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The role of physical variables in biodiversity patterns of intertidal macroalgae along European coasts

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In the frame of the COST ACTION 'EMBOS' (Development and implementation of a pan-European Marine Biodiversity Observatory System), coverage of intertidal macroalgae was estimated at a range of marine stations along the European coastline (Subarctic, Baltic, Atlantic, Mediterranean). Based on these data, we tested whether patterns in macroalgal diversity and distribution along European intertidal rocky shores could be explained by a set of meteo-oceanographic variables. The variables considered were salinity, sea surface temperature, photosynthetically active radiation, significant wave height and tidal range and were compiled from three different sources: remote sensing, reanalysis technique and in situ *measurement. These variables were parameterized to represent average conditions (mean values), variability (standard deviation) and extreme events (minimum and maximum values). The results obtained in this study contribute to reinforce the EMBOS network approach and highlight the necessity of considering meteo-oceanographic variables in long-term assessments. The broad spatial distribution of pilot sites has allowed identification of latitudinal and longitudinal gradients manifested through species composition, diversity and dominance structure of intertidal macroalgae. These patterns follow a latitudinal gradient mainly explained by sea surface temperature, but also by photosynthetically active radiation, salinity and tidal range. Additionally, a longitudinal gradient was also detected and could be linked to wave height.*

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INTRODUCTION

European coastal ecosystems have been modified by a range of pressures, such as habitat loss, eutrophication, pollution, species invasion and resource overexploitation (EEA, 2010). In addition, many of these impacts are exacerbated by climate change, mainly driven by ocean warming, acidification and sea level rise (Hoegh-Guldberg & Bruno, 2010; Philippart *et al.*, 2011). All these processes have led to changes in the ecosystem functioning of intertidal communities and have modified their biodiversity patterns, with the consequent loss of ecosystem goods and services they provide (Costanza *et al.*, 1997). Therefore, establishment of specific and regional to worldwide implementation of mitigation and adaptation strategies for global changes is urgently required (Apitz *et al.*, 2006).

Extensive and comprehensive information on littoral biodiversity patterns and their causes represents an essential resource for marine spatial planning and for the management of coastal areas to support sound decisions by managers and policymakers. However, the compilation of long-time series of biological data is costly and complex, and therefore, homogeneous information from wide biogeographic ranges is scarce. There is a growing interest to fill this gap by promoting the creation of global biodiversity monitoring programmes such as GEO BON (Group on Earth Observation, Biodiversity Observation Network) and open access biological databases at global, e.g. Global Biodiversity Information Facility (GBIF, 2013), Ocean Biogeographic Information (OBIS, 2015), or European level, e.g. Marine Biodiversity and Ecosystem Functioning (MarBEF data system) (Escaravage *et al.*, 2009; Heip *et al.*, 2009). Regarding macroalgae, Konar *et al.* (2010) analysed patterns of macroalgal diversity in the northern hemisphere based on field-collected samples using a standardized protocol. At the European scale, Ramos *et al.* (2014) carried out a first approach to characterize the NE Atlantic coast, providing homogeneous and standardized information about intertidal macroalgae on a semi-quantitative scale (absent, rare, common). However, none of these databases provides an adequate knowledge of the current distribution of species, due to at least one of the following reasons: (i) they do not cover the whole geographic area of interest, (ii) they are not based on standardized sampling protocols, (iii) most are only presence data, without any quantitative information regarding species abundance and (iv) acquisition of data is usually done once and not repeated over time.

The COST ACTION ES1003 EMBOS (Development and implementation of a pan-European Marine Biodiversity Observatory System) aims to address these problems by creating a permanent international pan-European network of observation stations. This network will ultimately allow us to assess long-term changes in marine biodiversity and investigate their possible causes. Specific protocols have been defined to sample soft bottoms, hard substrata and pelagic communities, aimed at standardizing future biodiversity observations. These protocols have been tested in a network of pilot sites throughout Europe in order to assess their efficacy, reliability and robustness.

In order to seek large-scale biodiversity patterns and explain their causes, such valuable biological information has to be linked with abiotic explanatory variables. The appropriate variables and indicators will depend on the habitat, community or species of interest, the spatial scale considered (Juanes *et al.*, 2016) and the ultimate goal of the study. In any case, it would be advisable to use physical variables with a very high and homogeneous spatial and temporal resolution. These variables could be used not only to characterize the present environmental conditions, but also to model species distributions or to predict their future shifts in different change scenarios. Biotic interactions are also important drivers of macroalgae distribution (Benedetti-Cecchi *et al.*, 2000), but their usefulness is limited at wide scales and can often be omitted at regional-scale assessments of diversity patterns (Benedetti-Cecchi & Trussell, 2014).

Among abiotic variables that determine regional-scale patterns of intertidal macroalgae, temperature is undoubtedly the key factor explaining the biogeographic patterns of macroalgae (Breeman, 1988; Lüning, 1990). However, the distribution of marine macroalgae is interactively set by several abiotic factors, such as wave exposure (Ballantine, 1961; Levin & Paine, 1974), tidal range (Lewis, 1955), solar radiation (Hanelt *et al.*, 1993) and salinity (Wallentinus, 1991). Nowadays, information on environmental variables can be obtained with high spatial and temporal resolution from a number of sources. Satellite imagery allows us to obtain standardized, continuous and extensive environmental characterization of physical conditions, with a global coverage and with the appropriate level of accuracy for different purposes (de Barbosa Araujo *et al.*, 2015). In addition, reanalysis techniques have become a valuable tool to obtain global homogeneous long-time series of climate variables when complete temporal or spatial records are not available (Reguero *et al.*, 2012). In spite of these powerful tools, few studies have combined meteo-oceanographic variables, rather than sole temperature gradients, in order to describe the biological patterns of benthic communities at broad scales (Ramos *et al.*, 2012, 2014).

