Marine Biodiversity (2020) 50: 15
https://doi.org/10.1007/s12526-019-01032-z

SENCKENBERG

ORIGINAL PAPER

Strong upwelling conditions drive differences in species abundance and community composition along the Atlantic coasts of Morocco and Western Sahara

Carla R. Lourenço[1] · Katy R. Nicastro[1,2] · Christopher D. McQuaid[1] · Lilian A. Krug[3] · Gerardo I. Zardi[1]

Received: 13 June 2019 / Revised: 28 November 2019 / Accepted: 19 December 2019 / Published online: 15 February 2020

Abstract

Upwelling strongly influences the composition and dynamics of coastal communities by affecting species abundances, recruitment, dispersal and distribution. Coastal upwelling areas are key model regions to study the responses of coastal species to climate change because they are characterized by cooler water conditions and experience lower warming rates than adjacent regions, making them effective 'control' or refuge sites. This is particularly true for the benthic species of rocky shores in upwelling areas because they are sedentary, inhabit the interface between marine and terrestrial habitats, are exposed to extremely severe and variable environmental conditions and often live near their tolerance limits. We sampled roughly 2000 km of the Atlantic coast of Morocco and Western Sahara to assess the influence of upwelling cells on patterns of diversity and abundance of northern African rocky shore species. We recorded 186 taxa, providing clarification of the distribution of 141 algae and documenting nine new species records for Morocco and Western Sahara. The results emphasize the influence of upwelling on the abundance and distribution of these organisms. The contrast between non-upwelling and upwelling areas highlights the direct and indirect importance of water temperature in shaping these communities, pointing to the consequences of large-scale warming. Such warming is likely to threaten intertidal species that already live close to their thermal tolerance limits and are not buffered by the effects of upwelling.

Keywords Biogeography · Intertidal · Biodiversity · Distributional shift

Introduction

Species distributions are shifting globally in response to climate change, with large variability in responses among taxa and regions (Lourenço et al. 2016). Therefore, describing and reporting changes in species ranges are necessary for the successful assessment of the impact of contemporary climate variability on species distributions (Johnson et al. 2011). Among the drivers of coastal species, abundances and distributions that are likely to undergo dramatic change is upwelling. Upwelling has important effects on the distribution of coastal marine organisms (Fenberg et al. 2015; Reddin et al. 2015; Cefalì et al. 2016) through several mechanisms. These include the enhancement of primary production by bringing cold, nutrient-rich water to the surface, an influence on local/regional recruitment of larvae through the advection of near-shore waters (e.g. Barshis et al. 2011; Moyano et al. 2014; Fenberg et al. 2015), and providing cooler areas that allow species persistence (e.g. Hu and Guillemin 2016; Lima et al. 2006; Lima et al. 2007; Lourenço et al. 2016).

Upwelling is spatially and temporally heterogeneous while its strength is site-specific (e.g. Wang et al. 2015; Sousa et al. 2017), so that its effects on intertidal assemblages differ and can be community-specific, for instance by causing cascading effects on the composition of the intertidal biota (Nielsen and

---

Communicated by I. Kjersti Sjøtun

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s12526-019-01032-z) contains supplementary material, which is available to authorized users.

✉ Gerardo I. Zardi
zardi73@yahoo.it

[1] Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa

[2] CCMAR-CIMAR – Associated Laboratory, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

[3] CIMA—Centre for Marine and Environmental Research, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

Navarrete 2004; Guerry and Menge 2017). Consequently, variations in the frequency and intensity of upwelling can determine the functional and trophic structure of intertidal communities (Bosman et al. 1987; Broitman et al. 2001; Blanchette et al. 2009; Reddin et al. 2015 but see Kelaher and Castilla 2005; Puccinelli et al. 2016a; Puccinelli et al. 2016b).

The Benguela (Bustamante and Branch 1996a), Humboldt and California Current (e.g. Broitman et al. 2001; Blanchette et al. 2008, Blanchette et al. 2009) upwelling systems are major upwelling systems that have long been the focus of studies aimed at describing and comparing the biological and environmental structure of intertidal rocky shore communities. In contrast, the Canary Current upwelling system, another major eastern boundary upwelling system, remains largely unexplored. Geographic data on current species distributions along northern African shores are so limited and outdated (e.g. Fischer-Piette 1957; Fischer-Piette and Prenant 1957) that the Census of Marine Life (http://comlmaps.org/mcintyre) describes this coastline as a major biodiversity gap requiring improved taxonomy and an improved understanding of the scales of temporal and spatial variability in nearshore habitats (Stuart-Smith et al. 2015). At the same time, analysis of the vulnerability of the world's shallow marine fauna based on their thermal preferences indicates that this region is among the most sensitive to long-term climate warming. Despite numerous studies of the oceanography and upwelling dynamics of the system (e.g. Marcello et al. 2011; Benazzouz et al. 2014; Cropper et al. 2014; Sousa et al. 2017) and focussed studies on groups of species (e.g. algae, Benhissoune et al. 2001, Benhissoune et al. 2002b, Benhissoune et al. 2002a, Benhissoune et al. 2003), we are aware of no large scale investigation linking environmental conditions and biological gradients among intertidal communities along this coast. Furthermore, the region includes an important biogeographic transition. The Iberian and north African shores are influenced by the Canary Current upwelling system and represent a biogeographic transition where warm- and cold-water species reach their northern and southern distributional limits, respectively (e.g. Smale et al. 2013; Neiva et al. 2015; Assis et al. 2017). Not only is the region strongly affected by ongoing climate change (Belkin 2009; Lima and Wethey 2012), with marked shifts in the ranges of ecosystem-structuring species in response to warming conditions (e.g. the macroalga *Fucus vesiculosus*, Nicastro et al. 2013), but reports of new species from Morocco (e.g. Hassoun et al. 2014; Belattmania et al. 2017) suggest that it may harbour higher levels of biodiversity than recognized.

Here, we describe patterns of diversity and abundance of intertidal rocky shore species along c. 2000 km of the Atlantic coast of Morocco and Western Sahara and identify upwelling-based drivers that influence to these patterns. Specifically, we: (a) create a baseline for future studies investigating climate-driven shifts in the distribution of intertidal rocky shore species along the north African Atlantic coast and (b) assess and relate biological (intertidal community) and environmental (upwelling) structure along the Canary Current system.

Material and methods

Study region

Qualitative and quantitative field surveys were conducted at 12 intertidal rocky shore sites in the Canary Current upwelling system (CCS) along the Atlantic shores of Morocco and Western Sahara (Marcello et al. 2011; Benazzouz et al. 2014; Table S1 supplementary material). Sites were sampled between September 2013 and October 2014. Sites were roughly equidistantly distributed along the region and selected based on similarity in wave exposure, habitat type, topography and proximity to upwelling cells. Due to the inaccessibility of Nouifed (24°54′30.29″N; 14°49′45.36″W) during the second survey, the closest accessible rocky shore, Hassi El Kraa (24°41′06.18″N; 14°54′08.87″W), was selected as its replicate (approx. distance 22 km; Table S1 in supplementary material; Fig. 1).

The CCS comprises multiple upwelling cells that vary in timing and intensity (Marcello et al. 2011; Benazzouz et al. 2014). Three main centres of upwelling can be detected through low sea surface temperatures (SST) or upwelling indices along this stretch of coast: the first at 31–32°N (north of Cap Ghir), a second at 26.5–28°N (south of Cap Juby) and a third at 21–25°N (north of Cap Blanc; Marcello et al. 2011; Benazzouz et al. 2014). Adjacent surrounding areas are intermittently affected by upwelling, the effects of which decrease as the distance from the upwelling centres increases (Marcello et al. 2011; Benazzouz et al. 2014). Northern Morocco (33–36°N) shows low seasonality and weak upwelling indices, central and south Morocco and northern Western Sahara (26–33°N) show the strongest seasonality and the highest upwelling indices (peak during late summer, August–September; (Marcello et al. 2011; Benazzouz et al. 2014), while central and southern Western Sahara (21–26°N) show high upwelling indices and very little seasonality (Benazzouz et al. 2014).

Environmental variables

Site-specific monthly sea surface temperature (SST) data with a 4-km resolution were retrieved from the Moderate Resolution Imaging Spectroradiometer-Aqua (MODIS-Aqua) dataset available from the National Aeronautics Space Administration (NASA) Goddard Earth Sciences (GES) Data and Information Services Center (DISC) for the period from January 2010 to December 2014 using Giovanni, a web-based application developed by the NASA GES DISC. An area of

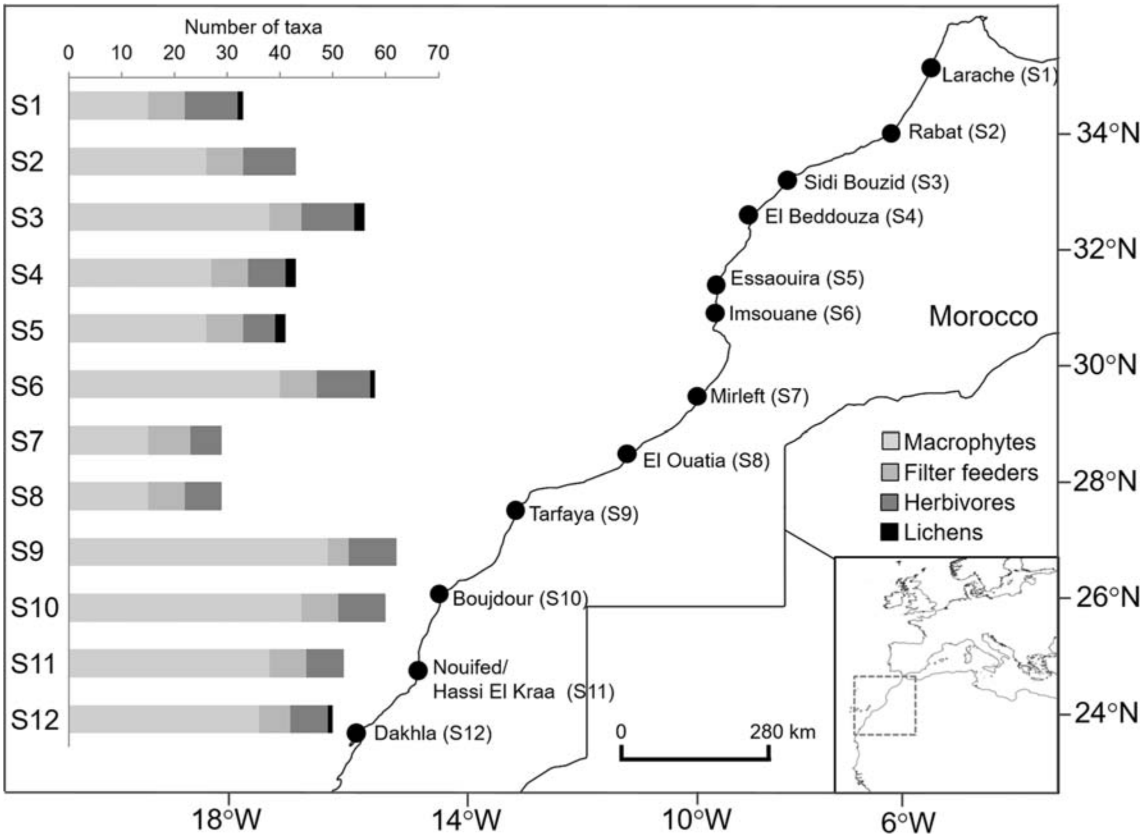


Fig. 1 Study site and species richness. Sites sampled and species richness at 12 sites along the coasts of Morocco and Western Sahara, categorized by functional group

25 km^2 situated 5 km offshore of each sampling site was selected to investigate annual minimum and maximum SST and SST variation (maximum SST–minimum SST). Annual minimum and maximum SST were obtained by selecting the lowest and highest monthly SST over each year, respectively. Annual minimum and maximum SST and SST variation values were then averaged over the 5-year period considered.

