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Changes in the structure and dynamics of marine assemblages dominated by *Bifurcaria bifurcata* and *Cystoseira* species over three decades (1977–2007)

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ABSTRACT

Two low intertidal assemblages dominated in 1977 by *Bifurcaria bifurcata* and *Cystoseira baccata-Saccorhiza polyschides* in the North coast of Spain show changes in the structure and dynamics after 30 years. A re-survey in 2007 detected phenological changes affecting the annual cycle of dominant canopy species. *B. bifurcata* has shortened its growth period and undergone a decrease in biomass, while *C. baccata* lengthened its period of growth and increased its biomass. Also important were the disappearance of *Saccorhiza polyschides* and the increase of *Cystoseira tamariscifolia*. These changes affect the rest of the species of the assemblages, with a shift in the main understory species and an increase in crustose coralline algae although the overall biomass of the subcanopy was similar. The species richness shows a sharp increase, at the expense of increasing epiphytes and simpler functional and morphological groups. These biological changes agree with the general trends of increasing sea surface temperature and the relaxation of the summer upwelling affecting the North coast of Spain, but the results were unexpected in the case of *Bifurcaria bifurcata*.

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1. Introduction

Fucoids are brown canopy-forming seaweeds dominating intertidal sheltered and semi-exposed rocky shores along the Atlantic coast of Europe (Lewis, 1964). They act as engineering species (Jones et al., 1997) and determine the structure and functioning of the assemblage through biotic and non-biotic interactions (Schiel, 2006). Among these species, it is possible to differentiate between cold-temperate and warm-temperate species according to the temperature tolerance (Lüning, 1990). On the north coast of Spain, cold-temperate fucoids colonize the high- and mid-littoral and they are restricted to the western region, due to the west-east thermal gradient of Biscay Bay (Lüning, 1990). Warm-temperate fucoids colonize the low littoral and the sublittoral but they are present all around the coast, especially at central and eastern parts (Fernández and Niell, 1982; Díez et al., 1999; Borja et al., 2004; Guinda et al., 2014).

Along the North coast of Spain the boundary between cold- and warm-temperate species has been moving eastwards and westwards by hundreds of kilometres over the last century (Sauvageau, 1897; Fischer-Piette, 1957, 1963; Anadón and Niell, 1981; Fernández and Niell, 1982). This displacement has been attributed to changes in the sea surface temperature (SST) and the summer upwelling intensity (Fernández and Anadón, 2008).

Over the last 40 years the global SST has warmed by 0.11 (±0.2) °C per decade, and this trend is projected to continue during the 21st century (IPCC, 2014). Therefore, a retreat of cold- and an expansion of warm-temperate species along European coasts is expected (Hiscock et al., 2004; Mieszkowska et al., 2005; Helmuth et al., 2006; Hawkins et al., 2008, 2009; Martínez et al., 2012, 2014) and biological shifts have been recently reported (Lima et al., 2007; Fernández, 2011; Díez et al., 2012; Lamela-Silvarrey et al., 2012; Duarte et al., 2013; Voerman et al., 2013). Nevertheless, apart from SST, other factors may be important stressors, such as the trend towards longer periods of stratification (Taboada and Anadón, 2012) or the relaxation of the summer deep-water upwelling affecting the Northern Spanish coast (Lavín et al., 2000; Cabanas et al., 2003; Llope et al., 2006; Pérez et al., 2010; Santos et al., 2011).

Long-term studies of species abundance and distribution allow us to identify population responses to climate change and other anthropogenic effects (Parmesan, 1996; Sagarin et al., 1999). In the absence of long-term data series, the use of a historical baseline is the only way to detect changes. It means the re-survey of the sites and the use of the same methodology, assuming that it may be difficult to assess causality to possible changes. This study uses a

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baseline of quantitative biomass data collected on the low intertidal assemblages, dominated by *Bifurcaria bifurcata* and *Cystoseira baccata*, in 1977, and compares it with data collected in 2007. The study completes those done by Lamela-Silvarrey et al. (2012) which focused on the mid and high littoral assemblages (dominated by cold-temperate fucoids) in the same location. The main objectives were: (1) to detect differences among community patterns of biomass and primary production for both assemblages, and (2) to assess whether any of these changes were consistent with changes in the coastal waters, especially temperature and upwelling intensity and duration. Due to the previous results of Lamela-Silvarrey et al., (op. cit.) and the evidence of the retreat of cold-temperate species along the North coast of Spain (Fernández, 2011; Díez et al., 2012; Duarte et al., 2013; Martínez et al., 2012, 2014) we hypothesize a substantial change in the canopy-species phenology and in the community structure and dynamics of both assemblages from 1977 to 2007.

2. Materials and methods

2.1. Study site

The sampling was carried out in Bañugues (43° 38′09″N 5°48′19″ W, Cape Peñas region, N. of Spain). This rocky shore is characterized by smooth slope platforms with large blocks and boulders and semi-exposed wave action (Arrontes, 1990). The low intertidal was characterized by four seaweed-dominated assemblages, which from high to low over the sea level were *Corallina elongata*, *Bifurcaria bifurcata*, *Gelidium latifolium* (now *Gelidium spinosum*) and a co-dominance *Saccorhiza polyschides* and *Cystoseira baccata* (Fernández and Niell, 1982). The assemblages studied were those dominated by brown seaweeds, *Bifurcaria bifurcata* and *Cystoseira baccata*. The former was placed in between 0.6 and 1.2 m above the Lowest Astronomic Tide (LAT) (Fernández et al., 1983), whereas the second was located below 0.3 m on the LAT (Fernández and Niell, 1982).

2.2. Temperature data

Sea Surface Temperature (SST) data from 1985 to 2006 were obtained from satellites NOAA-12 to NOAA-18 (Reynolds et al., 2007), recording as near as possible to Bañugues (43° 62′N 5°65′ W). Then, the (i) mean, (ii) number of days above 20 °C, (iii) number of days above the 90th percentile, (iv) mean summer (July, August, September) SST, (v) maximum SST and (vi) standard deviation per year were calculated, in order to detect whether average long-term trends or extreme warm conditions best explains the community changes. The 20 °C threshold was chosen because it represents the biological thermal limit of many cold-temperate species of seaweeds (Lüning, 1990).

2.3. Collection and analysis of data

A baseline of quantitative data collected in 1977 (Anadón, 1980; Fernández, 1980) was compared with data from 2007 using the same methodology. Samples were collected monthly during a complete year by removing all the algae in 2 randomly selected plots (50 × 50 cm). Then, the algae were identified to species, dried (60 °C, 48 h) and weighed to the nearest 0.01 g. Algal species taxonomy was updated using the World Register of Marine Species (WoRMS, Appeltans et al., 2010) and also divided into morphological-functional groups (Balata et al., 2011). Changes in the structure of both assemblages were analysed using two different analytical approaches:

1) A multivariate analysis of variance (PERMANOVA; Anderson, 2001), where two factors were defined: Year, considered as a fixed factor with two levels (1977 and 2007) and Season, also considered as fixed, with two levels (Summer –July, August and September- and Winter –January, February and March-). In the *Cystoseira baccata* assemblage for 2007, April was included in ‘Winter’ due to the lack of data for March. The statistical test was performed over the Bray-Curtis dissimilarity matrix applied to square root transformed data (Bray and Curtis, 1957). This matrix was also used to graphically represent the variation over time in the assemblages (Non-metric multidimensional scaling, nMDS ordination). To identify which species contribute the most to the similarity/dissimilarity within/between years and seasons, a two-way similarity percentage analysis (SIMPER) routine was applied (Clarke, 1993).

