, 1994) and thus reduce algal palatability. In addition, it has been shown that UVR can depress ammonium and nitrate uptake and the activity of the enzyme nitrate reductase (a key enzyme involved in nitrate assimilation) in some brown and red algal species (Döhler et al., 1995; Flores-Moya et al., 1998). In turn, this depression may ultimately reduce algal palatability because nitrate uptake and nitrate reduction can be important controls of nitrogen assimilation and hence nitrogen content (Lobban and Harrison, 1994). Accordingly, Altamirano et al. (2000a) found that in *U. olivascens* 78% and 79% of the variability in tissue carbon and nitrogen, respectively, could be explained by the level of incident UV-B radiation, with high levels of UVR-B coinciding with low levels of tissue carbon and nitrogen.

To our knowledge, this study is the first to consider the impact of UVR on both the pho-

tosynthesis and consumption of intertidal *U. lactuca*, an important producer and food resource in many coastal ecosystems. We present evidence that UVR may depress short-term photosynthetic rates and consumption by a generalist feeder. The relevance and implications of this study, however, are limited because the results have been obtained with short-term, simple experiments. Studies encompassing a longer time scale and the community of consumers (e.g., exposing both the algae and main consumers simultaneously to experimental UVR levels) are needed to elucidate whether the algae can offset UVR-deleterious effects through the induction of protective compounds and how these compounds and UVR exposure affect the activity of consumers. In any case, we believe that this article provides significant background data that should stimulate more thorough research on long-term, community-integrated UVR effects on the productivity and trophic dynamics of intertidal populations of *U. lactuca* and other coastal macroalgal stands.

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