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Effects of UV radiation and temperature on growth of germlings of three species of *Fucus* (Phaeophyceae)

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Abstract

Measurements of relative growth rates (RGR) of germlings of three species of *Fucus* (Fucales, Phaeophyceae) collected in Helgoland (North Sea, Germany) were carried out in the laboratory in order to determine the effects of different ultraviolet radiation (UVR, $\lambda = 280$–400 nm) conditions, UVR doses and temperatures. High ultraviolet-B radiation (UVBR, $\lambda = 280$–315 nm) levels and low temperature, as independent factors, led to a species-specific reduction in RGR which appears to be related to the vertical distribution of the species in the intertidal zone. The inhibition of RGR ranged from 10% to even death of the germling. For the most sensitive species, high temperature in combination with a high dose of UVBR caused the death of the germlings, whereas at low temperature germlings were able to survive. This suggest growth-related temperature dependence of sensitivity to UVBR.

Keywords: *Fucus*; Germling; Growth; Temperature; Ultraviolet radiation

1. Introduction

Stratospheric ozone depletion, which is now a problem not only in the Antarctic atmosphere (Chubachi, 1985) but also in the Northern Hemisphere (Pearce, 1996), causes an increase of ultraviolet-B radiation (UVBR) reaching the earth's surface (Seckmeyer and McKenzie, 1992). Effort has recently focused on understanding the role of current ultraviolet

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radiation (UVR) on marine primary producers, with studies on macroalgae concentrated on effects on photosynthesis, photosynthetic pigment concentrations, growth and DNA (Dring et al., 1996a,b; Altamirano et al., 2000a,b; Wiencke et al., 2000).

A principal feature of intertidal macroalgal vegetation on rocky shores is readily apparent: distinct bands of particular species or associations run parallel to the shoreline. It has been supposed that this distribution pattern reflects the capacity to withstand the physiological stresses associated with emersion at the upper limits (Lüning, 1990). Significantly, it has recently been demonstrated that the upper limits of the zonation patterns of large sublittoral kelps (*Laminaria*, *Alaria*, *Saccorhiza* and *Phyllariopsis*) from the Arctic and the Straits of Gibraltar are correlated with underwater UVR levels that could affect the survival of the single- and few-celled stages of their life histories (Wiencke et al., 2000). As UVR daily doses in the intertidal system are much higher than in the sublittoral zone, the possible relationship between UVR tolerance and vertical distribution of intertidal macroalgae remains as an important matter to be investigated.

Most of the studies designed to address the relationship between zonation patterns and their possible causes have focused on the adult stages in the life history of macroalgae (Schonbeck and Norton, 1980). However, considering the smaller size and greater structural simplicity of microscopic (single- and few-celled) stages, any kind of stress that affect the biology of any species may exert more evident effects on these stages that are more sensitive (Yakovleva et al., 1998; Wiencke et al., 2000). Hence that for prediction studies of environmental stress factors such as UVR, the knowledge of the sensitivity of these ontogenetic stages is crucial, since recruitment of the species depend on the survival of these stages, and conclusions obtained with macroscopic stages should not be extrapolated to microscopic ones.

Another important ecological factor for seaweeds is temperature as it controls survival, reproduction, growth and geographical distribution (Lobban and Harrison, 1994). Therefore the study of combined temperature and UVR effects might be of much interest related to possible effects of climate change (Shindell et al., 1998).

The present study examines the consequences of long-term UVR exposures, and the interactive effects with temperature, on growth and survival of germlings of three different species of *Fucus* that occupy different levels in the intertidal zone at Helgoland, Germany. Ultraviolet radiation doses and temperatures within the natural ranges (Dring et al., 2001) were tested in order to obtain the most realistic assessment of effects on growth, although natural UVA:PAR and UVB:PAR ratios were not used. Our results support the hypothesis that UVR-tolerance of germlings could determine the vertical distribution of adult plants.

