



Decades of biomass loss in the shallow rocky subtidal vegetation of the south-eastern Bay of Biscay

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Abstract

This study seeks to assess changes over time in the structure of subtidal macroalgal assemblages across depth in the south-eastern Bay of Biscay. The results reveal a large-scale decline in total macroalgal biomass between 1982 and 2014. However, the temporal pattern of shift differs from one depth to another: total biomass decreased at depths from 3 to 10 m, but increased at depths of 2 and 11 m. The strong decrease in biomass detected in the 3–10-m depth range is a consequence of a sharp net decline in large macroalgae biomass which was not offset by increased biomass of small species, mainly corresponding to turf-forming algae. The dominant canopy-forming *Gelidium corneum* in 1982 had practically disappeared by the end of the study period and its biomass loss was far from being offset by the small increase detected in the fucoid *Gongolaria baccata*. By contrast, at depths of 2 and 11 m, the most notable result is an increase in large species, mainly *Halopithys incurva* and *Codium decorticans* at 2 m and *G. baccata* at 11 m; however, at both depth levels, a new canopy was far from being developed. These findings evidence that biomass and habitat provision, two pivotal roles of canopy-forming species in ecosystem functioning, have been altered. Further research into potential changes in primary productivity and biodiversity linked to the shift detected in assemblage structure needs to be conducted in order to get information for conservation and management decisions associated with the loss of habitat-forming macroalgae.

Keywords Climate change · Macroalgal community · Species composition · Subtidal assemblages

Introduction

Canopy-forming macroalgae usually form extensive stands in rocky benthic subtidal communities in most temperate regions (Steneck et al. 2002; Smale et al. 2013; Strain et al. 2014). These large, often perennial macroalgae play a very important role in marine ecosystems as they create structurally complex assemblages analogous to forests on land (Ballesteros et al. 2009; Reed and Foster 2012; Gianni et al. 2013), i.e. they are foundation species. In this regard, these macroalgae increase three-dimensional complexity by providing biogenic habitats and protection for a great variety of marine organisms

(Steneck et al. 2002; Wernberg et al. 2011; Smale et al. 2013). They also act as ecosystem engineers, since they substantially modify the local environment by changing light conditions (Wernberg et al. 2005), water flow (Rosman et al. 2007) and sedimentation rates (Eckman et al. 1989) in ways that favour the settlement of other organisms. Canopy-dominated assemblages constitute some of the most diverse and productive ecosystems anywhere in the world, contribute significantly to nearshore primary productivity and also enhance secondary productivity (Mann 2000; Steneck et al. 2002; Tait and Schiel 2011; Smale et al. 2013). In addition, these foundation species supply many valuable ecosystem services such as reducing coastal erosion, CO₂ sinking, nutrient cycling and water quality control (Airoldi and Beck 2007; Smale et al. 2013; Wernberg et al. 2016).

However, in the last 30 years, drastic declines in these foundation species have been observed as a consequence of multiple anthropogenic pressures comprising harvesting, pollution, sedimentation, invasive species, overgrazing due to a decline in grazer predators, fishing nets, recreation and ocean warming (Steneck et al. 2002; Serisawa et al. 2004; Connell

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et al. 2008; Perkol-Finkel and Airoldi 2010; Smale et al. 2013; Mineur et al. 2015; Krumhansl et al. 2016; Wernberg et al. 2016). Whatever is driving the decline, a shift to less structurally complex communities dominated by turf-forming, filamentous or ephemeral macroalgae has been widely documented (Airoldi et al. 2008; Mangialajo et al. 2008; Perkol-Finkel and Airoldi 2010; Tait and Schiel 2011). To date, there has been little evidence of foundation species recovering from disturbances (Dayton et al. 1992, Martínez and Cárdenas 2003), mainly because once less structurally complex communities are established they may inhibit recolonisation by canopy species, resulting in alternative stable states (Strain et al. 2014; Wernberg et al. 2016). Loss of large perennial macroalgae in favour of less structured communities may have consequences for the whole ecosystem, and in this connection, numerous studies have linked the retreat of these ecosystem engineers to a decrease in species richness and abundance (Graham 2004; Norderhaug et al. 2007; Schiel and Lilley 2007; Wikström and Kautsky 2007), homogenisation with neighbouring habitats (Mangialajo et al. 2008) and loss of productivity (Tait and Schiel 2011; Crowe et al. 2013).

In the particular case of the south-eastern Bay of Biscay, local retreats in subtidal perennial canopy-forming *Gelidium corneum*, *Laminaria ochroleuca* and *Gongolaria baccata* (formerly *Cystoseira baccata*) have been reported in the past few decades (Díez et al. 2012; Borja et al. 2013, 2018; Muguerza et al. 2017, 2020). In addition to canopy decline, there has been an increase over the same period in richness and abundance of warm-affinity species (mainly ephemeral forms with simple morphology), coralline algae and crustose species have become abundant, and non-indigenous species have expanded (Díez et al. 2012; Muguerza et al. 2017). These studies point out that higher temperatures are probably the main driver of the changes observed. Indeed, a warming of 0.26 ± 0.03 °C every 10 years was detected in the Bay of Biscay for 1982–2014 (Costoya et al. 2015). However, other local factors such as nutrient availability, solar radiation, sunlight hours and wave height have been suggested as potential co-acting factors of change in combination with warming (Díez et al. 2012; Borja et al. 2013, 2018; Muguerza et al. 2017).

Most of the aforementioned research papers provide information on species abundance in terms of cover, but little information about loss of biomass due to canopy decline is available for the south-eastern Bay of Biscay. Only Borja et al. (2013) provide data on changes in *G. corneum* biomass for the eastern Basque coast, where a drastic reduction in its standing stock of about 7800 t across 30 km has been documented for 1993–2012. However, no data on the variability over time of the biomass of other species and areas are available. This paper seeks to assess changes over time (three sampling surveys: 1982, 2007 and 2014) in the structure of subtidal macroalgal assemblages in terms of composition

and taxon biomass in the westernmost part of the Basque coast. These assemblages can be considered representative of the south-eastern Bay of Biscay since they are distributed along large stretches of coastline in this region (Gorostiaga et al. 1998; Díez et al. 2003).

Materials and methods

Study area

The study area lies at the eastern end of the Cantabrian Sea (Northern Spain), on the south-eastern Bay of Biscay. It is over 192 km in length and is open to strong waves coming mostly from the NW, with an average height of 1.9 m (Díez et al. 2003; González et al. 2004; Galparsoro et al. 2010). The south-eastern Bay of Biscay is exposed to highly exposed to the prevailing NW swells, with high, mostly erosional, energy. It also features extensive vertical cliffs and abrasion platforms interspersed with sandy beaches. In shallow waters in the study area, the rocky bottom is almost continuous, but it becomes sandy as depth increases (Chust et al. 2011). The flora belongs to the warm temperate NE Atlantic Region according to the biogeographical scheme proposed by van den Hoek and Breeman (1990).

The study was carried out on a stretch of shoreline about 1.8 km long, between the locations of Kobaron and Muskiz ($43^{\circ}35'34''\text{N}$ $03^{\circ}15'44''\text{W}$ and $43^{\circ}35'52''\text{N}$ $03^{\circ}12'94''\text{W}$, respectively), in the province of Bizkaia (Fig. 1).

Field sampling and processing

The biomass of taxa composing in macroalgal assemblages was studied at six different depths (2, 3, 6, 9, 10 and 11 m) along seven transects in three sampling surveys (1982, 2007 and 2014). Each transect was set perpendicular to the coastline following a north-south orientation with a starting point at 2 m below extremely low tides (Fig. 1). Within each transect, a surface area of 2000 cm² was delimited at each depth using quadrats of 40 × 50 cm placed systematically at the midpoint of the cross section of the transect. This means that there were six quadrats per transect across each depth profile and sampling survey. In some transects, it was not possible to sample at certain depths due to a lack of appropriate substrate (continuous bedrock with slight to moderate slopes of <30°). Each surface was destructively sampled, with all macroalgal species within the quadrat being collected except the mostly calcareous crustose layer, which was not sampled. Once in the laboratory, samples were kept frozen in labelled plastic bags. For analysis, samples were thawed and the macroalgae were separated and identified. Algal taxonomy was updated following AlgaeBase (Guiry and Guiry 2021). The dry weight (DW) in

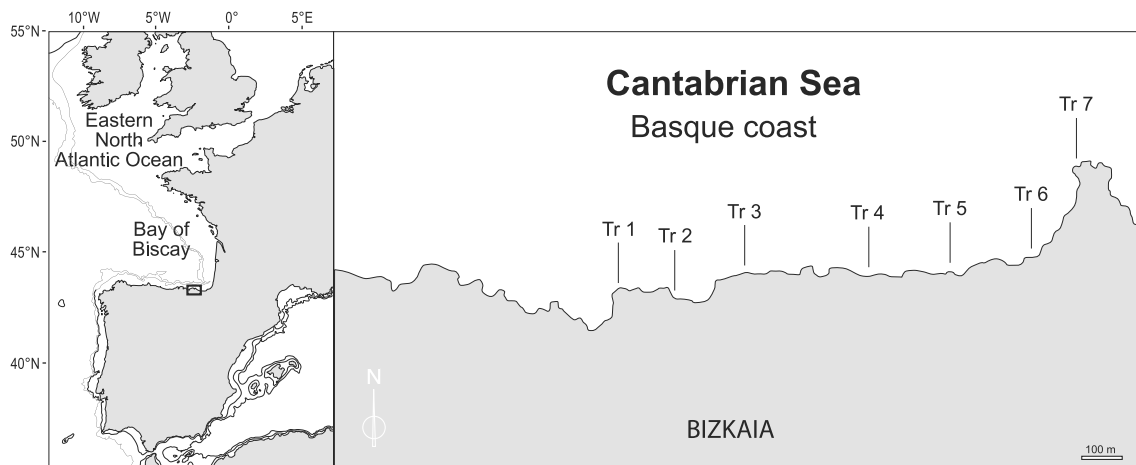


Fig. 1 Study area. Layout of the seven transects along the western end of the coast of Bizkaia. (Source: modified from Díez et al. 2000)

grammes (100–110 °C, 24 h) was then obtained for each species.