In this paper, we tested whether spatial patterns in macroalgal diversity and distribution along European intertidal rocky shores (EMBOS pilot survey 2014) can be associated with a set of meteo-oceanographic variables, which were compiled from different open-access and continuously updated databases. The analysis performed will contribute to validate and refine the sampling protocol proposed by EMBOS.

MATERIALS AND METHODS

Study area

In total, 17 EMBOS pilot sites sampled in 10 different countries (Belgium, Estonia, France, Greece, Ireland, Israel, Italy, Norway (Polish Polar Station of Hornsund), Portugal and Spain) were considered for this study (Figure 1, Table 1). These pilot sites are representatives of six of the Large Marine Ecosystems (Sherman, 1986): Barents Sea (Svalbard archipelago), Baltic Sea, North Sea (Southern Bight), Celtic – Biscay Bight (Irish Sea, English Channel), Iberian Coastal (Bay of Biscay, Western Iberian Peninsula, Azores) and Mediterranean (Alboran Sea, Western Basin, Ligurian – Tyrrhenian Sea, Sea of Crete, Eastern basin). According to the EMBOS sampling protocol, these sites are representatives of the locality, fairly sheltered to semi-exposed to waves, fully marine, comparatively unbroken bedrock, of moderate slope and unimpacted by sediment or anthropogenic stressors.

Environmental data compilation

Temporal data of five environmental variables were compiled for the 17 pilot sites: photosynthetically active radiation (PAR), sea surface temperature (SST), salinity (Sal), significant wave height (Hs) and tidal range (TR). These variables were parameterized to represent average conditions (annual mean), variability (standard deviation) and extreme events (minimum and maximum values). Time series longer than 20 years were used for most variables in order to properly characterize the climatic conditions in the study area. As an exception, PAR data comprised only five years due to the lack of longer series.

Environmental data were obtained from a combination of satellite (PAR), *in situ* (Sal) and reanalysis sources (SST, Hs, TR). The PAR data were obtained from the SeaWifs and Modis Aqua (NASA) satellite sensors through MyOcean L4 products. Data were provided with a spatial resolution of 2 km and a monthly temporal resolution for the period between 1999 and 2004. The SST values were supplied with daily temporal resolution from 1985 to 2013 by the Operational Sea Surface Temperature and Sea-Ice Concentration Analysis (OSTIA) dataset, which is under the MyOcean2 project by UK-Met Office (NASA) (Stark *et al.*, 2007). Specifically, the Group for High Resolution Sea Surface Temperature (GHRSST), L4 Gap-free gridded products were used, with a spatial resolution of 0.05°. Wave height data were obtained from the Global Ocean Wave reanalysis database (GOW) (Reguero *et al.*, 2012), which was generated with the third generation model WaveWatch III, and the results were validated with satellite measurements in time and space (Tolman, 2014). In this study, hourly data from 1985 to 2013 were extracted with a spatial resolution of 0.125° for all sites, except for the Hornsund site, whose values were obtained from a global spatial domain, with a resolution of 1 – 1.5°. In order to take into account the relevant component of sea level, tidal range was defined as the difference between the 1 and 99 percentiles of the accumulated distribution of both surge and astronomical tide components, collected between 1985 and 2013. The astronomical tide was generated using the harmonic constants derived from the TPXO7.2 global tides model, developed by the Oregon State University at 0.25° resolution full global grid (Egbert *et al.*, 1994; Egbert & Erofeeva, 2002). This information was used to reconstruct hourly time series of tide, which were compiled in the IH Cantabria database Global Ocean Tide (GOT). The meteorological component was obtained from the hourly IH Cantabria database Global Ocean Surges Reanalysis (GOS). This validated model was generated as the result of the dynamic downscaling from global atmospheric NCEP and ERA-Interim, with a spatial resolution of 0.125° (Cid *et al.*, 2014). The above-mentioned variables were acquired from the nearest point with information to the pilot sites (average distance of 5 km, range from 0.2 to 25 km, except in the case of PAR for the Hornsund station, which was 150 km apart). Finally, salinity values were obtained from *in situ* measurements provided by the World Ocean Database (WOD) of the National Oceanic and Atmospheric Administration (NOAA)-NESDIS National Oceanographic Data Centre (NODC) (Levitus *et al.*, 2013). Salinity profiles between 1985 and 2014 were obtained from *in situ* measurements provided by the World Ocean Database (WOD) of the National

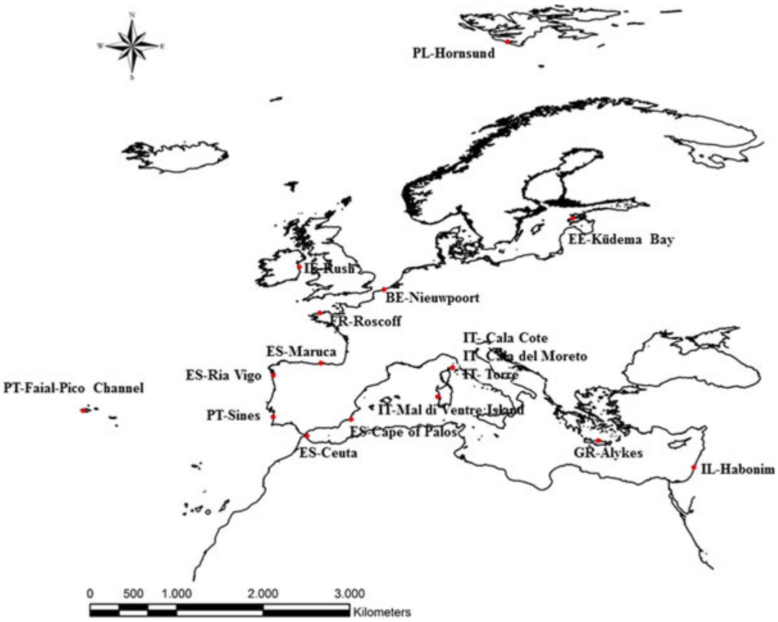

Fig. 1. EMBOS pilot sites considered in this study.

