

# Iberian intertidal turf assemblages dominated by *ErythroGLOSSUM lusitanicum* (Ceramiales, Rhodophyta): structure, temporal dynamics, and phenology

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## Abstract

*ErythroGLOSSUM lusitanicum* is a foliose, turf-forming member of the Delesseriaceae that colonizes sand-covered intertidal rocks on the Atlantic Iberian Peninsula. We examined (i) the phenology of this alga and (ii) the structure and temporal dynamics of its associated flora at two sites over one year. Species diversity was low in the assemblage, which was dominated by *E. lusitanicum*. Assemblage structure was essentially constant through the year. There were, however, significant differences in *E. lusitanicum* characteristics between the two sites. At one, *E. lusitanicum* was more abundant, thalli were longer and wider, and the proportion of plants with tetrasporangia was higher than at the second location. At the first site, the phenological traits tracked a temporal cycle. Thallus length and blade width were highest in April; after gradual deterioration of the apical portions of the plants, individual sizes reached minimum values in July. Subsequently, individual growth rate was low and plant length was nearly constant from September to February. Tetrasporangia were common throughout most of the year; only in July they were totally absent. Temperature and day-length were inversely related to reproduction. Sexual reproductive structures were not observed. The abundant growth of basal proliferations suggests that vegetative propagation very probably plays an important role in the maintenance of *E. lusitanicum* populations.

**Keywords:** assemblage structure; *ErythroGLOSSUM lusitanicum*; intertidal turf; phenology; temporal dynamics.

## Introduction

Macroalgal assemblages dominated by turf-forming algae abound on tropical and temperate intertidal and subtidal rocky shores (Hay 1981, Airoldi et al. 1995, Airoldi 2001, Irving and Connell 2002). In the most common interpretation, turfs are assemblages of densely packed, small macroalgae

often associated with trapped sediment (Stewart 1982, Kendrick 1991, Airoldi 2003). Although turfs are usually dominated by one or a few species, their composition on temperate coasts is extremely variable (Airoldi et al. 1995). For example, intertidal turf assemblages in northwestern Italy are dominated by *Boergenseniella fruticulosa* (Wulfen) Kylin, *Lophosiphonia cristata* Falkenberg and *Polysiphonia* spp. (Rindi and Cinelli 2000), while *Womersleyella setacea* (Hollenberg) R.E.Norris prevails in subtidal habitats (Airoldi et al. 1995, Rindi and Cinelli 2000). Likewise, two *Corallina* species dominate the intertidal turfs of California (Stewart 1982), while *Gelidium crinale* (Hare ex Turner) Gaillon is the most abundant turf-forming species in Texas (Whorff et al. 1995); *Polysiphonia adamsiae* Womersley dominates in New Zealand (Mei and Schiel 2007). On the Atlantic Iberian Peninsula, algal turfs are common on intertidal, sand-covered rocks. Floristic accounts and vegetation descriptions show that the red alga *ErythroGLOSSUM lusitanicum* Ardré typically dominates these turf assemblages, while other common constituents are: *Ophidocladus simpliciusculus* (P.L.Crouan et H.M.Crouan) Falkenberg ex Schmitz et Falkenberg; *Polysiphonia nigra* (Hudson) Batters; *Pterosiphonia pennata* (C.Agardh) Sauvageau; *P. ardreana* Maggs et Hommersand; *Ptilothamnion sphaericum* (P.L. Crouan et H.M. Crouan ex J. Agardh) Maggs et Hommersand; or *Rhodothamniella floridula* (Dillwyn) Feldmann (Ardré 1970, Pérez-Cirera 1976, Pérez-Cirera and Maldonado 1982, Díaz and Bárbara 2005a,b; 2010, Díaz et al. 2009).

*ErythroGLOSSUM lusitanicum* is endemic to the warm-temperate northeastern Atlantic subregion 1 (Hoek and Breeman 1990); its distribution is restricted to the Atlantic coast of the Iberian Peninsula and Morocco (see Díaz et al. 2009). The thallus consists of a basal discoid holdfast bearing a stipe from which erect blades develop; basal proliferations arise from the holdfast and form an elaborate, creeping rhizomatous base. This species forms turfs on sand-covered rocks (Ardré 1970), where the basal parts of the plants remain buried in a layer of sand and only the upper parts emerge. A detailed description of this species was provided by Díaz et al. (2009), who described very rare sexual structures for the first time. Tetrasporangia were common.

Despite their worldwide distribution, several features of algal turfs remain largely unexplored (e.g., Airoldi 1998, Kelaher et al. 2001, Stuercke and McDermid 2004, Díaz et al. 2009). Details of phenology are poorly known. Knowing when component turf species grow and reproduce is a particularly relevant first step in investigations of marine ecosystems dominated by benthic algae (Kain 1986); however, turf assemblages have been largely overlooked in phenological studies

(but see Airoidi et al. 1995, Rindi and Cinelli 2000, Prathep et al. 2009). Specifically, studies of *Erythroglossum* have focused mostly on morphological taxonomy (e.g., Mikami 1976, Yoshida and Mikami 1997, Díaz et al. 2009), and the few phenological details known for this red algal genus derive from observations obtained in a handful of mainly floristic accounts (Ardre 1970, Maggs and Hommersand 1993). Unfortunately, as this information was obtained in studies not specifically designed to explore patterns of growth and reproduction of this organism, its relevance and generality is difficult to assess.