2) An analysis of the temporal patterns of abundance (biomass), biodiversity and primary production. For the dominant species (*Bifurcaria bifurcata* and *Cystoseira baccata*) a two-way ANOVA was done with the same model in order to detect differences in the patterns of biomass. For the rest of species the significance levels of the differences in biomass between years for each species were assessed by the Mann-Whitney test due to lack of homogeneity in the response variable (biomass). Biodiversity was estimated analysing species richness (S), Shannon-Wiener (H', $\log_2$), Simpson ($1 - \lambda'$) and Pielou evenness (J') indices. Finally, the net primary production (NPP) was estimated as the increase of biomass at monthly intervals (Westlake, 1969; Anadón and Fernández, 1984).

Analyses were performed using the statistical packages vegan (Oksanen et al., 2015) and GAD (Sandrini-Neto and Camargo, 2015) in R software (R Core Team, 2014) and PRIMER 6 & PERMANOVA+ (Clarke and Gorley, 2006; Anderson et al., 2008) software.

3. Results

3.1. Temperature trends

Both the mean yearly SST and the mean summer SST underwent significant annual increases over the studied period, from 15.70 °C to 19.42 °C respectively in 1985 to 16.66 °C and 20.96 °C respectively in 2006. The numbers of days above 20 °C (Fig. 1) and the numbers of days above 90th percentile were the variables which best fit the regression line versus time ($r^2 = 0{,}26$ and $0{,}29$, respectively) and had the highest significance (p value = 0,0149* and 0,0092**, respectively). Far from it was the standard deviation of the mean annual SST, which depended more on annual and local factors. Maximum temperatures also increased but not significantly, probably due to the years 1993 and 2002 which were extremely cold. The maximum temperatures ranged from 19.73 °C in 1985 to 22.05 °C in 2006. Years 1990, 1999, 2003 and 2006 were especially warm.

3.2. Assemblage structure

The non-parametric multivariate analysis of variance (PERMANOVA) (Table 1) detected significant differences between the two years (1977 and 2007) and between the two seasons (summer and winter) in both assemblages. The nMDS (Fig. 2) shows clear differences for the two years (stress: 0.13). In 1977, all months are closer to each other, whilst in 2007, they are more scattered.

The biomass of the assemblages showed a seasonal pattern (Fig. 3), nonetheless there were significant differences between years (Table 2). In the assemblage dominated by *Bifurcaria bifurcata*, three periods of growth were observed in 1977 (Fig. 3a): spring, late summer-early autumn and January, being late summer-early autumn the most important growth period ($342.62 \text{ g DW} \cdot 0.25 \text{ m}^{-2}$). In 2007, only two periods of growth were detected, one during late spring-summer and the second in November, and their biomass were significantly lower than in 1977 (Table 3). This seasonal pattern was due to the dominant species *Bifurcaria bifurcata* (Fig. 3b). In 1977, the dominance was greater with a mean contribution of 82% to the total biomass, while in 2007, it was reduced to a 73%.

The biomass of the *Cystoseira baccata* assemblage showed a seasonal pattern with one period of growth (Fig. 3c), but different for both years. During 1977, it began in March and finished in September with a maximum of 302.99 g DW · 0.25 m^{-2}. In 2007, the growth lasted from May to October with a maximum of 496.81 g DW 0.25 m^{-2}. *C. baccata* was the responsible of this annual pattern (Fig. 3d) with a significant increase in biomass, from 1977 to 2007 (Table 2).

The net primary production and the turnover of both assemblages are shown in Table 3. Despite the biomass decrease of *Bifurcaria bifurcata* in 2007, the annual net primary production of the assemblage was similar in both years (Table 3). This was because of the increase of the biomass of the understory species. The same tendency is shown by the slight increase in the turnover, estimated as the rate NPP/Minimum biomass. In the assemblage dominated by *Cystoseira baccata*, the NPP almost doubled from 1977 to 2007, but as in 2007 the assemblage maintains a higher biomass over all the year, the turnover rate decreased.

Apart from the dominant species *Bifurcaria bifurcata* and *Cystoseira baccata*, the species that contribute the most to the dissimilarity between years and between seasons (SIMPER routine, Appendix 1), there are other species responsible of the differences between years. In the assemblage dominated by *B. bifurcata* (Fig. 4a), *Corallina elongata*, *Halopteris scoparia*, *Gelidium spinosum* and *Cladostephus spongiosus* were among the most abundant species in 1977 whereas in 2007 they were replaced by crustose coralline species (*Lithophyllum incrustans* and *Mesophyllum* spp.). *G. spinosum*, *H. scoparia* and *C. elongata* were still abundant. These crustose coralline species contributes up to 9.41% and 6.21% respectively to the dissimilarities between years. The assemblage dominated by *Cystoseira baccata* (Fig. 4b) shows a significant decrease in biomass of *Saccorhiza polyschides* and *Chondrus crispus* contributing up to 12.01% and 7.26% of the dissimilarities between years. In 2007 *S. polyschides* mostly disappeared and *Cystoseira tamariscifolia* is now the co-dominant canopy forming species. This species and one of its main epiphytes, *Calliblepharis jubata*, increased considerably their biomass from 1977 to 2007. In both assemblages *G. spinosum* was the main species responsible of the dissimilarity between seasons (8.52% and 9.52%). In 2007, it is also noticeable the presence of the invasive species *Sargassum muticum* and other non-native species, especially *Asparagopsis armata* and *Colpomenia sinuosa*, which have significantly increased their biomass.

Table 1
PERMANOVA for interannual, seasonal and monthly differences in the structure for *Bifurcaria bifurcata* and *Cystoseira baccata* assemblages.

Source	Df	*B. bifurcata* assemblage			*C. baccata* assemblage		
		Pseudo-F	P(perm)		Pseudo-F	P(perm)	
Year	1	5.9781	**0.0027**	**	12.739	**0.002**	**
Season	1	3.9693	**0.0024**	**	2.9916	**0.0083**	**
Year:Season	1	2.2446	**0.0301**	*	2.5815	**0.0049**	**
Year:Season:Month	8	1.3241	0.0912	.	1.6045	**0.007**	**
Residuals	12						

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.
Significant differences are shown in bold.

