

## Effects of environmental factors on net photosynthesis and growth of intertidal species of the genus *Gelidium* (Gelidiaceae, rhodophyta) in northern Spain\*

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**SUMMARY:** The effect of temperature, air exposure, salinity and light have been tested for three species of *Gelidium* on the basis of photosynthetic and growth responses in order to assess the zonation patterns observed on the Atlantic coasts of northern Spain. The vertical distribution of three *Gelidium* species is described: *G. sesquipedale* reaches its limit in the low intertidal zone, whereas both *G. latifolium* and *G. pulchellum* extend from the mid- to the lower intertidal zone. These differences in location on the shore gradient are in accordance with the physiological responses to the factors tested. *Gelidium sesquipedale* has the lowest saturated net photosynthesis ( $P_{max}$ ) and saturating ( $I_k$ ) Photosynthetic Photon Flux Density (PPFD) and is the less tolerant to changes in temperature and to dessication. Exposure to air causing water losses above 50% (wet weight) produced negative net photosynthesis values in *G. sesquipedale*. *Gelidium latifolium* showed broader tolerance ranges to the factors mentioned above, although exposure to long periods of dessication caused significant reductions in the photosynthetic response. *Gelidium pulchellum*, which has the highest vertical position in the shore, was the most tolerant to temperature and dessication. The response was similar when growth, instead of net photosynthesis, was tested against various combinations of temperature and salinity. These differences in net photosynthesis and growth are consistent with the observed zonation pattern. Although other causes can be invoked, it is concluded that tolerance ranges are decisive in determining the vertical distribution of these three species.

**Keywords:** environmental factors, *Gelidium*, Northern Spain, physiology, zonation.

**RESUMEN:** EFECTO DE FACTORES AMBIENTALES EN FOTOSÍNTESIS Y CRECIMIENTO DE ESPECIES INTERMAREALES DE *GELIDIUM* (GELIDIACEAE, RHODOPHYTA) DEL NORTE DE ESPAÑA. – En este artículo se analiza el efecto de la temperatura, la exposición al aire, la salinidad y la cantidad de luz sobre la fotosíntesis y el crecimiento de tres especies de *Gelidium*, a fin de establecer los posibles factores ambientales responsables del patrón de zonación de estas especies en la costa Norte de España. Se describe la distribución vertical de estas tres especies: *Gelidium sesquipedale* tiene su límite superior en el intermareal inferior, mientras que *G. latifolium* y *G. pulchellum* se extienden a lo largo del intermareal inferior y medio, respectivamente. Estas diferencias de posición vertical están relacionadas con las respuestas fisiológicas encontradas. *Gelidium sesquipedale* tiene el menor valor de fotosíntesis neta a saturación ( $P_{max}$ ) y de luz (PPFD) saturante ( $I_k$ ) y es la especie menos tolerante a cambios en temperatura o a exposición al aire. Cuando es expuesta durante 1.5 h, la pérdida de contenido hídrico superior al 50% (peso fresco) da lugar a fotosíntesis neta negativa. En el caso de *G. latifolium*, los rangos de tolerancia son más amplios, aunque largos periodos de exposición al aire (>1.5 h.) causan reducciones significativas en la respuesta fotosintética. *Gelidium pulchellum*, la especie que ocupa la posición más alta, es la más tolerante respecto a temperatura y desecación. Lo mismo sucede en el caso del crecimiento, cuando esta respuesta se analiza respecto a temperatura y salinidad. Sin perjuicio de otras causas, los rangos de tolerancia pueden utilizarse para explicar el patrón de distribución vertical de estas tres especies.

**Palabras clave:** factores ambientales, fisiología, *Gelidium*, norte de España, zonación.

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## INTRODUCTION

In the central area of the northern Spanish coast, the Eastern side of Cape Peñas exhibits a zonation pattern unique along 30 km of coastline (Anadon and Niell, 1981; Fernandez and Anadon, 1989). *Gelidium latifolium*<sup>1</sup> Bornet dominates the low intertidal area, whereas just a few km to the west the lower shore is dominated by fucoids such as *Fucus serratus* L. or *Himanthalia elongata* (L.) S. F. Gray. Because of the meticulous work of Faustino Miranda, it is possible to date the appearance of this *Gelidium*-dominated community between 1931 and the early 1980s (Miranda, 1931; Fischer-Piette, 1955; Anadon and Niell, 1981; Fernandez and Niell, 1982). Two other species coexist in the same area: *Gelidium sesquipedale* (Clem.) Born. et Thur. and *G. pulchellum* (Turn.) Kütz., although *G. latifolium* is the only species that forms almost unspecific intertidal communities (Fernández, 1991). In the whole, there is a pattern of zonation similar to that described for other *Gelidium*-dominated shores around the world (Santelices, 1978, 1991).