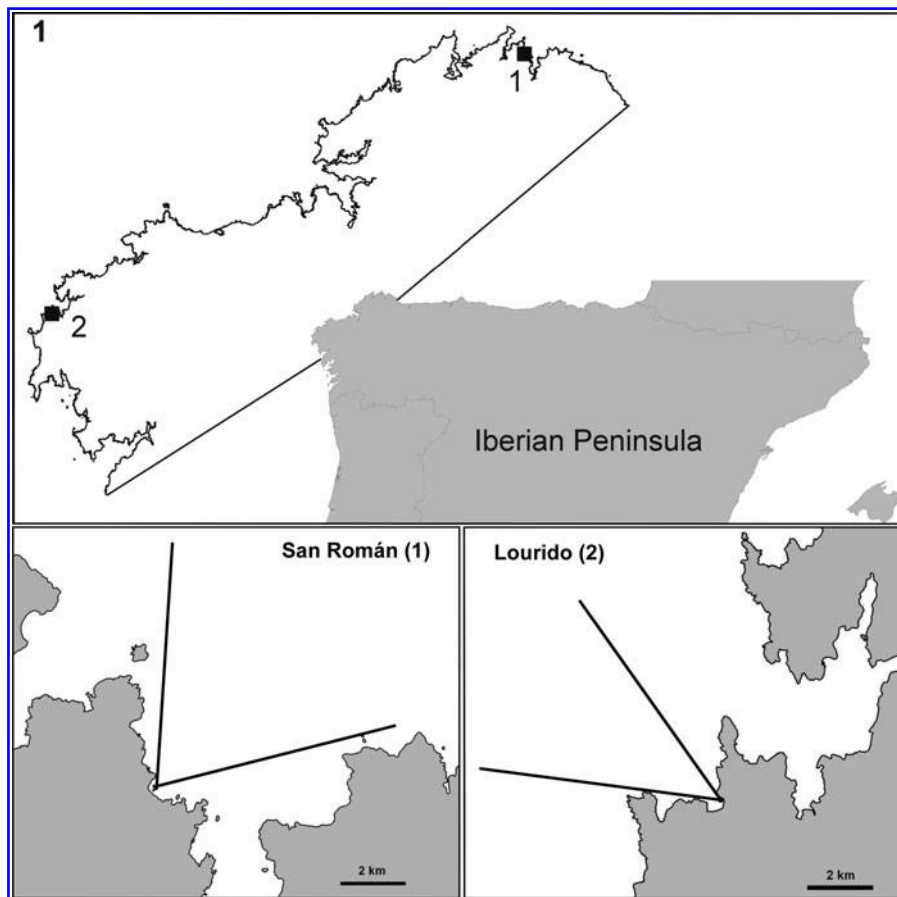
Although algal turfs dominate intertidal, sand-covered rocks on the Atlantic Iberian Peninsula, there are virtually no published quantitative data on their structure and temporal dynamics, or on the phenology of *Erythroglossum* spp. and other turf-forming species. In an effort to fill this knowledge gap, we monitored the turf assemblage that occurs in the lower intertidal zone of two sand-covered, rocky locations on the northwest Iberian Peninsula over one year. The aims of the study were to (i) describe the structure and temporal dynamics of these turf assemblages, and (ii) provide a detailed description of the phenology of the dominant species, *E. lusitanicum*. The phenological description includes vegetative (thallus length, blade width) and reproductive traits (proportion of

tetrasporic plants), and we put particular emphasis on investigating the role of potential controlling environmental factors (temperature and daylength). The structure and dynamics of the assemblage combine approaches based on species composition, vegetation layers, and functional groups.

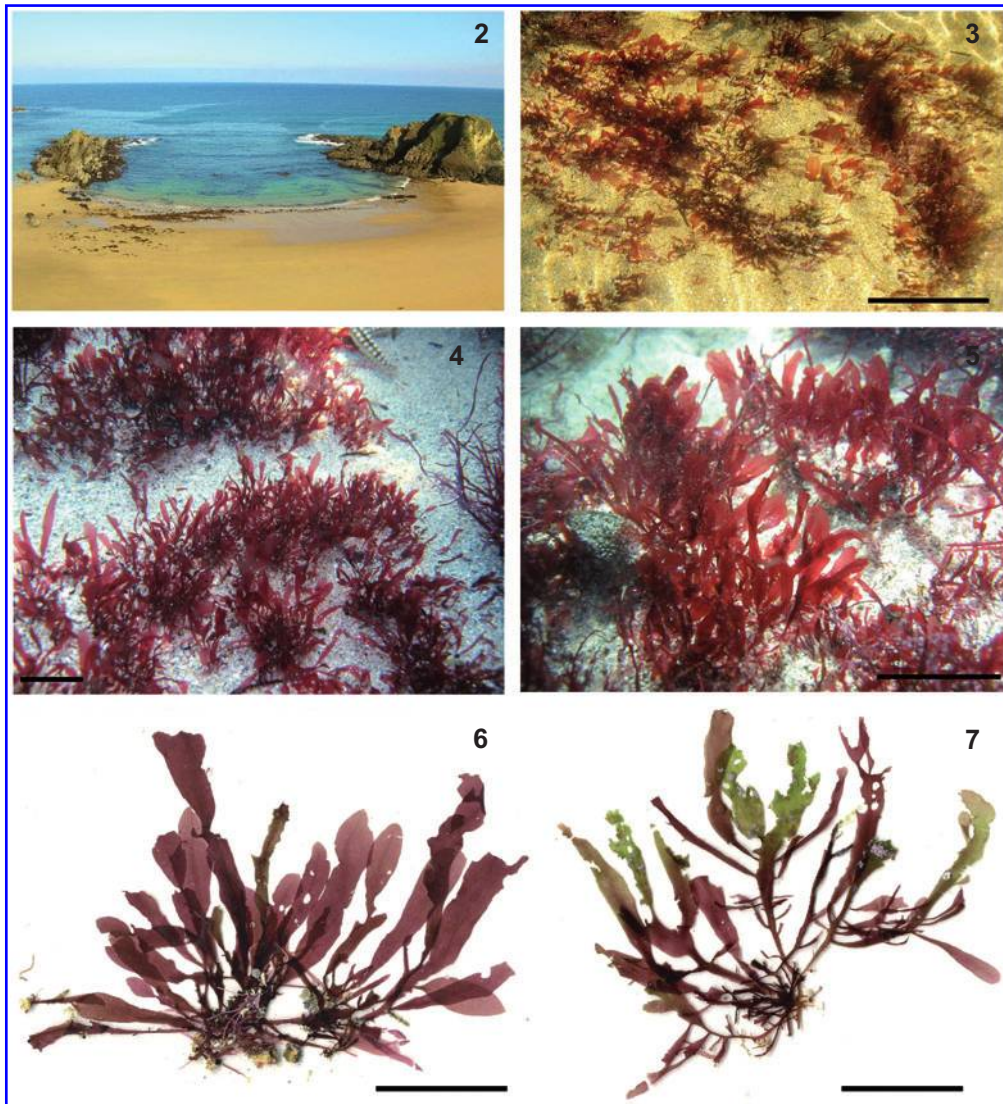
## Materials and methods

### Study area

Research was carried out in the lower intertidal of two wave-exposed shores on the northwestern Iberian Peninsula (Figures 1 and 2). Wave exposure was measured by cartographical methods using the Baardseth index (Baardseth 1970). The two replicate sites were randomly chosen between a set of 10 possible locations where *Erythroglossum lusitanicum* was previously known and that have similar environmental conditions. Sampling dates were randomly selected at intervals of between 40 and 60 days from December 2007 to January 2009. At both sites, the lower intertidal zone consists of rock outcrops surrounded by sand; algal assemblages from the upper sections of the outcrops (free of sand) were dominated by large brown



**Figure 1** Locations of the two study sites on the northwestern coast of the Iberian Peninsula. Site 1: San Román, 43°43' N, 7° 37' W; Baardseth index 10. Site 2: Lourido, 43°5' N, 9°13' W; Baardseth index 8. Radiating lines from each site represent the angle open to the sea in a radius of 7.5 km.