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Table 1. Coordinates and physical variables values for each pilot site (units are shown in parentheses).

LME	Pilot site	Lon (°)	Lat (°)	SST (°C)				Salinity (‰)				Hs (m)				PAR (mol m^{-2} d^{-1})				TR (m)
				av	min	max	std	av	min	max	std	av	min	max	std	av	min	max	std	
Barents Sea	PL-Hornsund	15.54	77.00	0.9	−2.0	7.1	0.4	33.2	32.9	33.5	0.3	1.32	0.15	7.17	0.91	26.3	11.9	40.7	10.8	2.11
Baltic Sea	EE-Küdema Bay	22.30	58.57	8.1	−2.0	23.2	0.7	6.7	6.7	6.7	0.0	0.64	0.01	3.46	0.52	31.9	10.4	51.2	15.9	0.84
North Sea	BE-Nieuwpoort	2.72	51.16	12.0	2.5	21.1	0.4	33.5	30.9	34.9	1.1	0.73	0.09	2.54	0.39	26.4	7.6	47.9	14.9	5.02
Celtic Biscay Shelf	IE-Rush	−6.08	53.53	11.1	4.8	18.3	0.2	33.9	29.6	34.4	0.7	0.69	0.04	3.33	0.50	24.1	5.9	40.2	12.0	4.25
	FR-Roscoff	−3.97	48.73	12.7	7.7	17.8	0.2	35.2	34.9	35.3	0.1	1.58	0.30	5.96	0.80	27.6	6.7	48.1	15.3	7.89
Iberian Coastal	ES-Maruca	−3.84	43.48	16.0	10.7	23.9	0.3	35.1	33.2	35.6	0.8	1.45	0.30	5.09	0.80	30.4	10.6	51.1	15.1	3.83
	ES-Ria Vigo	−8.80	42.20	15.1	11.6	20.0	0.2	35.2	33.0	35.8	0.9	0.84	0.20	1.61	0.35	33.2	11.3	56.8	17.1	3.24
	PT-Faial-Pico Channel	−28.55	38.54	18.7	14.1	24.9	0.3	36.3	36.3	36.3	0.0	2.19	0.60	9.22	1.19	33.7	13.4	54.5	14.7	1.31
	PT-Sines	−8.80	37.89	16.9	13.1	21.8	0.3	36.1	36.0	36.3	0.1	1.19	0.30	3.45	0.61	39.6	16.5	62.2	16.5	2.91
Mediterranean	IT- Cala Cote	9.79	43.02	18.5	11.8	28.1	0.3	38.0	37.9	38.2	0.1	0.64	0.03	4.52	0.54	33.6	8.8	59.0	17.8	0.54
	IT- Cala del Moreto	9.80	43.00	18.5	11.8	28.1	0.3	38.0	37.9	38.2	0.1	0.64	0.03	4.52	0.54	33.6	8.8	59.0	17.8	0.54
	IT- Torre	9.84	43.05	18.5	11.8	28.1	0.3	38.0	37.9	38.2	0.1	0.64	0.03	4.52	0.54	33.6	8.8	59.0	17.8	0.54
	IT-Mal di Ventre Island	8.30	39.99	18.4	11.6	27.5	0.3	37.9	37.9	37.9	0.0	1.03	0.04	6.41	0.91	36.3	13.9	59.9	16.9	0.46
	ES-Cape of Palos	−0.69	37.63	19.2	12.7	27.8	0.3	37.5	37.2	37.8	0.2	0.76	0.07	3.35	0.44	38.6	16.3	60.1	15.9	0.43
	ES-Ceuta	−5.28	35.89	18.2	14.0	23.9	0.2	36.6	36.3	37.0	0.2	0.96	0.21	4.55	0.59	37.7	16.1	59.9	16.0	0.93
	GR-Alykes	24.99	35.41	20.1	13.5	28.0	0.2	39.1	39.0	39.2	0.1	0.74	0.04	4.26	0.56	38.1	10.9	59.6	19.3	0.35
	IL-Habonim	34.92	32.63	22.5	15.4	29.9	0.2	39.2	39.1	39.3	0.1	0.80	0.09	4.69	0.56	43.3	20.4	63.2	15.7	0.50

LME, Large Marine Ecosystems, Lon, longitude; Lat, latitude; SST, sea surface temperature; Hs, significant wave height; PAR, photosynthetically active radiation; TR, tidal range.

Oceanic and Atmospheric Administration (NOAA)-NESDIS National Oceanographic Data Centre (NODC) (Levitus *et al.*, 2013). For each site, the salinity value in the first 40 m was calculated as the average of all data points within a 0.4° radius around the pilot sites.

Biological data

In each pilot site, macroalgal diversity data were collected following the protocol proposed for hard bottom communities sampling in the EMBOS project. The metadata describing the sampling campaign can be accessed at http://lifewww-00.her.hcmr.gr:8080/medobis/resource.do?r=embos_2014.