Statistical analysis

Multivariate analyses were performed in order to explore the spatio-temporal variability of the structure of assemblages in terms of composition and taxon biomass. Prior to analysis, the biomass values for each taxon were square root transformed to reduce the influence of the dominant ones. The similarity between pairs of samples was calculated using the Bray-Curtis index. The hypothesis that time and depth have no influence on the structure of macroalgal assemblages was tested by means of PERMANOVA (permutational multivariate analysis of variance, see Anderson et al. 2008) with an a priori chosen significance level of $\alpha = 0.05$. The design of the experiment was as follows: time (Year; set with three levels: 1982, 2007 and 2014) and depth (Depth; random with six levels: 2, 3, 6, 9, 10 and 11). Post hoc pairwise comparisons were performed using Gosset’s *t*-statistic to investigate the significant terms of the PERMANOVA (Anderson et al. 2008). In order to graphically visualise this spatio-temporal variation, a non-metric multidimensional scaling (nMDS) was conducted. Given that PERMANOVA tests the null hypothesis that centroids and/or dispersion of the groups defined by the factors of the experimental design is equivalent, we performed a permutational test for homogeneity of multivariate dispersions (PERMDISP) to check for differences in dispersion between the levels within the Year factor. By applying classification analysis (CLUSTER), samples were segregated into different groups according to their similarities. This analysis was followed by a similarity percentage (SIMPER) analysis to calculate the contribution of each taxon (%) to the dissimilarity between the clustering groups. All statistical analyses and the aforementioned routines were performed using the PERMANOVA+ for PRIMER6 software package (Clarke and Gorley 2006).

Results

The survey carried out in 1982 identified a total of 55 taxa, 94 species were documented in 2007 and 65 in 2014. Across all three surveys, the most widely represented phylum was Rhodophyta, with a total of 92 taxa, followed by Ochrophyta with 13 and Chlorophyta with 12 (Table 4).

PERMANOVA results (Table 1) show the partitioning of sample variation in the multivariate space based on the Bray-Curtis similarity in response to the Year and Depth factors. Differences between depths in the pattern of temporal change were detected, given that the Year x Depth interaction was significant ($p = 0.0028$). Pairwise comparisons reveal that at

Table 1 Summary of PERMANOVA results testing for the effect of Year (Y), Depth (D) and the interaction of the two factors (Y x D) on the community structure in terms of composition and taxon biomass. Pairwise comparisons for significant terms are shown at the bottom of the table

PERMANOVA					
	df	SS	MS	Pseudo-F	<i>p</i>
Y	2	59,978	29,989	9.929	0.0001
D	5	49,146	9829.2	4.61	0.0001
Y x D	10	32,517	3251.7	1.525	0.0028
Residuals	85	1.81E+05	2132.1		
Total	102	3.29E+05			
Pairwise comparisons					
	2 m	3 m		6 m	
	1982=2007	1982≠2007		1982≠2007	
	1982≠2014	1982≠2014		1982≠2014	
	2007≠2014	2007≠2014		2007≠2014	
	9 m	10 m		11 m	
	1982≠2007	1982≠2007		1982≠2007	
	1982≠2014	1982≠2014		1982≠2014	
	2007=2014	2007=2014		2007=2014	

Table 2 Summary of the test for homogeneity of multivariate dispersions (PERMDISP) based on the Bray-Curtis similarity matrix testing for Year. Pairwise comparisons for Year are shown

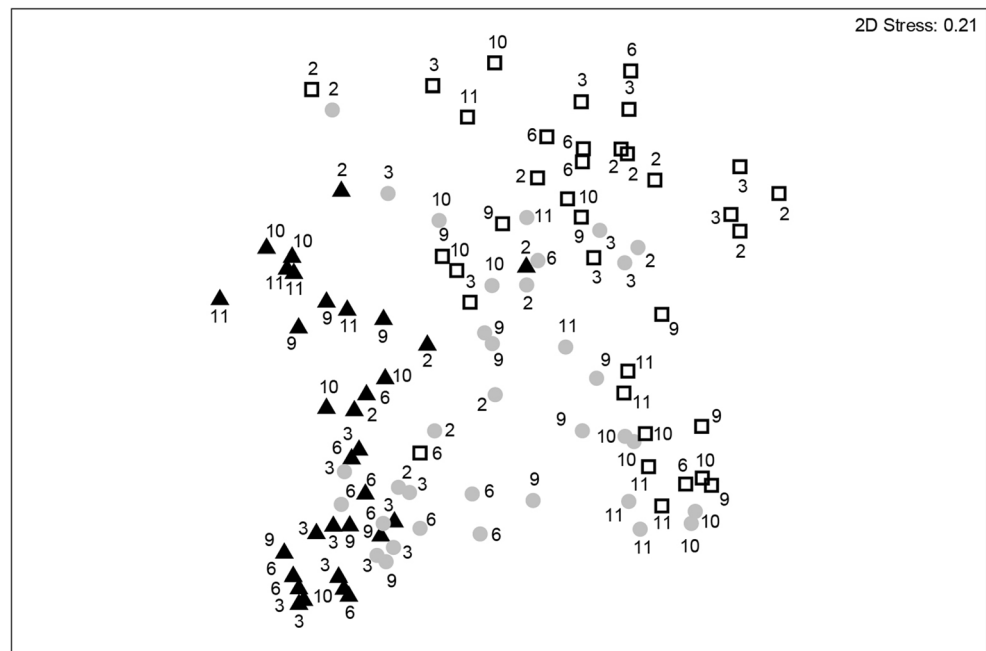
PERMDISP		
	Av. distance	SE
1982	44.958	2.069
2007	51.076	1.077
2014	52.591	1.278
Pairwise comparisons		
	<i>t</i>	<i>P</i>
1982 vs. 2007	2.688	0.017
1982 vs. 2014	3.214	0.004
2007 vs. 2014	0.904	0.369

a depth of 2 m, significant changes in the structure of assemblages start to occur in 2007. At depths of 3 and 6 m, significant differences are detected from 1982 onwards, whilst at depths from 9 to 11 m, the structure of assemblages changed between 1982 and 2007 but has not changed significantly since then (Table 1). Non-metric multidimensional scaling (nMDS) (Fig. 2) shows the PERMANOVA results in graphic form. A gradual shift in the structure of assemblages is found across the sampling surveys (1982, 2007 and 2014). The permutational test for homogeneity of multivariate dispersions (PERMDISP) for the Year factor shows an increase in multivariate dispersion from 1982 to 2007, indicating a rise in the heterogeneity of vegetation. However, no differences in the dispersion of samples are found between 2007 and 2014 (Table 2; Fig. 2).

In the dendrogram resulting from classification analysis (CLUSTER) of samples, two main groups, A and B, are distinguished at a similarity level of 14% (Fig. 3). Group A (average similarity between samples 42.9%) consists mainly of samples from 1982 but also contains some samples from 2007 and one from 2014. The samples from 2007 are all from depths of 3 and 6 m except for two which come from 2 and 9 m (Fig. 3). Group B (average similarity between samples 24.8%) comprises the rest of the samples from 2007 and 2014 and two samples from 1982 taken at a depth of 2 m (Fig. 3). The similarity percentage (SIMPER) analysis points to *Gelidium corneum* as the main species responsible for the separation of these two groups, with a contribution of 26.9%. The mean biomass of this rhodophyte is higher in group A. Apart from *G. corneum*, other species which make noteworthy contributions (>2%) to group A are *Pterosiphonia complanata*, *Plocamium cartilagineum*, *Asparagopsis armata* and *Dictyopteris polypodioides*. Of these species, *P. complanata*, *P. cartilagineum* and *D. polypodioides* are more abundant in group A, whilst the biomass of *A. armata* is similar in both groups. In addition to the lower presence of *G. corneum*, group B also shows a mosaic distribution of many species, dominated by *Gongolaria baccata*, *Codium decorticatum*, *Halopithys incurva* and *Corallina* spp. It is also noteworthy that this group shows a greater abundance of morphologically simple forms such as *Aphanocladia stichidiosa*, *Lychaete pellucida*, *Aglaothamniom pseudobyssoides* or *Microcladia glandulosa*, among others (Table 3).

Group A is divided into two subgroups (A1 and A2) at a similarity level of 24% (Fig. 3). Subgroup A1 consists of

Fig. 2 Non-metric MDS ordination analysis based on the Bray-Curtis similarity index showing sample distribution in relation to sampling surveys (1982, 2007 and 2014) and depths (2, 3, 6, 9, 10 and 11 m). Data are square root transformed. Black triangles: 1982; grey circles: 2007; white squares: 2014



samples from 1982 and the aforementioned samples from 2007 and 2014, mostly from depths of 3 and 6 m. These samples are characterised by the dominance of *G. corneum* accompanied mainly by *P. cartilagineum* (Table 3). By contrast, subgroup A2 comprises samples from 1982, mainly from deeper waters. In this case, the abundance of *G. corneum* is notably lower and the species that shows the greatest abundance is *P. complanata* (Table 3). Other species that show considerable biomass values are *A. armata*, *D. polypodioides*, *Calliblepharis ciliata* and *Heterosiphonia plumosa*, all of which are more abundant in subgroup A2 than in subgroup A1. The latter subgroup (samples from depths of 3 and 6 m) is divided, in turn, into two groups (A1.1 and A1.2) at a similarity level of 59% (Fig. 3). Subgroup A1.1 consists of samples from 1982 plus two samples from 2007, whilst subgroup A1.2 comprises the remaining samples from 2007 and the single sample from 2014. The dominant

species in both subgroups is *G. corneum*, but its abundance in subgroup A1.1 is greater. Other significant macroalgae in terms of biomass in the latter subgroup are *P. cartilagineum*, *P. complanata*, *D. polypodioides* and *Desmarestia ligulata*. In subgroup A1.2, the taxa with notable abundances are *G. baccata*, *Callithamnion tetragonum*, *P. cartilagineum*, *Dictyota dichotoma*, *A. armata*, *Rhodymenia pseudopalmata* and *Corallina* spp. The first two of these species are not found in subgroup A1.1 whilst the others all show higher biomass values in subgroup A1.2 (Table 3).