2. Materials and methods

2.1. Plant material and sampling site

Fertile receptacles of *F. spiralis* (eulittoral), *F. vesiculosus* (eulittoral-high sublittoral) and *F. serratus* (high sublittoral) were collected during low tide in December 1998 at the intertidal zone of Helgoland, North Sea, Germany (54°11′N 07°53′E). Only receptacles from plants which could be assigned unequivocally to a specific taxon were used as a source

of gametes or zygotes for experiments. Samples for an individual species were collected from the same shore height. Samples were taken to the laboratory inside plastic bags in an ice-chest and kept in darkness.

2.2. Release of gametes and isolation of zygotes

Receptacles were washed in cold seawater and wiped with paper towels to eliminate gross contaminants and previously-discharged gametes and zygotes. The protocol from McLachlan et al. (1971) was followed for the release of gametes and zygotes. Clean receptacles were placed on dry tissue at room temperature (18 °C, 30–45 min) in order to eliminate surface water. Partially dehydrated receptacles were placed well separated inside dry glass covered Petri dishes (20 cm diameter). They were kept inside a culture chamber at 8 °C and darkness until the release of gametes and zygotes from conceptacles was observed (8–12 h). After that, receptacles were put inside 8 cm diameter glass Petri dishes, covered with cold sterile seawater and kept inside a culture chamber at 8 °C and darkness. In less than 1 h gametes and zygotes were completely released from conceptacles and sank to the bottom of the Petri dish, where they could easily be isolated with a Pasteur pipette. Most of the medium, which by this time contained conspicuous mucilage, was decanted and replaced by cold sterile seawater and swirled vigorously. The gametes and zygotes were allowed to settle and the previous procedure repeated several times. In dioecious species (*F. vesiculosus* and *F. serratus*) fertilization was forced by pippeting a suspension of antherozoids into a suspension of female gametes (McLachlan et al., 1971). A sufficient quantity of synchronous zygotes was obtained in order to establish unialgal cultures of each of the three species. Approximately 100 zygotes of each species were cultured in separate 5 cm diameter Petri dishes with 12 ml sterile natural seawater.

2.3. Experimental design

For each species twelve different treatments were tested, to provide a combination of two culture temperatures, three UVR conditions and two UVR daily doses. Under each treatment, three Petri dishes of each species were incubated.

Two plastic trays (200 × 50 cm) were filled with circulating filtered seawater, with one held at 8 °C and the other at 16 °C. In both trays uncovered Petri dishes with zygotes were immersed 1 cm beneath the surface. The medium was renewed once a week.

For the different UVR conditions three UVA-340 lamps (Q-Panel Co., Cleveland, Ohio, US) were used as source of UVAR and UVBR, and four Duro-Test (Truelite II, Ohio, US) were used as source of PAR. These lamps were set alternately at 10 cm height above the water surface of each tray, supplying 150 μmol m^{-2} s^{-1} PAR, 17.0 W m^{-2} UVAR and 0.8 W m^{-2} UVBR, measured with a LI-1800 UW spectroradiometer. In order to obtain three different UVR conditions, three kinds of blocking filters were placed in each tray, and submerged at the top of the Petri dishes: two types of Ultraphan filters (Digefra GmbH, Munich, Germany) with transmission at $\lambda > 395$ nm and $\lambda > 295$ nm for the PAR only (P) and PAR + UVAR + UVBR (PAB) conditions, respectively; a Folex filter (Folex GmbH, Dreieich, Germany) with transmission at $\lambda > 320$ nm was used for the PAR + UVAR (PA) treatment. The transmission spectra of the blocking filters were shown in Figueroa et al. (1997).

Two different daily unweighted UVR doses were obtained changing the time of daily exposure. Germlings under low dose (LD) condition were exposed daily to 4 h less of UVR than those under the high dose (HD) condition; for this purpose, every day, 4 h before UVR lamps were switched off, Petri dishes of LD treatment were covered with an extra Ultraphan 395 filter, which was removed at the end of the daily UVR treatment. The HD condition consisted of 12 h of UVR daily whereas the LD condition was 8 h of UVR daily, yielding a difference of 33% between the doses related to both UVAR and UVBR. Duro-Test lamps were switched on for 14 h daily and, due to their relatively low irradiance it was not possible to keep the natural UVAR:PAR and UVBR:PAR ratios.