Sampling was performed in 2014 in early biological spring for each region (from March to May). Each pilot site comprised two stations separated by ~50–100 m. The stations were transects 5–15 m wide and included two tidal levels, mid and lower intertidal. As an exception, only the mid intertidal was sampled in ES-Cape of Palos and only lower intertidal in EE-Kudema Bay and IT-Mal di Ventre Island. The mid intertidal was defined as ~25% of the vertical extent of the shore centred on mean tidal level and the lower intertidal as 25% of the vertical extent of the shore working upwards from mean low water spring tide. Within each station, the coverage of macroalgal taxa was assessed in five replicate quadrats placed haphazardly in each tidal level. Quadrat size was 0.5 × 0.5 m (0.25 m^2) in the Subarctic, Baltic and NE Atlantic and 0.2 × 0.2 m (0.04 m^2) in the Mediterranean, to account for the narrow amplitude of the rocky intertidal habitat (Figure 2). Organisms were generally identified to the species level, except for encrusting corallines and small filamentous algae (<2 cm). The World Register of Marine Species (Costello *et al.*, 2013) was used as reference system for species nomenclature.

Data treatment

The ability of environmental variables to explain biodiversity patterns of macroalgae was tested using either ecological indices (richness, diversity and total coverage) or species composition and structure as dependent variables. Latitude and longitude were treated as variables in order to facilitate the explanation of the potential biogeographic gradients. In all cases, species cover of the five replicates per tidal level and station were averaged. Therefore, each pilot site was characterized by four samples (two stations and two tidal levels per station). That way, we gathered as much diversity as possible with the available data and avoided pseudoreplication when making spatial inferences. Firstly, the Spearman Rank correlation coefficient among all the environmental indicators considered and the values of richness (S, number of species), Shannon–Wiener diversity (H', Log_2) and total coverage (C) in each station and tidal level were calculated. Secondly, the multivariate spatial pattern of macroalgal assemblages was represented by a non-metric multidimensional scaling analysis (nMDS) and vectors defining correlations between ordinations of samples with the meteo-oceanographic variables were calculated. The resulting nMDS were based on cover data previously square-root-transformed, and the similarity matrix was calculated using the Bray–Curtis coefficient. In the first nMDS analysis, all pilot sites and both tidal levels were included in order to describe the general biodiversity pattern. Afterwards, more detailed separate analyses were carried out for each tidal level and focused in the Mediterranean and Atlantic sites, excluding samples from the Barents Sea and the Baltic Sea. Finally, a similarity percentage analysis (SIMPER) was used to identify the most characteristic species explaining the biogeographic patterns found. Correlations were calculated by means of MATLAB 7.7., and MDS and SIMPER analyses were carried out using the PRIMER-E software v.7 (Clarke & Gorley, 2015).

RESULTS

Environmental variables *vs* richness, diversity and total cover

The average, maximum, minimum and standard deviation of the five environmental variables considered in the analyses are shown in Table 1. The Spearman Rank correlations among environmental variables and the ecological indices were quite low and not significant in most of the cases, except for geographic coordinates (Table 2). Longitude was significantly negatively correlated with all the ecological indices and latitude correlated negatively with H', but only in the lower intertidal. Among the meteo-oceanographic variables, the low correlations obtained with averaged SST stood out, whereas its standard deviation was always significant and in the lower intertidal, even the minimum values were correlated with S and H'. Nevertheless, the parameters used to describe the swell conditions showed positive correlations with the ecological indices in most of the cases. One exception is the absence of a significant correlation in the lower intertidal with maximum Hs, whereas it was quite high in the middle intertidal. The PAR seemed to be more relevant in the middle intertidal where algal coverage decreased with PAR intensity. The variability of PAR was also negatively correlated with all the ecological indices. Finally, tidal range was only positively correlated to coverage in mid-intertidal assemblages.

Environmental variables *vs* community composition and structure

Considering all the stations and both tidal levels, nMDS results showed a high dispersion of biological data, although some patterns related to the environmental variables can be identified (Figure 3). Firstly, an evident latitudinal gradient (vertical axis) is defined by the extreme differentiation of Barents Sea samples and, to a lesser extent, Baltic sites. This latitudinal gradient highly reflected the increase in SST (average, maximum, minimum) from northern to southern Europe. Average conditions in PAR and salinity were positively correlated to this gradient, albeit to a lower degree. Secondly, a weaker longitudinal gradient (horizontal axis) was also defined, mainly driven in this case by minimum wave height and, to a lesser extent, tidal range and average wave height. No clear patterns depicted by biological data appeared along the horizontal axis, although some differentiation between Mediterranean and Atlantic regions can be distinguished. The explanatory role of the standard deviations of most of the variables was quite low, except for PAR, which showed the same pattern described for the SST parameters.

Middle intertidal

Considering only the stations from the middle intertidal in Mediterranean and Atlantic sites, similar latitudinal and longitudinal gradients can be identified, although with some differences in the role and importance of explanatory variables (Figure 4). Thus, the distribution of stations in the MDS followed a gradient from North (Celtic Sea and North Sea) to South (Mediterranean). Nonetheless, some Mediterranean samples showed greater similarities with Iberian Coastal ones than with other Mediterranean sites. This latitudinal

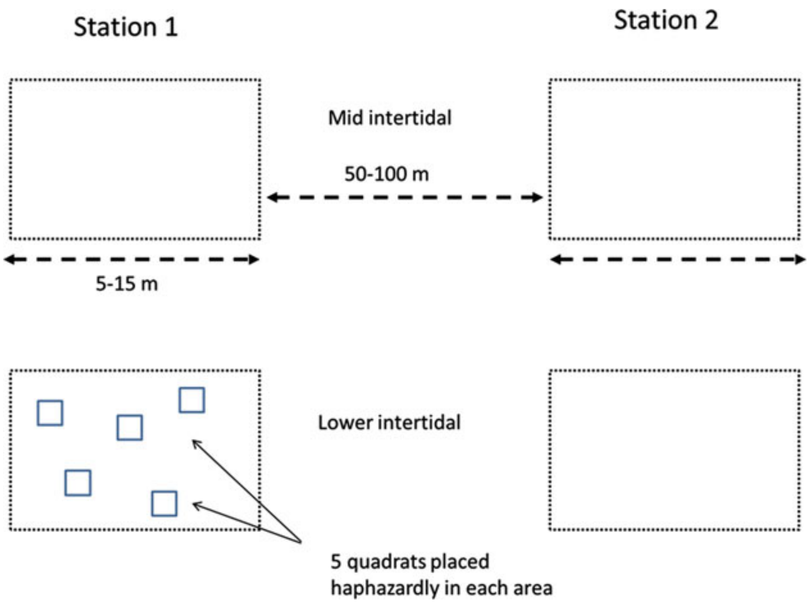

Fig. 2. Layout of stations, sampling areas and quadrats at each pilot site.