The annual pattern of biodiversity was similar for all indices used, so only Shannon-Wiener is shown (Fig. 5a, c). In general terms biodiversity was greater in 2007 in the assemblage dominated by *Bifurcaria bifurcata* but there was a slight loss in the case of *Cystoseira baccata* probably due to the significant increase in dominance of *C. baccata*.

In both assemblages there was a substantial increment in species richness (Fig. 5b, d). In the assemblage dominated by *Bifurcaria bifurcata* a total of 112 species were identified considering both years (52 species were found in 1977 and 106 species in 2007). From 1977 to 2007, 13 species significantly increased their biomass while only 2 significantly decreased their biomass. In most of the cases, the new species or those that increased their biomass belonged to either the simplest morph-functional group (filamentous and smaller-sized corticated) or to the calcareous (encrusting and articulated) group (Fig. 6a). Among the former, we found species of the genera *Callithamnion*, *Ceramium*, *Cladophora*, *Drachiella* and *Polysiphonia*, and species such as *Chondria coerulescens* and *Dasya hutchinsiae*. Among the calcareous, *Jania rubens*, *Mesophyllum* spp. and *Lithophyllum incrustans* were the most representative species.

In the assemblage of *Cystoseira baccata* a total of 121 species were identified, of which 54 occurred in 1977, and 109, in 2007. From 1977 to 2007, 13 species significantly increased their biomass whereas only 1 significantly decreased. Regarding morpho-functional groups (Fig. 6b), filamentous algae nearly increased 4-fold in number (i.e. *Aglaothamnion* spp, *Callithamnion* spp or *Ceramium* spp.). Other blade-like species such as *Ulva* spp. or

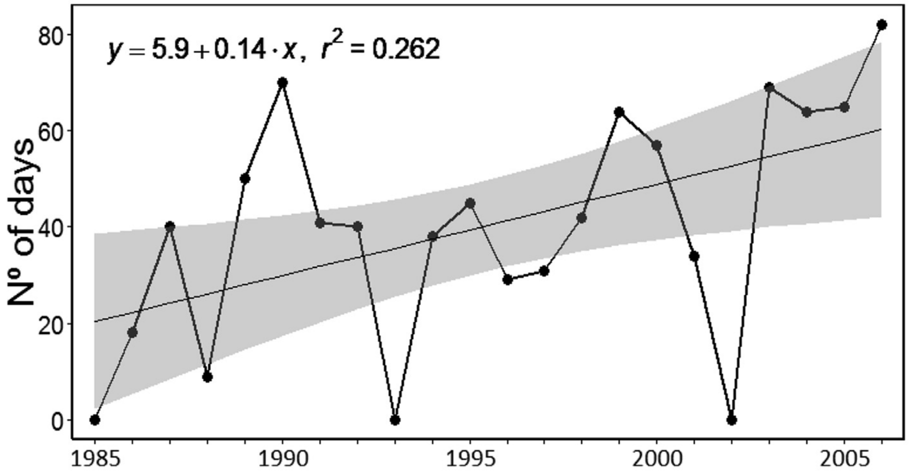

Fig. 1. Time series of the number of days above 20 °C for the annual sea surface temperature over the period 1985–2006. The grey area represents the 95% confidence intervals.

Fig. 2. nMDS based on Bray Curtis dissimilarity matrix applied to square root transformed data for *Bifurcaria bifurcata* assemblages (a) and for *Cystoseira baccata* assemblage (b). Each symbol represents the average between replicates for each month. ○ 1977, ● 2007.

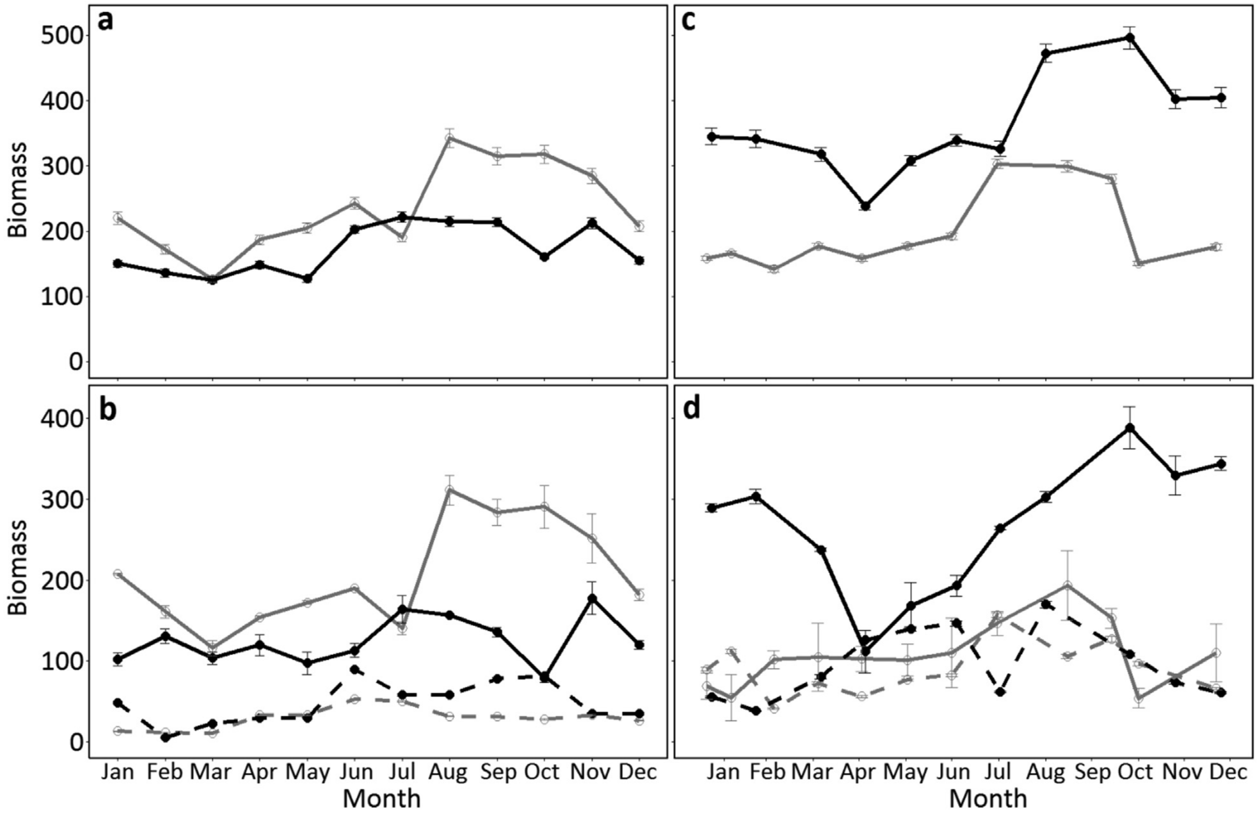

Fig. 3. Seasonal changes in biomass (g DW · 0.25 m^{-2}) of *Bifurcaria bifurcata* assemblage (a) and *B. bifurcata* (solid line) and the rest of species (dashed line) (b), *Cystoseira baccata* assemblage (c) and *C. baccata* (solid line) and the rest of species (dashed line) (d). ○ 1977, ● 2007. Bars indicate standard deviation.

smaller-sized corticated such as *Chondria* spp, *Polysiphonia* spp. or *Pterosiphonia* spp. also increased, whereas more complex morpho-functional groups underwent almost no variation.