**Figures 2–7** *ErythroGLOSSUM lusitanicum*.

(2) Sampling area in San Román beach. (3–5) Turf assemblages dominated by *ErythroGLOSSUM lusitanicum*. (6, 7). Herbarium specimens of *E. lusitanicum* collected in November (Figure 6) and June (Figure 7). Scale bars: Figures 3, 5: 4 cm; Figures 4, 6, 7: 1.5 cm.

seaweeds, mostly *Cystoseira baccata*, while lower (sand-buried) parts were covered by patches of algal turf dominated by several species and the crustose coralline seaweed *Lithophyllum incrustans*. *ErythroGLOSSUM lusitanicum* occurred as patches of turf (Figures 3–7) mainly where the sand layer was thicker (3–5 cm). Tidal cycles in the region are semidiurnal and the largest tidal amplitude during spring tides is 3.5–4 m. During the course of the study, sea surface temperature (data provided by Puertos del Estado) varied from 11.9°C in January to 20.6°C in July, and daylength (data provided by Meteogalicia) was longest in June (15 h) and shortest in December (8 h).

#### Algal assemblages

At each site, four replicate quadrats (20×20 cm) were haphazardly positioned. Quadrats (hereafter, samples) were divided into 16 subquadrats of 5×5 cm, and algal cover was non-

destructively assessed by visual estimates made by counting the number of subquadrats occupied by each species (Dethier et al. 1993). All macroalgae were identified to species level; when necessary, specimens that could not be identified in the field were brought to the laboratory for identification. Total algal cover was calculated by summing up the cover of each species. Following protocols previously applied to macroalgal assemblages (Verlaque and Fritayre 1994, Airoldi et al. 1995, Piazzini et al. 2002), algal species were classified into three categories of vegetation layer (encrusting, turf, or erect), and the cover of each layer was estimated for each sample. According to Littler (1980), and following Steneck and Dethier (1994), algal species were divided into six functional groups (crustose, filamentous, foliose, corticated-terete, articulated algae, and leathery macrophytes), and the cover of each functional group was calculated for each sample. Species number and the Shannon-Weaver diversity index

( $H'$ ) were calculated for each sample. The variables used to describe the structure of the macroalgal assemblage (total cover, cover of *Erythroglossum lusitanicum*, cover of each vegetation layer, functional group, species number, and species diversity) were analysed by two-way ANOVA with date (eight levels) as a fixed factor and site (two levels) as a random factor. Homocedasticity of data was tested prior to statistical analyses using Cochran's C-test, and normality was assessed using probability plots; when necessary, data were appropriately transformed to meet these assumptions.

To test whether species composition and abundance differed between sites and dates, a matrix of Bray-Curtis dissimilarities between pairs of samples (Clarke and Green 1998) was analysed using PERMANOVA (Anderson 2001). Bray-Curtis dissimilarities were calculated using raw (untransformed data) as preliminary tests using various transformations (square root, fourth root) provided mostly similar results. The contribution of each individual species to Bray-Curtis dissimilarities between sites was determined by the Similarities Percentages (SIMPER) procedure (Clarke 1993) for analysis of macroalgal abundance data. Bray-Curtis dissimilarities were also employed to construct a two-dimensional, non-metric multidimensional scaling (nMDS) ordination plot (Clarke 1993).

### Phenological patterns

On each sampling date, 10 individuals of *Erythroglossum lusitanicum* were haphazardly collected from each of the four quadrats, preserved in 4% formalin seawater, and stored in the dark for later study. In the laboratory, total thallus length and the width of the longest blade were measured for each specimen, and the proportion of plants bearing tetrasporangia (hereafter, proportion of tetrasporic plants) was recorded. Voucher specimens were deposited in the Herbarium of the University of Santiago de Compostela (SANT).

Changes in thallus length and blade width were tested by ANOVA with date as fixed factor, site as random factor, and quadrat as a random factor nested within site $\times$ date. Differences in reproductive status (as proportion of plants bearing tetrasporangia) were tested by a factorial ANOVA with date as a fixed factor and site as a random factor. When necessary, data were transformed to meet the assumptions of parametric procedures. Differences in phenological traits between dates for each site and between sites for every given date were assessed using Student-Newman-Keuls (SNK) tests. The relationship between the proportion of fertile plants and environmental variables was assessed with Pearson's product-moment correlation coefficients.

## Results

### Structure and temporal dynamics of the assemblage

A total of 38 macroalgal species was found in the assemblage: four Chlorophyta, six Phaeophyceae, and 28 Rhodophyta. Only 12 species exceeded 5% mean cover in at least 1 month; the other species were scarce and/or they were only

sporadically observed (Table 1). *Erythroglossum lusitanicum* clearly dominated the assemblage with 38–92% of the total cover. Its tangled basal parts formed a turf, sometimes monospecific, but more often mixed with other turf-forming species; *Rhodothaminella floridula* and *Pterosiphonia ardreana* were the most abundant species in this turf (up to 22% and 25% of the total cover, respectively). The turf extended over both bare-rock and crustose taxa (mainly *Lithophyllum incrustans*; up to 17% of cover). A true canopy over underlying turfs was never observed. *Jania longifurca*, *Corallina officinalis*, and *Chondria scintillans* were the most abundant erect species; however, individually they never covered more than 20% of the surface (maximum coverages were 18%, 11%, and 7%, respectively).

Total cover was significantly higher in San Román ( $103.13 \pm 3.84\%$ ; mean $\pm$ SE,  $n=32$ ) than in Lourido ( $88.88 \pm 2.68\%$ ) (Table 2, Figure 8A). Conversely, *E. lusitanicum* reached a significantly higher cover in Lourido than in San Román ( $68.91 \pm 3.03\%$  vs.  $46.56 \pm 2.64\%$ , respectively) (Table 2, Figure 8B). Neither total cover nor the cover of *E. lusitanicum* was significantly different among dates (Table 2, Figure 8).

Turf species dominated the assemblage at both sites throughout the study period. There was no significant difference in the cover of the turf layer between sites (Table 2, Figure 9). By contrast, encrusting and erect species, though occurring with low cover values, were significantly more abundant in San Román than in Lourido (Table 2, Figure 9). The six functional form groups identified in this study were found at the two sites. The foliose group, which includes *E. lusitanicum*, dominated throughout the year and was significantly more abundant in Lourido than in San Román (Table 2, Figure 10), while the articulated, crustose, and filamentous algae were more common in San Román (Table 2, Figure 10). In contrast, while there were significant differences between sites, none of these vegetation layers or functional group covers varied significantly with the time of year. Nevertheless, the two-way ANOVA detected a significant site $\times$ date interaction for corticated terete algae (Table 2). Cover for this functional group was generally higher in San Román except in September and November 2008 when a slight increase of *Chondria scintillans* in Lourido resulted in higher cover values for the corticated terete in this site in these 2 months.

Species richness and diversity were consistently low throughout the study at both sites (Figure 11). Both variables were significantly higher in San Román (Table 2, Figure 11). However, and particularly for species richness, differences between sites were more pronounced from December 2007 to April 2008, while the two sites were more similar from June 2008 to the end of the study. This decrease in the magnitude of intersite differences explains the significant site $\times$ date interaction and resulted from changes in opposite directions experienced by the assemblage at each site: a decrease in the estimates obtained in San Román from June 2008 (particularly evident in species number), and a gradual increase in species richness and diversity in Lourido from December 2007 to September 2008.

