

Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change

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ABSTRACT

Rising sea-surface temperatures (SSTs) over the last three decades in the south-eastern part of the Bay of Biscay could be affecting phyto-benthic assemblage distributions. This study assesses recent changes in species abundance and diversity along the western Basque coast by studying 18 locations in summer 1991 and in 2008. There were substantial changes in the structure of subtidal vegetation between the two surveys: 1) an increase in coralline algae; 2) changes in the distribution patterns of the canopy species; 3) disappearance of kelps; 4) increases in warm-water species, mainly morphologically simple forms; 5) introduction and expansion of non-indigenous species, and 6) increases in species richness and diversity. These results are consistent with the rise detected in SST, particularly in summer when SST was found to have risen by as much as 1 °C from 1980 to 2008. Furthermore, two extreme warming events occurred in the summers of 2003 and 2006. However, some biological shifts cannot be explained by warmer waters alone. Only limited data are available on changes in nutrient concentrations and water transparency, but these factors are also thought to be involved in the biological changes detected.

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1. Introduction

Over the last 15 years temperatures in many ocean areas have been warmer than ever before recorded. The 4th IPCC Report (2007) concludes that the global sea-surface temperature has increased by 0.13 °C per decade over the last 50 years, and for the next two decades a warming of about 0.2 °C per decade is projected. Responses from biological communities to gradual climate change are expected to be expressed mainly as changes in species distribution, abundance, timing of life-history events and diversity (Ling, 2008; Müller et al., 2009). Distribution shifts in marine organisms coincident with global warming have been detected in recent years (Hawkins et al., 2008). These changes are generally most evident near the northern and southern boundaries of the geographical distribution of species.

There is much evidence of northward shifts for both off-shore and coastal systems. Over the past 40 years warm-water calanoid copepod assemblages have moved 1000 km further north in the Northeast Atlantic, whereas cold-water assemblages have retreated (Beaugrand et al., 2002). Since 1970 the dinoflagellate *Ceratium trichoceros* has extended its northern limit from the south of the UK to the North Sea (Barnard et al., 2004). Exploited and non-exploited

North Sea fish species have responded markedly to recent increases in sea temperature, with shifts in mean latitude, depth or both being recorded for nearly two-thirds of them over 25 years (Perry et al., 2005). There is also evidence that benthic species are expanding into higher latitudes in association with climate warming. Barry et al. (1995) report significant increases in eight southern invertebrates in a central California intertidal community between 1931 and 1994. Seaweed migrations along European coastlines have also been documented. The brown macrophytes *Bifurcaria bifurcata* and *Cystoseira tamariscifolia* are extending northwards along the coasts of Britain and Ireland (Hiscock et al., 2004; Mieszkowska et al., 2005) and Lima et al. (2007) report that warm-water algae have expanded their range northwards along the Portuguese coastline.

Latitudinal shifts in species abundances and geographical boundaries are expressions of gradual climate change. However, explanations of changes in marine algae and predictions of future distribution shifts based on warmer temperatures alone are weak because there is also interplay between temperature and other factors (Schiel et al., 2004), including the photoperiodic responses of the species. If daylength triggers crucial steps in the life history of certain seaweeds when critical temperature demands are not met, then the distribution migrations of those species will not coincide with sea-surface isotherm shifts (Müller et al., 2009). In addition, the presence of hydrographical and geographical barriers may limit species spread (Hiscock et al., 2004). Global warming may also lead

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to nutrient input alterations due to changes in water column stratification (Roemmich and McGowan, 1995; Llope et al., 2006) and to changes in the geographical or seasonal distributions of rainfall and upwelling (Llope et al., 2006) with subsequent changes in primary production (Bakun, 1990; Llope et al., 2007). Similarly, changes in the carbon chemistry of seawater due to CO₂ emissions may have large-scale impacts on calcifying macroalgae, which are key species in a wide range of ecosystems (Beardall et al., 1998; Nelson, 2009). In addition, global warming may facilitate the spread of exotic species (Stachowicz, 2002). Climate-driven changes may affect the dispersion of non-indigenous species due to the alteration of current patterns and to competitive interactions between alien and native species as a result of the onset of new thermal optima and/or different water chemistry (Occhipinti-Ambrogi, 2007). Climate-induced changes may well be exacerbated by the synergistic effects between climate and other anthropogenic variables, particularly pollution and the over-exploitation of biological resources (Nelson, 2009). The overall response of a community to the complex interplay of various stress factors in combination with key ecological interactions is therefore unpredictable (Schiel et al., 2004).

Simulations for 2080–2099 show that the phytobenthos of northern Spain is likely to be one of those most affected by future sea-surface temperature increases around the world (Müller et al., 2009). The Basque coast extends over approximately 192 km at the eastern end of the Cantabrian Sea, northern Spain. Increases of about 0.26 °C per decade in SST for this area have been documented since 1977 (Goikoetxea et al., 2009). Recent surveys have revealed the disappearance of *Gelidium corneum* beds at the western end of the coast of Bizkaia (Gorostiaga et al., 2009). These local alterations led us to assess changes in species abundance and diversity along the whole western part of the Basque coast. The first quantitative study dealing with the sublittoral vegetation of this area was conducted in 1991 by the present research team (Díez et al., 2003) and then 17 years later we repeated our study to estimate changes in species composition, relative abundance of species and diversity.

2. Materials and methods

2.1. Study area

The Cantabrian Sea is the southernmost part of the Bay of Biscay, in the North-eastern Atlantic (Fig. 1). The sample area, which

extends approximately 108 km along the eastern Cantabrian Sea, corresponds to the western part of the Basque coast. This is an open coastline exposed to a large fetch where swell comes mainly from the WNW and NW. Rocky bottoms are almost continuous in shallow waters and soft ground is scarce. Mean water surface temperature off the Basque coast used to range between 12 °C in February and 22 °C in August (Valencia et al., 2004). The flora falls within the warm-temperate NE Atlantic sub-region according to the phytogeographical scheme proposed by Hoek and Breeman (1990).

2.2. Climate variables

The data used in this study include measurements of mean daily precipitation at the surface (expressed in kg m⁻² s⁻¹) and mean daily visible beam downward solar flux at the surface (expressed in W/m²) from January 1948 to December 2008. The data are reanalysis daily averages (Kalnay et al., 1996) obtained from the National Centers for Environmental Prediction (NOAA/NCEP, <http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.surfaceflux.html>). Data are centred on an area from 42.8564°N to 44.7611°N and 3.750°W to 1.875°W with 1.9° × 1.9° resolution. Wave energy flux was also obtained from NOAA/NCEP (<http://polar.ncep.noaa.gov/waves/index2.shtml>). WAVEWATCH III™ (Tolman, 2009) is a third-generation wave model developed at NOAA/NCEP in the spirit of the WAM model (WAMDIG, 1988; Komen et al., 1994). The data used run from January 1998 to December 2008. Wave energy flux (henceforth called *E* and expressed in kW m⁻¹) is the rate at which energy is transmitted in the direction of wave propagation, across a vertical plane perpendicular to the direction of wave advance and extending down the entire ocean depth (Dean and Dalrymple, 1991). The three-hourly data from the wave model and buoy data were used to compute *E* at the original three-hourly sampling rate, by means of the approximate equation $E = 0.5H_s2T_p$ (Dean and Dalrymple, 1991; Hagerman, 2001; Beyene and Wilson, 2006). The SST data, provided by the Fundación Oceanográfica de Guipúzcoa - Aquarium de Donostia-San Sebastián, run from January 1980 to December 2008 and were recorded daily at 10 a.m.

To provide an accurate indicator of the climate behaviour of each variable, the 25th and 75th percentiles were calculated on the basis of the longest available data series. The period and number of missing values (above 98% in all periods) differ from one variable to another: (a) Climate data (obtained from NCEP) for 1948–2008, (b)

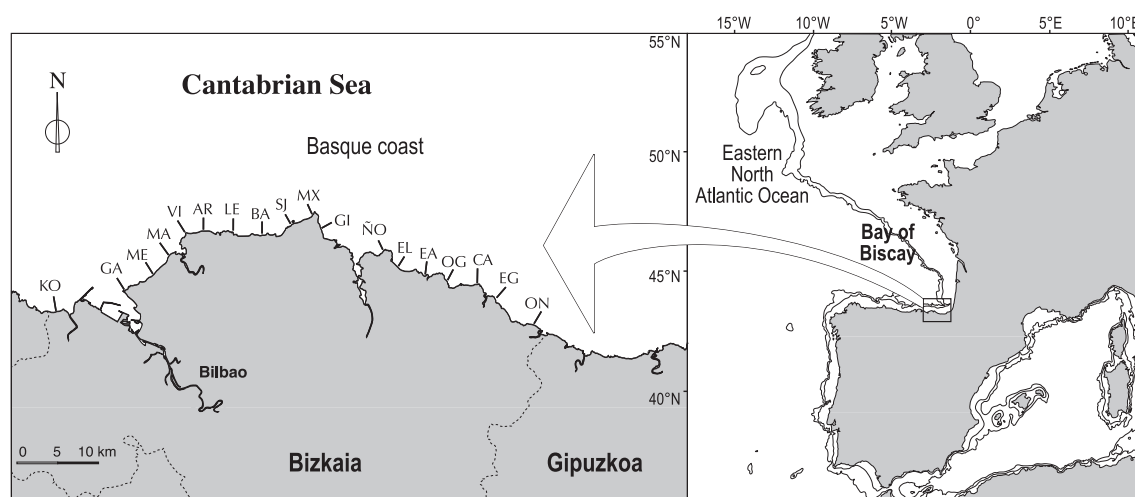


Fig. 1. Map of the study area showing locations of transects: Kobaron (KO); La Galea (GA); Meñakoz (ME); Matxilando (MA); Cabo Villano (VI); Arminza (AR); Lemoiz (LE); Bakio (BA); San Juan de Gaztelugatxe (SJ); Matxitxako (MX); Gibealeko (GI); Ogoño (ÑO); Elantxobe (EL); Ea (EA); Ogeia (OG); Santa Catalina (CA); Egiluz (EG); and Ondarroa (ON).

wave energy flux for 1998–2008 (WAVEWATCH model), (c) SST data for 1947–2008 (Aquarium data). The relationships between variables were analysed on the basis of Pearson's correlation and Linear Models (LM) (Verzani, 2005). The correlation coefficient was checked against the hypothesis that it was zero with a 95% confidence level (Wilks, 2006).