4. Discussion

Bifurcaria bifurcata forms monospecific stands covering flat low intertidal rocks on the North coast of Spain (Fernández et al., 1983). Similar assemblages were described in the central coast of Portugal (Ardré, 1971) and in some places of southern Ireland (De Valera, 1962). Since the species distribution northwards is limited by low temperatures (Todd and Lewis, 1984), an expansion of the species was predicted during periods of climate amelioration (de Valera, op. cit.). Recently, *B. bifurcata* was considered a good candidate for monitoring changes in a warming scenario (Hiscock et al., 2004). There is now evidence of an expansion of 150 km northwards along the British coasts (Mieszkowska et al., 2006) and an increase in abundance along the North coast of Spain is also expected (Martínez et al., 2014).

Cystoseira baccata, along with kelps (*Laminaria ochroleuca* and

Table 2
Analysis of variance for interannual, seasonal and monthly differences in biomass for *Bifurcaria bifurcata* and *Cystoseira baccata*.

Source	Df	*Bifurcaria bifurcata*			*Cystoseira baccata*		
		F Value	Pr(>F)		F Value	Pr(>F)	
Year	1	680.696	**0.00274**	**	704.832	**0.00229**	**
Season	1	515.137	**0.01121**	*	12.120	0.29253	
Year:Season	1	64.342	**0.02610**	*	60.072	**0.03054**	*
Year:Season:Month	8	122.622	**0.00011**	***	17.110	0.19634	
Residuals	12						

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.
Significant differences are shown in bold.

Table 3
Net primary production (NPP) and turnover (NPP/B_{min}) of *Bifurcaria* assemblage, *Bifurcaria bifurcata*, *Cystoseira* assemblage and *Cystoseira baccata*.

	NPP (g DW · 0.25 m^{-2} $year^{-1}$)		NPP/Bmin ($year^{-1}$)	
	1977	2007	1977	2007
Bifurcaria assemblage	324.37	330.93	2.56	2.64
Bifurcaria bifurcata	277.19	209.46	2.39	2.65
Cystoseira assemblage	398.41	521.84	2.80	2.19
Cystoseira baccata	198.69	305.48	3.70	2.74

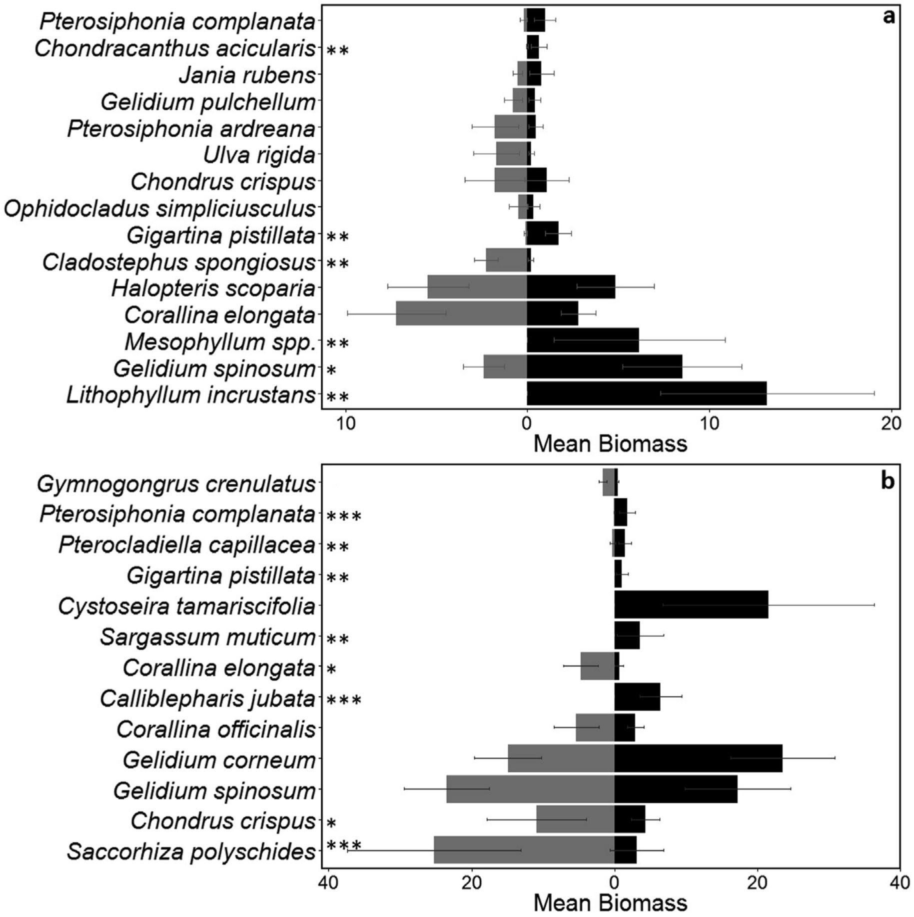

Fig. 4. Mean biomass (g DW · 0.25 m^{-2}) of the most discriminant species in differences detected between 1977 (grey) and 2007 (black) by SIMPER routine for *Bifurcaria bifurcata* assemblages (a) and for *Cystoseira baccata* assemblage (b). Only species who contributed more than 2% are shown, with the exception of *B. bifurcata* and *C. baccata*. It is also shown the significance levels (asterisks) for the Mann-Whitney test detecting differences between years (*<0.05; **<0.01; ***<0.001).

Saccorhiza polyschides) dominated the lowest intertidal and the shallow subtidal assemblages in sheltered and semiexposed shores on the central and east coast of the North of Spain (Fernández and Niell, 1982; Díez et al., 1999; Guinda et al., 2012). *C. baccata* is another warm-temperate species whose distribution is expected to expand northwards (Hiscock et al., 2004) while *S. polyschides* and *L. ochroleuca* are expected to decline together with most of the kelps (Müller et al., 2009; Fernández, 2011; Díez et al., 2012; Voerman et al., 2013).

Contrary to expected, there was a significant decrease in the abundance of *Bifurcaria bifurcata* from 1977 to 2007, especially in summer. Lamela-Silvarrey et al. (2012) have already reported changes in the seasonal growth-decay cycle for other intertidal fucoids in the same locality, and summer seems to be a non-favourable period, even for warm-temperate species, such as *B. bifurcata*. The increasing trend of warm periods (SST>20 °C), combined with the time the species is exposed to severe aerial conditions in summer (approx. 2 h/day during spring tides), may exceed the physiological temperature threshold of the species (23 °C, Martínez et al., 2014). Since the intensity and duration of the summer upwelling have decreased (Lavín et al., 2000; Cabanas et al., 2003; Llope et al., 2006; Pérez et al., 2010; Santos et al., 2011), nutrient availability is low (Llope et al., 2007). Therefore, both temperature and nutrients availability may limit growth and recruitment (Wethey et al., 2011), which is an explanation for the deterioration of the population.