Group B is divided into two subgroups (B1 and B2) at a similarity level of 17% (Fig. 3). Subgroup B1 is represented mainly by deeper samples from 2007 and 2014, with *G. baccata* as the dominant species (Table 3). Other species with noteworthy biomass values include *Phyllophora crispa*, and *Corallina* spp. Subgroup B2 mainly comprises shallower

Table 3 Summary of the SIMPER test indicating the average biomass (Av.Bio; g DW · 2000 cm⁻²) of each taxon and its contribution (C (%)) to the differentiation of the subgroups identified in the classification analysis. The biomass values expressed in this table are untransformed.

Only taxa that contribute more than 2% in any subgroup comparison are shown. The average dissimilarity (Av. Diss.) between subgroups is also indicated. ⁽¹⁾*Ellisolandia elongata* and *C. officinalis*; ⁽²⁾*P. harveyana* and *P. squamaria*

Taxa	Av. Diss. = 87.23%			Av. Diss. = 78.86%			Av. Diss. = 42.72%			Av. Diss. = 85.15%		
	Subgroups			Subgroups			Subgroups			Subgroups		
	A	B	C (%)	A1	A2	C (%)	A1.1	A1.2	C (%)	B1	B2	C (%)
	Av.Bio.	Av.Bio.	C (%)	Av.Bio.	Av.Bio.	C (%)	Av.Bio.	Av.Bio.	C (%)	Av.Bio.	Av.Bio.	C (%)
<i>Acrosorium ciliolatum</i>	-	-	-	-	-	-	0.00	0.12	2.4	-	-	-
<i>Aglaothamnion pseudobyssoides</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aphanocladia stichidiosa</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Asparagopsis armata</i>	0.77	0.79	3.26	0.10	2.86	6.0	0.06	0.21	3.7	0.16	0.90	2.8
<i>Calliblepharis ciliata</i>	-	-	-	0.00	1.56	5.3	-	-	-	-	-	-
<i>Callithamnion tetragonum</i>	-	-	-	-	-	-	0.00	0.15	3.0	-	-	-
<i>Cladostephus spongiosum</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Codium decorticatedum</i>	0.18	1.72	6.39	-	-	-	-	-	-	0.01	5.81	7.6
<i>Corallina</i> spp. ⁽¹⁾	0.21	1.10	3.57	-	-	-	0.04	0.10	2.7	1.06	1.25	4.0
<i>Cryptopleura ramosa</i>	-	-	-	-	-	-	-	-	-	0.67	0.01	2.5
<i>Desmarestia ligulata</i>	-	-	-	-	-	-	0.18	0.00	3.1	-	-	-
<i>Dictyopteris polypodioides</i>	0.66	0.09	2.39	0.12	1.66	5.0	0.28	0.00	4.1	-	-	-
<i>Dictyota dichotoma</i>	-	-	-	0.14	0.10	2.0	0.03	0.72	61	-	-	-
<i>Gelidium corneum</i>	8.03	0.56	26.94	124.32	3.24	37.8	167.44	62.73	37.1	0.20	0.37	2.6
<i>Gelidium spinosum</i>	-	-	-	-	-	-	-	-	-	0.27	0.18	2.5
<i>Gongolaria baccata</i>	0.25	2.62	8.59	-	-	-	0.00	1.32	7.2	71.57	0.03	27.2
<i>Halopithys incurva</i>	0.10	1.53	5.12	-	-	-	-	-	-	0.10	4.20	6.4
<i>Halopteris scoparia</i>	0.07	0.65	2.27	-	-	-	-	-	-	0.01	0.79	2.8
<i>Heterosiphonia plumosa</i>	-	-	-	0.00	1.12	4.3	-	-	-	-	-	-
<i>Jania rubens</i>	0.06	0.77	2.55	-	-	-	-	-	-	0.10	0.92	2.8
<i>Peyssonnelia</i> spp. ⁽²⁾	-	-	-	-	-	-	-	-	-	-	-	-
<i>Phyllophora crispa</i>	0.03	0.64	2.02	-	-	-	-	-	-	3.76	0.01	5.9
<i>Plocamium cartilagineum</i>	0.69	0.37	2.42	0.74	0.13	3.2	0.79	0.81	6.2	0.64	0.03	2.3
<i>Pterosiphonia complanata</i>	1.19	0.46	4.18	0.14	7.95	10.3	0.28	0.01	3.6	0.55	0.12	2.0
<i>Rhodymenia pseudopalmata</i>	-	-	-	-	-	-	0.02	0.14	2.6	-	-	-

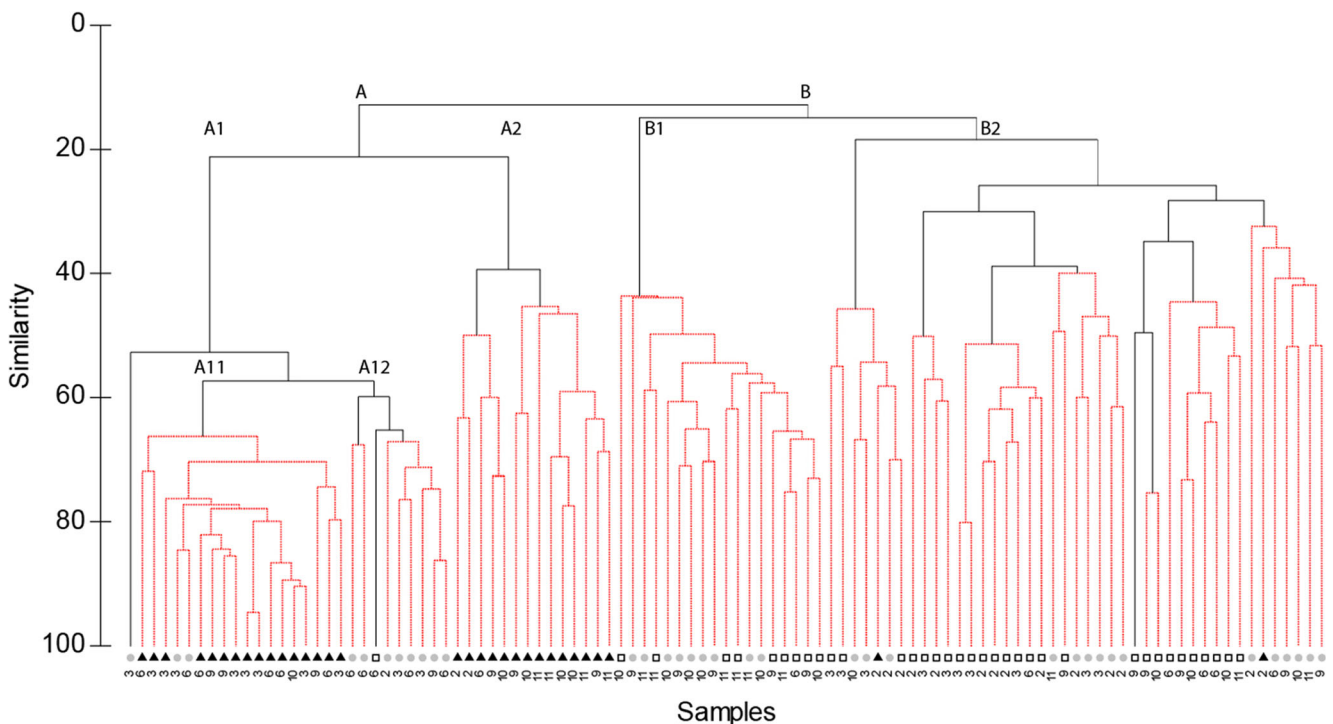


Fig. 3 Dendrogram resulting from classification analysis of samples based on taxon square root transformed biomass data and Bray-Curtis similarity index. Black lines represent significantly different groups,

whilst red lines denote groups that do not differ significantly according to the SIMPROF test. Black triangles: 1982; grey circles: 2007; white squares: 2014

samples from 2007 and 2014, and is characterised by higher values of *C. decortatum*, *H. incurva*, *Corallina* spp. and *Jania rubens* (Table 3). This latter heterogeneous group is further divided into different subgroups with no defined spatio-temporal pattern (Fig. 3).

Mean total biomass decreases from 106.75 g DW · 2000 cm⁻² in 1982 to 70.82 g DW · 2000 cm⁻² in 2007, but remains nearly constant in 2014 (72.68 g DW · 2000 cm⁻²). Biomass corresponding to small species (<5 cm) (3.07 vs. 10.73 g DW · 2000 cm⁻²) and medium-size species (5–15 cm) (7.59 vs. 9.18 g DW · 2000 cm⁻²) increases slightly between 1982 and 2014, whereas that of aggregated large-size (>15 cm) species shows a noteworthy decline (96.08 vs. 52.77 g DW · 2000 cm⁻²) (Table 4). Changes in both the total biomass and the thallus size vary in relation to depth (Table 5 in the Appendix).

The trend over time across depths of the mean total biomass and the biomass of those species that SIMPER indicates contribute most (>7%) to the groups detected in the CLUSTER which is shown in Fig. 4. The highest total biomass figures for 1982 are found at depths of 3 and 6 m with 194.56 and 154.47 g DW · 2000 cm⁻², respectively (Fig. 4). Intermediate values are found at depths of 9 and 10 m (77.36 and 71.51 g DW · 2000 cm⁻²) and the lowest values at depths of 2 and 11 m (46.18 and 30.18 g DW · 2000 cm⁻²). These biomass records in 1982 at depths of 3, 6, 9 and 10 m are consistent with the high abundance of *G. corneum* (189.36, 149.51, 63.74 and 43.67 g

DW · 2000 cm⁻², respectively). However, at 2 m, *H. incurva* is the most abundant species (18.65 g DW · 2000 cm⁻²), whilst at 11 m, the biggest contributor to biomass is *P. complanata* (7.31 g DW · 2000 cm⁻²). In 2007 and 2014, the total biomass does not exceed 93 g DW · 2000 cm⁻² at any depth and it is more homogeneously distributed than in 1982.