Zonation of intertidal species has been related to environmental factors (Doty, 1946; Lewis, 1964; Schonbeck and Norton, 1978) as well as to interspecific interactions (Connell, 1972; Schonbeck and Norton, 1980; Hawkins and Hartnoll, 1985) which may create competitive differences along an ecological gradient (Zaneveld, 1969; Chapman, 1974). In the case of zonation of Gelidiales, environmental factors have been suggested as the primary cause of their vertical distribution (Santelices, 1978; Oliger and Santelices, 1981).

Among the possible environmental factors explaining zonation of intertidal seaweeds, dessication tolerance has been frequently used, sometimes as the main cause (Schonbek and Norton, 1980; Oates and Murray, 1983) or sometimes in a more critical fashion (Dring and Brown, 1982). Associated to the emersion stress, salinity may also play a significant adaptative role (Reed *et al.*, 1980; Macler, 1988).

The purpose of the present study is to test the effect of temperature, light requirements, air expo-

sure, salinity and dessication on the physiological response of three species of *Gelidium*, based on short term (photosynthesis) and medium term (growth) bioassays. A precise description of zonation of the species studied is also provided in order to define the specific limits of the vertical distribution on the shore.

## MATERIALS AND METHODS

### Vertical distribution

The vertical distribution of *Gelidium* species in the low intertidal zone was studied in the spring of 1991 at Aramar beach (42° 37' N, 5° 46' W), in the central region of Cape Peñas on the north coast of Spain (Fig. 1). The shore studied is oriented to the north, and has a slope of 1 in 3 and is moderately exposed (Rico, 1992) due to the presence of a reef that protects it from prevailing northerly waves. Annual temperature ranges are 10-21 °C (seawater) and 9-24 °C (air) (Rico, 1992). Fifty-two 60 x 60 cm randomly distributed grids were sampled (this area is slightly greater than the structural minimal area defined for this community: Fernandez and Niell, 1981), along four transects perpendicular to the coastline and 100 m apart. For each grid, percentage cover of the dominant species was estimated using the point-intercept technique, using 144 random points per sample. The position of the grid with respect to the water level was determined using the 'bottle and tube' method (Baker and Crothers, 1987) from the water level at that time. These data were converted to height above Lowest Astronomical Tide (LAT) using tide tables (Anonymous, 1991) with corrections being made for barometric pressure.

From the percentage-cover data obtained, we calculated for each species the spatial niche parameters proposed by Rørslett (1987) :

$z_h$ : height of highest record

$z_l$ : height of lowest record

$b_{hl}$ : vertical extension ( $|z_h - z_l|$ )

$b_w$ : band width (maximum distance between highest and lowest records  $\geq 50\%$  maximum cover).

### Photosynthetic measurements

All photosynthetic measurements were carried out in January at the Laboratorio de Ecología, 30 km inland from the sampling site. Intertidal populations

<sup>1</sup>The name *G. latifolium* Bornet is used here, although it is possible that two entities are present at the low intertidal: *G. latifolium* and *G. attenuatum* (Turn.) Thur. (Freshwater and Rueness, 1994). Even though Bornet and Thuret (1876) are generally credited with making the combination *Gelidium latifolium*, there is no reference to Greville's *Gelidium corneum* var. *latifolium* in Bornet and Thuret (1876). The combination would appear to have been first made by Bornet (Bornet and Thuret, 1876, p. 58).

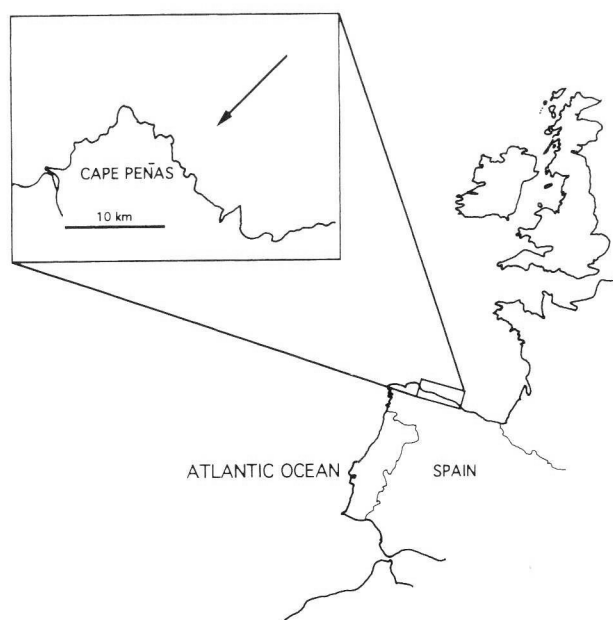


FIG. 1. — Area of study. The enlarged detail shows the region of Cape Peñas, in northern Spain (Bay of Biscay). The arrow points to the location of Aramar, on the east side of Cape Peñas.