2.3. Biological data

The methods used were adapted from earlier research (Díez et al., 2003) to ensure comparable datasets. In the reference study, sampling was carried out in the summer of 1991 using SCUBA. Twenty-one 100 m long equidistant transects were set up perpendicularly along 108 km of coastline and 18 of these transects were revisited in the summer of 2008 (from July 14 to September 19) (Fig. 1). The relocation of each transect was calculated using photographic records of the starting point in combination with the transect orientation and bathymetric profile (see Annex Table A1 for georeference details). Each transect started at 2–4 m below mean low water at spring tide, with depth being determined with a digital gauge, and the tide tables were corrected for the diving time. The average depth range covered by transects was 3–9 m (2 m minimum; 13 m maximum depth). Macrophyte abundances were assessed by visually estimating their cover (%) in 1 m² quadrats at 5 m intervals along each transect, according to the scale of Braun-Blanquet (1951). Average species cover among quadrats was calculated using the median value for each Braun-Blanquet interval. To minimise the differences between the years and prevent possible misidentification of species, some species were aggregated into genera.

Permutational multivariate analysis of variance (PERMANOVA) was performed to test the hypothesis that assemblages differed

from one year to the other. Non-metric multidimensional scaling (nMDS) ordination on the basis of a Bray–Curtis dissimilarity matrix calculated for square-root transformed data was used to provide a graphic visualisation of variation over time in communities. The SIMPER (Similarity Percentage Analysis) routine was applied to identify species that could discriminate between the two years. For each site the significance levels of the differences in species cover from one year to the other were evaluated by the Wilcoxon signed-rank test. Species richness (S), Shannon diversity (H' , \log_e), Simpson ($1 - \lambda$) diversity and Pielou J' evenness were calculated for each quadrat. The PRIMER software package (Anderson et al., 2008) was used to perform the analyses.

3. Results

3.1. Climate variable trends

Annual increases in SST occurred from 1980 to 2008 (Fig. 2a), particularly in Spring and Summer (Table 1). The number of days in summer with SST over the 75th percentile value (22.1 °C) increased from less than 9.88 to 36.67 over this period (Fig. 2b). The average SST in this season increased from 20.8 °C to 21.7 °C. The average summer temperatures above the 75th percentile significantly increased from 22.4 °C to 23.2 °C (Fig. 2c). The maximum temperatures reached in summer also increased, with the summers of 1997, 2003 and 2006 being especially hot (Maximum SST > 25 °C) (Fig. 2d). The daily precipitation rate at surface suffered a significant (99%) annual decline over the period 1980–2008, which was significant (99%) in both spring and summer (Table 1). The mean daily visible (photosynthetically active, PAR) beam downward solar flux at surface showed no significant changes (1980–2008) (Table 1). Only an annual increase of 2.9 days per decade of

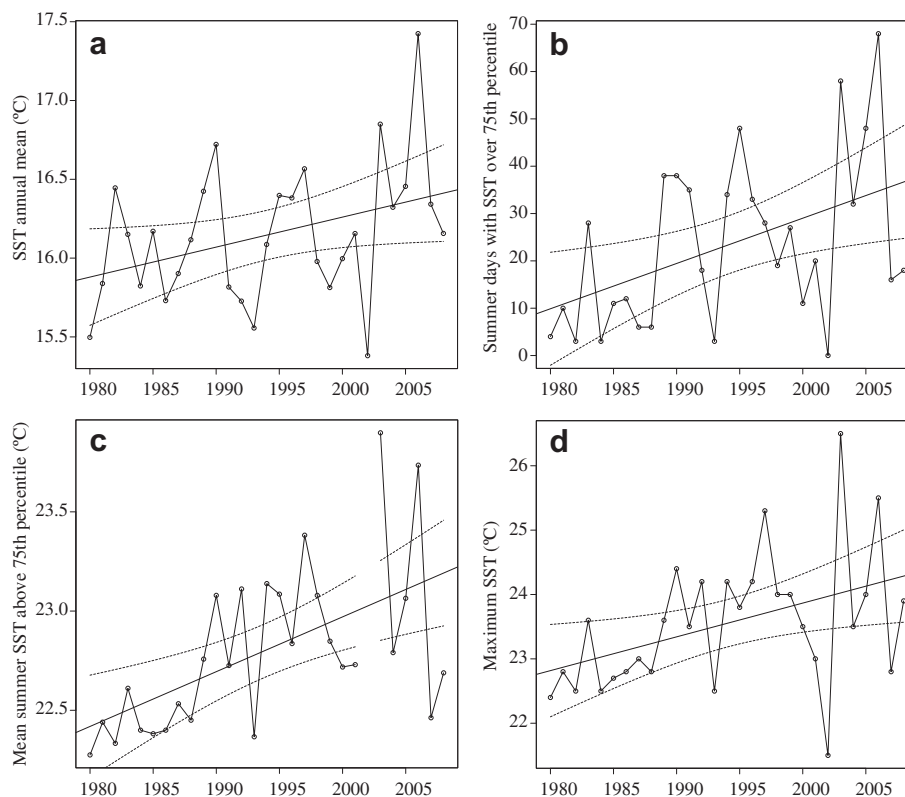


Fig. 2. Time series of sea-surface temperature: annual mean (a), number of summer days exceeding the 75th percentile (b), summer mean of values over 75th percentile (c), and maxima (d) over the period 1980–2008. The dashed lines represent the 95% confidence intervals.

Table 1

Linear trends (slope and significance: 90%, 95%, 99%**) of seasonal (Winter: January–March; Spring: April–June; Summer: July–September; Autumn: October–December) and annual sea-surface temperature (SST), mean daily precipitation rate (DPR), and mean daily visible beam downward solar flux at surface (PAR beam) over the period 1980–2008. Mean = Average of all values; Mean ($P > 75$) = Average of values over 75th percentile; Days ($P > 75$) = Number of days exceeding the 75th percentile; Max = Maximum value of SST.

| | Winter | Spring | Summer | Autumn | Annual |
|-------------------|-------------|-------------|--------------|--------------|---------------|
| SST | | | | | |
| Mean | 0.016 | 0.036* | 0.033* | 0.001 | 0.019* |
| Mean ($P > 75$) | 0.001 | 0.023 | 0.028** | 0.015 | 0.017 |
| Days ($P > 75$) | 0.735 | 0.499* | 0.957** | 0.131 | 1.278** |
| Max | 0.019 | 0.043 | 0.052* | 0.002 | 0.052* |
| DPR | | | | | |
| Mean | -2.4245e-07 | -6.2430e-07 | -6.3307e-07* | -8.60522e-08 | -3.9678e-07** |
| PAR beam | | | | | |
| Mean | 0.037 | 0.065 | 0.104 | 0.069 | 0.069 |
| Mean ($P > 75$) | 0.059 | -0.009 | 0.033 | 0.020 | 0.008 |
| Days ($P > 75$) | 0.097 | 0.091 | 0.116 | -0.037 | 0.294 |

radiation above the 75th percentile (beam PAR > 95.9 W/m²) at 90% significance was detected. No significant change in wave energy was detected, although it should be noted that the time series (1998–2008) is too short to confirm trends.

3.2. Changes in vegetation structure

Permutational multivariate analysis of variance (PERMANOVA) detected significant differences between the two years (Table 2). The diagram resulting from nMDS ordination graphically represents the variation of assemblages over time (Fig. 3). The ordination analysis shows clear differences between the two surveys and the species contributing most to the discrimination of the time pattern detected were identified by the similarity percentage procedure (SIMPER routine). Each of the 28 taxa listed in Table 3 contributes in excess of 1% to the average dissimilarity between the two years (59.5%), and their cumulative contribution is 68%. Changes in the abundance of these taxa are detailed below.

The only encrusting calcareous species reported in 1991 was *Mesophyllum* spp. (reported as *Mesophyllum licheoides*), whereas in 2008 *Lithophyllum incrustans* (average cover: 3.2 ± 0.4 SE) was also found in 54% of the quadrats. *Mesophyllum* spp., the dominant species of the crustose layer, showed no significant changes in most of the sites (Fig. 4). A widespread increase was detected in the brown alga *Zanardinia typus*, which showed significant increases at ten sampling sites. In general terms, the crustose layer of subtidal vegetation in the study area has experienced greater development.