The canopy-forming species belonging to the assemblage of *Cystoseira baccata* show a change in line with predictions. Since *C. baccata* shows high acclimation capacity to increased

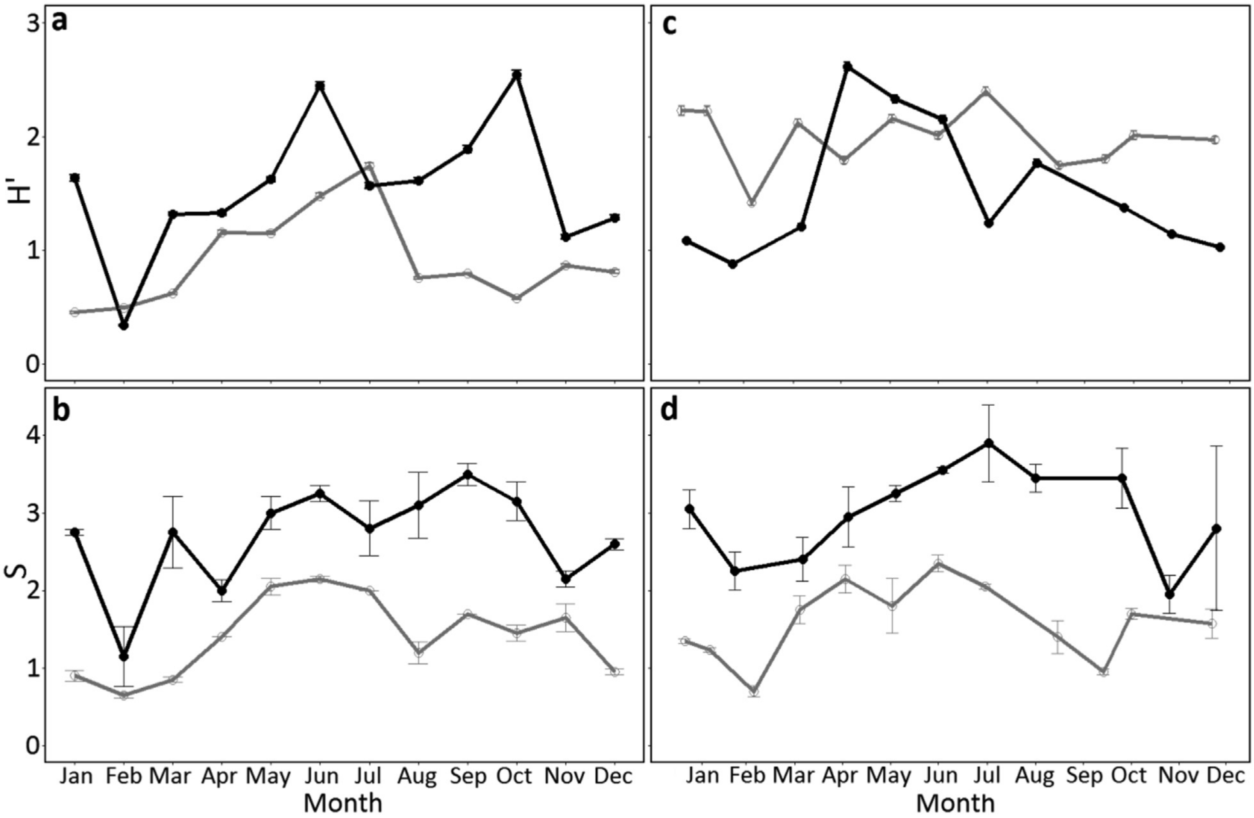

Fig. 5. Seasonal changes in the Shannon-Wiener index and species richness for *Bifurcaria bifurcata* assemblage (a and b, respectively) and for *Cystoseira baccata* assemblage (c and d, respectively). ○ 1977 (grey), ● 2007 (black). Bars indicate standard deviation.

temperature and irradiance (Miguel-Vijandi et al., 2010), it expanded its growth period to the autumn and nearly doubled its maximum of biomass. Other species of *Cystoseira*, such as *C. tamariscifolia*, also increased in biomass, and *Saccorhiza polyschides* practically disappeared.

These changes in the seasonal cycle of the dominant species have major effects on the structure of the assemblage, changing both the available space and the resources (Crowe et al., 2013). If there is a reduction in dominance by the species that monopolize the space, as we show in the case of *B. bifurcata*, the new allowable space might facilitate the settlement of other species, increasing the species richness and diversity. Most of the available space was covered by calcareous crustose algae, such as *Lithophyllum incrustans* and *Mesophyllum* spp., reducing the abundance of understory species such as *Cladostephus spongiousus*, *Pterosiphonia ardreana* and *Corallina elongata*. It is known that increasing temperature stimulates calcification, but the increase in light availability and water transparency should be considered (Díez et al., 2012). In the assemblage dominated by *Cystoseira baccata* there was a replacement of an annual canopy-forming species (*S. polyschides*) by a denser perennial canopy species (*C. tamariscifolia*), that affects the heterogeneity of the assemblage physical environment and the structure of the understory species. These shifts in species composition agree with the general kelp retreat detected along the Northern Spanish coast (Fernández, 2011; Díez et al., 2012; Voerman et al., 2013) and the poleward move of *Cystoseira* spp. already mentioned. Differences in thallus morphology and architecture also might be responsible of the observed changes in the species richness. This showed a considerable increase in 2007, mainly due to the presence of a great number of epiphytes, favoured by the roughness of the thallus of *Cystoseira* species.

Both assemblages showed the same pattern in terms of increasing species richness, and most of the new species belong to the simplest morphological and functional groups. From 1977 to 2007 the number of filamentous species has increased three-fold in the lower cases, and smaller-sized corticated or blade-like species have also increased. The large number of simpler morphological forms with short life cycle leads to a higher variations in time of the subcanopy. This evidence was already reported by Díez et al. (2012) for subtidal assemblages in the eastern coast of the North of Spain and by Araújo et al. (2009) on the coast of Portugal. However, while range shifts are widely studied for large species, simple and short-life species are scarcely considered.

Lamela-Silvarrey et al. (2012) have also detected changes in the intermediate and upper intertidal assemblages in the same locality, similarly to the results of the present study, and have attributed those shifts to climate change. Here, we have detected changes in the lower intertidal assemblages, but these results should only be considered as an evidence of change. With only two years of data, and not the complete time-series, it is not possible to infer causality. Nevertheless, there is clear evidence that shifts are taking place on the North Coast of Spain.