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Table 2. Spearman Rank correlations among the environmental variables and the community parameters.

		Middle intertidal			Lower intertidal		
		S	H	C	S	H	C
Longitude		−0.20	−0. 24	−0.03	**−0.59*****[***]	**−0.66*****[***]	**−0.54**[**]
Latitude		0.08	0.03	0.29	−0.33	**−0.39**[*]	−0.21
SST	Avg	−0.04	0.00	−0.26	0.23	0.21	0.14
	Min	0.09	0.14	−0.15	**0.37**[*]	**0.39**[*]	0.30
	Max	−0.13	−0.13	−0.29	0.01	−0.06	−0.05
	Std	**−0.36**[*]	**−0.38**[*]	−0.31	**−0.42**[*]	**−0.48**[**]	**−0.51**[**]
Salinity	Avg	−0.05	−0.04	−0.24	0.17	0.13	0.09
	Min	−0.05	−0.04	−0.22	0.14	0.10	0.05
	Max	−0.13	−0.11	−0.33	0.12	0.10	0.02
	Std	−0.18	−0.22	0.06	−0.02	−0.01	−0.09
Hs	Avg	**0.48**[**]	**0.53**[**]	**0.39**[*]	**0.50**[**]	**0.60**[***]	**0.49**[**]
	Min	**0.45**[*]	**0.49**[**]	0.30	**0.60**[***]	**0.68**[***]	**0.53**[**]
	Max	**0.59**[***]	**0.60**[***]	**0.54**[**]	0.22	0.24	0.32
	Std	**0.58**[***]	**0.61**[***]	**0.47**[**]	0.35	**0.41**[*]	**0.37**[*]
PAR	Avg	−0.08	−0.04	**−0.37**[*]	0.21	0.26	0.09
	Min	−0.01	0.03	−0.24	0.15	0.26	0.05
	Max	−0.13	−0.10	**−0.38**[*]	0.16	0.19	0.02
	Std	**−0.42**[*]	**−0.39**[*]	**−0.58**[*]	−0.02	−0.06	−0.25
TR		0.30	0.28	**0.39**[*]	0.23	0.23	0.27

S, richness, number of species; H, Shannon–Wiener diversity; C, % cover; SST, sea surface temperature; Hs, significant wave height; PAR, photosynthetically active radiation; TR, tidal range; avg, average; min, minimum; max, maximum; std, standard deviation.
$^{*}=P \le 0.05$; $^{**}=P \le 0.01$; $^{***}=P \le 0.001$.

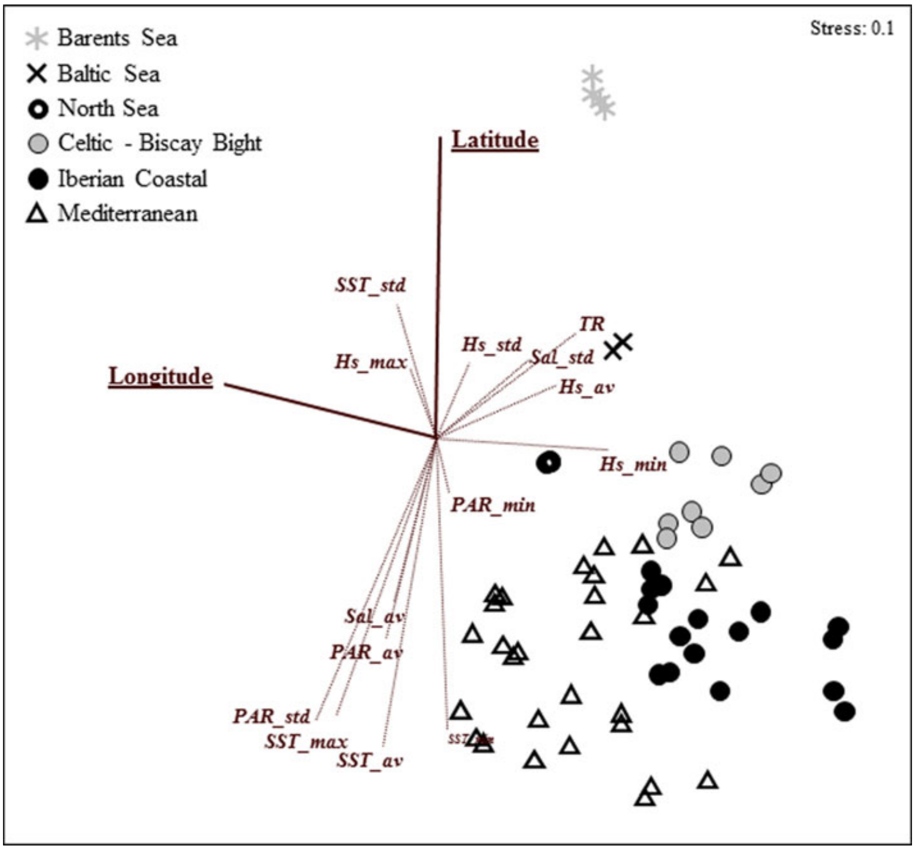

Fig. 3. Results of nMDS analysis considering all the pilot sites (each dot corresponds to the middle or lower tidal level of a station). SST, sea surface temperature; Hs, significant wave height; PAR, photosynthetically active radiation; TR, tidal range; avg, average; min, minimum; max, maximum; std, standard deviation.