The results show increases in the abundance of articulated coralline algae. The most abundant genus *Corallina* showed significant increases at 15 sampling sites (Fig. 4) with a mean increase of $14.5 \pm 3.8\%$ (mean \pm SE). Two species were found, *Corallina officinalis* and *Corallina elongata*, with the latter being more abundant. Similarly, the genus *Jania*, including the species *Jania rubens* and *Jania longifurca*, showed significant increases at 15 locations. Epiphytic filamentous forms, mainly ceramiceous algae, also

showed significant increases, e.g. *Gayliella flaccida* and *Aglaothamnion tenuissimum*. Another taxon that discriminates between the two surveys is the genus *Pterosiphonia*. The species *Pterosiphonia ardreana* and *Pterosiphonia pennata*, treated as a group (*Pterosiphonia* spp.), showed significant increases at eleven sampling sites. However, changes in *Pterosiphonia complanata* varied from site to site. Other basal species that increased along the coast, albeit with low cover values, were *Acrosorium ciliolatum*, *Cladostephus spongiosus*, *Cladophora pellucida*, *Chondria coeruleascens* and *Bornetia secundiflora*.

The key structural seaweeds *Cystoseira baccata* and *Gelidium corneum* (formerly *G. sesquipedale*) underwent significant distributional changes between 1991 and 2008. *Cystoseira baccata* significantly increased at four sites (KO, LE, SJ, ÑO) but decreased at three (BA, MX, EG) (Fig. 4). The agarophyte *G. corneum* decreased in clean, transparent waters (KO, BA, EA) but increased at those sites where water quality had improved (MA, VI, SJ, ÑO) (Díez et al., 2010; Gorostiaga et al., 2010). *Plocamium cartilagineum* growing epiphytically on canopy species increased. In 1991 two populations of the kelp *Laminaria ochroleuca* were detected in Bakio (cover: 20%, frequency: 80%) and San Juan de Gaztelugatze (cover: 39%, frequency: 78%), along with scattered specimens along the coast, whereas in 2008 was not found. Similarly, the annual kelp *Saccorhiza polyschides* was present in 24.6% of the quadrats sampled in 1991 but was not observed at all in 2008.

Table 2

PERMANOVA results based on Bray–Curtis dissimilarities of square-root transformed data showing the effect of Year (Y) on algal assemblages (140 variables). P values were obtained using 9999 permutations of given permutable units.

| PERMANOVA – permutational multivariate analysis of variance | | | | | | |
|---|----|--------|--------|----------|------------|--------------|
| Source | df | SS | MS | Pseudo-F | P (perm) | Unique perms |
| Y | 1 | 10,878 | 10,878 | 8.4823 | 0.0001 | 9928 |
| Res | 34 | 43,601 | 1282.4 | | | |
| Total | 35 | 54,479 | | | | |

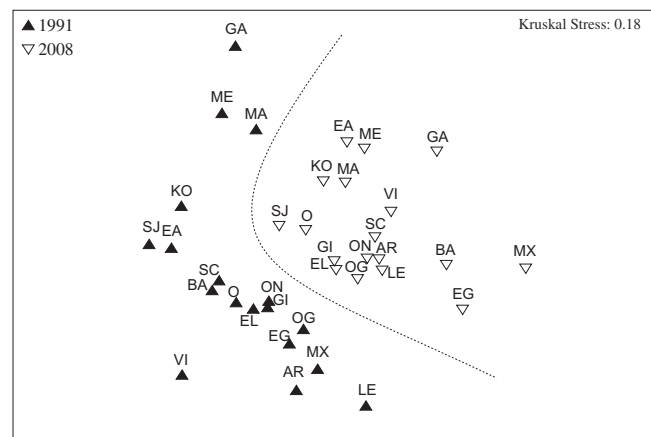


Fig. 3. Non-metric MDS ordination based on the Bray–Curtis dissimilarity coefficient applied to square-root transformed data. Each symbol is the 'average sample' obtained by averaging across site quadrats in each sampling survey. Black triangles: 1991 survey; white triangles: 2008 survey. For site abbreviations, see legend to Fig. 1.

Table 3
Average cover in % (C) and frequency in % (F) of the species in 1991 and 2008 and contribution of each taxon to the average dissimilarity between the two surveys according to the SIMPER routine. The 28 taxa listed have a contribution of over 1% of the total dissimilarity. They are ordered on the basis of their cold or warm-water affinity. Northern distribution limit: (a) Scandinavia; (b) British Isles. (1) *C. elongata* and *C. officinalis*; (2) *M. expansum* and *M. alternans*; (3) *P. pennata* and *P. ardreaana*; (4) *P. cartilagineum* and *P. raphelisanum*; (5) *J. rubens* and *J. longifurca*.

| SIMPER results – similarity percentages – species contributions | | | | | |
|---|------|------|------|------|------------|
| Taxa list | 1991 | | 2008 | | Contrib. % |
| | C | F | C | F | |
| Lusitanic species | | | | | |
| <i>Cystoseira baccata</i> (S.G. Gmel.) P.C. Silva | 23.6 | 39.0 | 23.2 | 41.5 | 6.31 |
| <i>Gelidium corneum</i> (Huds.) J.V. Lamour. | 13.4 | 45.5 | 15.0 | 69.8 | 5.06 |
| <i>Pterosiphonia complanata</i> (Clemente) Falkenb. | 9.2 | 58.8 | 5.8 | 61.9 | 3.19 |
| <i>Laminaria ochroleuca</i> Bach. Pyl. | 2.9 | 11.6 | – | – | 1.10 |
| Warm-water species (a) | | | | | |
| <i>Cladostephus spongiosus</i> (Huds.) C. Agardh | 0.6 | 15.0 | 2.2 | 40.7 | 1.81 |
| <i>Dictyota dichotoma</i> (Huds.) J.V. Lamour. | 2.4 | 44.6 | 1.6 | 50.3 | 1.76 |
| <i>Phyllophora crispa</i> (Huds.) P.S. Dixon | – | – | 0.9 | 18.6 | 1.06 |
| Warm-water species (b) | | | | | |
| <i>Corallina</i> spp. (1) | 4.1 | 47.2 | 15.8 | 86.4 | 4.26 |
| <i>Zanardinia typus</i> (Nardo) G. Furnari | 7.5 | 50.6 | 13.3 | 77.1 | 4.00 |
| <i>Aglaothamnion tenuissimum</i> (Bonnem.) Feldm.-Maz. | – | – | 7.00 | 64.1 | 3.95 |
| <i>Mesophyllum</i> spp. (2) | 28.0 | 85.0 | 32.5 | 96.0 | 3.51 |
| <i>Codium decortcatum</i> (Woodw.) M.A.Howe | 6.0 | 18.2 | 6.1 | 25.1 | 3.28 |
| <i>Gayliella flaccida</i> (Harv. ex Kütz.) T.O.Cho & L.J.McIvor | 0.0 | 2.5 | 4.0 | 61.9 | 2.78 |
| <i>Lithophyllum incrustans</i> Phil. | – | – | 3.2 | 54.5 | 2.77 |
| <i>Pterosiphonia</i> spp. (3) | 0.5 | 15.0 | 4.0 | 50.3 | 2.36 |
| <i>Plocamium</i> spp. (4) | 0.7 | 38.4 | 3.6 | 68.4 | 2.07 |
| <i>Acrosorium ciliolatum</i> (Harv.) Kylin | 0.0 | 5.1 | 1.8 | 73.7 | 1.94 |
| <i>Jania</i> spp. (5) | 0.2 | 11.6 | 2.2 | 61.0 | 1.77 |
| <i>Chondria coerulea</i> (J. Agardh) Falkenb. | 0.6 | 15.3 | 1.7 | 18.6 | 1.45 |
| <i>Haematocelis rubens</i> J. Agardh | 1.1 | 21.5 | 1.3 | 37.9 | 1.43 |
| <i>Rhodymenia pseudopalmata</i> (J.V. Lamour.) P.C. Silva | 1.2 | 27.7 | 0.8 | 32.2 | 1.41 |
| <i>Cladophora pellucida</i> (Huds.) Kütz. | 0.3 | 30.5 | 1.2 | 42.9 | 1.08 |
| <i>Bornetia secundiflora</i> (J. Agardh) Thur. | 0.0 | 1.1 | 0.4 | 49.4 | 1.04 |
| <i>Cryptopleura ramosa</i> (Huds.) Kylin ex L. Newton | 0.8 | 44.9 | 0.8 | 50.8 | 1.03 |
| <i>Peyssonnelia atropurpurea</i> P. Crouan & H. Crouan | – | – | 0.9 | 24.0 | 1.00 |
| Alien species | | | | | |
| <i>Falkenbergia rufolanosa</i> (Harv.) F. Schmitz | 3.7 | 51.7 | 12.5 | 83.9 | 3.18 |
| <i>Herposiphonia</i> sp. | – | – | 4.3 | 30.8 | 2.28 |
| <i>Heterosiphonia japonica</i> Yendo | – | – | 1.9 | 31.9 | 1.37 |

The study reveals the introduction and expansion of non-indigenous species. The alien species *Heterosiphonia japonica* was found at 17 sampling sites, although its abundance was high at only one location (EG). Several recently introduced species of Ceramiales were also found, such as *Antithamnion amphigenum*, *Antithamnion nipponicum* and *Scageliopsis patens*, all with low cover values. Likewise, an unidentified species of the genus *Herposiphonia* whose abundance ranges from occasional presence to 26% cover (Fig. 4) is probably a newly introduced species. The tetrasporophytic phase (*Falkenbergia rufolanosa*) of the established non-indigenous species *Asparagopsis armata* was significantly greater at ten of the eighteen locations studied (Fig. 4). Its mean cover change in the study area was $8.9\% \pm 2.4\%$ (SE). Similarly, the tetrasporophytic phase (*Trailliella intricata*) of the non-native species *Bonnemaisonia hamifera*, which was not recorded in 1991, was found in eight locations.

