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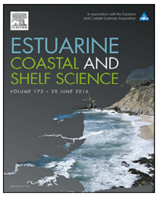

Changes in the structure and dynamics of marine assemblages dominated by *Bifurcaria bifurcata* and *Cystoseira* species over three decades (1977–2007)

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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*.

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 g DW · 0.25 m^{-2}). In 2007, only two periods of growth were detected, one