As for temporal changes in biomass (Fig. 4), at a depth of 2 m, the total biomass increases from 1982 to 2007 (78.17 g DW · 2000 cm⁻²), with no changes being shown in 2014 (78.18 g DW · 2000 cm⁻²). This increase is mainly associated with *C. decortatum* (0 vs. 24.66 g DW · 2000 cm⁻²; in 1982 and 2007, respectively) and *H. incurva* (18.66 vs. 45.24 g DW · 2000 cm⁻²; in 1982 and 2014, respectively). At depths of 3 and 6 m, the total biomass sharply declines to 92.99 and 58.85 g DW · 2000 cm⁻², respectively, between 1982 and 2014. In this regard, the increases from 1982 to 2014 in *C. decortatum* (0 vs. 21.79 g DW · 2000 cm⁻²) and *H. incurva* (0.00 vs. 15.10 g DW · 2000 cm⁻²) at a depth of 3 m and *G. baccata* (0.00 vs. 25.19 g DW · 2000 cm⁻²) at 6 m do not offset the drastic decrease in biomass detected for *G. corneum* towards the end of the study period (1.21 and 13.37 g DW · 2000 cm⁻²; for depths of 3 and 6 m, respectively). At depths of 9 and 10 m, the total biomass decreases to 53.44 and 62.05 g DW · 2000 cm⁻², respectively, between 1982 and 2014. *G. corneum* sharply decreases at both depths (0.33 and 0.45 g DW · 2000 cm⁻²; for depths of 9 and 10 m, respectively). To a lesser extent, *P. complanata* also decreases (9 m: 3.92 vs. 0.44; 10 m: 14.67 vs. 0.19 g

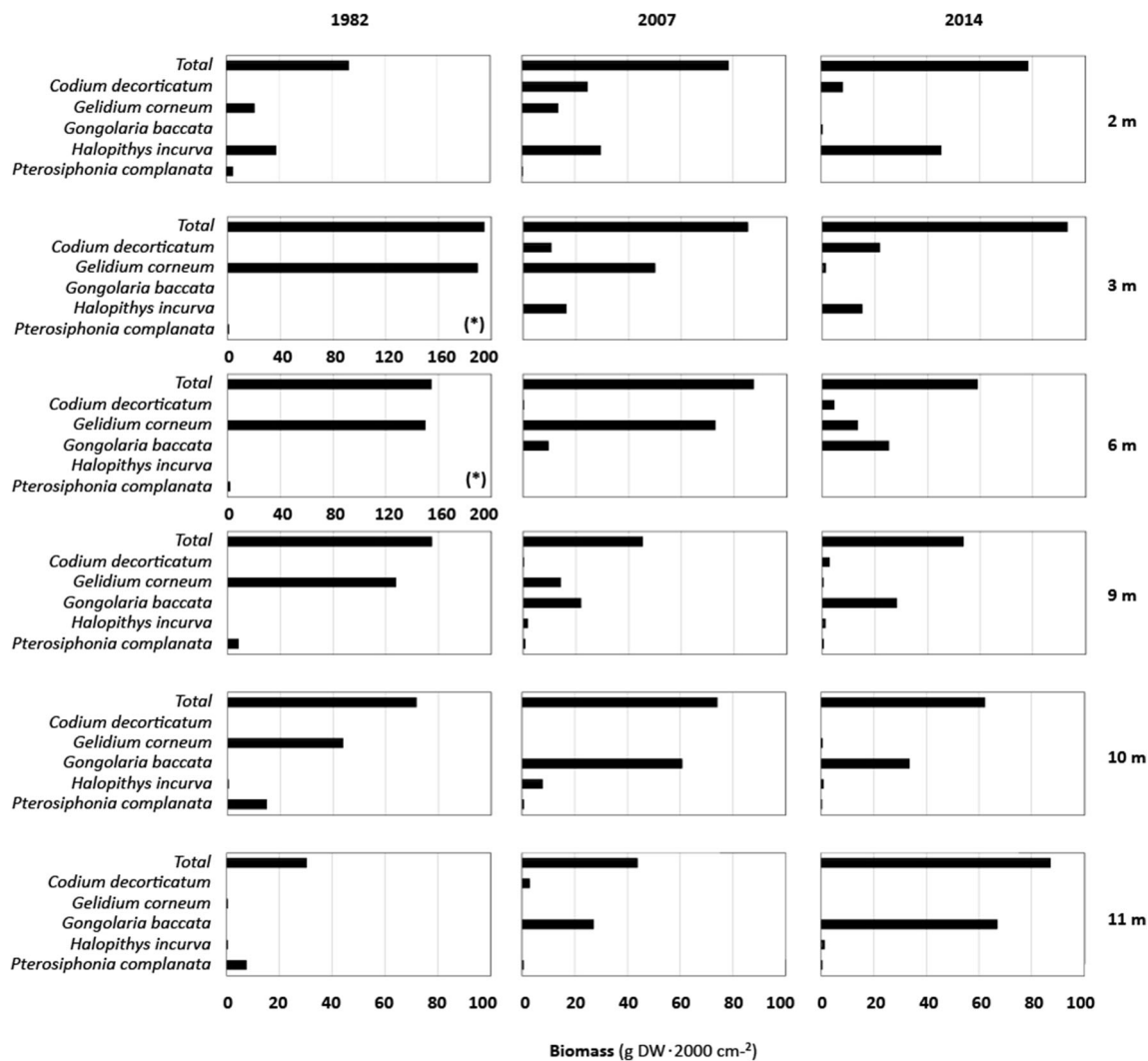


Fig. 4 Mean biomass (g DW · 2000 cm⁻²) of the whole community (Total) and the five species contributing most (>7%) to differences detected between surveys at different depths. At depths of 3 and 6 m (*), the biomass ranges from 0 to 200 g dry weight · 2000 cm⁻²

DW · 2000 cm⁻²; in 1982 and 2014, respectively). By contrast, *G. baccata* moderately increases between 1982 and 2014 (0.00 vs. 28.14 and 0.00 vs. 33.45 g DW · 2000 cm⁻²; for depths of 9 and 10 m, respectively). The deepest assemblages (11 m) show an increase in total biomass (86.87 g · 2000 cm⁻²) by the end of the study period (2014), mainly related to the development of *G. baccata* (0.00 vs. 66.73 g DW · 2000 cm⁻², in 1982 and 2014, respectively). The greatest decrease at this depth is detected for *P. complanata* (7.31 vs. 0.37 g DW · 2000 cm⁻², in 1982 and 2014, respectively). Mean biomass figures for all taxa over the years are shown in Table 4.

Discussion

This research reveals a large-scale decline in total macroalgal biomass between 1982 and 2014. However, the temporal pattern of the shift differs from one depth to another: total biomass

decreased at depths from 3 to 10 m but increased at 2 and 11 m. The strong decrease in biomass detected in the 3–10-m depth range is a consequence of the sharp net decline in large macroalgal biomass, which was not offset by the increased biomass of small species, mainly turf-forming forms. The dominant large macroalga in 1982, the canopy-forming *G. corneum*, had practically disappeared by the end of the study, and its biomass loss was far from offset by the small increase detected in the fucoid *Gongolaria baccata*. By contrast, at depths of 2 and 11 m, the most notable result is the increase in large species, mainly *Halopithys incurva* and the annual chlorophyte *C. decorticans* at 2 m, and *G. baccata* at 11 m; however, at both depth levels, a new canopy is far from being developed.

The decline of *G. corneum* detected in this study is in line with that recorded along the Basque coast in the last 30 years (Díez et al. 2012; Muguerza et al. 2017). Increased water temperature, irradiance and wave height are suggested as being among the main drivers underlying this regression (Díez

Table 4 List of all the taxa recorded, showing their mean biomass (g DW · 2000 cm⁻²) and the standard deviation (SD) for the three sampling surveys. ⁽¹⁾*Ellisolandia elongata* and *C. officinalis*; ⁽²⁾*P. harveyana* and*P. squamaria*; ⁽³⁾*P. ardreana* and *P. pennata*. T.S. refers to thallus size (S, small; M, medium; L, large)