In total 140 macroalgal taxa were found, 86 in 1991 and 133 in 2008 (see Annex Table A2 for full species list with their relative abundances). Seventy-nine of them were recorded in both surveys and 54 species were new additions, distributed as follows: 44 Rhodophyceae, 6 Chlorophyceae, and 4 Phaeophyceae. The total number of species per site found was higher at 17 of the 18 sampling sites in 2008 (Fig. 5a). The increases ranged from 4.3% (2 species) to 126.7% (38 species). Similarly, the species richness per quadrat was higher at all sampling sites, with an average increase of

10.6 ± 4.3 SD (Fig. 5b). Changes in the number of species per sampling unit were also estimated, considering only conspicuous species (cover higher than 1%). Increases were detected at all locations, with an average increase of 5.9 ± 1.7 SD (Fig. 5c). Diversity also increased throughout the study area. Shannon diversity measurements gave figures of over 1.5 in all cases in 2008, whereas only subtidal vegetation at Matxilando (MA) showed such a figure in 1991 (Fig. 5d). Simpson diversity measurements were significantly higher at 17 sites in 2008 (Fig. 5e). It was also observed that differences in Simpson diversity from site to site were lower in 2008. Similarly, Pielou's evenness was higher at most sites in 2008 (Fig. 5f).

4. Discussion

The results obtained in this study reveal significant changes in the structure of subtidal vegetation along the western Basque coast from 1991 to 2008. The most important results are: 1) an increase in coralline algae; 2) changes in the distributional patterns of the canopy-forming species; 3) disappearance of kelps; 4) increases of meridional affinity species, mainly morphologically simple forms; 5) introduction and expansion of non-indigenous species, and 6) increases in species richness and diversity. All these biological changes have coincided with upward trends in sea-surface temperature over the last three decades, particularly in summer.

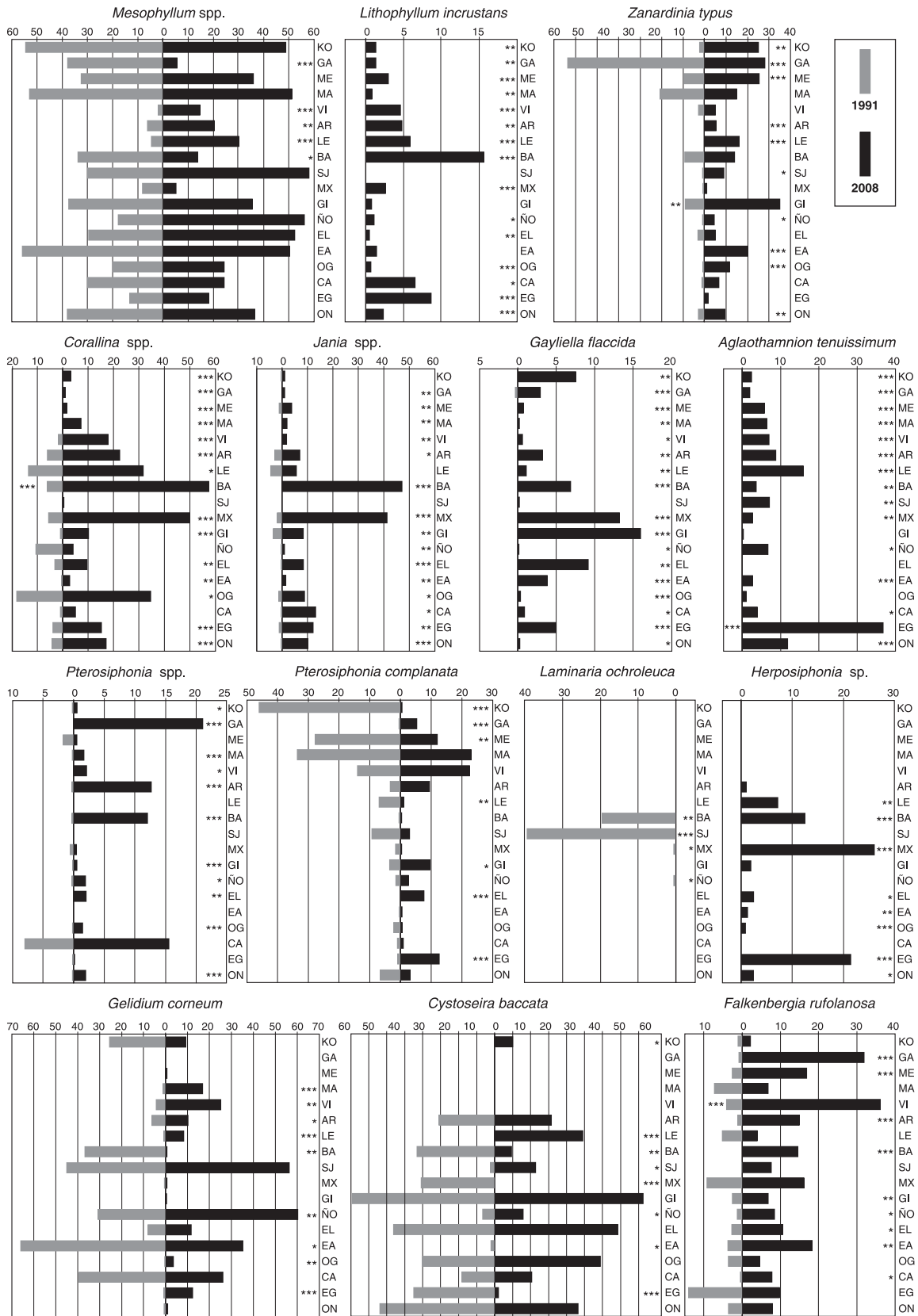


Fig. 4. Percentage cover of the most discriminant species in differences detected between 1991 and 2008. Asterisks *, ** and *** indicate significance levels $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively, for the Wilcoxon signed-rank test of differences between means. For site abbreviations, see legend to Fig. 1.