of *Gelidium* in this area show maximum photosynthesis and minimum growth during winter (Rico, 1992). Samples collected at the centre of each species' distributional range were transported in isotherm bags ( $< 4^{\circ}\text{C}$ ) in damp, dark conditions. On arrival, they were cleaned of visible epiphytes, rinsed with filtered seawater and placed in 500 ml or 1000 ml (to maintain a constant plant size-to incubation volume ratio of around 0.5 g per l) glass incubation bottles filled with filtered seawater. Filling procedures were standardised to avoid as much experimental variability as possible. The incubations were carried out under direct sunlight in water-cooled incubators. Different Photosynthetic Photon Flux Densities (PPFD) were obtained by placing various layers of neutral density filters over the incubators. Four replicates were used at each light level, and three bottles were used for dark incubations (samples in bottles wrapped in several layers of aluminium foil) and controls (Littler and Arnold, 1985), respectively. Temperature and PPFD were continuously monitored during the incubations, and the temperature was maintained at  $15^{\circ}\text{C}$  (the same as that of seawater at the moment of collection) during the experiment.  $\text{O}_2$  concentration was measured after 2 h of incubation using the Winkler method (Dawes, 1988). The photosynthetic parameters were calculated, from each individual curve, using non-linear multiple iteration procedures contained in the SAS statistical package.

The photosynthetic response after different

periods of exposure to air was measured in fronds dessicated for different periods of time (0.5, 1, 1.5 and 2 h) in controlled temperature chambers, at  $15 \pm 1^{\circ}\text{C}$  in the dark. After these treatments, they were placed in the incubation bottles and the incubations were performed at full sunlight as described above. The tolerance to dessication was expressed as photosynthetic activity vs. percent water loss, calculated from the weight before and after the exposure treatment (Dring and Brown, 1982).

The effect of temperature on the photosynthetic response was determined in incubations at different temperatures: 12, 17, 20 and  $25^{\circ}\text{C}$ . These first three values are within the typical range of seawater temperatures at Aramar, while  $25^{\circ}\text{C}$  is the highest seawater temperature recorded over a two-year period (Rico, 1992). Prior to incubation samples were left for 2 h at the temperature to be assayed under saturating light from Cool-White fluorescent tubes.

## Growth experiments

A factorial experiment similar to that described by Yarish *et al.* (1979) was used to test salinity and temperature effects on growth. PPFD was  $40 \mu\text{mol photons m}^{-2}\text{s}^{-1}$  (previous experiments showed that growth is saturated at  $40\text{--}50 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ ; Rico, 1992) and with a daylight regime of 16:8 h. Petri dishes containing 25 ml IMR/2 sea water medium (Eppley *et al.* 1967) were adjusted to three different salinities (15, 30, 45‰ S). Three replicated thalli sections were placed in these substrata and left for several days at different temperatures (10, 20,  $28^{\circ}\text{C}$ ). Experiments were run separately for the three species. Growth rate was measured for *G. sesquipedale*, *G. latifolium* and *G. pulchellum* after 36, 40 and 48 days, respectively, by using the formula

$$\mu(\%) \text{ day}^{-1} = [(\ln N_t/N_0)/t] * 100$$

where  $N_0$ =initial biomass,  $N_t$ =biomass on day  $t$ ,  $t$ =time interval in days. Results were analyzed using ANOVA.