Taxa	T.S.	1982		2007		2014	
		Mean	SD	Mean	SD	Mean	SD
Chlorophyta							
<i>Bryopsis hypnoides</i> J.V.Lamour	S	-	-	-	-	0.00	0.01
<i>Bryopsis plumosa</i> (Huds.) C.Agardh	S	-	-	0.00	0.02	0.00	0.02
<i>Chaetomorpha linum</i> (O.F.Müller) Kütz.	S	-	-	0.00	0.00	-	-
<i>Cladophora lehmanniana</i> (Lindenb.) Kütz.	S	-	-	0.00	0.00	0.16	0.38
<i>Cladophora prolifera</i> (Roth) Kütz.	S	-	-	0.05	0.15	-	-
<i>Codium decorticatum</i> (Woodw.) M.A.Howe	L	-	-	6.74	17.76	13.59	31.02
<i>Derbesia tenuissima</i> (Moris & De Not.) P.Crouan & H. Crouan	S	0.00	0.00	-	-	-	-
<i>Lychaete pellucida</i> (Hudson) M.J.Wynne	S	0.01	0.06	0.06	0.15	0.23	0.38
<i>Rhizoclonium riparium</i> (Roth) Harv.	S	-	-	0.00	0.00	-	-
<i>Ulva pseudocurvata</i> Koeman & Hoek	S	-	-	-	-	0.00	0.02
<i>Ulva clathrata</i> (Roth) C.Agardh	S	0.00	0.00	-	-	-	-
<i>Ulva rigida</i> C.Agardh	S	0.13	0.60	0.06	0.20	0.00	0.01
Ochrophyta							
<i>Cladostephus spongiosum</i> (Huds.) C.Agardh	M	0.01	0.06	0.07	0.25	0.65	1.39
<i>Colpomenia peregrina</i> Sauv.	S	0.00	0.01	0.01	0.24	0.00	0.01
<i>Desmarestia ligulata</i> (Stackh.) J.V.Lamour.	L	0.54	1.76	-	-	0.00	0.00
<i>Dictyopteris polypodioides</i> (D.C) J.V.Lamour.	L	1.93	4.28	0.02	0.05	0.11	0.37
<i>Dictyota dichotoma</i> (Huds.) J.V.Lamour	M	0.22	0.71	0.60	1.20	0.05	0.23
<i>Gongolaria baccata</i> (S.G. Gmelin) Molinari & Guiry	L	0.00	0.00	18.86	37.95	22.89	46.11
<i>Halopteris filicina</i> (Gratel.) Kütz.	S	0.10	0.29	0.08	0.16	0.01	0.03
<i>Halopteris scoparia</i> (L.) Sauv.	M	0.04	0.13	0.02	0.03	3.18	7.08
<i>Hinckesia granulosa</i> (Sm.) P.C.Silva	S	0.00	0.00	-	-	-	-
<i>Phyllariosopsis brevipes</i> (C.Agardh) E.C.Henry & South	L	0.00	0.00	-	-	0.01	0.03
<i>Saccorhiza polyschides</i> (Lightf.) Batters	L	-	-	0.00	0.00	-	-
<i>Sphacelaria cirrosa</i> (Roth) C.Agardh	S	-	-	0.03	0.16	-	-
<i>Taonia atomaria</i> (Woodw.) J.Agardh	S	-	-	-	-	0.29	1.03
Rhodophyta							
<i>Acrosorium ciliolatum</i> (Harv.) Jylin	S	0.05	0.18	0.35	0.54	0.03	0.06
<i>Aglaothamnion pseudobyssoides</i> (P.Crouan & H. Crouan) Halos	S	-	-	-	-	0.36	0.69
<i>Aglaothamnion tenuissimum</i> (Bonnem.) Feldm.-Maz.	S	-	-	0.01	0.03	0.00	0.01
<i>Algaothamnion tripinnatum</i> (C.Agardh) Feldm.-Maz.	S	0.00	0.00	0.01	0.02	0.00	0.01
<i>Anotrichium furcellatum</i> (J.Agardh) Baldock	S	-	-	0.00	0.00	0.00	0.01
<i>Antithamnion amphigeneum</i> A. Miller	S	-	-	0.00	0.00	-	-
<i>Antithamnion nipponicum</i> Yamada & Inagaki	S	-	-	0.00	0.00	-	-
<i>Antithamnion villosum</i> (Kütz.) Athanasiadis	S	-	-	0.00	0.00	-	-
<i>Antithamnionella ternifolia</i> (J.D.Hooker & Harvey) Lyle	S	0.00	0.00	0.00	0.00	-	-
<i>Aphanocladia stichidiosa</i> (Funk) Ardré	S	-	-	0.02	0.07	0.44	0.68
<i>Apoglossum ruscifolium</i> (Turner) J.Agardh	S	-	-	0.03	0.04	0.00	0.01
<i>Asparagopsis armata</i> Harv.	M	1.90	3.07	0.41	0.60	1.62	2.31
<i>Bonnemaisonia hamifera</i> Har.	M	-	-	0.02	0.04	0.00	0.00
<i>Bonnemaisonia asparagoides</i> (Woodw.) C.Agardh	M	0.09	0.17	0.04	0.07	0.01	0.03
<i>Bornetia secundiflora</i> (J.Agardh) Thur.	S	-	-	0.02	0.05	0.03	0.08
<i>Calliblepharis ciliata</i> (Huds.) Kütz.	L	1.61	3.71	0.05	0.23	0.14	0.45
<i>Callithamnion tetragonum</i> (Withering) S.F.Gray	S	-	-	0.10	0.21	0.00	0.00

Table 4 (continued)

Taxa	T.S.	1982		2007		2014	
		Mean	SD	Mean	SD	Mean	SD
<i>Callithamnion corymbosum</i> (Smith) Lyngb.	S	0.00	0.00	0.01	0.02	-	-
<i>Callithamnion granulatum</i> (Ducluz.) C.Agardh	S	0.00	0.00	-	-	-	-
<i>Centroceras clavulatum</i> (C.Agardh) Mont.	S	-	-	0.00	0.00	-	-
<i>Ceramium cimbricum</i> H.E.Petersen	S	-	-	0.01	0.05	-	-
<i>Ceramium secundatum</i> Lyngb.	S	-	-	0.01	0.04	0.00	0.00
<i>Ceramium virgatum</i> Roth	S	0.02	0.07	-	-	-	-
<i>Ceramium ciliatum</i> (J.Ellis) Ducluz.	S	0.00	0.00	0.00	0.00	0.01	0.03
<i>Ceramium diaphanum</i> (Lightf.) Roth	S	0.01	0.06	-	-	-	-
<i>Ceramium echionotum</i> J.Agardh	S	0.00	0.00	-	-	0.07	0.35
<i>Champia parvula</i> (C.Agardh) Harv.	S	0.00	0.01	0.00	0.02	0.02	0.10
<i>Chondracanthus acicularis</i> (Roth) Fredericq	S	-	-	0.11	0.64	-	-
<i>Chondracanthus teedei</i> (Mert. ex Roth) Kütz.	S	-	-	0.00	0.01	-	-
<i>Chondria coerulecens</i> (J.Agardh) Falkenb.	S	-	-	0.00	0.00	-	-
<i>Chondria dasyphylla</i> (woodw.) C.Agardh	S	-	-	-	-	0.00	0.00
<i>Colaconema caespitosum</i> (J.Agardh) Jackelman, Stegenga & J.J.Bolton	S	-	-	0.01	0.03	-	-
<i>Colaconema daviesii</i> (Dillwyn) Stegenga	S	-	-	0.00	0.02	-	-
<i>Compsothamnion gracillimum</i> De Toni	S	-	-	0.01	0.02	-	-
<i>Compsothamnion thuyoides</i> (Sm.) Nägeli	S	-	-	0.00	0.01	-	-
<i>Corallina</i> spp. ⁽¹⁾	S	0.28	0.75	1.68	3.78	2.75	4.34
<i>Crouania attenuata</i> (C.Agardh) J.Agardh	S	0.00	0.00	0.04	0.12	-	-
<i>Cryptonemia lomation</i> (Bertol.) J.Agardh	S	0.06	0.17	-	-	-	-
<i>Cryptopleura ramosa</i> (Huds.) Kylin ex L.Newton	S	0.17	0.31	0.09	0.15	0.58	1.10
<i>Dasya ocellata</i> (Gratel.) Harv.	S	-	-	0.01	0.03	0.24	0.33
<i>Dasya hutchinsiae</i> Harv.	S	0.00	0.01	0.02	0.07	0.04	0.09
<i>Dasyisiphonia japonica</i> (Yendo) H.-S.Kim	S	-	-	0.00	0.00	0.00	0.01
<i>Dermocorynus dichotomus</i> (J.Argardh) Gargiulo, M.Morabito & Manghisi	S	-	-	-	-	0.00	0.01
<i>ErythroGLOSSUM laciniatum</i> (Lightf.) Maggs & Hommers.	S	-	-	0.00	0.03	-	-
<i>Gaillona gallica</i> (Nägeli) Athanasiadis	S	-	-	0.00	0.00	-	-
<i>Gayliella flaccida</i> (Harvy ex Kützing) T.O.Cho & L.J.Mclvor	S	0.00	0.00	0.01	0.02	0.02	0.07
<i>Gelidium spinosum</i> (S.G.Gmel.) P.C.Silva	L	0.33	1.19	0.08	0.38	1.36	3.55
<i>Gelidium corneum</i> (Huds.) J.V.Lamour.	S	89.57	99.02	27.22	44.83	2.69	13.38
<i>Gelidium pusillum</i> (Stackh.) Le Jol.	S	0.54	2.27	0.00	0.00	-	-
<i>Gigartina pistillata</i> (S.G.Gmel.) Stackh.	M	0.02	0.10	0.01	0.07	-	-
<i>Gracilaria multipartita</i> (Clemente) Harv.	S	0.01	0.05	-	-	-	-
<i>Gymnogongrus crenulatus</i> (Turner) J.Agardh	S	0.11	0.34	-	-	0.01	0.05
<i>Halopithys incurva</i> (Huds.) Batters	L	2.44	13.17	9.90	33.41	13.33	55.19
<i>Halurus equisetifolius</i> (Lightf.) Kütz.	S	0.03	0.12	0.08	0.20	0.16	0.52
<i>Herposiphonia</i> sp.	S	-	-	-	-	0.03	0.09
<i>Herposiphonia tenella</i> (C.Agardh) Ambronn.	S	-	-	0.01	0.02	-	-
<i>Heterosiphonia plumosa</i> (J.Ellis) Batters	S	0.89	2.26	0.03	0.09	0.11	0.29
<i>Hypoglossum hypoglossoides</i> (Stackh.) Collins & Herv.	S	-	-	0.00	0.01	-	-
<i>Jania rubens</i> (L.) J.V.Lamour.	S	0.06	0.18	0.65	1.61	2.44	7.77
<i>Kallymenia reniformis</i> (Turner) J.Agardh	M	-	-	0.00	0.01	-	-
<i>Lomentaria clavellosa</i> (Lightf. ex Turner) Gaillon	S	0.00	0.00	0.00	0.00	-	-
<i>Meredithia microphylla</i> (J.Agardh) J.Agardh	S	-	-	-	-	0.05	0.28
<i>Metacallophyllis laciniata</i> (Hudson) A.Vergés & L.Le Gall	M	-	-	0.01	0.04	-	-
<i>Microcladia glandulosa</i> (Sol. ex Turner) Grev.	S	0.00	0.02	0.05	0.09	0.16	0.56