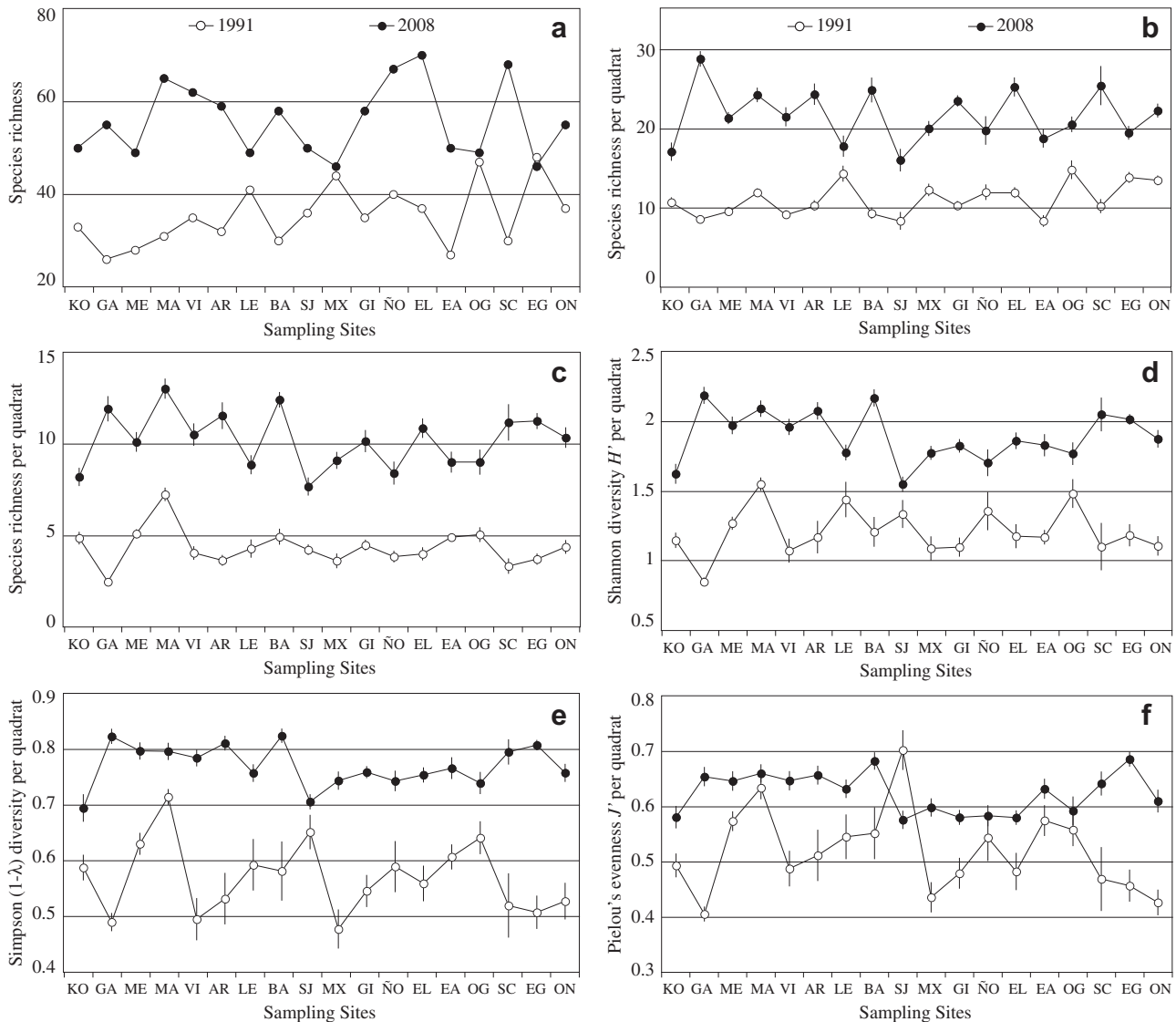


Fig. 5. Cumulative species richness (a), mean values of species richness derived from full species dataset (b), species richness after the removal of occasional species (c), Shannon–Wiener H' diversity (d), Simpson $(1-\lambda)$ diversity (e) and Pielou evenness J' (f) for each sampling site and year. Bars show standard error (SE). For site abbreviations, see legend to Fig. 1.

4.1. Increase in coralline algae

The study reveals increases in the cover of coralline algae, mainly *Corallina elongata*, *Jania rubens* and *Lithophyllum incrustans*. These changes may be related to the warming trend detected since 1980 (0.21 °C per decade in mean annual SST). Stimulation of calcification and growth by increasing temperature has already been documented for coralline algae (Mohamed and Khaled, 2005; Steller et al., 2007; Jian-Zhang et al., 2010). Nevertheless, given that these species are common macrophytes thriving in sun-exposed intertidal habitats along the Basque coast (Díez et al., 2009), their downward extension into the subtidal zone may also be attributable to increases in light availability. The interactive effects of temperature and irradiance levels are known to exert control over the rate of calcification of temperate coralline algae (Martin et al., 2006). Our results show no evidence that PAR radiation levels have changed significantly since 1980, so we suggest that there may have been increases in water transparency. The combination of the decrease suggested in the productivity of the inner Bay of Biscay (Llope et al., 2007; Valdés et al., 2007), pollution abatement

(Gorostiaga and Díez, 1996; García-Barcina et al., 2006; Díez et al., 2010; Gorostiaga et al., 2010) and the decrease detected in rainfall could have resulted in greater clarity of seawater. Changes in depth distributions of seaweeds concordant with water transparency increases have been reported recently for other European areas (Pehlke and Bartsch, 2008).

On the other hand, changes in the carbonate chemistry of seawater are predicted to have profound negative consequences for calcifying algae (Gao et al., 1993; Martin and Gattuso, 2009). According to the IPCC, for a three-fold increase in atmospheric CO_2 from the pre-industrial level (a rise to 840 ppm), dissolved CO_2 would cause a decrease in average ocean surface pH to ca. 7.77 (assuming a temperature of 18 °C) by 2100 (Raven et al., 2005). Studies on volcanic hydrothermal vents (Hall-Spencer et al., 2008; Couto et al., 2010) report large-scale decreases in the abundance of coralline algae at lowered pH levels of 7.6. The current seawater pH in the study area (8.2–8.3) is far from levels that would inhibit calcification, but it is possible that by the end of this century net dissolution may exceed net calcification in coralline algae along the Basque coast.

4.2. Changes in the distribution patterns of canopy species

The impact of climate change on key species is expected to have major negative consequences in coastal ecosystems (Breeman, 1990; Hiscock et al., 2004). Seaweed vegetation in unpolluted shallow waters throughout the study area was characterised in 1991 by the presence of a perennial canopy of *Gelidium corneum* or *Cystoseira baccata* (Díez et al., 2003) and significant changes in the distribution of both species have been detected. The macrophyte *G. corneum* exhibited high covers at six locations in 1991 (KO, BA, SJ, ÑO, EA, CA), all of them exposed to high wave action. Our results show that this agarophyte has significantly decreased in three of these locations (KO, BA, EA), and shows stress symptoms such as partial frond yellowing and an unusual branch breakdown pattern. By contrast, *G. corneum* has increased in those exposed sites where extra loads of nutrients and turbidity are available but water quality has improved as result of pollution mitigation (MA, VI, SJ, ÑO) (Díez et al., 2010; Gorostiaga et al., 2010). These results suggest that warming of the waters in the past three decades does not fully explain the decline of *G. corneum* beds. Miguel-Vijandi et al. (2010) conducted multifactorial experiments to examine the effects of the interaction between temperature, photosynthetic irradiance, UV radiation, and nutrient availability on the acclimation capacity of *G. corneum* collected from Basque populations. They found that nitrogen supply exerts a positive effect on photosynthesis performance, as opposed to the stress factors of increased temperature and irradiance, as reported for other macrophytes such as *Gracilaria conferta* (Figueroa et al., 2010). Some studies (Llope et al., 2007; Valdés et al., 2007) have suggested that the Cantabrian Sea is becoming less productive, for example, a decreasing trend in nitrate availability has been reported for the southern Bay of Biscay, as result of decreases in upwelling intensity and an increase in the period of summer stratification (Llope et al., 2007). In addition, the decrease in summer rainfall recorded on the Basque coast since 1980, and the consequent decrease in the input of nutrient-rich continental waters during the stratification period, may also have contributed to the hypothetical decline in nutrient availability in waters off that coast. Nutrient depletion, increased temperature and water transparency in summer may be acting synergetically as a complex stress factor for those *G. corneum* populations that live in clean coastal stretches.

The key structural seaweed *Cystoseira baccata* also underwent significant distributional changes in the study area from 1991 to 2008. It significantly increased at four sites (KO, LE, SJ, ÑO) but significantly decreased at three others (BA, MX, EG). Multifactorial laboratory experiments carried out to examine the effects of the interaction between several stress factors suggest that *C. baccata* shows a high acclimation capacity to increased temperature and irradiance (Miguel-Vijandi et al., 2010). This brown macrophyte is predicted to migrate northwards along European coastlines (Hiscock et al., 2004). This shift seems to be occurring now as this species has become dominant on the neighbouring coast of Asturias in those habitats where kelps beds have retreated (J. Rico in Müller et al., 2009).

4.3. Disappearance of kelps

Two dense populations of *Laminaria ochroleuca* were detected in Bakio and San Juan de Gaztelugatxe in 1991, as well as scattered individuals of *Saccorhiza polyschides* along the coast. Neither of these two species was observed in 2008. According to Fernández (2011) these kelps have been retreating westward on the north coast of Spain since the 1980s, and they are currently reduced to small patches and isolated individuals east of Cabo Peñas. *Laminaria ochroleuca* is considered to be a warm-temperate species since it exhibits optimum growth at between

15 and 20 °C and an upper lethal temperature of 22–23 °C for its sporophytes (tom Dieck, 1992). Similarly, *S. polyschides* has a survival interval of between 5 and 23 °C (van den Hoek, 1982). Our results suggest that the number of summer days with temperatures above 22.1 °C has increased from less than 10 to more than 35 from 1980 to 2008. These long warm periods in combination with the pronounced warming up to 26.5 °C in 2003 and 25.5 °C in 2006 probably had a lethal effect on both species. The regression of kelps has already been documented along European coastlines (Cosson, 1999; Husa, 2007). However, although kelps are considered particularly vulnerable to climate change due to their cold-water affinities, there is no evidence of a worldwide shift to higher latitudes (Merzouk and Johnson, 2011).

4.4. Introduction and expansion of non-indigenous species

This study also detected the alien species *Antithamnion amphigenum*, *Scageliopsis patens*, *Antithamnion nipponicum* and *Heterosiphonia japonica*, recently introduced into Atlantic European waters (Secilla et al., 1997, 2007, 2008; Husa et al., 2004; Rueness et al., 2007), as well as the proliferation of one unidentified exotic species of the genus *Herposiphonia*. The introduction of species into new ecosystems is a major threat to biodiversity because it may lead to biotic homogenisation, especially in synergy with other anthropogenic disturbances such as climate change and coastal pollution (Schaffelke et al., 2006). Currently none of the alien species detected in this study is considered invasive because they all have low cover values. However, it is important that they are closely tracked because as climate-driven changes ensue, the new environmental conditions could alter the competitive interactions between alien and native species (Occhipinti-Ambrogi, 2007). In this sense, we have detected a significant spread of the established alien *Falkenbergia rufolanosa* (tetrasporophytic phase of *Asparagopsis armata*), mainly at those sites where the vegetation has no canopy. Although no disappearance of native species can be related to the increase in *F. rufolanosa*, its expansion may be affecting the relative abundance of native species. Our finding agrees with that of Lima et al. (2007), who estimate that *Asparagopsis armata* has shifted 287 km northwards along the Portuguese coast over the last 50 years.