The spectral irradiances under each treatment were measured with a LI-1800UW spectroradiometer. In order to estimate the wavelength-dependent effectiveness of the UV-irradiances applied in each treatment (biologically effective dose, BED), spectral irradiances in the range 300–400 nm were weighted using an effective biological spectrum for inhibition of photosynthesis in the diatom *Phaeodactylum* (Cullen et al., 1992). The biologically effective spectral irradiance (BESI) was calculated according to Madronich and Flocke (1997), as follows:

$$\mathrm{BESI} = \int_{300\,\mathrm{nm}}^{400\,\mathrm{nm}} I(\lambda)\,\varepsilon(\lambda)\,\mathrm{d}\lambda$$

where $I(\lambda)$ and $\varepsilon(\lambda)$ are the spectral irradiance and biological response at λ nm, respectively. Time integration (from initial, t_0 to final t_f, the time period of exposure) of this quantity gives the BED:

$$\mathrm{BED} = \int_{t_0}^{t_f} \int_{300\,\mathrm{nm}}^{400\,\mathrm{nm}} I(\lambda)\,\varepsilon(\lambda)\,\mathrm{d}\lambda\,\mathrm{d}t$$

Both daily unweighted doses and daily BEDs are compiled in Table 1. Weighting of irradiances in the range 280–300 nm could not be done due to limitation of the spectroradiometer, so BED are underestimated. In each species estimated BED causing 50% inhibition of growth were calculated by regression analysis of the dose-response data using weighted irradiances.

Table 1
Daily unweighted doses (kJ m^{-2}) of PAR, UVA and UVB radiation, and daily biologically effective dose (BED: kJ m^{-2}: Cullen et al., 1992), under each light treatment

Dose	PAB/HD	PAB/LD	PA/HD	PA/LD	P/HD	P/LD
Unweighted dose						
PAR	1276.0	1162.8	1221.6	1118.9	1257.4	1126.5
UVAR	656.1	445.5	521.1	351.1	15.4	11.7
UVBR	26.9	18.2	0.7	0.5	0.4	0.3
BED						
Cullen et al., 1992	24.3	16.4	13.8	9.3	0.4	0.3

PAB: PAR + UVAR + UVBR: PA: PAR + UVAR: P: PAR: HD: high dose of UVR: LD: low dose of UVR.

2.4. Growth measurements

The relative growth rate ((RGR) of germlings of *Fucus* was estimated from changes in length of the major axis of the germlings without taking into account the length of primary and secondary rhizoids, or apical hairs. Relative growth rate was estimated from the following equation:

$$\mathrm{RGR(\%per\ day)} = 100 \times (\ln L_f - \ln L_0) \times t^{-1}$$

where L_0 is the initial diameter of the zygote (57 μm for *F. spiralis* and *F. serratus* and 67 μm for *F. vesiculosus*), and L_f is the length after 7 and 14 days of incubation under the different treatments. Length of germlings was measured with an ocular micrometer of an inverted microscope (Leitz Labovert, Germany). From each of the three Petri dishes incubated under each treatment, ten germlings were randomly chosen and measured, and the Petri dishes were immediately returned to the cultures.

2.5. Statistical analysis

The RGR data were compared by a three-way (temperature, UVR condition and UVR dose) model I ANOVA. The arcsine transformation was applied to the RGR percentages. Homocedasticity was checked by the $F_{\max}$-test. The least significant distance (L.S.D.) test was applied to separate the means when significance was found. For UVR condition to maintain the overall experiment wise error rate ($P < 0.05$) each comparison was tested using a lower comparison wise error rate calculated by Bonferroni method: $P < 0.017$. In all the cases the mean RGR value of each Petri dish was considered as a replicate, so for each treatment and species the number of replicates was three. All the statistical tests were performed in accordance with Sokal and Rohlf (1995).