The wind-based upwelling index cross-shore Ekman transport (CSET) was used to estimate upwelling intensity during the period 2010–2014 following (Krug et al. 2017). Daily sea surface wind fields (speed and direction) at a spatial resolution of 0.25° were obtained from the Blended Sea Winds dataset (National Climatic Data Centre—National Oceanic and Atmospheric Administration, NCFC-NOAA, http://www.ncdc.noaa.gov/oa/rsad/air-sea/seawinds.html). The Blended Sea Winds dataset combines multiple scatterometers standardized across platforms, resulting in high-quality temporal and spatial coverage of ocean wind vectors (Zhang 2006). CSET values were estimated for 13 locations along the meridionally oriented Atlantic coast of northern Africa (Table S1 in supplementary material). For each location, CSET values represented the average of a 0.75 × 0.75° box centred on the target location.

The zonal component of the Ekman transport (CSET$_x$), induced by the meridional component of wind-stress (τ_y), was used as an upwelling index for each station. CSET$_x$ (m^3 s^{-1} km^{-1} coastline) was calculated following Bakun (1973), as modified by Alvarez et al. (2011):

$$\mathrm{CSET}_x = \frac{1000\ \mathrm{T_y}}{\rho_\mathrm{w}\ \mathrm{f}} = \frac{\rho_a\, C_d}{\rho_\mathrm{w}\ \mathrm{f}} \left(W_x^2 + W_y^2\right)^{1/2} 1000\ W_y$$

where W represents wind velocity (m s^{-1}), ρ_w is seawater density (1025 kg m^{-3}), ρ_a is air density (1.22 kg m^{-3}), C_d is the drag coefficient (1.4 × 10^{-3}) and f is the Coriolis parameter, estimated as 2 Ω sin(θ) where Ω and θ represent the vertical component of the Earth's angular velocity and local latitude, respectively. Negative CSET$_x$ values indicate upwelling-favourable periods with offshore Ekman transport and conversely, positive values indicate downwelling-favourable periods and onshore Ekman transport.

Daily CSET data were first monthly averaged to reduce the influence of daily anomalies. Over each year, the lowest CSET monthly average was identified to obtain the annual minimum. The overall minimum (UImin) and mean (UImean) upwelling indices for the 5-year period (2010–2014) were estimated for each site and used in statistical analyses. The UImin was obtained by selecting the lowest upwelling index of the 5-year period, while the overall UImean was obtained by averaging the five minimum annual CSET (i.e.

one value per year). Annual probability of upwelling (UIp in %) was calculated as the average of the monthly frequency of upwelling favourable days (CSET values < 0). The overall UIp was the average over the 5-year period.

Biological sampling design

A point-intercept sampling method was used to quantify relative abundance (% cover) of sessile invertebrates, macrophytes and lichen species at each site (adapted from Blanchette et al. 2008). A representative shore section was designated at each site and a measuring tape was laid out from the upper edge of the highest intertidal barnacle zone, perpendicular to the shore, to the lowest level of the low tide. Vertical point-intercept transects ($n = 2$ each site) were divided into 50 equidistant points. Intervals between points were adjusted at each site and depended on the width of the shore. The five species under each point, including layering and epibionts, or closest to the point directly attached to the substratum were recorded. Tide pools and gulleys were not sampled to avoid a misrepresentation of the intertidal height. If an intercept point fell on a tide pool or gulley, the closest horizontal non-tide pool/inundated area was sampled instead.

When species identification was not possible in the field, specimens were collected for identification in the laboratory. Algae and lichen specimens were preserved in KEW solution (40% ethanol (70%), 40% seawater, 10% glycerine and 10% formaldehyde (4%)) and sessile invertebrates were preserved in 96% ethanol. A random search of 15 min at each site was performed to include species that did not comprise one of the five taxa at each point but which were present along the transect. Species were identified and accounted for in the overall qualitative description of the site's community composition, but that were not considered in the statistical analyses.

The abundances of mobile species were determined using 30 × 30 cm quadrats placed along the transect following (Engle 2008). Specifically, three quadrats were placed haphazardly on the substratum in each of the low, mid and high shore and the macroinvertebrate target taxa (limpets, gastropods and pulmonate species) > 5 mm found within the quadrat were identified and counted. The abundance of littorinids (mostly < 5 mm) was only determined in the high zone and this species were sub-sampled in a 7.5 × 10 cm section of the quadrat due to their high densities. When species identification was not possible in the field, specimens were collected and preserved in 96% ethanol for further morphological or genetic identification in the laboratory. Again, tide pools and gulleys were not sampled to avoid a misrepresentation of the intertidal height.

Main sources for identification were: Sansón and Carrillo 1999, Gómez-Garreta 2002, Brodie et al. 2007, Cabioc'h et al. 2006, Rodríguez Prieto et al. 2013, Fish and Fish 2011, Preston-Mafham 2010, taxonomic notes and references from Algaebase (http://www.algaebase.org/).

Historical data on the distributions of algae in northern Africa described in the literature and in Algaebase (http://www.algaebase.org/) were used as a baseline for the distributional patterns of the species identified in this work. Published literature was screened up until January 2017 using Google Scholar and the ISI Web of Knowledge by using the names of the species identified in the present study in combination with the following keywords: Morocco, Maroc, Western Sahara, Spanish Sahara. New local records depicted novel descriptions of a species at a site, despite its confirmed presence in the country. A new southern limit recorded a species farther south than its previous historical limit. A new record was defined as the first record of a species from Moroccan or Western Saharan shores.

Data analyses

Site-specific species richness was estimated by summing the total number of taxa identified at each site from both transect and quadrat surveys. Species were categorized into functional groups based on their feeding guilds (macrophytes, filter-feeders, herbivores and lichens (as in Blanchette et al. 2009).

To examine similarity of spatial patterns in the biological and environmental data along the study area and to understand if the composition of intertidal communities was influenced by upwelling-related variables, the multivariate methods of Clarke (Clarke 1993) in PRIMER 6.1.3 (Plymouth Routines in Multivariate Ecological Research) software package were used. Abundances of sessile and sedentary species on transects were calculated by determining the total percentage (%) of species presence detected along the 50 points of each transect. Abundances of mobile species in quadrats were determined by estimating species density in each quadrat. Taxon abundance was averaged across sampling replicates (transects or quadrats) for each site. The data matrix of taxon abundances was fourth-root transformed to reduce the contribution of very abundant species and increase that of rare species (as in Blanchette et al. 2009). A biological similarity matrix was constructed using the Bray–Curtis similarity coefficient and cluster analysis was performed using a hierarchical method with group-average linking. Environmental data were normalized after fourth-root transformation and a similarity matrix was constructed using Euclidean distance. A SIMPROF test was run for the biological and environmental dendrograms separately using 9999 permutations to indicate group structure at a significance level of 5%.

The SIMPER routine was performed to identify the taxa of each group that were most responsible for the differences among groupings, with a cut-off of 25% contribution. Sites were assigned to groups defined a priori based on SIMPROF analyses of the biological dendrogram.

Two-dimensional, non-metric multidimensional scaling (nMDS) was performed on the environmental variables to examine regional segregation among sites (Kruskal and Wish 1978).

The RELATE routine was used in PRIMER to match the environmental resemblance matrices with the resemblance matrices of taxon richness, abundance of functional groups, taxon abundance based on transects (TAT) and based on quadrats (TAQ) separately, running 9999 permutations under the Spearman rank correlation method at a significance level of 5%.

Distance-based linear models (DistLM) were carried out to determine the contribution of the environmental variables to the variability in community composition. DistLM analyses were performed through a dissimilarity matrix, using the ‘all specified’ selection procedure under the Akaike Information Criterion (AIC), performing 9999 permutations for taxon richness, abundance of functional groups, TAT, TAQ, and presence/absence for the taxa identified in transects, separately. The environmental variables were analysed individually (marginal tests) and a sequential test was employed to evaluate the cumulative effect of each variable once the previous variable(s) had been accounted for.

Results

Environmental data

The environmental variables were averaged over the 5-year period (2010–2014) for each site (Table 1) and analysed to detect geographical clustering of sites. The minimum (UImin) and mean (UImean) values of wind-based upwelling indices ranged from − 1723.51 $m^3 s^{-1} km^{-1}$ coastline (at Imsouane, site S6) to − 418.99 $m^3 s^{-1} km^{-1}$ coastline (at Rabat, site S2) and − 1543.06 $m^3 s^{-1} km^{-1}$ coastline (at Imsouane) and − 312.55 $m^3 s^{-1} km^{-1}$ coastline (at Rabat, site S2), respectively. Favourable wind-conditions for upwelling phenomena occurred between 68.9% (at Rabat) and 95.73% (at Dakhla, site S12) of the time over the 5-year period. Maximum and minimum sea surface temperature (SSTmax and SSTmin) ranged between 20.41 °C (at Essaouira, site S5) and 23.33 °C (at Rabat) and between 16.08 °C (at Imsouane) and 17.12 °C (at Tarfaya, site S9), respectively. SST variation (SSTv) ranged from 4.05 °C (at SNouifed/Hassi El Kraa, site 11) to 6.94 °C (at Rabat).

Hierarchical cluster analysis based on the six environmental variables revealed significant geographical structure (Fig. 2). The SIMPROF test identified three significant groups (E1, E2 and E3). Group E1 contained Imsouane (site S6) only. Group E2 comprised sites Larache (site S1), Rabat (site S2), Sidi Bouzid (site S3) and El Beddouza (site S4; the four northernmost sites). Group E3 comprised sites Essaouira (site S5) and Mirleft (site S7), El Ouatia (site 8), Tarfaya (site S9), Boujdour (site S10), Nouifed/Hassi EL Kraa (site S11) and Dakhla (site S12; central and southern sites).