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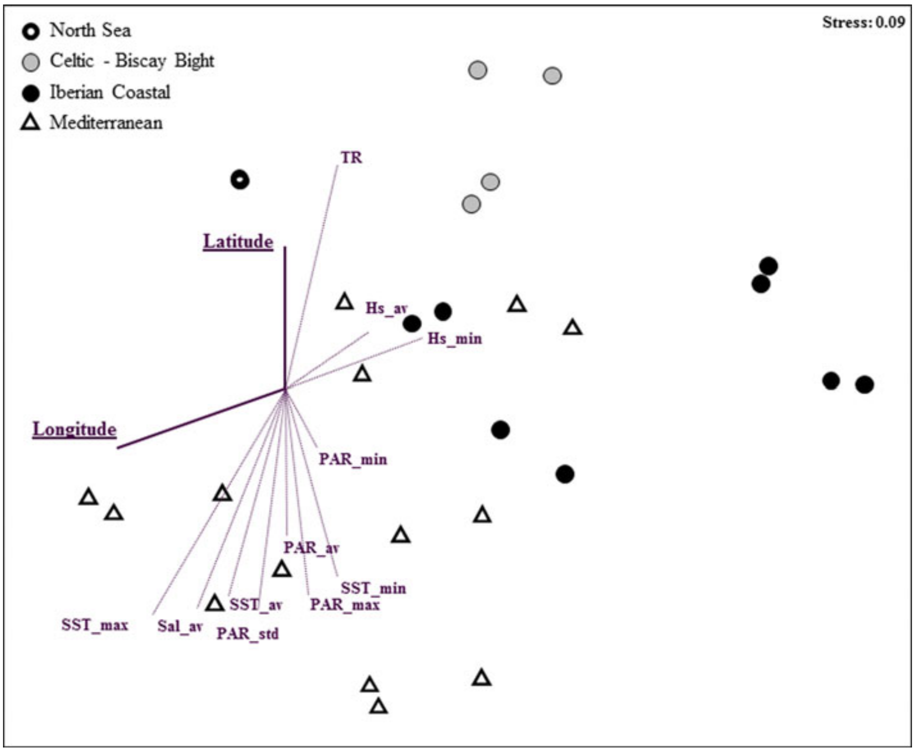

Fig. 4. Results of nMDS analysis considering Mediterranean and NE-Atlantic sites in the middle intertidal (each dot corresponds to a station). SST, sea surface temperature; Hs, significant wave height; PAR, photosynthetically active radiation; TR, tidal range; avg, average; min, minimum; max, maximum; std, standard deviation.

gradient is highly positively correlated with tidal range and inversely with most of the other environmental parameters. Additionally, a secondary longitudinal gradient can be identified, in this case explained by wave height (either average or minimum).

Lower intertidal

The ordination analysis performed with samples from the lower intertidal reflects the latitudinal gradient described for the middle intertidal, although in this case, the standard deviations of salinity and tidal range are positively and significantly correlated with latitude (Figure 5). The main difference to the middle intertidal was the loss of the longitudinal gradient in the horizontal axis, appearing in this case opposite to latitude. Wave height also played an important role in the ordination of the samples, but in this case, it was not correlated to longitude.

Differences in species composition between biogeographic regions

All the taxa identified are listed in Appendix A (Supplementary material). Based on the results of SIMPER analysis on the biogeographic differences among regions (Table 3), the northernmost stations were characterized by very few species, with *Fucus distichus* dominating in the Barents Sea and *Fucus vesiculosus* in the Baltic, together with *Pylaiella littoralis* in both sites. North Sea sites were dominated by *Ulva* spp., in both tidal levels. On the other hand, Celtic Sea and Iberian Coastal sites were much more variable and diversified. The most relevant species in Celtic Sea sites were *Chondrus crispus* in both tidal levels, *Osmundea pinnatifida* and *F. vesiculosus* in the mid intertidal and *Fucus serratus* and *Ellisolandia elongata* in the lower intertidal. In the Iberian Coastal sites, the dominance of this species was replaced by *E. elongata* in both tidal levels and *Bifurcaria bifurcata* in the lower. Regarding the Mediterranean, *Laurencia obtusa* was well represented across the whole area. *Polysiphonia* spp. and *Rissoella verruculosa* were also important in the middle intertidal, whereas *Cystoseira amentacea* dominated the lower intertidal.

DISCUSSION

The results obtained in this study contribute to reinforce the EMBOS network approach and highlight the necessity of considering meteo-oceanographic variables in long-term assessments (Ramos *et al.*, 2012, 2014; Juanes *et al.*, 2016). The broad spatial distribution of pilot sites has allowed us to identify latitudinal and longitudinal gradients manifested through species composition, diversity and dominance structure of intertidal macroalgae. In addition, the meteo-oceanographic variables analysed properly reflect the well-known physical gradients in the Atlantic (Ramos *et al.*, 2012) and in the Mediterranean Sea (Coll *et al.*, 2010).