According to historical data (Sauvageau, 1897; Miranda, 1931; Fischer-Piette, 1957, 1963; Anadón and Niell, 1981; Fernández and Niell, 1982), shifts on the distribution patterns of canopy-forming seaweeds along the North coast of Spain have been occurring during the last century. In general terms, these shifts eastwards or westwards coincide with cold and warm SST periods. From 1854 onwards, two consecutive warm-cold periods were identified (DeCastro et al., 2009). The last warm period began in 1974 and continues, with an estimated increase of 0.17–0.22 °C per decade (DeCastro et al., 2009; Taboada and Anadón, 2012; IPCC, 2014). But SST is not the only causal factor responsible of these changes. The reduction in both, the strength and duration (number of days) of

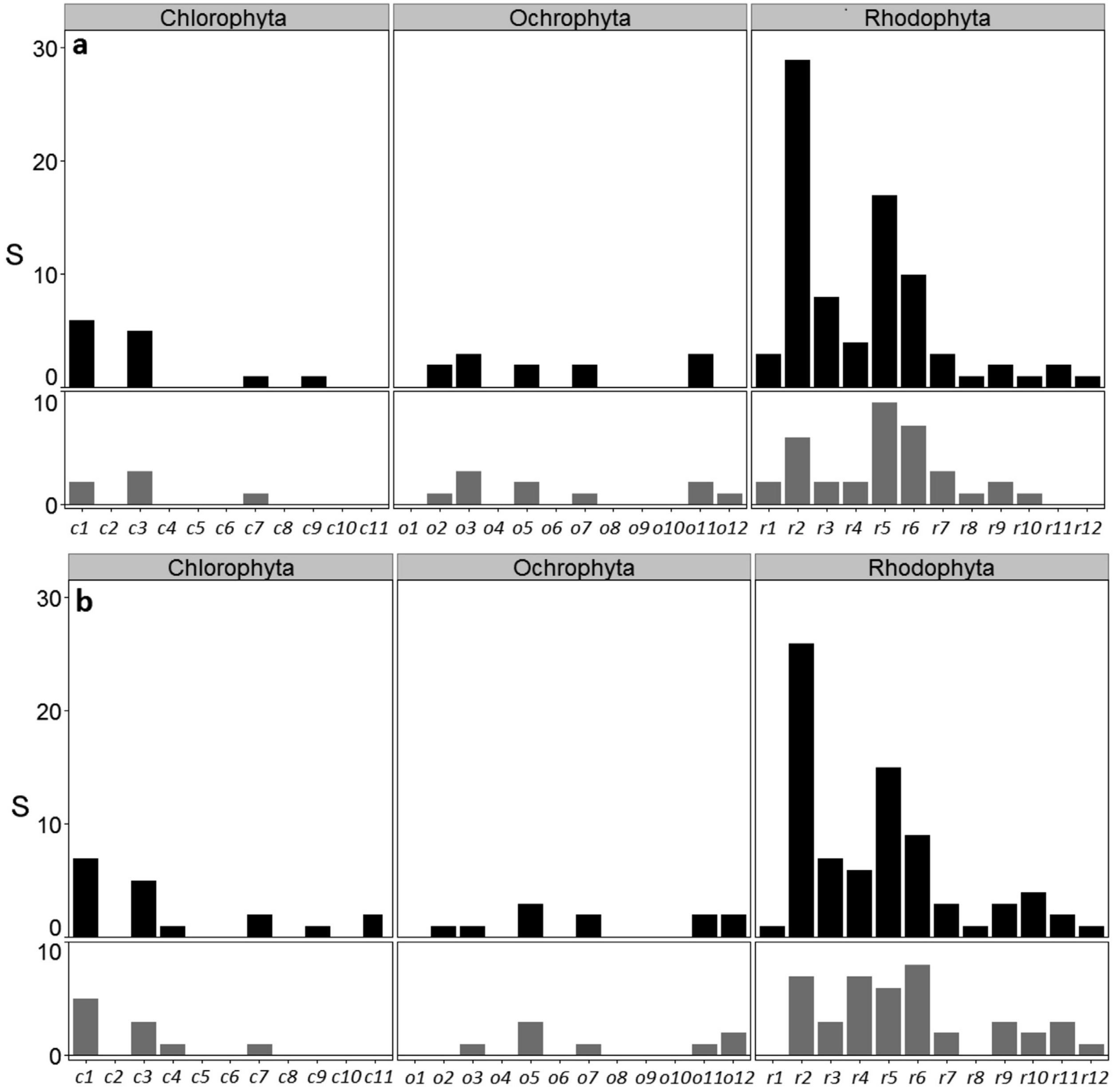

Fig. 6. Number of species (S) in each functional and morphological group for *Bifurcaria bifurcata* (a) and *Cystoseira baccata* assemblage (b) in 1977 (grey) and 2007 (black). Groups were ordered from the simplest to the more complex. Chlorophyta: Filamentous uniseriate (*c1*), palmelloid (*c2*), blade-like (*c3*), tubular (*c4*), siphonous with thin separate filaments (*c5*), siphonous with thin compacted filaments (*c6*), siphonous with vesicle-like thallus (*c7*), siphonous with dasyclad-like thallus (*c8*), siphonous with creeping axes (*c9*), codium with erect thallus (*c10*) and codium with encrusting thallus (*c11*). Ochrophyta: Filamentous uniseriate (*o1*), smaller-sized filamentous pluriseriate (*o2*), larger-sized filamentous pluriseriate (*o3*), compressed with blade-like habit (*o4*), compressed with branched or divided thallus (*o5*), tubular (*o6*), hollow with spherical or subspherical shape (*o7*), prostrate not strictly adherent to the substratum (o8), encrusting (*o9*), corticated macrophytes with cylindrical or compressed thallus (*o10*), thick leathery macrophytes (*o11*), kelp-like (*o12*). Rhodophyta: Filamentous uniseriate and pluriseriate with extensive prostrate filaments (*r1*), filamentous uniseriate and pluriseriate with erect thallus (*r2*), blade-like with one or few layers of cells (*r3*), flattened macrophytes with cortication (*r4*), smaller-sized corticated (*r5*), larger-sized corticated (*r6*), corticated with hollow thallus (*r7*), smaller-sized articulated corallines (*r8*), larger-sized articulate corallines (*r9*), prostrate not strictly adherent to the substratum (*r10*), encrusting calcified (*r11*), encrusting not calcified (*r12*).

the summer upwelling (Lavín et al., 2000; Cabanas et al., 2003; Llope et al., 2006; Anadón et al., 2009; Álvarez et al., 2010; Pérez et al., 2010; Santos et al., 2011) is another important factor to take into account. Consequently, these changes may affect other environmental factors such as a decrease in nutrients availability in summer (Llope et al., 2007) or a possible increase in water transparency (Díez et al., 2012) already reported for other European seas (Pehlke and Bartsch, 2008). These environmental changes allow warm-temperate species spread westwards along the north coast of Spain while cold-temperate species retreat to the northwest corner of the Iberian Peninsula or disappear (Díez et al., 2012; Fernández, 2011, 2016; Voerman et al., 2013).