Biological sampling

A total of 186 taxa (26 Ochrophyta, 107 Rhodophyta, 26 Chlorophyta, 2 Ascomycota, 3 Cnidaria, 16 Mollusca, 1 Annelida, 4 Arthropoda, 1 Chordata) inhabiting the intertidal shores of Atlantic Morocco and Western Sahara were identified (Table 2). A considerably greater number of algal taxa were identified in comparison with lichens or animals. Algae constituted 85.5% of the identified taxa, while animals and lichens constituted 13.4% and 1.1%, respectively. The surveys reported 376 new local records of algae; new overall southern

Table 1 Summary of the environmental variables analysed at each sampling site

Sites	UImin ($m^3 s^{-1} km^{-1}$)	UImean ($m^3 s^{-1} km^{-1}$)	UIp (%)	SSTmax (°C)	SSTmin (°C)	SSTv (°C)
S1	− 430.19	− 340.36	70.52	22.53	16.17	6.37
S2	− 418.99	− 312.55	68.94	23.33	16.39	6.94
S3	− 820.64	− 702.49	77.97	22.76	16.38	6.38
S4	− 1077.05	− 909.97	80.93	22.23	16.54	5.69
S5	− 1611.04	− 1441.31	83.24	20.41	16.15	4.26
S6	− 1723.51	− 1543.06	84.22	20.80	16.08	4.72
S7	− 1704.03	− 1263.98	83.98	22.16	16.62	5.55
S8	− 1140.94	− 1014.64	88.16	21.88	16.77	5.11
S9	− 1330.26	− 1050.61	90.28	21.79	17.12	4.67
S10	− 1301.84	− 1209.70	92.66	22.62	16.76	5.86
S11	− 1058.47	− 953.61	93.26	20.48	16.43	4.05
S12	− 1072.76	− 924.01	95.73	21.15	16.98	4.17

UImin minimum Upwelling Index, *UImean* mean Upwelling Index, *UIp* probability of upwelling events, *SSTmax* maximum sea surface temperature, *SSTmin* minimum sea surface temperature; *SSTv* variation of sea surface temperature (maximum-minimum SST)

Sampling sites are coded as in Table S1 in supplementary material

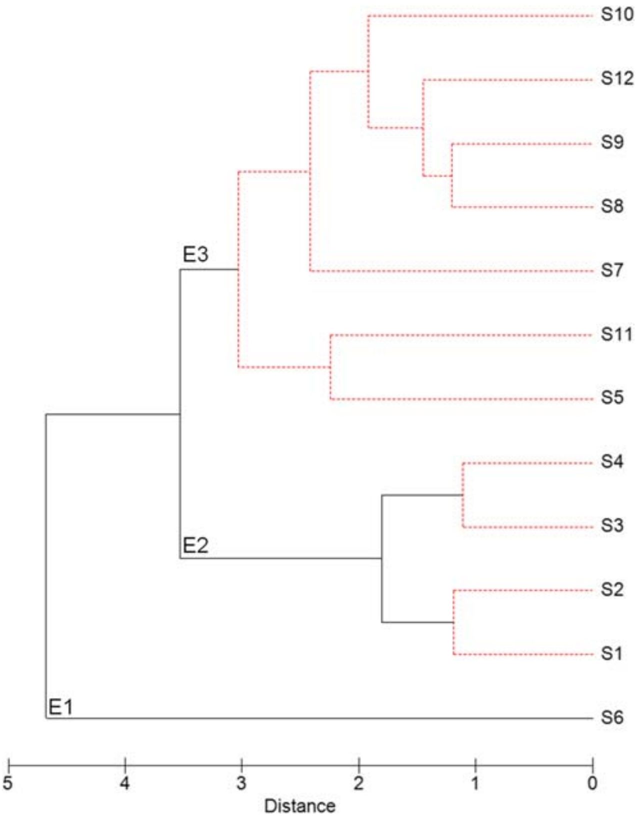


Fig. 2 Dendrogram based on environmental variables. Euclidean distance dendrogram of the similarity of sites based on environmental variables. Labelled nodes depict significant clustering ($p < 0.05$)

limits were detected for 25 algal species and nine algal species were recorded for the first time from the study area. Overall, distribution novelties or changes were described for 89% (141 species) of the algal taxa identified.

Taxon richness varied along the study area, but did not follow a clear latitudinal gradient (Fig. 1). However, the four southernmost sites showed a trend of decreasing taxon richness towards the south. Average taxon richness across all sites was 46, but some sites had particularly low (29 taxa, Mirleft and El Ouatia) or high (62 taxa, Tarfaya) richness. Macrophyte, filter-feeder, herbivore and lichen taxa ranged between 15 and 49, 4–8, 6–10 and 0–2 taxa per site, respectively.

Hierarchical cluster analyses based on taxon abundance from the transect (TAT) matrix revealed significant geographic structure that was not related to latitude, while no significant structure was detected for taxon abundance from quadrats (TAQ; Fig. 3). The SIMPROF test performed on TAT data identified three significantly different clusters (groups B1, B2 and B3). Group B1 included only Imsouane. Group B2 comprised sites Larache, Rabat, Mirleft and El Ouatia at a Bray-Curtis similarity of around 64%. Groups B1 and B2 showed significant similarity of around 55%. Group B3 comprised sites Sidi Bouzid, El Beddouza and Essaouira and Tarfaya, Boujdour, Nouifed/Hassi El Kraa and Dakhla at a similarity level of 53%.

The SIMPER results showed that a total of 19 algae, two animal taxa and one lichen contributed the most to the dissimilarities among the three groups (B1B2, B1B3 and B2B3, Table 2). While seven taxa contributed the most to differences between groups B1 and B2 (dissimilarity of 45.04%), 11 and 12 taxa contributed the most to differences between groups B1 and B3 (dissimilarity of 51.01%) and B2 and B3 (dissimilarity of 50.82%), respectively (Table 3). SIMPER contributions based on TAT per site highlighted dissimilar distributional arrangements and changes in species abundance among and within groups (Fig. 4). Species that most contributed to dissimilarities among groups were sessile species, namely the algae species *Bifurcaria bifurcata*, *Ulva clathrata*, *Osmundea pinnatifida*, *Padina pavonica*, *Codium adhaerens*, *Jania rubens* and *Fucus guiryi*. Abundance of *B. bifurcata* gradually increased from group B3 (Sidi Bouzid) to its maximum abundance in group B1 (Imsouane; Fig. 4) and was absent south of Imsouane. *Ulva clathrata* was exclusive to Imsouane (group B1), where it was the most abundant, and Boujdour (group B3). *Osmundea pinnatifida* was present at all sites of group B3, but absent from the remaining two groups. *Padina pavonica*, *C. adhaerens* and *J. rubens* were relatively abundant in group B1 (Imsouane), but absent or extremely rare in the other two groups. Finally, *F. guiryi* was abundant at most sites of group B3, with a gradual increase of abundance from Sidi Bouzid to Essaouira, but it was absent from groups B1 and B2.

Abundances of macrophytes, filter feeders and lichens differed among the study sites, but did not follow a latitudinal gradient (Fig. 5). Macrophytes were the only functional group present at all sites. Lichens were the least abundant. The highest abundance for filter feeders was observed at Imsouane, Mirleft and El Ouatia.

Biological-environmental comparison

The RELATE routine did not identify significant similarity between the environmental variables and taxon richness (Rho = − 0.163, p = 0.086), abundance of functional groups (Rho = − 0.079, p = 0.262), TAT (Rho = 0.121, p = 0.795), TAQ (Rho = 0.022, p = 0.584) or presence/absence data from taxa identified on transects (Rho = 0.098, p = 0.762). However, both biological (transect based) and environmental hierarchical cluster analyses showed similar clustering structure. Site S6 (Imsouane) was depicted as an outlier group in both cluster analyses. Additionally, both cluster analyses grouped sites Larache and Rabat in B2/E2 and Essaouira and Tarfaya, Boujdour, Nouifed/Hassi El Kraa and Dakhla in B3/E3.

DistLM mostly retrieved non-significant contributions of the environmental variables to the variability of taxon richness, abundance of functional groups, TAT, TAQ and presence/absence data from taxa identified in transects (most

Table 2 List of all species recorded along intertidal Atlantic Moroccan and Western Sahara shores

Taxon	Larache	Rabat	Sidi Bouzid	El Beddouza	Essaouira	Imsouane	Mirleft	El Ouatia	Tarfaya	Boujdour	Nouifed/ Hassi El Kraa	Dakhla
Ochrophyta												
Acinetospora crinita		x̲				x						
Bifurcaria bifurcata			x	x	x	x						
Cladostephus spongiosus^{S}									x̲			
Colpomenia peregrina	x̲	x̲		x̲		x̲	x					
Colpomenia sinuosa						x̲	x̲			x̲	x̲	
Cystoseira humilis			x						x̲			
Cystoseira sedoides^{R}								x̲				x̲
Cystoseira sp			x		x	x		x	x̲	x̲	x̲	x̲
Dictyopteris polypodioides									x̲			
Dictyota cyanoloma^{R}											x̲	
Dictyota dichotoma	x̲		x	x̲	x	x̲	x̲	x	x̲	x̲	x̲	
Fucus guiryi			x	x	x	x			x			x
Halopteris scoparia									x̲	x̲		
Hincksia mitchelliae						x̲						
Laminaria ochroleuca			x		x							
Padina pavonica		x				x̲			x̲			
Phyllariopsis brevipes		x̲										
Phyllariopsis purpurascens			x̲									
Ralfsia verrucosa^{s}	x̲	x̲	x	x̲	x	x̲	x̲	x̲	x̲	x̲	x̲	
Saccorhiza polyschides			x		x							
Sargassum sp.			x									
Sargassum vulgare			x									
Sphacelaria cirrosa^{S}						x̲				x̲		
Sphacelaria fusca						x̲						
Sphacelaria rigidula			x			x̲	x̲					
Sphacelaria tribuloides						x̲						
Rhodophyta												
Ahnfeltiopsis devoniensis^{S}		x̲	x̲		x̲		x̲	x̲	x̲	x̲	x̲	x̲
Acrosorium ciliolatum		x	x				x		x̲	x̲		
Amphiroa beauvoisii		x	x			x̲						
Amphiroa rigida								x̲				
Amphiroa vanbosseae^{R}						x̲						
Antithamnion cruciatum		x̲				x̲	x̲				x̲	
Aphanocladia stichidiosa^{S}			x̲			x̲						
Apoglossum ruscifolium							x̲					
Asparagopsis armata										x̲		
Bangia fuscopurpurea												x̲
Boergeseniella thuyoides^{S}				x̲					x̲			
Bornetia secundiflora			x					x				
Calliblepharis ciliata									x̲			
Calliblepharis jubata			x		x			x	x̲	x̲		
Callithamnion corymbosum		x̲		x̲								
Callithamnion tetragonum		x	x	x̲	x̲		x	x	x̲	x̲	x̲	x̲
Callithamnion tetricum^{S}									x̲			
Catenella caespitosa	x̲	x				x̲						
Caulacanthus ustulatus	x	x	x	x̲	x	x	x	x	x̲	x̲	x̲	x̲