Nonetheless, the great variability existing along the European coasts (Ramos *et al.*, 2012, 2014) demands the incorporation of a further larger amount of pilot sites in order to cover the wide range of environmental conditions in European coastal waters and the singularity of the different regions. Otherwise, some of the biological differences observed and potentially attributed to geographic factors could be caused by local environmental conditions at sampling stations,

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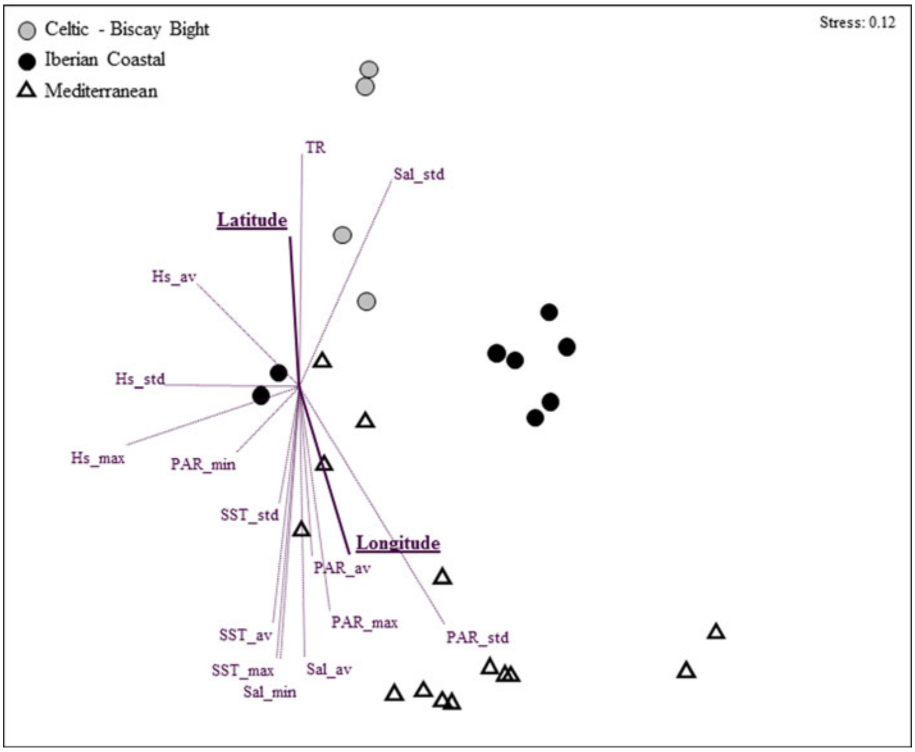

Fig. 5. Results of nMDS analysis considering Mediterranean and Atlantic samples from lower intertidal (each dot corresponds to a station). SST, sea surface temperature; Hs, significant wave height; PAR, photosynthetically active radiation; TR, tidal range; avg, average; min, minimum; max, maximum; std, standard deviation.

such as the nature of the substratum (Guidetti *et al.*, 2004), geomorphology (Cefalì *et al.*, 2016; Ramos *et al.*, 2016a), nutrient availability (Arévalo *et al.*, 2007) or biological interactions (Benedetti-Cecchi *et al.*, 2000). The selection of sites sharing analogous environmental conditions (wave exposure, slope, sedimentation), as the EMBOS protocol states, reduces the uncertainty introduced by the natural variability, but still some other uncontrolled factors could represent a source of noise in the long-term assessment of macroalgae communities (Puente & Juanes, 2008).

The availability of physical data at European or global scales is increasingly noteworthy. However, these data

Table 3. Breakdown of average similarity into contributions (%) from each taxa in middle and lower intertidal levels that contribute to similarity in each biogeographic region, according to the SIMPER analysis results.

	Middle intertidal		Lower intertidal	
Region	**Species**	**Contribution (%)**	**Species**	**Contribution (%)**
Barents Sea	*Fucus distichus*	83.0	*Fucus distichus*	95,7
	Pylaiella littoralis	15.5	*Pylaiella littoralis*	4,3
Baltic			*Pylaiella littoralis*	50.9
			Fucus vesiculosus	48.3
North Sea	*Ulva* spp.	100	*Ulva* spp.	98.8
Celtic – Biscay Bight	*Osmundea pinnatifida*	31.0	*Chondrus crispus*	38.2
	Fucus vesiculosus	19.4	*Fucus serratus*	20.3
	Chondrus crispus	14.4	*Ellisolandia elongata*	12.2
	Lithothamnion	9.6	*Laminaria digitata*	7.7
	Fucus serratus	8.6		
	Lomentaria articulata	5.9		
Iberian Coastal	*Ulva* spp.	38.8	*Bifurcaria bifurcata*	41.0
	Ellisolandia elongata	22.7	*Ellisolandia elongata*	13.1
	Lithophyllum	9.9	*Plocamium cartilagineum*	6.3
	Lithophyllum byssoides	7.9	*Ulva* spp.	5.6
Mediterranean	*Laurencia obtusa*	33.0	*Cystoseira amentácea*	78.0
	Polysiphonia spp.	24.3	*Ellisonlandia elongata*	6.9
	Rissoella verruculosa	13.5	*Laurencia obtusa*	60.5
	Lithophyllum	8.8		
	Ellisolandia elongata	6.3		

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usually come from different sources, which makes it difficult to obtain information with the same geographic resolution and for the same time period. In any case, this constraint does not invalidate the results of our study, because the environmental data used here properly characterized the average conditions in the area during the last decades. We also have to take into account the relative importance of these factors at different scales (Juanes *et al*., 2016). For example, temperature is a key factor at the biogeographic scale, but can be less relevant at the local scale (Ramos *et al*., 2016b). Conversely, geomorphology can explain changes at regional or local scales, but it is much more difficult to identify patterns at broader scales (Ramos *et al*., 2016a).

As stated by other authors (van den Hoek, 1982a; Ramos *et al*., 2014), a latitudinal gradient in the composition and structure of the macroalgal assemblages has been found along the European coasts. In accordance with other studies, this gradient is mainly explained by SST (van den Hoek, 1982b; Lüning, 1990; Ramos *et al*., 2012), but also by PAR (Wahl *et al*., 2004), salinity (Jakobsen, 1997) and tidal range (Briggs *et al*., 1997). Based on our study, biotic patterns responded very similarly to variation in minimum, maximum and average values of environmental variables, although it is well known that climatic conditions do not always follow the same patterns as those representing extreme events or their variability. Regarding this issue, Ramos *et al*. (2016c) recommended the use of more specific wave variables, such as the bottom shear stress or the frequency of extreme events, in order to increase the prediction accuracy of macroalgae distribution based on physical variables.