But the response is species-specific, since it depends on the life history traits of each species (Sexton et al., 2009) Under this scenario, the species respond to an increase of temperature and a decrease in the importance of the summer upwelling by shifts in their climatic niches: changes in phenology (Lamela-Silvarrey et al., 2012) in the range of distribution and, possibly in physiology (Bellard et al., 2012). But apart from that, we have also to consider the importance of extreme events (Wethey et al., 2011), especially heat waves (García-Herrera et al., 2010) affecting the species in the emersion times.

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Appendix 1. SIMPER routine results for (a) *Bifurcaria bifurcata* and (b) *Cystoseira baccata* assemblages.

(a) *Bifurcaria bifurcata* assemblage

Examines Year groups (across all Season groups)

Group 1977

Average similarity: 68.36

Species	Av.Abund	Contrib%	Cum.%
Bifurcaria bifurcata	14.02	72.47	72.47
Halopteris scoparia	1.68	5.81	78.28
Ellisolandia elongata	1.8	5.54	83.81
Cladostephus spongiosus	1.32	5.14	88.95
Ulva rigida	1.06	3.23	92.19

Group 2007

Average similarity: 63.05

Species	Av.Abund	Contrib%	Cum.%
Bifurcaria bifurcata	11.43	59.36	59.36
Gelidium spinosum	2.16	7.62	66.97
Halopteris scoparia	2.01	5.72	72.7
Mesophyllum lichenoides	1.88	4.42	77.12
Lythophyllum incrustans	2.55	4.38	81.5
Gigartina pistillata	0.98	3.01	84.51
Ellisolandia elongata	1.08	2.5	87.01
Chondracanthus acicularis	0.59	1.25	88.25
Pterosiphonia complanata	0.47	0.95	89.21
Pterosiphonia ardreana	0.36	0.93	90.13

Groups 1977 & 2007

Average dissimilarity = 44.76

Species	1977 Av.Abund	2007 Av.Abund	Contrib%	Cum.%
Bifurcaria bifurcata	14.02	11.43	11.28	11.28
Lythophyllum incrustans	0	2.55	9.41	20.69
Gelidium spinosum	0.93	2.16	6.52	27.21
Mesophyllum lichenoides	0	1.88	6.21	33.42
Ellisolandia elongata	1.8	1.08	5.48	38.9
Halopteris scoparia	1.68	2.01	5.44	44.33
Cladostephus spongiosus	1.32	0.33	4.29	48.63
Gigartina pistillata	0.19	0.98	4.11	52.74
Ophidocladus simpliciusculus	0.54	0.47	3.23	55.97
Chondrus crispus	0.58	0.34	3.15	59.12
Ulva rigida	1.06	0.3	2.84	61.96
Pterosiphonia ardreana	0.63	0.36	2.81	64.77
Gelidium pulchellum	0.52	0.36	2.57	67.33
Jania rubens	0.44	0.38	2.3	69.63
Chondracanthus acicularis	0.02	0.59	2.09	71.72
Pterosiphonia complanata	0.23	0.47	2.05	73.77
Gymnogongrus crenulatus	0.21	0.39	1.62	75.39
Corallina officinalis	0.51	0.13	1.62	77.01
Calliblepharis jubata	0	0.38	1.36	78.37
Ceramium echionotum	0	0.41	1.32	79.7
Gymnogongrus griffithsiae	0.33	0	1.32	81.01
Osmundea pinnatifida	0.24	0.11	1.03	82.04
Ceramium gaditanum	0.28	0.01	0.92	82.96
Pleonosporium borreri	0.06	0.23	0.83	83.79
Gastroclonium ovatum	0	0.25	0.82	84.61
Ceramium diaphanum	0.21	0.01	0.74	85.34
Gelidium corneum	0.21	0.02	0.72	86.06
Peyssonnelia dubyi	0	0.15	0.7	86.76
Cutleria multifida	0.21	0	0.66	87.41
Asparagopsis armata	0	0.13	0.59	88.01
Audouinella	0.05	0.09	0.58	88.58
Polysiphonia denudata	0.14	0.01	0.5	89.08
Gayliella flaccida	0	0.14	0.48	89.56
Hypoglossum hypoglossoides	0	0.09	0.43	89.99
Gastroclonium reflexum	0.04	0.07	0.4	90.39

(b) *Cystoseira baccata* assemblage

Examines Year groups (across all Season groups)

Group 1977

Average similarity: 71.51

Species	Av.Abund	Contrib%	Cum.%
Cystoseira baccata	10.57	39.29	39.29
Saccorhiza polyschides	4.6	16.47	55.76
Gelidium spinosum	4.67	13.86	69.62
Gelidium corneum	3.63	12.3	81.93
Chondrus crispus	3.09	6.66	88.59
Ellisolandia elongata	1.66	4.47	93.06

Group 2007

Average similarity: 66.86

Species	Av.Abund	Contrib%	Cum.%
Cystoseira baccata	16.23	55.38	55.38
Gelidium spinosum	3.99	10.13	65.51
Gelidium corneum	4.38	9.96	75.47
Calliblepharis jubata	1.83	4.8	80.28
Corallina officinalis	1.59	4.15	84.42
Gymnogongrus crenulatus	0.6	1.71	86.13
Chondrus crispus	1.08	1.65	87.79
Pterosiphonia complanata	0.85	1.51	89.29
Sargassum muticum	1.54	1.46	90.76

Groups 1977 & 2007

Average dissimilarity = 49.55

Species	1977 Av.Abunc	2007 Av.Abund	Contrib%	Cum.%
Cystoseira baccata	10.57	16.23	16.48	16.48
Saccorhiza polyschides	4.6	0.19	12.01	28.49
Chondrus crispus	3.09	1.08	7.26	35.75
Gelidium spinosum	4.67	3.99	6.39	42.14
Gelidium corneum	3.63	4.38	6.24	48.38
Corallina officinalis	1.07	1.59	5.2	53.58
Calliblepharis jubata	0	1.83	4.68	58.26
Ellisolandia elongata	1.66	0.22	4.01	62.27
Sargassum muticum	0	1.54	3.91	66.18
Cystoseira tamariscifolia	0	1.57	3.63	69.81
Gigartina pistillata	0	0.87	2.52	72.33
Pterocladiella capillacea	0.11	0.93	2.3	74.63
Pterosiphonia complanata	0.03	0.85	2.08	76.71
Gymnogongrus crenulatus	0.89	0.6	2.02	78.73
Mesophyllum lichenoides	0.48	0.57	1.94	80.67
Plocamium cartilagineum	0.45	0.67	1.73	82.4
Ulva rigida	0.26	0.85	1.63	84.03
Halopteris scoparia	0.03	0.6	1.48	85.51
Sphacelaria fusca	0.12	0.34	1.11	86.62
Hypnea musciformis	0.38	0	0.91	87.53
Lomentaria articulata	0.01	0.27	0.8	88.32
Schizymenia dubyi	0.25	0	0.58	88.9