**Table 1** Seasonal variations in mean percentage cover ( $\pm$ SD) of the macroalgae found in the two study sites (San Román and Lourido, Figure 1).

FG	San Román						Lourido									
	December 2007	February 2008	April 2008	June 2008	July 2008	September 2008	January 2009	December 2007	February 2008	April 2008	June 2008	July 2008	September 2008	November 2008	January 2009	
Encrusting layer																
C	+	12.5 $\pm$ 5.0	7.8 $\pm$ 4.8	17.5 $\pm$ 23.6	+	13.75 $\pm$ 18.0	8.8 $\pm$ 14.4	5 $\pm$ 10.0	+		+	6.3 $\pm$ 9.5	+	+		
		<i>Lithophyllum incrustans</i> Philippi														
C			+											+		
		<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini														
C		+	+													
		<i>Melobesia membranacea</i> (Esper) J.V. Lamouroux														
Turf																
Fo	45 $\pm$ 19.1	52.5 $\pm$ 9.6	42.5 $\pm$ 5.0	45 $\pm$ 17.3	45 $\pm$ 12.9	55 $\pm$ 23.8	37.5 $\pm$ 5.0	50 $\pm$ 21.6	75 $\pm$ 12.9	75 $\pm$ 5.8	67.5 $\pm$ 15.0	65 $\pm$ 23.8	57.5 $\pm$ 15.0	55 $\pm$ 12.9	68.8 $\pm$ 21.7	87.5 $\pm$ 12.6
		<i>ErythroGLOSSUM lusitanicum</i> Ardé														
Fi	18.8 $\pm$ 22.5	8.8 $\pm$ 8.5	22.5 $\pm$ 26.3	16.25 $\pm$ 16.0	10 $\pm$ 7.1	6.5 $\pm$ 9.3								+	+	
		<i>Rhododhamniella floridula</i> (Dillwyn) Feldmann														
Fi	5 $\pm$ 7.1	+	11.3 $\pm$ 12.5	+	7.5 $\pm$ 5.0	+	23.75 $\pm$ 12.5	13.75 $\pm$ 12.5	5.5 $\pm$ 9.7	+	10 $\pm$ 20.0		+	+		
		<i>Pterosphonia ardreana</i> Maggs et Hommersand														
Fo	+	+	5 $\pm$ 5.8	12.5 $\pm$ 11.9	+	+	+	5 $\pm$ 1.5			5.3 $\pm$ 9.8	+	+			
		<i>Phyllophora sicula</i> (Kützing) Guiry et L.M. Irvine														
Fi	11.3 $\pm$ 8.5	+												+		
		<i>Pterosphonia pennata</i> (C. Agardh) Sauvageau														
Fi	+		5 $\pm$ 5.8													
		<i>Ophidocladus simpliciusculus</i> (P.L. Crouan et H.M. Crouan) Falkenberg														
Fo	5 $\pm$ 10.0															
		<i>Hypoglossum hypoglossoides</i> (Stackhouse) F.S. Collins et Hervey														





(Table 1 continued)

FG	San Román						Lourido									
	December 2007	February 2008	April 2008	June 2008	July 2008	September 2008	November 2008	January 2009	December 2007	February 2008	April 2008	June 2008	July 2008	September 2008	November 2008	January 2009
Fi	<i>Bryopsis plumosa</i> (Hudson) C. Agardh	+														
Fi	<i>Chaetomorpha aerea</i> (Dillwyn) Kützting		+													
Ct	<i>Colpomenia peregrina</i> Sauvageau		+													
Fi	<i>Polyisiphonia brodiaei</i> (Dillwyn) Sprengel															

FG indicates the functional group of each species. A, articulated; C, crustose; Ct, corticated-terete; Fi, filamentous; Fo, foliose; Lm, leathery macrophytes. + indicates mean cover <5.

The nMDS ordination depicts the distinctive species composition and relative abundances of the assemblages at the two sites: there was no overlapping between site clusters (Figure 12). This clear-cut distinction in species composition of the assemblage at each site was confirmed by the significant intersite differences detected by PERMANOVA (Pseudo- $F=15.62$ ;  $p<0.001$ ; site $\times$ date interaction non-significant). According to the SIMPER procedure, *Erythroglossum lusitanicum*, *Rhodothamniella floridula*, *Pterosiphonia ardreana*, *Jania longifurca*, and *Lithophyllum incrustans* were the most important species separating the assemblages of the two sites (cumulative percentage contribution to the significant differences between sites: 73.24%). Thus, Lourido was characterized by a higher cover of *E. lusitanicum*, while the other four algae were more abundant in San Román. PERMANOVA did not detect significant differences between dates (Pseudo- $F=1.113$ ;  $p=0.411$ ). However, the circular annual trajectory followed by the assemblage of Lourido in the nMDS ordination seems indicative of a cyclical temporal fluctuation (Figure 12) and may reflect temporal fluctuation in species number and diversity in this site. No obvious trajectory was detected in San Román.

#### Phenology of *Erythroglossum lusitanicum*

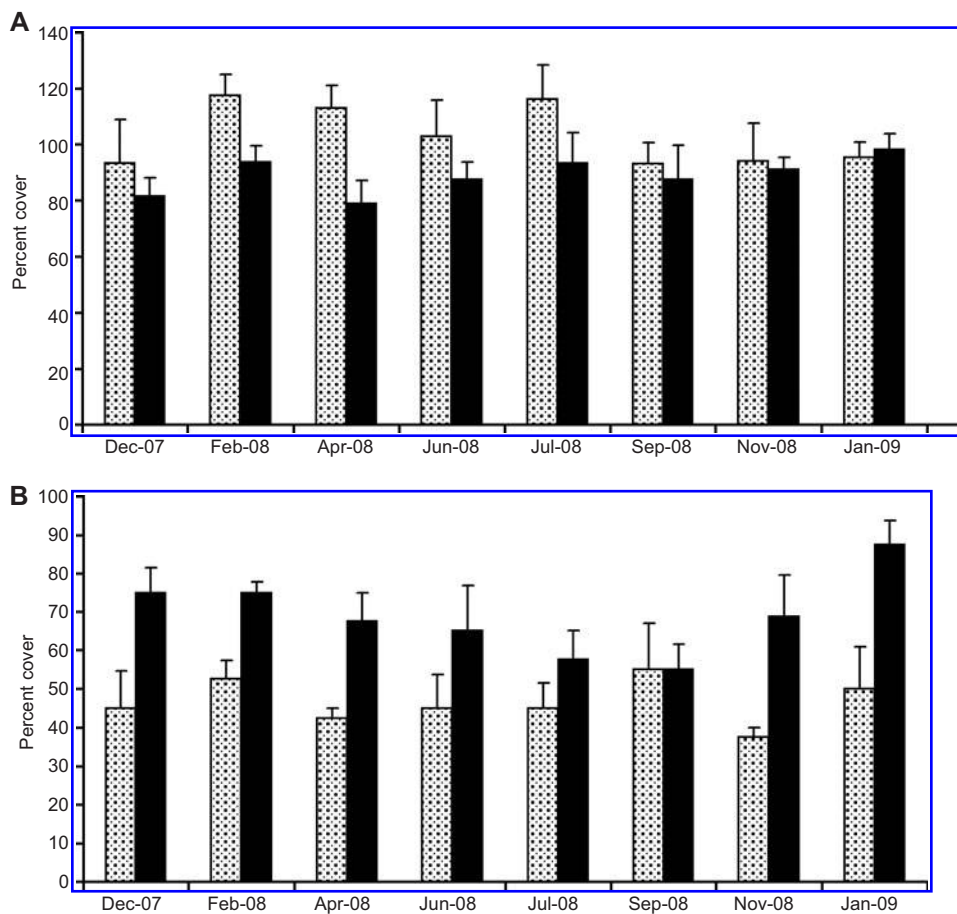
On a local scale, the morphology of *E. lusitanicum* varied among patches, producing significant differences in thallus length and blade width between the various quadrats collected in each combination of site $\times$ date (Table 3). Despite the local variability, length and width were significantly different between sites; plants were, on average,  $0.8\pm 0.27$  cm longer (mean $\pm$ SE) and  $0.1\pm 0.03$  cm (mean $\pm$ SE) wider in Lourido than in San Román (Figure 13). Blade width varied synchronously between sites, with a statistically significant peak in April 2008 (SNK unplanned contrasts). Subsequently, blades bleached and deteriorated in June–July (Figures 6, 7). Deterioration started with a colour change from red to brownish-yellow and was accompanied by an increase in epiphytism; it ended with the breakage of the apical parts. Apart from the April peak, blade width remained mostly stable at both sites. There were no statistically significant differences in thallus length between dates noted at either site.