Table 4 (continued)

Taxa	T.S.	1982		2007		2014	
		Mean	SD	Mean	SD	Mean	SD
<i>Monosporus pedicellatus</i> (Sm.) Solier	S	-	-	0.00	0.01	-	-
<i>Nitophyllum punctatum</i> (Stackh.) Grev.	S	0	0.02	0.00	0.00	-	-
<i>Peyssonmelia</i> spp. ⁽²⁾	S	0.00	0.02	0.35	1.41	0.59	2.11
<i>Phyllophora crispa</i> (Huds.) P.S.Dixon	M	-	-	0.79	2.58	2.68	9.67
<i>Pleonosporium borneri</i> (Sm.) Nägeli	S	-	-	0.00	0.00	-	-
<i>Pleonosporium flexuosum</i> (C.Agardh) Bornet ex De Toni	S	-	-	0.00	0.00	-	-
<i>Plocamium cartilagineum</i> (L.) P.S.Dixon	M	0.59	0.93	0.90	1.71	0.46	1.16
<i>Polysiphonia brodiei</i> (Dillwyn) Sprengel	S	-	-	0.01	0.04	-	-
<i>Polysiphonia polyspora</i> (C.Agardh) Mont.	S	-	-	0.00	0.00	0.00	0.02
<i>Polysiphonia</i> sp.	S	-	-	-	-	0	0
<i>Polysiphonia atlantica</i> Kapraun & J.N.Norris	S	-	-	0	0	-	-
<i>Pterosiphonia parasitica</i> (Huds.) Falkenb.	S	-	-	0.04	0.09	0.09	0.16
<i>Pterosiphonia</i> spp. ⁽³⁾	S	0.16	0.29	0.05	0.10	0.42	0.77
<i>Pterosiphonia complanata</i> (Clemete) Falkenb.	M	4.69	7.02	0.31	0.53	0.37	0.70
<i>Pterothamnion crispum</i> (Ducluz.) Nägeli	S	-	-	0.08	0.23	0.00	0.00
<i>Pterothamnion plumula</i> (J.Ellis) Nägeli	S	0.01	0.03	-	-	-	-
<i>Rhodophyllis divaricata</i> (Stackh.) Papenf.	S	0.00	0.00	0.02	0.08	-	-
<i>Rhodymenia holmesii</i> Ardiss.	S	-	-	0.00	0.00	-	-
<i>Rhodymenia pseudopalmata</i> (J.V.Lamour.) P.C.Silva	M	0.03	0.05	0.11	0.26	0.14	0.40
<i>Scageliopsis patens</i> Wollaston	S	-	-	0.00	0.00	-	-
<i>Schizymenia dubyi</i> (Chauv. ex Duby) J.Agardh	M	-	-	0.00	0.01	-	-
<i>Seirospora interrupta</i> (Sm.) F.Schmitz	S	0.00	0.00	0.00	0.01	-	-
<i>Spermothamnion repens</i> (Dillwyn) Rosenv.	S	-	-	0.07	0.36	-	-
<i>Sphaerococcus coronopifolius</i> Stackh.	L	-	-	0.25	0.91	0.01	0.05
<i>Sphondylothamnion multifidum</i> (Huds.) Nägeli	S	0.10	0.28	0.07	0.40	0.01	0.03
<i>Tiffaniella capitata</i> (Schousboe ex Bornet) Doty & Meñez	S	-	-	0.01	0.04	-	-
<i>Vertebrata fruticulosa</i> (Wulfen) Kuntze	S	-	-	-	-	0.00	0.00
<i>Vertebrata thuyoides</i> (Harvey) Kuntze	S	-	-	0.00	0.00	-	-
Total biomass		107		70.8		72.7	
Small size (<5 cm)		3.07		4.48		10.73	
Medium size (5–15 cm)		7.59		3.29		9.18	
Large size (>15 cm)		96.09		63.05		52.77	

et al. 2012; Borja et al. 2013; Muguerza et al. 2017; Quintano et al. 2019). The loss of the biomass and canopy functions provided by *G. corneum* in 1982 in the 3–10-m depth range may have severe, long-lasting consequences for benthic assemblages, as no other large macroalga has shown conspicuous development in this depth range. At the end of the study period, scattered individuals and small patches of the large macroalga *G. baccata* were detected. However, the ability of this furoid to colonise shallow rocky reefs in coastal stretches exposed to strong waves is rather limited (Díez et al. 2003). Accordingly, the increase in wave energy detected since the early 1990s on the Basque coast (Borja et al. 2013) is

suggested as the main factor of change explaining the decline of *G. baccata* in some pristine locations along this coast (Muguerza et al. 2017). This macroalga is a warm-temperate species whose distribution is expected to expand northwards in the context of ongoing climate change (Hiscock et al. 2004). It has a high capacity for acclimation to increased temperature and irradiance levels (Miguel-Vijandi et al. 2010), which may be the reason for the lengthening of its growth period and the increase in biomass detected in semi-exposed coastal stretches of the southern Bay of Biscay since 2007 (Méndez-Sandín and Fernández 2016). Likewise, the physiological traits of *G. baccata* may explain the increase detected

in the present study at a depth of 11 m, where the bottom friction exerted by waves is low enough for *G. baccata* to cope with it, whilst the increases in water temperatures and irradiance registered in the study area (Quintano et al. 2019) may have favoured its development.

Concurrently with the strong net decrease in canopy-forming macroalgae at depths of 3–10 m, turf-forming species comprising articulated coralline macroalgae (*Corallina* spp., *J. rubens*) and morphologically simple and ephemeral algal forms (*Aphanocladia stichidiosa*, *Lychaete pellucida*, *Aglaothamnium pseudobyssoides*, *M. glandulosa*) have expanded. By contrast, at a depth of 2 m, where the warm-temperate affinity species *H. incurva* and *C. decorticutum* increased, and at the depth of 11 m where *G. baccata* increased, no expansion of turf-forming species was detected. Large macroalgae competitively exclude some species by monopolising resources, particularly space (Maggi et al. 2009), and numerous studies indicate that opportunistic species readily colonise space made available by canopy loss (Benedetti-Cecchi et al. 2001; Bulleri et al. 2002; Airoidi et al. 2008). The net loss of biomass linked to the shift detected in assemblage structure may be long-lasting (Tait and Schiel 2011; Crowe et al. 2013), since once turfing vegetation is well established, it may inhibit canopy-forming macroalgae from recruiting (Airoidi et al. 2008). In this regard, a shift to stable turfing assemblages in the vicinity of the study area has already been documented (Díez et al. 2014).

Canopy-forming macroalgae act as ecosystem engineer species and directly or indirectly modulate the availability of resources (Steneck et al. 2002). One consequence of canopy loss is a decline in the richness and abundance of the associated flora and fauna (Steneck et al. 2002; Graham 2004; Norderhaug et al. 2007; Schiel and Lilley 2007; Wikström and Kautsky 2007). In the study reported here, this functional role provided by *G. corneum* in 1982 was not replaced in 2014 by the expansion of *H. incurva* and *C. decorticutum* at a depth of 2 m, or by *G. baccata* at 11 m, since at both these levels, a new canopy was far from being developed. The complex habitat formed by *G. corneum* is essential for the functioning of the ecosystem since it preserves understory and epiphytic assemblages of smaller macroalgae, as well as sessile and vagile invertebrates (Borja et al. 2004; Bustamante et al. 2017). This habitat has become extinct in most of the study area, which may have consequences for the whole benthic ecosystem (Bustamante et al. 2017).

Branched canopies of species of the genus *Cystoseira* (*G. baccata* was formerly *Cystoseira baccata*) increase coastal primary production (Ballesteros et al. 2009), preserve biodiversity (Bianchelli et al. 2016), offer nursery areas for juvenile fish (Cheminée et al. 2013) and provide a home for outstanding species richness and density in coastal fish assemblage (Orlando-Bonaca and Lipej 2005). Therefore, the potential

development of deepwater forests of *G. baccata* may take over the ecosystem functional role previously played by *G. corneum*. However, at present, this functional replacement has not yet occurred, since *G. baccata* stands are poorly developed. In addition, the newly established turf-forming macroalgae typically consist of species with less ecological and functional value than those replaced (Crowe et al. 2013). A decrease in the richness and abundance of associated organisms may therefore be expected. Furthermore, recent research in the study area has shown a sharp decrease in invertebrate taxonomic and functional density and diversity after canopy loss (Bustamante et al. 2014, 2017). Although species richness increased only slightly by the end of the study period for this research, significant increases (mainly in ephemeral forms) have been detected along the Basque coast (Muguerza et al. 2017, 2020). The latter finding has been related to the intermediate disturbance hypothesis, which predicts maximal diversity at intermediate levels of disturbance (Connell 1978).

Foundation species are very important for marine food webs as they facilitate the capture and export of carbon (Dayton 1985; Krumhansl and Scheibling 2012; Smale et al. 2013). Moreover, much of their biomass is not consumed directly by herbivores, so canopy species are a major source of nutrition for other nearshore ecosystems (Duggins and Eckman 1997, Mann 2000, Steneck et al. 2002). Although no specific productivity measurements are made in this study, there may be a high risk of future primary productivity being significantly lower if the biogenic habitat previously provided by *G. corneum* is not recovered. Thus, previous experimental research on the impact of canopy loss on ecosystem functioning (Tait and Schiel 2011) has reported long-term reductions in primary productivity of macroalgal assemblages following canopy removal.

In addition to changes in ecosystem functions, canopy loss and subsequent decrease in macroalgal biomass in the study area could also impair the ecosystem services that canopy species provide. As mentioned above, these ecosystem engineers provide refuge for numerous other species, including many that are economically important for humans (Graham 2004; Smale et al. 2013). In this regard, the fact that the species that have replaced *G. corneum* cannot perform the same functional role means that the exploitation of some species in the study area might decline. *G. corneum* used to be the main raw material for agar extraction along the Atlantic shores of Spain, Portugal and Morocco (McHugh 1991). In the particular case of the study area, this resource has not been exploited since 1999 due to its decline (Borja et al. 2013).