Table 2 (continued)

Taxon	Larache	Rabat	Sidi Bouzid	El Beddouza	Essaouira	Imsouane	Mirleft	El Ouatia	Tarfaya	Boujdour	Nouifed/ Hassi El Kraa	Dakhla
Centroceras clavulatum										**x**		
Ceramium ciliatum			x	**x**	x	**x**	x	x	**x**	**x**	**x**	
Ceramium diaphanum		x	**x**			**x**						
Ceramium echionotum			x			**x**	x	x	**x**			
Ceramium gaditanum^{S}												**x**
Ceramium sp		x										
Ceramium tenerrimum	**x**											
Ceramium virgatum	x	x	x	x	x	x	x	x	x	x	x	x
Champia compressa^{S}							**x**					
Champia parvula		x		**x**	x							
Chondracanthus acicularis	x	x	x	**x**	x	x	x		x	x	x	x
Chondracanthus teedei		x	x		x				**x**			
Chondria coerulescens			x			**x**			**x**			
Chondria dasyphylla			x									
Corallina caespitosa^{R}	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Crouania attenuata			**x**									
Cryptonemia lomation^{S}									**x**			
Cryptonemia seminervis			x									
Dasya corymbifera^{S}							**x**					**x**
Dasya hutchinsiae						**x**						**x**
Dasya ocellata			x									
Drachiella spectabilis^{R}							**x**					
Ellisolandia elongata	x		x			**x**						
Erythrotrichia carnea						**x**						
Falkenbergia rufolanosa state						**x**	x	x				
Gaillona hookeri		**x**	**x**	**x**	**x**							**x**
Gastroclonium ovatum				**x**			x	x				**x**
Gastroclonium reflexum^{S}		**x**	**x**	**x**	x				**x**	**x**	**x**	**x**
Gayliella flaccida				**x**		**x**	**x**	**x**		**x**	**x**	
Gelidium corneum			x		x						**x**	
Gelidium crinale									**x**	**x**		
Gelidium pulchellum	x	x	x						**x**	**x**		
Gelidium pusillum			x			**x**	**x**		**x**	**x**	**x**	**x**
Gelidium sp		x	x						**x**	**x**		
Gelidium spathulatum		x										
Gelidium spinosum									**x**	**x**		
Gigartina pistillata									**x**			
Gracilaria multipartita		x	x	**x**	x				**x**	**x**		
Grateloupia filicina		x										
Grateloupia lanceola	x	x	x	**x**		**x**			**x**			
Gymnogongrus crenulatus	x			x	x				**x**			
Gymnogongrus griffithsiae		x								**x**		
Halopithys incurva			x		x				**x**	**x**		
Halurus equisetifolius				**x**			**x**	**x**	**x**			
Halymenia latifolia^{R}									**x**			
Herposiphonia secunda			x		x	**x**	**x**		**x**	**x**	**x**	**x**
Heterosiphonia crispella		**x**										**x**

Table 2 (continued)

Taxon	Larache	Rabat	Sidi Bouzid	El Beddouza	Essaouira	Imsouane	Mirleft	El Ouatia	Tarfaya	Boujdour	Nouifed/ Hassi El Kraa	Dakhla
Hypnea musciformis			x			**x**	x		**x**	**x**		**x**
Hypoglossum hypoglossoides			x	**x**		**x**	**x**		**x**	**x**	**x**	**x**
Jania longifurca					x							**x**
Jania rubens				**x**		**x**			**x**	**x**	**x**	
Laurencia obtusa									**x**	**x**		
Leptosiphonia schousboei			x									
Lithophyllum byssoides	x	x	x	**x**	x	x	x				**x**	
Lithophyllum incrustans	x	x	x	**x**	x	**x**	x	x	**x**	**x**	**x**	**x**
Lomentaria articulata^{S}	x		x	x	x				**x**	**x**		
Mastocarpus stellatus								x			**x**	
Melanothamnus collabens		x	x	**x**		**x**	**x**	x	**x**	**x**	**x**	**x**
Melanothamnus ferulaceus^{R}				**x**			**x**					
Melobesia membranacea					x			**x**		**x**		
Mesophyllum lichenoides	x	x	x	**x**	x	**x**	x	x		**x**	**x**	
Metacallophyllis laciniata^{S}			x									**x**
Ophidocladus simpliciusculus			x			**x**			**x**		**x**	
Osmundea osmunda			**x**	**x**	**x**				**x**	**x**		**x**
Osmundea pinnatifida		x	x	**x**	x		x		**x**	**x**	**x**	**x**
Osmundea sp							x			**x**	**x**	**x**
Peyssonnelia sp				**x**								
Phyllophora sp			x									
Plocamium cartilagineum			x	**x**	x	**x**	x	x	**x**	**x**	**x**	**x**
Polysiphonia atlantica												**x**
Polysiphonia brodiei^{S}						**x**		**x**				
Polysiphonia funebris^{S}			**x**			**x**			**x**			
Polysiphonia scopulorum^{S}											**x**	
Porphyra umbilicalis	**x**	x	**x**	**x**	x						**x**	
Porphyrostromium boryanum											**x**	
Pterocladiella capillacea			x		x					**x**		
Pterosiphonia complanata		x	x	**x**		**x**	**x**	**x**		**x**	**x**	
Rhodochorton purpureum									**x**			
Rhodymenia pseudopalmata					x				**x**	**x**		
Rhodymenia sp				**x**								
Stylonema alsidii		**x**										
Symphyocladiella parasitica						x						
Titanoderma pustulatum					x							
Vertebrata fruticulosa		x	x	**x**		**x**	**x**	**x**	**x**	**x**	**x**	**x**
Vertebrata fucoides^{S}			**x**									
Vertebrata reptabunda^{S}									**x**	**x**	**x**	**x**
Xiphosiphonia ardreana^{R}			**x**	**x**	**x**	**x**	**x**		**x**		**x**	**x**
Xiphosiphonia pennata			x	**x**	**x**	**x**			**x**		**x**	**x**
Chlorophyta												
Bryopsis duplex					**x**							
Bryopsis plumosa												**x**
Chaetomorpha aerea		x								**x**	**x**	
Chaetomorpha ligustica						**x**				**x**		
Cladophora albida						**x**						**x**

Table 2 (continued)

Taxon	Larache	Rabat	Sidi Bouzid	El Beddouza	Essaouira	Imsouane	Mirleft	El Ouatia	Tarfaya	Boujdour	Nouifed/ Hassi El Kraa	Dakhla
Cladophora hutchinsiae^{S}						**x**				**x**		**x**
Cladophora laetevirens^{S}						**x**				**x**		
Cladophora lehmanniana^{S}				**x**		**x**		**x**				
Cladophora rupestris^{S}										**x**	**x**	
Cladophora sp.												**x**
Codium adhaerens					x	**x**	x					
Codium sp.		x	x						**x**			
Codium tomentosum var. mucronatum	**x**	x		**x**		**x**	x	**x**	**x**		**x**	**x**
Pedobesia simplex											**x**	
Ulva clathrata						**x**				**x**		
Ulva compressa		x		**x**	x					**x**	**x**	**x**
Ulva flexuosa						**x**						
Ulva intestinalis		x		**x**								
Ulva lactuca									**x**	**x**		
Ulva linza^{S}										**x**		
Ulva prolifera		x				**x**				**x**	**x**	
Ulva pseudolinza^{R}											**x**	
Ulva rigida	x	x	x	**x**	x	**x**	x	**x**	**x**	**x**	**x**	**x**
Ulva sp.	x	x			x	**x**	x		**x**	**x**	**x**	**x**
Ulvaria obscura^{S}			**x**		x	**x**	x	**x**	**x**	**x**		**x**
Valonia utricularis^{S}									**x**	**x**		
Ascomycota												
Lichina pygmaea			x	x	x							
Verrucaria maura	x		x	x	x	x					x	x
Cnidaria												
Actinia equina						x				x		
Actinia fragacea				x			x			x		
Anemonia viridis							x			x		
Mollusca												
Cymbula safiana	x	x	x	x		x		x	x	x	x	x
Echinolittorina punctata	x	x	x	x	x	x	x	x	x	x	x	x
Fissurella nubecula	x	x	x			x	x	x	x	x		x
Melarhaphe neritoides	x	x	x	x	x	x	x	x	x	x	x	x
Mytilus galloprovincialis	x	x	x	x	x	x	x	x	x	x	x	x
Patella depressa	x	x	x	x	x	x	x	x	x	x	x	x
Patella rustica	x		x		x						x	x
Patella ulyssiponensis	x	x	x	x	x	x	x	x	x	x	x	x
Perna perna	x	x	x	x	x	x	x	x		x	x	x
Phorcus lineatus			x	x	x	x			x	x	x	
Phorcus sauciatus	x	x		x		x	x	x	x	x	x	x
Siphonaria pectinata	x	x	x		x	x	x	x	x	x	x	x
Steromphala pennanti		x				x		x		x		
Steromphala umbilicalis	x	x	x	x	x	x	x	x	x	x		
Stramonita haemastoma				x		x			x			
Vexillum zebrinum						x	x			x		
Annelida												
Sabellaria alveolata	x	x	x	x	x	x	x	x	x	x	x	x

Table 2 (continued)

Taxon	Larache	Rabat	Sidi Bouzid	El Beddouza	Essaouira	Imsouane	Mirleft	El Ouatia	Tarfaya	Boujdour	Nouifed/ Hassi El Kraa	Dakhla
Arthropoda												
Chthamalus montagui	x	x	x	x	x	x	x	x	x	x	x	x
Chthamalus stellatus	x	x	x	x	x	x	x	x	x	x	x	x
Perforatus perforatus	x	x	x	x	x	x	x	x		x	x	
Pollicipes pollicipes	x	x	x	x	x		x			x	x	x
Chordata												
Pyura herdmani						x	x	x				

The phylum of each taxon is depicted in bold. Locations as is Table 1 in supplementary material. x, presence; **x**, new local record; S new southern limit detected, R first record from Morocco and Western Sahara

marginal and sequential tests on environmental variables $p > 0.05$, Table S2 in supplementary material). Although marginal tests on the individual environmental variables explaining TAQ were all non-significant (all $p > 0.05$, Table S2 in supplementary material), sequential tests showed that UImin, UImean, UIp and SSTmax together explained 47% of the variation ($p = 0.0426$, Table S2 in supplementary material). Additionally, a DistLM analysis retrieved a significant contribution of UIp (marginal tests, $p = 0.0357$) to the variability of presence/absence data from taxa identified in transects, explaining ~ 16% of the variation (Table S2 in supplementary material).