Sexual structures were never observed in this study, but tetrasporangia were common. The significant interaction between date and site in the two-way ANOVA (Table 4) indicates that the temporal pattern in the proportion of tetrasporic plants was site-specific. A temporal cycle was detected in Lourido with a peak in the proportion of tetrasporic plants in January–February (average values from 30–93%) and nearly zero values in June–July (Figure 14). Pearson correlation coefficients and Figure 8 show that the proportion of fertile plants in Lourido was inversely correlated with both daylength ( $r=-0.6632$ ,  $p<0.001$ ) and temperature ( $r=-0.6444$ ,  $p<0.001$ ). By contrast, *E. lusitanicum* in San Román followed a seemingly oscillating pattern in which dates with a low proportion of plants bearing tetrasporangia (mostly <25%, except for January 2009 when

**Table 2** Two-way ANOVA tests testing differences in percentage cover, species richness, and diversity between sites across all dates and between sampling dates across all sites, with site as random factor and date as fixed factor.

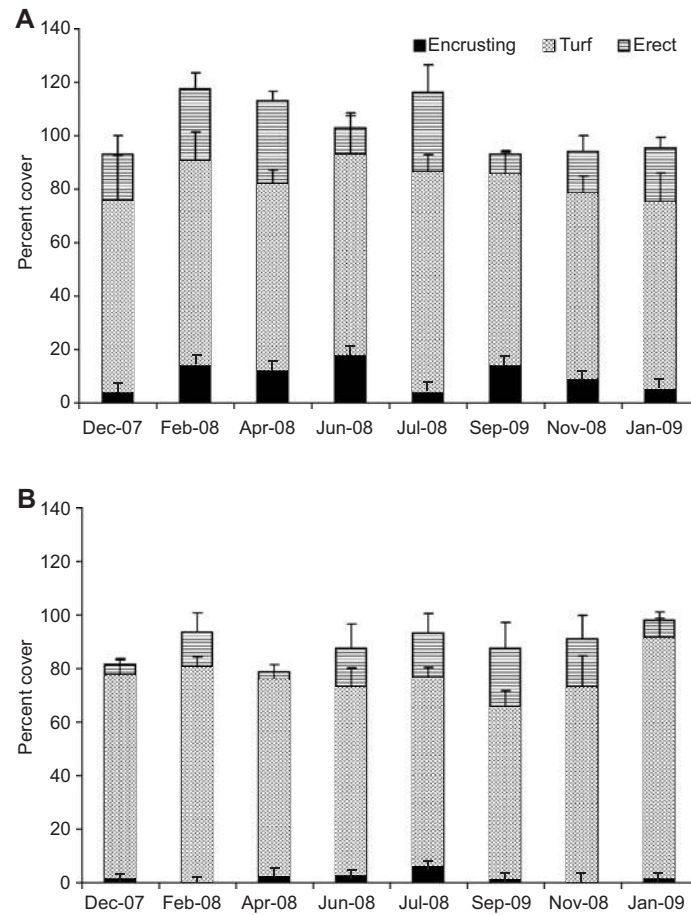
	Site			Date			Site×Date		
	MS	F	p-Value	MS	F	p	MS	F	p-Value
Total cover	3249.0	8.99	<0.01	328.79	1.07	n.s.	306.0	0.85	n.s.
<i>Erythroglossum lusitanicum</i> cover	7987.89	31.77	<0.001	283.87	1.02	n.s.	278.96	1.11	n.s.
Vegetation layer cover									
Erect algae	833.77	5.09	<0.05	149.64	0.47	n.s.	320.94	1.96	n.s.
Encrusting algae	992.25	8.06	<0.01	50.46	0.67	n.s.	75.11	0.61	n.s.
Turf algae	12.25	0.04	n.s.	147.92	0.77	n.s.	192.32	0.57	n.s.
Functional group cover									
Articulated	892.52	9.20	<0.05	79.66	0.57	n.s.	140.02	1.44	n.s.
Crustose	992.25	8.06	<0.01	50.46	0.67	n.s.	75.11	0.61	n.s.
Corticated-terete	23.77	0.96	n.s.	34.66	0.52	n.s.	66.27	2.66	<0.05
Filamentous	5568.89	30.30	<0.001	85.32	0.93	n.s.	91.71	0.50	n.s.
Foliose	5494.52	25.59	<0.001	177.37	0.81	n.s.	218.23	0.82	n.s.
Leathery macrophytes	14.06	2.57	n.s.	4.24	0.54	n.s.	7.81	1.43	n.s.
Species number	112.89	22.79	<0.001	6.28	0.47	n.s.	13.25	2.67	<0.05
H'	7.47	36.02	<0.001	0.16	0.38	n.s.	0.42	2.03	n.s.

df are 1 for site, 7 for date, 7 for site × date and 48 for residual. n.s., Not significant.