## RESULTS

### Vertical distribution

*Gelidium sesquipedale*, *G. latifolium* and *G. pulchellum* exhibit a marked vertical segregation in the exposed zone at Aramar (Fig. 2). *Gelidium sesquipedale* is

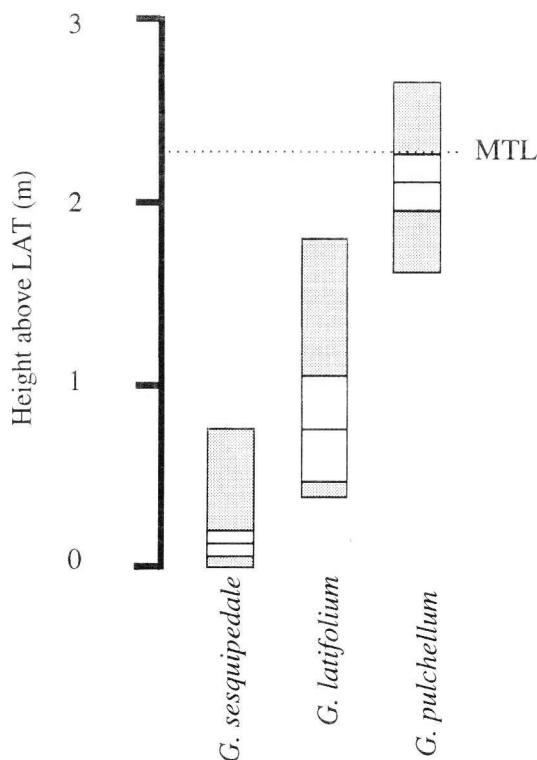


FIG. 2. – Vertical distribution of the three species of *Gelidium* at Aramar (N Spain). The blank bar represent the band width ( $b_w$ , see Material and Methods), and the filled one the vertical extension ( $b_{hi}$ ). The broken line marks the mean tide level (MTL) for 1991.

found only in the sublittoral fringe (Lewis, 1964), and occupies a relatively narrow band, even though it occurs also to a depth of 20 m in this area. *Gelidium latifolium* forms a wide band below the mean tide level, although its vertical distribution is markedly asymmetrical, being more abundant towards the lower shore. *Gelidium pulchellum* is the shallowest in the intertidal zone, frequently above the mean tide level (Fig. 2). This species has lowest cover values (Table 1), not forming a cons-

TABLE 1. – Spatial niche parameters (Rørslett, 1987) and maximum percentage cover for the three species of *Gelidium* in Aramar.

Niche parameters	Species of <i>Gelidium</i>		
	<i>sesquipedale</i>	<i>latifolium</i>	<i>pulchellum</i>
$z_h$	0.74	1.80	2.65
$z_l$	0.00	0.39	1.60
$b_{hi}$	0.74	1.41	1.05
$b_w$	0.12	0.58	0.35
Max. % cover	21%	59%	10%

For abbreviations see Material and Methods. All distances and widths in m.

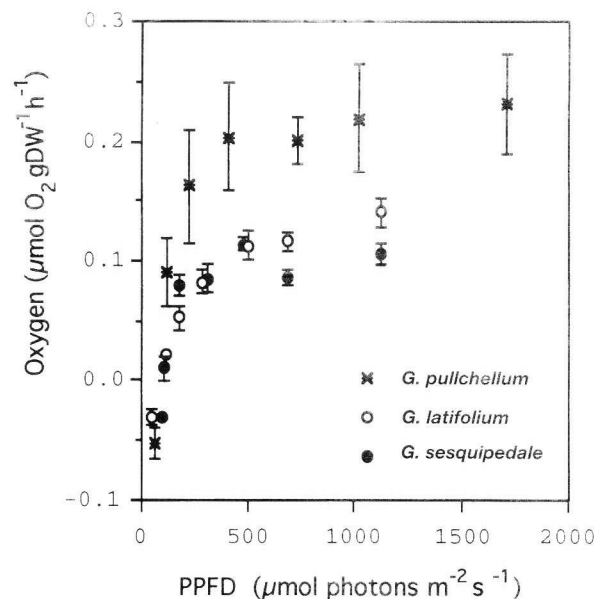


FIG. 3. – Photosynthesis-PPFD curves for the three species of *Gelidium*. Values are mean  $\pm$  standard error ( $n=4$  for photosynthesis,  $n=3$  for respiration).

picuous belt, but instead appearing as scattered mats in a zone dominated by encrusting coralline algae (mainly species of *Lithophyllum*) and bare rock.

### Light requirements

The three species differ significantly (Least Significant Difference test,  $p < 0.05$ ) in their photosynthetic activities above saturation (Fig. 3), the values of  $P_{max}$  increasing with vertical position on the shore (Table 2). No significant differences were found, however, in the photosynthetic response below saturation, so that the differences in saturation PPFD ( $I_k$ , Table 2) can be attributed to the differences in maximum photosynthesis.