Discussion

The results of this study suggest that strong upwelling conditions influence community structure of intertidal benthic biota of Atlantic Moroccan and Western Sahara shores. Here, we further discuss the intertidal biodiversity of the region and the importance of upwelling as a thermal buffer in the context of climate change.

Upwelling influence on intertidal benthic communities

The distribution and abundance of coastal marine species are strongly influenced by large-scale oceanographic processes (Bosman et al. 1987; Broitman et al. 2001; Blanchette et al. 2008).The environmental analysis structured our study area into three groups: an outlier location (site Imsouane, group E1, western Morocco), a northern region (Larache, Rabat, Sidi Bouzid and El Beddouza, group E2, northern Morocco) and a southern region (Essaouira and Mirleft, El Ouatia, Tarfaya, Boujdour, Nouifed/Hassi El Kraa and Dakhla, group E3, southern Morocco and Western Sahara). Imsouane was most likely identified as an independent group due to the combined effects of the strongest upwelling indices (UI), some of the lowest maximum sea surface temperature (SSTmax) and the lowest minimum SST (SSTmin), highlighting a location characterized by the coldest water conditions and most intense upwelling of the entire study area. In sharp contrast, E2 combined the weakest UI with the lowest probability of upwelling (UIp) and the greatest SST variation, which matches previous studies describing northern Morocco as a region characterized by weak upwelling indices (Marcello et al. 2011; Benazzouz et al. 2014; Cropper et al. 2014). In agreement with the described intense upwelling events and the lack of seasonality along southern Morocco and Western Sahara due to conditions that are favourable to year-round upwelling (Marcello et al. 2011; Benazzouz et al. 2014), E3 revealed strong upwelling indices and the greatest probability of upwelling.

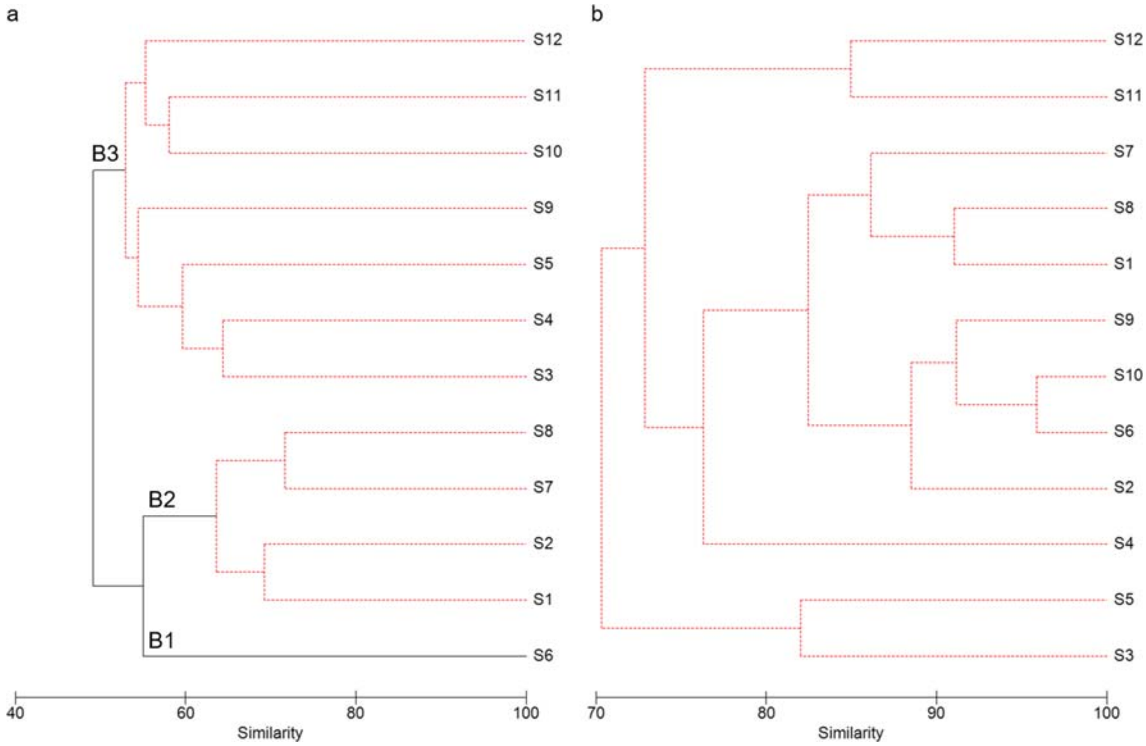


Fig. 3 Dendrograms based on community composition. Bray-Curtis similarity dendrograms based on the community composition of **a** taxon abundance from transect data and **b** taxon abundance from quadrat data. Labelled nodes depict significant clustering ($p < 0.05$). B1–B3 refers to the clustering groups

Because they can interrupt the general pattern of warmer SST towards the equator, oceanographic features such as fronts, currents or upwelling cells cause latitudinal thermal discontinuities that influence the distribution of intertidal assemblages (e.g. Blanchette et al. 2008; Ling et al. 2009). Latitudinal discontinuities associated with upwelling are key elements in explaining the community structure of benthic intertidal biota (e.g. Humboldt Current system: Broitman et al. 2001; Tapia et al. 2014; California Current system: Blanchette et al. 2008). For example, upwelling conditions were proposed as major drivers of biogeographic variation of the intertidal fauna and flora in South Africa (Bustamante and Branch 1996b; Xavier et al. 2007). In this study, we demonstrate that strong upwelling-related conditions (i.e. the strongest upwelling indices coupled to the lowest SST) drive changes in species abundance and community composition, as suggested by DistLM analyses of species abundances in quadrats and of presence/absence data, and by the agreement between environmental and biological dendrograms for Imsouane. This influence seems to be exclusive to the site where environmental variables were particularly different from the surrounding locations. Specifically, the strongest upwelling indices and the lowest SST displayed by Imsouane most likely drive an effect on the abundance of the intertidal biota, primarily algae, at this location. In fact, the community patterns described largely reflect variations in the relative abundances of taxa rather than changes in species composition. This pattern has been previously described by Blanchette et al. (2008) from the intertidal shores of the California Current system. In the present study, many of the species that contributed most to differences between groups did not show large scale presence/absence patterns, but rather had striking differences in abundances, with particular expression where upwelling was stronger. For example, *Bifurcaria bifurcata*, *Padina pavonica* and *Ulva chlathrata* were relatively abundant in group B1/E1 (i.e. Imsouane) but extremely rare in the other groups. *Bifurcaria bifurcata* is a warm temperate species distributed from the British Isles to Morocco, on moderately exposed rocky shores in the mid/low intertidal and in rock-pools (e.g. Boaventura et al. 2002; Cires Rodríguez and Cuesta Moliner 2009; Neiva et al. 2015). Group B1/E1 most likely provides optimum conditions as a thermal refugium for the persistence of this brown alga. For example, cover and abundance of *B. bifurcata* were particularly high at Imsouane, where upwelling indices were the greatest, while minimum and maximum SST were the lowest. This is in line with recent evidence highlighting the role of upwelling cells as contemporary refugia for marine species in a context of warming climate (Riegl and Piller 2003; Hu and Guillemin 2016; Lourenço et al. 2016), by delivering cold upwelled waters that counter the effect of warming SST, allowing the long-term persistence of species and relatively high within-species genetic diversity (Lourenço et al. 2016).

Table 3 Results of Simper analysis

Taxon	B1B2	B1B3	B2B3
Ellisolandia elongata	2.78	–	–
Verrucaria maura	2.9	–	–
Jania rubens	3.2	2.11	–
Codium adhaerens	3.55	2.72	–
Padina pavonica	3.81	2.86	–
Ulva clathrata	4.21	2.69	–
Bifurcaria bifurcata	4.72	2.68	–
Colpomenia peregrina	–	2.23	–
Pyura herdmani	–	1.88	–
Sphacelaria fusca	–	1.88	–
Perforatus perforatus	–	2.08	1.72
Fucus guiriy	–	2.18	2.86
Osmundea pinnatifida	–	2.96	3.86
Osmundea sp	–	–	1.67
Ralfsia verrucosa	–	–	1.69
Hypoglossum hypoglossoides	–	–	1.78
Lithophyllum byssoides	–	–	1.91
Ulva compressa	–	–	1.92
Neosiphonia collabens	–	–	1.94
Chondracanthus acicularis	–	–	1.95
Plocamium cartilagineum	–	–	2.23
Osmundea osmunda	–	–	2.36

Results of similarities percentages (SIMPER) analyses showing the percentage contributions of the species that contributed the most to dissimilarity between groups

Upwelled waters also enhance algal growth as a result of increased nutrient supply (Bosman et al. 1987; Ormond and Banaimoon 1994). *Ulva chlathrata*, an opportunistic foliose algae characterized by fast growth (Gaspar et al. 2017), reached its greatest relative abundance at Imsouane. This suggests a bottom-up effect of increased nutrient supply through upwelling (Bustamante et al. 1995; Head et al. 1996). Importantly, as our biological dataset was dominated by algae, the patterns observed in dendrogram analyses may largely reflect the influence of nutrients. While the key role of nutrient-rich upwelling waters in structuring assemblage composition across the Canary Current upwelling system (CCS) has been recently demonstrated for pelagic communities (Anabalón et al. 2014), the drivers of community structure of intertidal benthic biota along Moroccan and Western Sahara shores still warrant further investigation.

Importantly, local and meso scale features, not directly linked to larger environmental gradients, can be key drivers of intertidal community composition and abundance (Hawkins et al. 1992; Helmuth et al. 2006b; Raffaelli and Hawkins 2012). At small spatial scales, topographic and hydrodynamic features such as shore elevation and wave exposure play an important role in the trophic structure and diversity in rocky intertidal habitats (Blanchette et al. 2008; Nicastro et al. 2010; Zardi et al. 2006a; Waters et al. 2014). For example, experimental manipulation of hydrodynamics at cm-scales significantly laters mussel growth rates (McQuaid and Mostert 2010), while small scale thermal heterogeneity can exceed large-scale variability (Helmuth et al. 2006a). At meso scales both physical factors and biological interactions affect the biotic landscape of intertidal rocky shores. For example, coastal topography and habitat continuity are critical in shaping species richness gradients, boundaries and genetic structure (Fenberg and Rivadeneira 2019; Nicastro et al. 2008). In addition, periodic phenomena such as sand inundation have large effects on species richness, composition and competitive interactions (e.g. Zardi et al. 2008; Zardi et al. 2006b). Pollution has also been identified as a determinant of alterations of macrofaunal intertidal communities with significant repercussions for the functioning of ecosystems (e.g. Leopardas et al. 2016; Sabri et al. 2017), however, except after acute oils spills, its influence on more exposed rocky shores is limited compared to other anthropogenic stressors (Thompson et al. 2002). In the case of intertidal benthic animals with planktonic larvae, the processes of larval supply (influenced by coastal geomorphology and nearshore hydrodynamic features) and settlement from the water column into the benthos are key to population regulation (e.g. Poloczanska et al. 2008; Porri et al. 2007).