3. Results

In general for the three species, the effects of the three independent factors (UVR condition, dose and temperature) on growth of germlings were similar, although with quantitative species-specific differences (Table 2). All factors tested as well as most of their interactions were significant. After 7 days, temperature generally explained most of the variance (Table 2), but in *F. serratus* UVR condition also explained much (≈40 %). After 14 days, the contribution of UVR condition to total variance had increased substantially. Overall, growth was always higher at the low dose of UVR and at the higher temperature (Table 2). Related to the UVR condition, the highest RGR values were always measured when all UVR was depleted, followed by the treatment with UVAR but without UVBR (PA) (Figs. 1–3). The lowest RGR values were always recorded in the presence of UVBR (PAB treatment). Susceptibility of germlings to UVBR differed among species. After 14 days under PAB condition, the decrease in RGR of germlings of *F. spiralis* was never higher than 43%, whereas that of *F. vesiculosus* reached nearly 90%, and in *F. serratus* the presence of UVBR meant the death of the germlings (Figs. 1–3). Those germlings incubated under the HD condition of UVR in each temperature showed significantly lower RGR than those

Table 2
Three-way (UVR condition, UVR dose and temperature) model I ANOVA for RGR (% per day) after arcsine transformation, of *F. spiralis*, *F. vesiculosus* and *F. serratus* after 7 and 14 days of incubation under the different treatments

	F. spiralis			*F. vesiculosus*			*F. serratus*		
	d.f.	% SS	*P*	d.f.	% SS	*P*	d.f.	% SS	*P*
7 day									
UVR	2	4.0	<0.0001*	2	6.1	<0.0001*	2	38.5	<0.0001*
	L.S.D.: P > PA >PAB			L.S.D.: P > PA >PAB			L.S.D.: P > PA > PAB		
Dose	1	3.4	<0.0001*	1	3.2	<0.0001*	1	1.6	<0.0001*
T	1	90.7	<0.0001*	1	88.3	<0.0001*	1	42.5	<0.0001*
UVR × dose	2	0.8	<0.0001*	2	0.2	0.0837ns	2	2.1	<0.0001*
UVR × T	2	0.3	0.0023*	2	0.1	0.5171ns	2	13.0	<0.0001*
Dose × *T*	1	0.1	0.0325*	1	0.4	0.0043*	1	0.4	0.0099*
UVR × dose × T	2	0.3	0.0011*	2	0.6	0.0027*	2	0.7	0.0067*
Error	24	0.4		24	1.0		24	1.3	
14 day									
UVR	2	31.9	<0.0001*	2	26.7	<0.0001*	2	80.8	<0.0001*
	L.S.D.: P > PA >PAB			L.S.D.: P > PA >PAB			L.S.D.: P > PA > PAB		
Dose	1	1.8	<0.0001*	1	0.2	<0.0001*	1	4.1	<0.0001*
T	1	61.7	<0.0001*	1	63.7	<0.0001*	1	0.4	<0.0001*
UVR × dose	2	1.3	<0.0001*	2	2.0	0.0007*	2	1.2	<0.0001*
UVR × T	2	0.2	0.1985ns	2	0.9	0.0211*	2	8.8	<0.0001*
Dose × T	1	1.0	<0.0001*	1	0.0	0.7172ns	1	0.6	<0.0001*
UVR × dose × T	2	1.1	0.0002*	2	0.4	0.1685ns	2	3.9	<0.0001*
Error	24	1.0		24	2.3		24	0.3	

UVR: UVR condition; PAB: PAR + UVAR + UVBR; PA: PAR + UVAR; P: PAR; T: temperature; HD: high dose of UVR; LD: low dose of UVR; d.f.: degrees of freedom; % SS: percentage of the total sum of squares [% SS = (factor SS/total SS)/100]; ns: non-significant; L.S.D.: results of the L.S.D. test.

* Significant at $P < 0.05$.

incubated under the LD condition (Table 2). Germlings of the three species incubated at 8 °C showed significantly slower RGR values than those at 16 °C (Figs. 1–3).

3.1. *Fucus spiralis*

Germlings increased in size under all treatments. The RGR values ranged, independently of the dose, from an overall mean value of 4.2 ± 0.1% day over 14 days under PAB at 8 °C (Fig. 1b), to a mean value of 17.8 ± 0.1% day over 7 days under P at 16 °C (Fig. 1a). If the treatment P is considered as a control, then the percentage of decrease of RGR of those germlings incubated under PAB was much higher (10–43%) than those germlings incubated only under PA (1–25%). In the same way, the percentage of decrease in RGR under PAB treatment, was higher after 14 days of incubation (overall mean value of 36.9 ± 11.9%) than after the first 7 days period (overall mean value of 19.6 ± 7.4%), whereas this decrease remained the same for those germlings incubated under the PA treatment (overall mean value of 15.5 ± 8.9%).