4.5. Increases in species with meridional affinity

Warm-temperate species have increased significantly throughout the study area, a result consistent with the increases detected in SST. While warming may have allowed some species such as *Aglaothamnion tenuissimum*, *Aphanocladia stichidiosa* or *Centroceras clavulatum* to migrate northwards, the new thermal conditions could have enhanced the growth and/or reproduction of some warm-temperate species already recorded in 1991 such as *Gayliella flaccida*, *Acrosorium ciliolatum*, and *Zanardinia typus*. Most of the species that exhibit increased cover are filamentous or polysiphonated annual forms. The northward expansion of warm-temperate species has already been observed along European coasts. According to Helmuth et al. (2006) the poleward range limits of intertidal biota have shifted by as much as 50 km per decade, faster than recorded shifts of most terrestrial species. Most of the changed documented in algae distributions coinciding with global warming are focussed on large-sized species such as *Bifurcaria bifurcata*, *Cystoseira tamariscifolia*, *Halopithys incurva* and *Hypnea musciformis* (Hiscock et al., 2004; Mieszkowska et al., 2005; Lima et al., 2007). In contrast, reports on changes in the distribution of small, inconspicuous species are scarce. Araújo et al. (2009) report northwards expansion in the distributional range of the southern warm-temperate small

species *A. stichidiosa*, *Ctenosiphonia hypnoides* and *Griffithsia schousboei* in northern Portugal.

4.6. Changes in species richness and diversity

Our results reveal that subtidal phytobenthic assemblages along the western Basque coast underwent large-scale increases in species richness and diversity from 1991 to 2008. Approximately 70% of the species that account for the increase in taxon richness are morphologically simple forms with short life-cycles and warm-water affinity. Such changes could be due to physiological responses of species to new environmental conditions, but may also be related to shifts in interspecific interactions. The first explanation is consistent with the evidence of the positive relationship between SST and marine biodiversity (Tittensor et al., 2010). Higher temperatures increase metabolic rates, resulting in latitudinal gradients of increasing species richness from polar to equatorial regions (Gaston and Spicer, 2004). But the instability shown by the perennial canopy species *Cystoseira baccata* and *Gelidium corneum* could also have benefited opportunistic species. Underlying this non-equilibrium approach is the intermediate disturbance hypothesis, which predicts maximal diversity at intermediate levels of disturbance (Connell, 1978; Valdivia et al., 2005). Nevertheless, global climate change is predicted to have major negative consequences for marine biodiversity, particularly if important habitat-modifying species undergo range shifts (Ling, 2008). In addition, warming is expected to reduce compositional stability and increase temporal species turnover (Hillebrand et al., 2010).

The present study suggests that global warming could already be affecting the eastern Cantabrian coastal ecosystems. Most of the

changes detected are probably attributable to the observed increase in SST, but changes in water clarity and nutrient availability may also have had an effect. There is great uncertainty in forecasting future trends in seaweed distributions since global climate change involves the interplay of ocean warming with other environmental factors plus indirect effects that operate through ecological interactions such as trophic relationships and competition. Hence biological and modelling studies are needed to identify sentinel species and sites in order to track future changes and build more accurate predictive models for the responses of benthic assemblages to climate change.

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Annex

Table A1

Georeference of the starting point on land, direction and starting point depth of the transects.

| Location | Latitude | Longitude | Direction | Starting depth |
|-------------------------------|---------------|--------------|-----------|----------------|
| Kobaron (KO) | 43°21'17.65"N | 3°07'46.40"O | NW 355° | –3 m |
| La Galea (GA) | 43°22'24.06"N | 3°02'11.88"O | NW 315° | –3 m |
| Meñakoz (ME) | 43°23'37.70"N | 2°59'25.44"O | NW 315° | –3 m |
| Matxilando (MA) | 43°24'51.44"N | 2°58'00.39"O | NW 315° | –4 m |
| Cabo Villano (VI) | 43°26'09.80"N | 2°56'47.94"O | N 330° | –4 m |
| Arminza (AR) | 43°26'18.72"N | 2°54'34.31"O | N 30° | –4 m |
| Lemoiz (LE) | 43°25'54.18"N | 2°52'05.95"O | N 30° | –2 m |
| Bakio (BA) | 43°25'53.65"N | 2°49'48.03"O | N 0° | –3 m |
| San Juan de Gaztelugatxe (SJ) | 43°26'44.12"N | 2°47'16.45"O | W 290° | –4 m |
| Matxitxako (MX) | 43°27'19.82"N | 2°45'14.35"O | N 355° | –4 m |
| Gibeleko (GI) | 43°25'54.60"N | 2°44'22.92"O | E 75° | –2 m |
| Ogoño (ÑO) | 43°24'49.73"N | 2°38'58.66"O | NW 315° | –3 m |
| Elantxobe (EL) | 43°23'38.50"N | 2°37'18.49"O | NE 45° | –4 m |
| Ea (EA) | 43°23'16.89"N | 2°35'00.66"O | NE 45° | –3 m |
| Ogeia (OG) | 43°22'55.27"N | 2°33'12.60"O | NE 45° | –2 m |
| Santa Catalina (CA) | 43°22'34.17"N | 2°30'51.85"O | NW 315° | –3 m |
| Egiluz (EG) | 43°21'32.79"N | 2°29'06.97"O | NE 45° | –2 m |
| Ondarroa (ON) | 43°19'44.75"N | 2°25'19.10"O | NE 45° | –3 m |

Table A2

Average cover in % (C), standard error (SE) and frequency in % (F) of the species in 1991 and 2008.

| Taxa list | 1991 | | | 2008 | | |
|---|------|-----|------|------|-----|------|
| | C | SE | F | C | SE | F |
| RHODOPHYTA | | | | | | |
| <i>Acrosorium ciliolatum</i> (Harv.) Kylin | 0.0 | 0.0 | 5.1 | 1.8 | 0.2 | 73.7 |
| <i>Aglaothamnion cordatum</i> (Børgesen) Feldm.-Maz. | 0.1 | 0.0 | 10.5 | 0.1 | 0.0 | 6.5 |
| <i>Aglaothamnion gallicum</i> (Nägeli) Halos ex Ardré | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Aglaothamnion tenuissimum</i> (Bonnem.) Feldm.-Maz. | – | – | – | 7.0 | 0.8 | 64.1 |
| <i>Aglaothamnion tripinnatum</i> (C. Agardh) Feldm.-Maz. | – | – | – | 0.0 | 0.0 | 2.5 |
| <i>Ahnfeltia plicata</i> (Huds.) Fr. | 0.0 | 0.0 | 0.3 | – | – | – |
| <i>Ahnfeltiopsis devoniensis</i> (Grev.) P.C. Silva & DeCew | 0.0 | 0.0 | 1.1 | 0.0 | 0.0 | 1.7 |

Table A2 (continued)