Intertidal biodiversity along the Atlantic shores of Morocco and Western Sahara in the context of climate change

In spite of the multiple expeditions performed within the CCS since the 19th century (reviewed in Ramos et al. 2015), benthic communities in the northwest African region are among the least known globally (Decker et al. 2003; Brito et al. 2014; Ramos et al. 2015), with most studies being limited to the Atlantic coast of northwest Morocco or Mediterranean Moroccan shores, and little sampling effort in southern Morocco or the Western Sahara (Franchimont and Saadaoui 2001).

While we omitted many small taxa such as crustaceans, our data clarify the ranges of 141 algal species, particularly along the southern region, and add nine novel records for Morocco and Western Sahara, highlighting the gaps in our knowledge of the composition and distribution of intertidal algal species in northern Africa (Franchimont and Saadaoui 2001; Ramos et al. 2015). These gaps also extend to macroinvertebrates from Moroccan shores (Franchimont and Saadaoui 2001). For example, the sandworm *Sabellaria alveolata* has been described in multiple studies as being distributed from Scotland to southern Morocco (e.g. Mieszkowska et al. 2006; Dubois et al. 2007; Plicanti et al. 2016). While its distribution is well described from the northern part of the range

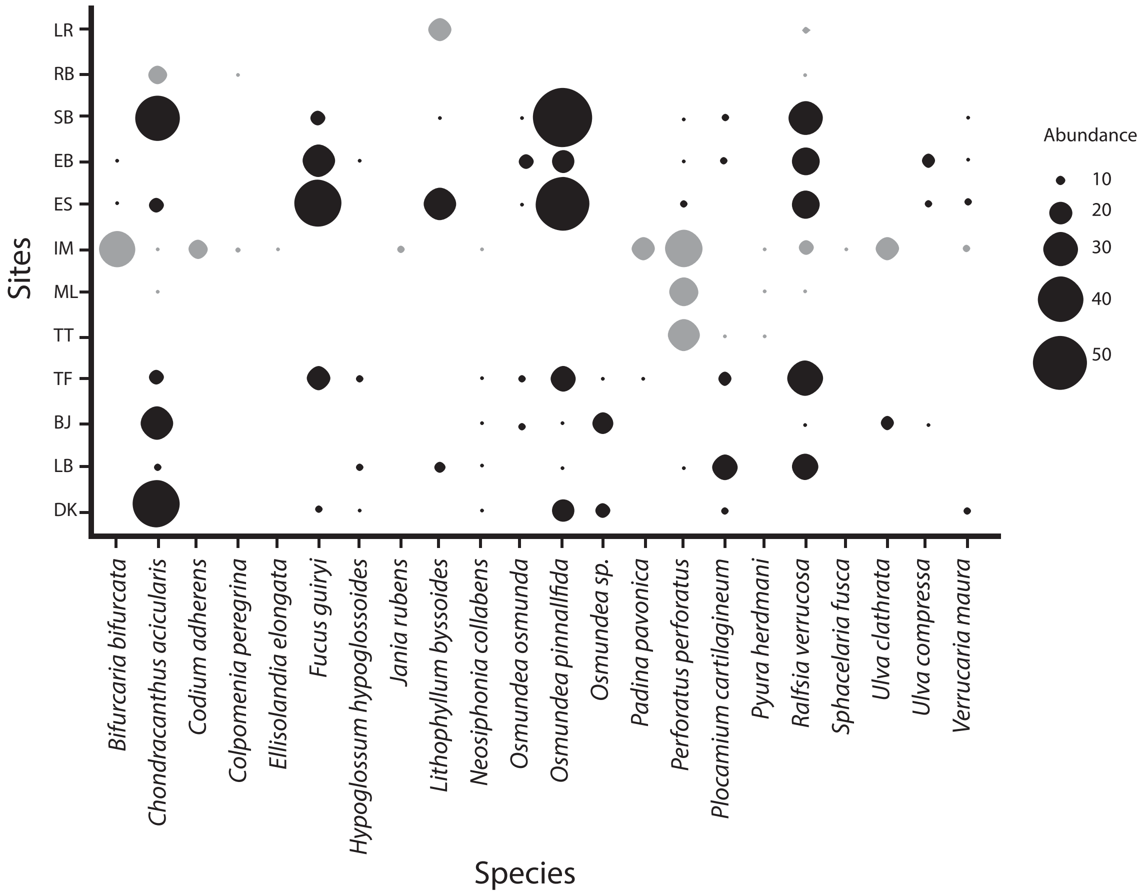
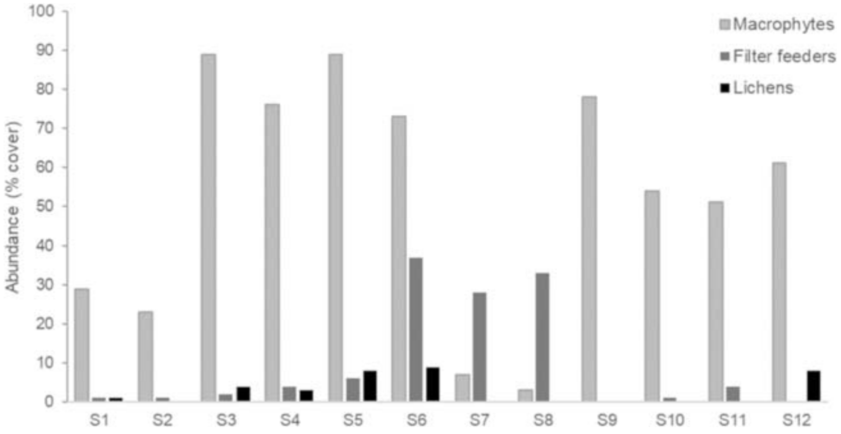


Fig. 4 SIMPER results. Geographic pattern of distribution and abundance for the species that contributed most to the dissimilarity between groups B1B2, B1B3 and B2B3. Sites belonging to groups B1, B2 and B3 are represented in light grey, grey and dark grey, respectively. Species abundance is represented by total percentage (%) of presence detected along the 50 points of each transect, averaging the abundance of each of the two replicates at each site. Study sites are as in Table 1

(e.g. Dubois et al. 2007; Mieszkowska et al. 2013; Firth et al. 2015), few studies refer to specific locations along the southern range (Ocaña et al. 2005; Rouhi et al. 2007; Muir et al. 2016). Here, we showed that *S. alveolata* extends towards the Western Sahara, at least as far south as Dakhla (site S12), approximately 24°S.

Importantly, the region is experiencing variable, severe and rapid climatic change, particularly in terms of warming (Lima and Wethey 2012). Climate change is expected to further alter species richness and community composition worldwide (Molinos et al. 2016; Woodworth-Jefcoats et al. 2016). The CCS is a temperate zone bordered by the Mediterranean Sea,

Fig. 5 Cover abundance. Abundance by cover of sessile or sedentary species at 12 sites along the coasts of Morocco and Western Sahara, for functional groups that contributed most to the dissimilarity between groups



the shores of tropical West Africa and the cool temperate northeastern Atlantic (Spalding et al. 2007), representing a biogeographical transition where several warm and cold water species meet and reach their northern or southern range limits (e.g. Lima et al. 2007; Lourenço et al. 2012; Nicastro et al. 2013; Neiva et al. 2015). In particular, Moroccan and Western Saharan shores have experienced warming of sea surface temperature of 0.02–0.30 and − 0.02–0.29 °C decade^{-1} over the last 30 years, respectively (Lima and Wethey 2012), and are characterized by distributional shifts linked to climatic changes (Nicastro et al. 2013; Lourenço et al. 2016). Recent studies have focused on understanding how upwelling intensity is changing and will change worldwide as a consequence of climate change (McGregor et al. 2007; Bakun et al. 2010; Wang et al. 2015; Sousa et al. 2017). Regardless of the expected increase in upwelling intensity in northern Africa (Wang et al. 2015 but see also Sousa et al. 2017), which could mitigate the negative effects of climate change, warming is expected to continue to increase (Collins et al. 2013; IPCC 2014), threatening intertidal species that already live close to their thermal tolerance limits. This study provides a baseline for studies investigating how intertidal benthic communities shift in a globally important upwelling systems.

Acknowledgements We thank I. Bárbara, A.M. Tavares and M. Namora for assistance with species identification. We thank R. Jacinto, M. Silva and P. Madeira for field assistance. We thank Stephen Hawkins and an anonymous referee for their comments.

Funding This research was funded by projects UID/Multi/04326/2019 and IF/01413/2014/CP1217/CT0004 from the Fundação para a Ciência e Tecnologia (FCT-MEC, Portugal) and based upon research supported by the National Research Foundation of South Africa (Grant number 64801). LAK was supported by a PhD scholarship from the Programme Science without Borders (Conselho Nacional de Desenvolvimento Científico e Tecnológico, of the Ministry of Science, Technology and Innovation of Brazil—237998/2012-2).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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

Sampling and field studies No specific permits were necessary as the species collected were not endangered or legally protected, and all sampling sites had free public access and were not protected or privately owned.

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

Author contribution GIZ and KRN conceived, designed research conducted survey. CDM conducted survey and contributed to statistical analyses. KRN and CRL conducted statistical analyses. CRL conducted field survey. LAK contributed to analyses. CRL, KRN and GIZ wrote the manuscript. All authors read and approved the manuscript.