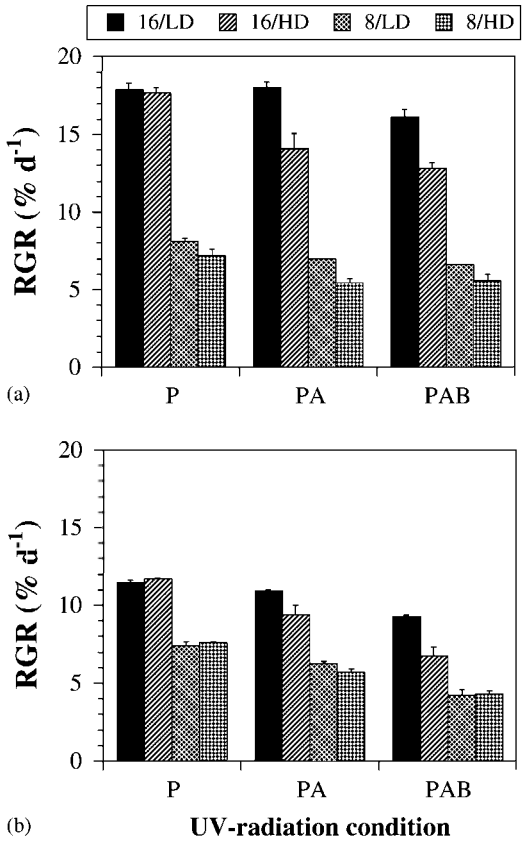

Fig. 1. *Fucus spiralis*: relative growth rates (RGR; % day) of germlings after 7 days (a) and 14 days (b), under the different UVR- and temperature-combined conditions. Data are expressed as mean values ± S.D. ($n = 3$). Treatments are indicated as follows: 16/HD: 16 °C/high dose of UVR; 16/LD: 16 °C/low dose of UVR; 8/HD: 8 °C/high dose of UVR; 8/LD: 8 °C/low dose of UVR; P: PAR; PA: PAR + UVAR; PAB: PAR + UVAR + UVBR.

3.2. *Fucus vesiculosus*

For this species not all the experimental conditions allowed the germlings to grow; under PAB and HD at 8 °C the RGR was negative, which meant a reduction in size (Fig. 2a). The highest RGR value was observed, as for *F. spiralis*, under the treatment depleted of all UVR (P) and at 16 °C, with an overall mean value for both dose conditions of 13.3 ± 0.4% day (Fig. 2a). The decrease in RGR under the PAB treatment was greater than under the PA treatment (Table 2).

3.3. *Fucus serratus*

Germlings incubated with UVBR at 16 °C were not able to survive longer than 7 days, independent of the dose; the same was true of the germlings exposed to the PAB treatment