### Temperature effect

The effect of temperature on photosynthesis is similar in the two intertidal species, *G. latifolium* and *G. pulchellum*. Both have higher photosynthetic activities as temperature increases in the range tested, while *G. sesquipedale*, the sublittoral fringe species, appears to be less tolerant to temperatures above 20 °C. Also, the intensity of the response (e.g., relative increase in photosynthesis with respect to temperature increase) is higher in *G. sesquipedale* (Fig. 4). Respiration values also showed a temperature response in the three species, with a marked tendency to increase with increasing temperature.

TABLE 2. – Photosynthetic parameters for three species of *Gelidium* studied. Respiration, in mmoles O<sub>2</sub> g DW<sup>-1</sup> h<sup>-1</sup> (mean ± SD); I<sub>k</sub>: irradiance at light-saturated photosynthesis, in μmol photons m<sup>-2</sup> s<sup>-1</sup>; P<sub>max</sub>: maximum photosynthetic rate, in mmoles O<sub>2</sub> g DW<sup>-1</sup> h<sup>-1</sup> (mean ± SD).

Species of <i>Gelidium</i>	Respiration	I <sub>k</sub>	P <sub>max</sub>
<i>G. pulchellum</i>	0.025 ± 0.008	43-223	0.212 ± 0.015
<i>G. latifolium</i>	0.013 ± 0.006	217-312	0.128 ± 0.007
<i>G. sesquipedale</i>	0.005 ± 0.004	77-154	0.100 ± 0.005

### Dessication effects

The dessication process was different in the three species (Fig. 5). *Gelidium sesquipedale* showed a linear relationship between time of exposure and water loss. *Gelidium latifolium* showed an attenuation in the rate of water loss when the exposure was longer than 2 h, and this attenuation was even more

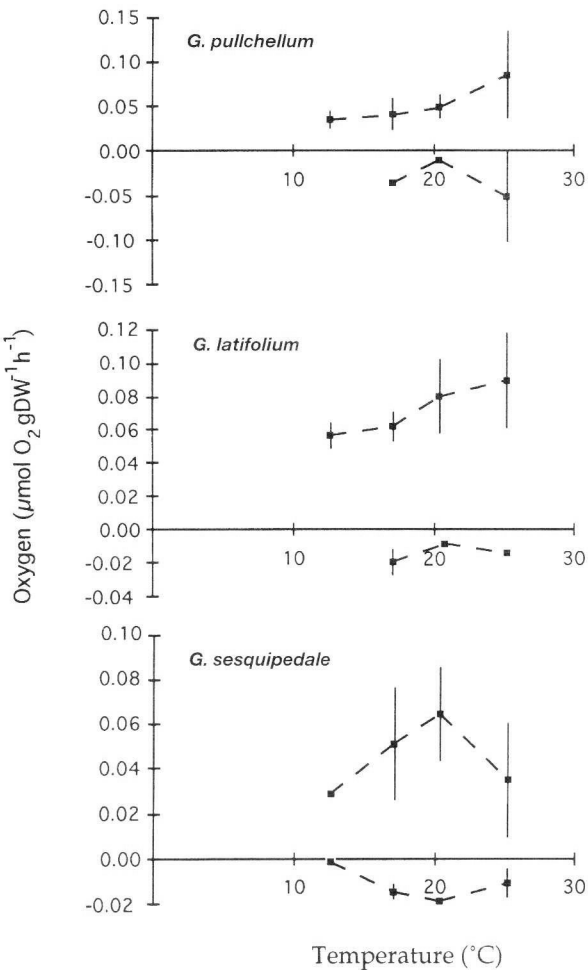


FIG. 4. – Values of gross photosynthesis and respiration vs. temperature for the three species of *Gelidium*. Means ± standard error as in Fig. 3.

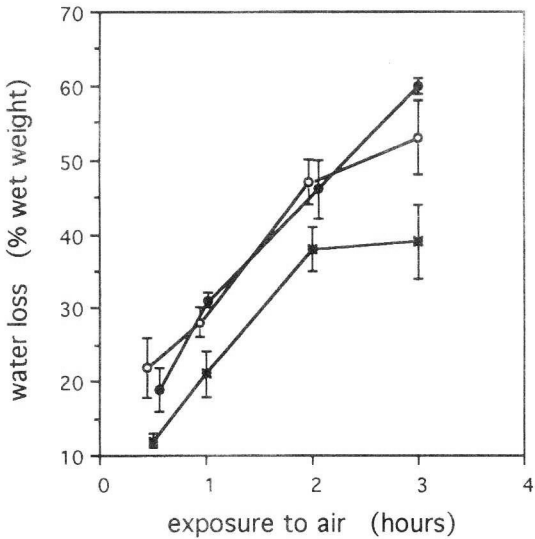


FIG. 5. – Rate of water loss (% fresh weight) in relation to the duration of the exposure period in the three species of *Gelidium*. Symbols as in Fig. 3.