References

Alvarez I, Gomez-Gesteira M, de Castro M, Lorenzo MN, AJC C, Dias JM (2011) Comparative analysis of upwelling influence between the western and northern coast of the Iberian Peninsula. Cont Shelf Res 31:388–399. https://doi.org/10.1016/j.csr.2010.07.009

Anabalón V et al (2014) The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa). Prog Oceanogr 120:320–339. https://doi.org/10.1016/j.pocean.2013.10.015

Assis J, Berecibar E, Claro B, Alberto F, Reed D, Raimondi P, Serrão EA (2017) Major shifts at the range edge of marine forests: the combined effects of climate changes and limited dispersal. Sci Rep 7: 44348. https://doi.org/10.1038/srep44348

Bakun A (1973) Coastal upwelling indexes, west coast of North America, 1946–71. NOAA Technical Report NMF 671

Bakun A, Field DB, Redondo-Rodriguez ANA, Weeks SJ (2010) Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. Glob Chang Biol 16:1213–1228. https://doi.org/10.1111/j.1365-2486.2009.02094.x

Barshis DJ, Sotka EE, Kelly RP, Sivasundar A, Menge BA, Barth JA, Palumbi SR (2011) Coastal upwelling is linked to temporal genetic variability in the acorn barnacle *Balanus glandula*. Mar Ecol Prog Ser 439:139–150. https://doi.org/10.3354/meps09339

Belattmania Z, Chaouti A, Machado M, Engelen A, Serrão EA, Reani A, Sabour B (2017) *Ampelisca lusitanica* (Crustacea: Amphipoda): new species for the Atlantic coast of Morocco. Mar Biodivers Rec 10:7. https://doi.org/10.1186/s41200-017-0110-5

Belkin IM (2009) Rapid warming of large marine ecosystems. Prog Oceanogr 81:207–213. https://doi.org/10.1016/j.pocean.2009.04.011

Benazzouz A et al (2014) An improved coastal upwelling index from sea surface temperature using satellite-based approach – the case of the canary current upwelling system. Cont Shelf Res 81:38–54. https://doi.org/10.1016/j.csr.2014.03.012

Benhissoune S, Boudouresque CF, Perret-Boudouresque M, Verlaque M (2002a) A check-list of marine seaweeds of the Mediterranean and Atlantic coasts of Morocco III. Rhodophyceae (excluding Ceramiales) Bot Mar 45:391–412. https://doi.org/10.1515/BOT.2002.041

Benhissoune S, Boudouresque CF, Perret-Boudouresque M, Verlaque M (2003) A check-list of marine seaweeds of the Mediterranean and Atlantic coasts of Morocco IV. Rhodophyceae - Ceramiales Bot Mar 46:55–68. https://doi.org/10.1515/BOT.2003.008

Benhissoune S, Boudouresque CF, Verlaque M (2001) A check-list of marine seaweeds of the Mediterranean and Atlantic coasts of Morocco I. Chlorophyceae Wille s. l. Bot Mar 44:171–182. https://doi.org/10.1515/BOT.2001.023

Benhissoune S, Boudouresque CF, Verlaque M (2002b) A check-list of marine seaweeds of the Mediterranean and Atlantic coasts of Morocco II. Phaeophyceae Bot Mar 45:217–230. https://doi.org/10.1515/BOT.2002.021

Blanchette C, Wieters E, Broitman B, Kinlan B, Schiel D (2009) Trophic structure and diversity in rocky intertidal upwelling ecosystems: a comparison of community patterns across California. Chile, South Africa and New Zealand. Prog Oceanogr 83:107–116. https://doi.org/10.1016/j.pocean.2009.07.038

Blanchette CA, Melissa Miner C, Raimondi PT, Lohse D, Heady KEK, Broitman BR (2008) Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. J Biogeogr 35:1593–1607. https://doi.org/10.1111/j.1365-2699.2008.01913.x

Boaventura D, Ré P, Cancela da Fonseca L, Hawkins SJ (2002) Intertidal rocky shore communities of the continental portuguese coast: analysis of distribution patterns. Mar Ecol 23:69–90. https://doi.org/10.1046/j.1439-0485.2002.02758.x

Bosman AL, Hockey PAR, Siegfried WR (1987) The influence of coastal upwelling on the functional structure of rocky intertidal communities. Oecologia 72:226–232

Brito JC et al (2014) Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. Biol Rev 89:215–231. https://doi.org/10.1111/brv.12049

Brodie J, Maggs CA & Jonh DM (2007) Green seaweeds of Britains and Ireland. British Phycological Society, 250 pp

Broitman BR, Navarrete SA, Smith F, Gaines SD (2001) Geographic variation of southeastern Pacific intertidal communities. Mar Ecol Prog Ser 224:21–34. https://doi.org/10.3354/meps224021

Bustamante R, Branch G (1996a) Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. J Biogeogr 23:339–351. https://doi.org/10.1046/j.1365-2699.1996.00026.x

Bustamante RH, Branch GM (1996b) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. J Exp Mar Biol Ecol 196:1–28. https://doi.org/10.1016/0022-0981(95)00093-3

Bustamante RH et al (1995) Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102:189–201. https://doi.org/10.1007/bf00333251

Cabioc'h, J., Floc'h, J. Y., Le Toquin, A., Boudouresque, C. F., Meinesz, A., Verlaque, M. (2006) Guide des algues des mers d'Europe. Delachaux et Niestlé.272 pp

Cefalì ME, Cebrian E, Chappuis E, Pinedo S, Terradas M, Mariani S, Ballesteros E (2016) Life on the boundary: environmental factors as drivers of habitat distribution in the littoral zone Estuar Coast Shelf Sci 172:81–92 doi:https://doi.org/10.1016/j.ecss.2016.01.043

Cires Rodríguez E, Cuesta Moliner C (2009) Más de un siglo de investigaciones Ficológicas en Asturias (1836-2007) Boletín de Ciencias de la Naturaleza, 50

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Collins M et al (2013) Long-term climate change: projections, commitments and irreversibility. In: Stocker TF et al (eds) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Cropper TE, Hanna E, Bigg GR (2014) Spatial and temporal seasonal trends in coastal upwelling off Northwest Africa, 1981–2012. Deep-Sea Res I Oceanogr Res Pap 86:94–111. https://doi.org/10.1016/j.dsr.2014.01.007

Decker C, Griffiths C, Prochazka K, Ras C, Whitfield A (2003) Marine biodiversity in sub-Saharan Africa: the known and the unknown. In: Proceedings of the Marine Biodiversity in Sub-Saharan Africa: The Known and the Unknown, Cape Town, South Africa, 23–26 September 2003. p 310

Dubois S, Comtet T, Retière C, Thiébaut E (2007) Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel. France Mar Ecol Prog Ser 346:243–254. https://doi.org/10.3354/meps07011

Engle JM (2008) Unified monitoring protocols for the multi-agency rocky intertidal network. Marine Science Institute, University of California, Santa Barbara, CA, USA

Fenberg PB, Menge BA, Raimondi PT, Rivadeneira MM (2015) Biogeographic structure of the northeastern Pacific rocky intertidal: the role of upwelling and dispersal to drive patterns. Ecography 38:83–95. https://doi.org/10.1111/ecog.00880

Fenberg PB, Rivadeneira MM (2019) On the importance of habitat continuity for delimiting biogeographic regions and shaping richness gradients. Ecol Lett 22:664–673. https://doi.org/10.1111/ele.13228

Firth LB et al (2015) Historical comparisons reveal multiple drivers of decadal change of an ecosystem engineer at the range edge. Ecol Evol 5:3210–3222. https://doi.org/10.1002/ece3.1556

Fish JD, Fish S (2011) A student's guide to the seashore. Cambridge University Press, 572 pp

Fischer-Piette E (1957) Sur des deplacements de frontieres biogeographiques, observes au long des cotes iberiques dans le domaine intercotidal Publ Inst Biol Apl Barc 26:35-40

Fischer-Piette E, Prenant M (1957) Quelques données ecologiques sur les cirripedes intercotidaux du Portugal, de l'Espagne du sud et du nord du Maroc Bulletin du Centre d'Etudes et Recherches Scientifiques Biarritz 1:361-368

Franchimont J, Saadaoui EM (2001) National study on biodiversity synthesis report. Ministry of Territorial Planning, Water and Environment, Kingdom of Morocco

Gaspar R, Pereira L, Neto JM (2017) Intertidal zonation and latitudinal gradients on macroalgal assemblages: species, functional groups and thallus morphology approaches Ecol Indicators 81:90-103. https://doi.org/10.1016/j.ecolind.2017.05.060

Gómez-Garreta, A. (2002) Flora Phycologica Iberica. Vol. 1. Fucales. Scientia Marina; Vol 66, No 2

Guerry AD, Menge BA (2017) Grazer impacts on algal community structure vary with the coastal upwelling regime. J Exp Mar Biol Ecol 488:10–23. https://doi.org/10.1016/j.jembe.2016.12.011

Hassoun M, Salhi G, Bouksir H, Moussa H, Riadi H, Kazzaz M (2014) *Codium tomentosum var. mucronatum* et son epiphyte *Aglaothamnion pseudobyssoides*, deux nouvelles espèces d'algues benthiques pour la phycoflore du Maroc. Acta Botanica Malacitana 39:37–44

Hawkins SJ, John DM, Price JH (1992) Plant-animal interactions in the marine benthos. Systematics Association, https://doi.org/10.1017/S0025315400053492

Head E, Harrison W, Irwin B, Horne E, Li W (1996) Plankton dynamics and carbon flux in an area of upwelling off the coast of Morocco Deep Sea Research Part I: oceanographic research papers, vol 43, pp 1713–1738. https://doi.org/10.1016/S0967-0637(96)00080-5

Helmuth B et al (2006a) Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecol Monogr 76:461–479. https://doi.org/10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2

Helmuth B, Mieszkowska N, Moore P, Hawkins SJ (2006b) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. Annu Rev Ecol Evol Syst 37:373–404. https://doi.org/10.1146/annurev.ecolsys.37.091305.110149

Hu Z-M, Guillemin M-L (2016) Coastal upwelling areas as safe havens during climate warming. J Biogeogr 43:2513–2514. https://doi.org/10.1111/jbi.12887

IPCC (2014) Climate change 2014: synthesis report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland

Johnson CR et al. (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania J Exp Mar Biol Ecol 400:17-32. https://doi.org/10.1016/j.jembe.2011.02.032

Kelaher BP, Castilla JC (2005) Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale coastal upwelling on the coast of northern Chile. Estuar Coast Shelf Sci 63:155–165. https://doi.org/10.1016/j.ecss.2004.10.017

Krug LA, Platt T, Sathyendranath S, Barbosa AB (2017) Unravelling region-specific environmental drivers of phytoplankton across a complex marine domain (off SW Iberia) remote. Sens Environ 203:162–184. https://doi.org/10.1016/j.rse.2017.05.029

Kruskal JB, Wish M (1978) Multidimensional scaling, quantitative applications in the social sciences. Beverly Hills. CA: Sage Publications, Inc,

Leopardas V et al (2016) Variation in macrofaunal communities of sea grass beds along a pollution gradient in Bolinao, northwestern Philippines. Mar Pollut Bull 105:310–318. https://doi.org/10.1016/j.marpolbul.2016.02.004