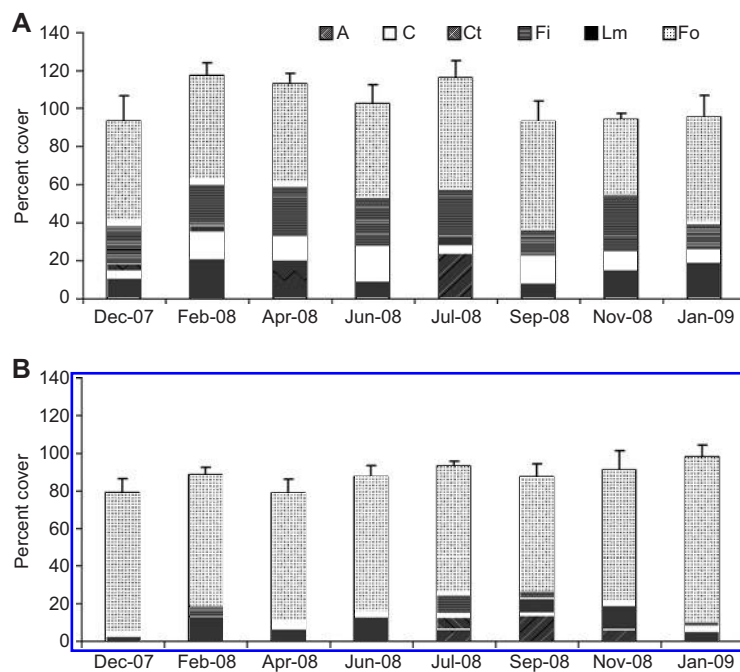


**Figure 8** Temporal variation in (A) total cover of the assemblage and (B) cover of *Erythroglossum lusitanicum* in San Román (grey) and Lourido (black).

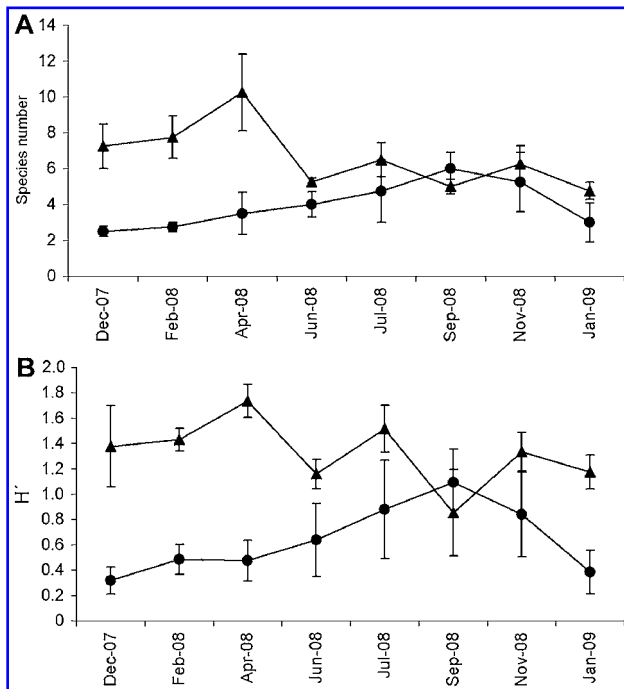
Values are means (+SE, n=4).



**Figure 9** Abundance (as cover) of the vegetation layers in San Román (A) and Lourido (B) through time (mean+SE, n=4).

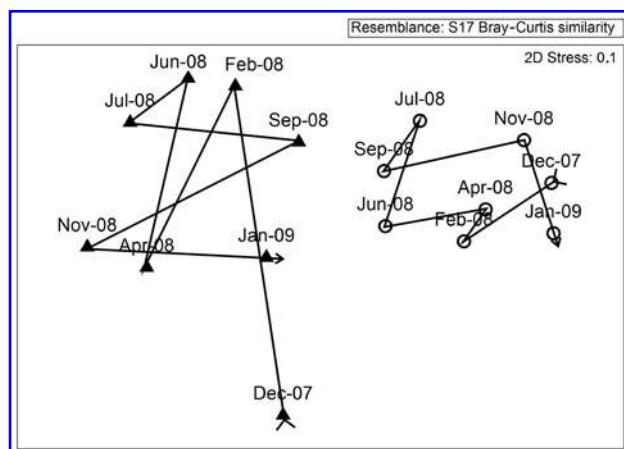


**Figure 10** Abundance (as cover) of seaweed functional form groups in San Román (A) and Lourido (B) through time (mean+SE, n=4). A, articulated; C, crustose; Ct, corticated terete; Fi, filamentous; Lm, leathery macrophytes; Fo, foliose.



**Figure 11** Changes in species number (A), and Shannon-Weaver diversity index  $H'$  (B) through time in San Román (triangles) and Lourido (circles). Values are mean  $\pm$  SE ( $n=4$ ).

the proportion of tetrasporic plants reached a high of 50%) alternated with dates when no fertile plant was observed. Planned statistical contrasts show that the proportion of fertile plants in Lourido was significantly higher than in San Román during the peak months (February, April, November, and December).



**Figure 12** Nonmetric multidimensional scaling (nMDS) ordination plot of samples from San Román (closed triangles) and Lourido (open circles) based on relative abundances and Bray-Curtis similarities. Lines reflect the trajectory in the nMDS space of the macroalgal assemblage of each site through time. Two-dimensional stress is the stress coefficient for the two-dimensional solution; values  $\leq 0.1$  correspond to a good ordination.

## Discussion

Despite our efforts to select similar wave-exposed shores, we found conspicuous inter-site differences in traits of *Erythrogllossum lusitanicum*. Thallus length, blade width, and the proportion of tetrasporic plants were significantly higher in Lourido suggesting that this location provides a more appropriate habitat for this species than San Román. Intersite differences also affected some aspects of phenology; the reproductive status of the population, as well as plant length, tracked a temporal pattern in Lourido, but not in San Román. One possible explanation for this variability is that the peculiarities of the local shore profile may have resulted in slight differences in the severity of the wave action experienced at each site. Sampling sites in San Román faced totally open waters, while a short bend of the beach may have provided some protection from wave action in Lourido (Figure 1). In retrospect, a heavier wave action in San Román would be consistent with more frequent damage observed in *E. lusitanicum* thalli. Other authors have noted that wave-swept organisms tend to be smaller than more sheltered ones (Lobban and Harrison 1997, Prathep et al. 2009). Changes in blade width, by contrast, were synchronized between the two sites, with wider blades in April and narrower ones in July. Width recovered slightly after the July minimum and remained largely unaltered between September and February.

The detection of significant differences in thallus length and width between the various replicate samples (quadrats) collected on each site  $\times$  date combination revealed a considerable patchiness in the morphology of *E. lusitanicum*. Patchiness is a basic feature of the structure of rocky intertidal areas (Nybakken 1997); other studies have repeatedly demonstrated that nearly all populations and assemblages of benthic organisms have a patchy distribution at the scale of centimetres (reviewed in Fraschetti et al. 2005). We detected small-scale patchiness in abundance and distribution, and also in morphology.

The proportion of tetrasporic plants followed very different patterns with time at each site. The clear temporal cycle detected in Lourido was negatively correlated with daylength and temperature. Tetrasporangia were absent during July when blade widths were minimal, suggesting that tetrasporangial development stops towards the end of the process of blade deterioration when daylength and temperature were maximal. The proportion of tetrasporic plants was highest some months before the blades reached their greatest width. By contrast, the proportion of tetrasporic plants in San Román alternated between rare and absent, with no obvious temporal pattern.