| Taxa list | 1991 | | | 2008 | | |
|--|------|-----|------|------|-----|------|
| | C | SE | F | C | SE | F |
| <i>Anotrichium furcellatum</i> (J. Agardh) Baldock | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.6 |
| <i>Antithamnion amphigeneum</i> A. Millar | – | – | – | 0.2 | 0.1 | 6.8 |
| <i>Antithamnion nipponicum</i> Yamada & Inagaki | – | – | – | 0.0 | 0.0 | 4.0 |
| <i>Antithamnionella multiglandulosa</i> A.Secilla, A.Santolaria, I.Díez & J.M.Gorostiaga | – | – | – | 0.0 | 0.0 | 2.3 |
| <i>Antithamnionella ternifolia</i> (J.D.Hooker & Harvey)Lyle | 0.1 | 0.0 | 4.0 | 0.4 | 0.1 | 26.3 |
| <i>Aphanocladia stichidiosa</i> (Funk) Ardré | – | – | – | 0.4 | 0.1 | 9.3 |
| <i>Apoglossum ruscifolium</i> (Turner) J. Agardh | 0.0 | 0.0 | 8.5 | 0.1 | 0.0 | 24.0 |
| <i>Asparagopsis armata</i> Harv. | 0.1 | 0.0 | 13.3 | 0.1 | 0.0 | 3.4 |
| <i>Bonnemaisonia asparagoides</i> (Woodw.) C. Agardh | 0.2 | 0.2 | 6.2 | 0.2 | 0.0 | 15.8 |
| <i>Bonnemaisonia clavata</i> Hamel | – | – | – | 0.0 | 0.0 | 1.1 |
| <i>Bonnemaisonia hamifera</i> Harv. | 0.4 | 0.1 | 29.7 | 0.0 | 0.0 | 5.4 |
| <i>Bornetia secundiflora</i> (J. Agardh) Thur. | 0.0 | 0.0 | 1.1 | 0.4 | 0.0 | 49.4 |
| <i>Calliblepharis ciliata</i> (Huds.) Kütz. | 0.4 | 0.2 | 13.8 | 0.0 | 0.0 | 1.4 |
| <i>Callithamnion granulatum</i> (Ducluz.) C. Agardh. | – | – | – | 0.0 | 0.0 | 1.7 |
| <i>Callithamnion tetragonum</i> (With.) Gray | – | – | – | 0.0 | 0.0 | 3.4 |
| <i>Callophyllis laciniata</i> (Huds.) Kütz. | 0.3 | 0.1 | 20.1 | 0.0 | 0.0 | 4.8 |
| <i>Centroceras clavulatum</i> Mont. | – | – | – | 0.1 | 0.0 | 8.5 |
| <i>Ceramium ciliatum</i> (J. Ellis) Ducluz. | 0.1 | 0.0 | 4.0 | 0.1 | 0.0 | 1.4 |
| <i>Ceramium echionotum</i> J. Agardh | – | – | – | 0.3 | 0.1 | 5.4 |
| <i>Ceramium pallidum</i> (Nägeli ex Kütz.) Maggs & Hommers. | – | – | – | 0.0 | 0.0 | 0.6 |
| <i>Ceramium secundatum</i> Lyngb. | 0.4 | 0.2 | 3.7 | 0.1 | 0.0 | 14.4 |
| <i>Champia parvula</i> (C. Agardh) Harv. | 0.2 | 0.1 | 6.5 | 0.5 | 0.1 | 24.6 |
| <i>Chondracanthus acicularis</i> (Roth) Fredericq | 0.0 | 0.0 | 1.7 | 0.2 | 0.1 | 7.6 |
| <i>Chondracanthus teedei</i> (Mert. ex Roth) Kütz. | 0.0 | 0.0 | 2.3 | 0.1 | 0.0 | 4.8 |
| <i>Chondria coerulea</i> (J. Agardh) Falkenb. | 0.6 | 0.2 | 15.3 | 1.7 | 0.4 | 18.6 |
| <i>Chrysymenia ventricosa</i> (J.V. Lamour.) J. Agardh | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.6 |
| <i>Chylocladia verticillata</i> (Lightf.) Bliding | 0.0 | 0.0 | 0.3 | – | – | – |
| <i>Composothamnion thuyoides</i> (Sm.) Nägeli | 0.0 | 0.0 | 3.7 | 0.1 | 0.0 | 8.2 |
| <i>Corallina elongata</i> J. Ellis & Solander | – | – | – | 10.4 | 1.1 | 64.7 |
| <i>Corallina officinalis</i> Linnaeus | 4.1 | 0.7 | 47.2 | 4.9 | 0.5 | 54.2 |
| <i>Crouania attenuata</i> (C. Agardh) J. Agardh | – | – | – | 0.0 | 0.0 | 5.4 |
| <i>Cryptonemia lomation</i> (Bertol.) J. Agardh | 0.1 | 0.0 | 4.8 | 0.0 | 0.0 | 0.8 |
| <i>Cryptopleura ramosa</i> (Huds.) Kylin ex L. Newton | 0.8 | 0.1 | 44.9 | 0.8 | 0.1 | 50.8 |
| <i>Dasya hutchinsiae</i> Harv. | – | – | – | 0.0 | 0.0 | 2.8 |
| <i>Dasya ocellata</i> (Gratel.) Harv. | – | – | – | 0.1 | 0.0 | 1.7 |
| <i>Drachiella minuta</i> (Kylin) Maggs & Hommers. | 0.3 | 0.1 | 13.3 | 0.1 | 0.0 | 10.5 |
| <i>Dudresnaya verticillata</i> (With.) Le Jol. | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.3 |
| <i>ErythroGLOSSUM laciniatum</i> (Lightf.) Maggs & Hommers. | – | – | – | 0.0 | 0.0 | 2.5 |
| <i>Falkenbergia rufolanosa</i> (Harv.) F. Schmitz | 3.7 | 0.6 | 51.7 | 12.5 | 0.9 | 83.9 |
| <i>Gastroclonium ovatum</i> (Huds.) Papenf. | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.3 |
| <i>Gastroclonium reflexum</i> (Chauv.) Kütz. | – | – | – | 0.1 | 0.0 | 9.3 |
| <i>Gayliella flaccida</i> (Harvey ex Kützling) T.O.Cho & L.J.Mclvor | 0.0 | 0.0 | 2.5 | 4.0 | 0.4 | 61.9 |
| <i>Gelidium attenuatum</i> (Turner) Thur. | – | – | – | 0.1 | 0.1 | 5.6 |
| <i>Gelidium corneum</i> (Huds.) J.V. Lamour. | 13.4 | 1.5 | 45.5 | 15.0 | 1.3 | 69.8 |
| <i>Gelidium crinale</i> (Turner) Gaillon | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Gelidium pusillum</i> (Stackh.) Le Jol. | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Gelidium spinosum</i> (S.G. Gmel.) P.C. Silva | 0.0 | 0.0 | 4.0 | 0.2 | 0.1 | 7.3 |
| <i>Gigartina pistillata</i> (S.G. Gmel.) Stackh. | 0.1 | 0.1 | 6.2 | 0.0 | 0.0 | 2.5 |
| <i>Gracilaria bursa-pastoris</i> (S.G. Gmel.) P.C. Silva | 0.0 | 0.0 | 2.5 | – | – | – |
| <i>Grateloupia dichotoma</i> J. Agardh | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Grateloupia filicina</i> (J.V. Lamour.) C. Agardh | 0.2 | 0.1 | 2.0 | 0.0 | 0.0 | 1.1 |
| <i>Gymnogongrus crenulatus</i> (Turner) J. Agardh | 0.1 | 0.0 | 18.4 | 0.0 | 0.0 | 8.2 |
| <i>Gymnogongrus griffithsiae</i> (Turner) Mart. | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Haematocelis rubens</i> J. Agardh | 1.1 | 0.4 | 21.5 | 1.3 | 0.2 | 37.9 |
| <i>Halophthys incurva</i> (Huds.) Batters | 0.0 | 0.0 | 5.9 | 0.7 | 0.2 | 14.1 |
| <i>Halurus equisetifolius</i> (Lightf.) Kütz. | 0.2 | 0.0 | 24.3 | 0.6 | 0.1 | 48.3 |
| <i>Halymenia latifolia</i> P. Crouan & H. Crouan ex Kütz. | 0.1 | 0.0 | 5.4 | 0.0 | 0.0 | 0.6 |
| <i>Herposiphonia</i> sp. | – | – | – | 4.3 | 0.6 | 30.8 |
| <i>Heterosiphonia japonica</i> Yendo | – | – | – | 1.9 | 0.4 | 31.9 |
| <i>Heterosiphonia plumosa</i> (J. Ellis) Batters | 0.2 | 0.1 | 15.8 | 0.1 | 0.0 | 15.0 |
| <i>Hypnea musciformis</i> (Wulfen) J.V. Lamour. | – | – | – | 0.1 | 0.0 | 5.4 |
| <i>Hypoglossum hypoglossoides</i> (Stackh.) Collins & Herv. | – | – | – | 0.1 | 0.0 | 13.6 |
| <i>Itonoa marginifera</i> (J. Agardh) Masuda & Guiry | – | – | – | 0.0 | 0.0 | 0.6 |
| <i>Jania longifurca</i> Zanardini | – | – | – | 0.6 | 0.1 | 19.8 |
| <i>Jania rubens</i> (Linnaeus) J.V.Lamouroux | 0.2 | 0.1 | 11.6 | 1.7 | 0.2 | 45.8 |
| <i>Kallymenia reniformis</i> (Turner) J. Agardh | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 1.7 |
| <i>Liagora viscida</i> (Forsk.) C. Agardh | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.8 |
| <i>Lithophyllum incrustans</i> Phil. | – | – | – | 3.2 | 0.4 | 54.5 |
| <i>Meredithia microphylla</i> (J. Agardh) J. Agardh | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.3 |
| <i>Mesophyllum</i> spp. | 28.0 | 1.5 | 85.0 | 32.5 | 1.4 | 96.0 |
| <i>Microcladia glandulosa</i> (Sol. ex Turner) Grev. | 0.0 | 0.0 | 0.3 | 0.5 | 0.1 | 20.6 |
| <i>Monosporus pedicellatus</i> (Sm.) Solier | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Naccaria wiggii</i> (Turner) Endl. | 0.0 | 0.0 | 0.3 | – | – | – |

(continued on next page)