Lima FP, Queiroz N, Ribeiro PA, Hawkins SJ, Santos AM (2006) Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. J Biogeogr 33:812–822. https://doi.org/10.1111/j.1365-2699.2006.01457.x

Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, Santos AM (2007) Do distributional shifts of northern and southern species of algae match the warming pattern? Glob Chang Biol 13:2592–2604. https://doi.org/10.1111/j.1365-2486.2007.01451.x

Lima FP, Wethey DS (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat Commun 3: 704. https://doi.org/10.1038/ncomms1713

Ling SD, Johnson CR, Ridgway K, Hobday AJ, Haddon M (2009) Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. Glob Chang Biol 15:719–731. https://doi.org/10.1111/j.1365-2486.2008.01734.x

Lourenço C, Nicastro KR, Serrão EA, Zardi GI (2012) First record of the brown mussel (Perna perna) from the European Atlantic coast marine biodiversity record 5:e39. https://doi.org/10.1017/S1755267212000280

Lourenço CR, Zardi GI, McQuaid CD, Serrão EA, Pearson GA, Jacinto R, Nicastro KR (2016) Upwelling areas as climate change refugia for the distribution and genetic diversity of a marine macroalga. J Biogeogr 43:1595–1607. https://doi.org/10.1111/jbi.12744

Marcello J, Hernández-Guerra A, Eugenio F, Fonte A (2011) Seasonal and temporal study of the northwest African upwelling system. Int J Remote Sens 32:1843–1859. https://doi.org/10.1080/01431161003631576

McGregor HV, Dima M, Fischer HW, Mulitza S (2007) Rapid 20th-century increase in coastal upwelling off Northwest Africa. Science 315:637–639. https://doi.org/10.1126/science.1134839

McQuaid CD, Mostert BP (2010) The effects of within-shore water movement on growth of the intertidal mussel Perna perna: an experimental field test of bottom-up control at centimetre scales. J Exp Mar Biol Ecol 384:119–123. https://doi.org/10.1016/j.jembe.2010.01.005

Mieszkowska N, Firth L, Bentley M (2013) Impacts of climate change on intertidal habitats. In: Marine climate change impacts partnership: science review, vol 4, pp 180–192

Mieszkowska N, Kendall M, Hawkins S, Leaper R, Williamson P, Hardman-Mountford N, Southward A (2006) Changes in the range of some common rocky shore species in Britain–a response to climate change? Hydrobiologia 555:241–251. https://doi.org/10.1007/1-4020-4697-9_20

Molinos JG et al (2016) Climate velocity and the future global redistribution of marine biodiversity. Nat Clim Chang 6:83–88. https://doi.org/10.1038/nclimate2769

Moyano M, Rodríguez JM, Benítez-Barrios VM, Hernández-León S (2014) Larval fish distribution and retention in the Canary Current system during the weak upwelling season. Fish Oceanogr 23:191–209. https://doi.org/10.1111/fog.12055

Muir AP, Nunes FL, Dubois SF, Pernet F (2016) Lipid remodelling in the reef-building honeycomb worm, *Sabellaria alveolata*, reflects acclimation and local adaptation to temperature. Sci Rep 6:35669. https://doi.org/10.1038/srep35669

Neiva J, Assis J, Coelho NC, Fernandes F, Pearson GA, Serrão EA (2015) Genes left behind: climate change threatens cryptic genetic diversity in the canopy-forming seaweed *Bifurcaria bifurcata*. PLoS ONE 10: e0131530. https://doi.org/10.1371/journal.pone.0131530

Nicastro KR, Zardi GI, McQuaid CD (2010) Differential reproductive investment, attachment strength and mortality of invasive and indigenous mussels across heterogeneous environments Biol Invasions 12:2165-2177 doi:https://doi.org/10.1007/s10530-009-9619-9

Nicastro KR, Zardi GI, McQuaid CD, Teske PR, Barker NP (2008) Coastal topography drives genetic structure in marine mussels. Mar Ecol Prog Ser 368:189–195. https://doi.org/10.3354/meps07607

Nicastro KR, Zardi GI, Teixeira S, Neiva J, Serrao EA, Pearson GA (2013) Shift happens: trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga Fucus vesiculosus. BMC Biol 11:6. https://doi.org/10.1186/1741-7007-11-6

Nielsen KJ, Navarrete SA (2004) Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecol Lett 7:31–41. https://doi.org/10.1046/j.1461-0248.2003.00542.x

Ocaña O, Brito A, González G (2005) The genus *Actinia* in the Macaronesian archipelagos: a general perspective of the genus focussed on the North-Oriental Atlantic and Mediterranean species (Actiniaria: Actiniidae) Vieraea 33:477-494

Ormond RFG, Banaimoon SA (1994) Ecology of intertidal macroalgal assemblages on the Hadramout coast of southern Yemen, an area of seasonal upwelling. Mar Ecol Prog Ser 105:105–120

Plicanti A, Domínguez R, Dubois SF, Bertocci I (2016) Human impacts on biogenic habitats: effects of experimental trampling on *Sabellaria alveolata* (Linnaeus, 1767) reefs. J Exp Mar Biol Ecol 478:34–44. https://doi.org/10.1016/j.jembe.2016.02.001

Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modeling the response of populations of competing species to climate change. Ecology 89:3138–3149. https://doi.org/10.1890/07-1169.1

Porri F, Zardi GI, McQuaid CD, Radloff S (2007) Tidal height, rather than habitat selection for conspecifics, controls settlement in mussels. Mar Biol 152:631–637. https://doi.org/10.1007/s00227-007-0716-y

Preston-Mafham, K (2010) Seashore of Britain & Europe. Collins Nature Guides. 256 pp

Puccinelli E, McQuaid CD, Noyon M (2016a) Spatio-temporal variation in effects of upwelling on the fatty acid composition of benthic filter feeders in the Southern Benguela ecosystem: not all upwelling is equal. PLoS ONE 11:e0161919. https://doi.org/10.1371/journal.pone.0161919

Puccinelli E, Noyon M, McQuaid CD (2016b) Hierarchical effects of biogeography and upwelling shape the dietary signatures of benthic filter feeders. Mar Ecol Prog Ser 543:37–54. https://doi.org/10.3354/meps11567

Raffaelli D, Hawkins SJ (2012) Intertidal ecology. Springer Science & Business Media,

Ramos A, Ramil F, Mohamed S, Barry A (2015) The benthos of Northwest Africa. In: Valdés L, Déniz-González I (eds) Oceanographic and biological features in the canary current large marine ecosystem, IOC technical series, vol 115. IOC-UNESCO, Paris, pp 231–244

Reddin CJ, Docmac F, O'Connor NE, Bothwell JH, Harrod C (2015) Coastal upwelling drives intertidal assemblage structure and trophic ecology. PLoS ONE 10:e0130789. https://doi.org/10.1371/journal.pone.0130789

Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. Int J Earth Sci 92:520–531. https://doi.org/10.1007/s00531-003-0328-9

Rodríguez Prieto C, Ballesteros E, Boisset F, Afonso-Carrillo J (2013) Guía de las macroalgas y fanerógamas marinas del Mediterráneo occidental. Omega.:656 pp

Rouhi A, Sif J, Ferssiwi A, Chemaa A (2007) Bioaccumulation de quelques éléments métalliques par deux espèces d'Annélides Polychètes du littoral de Jorf Lasfar (région d'El Jadida, Maroc) Bulletin de l'Institut Scientifique 29:81-87

Sabri H, Cherifi O, Maarouf A, Cheggour M, Bertrand M, Mandi L (2017) Wastewater impact on macroalgae biodiversity in Essaouira coast (Morocco). J Mater Environ Sci 8:857–862

Sansón, Martan & Carrillo, Julio Afonso (1999) Algas, hongos y fanerógamas marinas de las Islas Canarias: clave analítica. Serie Biologia ½. 256 pp

Smale DA, Burrows MT, Moore P, O'Connor N, Hawkins SJ (2013) Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. Ecol Evol 3:4016–4038. https://doi.org/10.1002/ece3.774

Sousa MC, Alvarez I, de Castro M, Gomez-Gesteira M, Dias JM (2017) Seasonality of coastal upwelling trends under future warming scenarios along the southern limit of the Canary upwelling system. Prog Oceanogr 153:16–23. https://doi.org/10.1016/j.pocean.2017.04.002

Spalding MD et al (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573–583. https://doi.org/10.1641/b570707

Stuart-Smith RD, Edgar GJ, Barrett NS, Kininmonth SJ, Bates AE (2015) Thermal biases and vulnerability to warming in the world's marine fauna. Nature 528:88. https://doi.org/10.1038/nature16144

Tapia FJ, Largier JL, Castillo M, Wieters EA, Navarrete SA (2014) Latitudinal discontinuity in thermal conditions along the nearshore of Central-Northern Chile. PLoS One 9:e110841. https://doi.org/10.1371/journal.pone.0110841.g001

Thompson RC, Crowe TP, Hawkins SJ (2002) Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environ Conserv 29:168–191. https://doi.org/10.1017/S0376892902000115

Wang D, Gouhier TC, Menge BA, Ganguly AR (2015) Intensification and spatial homogenization of coastal upwelling under climate change. Nature 518:390–394. https://doi.org/10.1038/nature14235

Waters JM, Condie SA, Beheregaray LB (2014) Does coastal topography constrain marine biogeography at an oceanographic interface? Mar Freshw Res 65:969–977. https://doi.org/10.1071/MF13307

Woodworth-Jefcoats PA, Polovina JJ, Drazen JC (2016) Climate change is projected to reduce carrying capacity and redistribute species richness in North Pacific pelagic marine ecosystems. Glob Chang Biol 23:1000–1008. https://doi.org/10.1111/gcb.13471

Xavier BM, Branch GM, Wieters EA (2007) Abundance, growth and recruitment of *Mytilus galloprovincialis* on the west coast of South Africa in relation to upwelling. Mar Ecol Prog Ser 346:189–201. https://doi.org/10.3354/meps07007

Zardi GI, Nicastro KR, McQuaid CD, Erlandsson J (2008) Sand and wave induced mortality in invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) mussels. Mar Biol 153:853–858. https://doi.org/10.1007/s00227-007-0857-z

Zardi GI, Nicastro KR, McQuaid CD, Rius M, Porri F (2006a) Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy Mar Biol 150:79-88. https://doi.org/10.1007/s00227-006-0328-y

Zardi GI, Nicastro KR, Porri F, McQuaid CD (2006b) Sand stress as a non-determinant of habitat segregation of indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels in South Africa. Mar Biol 148:1031–1038. https://doi.org/10.1007/s00227-005-0155-6

Zhang H-M (2006) Blended and gridded high resolution global sea surface winds from multiple satellites NOAA NESDIS National Climatic Data Center