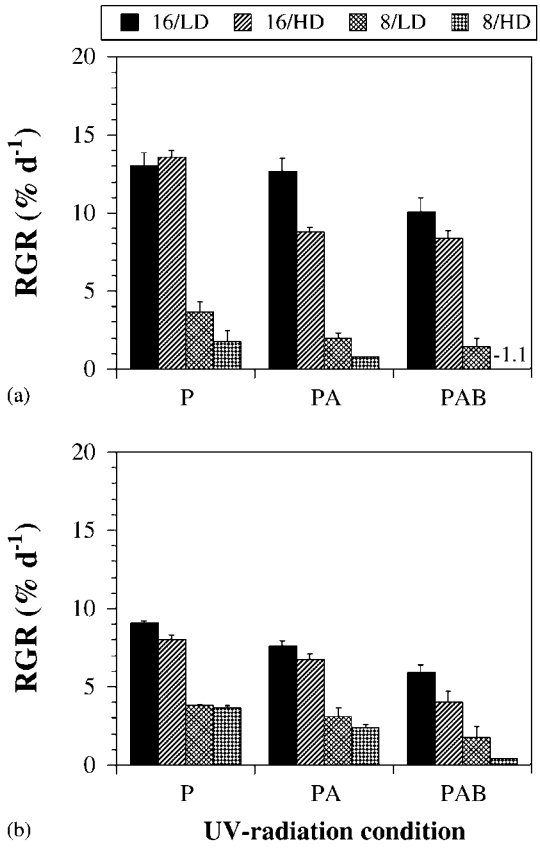

Fig. 2. *Fucus vesiculosus*: details as in Fig. 1.

at 8 °C, but only under the HD treatment (Fig. 3b). After 14 days under the PAB treatment and LD at 8 °C the germlings were able to grow (3.1 ± 0.1% day) (Fig. 3b). The highest RGR value (17.8 ± 0.8% day) was measured under the same conditions and period of time as the other two previous species, i.e. after 1 week without UVR at 16 °C (Fig. 3a). Again, when P treatment is considered as a control, the decrease of RGR of germlings incubated with UVBR, compared to this control, is higher at 16 °C than at 8 °C, after 1 week.

3.4. Inter-species specific differences

Among the species investigated, *F. spiralis* was the least sensitive to UVR (Fig. 1). After the first week of incubation, under 16 °C, the BED causing 50% inhibition of growth was the highest in *F. spiralis* (38.2 kJ m^{-2}), followed by *F. vesiculosus* (28.7 kJ m^{-2}), and *F. serratus* (18.5 kJ m^{-2}). After 14 days under PAB conditions, the decrease of RGR of *F. spiralis* was always lower than for the other two species (Fig. 1). At the end of the experiment *F. serratus* was quite more sensitive to UVR than *F. vesiculosus* (Fig. 3).

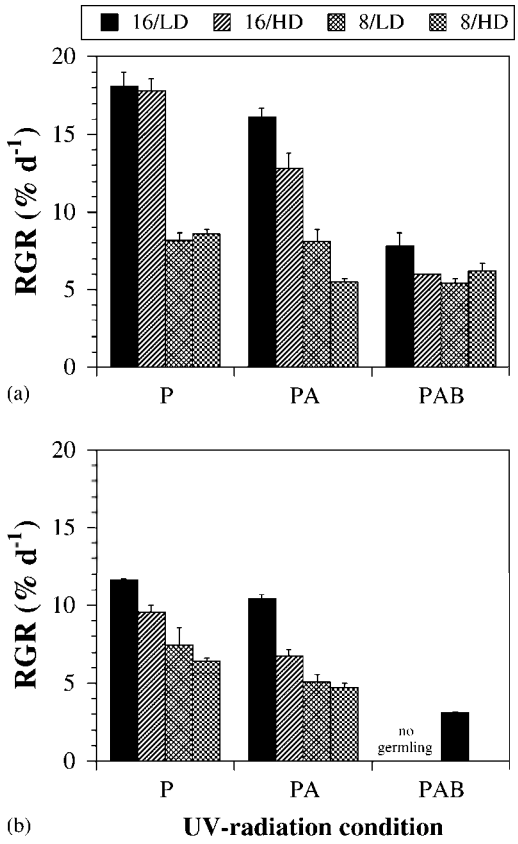

Fig. 3. *Fucus serratus*: details as in Fig. 1.

4. Discussion

Growth rates of *Fucus* germlings measured under the different light treatments suggest a relationship between the position of the adult plant on the shore and the sensitivity to UVR of the germlings. Species inhabiting the higher intertidal zone seem to be less sensitive to UVR. Ultraviolet B radiation represents a strong stress factor resulting in a 10% growth reduction up to death of the germlings. Ultraviolet A radiation also affected growth, although less than UVBR. In general, harmful effects on growth increased with increasing the biologically effective dose. This indicates an important role for UVR in determining the vertical distribution of species under natural conditions. However, direct extrapolations of our laboratory results to the field are not justified, since the reciprocity between time and dose has been assumed, and natural UVAR:PAR and UVBR:PAR ratios have not been used.