Table A2 (continued)

| Taxa list | 1991 | | | 2008 | | |
|--|------|-----|------|------|-----|------|
| | C | SE | F | C | SE | F |
| <i>Nitophyllum punctatum</i> (Stackh.) Grev. | 0.1 | 0.0 | 16.9 | 0.2 | 0.0 | 29.7 |
| <i>Osmundea osmunda</i> (S.G.Gmelin) K.W.Nam & Maggs | – | – | – | 0.0 | 0.0 | 2.0 |
| <i>Osmundea pinnatifida</i> (Huds.) Stackh. | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Peyssonnelia atropurpurea</i> P. Crouan & H. Crouan | – | – | – | 0.9 | 0.2 | 24.0 |
| <i>Peyssonnelia coriacea</i> Feldmann | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 4.8 |
| <i>Peyssonnelia harveyana</i> P.L.Crouan & H.M.Crouan ex J. Agardh | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Peyssonnelia</i> sp. | 0.0 | 0.0 | 0.6 | – | – | – |
| <i>Peyssonnelia squamaria</i> (S.G.Gmelin) Decaisne | 0.0 | 0.0 | 1.4 | 0.0 | 0.0 | 5.4 |
| <i>Phyllophora crispa</i> (Huds.) P.S. Dixon | – | – | – | 0.9 | 0.2 | 18.6 |
| <i>Pleonosporium borrieri</i> (Sm.) Nägeli ex Hauck | – | – | – | 0.0 | 0.0 | 2.5 |
| <i>Pleonosporium flexuosum</i> (C. Agardh) Bornet | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 1.7 |
| <i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon | – | – | – | 3.3 | 0.4 | 63.3 |
| <i>Plocamium raphelisianum</i> P.J.L.Dangeard | – | – | – | 0.3 | 0.1 | 23.7 |
| <i>Polysiphonia polyspora</i> (C. Agardh) J. Agardh | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 2.5 |
| <i>Polysiphonia scopulorum</i> Harv. | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Pterocladiaella capillacea</i> (S.G. Gmel.) Santelices & Hommers. | 0.0 | 0.0 | 1.4 | 0.0 | 0.0 | 0.3 |
| <i>Pterosiphonia complanata</i> (Clemente) Falkenb. | 9.2 | 0.9 | 58.8 | 5.8 | 0.6 | 61.9 |
| <i>Pterosiphonia parasitica</i> (Huds.) Falkenb. | 0.0 | 0.0 | 1.1 | 0.5 | 0.1 | 30.5 |
| <i>Pterosiphonia ardreana</i> Maggs & Hommersand | – | – | – | 3.3 | 0.4 | 46.0 |
| <i>Pterosiphonia pennata</i> (C.Agardh) Sauvageau | 0.48 | – | 15.0 | 0.7 | 0.2 | 11.3 |
| <i>Pterothamnion crispum</i> (Ducluz.) Nägeli | – | – | – | 0.4 | 0.2 | 25.4 |
| <i>Pterothamnion plumula</i> (J. Ellis) Nägeli | 0.1 | 0.0 | 4.5 | – | – | – |
| <i>Radicilingua thysanorhizans</i> (Holmes) Papenf. | – | – | – | 0.0 | 0.0 | 0.6 |
| <i>Rhodophyllis divaricata</i> (Stackh.) Papenf. | – | – | – | 0.0 | 0.0 | 1.1 |
| <i>Rhodothamniella floridula</i> (Dillwyn) Feldmann | – | – | – | 0.1 | 0.0 | 0.8 |
| <i>Rhodymenia holmesii</i> Ardiss. | 0.1 | 0.0 | 3.7 | 0.1 | 0.0 | 5.9 |
| <i>Rhodymenia pseudopalmata</i> (J.V. Lamour.) P.C. Silva | 1.2 | 0.2 | 27.7 | 0.8 | 0.1 | 32.2 |
| <i>Scageliopsis patens</i> Wollaston | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Schizymenia dubyi</i> (Chauv. ex Duby) J. Agardh | 0.0 | 0.0 | 5.6 | 0.0 | 0.0 | 4.5 |
| <i>Scinaia furcellata</i> (Turner) J. Agardh | 0.0 | 0.0 | 1.4 | 0.0 | 0.0 | 0.8 |
| <i>Seirospora interrupta</i> (Sm.) F. Schmitz | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Spermothamnion repens</i> (Dillwyn) Rosenv. | – | – | – | 0.1 | 0.0 | 2.8 |
| <i>Sphaerococcus coronopifolius</i> Stackh. | 0.1 | 0.0 | 11.6 | 0.2 | 0.1 | 15.0 |
| <i>Sphondylothamnion multifidum</i> (Huds.) Nägeli | 0.0 | 0.0 | 7.3 | 0.0 | 0.0 | 4.8 |
| <i>Stenogramme interrupta</i> (C. Agardh) Mont. ex Harv. | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.8 |
| <i>Trilliella intricata</i> Batters | – | – | – | 0.5 | 0.1 | 14.1 |
| OCHROPHYTA | | | | | | |
| <i>Cladostephus spongiosus</i> (Huds.) C. Agardh | 0.6 | 0.2 | 15.0 | 2.2 | 0.4 | 40.7 |
| <i>Colpomenia peregrina</i> (Sauv.) Hamel | 0.0 | 0.0 | 1.1 | 0.1 | 0.0 | 9.6 |
| <i>Cutleria adspersa</i> (Mert. ex Roth) De Not. | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Cystoseira baccata</i> (S.G. Gmel.) P.C. Silva | 23.6 | 2.0 | 39.0 | 23.2 | 1.9 | 41.5 |
| <i>Cystoseira tamariscifolia</i> (Huds.) Papenf. | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.6 |
| <i>Desmarestia ligulata</i> (Lightf.) J.V. Lamour. | 0.2 | 0.1 | 11.0 | 0.0 | 0.0 | 1.4 |
| <i>Dictyopteris polypodioides</i> (DC.) J.V. Lamour. | 0.3 | 0.0 | 38.7 | 0.2 | 0.0 | 26.3 |
| <i>Dictyota dichotoma</i> (Huds.) J.V. Lamour. | 2.4 | 0.4 | 44.6 | 1.6 | 0.2 | 50.3 |
| <i>Halidrys siliquosa</i> (L.) Lyngb. | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Halopectis filicina</i> (Gratel.) Kütz. | 0.0 | 0.0 | 6.8 | 0.1 | 0.0 | 11.0 |
| <i>Hincksia granulosa</i> (Smith) P.C. Silva | – | – | – | 0.0 | 0.0 | 0.8 |
| <i>Laminaria ochroleuca</i> Bach. Pyl. | 2.9 | 0.7 | 11.6 | – | – | – |
| <i>Phyllariopsis brevipes</i> (C. Agardh) E.C. Henry & South | 0.0 | 0.0 | 5.1 | 0.0 | 0.0 | 3.1 |
| <i>Saccorhiza polyschides</i> (Lightf.) Batters | 0.9 | 0.4 | 24.6 | – | – | – |
| <i>Sargassum vulgare</i> C. Agardh | – | – | – | 0.0 | 0.0 | 0.6 |
| <i>Spatoglossum solieri</i> (Chauv. ex Mont.) Kütz. | 0.0 | 0.0 | 3.1 | 0.0 | 0.0 | 2.0 |
| <i>Stypocaulon scoparium</i> (L.) Kütz. | 0.0 | 0.0 | 0.8 | 0.4 | 0.1 | 7.6 |
| <i>Taonia atomaria</i> (Woodw.) J. Agardh | 0.1 | 0.0 | 7.1 | 0.4 | 0.1 | 11.6 |
| <i>Zanardinia typus</i> (Nardo) G. Furnari | 7.5 | 0.9 | 50.6 | 13.3 | 0.9 | 77.1 |
| CHLOROPHYTA | | | | | | |
| <i>Bryopsis pennata</i> J.V. Lamour. | – | – | – | 0.0 | 0.0 | 0.6 |
| <i>Bryopsis plumosa</i> (Huds.) C. Agardh | – | – | – | 0.1 | 0.0 | 7.3 |
| <i>Chaetomorpha linum</i> (O.F. Müll.) Kütz. | – | – | – | 0.0 | 0.0 | 0.6 |
| <i>Chaetomorpha mediterranea</i> (Kütz.) Kütz. | – | – | – | 0.0 | 0.0 | 0.3 |
| <i>Cladophora hutchinsiae</i> (Dillwyn) Kütz. | – | – | – | 0.0 | 0.0 | 2.8 |
| <i>Cladophora lehmanniana</i> (Lindenb.) Kütz. | – | – | – | 0.1 | 0.0 | 8.5 |
| <i>Cladophora pellucida</i> (Huds.) Kütz. | 0.3 | 0.0 | 30.5 | 1.2 | 0.2 | 42.9 |
| <i>Cladophora prolifera</i> (Roth) Kütz. | 0.0 | 0.0 | 2.3 | 0.2 | 0.1 | 16.1 |
| <i>Codium adhaerens</i> C. Agardh | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.6 |
| <i>Codium decorticatum</i> (Woodw.) M.A.Howe | 6.0 | 1.1 | 18.9 | 6.1 | 0.9 | 25.1 |
| <i>Codium fragile</i> (Suringar) Hariot | – | – | – | 0.0 | 0.0 | 2.3 |
| <i>Codium vermilara</i> (Oliv.) Chiaje | – | – | – | 0.5 | 0.1 | 15.5 |
| <i>Derbesia tenuissima</i> (Moris & De Not.) P. Crouan & H. Crouan | – | – | – | 0.5 | 0.1 | 17.2 |
| <i>Halicystis parvula</i> Schmitz ex Murray | 0.0 | 0.0 | 2.0 | 0.1 | 0.0 | 22.3 |
| <i>Ulva pseudocurvata</i> Koeman & Hoek | 0.0 | 0.0 | 0.8 | 0.3 | 0.1 | 27.1 |
| <i>Ulva rigida</i> C. Agardh | 0.2 | 0.0 | 26.8 | 0.1 | 0.1 | 1.7 |
| <i>Umbraulva olivascens</i> (P.J.L.Dangeard) G.Furnari | – | – | – | 0.1 | 0.0 | 5.6 |

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