A longitudinal gradient was also detected, partially explained by wave height, which reached its maximum values in the Azores. This longitudinal gradient does not reflect the eastward increase in SST in the Mediterranean (Coll *et al*., 2010), neither that described along the Bay of Biscay (Fraga, 1981; Ramos *et al*., 2016c). This fact can be due to the extreme differences between northern and southern Europe (from minimum average values of 0.85°C in Hornsund to maximum average values of 22.5°C in Habonim) that mask differences at a regional scale. In other cases, local conditions, such as coastal orientation or geomorphology, can reduce the incoming ocean swell (e.g. ría de Vigo) (Ballantine, 1961).

Species distribution changed according to gradients, as described previously in many biogeographic studies. Therefore, the northern areas are distinguished by cold-temperate Ochrophyta (Fucaceae and Laminariaceae) (Steneck *et al*., 2002; Araújo *et al*., 2016), whereas the South NE-Atlantic region is mostly characterized by *Ellisolandia elongata* and *Bifurcaria bifurcata* (Anadón, 1983; Díez *et al*., 1999; Ramos *et al*., 2014, 2016c). According to their geographic distribution pattern (Lüning, 1990), Fucaceae are dominant in northern sites, with *Fucus distichus* being restricted to Barents Sea sites (Ramos *et al*., 2014). On the other hand, the Mediterranean Sea presents fewer species, with a strong dominance of *Cystoseira amentacea* in the lower intertidal of the western area and *Laurencia obtusa* in both levels at the eastern coast (Thibaut *et al*., 2014). The abundance of *C. amentacea* reflects the low-pressure level of the sampling sites, which were located on islands in relatively pristine conditions. Conversely, assemblages of turf-forming algae often colonize Mediterranean areas subjected to anthropogenic disturbances (Benedetti-Cecchi *et al*., 2001, 2015).

An interesting result of our study is that correlations of ecological indices with environmental parameters do not follow the same pattern in both tidal levels. For example, they are correlated with geographic coordinates only in the case of the lower intertidal, whereas PAR and tidal range showed a negative correlation with cover only in the middle intertidal assemblages. Despite these differences, the significant correlations found with wave height conditions in both tidal levels stand out. The relevance of exposure to wave action as an explanatory variable of the macroalgal assemblage distribution at regional and local scales has been described before by many authors (Ballantine, 1961; Nybakken, 1997; Cefalì *et al*., 2016; Ramos *et al*., 2016b). Our data reflect an increase in coverage, besides richness and biomass, with wave height. Conversely, many other studies described a negative relation between hydrodynamics and macroalgae abundance, although this pattern cannot be generalized (Nishihara & Terada, 2010). For example, Nishihara & Terada (2010) found an increase in Phaeophyta richness with increasing wave exposure, but Chlorophyta and Rhodophyta showed a clear decrease. Waves can be a limiting factor in very exposed shores, due to mechanical stress, because the smashing and tearing effects of waves are higher in this zone (Nybakken, 1997), but their influence decreases in semi-exposed or sheltered environments, such as those sampled for the EMBOS project.

Moreover, in moderate levels of exposure, hydrodynamics can have positive effects, such as reducing hydrological stress due to prolonged emersion times (Chappuis *et al*., 2014; Cefalì *et al*., 2016) or enhancing nutrient availability (Ballesteros, 1989). In any case, the effect of wave action preventing the colonization and development of seaweeds will also depend on the size of the macroalgae, being less critical for turf-forming, encrusting or small size algae (e.g. *Corallina* spp.) than for larger species such as Fucaceans or kelps (e.g. *Fucus* spp., *B. bifurcata, L. ochroleuca*, etc.). Besides, some confounding effects can appear due to the fact that Mediterranean sites are the most sheltered and warmest, mixing up the role of temperature and wave exposure as explanatory variables.

On the other hand, changes in composition and structure along the study sites can be explained, at least partially, by wave intensity. This factor seems to be especially important in the middle intertidal (Nybakken, 1997; Wallenstein & Neto, 2006; Cefalì *et al*., 2016; Ramos *et al*., 2016b, c) as lower shore levels are less subjected to wave action while immersed (Wallenstein & Neto, 2006).

The results presented here support the application of the sampling protocol developed in the framework of the EMBOS project for the assessment of hard-bottom intertidal communities in a long-term pan-European network of observation stations. Although some improvements are needed, including temporal and further spatial replication, this work, and others linked to the EMBOS project (Dal Bello *et al*., 2016; Hummel *et al*., 2016; Kotta *et al*., 2016), could demonstrate the feasibility of carrying out large-scale studies in a cost-effective and collaborative way. These approaches are becoming increasingly necessary due to global threats such as climate change, spread of invasive species and biodiversity loss, as well as to inform the management needs to mitigate and adapt to these phenomena, which include detailed habitats and species mapping along the European coasts and across the world.

In synthesis, the main conclusions of this study are that: (i) the meteo-oceanographic variables and parameters selected explained the spatial patterns in macroalgae diversity and distribution along European coastlines and therefore may provide further lines of evidence for retrospective and prospective hypotheses; (ii) a latitudinal gradient in the composition and structure of benthic assemblages was found, as expected, but also a longitudinal gradient, which can help to explain some of the spatial patterns identified; (iii) the latitudinal gradient was mainly explained by SST, but also by PAR, salinity and tidal range, whereas the longitudinal one was mainly linked with wave height; (iv) the standardized methodology proposed allowed characterization of the global diversity patterns of intertidal macroalgae at pan-European scale, even if some aspects should be improved in order to increase the robustness of the protocol.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/S0025315416001673.

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