In summary, the findings reported here evidence that two pivotal roles of canopy-forming species in coastal ecosystem functioning (biomass and habitat provision) have been altered in shallow rocky bottoms in the south-eastern Bay of Biscay. It seems that at present there are no native canopy-forming species that can adapt to the environmental

Appendix

Table 5 List of all the taxa recorded, showing their mean biomass (g DW · 2000 cm⁻²) for the six depths and the three sampling surveys. ⁽¹⁾*Ellisolandia elongata* and *C. officinalis*; ⁽²⁾*P. harveyana* and *P. squamaria*; ⁽³⁾*P. ardreana* and *P. pennata*. T.S. refers to thallus size (S, small; M, medium; L, large)

Taxa	T.S.	2 m			3 m			6 m			9 m			10 m			11 m		
		1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014
Chlorophyta																			
<i>Bryopsis hypnoides</i>	S	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bryopsis plumosa</i>	S	-	0.02	0.02	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetomorpha linum</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	-	-
<i>Cladophora lehmanniana</i>	S	-	0.00	0.42	-	0.00	0.10	-	0.29	-	-	0.04	-	-	-	-	-	-	0.01
<i>Cladophora prolifera</i>	S	-	0.13	-	-	0.06	-	0.00	-	0.07	-	-	-	-	-	-	-	-	-
<i>Codium decorticatum</i>	L	-	24.66	16.87	-	10.61	45.68	-	0.23	5.23	-	3.20	-	0.02	0.18	-	2.75	-	-
<i>Derbesia tenuissima</i>	S	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lychaete pellucida</i>	S	0.08	0.09	0.41	-	0.04	0.21	-	0.02	0.49	-	0.10	0.04	0.00	0.10	0.11	-	0.01	0.01
<i>Rhizoclonium riparium</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00
<i>Ulva clathrata</i>	S	0.00	-	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ulva pseudocurvata</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
<i>Ulva rigida</i>	S	-	-	0.00	-	0.00	0.00	-	0.03	-	0.56	0.20	0.02	-	0.05	0.00	0.19	0.14	-
Ochrophyta																			
<i>Cladostephus spongiosus</i>	M	-	0.00	0.81	-	0.00	0.84	-	0.12	0.09	0.05	0.21	0.32	0.03	0.06	0.99	-	-	0.86
<i>Colpomenia peregrina</i>	S	0.01	0.02	-	-	0.20	0.01	-	-	-	-	-	-	-	-	-	-	-	-
<i>Desmaresia ligulata</i>	L	0.00	-	-	-	2.43	-	-	0.01	-	-	-	-	-	-	-	-	-	-
<i>Dicyopteris polypodioides</i>	L	-	0.00	-	-	0.37	-	0.01	0.58	-	2.71	0.01	0.08	2.29	0.07	0.23	7.03	-	0.42
<i>Dicyota dichotoma</i>	M	0.01	0.01	0.20	0.01	0.60	0.00	0.57	1.38	0.03	0.05	0.98	0.00	0.11	0.18	0.00	0.68	0.40	0.04
<i>Gongolaria baccata</i>	L	-	0.06	0.46	-	-	-	-	9.44	25.19	-	21.84	28.15	0.00	60.63	33.45	-	27.07	66.73
<i>Halopteris filicina</i>	S	0.02	0.19	0.01	0.00	0.03	0.00	0.01	0.03	0.03	0.08	0.03	-	0.13	0.05	0.00	0.45	0.16	-
<i>Halopteris scoparia</i>	M	0.24	0.03	6.64	0.01	0.02	6.09	0.00	0.00	0.67	0.03	0.01	3.26	0.04	0.02	0.20	0.00	-	0.20
<i>Hinckia granulosa</i>	S	-	-	-	-	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-
<i>Phyllariopsis brevipes</i>	L	-	-	-	-	0.00	-	-	-	0.01	-	-	-	-	-	0.03	-	-	0.02
<i>Saccorhiza polyschides</i>	L	-	-	-	-	-	-	-	-	-	-	0.00	-	-	0.00	-	-	-	-
<i>Sphacelaria cirrosa</i>	S	-	0.00	-	-	0.00	-	-	0.00	-	-	0.00	-	-	0.16	-	-	-	-
<i>Taonia atomaria</i>	S	-	-	0.04	-	-	0.08	-	-	0.82	-	-	0.78	-	-	0.02	-	-	-
Rhodophyta																			
<i>Acrosorium ciliolatum</i>	S	0.00	0.09	-	0.00	0.51	0.02	0.00	0.15	0.02	0.11	0.33	0.08	0.16	0.59	0.04	0.04	0.43	0.01
<i>Aglaothamnion pseudobyssoides</i>	S	-	-	0.02	-	-	0.17	-	-	0.81	-	-	0.47	-	-	0.43	-	-	0.40
<i>Aglaothamnion tenuissimum</i>	S	-	0.01	-	-	0.00	-	-	-	-	-	0.02	-	0.02	0.01	-	-	0.01	-

Table 5 (continued)

Taxa	T.S.		2 m			3 m			6 m			9 m			10 m			11 m		
	1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014		
<i>Aglaothamnion trippinatum</i>	S	-	0.01	0.01	0.01	-	0.00	-	0.00	0.00	-	0.00	0.00	0.01	-	-	-	-	-	
<i>Anotrichium furcellatum</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	0.00	0.00	0.00	
<i>Anitithamnion amphigenum</i>	S	-	-	-	0.00	-	0.00	-	-	-	-	-	-	0.00	-	-	0.00	0.00	-	
<i>Anitithamnion nipponicum</i>	S	-	0.00	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-	0.00	-	
<i>Anitithamnion villosum</i>	S	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	
<i>Anitithamnionella ternifolia</i>	S	-	0.00	-	0.00	-	0.00	-	0.00	0.00	-	0.00	-	0.00	-	-	0.00	-	-	
<i>Aphanocladia stichidiosa</i>	S	-	0.05	0.36	-	0.03	0.35	-	0.05	1.25	-	0.00	0.15	0.00	0.01	0.22	0.01	0.24	0.24	
<i>Apoglossum ruscifolium</i>	S	-	0.01	-	0.03	0.00	0.00	-	0.01	-	-	0.01	-	0.02	0.00	0.00	0.03	-	-	
<i>Asparagopsis armata</i>	M	5.74	0.48	0.51	0.22	0.42	0.68	0.95	0.25	1.81	1.75	2.37	2.07	0.42	2.47	2.07	0.36	2.11	2.11	
<i>Bonnenmaisonia asparagoides</i>	M	0.17	0.00	0.01	0.01	0.00	0.00	0.11	0.02	0.01	0.09	0.06	0.06	0.06	0.01	0.15	0.16	0.05	0.05	
<i>Bonnenmaisonia hamifera</i>	M	-	0.00	-	-	0.01	0.00	-	0.02	-	-	-	-	0.01	-	-	0.02	-	-	
<i>Bornetia secundiflora</i>	S	-	0.01	0.00	-	0.02	0.00	-	0.02	0.04	-	0.04	0.06	0.04	0.06	-	-	0.06	0.06	
<i>Calliblepharis ciliata</i>	L	-	-	-	0.18	-	-	0.01	-	0.30	1.84	3.79	5.04	0.01	0.06	5.04	0.13	0.60	0.60	
<i>Callithamnion corymbosum</i>	S	-	0.02	-	0.00	0.00	-	-	0.01	-	-	-	-	-	-	-	-	-	-	
<i>Callithamnion granulatum</i>	S	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	-	
<i>Callithamnion tetragonum</i>	S	-	0.07	-	-	0.13	-	-	0.30	-	-	-	-	0.00	0.00	-	0.00	-	-	
<i>Centroceras clavulatum</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	
<i>Ceramium ciliatum</i>	S	0.00	0.00	0.03	0.00	-	0.00	0.00	-	-	0.00	0.00	-	0.00	-	0.00	-	-	-	
<i>Ceramium cimbricum</i>	S	-	0.05	-	-	0.01	-	-	0.00	-	-	-	-	-	-	-	-	-	-	
<i>Ceramium diaphanum</i>	S	0.00	-	-	0.00	-	0.00	-	-	-	0.06	-	-	-	-	-	-	-	-	
<i>Ceramium echionotum</i>	S	0.00	-	0.29	-	-	0.00	-	-	0.08	-	-	0.00	-	-	0.00	-	-	-	
<i>Ceramium secundatum</i>	S	-	0.06	-	-	0.01	0.00	-	0.00	-	-	-	-	-	-	0.00	-	-	-	
<i>Ceramium virgatum</i>	S	0.09	-	-	0.02	-	-	0.00	-	-	0.00	-	-	0.00	-	-	-	-	-	
<i>Champia parvula</i>	S	0.00	0.00	0.02	0.00	0.02	0.10	0.01	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	
<i>Chondracanthus acicularis</i>	S	-	0.02	-	-	-	-	-	-	-	-	-	-	0.63	-	-	-	-	-	
<i>Chondracanthus teedei</i>	S	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Chondria coerulescens</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Chondria dasyphylla</i>	S	-	-	-	-	-	0.00	-	-	-	-	0.00	-	-	-	-	-	-	-	
<i>Colaconema caespitosum</i>	S	-	0.02	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-	-	-	
<i>Colaconema daviesii</i>	S	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Composothamnion gracillimum</i>	S	-	0.02	-	-	0.01	-	-	0.00	-	-	-	-	0.00	-	-	-	-	-	
<i>Composothamnion thuyoides</i>	S	-	-	-	-	0.00	-	-	-	-	-	-	-	0.01	-	-	-	-	-	
<i>Corallina spp.⁽¹⁾</i>	S	1.36	5.99	1.34	0.27	1.41	5.01	0.17	0.25	0.74	0.09	0.00	0.00	0.09	3.95	0.00	1.73	1.52	1.52	
<i>Crouania attenuata</i>	S	0.00	0.02	-	0.00	0.02	-	0.00	0.00	-	0.00	-	-	0.11	-	-	0.09	-	-	