Growth and reproductive patterns are very variable among seaweed species. In many algae, growth starts in winter and stops, or reduces to a minimum, in summer (Lüning 1993). However, this general pattern is far from universal and the specific details of phenological pattern are variable between species (e.g., Mathieson 1989, Bottalico et al. 2008). Unfortunately, information on the growth and reproductive patterns of turf-forming species is very scarce. Rindi and Cinelli (2000) found that the season of maximum and minimum heights

**Table 3** Nested crossed ANOVAs examining differences between sites and between dates in thallus length and blade width of *Erythrogllossum lusitanicum* plants sampled from two sites on several dates throughout one year.

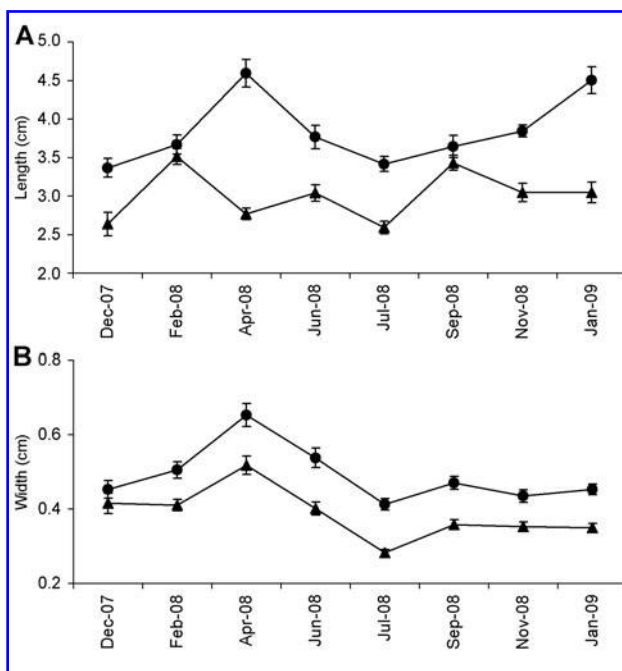
Source	df	Length			Width		
		MS	F	p-Value	MS	F	p-Value
Site	1	113.232	38.16	<b>&lt;0.001</b>	1.2789	26.74	<b>&lt;0.001</b>
Date	7	6.6892	1.04	n.s.	0.4393	4.43	<b>&lt;0.05</b>
Quadrat (site×date)	48	2.9669	6.97	<b>&lt;0.001</b>	0.0478	3.98	<b>&lt;0.001</b>
Site×date	7	6.4267	2.17	n.s.	0.0992	2.07	n.s.
Residual	576	0.4258			0.0120		

Dependent variables were measurements made on 10 plants collected from each of four quadrats randomly sampled in each combination of site×date. Date was treated as fixed factor, site and quadrat were treated as random factors; quadrat is nested within each combination of site×date. n.s., Not significant. Significant p-values in bold.

of the thallus is species-specific in several turf-forming rhodomelaceans from the Mediterranean. The reproductive pattern of *E. lusitanicum* differs from the rhodomelaceans studied in the Mediterranean because the latter included species with a reproductive period extending over the whole annual cycle, species with reproduction concentrated in one or two seasons, and even species that seem to reproduce only by vegetative growth and fragmentation (Airoldi et al. 1995, Rindi and Cinelli 2000). By contrast, *E. lusitanicum* had an extended fertile period that was only briefly interrupted in July. This temporal pattern resembles that described for *Gelidium pusillum* from Thailand, although the infertile period in the latter coincides with the rainy season, and is not associated with deterioration of thalli (Prathep et al. 2009). There is also similarity in growth because the upright fronds of *G. pusillum* also bleach in summer, becoming shorter afterwards.

Turf-forming algae commonly produce more tetrasporophytes than gametophytes (Rindi and Cinelli 2000, Prathep et al. 2009, Díaz and Bárbara 2010) and some species even have incomplete, or asexual, life histories (Norton et al. 1982, Airoldi et al. 1995). In the present study, no sexual structures were observed for *E. lusitanicum* in agreement with the previous observation that these structures are very rare in this species (Díaz et al. 2009). The relative abundance of tetrasporic plants and absence of gametophytic ones suggests that, possibly, the life-cycle is asexual. In this regard, the high number of basal proliferations with a potential to re-attach to the substratum could be an indication that vegetative propagation plays an important role in the maintenance of its turfs. Alternatively, the Rhodophyta includes many examples of apomixis (Hawkes 1990). In the particular case of the family Delesseriaceae, apomeiosis is the only reproductive pattern found in several populations of *Caloglossa leprieurii* (Montagne) G. Martens where tetrasporophytes recycle by tetrasporangia and bisporangia (West et al. 2001). Whether a similar mechanism is also applicable to *E. lusitanicum* surely deserves further research. *Ptilothamnion sphaericum*, another turf-forming red alga from sand-covered rocks, also propagates mostly through asexual mechanisms, and its sexual structures were described only recently (Díaz and Bárbara 2005a, 2010). The high potential for propagating vegetatively is common in algae from sediment-influenced habitats and in turf-forming species (Norton et al. 1982, D'Antonio 1986, Airoldi et al. 1995, Airoldi 1998, Eriksson and Johansson 2005, Mei and Schiel 2007, Prathep et al. 2009). Indeed, *E. lusitanicum* shares other morphological features with these species: (i) a perennial base that tolerates sediment burial and scour; from this base, upright portions of plants may regenerate (Daly and Mathieson 1977, Norton et al. 1982, Stewart 1983, D'Antonio 1986, Airoldi et al. 1995, Mei and Schiel 2007); and (ii) apical meristems that maintain dividing cells above sediment (Stewart 1983). This set of morphological and reproductive traits is thought to be advantageous in environments influenced by moving sand (Stewart 1983, Airoldi 2003, Eriksson and Johansson 2005).

The genus *Erythrogllossum* contains more than 10 species and there are virtually no quantitative studies specifically designed to describe their phenology. The erect *E. laciniatum* is the only species for which information is available. In the British Isles,



**Figure 13** *Erythrogllossum lusitanicum*. Temporal variation in (A) thallus length and (B) blade width (mean±SE, n=40) at San Román (triangles) and Lourido (circles).

**Table 4** Two-way ANOVA test examining effects of site and date on the proportion of *ErythroGLOSSUM lusitanicum* individuals bearing tetrasporangia.

Source	Proportion of tetrasporic plants			
	df	MS	F	p-Value
Site	1	2.14958	22.76	<b>&lt;0.001</b>
Date	7	0.675739	2.70	n.s.
Site×date	7	0.250052	2.65	<b>&lt;0.05</b>
Residual	48	0.0944382		

Data are estimates based on 10 individuals collected from each of 4 quadrats haphazardly sampled on each combination of site×date. Site was treated as random factor and date was treated as fixed factor. n.s., Not significant. Significant p-values in bold.