Two questions emerge from the results of this study. The first is on the mechanisms, i.e. how and where does UVR affect the germling. The second is on the wider ecological consequences, i.e. how does this phenomenon affect algal performance in the intertidal.

In macrothallus stages UVBR has been suggested to affect growth by negative effects on specific metabolic processes and cell division (Grobe and Murphy, 1998; Altamirano et al., 2000b). However, possible targets and effects of UVR found in adult plants should not be extrapolated to microscopic stages. Dring et al. (1996b) and Yakovleva et al. (1998) suggested that tolerance to UVR depends on the stage of the life-history in brown and red macroalgae respectively, with higher sensitivity found in microscopic stages. These differences may be explained by the structural and cellular simplicity of microscopic stages that allows UVR easily penetrate to UV sensitive cellular molecules. Wiencke et al. (2000) observed a direct relationship between DNA damage and mortality of zoospores of kelp species, and also suggested that the motility or phototaxis of these biflagellate zoospores might be affected by UVR as in the flagellate *Euglena gracilis* (Ekelund, 1996). Ultraviolet radiation might damage the DNA of *Fucus* germlings too, although perhaps in a less serious way than in zoospores. Both lower transmittance of light and diploid genetic information may mean a defence against DNA damage in zygotes and germlings compared to haploid zoospores. The hypothesis for the latter is that any damage in a haploid organism could be expressed in the phenotype in a more serious way than in a diploid organism.

The second question refers to the role of UVR in the distribution of these species in the intertidal zone. *Fucus spiralis* grows clearly higher within the intertidal compared with *F. vesiculosus* and *F. serratus*, which grow mixed in the same littoral zone at Helgoland, although *F. vesiculosus* can reach higher zones in the intertidal than *F. serratus* (Munda and Markham, 1982). This latter species generally experiences the longest daily period of submergence. In the present laboratory experiment *F. serratus* was the most sensitive species to UVBR, with a significant interaction with temperature effects, as in the presence of UVBR only those germlings grown at low temperatures could survive. Therefore, these results of this study suggest two hypotheses: (1) that the sensitivity of macroalgal growth to UVBR is less at lower temperature, and (2) that within the genus *Fucus* sensitivity to UVR may affect the vertical distribution of the different species. Concerning the first hypothesis, there is still no general trend on thermal-dependence UVR damage. On cyanobacteria Roos and Vincent (1998) found that UVR inhibition of growth increased linearly with decreasing temperature, but no relationship was found related to photosynthesis. An interesting point of view was reported by Pakker et al. (2000) who suggested that on macroalgae photorepair processes may have different temperature characteristics. Results on *F. serratus* suggest that the subtraction damage minus repair may be worsened by inefficiency of certain repair mechanisms at higher temperatures. Concerning the second hypothesis, the idea that the degree of sensitivity to UVR governs the vertical distribution of the species is not new for macrothallus stages of macroalgae (Dring et al., 1996a; Bischof et al., 1998), but extrapolations to microscopic stages are still scarce (Yakovleva et al., 1998; Wiencke et al., 2000).

The microhabitat in which zygotes and germlings settle is a very important factor for survival and development (Brawley and Johnson, 1991). In the case of *Fucus* germlings, it could be thought that most of them will settle under adult plants, where they will find a good protecting screen against solar UVR during the uni- and few-celled stages of the life cycle. But what happens to those germlings that are carried to less protected microhabitats, i.e. those that colonise new habitats and spread the canopy? Under presently prevailing spring UVR doses both *F. spiralis* and *F. vesiculosus* germlings would be able to develop, although with some growth inhibition. Under the same radiation conditions however, *F.*

serratus germlings would only survive at low temperature. When our experimental results are extrapolated to conditions of increased UVBR doses due to ozone depletion combined with predicted increased temperature, we speculate that growth will be seriously reduced in all three *Fucus* species investigated. The consequences for tidal zonation are as yet difficult to predict.

Finally, reproductive timing also appears to be in tune with seasonal variation of UVBR. The least sensitive species, *F. spiralis*, happens to reproduce in months (between April and November) with higher doses than the other two species (between September and May; Kornmann and Sahling, 1983).

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