Table 5 (continued)

Taxa	T.S.	2 m				3 m				6 m				9 m				10 m				11 m				
		1982	2007	2014	2014	1982	2007	2014	2014	1982	2007	2014	2014	1982	2007	2014	2014	1982	2007	2014	2014	1982	2007	2014	2014	
<i>Cryptonemia lomation</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cryptopteura ramosa</i>	S	0.06	0.02	0.00	0.00	0.01	0.07	-	0.10	0.05	0.82	0.08	0.08	0.24	0.17	1.19	0.46	0.22	1.05							
<i>Dasya hutchinsiae</i>	S	0.00	0.00	0.01	0.08	0.01	0.06	0.08	-	0.00	0.02	0.06	0.06	0.00	0.03	0.04	0.00	0.00	0.03							
<i>Dasya ocellata</i>	S	-	0.01	0.23	-	-	0.01	0.21	-	-	0.44	-	0.22	-	0.00	0.15	-	0.04	0.17							
<i>Dasydiphonia japonica</i>	S	-	-	-	-	-	0.00	-	-	-	-	0.01	-	-	-	0.00	-	-	-							
<i>Dermocorynus dichotomus</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01							
<i>Erythrogllossum laciniatum</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	-	-	-							
<i>Gaillona gallica</i>	S	-	0.00	-	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-	-							
<i>Gayiella flaccida</i>	S	-	0.03	0.00	-	0.01	0.00	-	-	0.01	0.02	-	0.02	-	0.01	0.02	0.00	0.02	0.08							
<i>Gelidium corneum</i>	L	10.48	13.58	0.04	1.64	189.36	49.94	1.64	149.51	72.70	13.37	14.05	0.40	43.67	0.10	0.48	0.25	0.15	0.01							
<i>Gelidium pusillum</i>	S	3.96	-	-	-	0.19	-	-	-	0.00	-	0.00	-	0.00	-	-	-	-	-							
<i>Gelidium spinosum</i>	S	2.45	0.43	1.51	0.79	0.05	0.00	0.79	0.06	0.00	2.47	0.01	2.78	-	0.02	-	0.00	-	0.28							
<i>Gigartina pistillata</i>	M	-	-	-	-	-	-	-	0.10	-	-	0.00	-	-	0.07	-	-	-	-							
<i>Gracilaria multipartita</i>	S	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	-	-							
<i>Gymnogongrus crenulatus</i>	S	-	-	-	0.00	0.00	-	0.00	0.00	-	0.00	-	-	0.20	-	-	0.25	-	0.06							
<i>Halophytis incurva</i>	L	18.66	29.68	45.24	-	0.02	-	16.15	20.85	0.27	0.00	0.01	1.70	0.21	7.54	0.79	0.20	-	1.22							
<i>Halurus equisetifolius</i>	S	-	0.01	-	0.00	0.00	0.03	0.09	0.07	0.00	0.46	0.21	0.04	0.11	0.15	0.03	0.00	0.09	0.43							
<i>Herposiphonia</i> sp.	S	-	-	0.00	-	-	-	0.12	-	-	0.01	-	0.00	-	-	0.00	-	-	0.00							
<i>Herposiphonia tenella</i>	S	-	0.01	-	-	-	0.01	-	-	0.01	-	0.00	-	-	0.00	-	-	0.02	-							
<i>Heterosiphonia plumosa</i>	S	0.11	0.00	0.00	0.01	0.00	0.00	0.01	0.01	-	0.16	0.12	0.07	0.97	0.02	0.26	4.92	0.07	0.25							
<i>Hypoglossum hypoglossoides</i>	S	-	-	-	-	-	-	-	-	-	-	0.01	-	-	0.01	-	-	-	-							
<i>Jania rubens</i>	S	0.10	0.28	2.62	9.38	0.00	2.03	0.00	0.00	0.02	0.23	0.08	0.24	0.17	0.33	0.13	-	0.17	0.10							
<i>Kallymenia reniformis</i>	M	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-							
<i>Lomentaria clavellosa</i>	S	0.00	0.00	-	0.00	-	0.00	-	-	0.00	-	0.00	-	-	0.00	-	-	0.00	-							
<i>Mereditia microphylla</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	-	-							
<i>Metacallophyllis laciniata</i>	M	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05	-							
<i>Microcladia glandulosa</i>	S	0.00	0.02	0.01	0.02	0.00	0.01	0.00	-	0.12	0.06	0.00	0.01	0.00	0.09	0.20	0.03	0.04	0.72							
<i>Monosporus pedicellatus</i>	S	-	-	-	-	-	0.00	-	-	-	-	-	-	-	0.00	-	-	0.00	-							
<i>Nitophyllum punctatum</i>	S	0.03	-	-	-	-	-	-	0.00	-	-	0.00	0.00	0.00	-	-	0.00	-	-							
<i>Peyssonnelia</i> spp. ⁽²⁾	S	-	0.14	0.01	-	-	0.00	-	-	0.01	0.86	0.02	2.33	-	0.68	0.01	-	1.85	0.37							
<i>Phyllophora crispa</i>	M	-	0.03	-	-	-	0.04	-	-	0.06	0.67	-	0.63	-	0.42	13.22	-	4.99	4.55							
<i>Pleonosporium borneri</i>	S	-	0.00	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	0.00	-							
<i>Pleonosporium flexuosum</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	0.00	-							
<i>Plocamium cartilagineum</i>	M	0.16	0.62	-	0.60	1.59	0.01	0.01	0.27	1.68	1.05	0.63	0.30	1.67	0.21	1.21	0.05	0.92	0.72							

Table 5 (continued)

Taxa	T.S.	2 m			3 m			6 m			9 m			10 m			11 m		
		1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014	1982	2007	2014
<i>Polysiphonia atlantica</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polysiphonia brodiei</i>	S	-	0.04	-	-	0.00	-	0.02	-	-	-	-	0.00	-	-	-	0.00	-	0.01
<i>Polysiphonia polyspora</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
<i>Polysiphonia</i> sp.	S	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pterosiphonia complanata</i>	M	2.28	0.22	0.03	0.77	0.03	0.06	1.59	0.06	0.08	3.92	0.65	0.54	14.67	0.58	0.35	7.31	0.39	1.41
<i>Pterosiphonia parasitica</i>	S	-	0.00	0.00	-	0.00	0.02	-	0.00	0.02	-	0.04	0.07	-	0.08	0.16	-	0.14	0.31
<i>Pterosiphonia</i> spp. ⁽³⁾	S	0.14	0.03	0.00	0.00	0.06	0.33	0.03	0.00	0.06	0.09	0.07	0.32	0.38	0.08	0.67	0.44	0.12	1.42
<i>Pterothamnion crispum</i>	S	-	0.03	0.00	-	0.19	0.00	-	0.00	-	-	0.01	-	-	0.03	0.00	-	0.25	0.00
<i>Pterothamnion plumula</i>	S	0.04	-	-	0.00	-	-	0.00	-	-	0.00	-	-	0.00	-	-	0.00	-	-
<i>Rhodophyllis divaricata</i>	S	0.00	0.00	-	-	0.00	-	-	0.01	-	-	0.00	-	-	0.00	-	-	0.11	-
<i>Rhodymenia holmesii</i>	S	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	-	-
<i>Rhodymenia pseudopalmeta</i>	M	-	0.01	-	0.03	0.05	0.02	0.02	0.21	0.14	0.03	0.21	0.24	0.07	0.03	0.23	-	0.23	0.31
<i>Scagelopsis patens</i>	S	-	0.00	-	-	-	-	-	-	-	-	0.00	-	-	0.00	-	-	-	-
<i>Schizymenia dubyi</i>	M	-	-	-	-	-	-	-	-	-	-	0.00	-	-	-	-	-	0.02	-
<i>Seirospora interrupta</i>	S	-	0.01	-	-	-	-	-	0.00	-	-	0.00	-	-	-	-	0.00	0.00	-
<i>Spermothamnion repens</i>	S	-	0.36	-	-	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-
<i>Sphaerococcus coronopifolius</i>	L	-	-	-	-	0.68	-	-	0.04	-	-	-	0.06	-	0.49	-	-	0.25	0.03
<i>Sphondylthamnion multifidum</i>	S	0.00	0.39	-	0.00	-	0.00	-	0.00	-	0.25	0.00	0.01	0.08	0.00	0.04	0.34	-	0.02
<i>Tiffaniella capitata</i>	S	-	0.04	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vertebrata fruticulosa</i>	S	-	-	-	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-	-
<i>Vertebrata thuyoides</i>	S	-	0.00	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
Total biomass		46.19	78.18	78.18	194.56	85.19	93	154.47	87.34	58.85	77.36	45.19	53.45	71.51	73.94	62.05	30.18	43.64	86.87
Small size (<5 cm)		8.45	8.79	7.38	0.58	5.05	17.11	0.51	1.14	10.20	2.51	3.52	12.51	2.52	2.96	8.15	7.41	5.76	7.60
Medium size (5–15 cm)		8.60	1.40	8.20	1.64	2.76	7.70	3.59	3.80	4.55	6.55	3.65	7.85	19.04	2.11	18.68	10.26	7.53	10.24
Large size (>15 cm)		29.14	67.98	62.60	192.34	77.37	68.18	150.37	82.41	44.10	68.30	38.02	33.09	49.95	68.87	35.22	12.52	30.36	69.03

conditions in the 3–10-m depth range where *G. corneum* previously thrived. Further research on potential changes in primary productivity and biodiversity linked to the shift detected in assemblage structure needs to be conducted to obtain information of elementary importance for conservation and management decisions associated with the loss of habitat-forming macroalgae.

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Declarations

Conflict of interest The authors declare no competing interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Author contributions JMG, ID and NM conceived and designed this research. NM, EQ and JMG conducted data collection and field work. NM analysed data. NM, ID and EQ wrote the manuscript. All authors read the manuscript and contributed to make improvements for approval and submission to Marine Biodiversity.

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