marked in the case of *G. pulchellum*. Whatever the duration of the exposure period, the water loss was lower in *G. pulchellum* than in *G. latifolium* or *G. sesquipedale* (Fig. 5). After the longest exposure period, differences in water loss were significant between the three species (LSD,  $p < 0.05$ ). The effect of air exposure on photosynthesis was highest in the subtidal species compared to the intertidal species. *Gelidium sesquipedale* maintains positive net photosynthesis when the water loss is lower than 40-50% (wet weight), and there is a significant relationship between water loss and reduction in photosynthesis ( $R^2 = 0.924$ ; Fig. 6C). Dessication also causes also a significant reduction in photosynthesis in *G. latifolium* ( $R^2 = 0.809$ ; Fig. 6B) whereas losses of 50-60% in *G. pulchellum* had not a significant reduction in photosynthesis (Fig. 6A).

### Temperature and/or salinity effect

Over a longer time scale, the three species also exhibited a response to both temperature and salinity as well as an interaction of species and salinity (Table 3). This is especially clear from the very different response curves and maxima growth values for the three species, with *G. sesquipedale* exhibiting an optimal of growth at 30‰ S and 20 °C (Fig. 7C), whereas *G. latifolium* and *G. pulchellum* showed no significant differences between growth rates at 30 and 45‰ S (Fig. 7A, B). In all three species, growth at 20 °C was significantly higher at the 'opti-

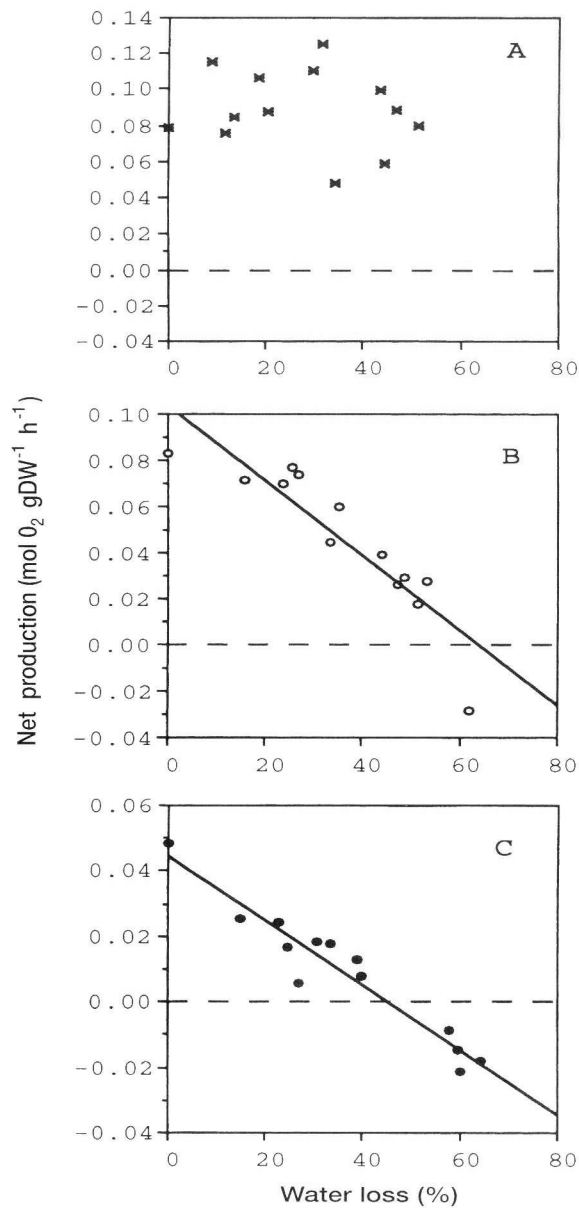


FIG. 6. – Values of net photosynthesis against % water loss after exposure to air. Symbols as in Fig. 3. The lines in B and C are the linear regression lines (no significant linear regression was found for 6A).