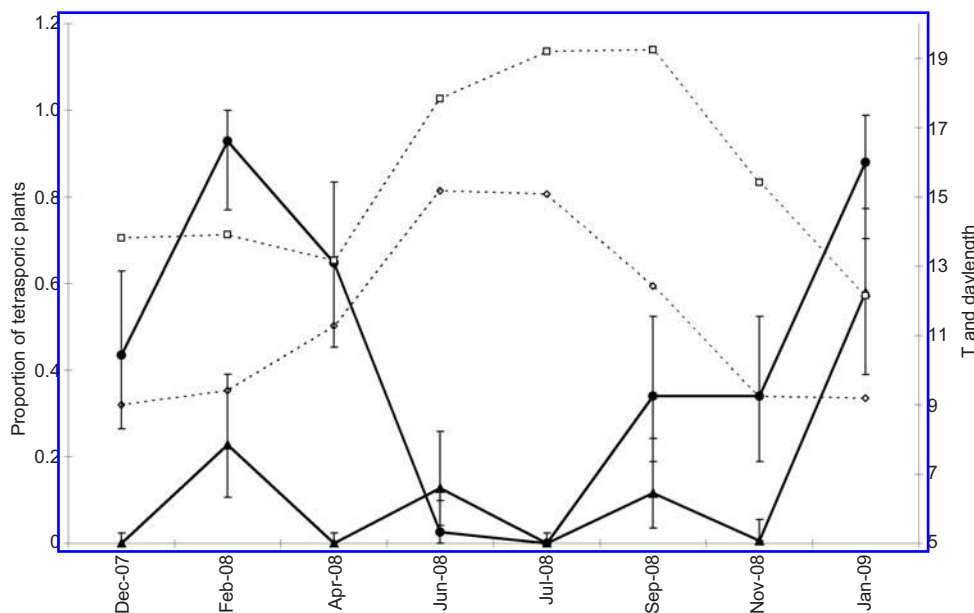
this species follows a seasonal pattern comparable to that which we observed in *E. lusitanicum*, although the maximum development of the thallus and subsequent degeneration of blades take place later in *E. laciniatum* (Maggs and Hommersand 1993). Also, *E. laciniatum* apparently experiences two reproductive periods in the course of a year (Maggs and Hommersand 1993) instead of the single period observed in *E. lusitanicum* from Northern Spain. It is unclear whether these differences are species-specific or just a consequence of the latitudinal changes in ambient conditions between the British Isles and Northern Spain. Certainly, more work is needed to ascertain the similarities and differences in the phenological patterns of the various members of the genus *ErythroGLOSSUM*.

The intertidal assemblage studied was permanently dominated by *E. lusitanicum*. The assemblage was organized as a turf, sometimes monospecific but more often mixed with tangled filaments of *Rhodothamniella floridula* and

other turf-forming species. Still, species richness and diversity were consistently low throughout the study period. Interestingly, several of the attributes of this assemblage compare well with those reported for turf assemblages from the Mediterranean (Airoldi et al. 1995), i.e., dominance by a single species, low diversity, and similar relative abundances among the various vegetation layers. In our study, *Jania longifurca* was the only abundant erect seaweed, and encrusting species were rare. The presence of *J. longifurca* agrees with the perception of this species as a common occupant of sand-influenced habitats around the Atlantic shores of the Iberian Peninsula (Ardré 1970) and is likewise consistent with the observation that some erect seaweeds sometimes reach higher densities on sand covered rocks than on sand-free substrata (e.g., Markham 1973, D'Antonio 1986).

The conspicuous dominance of Rhodophyta found in our assemblage largely agrees with descriptions of algal turfs elsewhere (Stewart 1982, Kendrick 1991, Price and Scott 1992, Airoldi et al. 1995, Rindi and Cinelli 2000, Stuercke and McDermid 2004, Mei and Schiel 2007). However, the predominance of a foliose species must be considered rather unusual because temperate marine algal turfs are often populated by filamentous species (Piazzi and Cinelli 2001, Gorgula and Connell 2004, Balata et al. 2007). Yet, other functional groups of algae are also known to occur in turf assemblages (Airoldi 2001, Stuercke and McDermid 2004).

Our results revealed significant differences in species composition and relative abundance between the two study sites. Although the abundance of *E. lusitanicum* was the variable that most clearly discriminated between sites, there were also intersite differences in that the assemblage was more abundant (total cover), species rich, and diverse in San Román than in



**Figure 14** *ErythroGLOSSUM lusitanicum*.

Temporal variation in proportion of tetrasporic plants from San Román (triangles) and Lourido (circles) (mean±SE, n=4), and temporal variation in temperature (quadrats) and daylength (diamonds) in the study area. T, temperature.

Lourido. Both sites are located in wave-swept beaches that are not particularly distant from one another (ca. 200 km). Therefore, it is reasonable to postulate that significant differences in the abundance and structure of the turfs must depend on rather small differences in the particular conditions experienced at each site. The intensity of wave exposure may be the relevant variable because it was slightly stronger in San Román, which may explain the reduced abundance of *E. lusitanicum* and increased abundances of other, less-competitive species (Connell 1978, Dial and Roughgarden 1998). A conclusive testing of this postulate will require manipulative experiments.

Despite the signs of temporal changes noticed in one of the two locations, PERMANOVA did not detect significant differences in the taxonomic structure of the turfs between sampling dates. This seemingly stable composition throughout the study period is consistent with a description of subtidal turfs in northwestern Italy (Airoldi et al. 1995) and of anchor species in intertidal algal turfs in California (Stewart 1982). In other cases, turf assemblages have been reported to retain a stable species composition throughout the year though with temporal fluctuations in species abundances (Rindi and Cinelli 2000, Prathep et al. 2009). Temporal changes in the abundances of epiphytes of *Corallina* spp. turfs have been recorded on rocky shores seasonally inundated by sand (Stewart 1982). Likewise, opportunistic macrophytes reportedly experience marked reductions in abundance after periods of maximum sand influence (Littler et al. 1983). Altogether, these results show a range of temporal dynamics that may be related to the considerable differences in the species composition of turfs studied, but may also be related to the particular conditions of sediment deposition. Thus, sediment deposition is continuous throughout the year in subtidal habitats in northwestern Italy (Airoldi et al. 1995), while intertidal rocks from California are seasonally inundated by sand (Stewart 1982, Littler et al. 1983), and a layer of sand permanently covers the intertidal rocks on the northwestern Iberian Peninsula (this work).

## Acknowledgements

We thank Puertos de España and Meteogalicia for providing data for seawater surface temperature and daylength, respectively. We thank V. Peña for assistance with some field work. We thank A.R.O. Chapman and anonymous reviewers for helpful suggestions and comments on the manuscript. This study was funded by a grant from Deputación da Coruña and it is a contribution to the projects CTM2007-61011 and CGL2009-09495/BOS (Ministerio de Ciencia e Innovación, partially founded by FEDER).

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Received 26 January, 2011; accepted 18 October, 2011; online first 24 November, 2011