(a) *Bifurcaria bifurcata* assemblage

Examines Season groups (across all Year groups)

Group Winter

Average similarity: 66.99

Species	Av.Abund	Contrib%	Cum.%
Bifurcaria bifurcata	11.58	75.81	75.81
Halopteris scoparia	1.54	5.84	81.64
Cladostephus spongiosus	0.79	3.49	85.14
Ellisolandia elongata	1.15	2.9	88.04
Gigartina pistillata	0.68	2.29	90.33

Group Summer

Average similarity: 64.62

Species	Av.Abunc	Contrib%	Cum.%
Bifurcaria bifurcata	13.87	56.16	56.16
Gelidium spinosum	2.36	6.71	62.87
Halopteris scoparia	2.16	5.69	68.56
Ellisolandia elongata	1.73	5.3	73.86
Mesophyllum lichenoides	1.68	4.16	78.03
Ulva rigida	1.15	3.45	81.48
Lythophyllum incrustans	1.52	2.85	84.33
Cladostephus spongiosus	0.87	2.43	86.76
Chondrus crispus	0.65	1.13	87.89
Gelidium pulchellum	0.66	1.02	88.91
Chondracanthus acicularis	0.5	0.98	89.89
Corallina officinalis	0.64	0.88	90.77

Groups Winter & Summe

Average dissimilarity = 42.20

Species	Winter Av.Abund	Summer Av.Abund	Contrib%	Cum.%
Bifurcaria bifurcata	11.58	13.87	11.43	11.43
Gelidium spinosum	0.73	2.36	8.52	19.95
Mesophyllum lichenoides	0.2	1.68	5.96	25.91
Halopteris scoparia	1.54	2.16	5.95	31.85
Lythophyllum incrustans	1.03	1.52	5.67	37.53
Ellisolandia elongata	1.15	1.73	5.47	43
Ulva rigida	0.21	1.15	4.3	47.3
Chondrus crispus	0.27	0.65	3.61	50.91
Ophidocladus simpliciusculu	0.45	0.56	3.39	54.3
Pterosiphonia ardreana	0.33	0.67	3.12	57.42
Gelidium pulchellum	0.22	0.66	3.01	60.42
Cladostephus spongiosus	0.79	0.87	2.79	63.22
Corallina officinalis	0	0.64	2.73	65.94
Gigartina pistillata	0.68	0.49	2.6	68.55
Jania rubens	0.31	0.51	2.37	70.91
Pterosiphonia complanata	0.28	0.43	1.98	72.89
Chondracanthus acicularis	0.11	0.5	1.72	74.61
Gymnogongrus crenulatus	0.4	0.2	1.63	76.25
Ceramium echionotum	0.01	0.39	1.53	77.78
Ceramium gaditanum	0.01	0.28	1.23	79.01
Pleonosporium borreri	0.03	0.27	1.08	80.1
Osmundea pinnatifida	0.13	0.21	1.07	81.17
Gymnogongrus griffithsiae	0.13	0.2	1.06	82.23
Calliblepharis jubata	0.1	0.29	1.03	83.26
Ceramium diaphanum	0.01	0.21	0.98	84.24
Gelidium corneum	0.02	0.21	0.93	85.18
Cutleria multifida	0	0.21	0.91	86.09
Gastroclonium ovatum	0.02	0.23	0.84	86.93
Polysiphonia denudata	0.01	0.14	0.65	87.58
Audouiniella	0.14	0	0.54	88.12
Peyssonnelia dubyi	0.13	0.03	0.51	88.63
Pterocladiella capillacea	0	0.12	0.49	89.12
Schizymenia dubyi	0	0.11	0.46	89.59
Boergeseniella thuyoides	0.01	0.1	0.45	90.04

(b) *Cystoseira baccata* assemblage

Examines Season groups (across all Year groups)

Group Winter

Average similarity: 71.26

Species	Av.Abund	Contrib%	Cum.%
Cystoseira baccata	12.91	51.75	51.75
Gelidium corneum	3.7	11.51	63.26
Saccorhiza polyschides	2.17	10.58	73.84
Gelidium spinosum	3.17	9.9	83.75
Chondrus crispus	2.75	5.31	89.06
Corallina officinalis	1.08	3.16	92.22

Group Summer

Average similarity: 67.12

Species	Av.Abund	Contrib%	Cum.%
Cystoseira baccata	13.9	42.09	42.09
Gelidium spinosum	5.49	14.35	56.44
Gelidium corneum	4.31	10.81	67.25
Saccorhiza polyschides	2.63	6.41	73.66
Ellisolandia elongata	1.69	4.72	78.38
Calliblepharis jubata	1.24	3.11	81.49
Chondrus crispus	1.43	3.11	84.6
Gymnogongrus crenulatus	0.95	2.15	86.75
Corallina officinalis	1.58	2.05	88.79
Ulva rigida	1.06	1.41	90.2

Groups Winter & Summer

Average dissimilarity = 37.34

Species	Winter Av.Abund	Summer Av.Abund	Contrib%	Cum.%
Gelidium spinosum	3.17	5.49	10.64	10.64
Cystoseira baccata	12.91	13.9	9.42	20.06
Chondrus crispus	2.75	1.43	8.73	28.79
Gelidium corneum	3.7	4.31	8.02	36.81
Ellisolandia elongata	0.19	1.69	6.82	43.63
Corallina officinalis	1.08	1.58	5.76	49.39
Saccorhiza polyschides	2.17	2.63	4.95	54.34
Cystoseira tamariscifolia	0.44	1.13	4.1	58.44
Ulva rigida	0.05	1.06	3.38	61.82
Sargassum muticum	0.61	0.93	3.02	64.84
Gymnogongrus crenulatus	0.55	0.95	2.91	67.75
Mesophyllum lichenoides	0.53	0.52	2.42	70.17
Plocamium cartilagineum	0.5	0.62	2.15	72.32
Calliblepharis jubata	0.59	1.24	2.11	74.43
Pterocladiella capillacea	0.4	0.64	2.01	76.44
Gigartina pistillata	0.48	0.39	1.78	78.22
Pterosiphonia complanata	0.23	0.64	1.68	79.91
Halopteris scoparia	0.13	0.5	1.56	81.47
Hypnea musciformis	0.03	0.36	1.42	82.89
Sphacelaria fusca	0.18	0.29	1.37	84.25
Elachista flaccida	0.01	0.32	1.23	85.48
Schizymenia dubyi	0	0.25	1.02	86.5
Lomentaria articulata	0.15	0.14	0.73	87.24
Laminaria ochroleuca	0	0.17	0.69	87.92
Cryptopleura ramosa	0.02	0.22	0.67	88.6
Cutleria multifida	0	0.21	0.67	89.26
Nitophyllum punctatum	0.02	0.16	0.63	89.89
Dictyota dichotoma	0.12	0.16	0.62	90.51

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