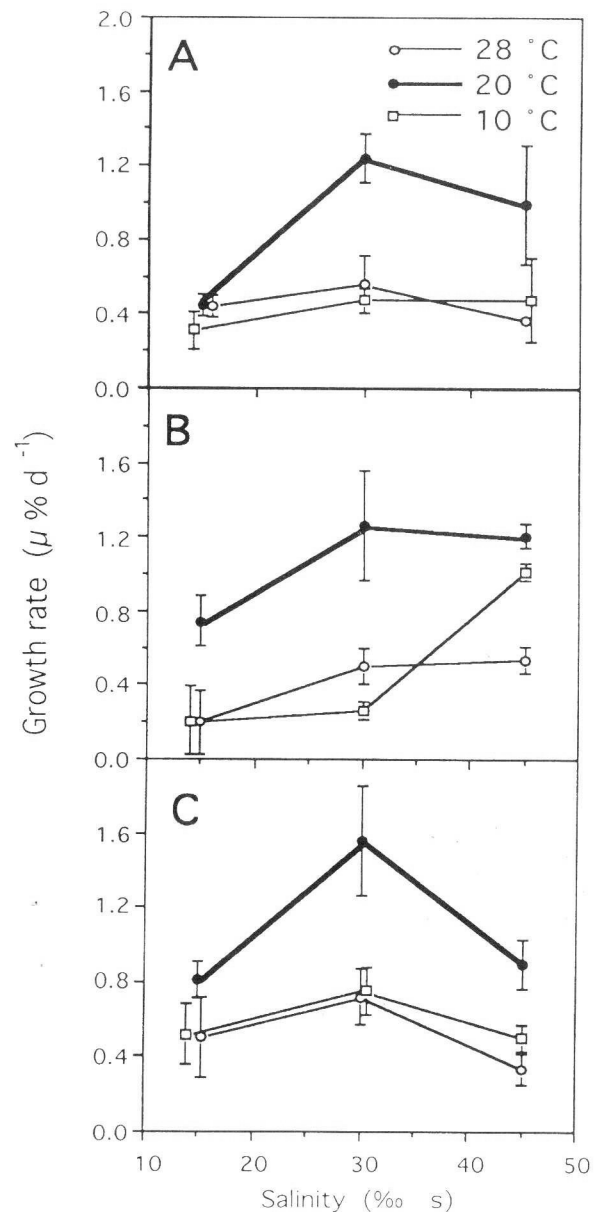


FIG. 7. – Growth rates of *G. pulchellum* (A), *G. latifolium* (B) and *G. sesquipedale* (C) under various combinations of salinity and temperature. Symbols as in Fig. 3

TABLE 3. – Two-way ANOVA for the temperature x salinity growth experiment. df: degrees of freedom; SS: sum of squares; MS: mean square. ns: not significant

Source	df	SS	MS	F-value	
SPECIES	2	0.285	0.143	5.778	**
TEMPERATURE	2	5.162	2.581	104.528	***
SALINITY	2	1.584	0.792	32.079	***
SPECIES x TEMPERATURE	4	0.108	0.027	1.096	ns
SPECIES x SALINITY	4	1.192	0.298	12.071	***
TEMPERATURE x SALINITY	4	1.171	0.293	11.858	***
SPECIES x TEMPERATURE x SALINITY	8	0.414	0.052	2.097	ns
RESIDUAL	54	1.333	0.025		
TOTAL	80				

\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$

mal' salinity value. In any case, the three species were able to grow in salinity values above and below the normal ranges in seawater (Fig. 7).

## DISCUSSION

The zonation pattern of wave-exposed rocky shores on the Asturian coasts of northern Spain is characterized by a conspicuous belt of *Gelidium latifolium*, a medium-sized species with a highly branched thallus (Dixon and Irvine, 1977, fig. 47E). Above and below, two other species of *Gelidium* occur, but never forming dominant intertidal communities. *Gelidium sesquipedale*, which has a pyramidal outline (Dixon and Irvine, 1977, Fig. 49) is present, but this species reaches its upper vertical limit in the low intertidal zone, and dense stands are found in the subtidal region to a depth of 20 m. Another species, *G. pulchellum* (Fredriksen *et al.*, 1994), is found at higher levels than the other two, well above mean tide level. Thus, three species of the same genus, with different morphologies, occupy very different environments in relation to tidal levels. This pattern is not exceptional to the northern coast of Spain, and has been described for other species of Gelidiales in various cold- and warm-temperate seas of the world (Santelices, 1991, 1988). It has been suggested that this pattern indicates a close similarity among species with respect to environmental tolerance, particularly in relation to interspecies competition (Santelices, 1991; Montalva and Santelices, 1981). On the other hand, it has been considered that physiological differences (optimum values and tolerance limits) with respect to photon irradiance and water movement (Santelices, 1978) are paramount.

We have shown that, in the *Gelidium*-dominated lower shore of northern Spain, irradiance does not appear to be a critical factor for photosynthesis or growth, as saturating PPFD levels reaching the three *Gelidium* populations are present throughout the year (Rico, 1992). However, because of morphological differences (*Gelidium sesquipedale* is 'flat' in outline, with branches in one plane, while both *G. latifolium* and *G. pulchellum* have a 'bushy' morphology) irradiance may be at subsaturating conditions in clumped fronds or in closely-knit populations (M. D. Guiry, pers. comm.) so the actual light regime throughout the year may be different, and would explain the differences in the values of  $P_{max}$ .

The lowest intertidal species (*G. sesquipedale*) reaches maximum photosynthetic levels at lower PPFD values than those needed to saturate *G. latifolium* and *G. pulchellum*—which occur higher up on the shore—but also has lower production values. A similar pattern has been described for species belonging to the Gelidiales in the Azores (Fralick *et al.*, 1990) and for *Pterocladia capillacea* (S. G. Gmel.) Born. et Thur. growing at different tidal levels in Brazil (Coutinho and Yoneshigue, 1988). In the absence of photoinhibition, it may be concluded that the higher the photosynthetic production, the higher the growth, and thus the most favoured in the competition. This competitive advantage is related to other physiological responses: rates of water loss were different between the three species, and at the same levels of exposure, this may cause the differences observed in net photosynthesis; both intertidal species showed broader temperature and dessication tolerances (with respect to photosynthesis) than *Gelidium sesquipedale*, and net photosynthesis was positive in the range of exposures tested. Exposure to air also means dessication stress, resulting from several factors: photosynthetic metabolism stress, changes in C-source and pressure, lack of nutrient supply and high osmotic gradient (Reiskind *et al.*, 1989). Dessication tolerance examined here showed that the species have significant differences in their photosynthetic performance after reimmersion (as defined by Dring and Brown, 1982), which is also the case in other species of *Gelidium* (Ogata and Matsui, 1964). To resist exposure to air, marine plants can either produce adaptations to retard dessication (i.e., reduce water loss) or to maintain photosynthesis when dessicated (Droomgole, 1980; Oates and Murray, 1983). As shown here in the case of *Gelidium pulchellum*, both strategies can work at the same time, and this dessication tolerance should be considered a major factor in determining the upper vertical limit of less immersion-tolerant species of Gelidiales. Also, as will be discussed in the case of growth, the ability to tolerate higher salinities is consistent with this photosynthetic tolerance, as dessication amounts to a progressive increase in salinity (Macler, 1988).

Photosynthetic responses to temperature have been attributed to acclimation, if short-term; if long-term, to adaptation (Davison, 1991). The latter condition may be genetically determined, but with a basis similar to temperature acclimation, so algae from different temperature regimes may exhibit different responses (Davison, 1991). The temperature

changes expected at the higher tidal levels, exposed twice a day every day in localities with semidiurnal tides -as is the case in northern Spain (Anonymous 1991)- are more extreme than those experienced by algae covered by seawater for longer periods of time, especially during temperature extremes in the winter and summer. Intertidal species able to maintain photosynthetic levels while exposed to abnormally high or low temperatures would have an advantage over subtidal species unable to tolerate these changes (e.g., Schonbeck and Norton, 1978; Norton, 1986).

However, one factor in isolation can give an incomplete picture of the ecophysiological response of a species. The parameters of the spatial niche occupied by these species provide an adequate picture of the distribution along the exposure gradient, but the physiological response is best described by the response curves to the environmental factors. Growth is a longer-term response than photosynthesis, and the three species of *Gelidium* occupying different environments differ in this response to the two factors previously considered, so a significant response both to salinity (or osmotic stress) and temperature has been demonstrated, thus corroborating the short-term differences. In fact, adaptation to salinity changes in the Rhodophyta *Gelidium coulteri* may take several weeks, which suggests that the discussion of the ecological significance of short-term comparisons, alone, may not give the complete picture (Macler, 1988).

Ecophysiological differences between the three species of *Gelidium* have been related here to their vertical distribution. These results, however, are evidence from a set of short to long-term experiments, and no 'causal' relation between vertical position on the shore (Zaneveld, 1969) has been demonstrated. It should be firmly borne in mind, however, that there are no descriptions of the exact physiological causes or precise environmental factors controlling specific vertical limits (Dring, 1982). Species zonation should be considered as expression of the array of ecological relations between macroalgal communities and the intertidal environment.

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