SPECIAL ISSUE

CSIRO PUBLISHING

Marine and Freshwater Research, 2016, **67**, 113–122
http://dx.doi.org/10.1071/MF14318

Spatial and temporal variation of kelp forests and associated macroalgal assemblages along the Portuguese coast

Daniela Pinho[A,E], *Iacopo Bertocci*[A], *Francisco Arenas*[A], *João N. Franco*[A], *David Jacinto*[B], *João J. Castro*[B], *Raquel Vieira*[A], *Isabel Sousa-Pinto*[A], *Thomas Wernberg*[C] *and Fernando Tuya*[D]

[A]CIIMAR/CIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, Rua dos Bragas 289, PT-4050-123 Porto, Portugal.
[B]MARE – Marine and Environmental Sciences Centre, Laboratório de Ciências do Mar, Universidade de Évora, Apartado 190, PT-7521-903 Sines, Portugal.
[C]School of Plant Biology & UWA Oceans Institute (M470), University of Western Australia, Crawley, WA 6009, Australia.
[D]ECOAQUA, Universidad de Las Palmas de Gran Canaria, E-35017, Las Palmas de Gran Canaria, Canary Islands, Spain.
[E]Corresponding author. Email: danielalealcmp@gmail.com

Abstract. Kelp communities are in decline in many regions. Detecting and addressing population declines require knowledge of patterns of spatial and temporal variation in the distribution and abundance of kelps and their associated organisms. We quantified kelp and associated macroalgal assemblages three times over a period of 2 years, at three regions along a natural gradient in temperature and nutrient availability across the Portuguese coast. Kelps were mostly found at the northern cool region (Viana do Castelo), which was also clearly separated from the two more southerly regions (Peniche, Sines) in terms of algal assemblage structure. This pattern was consistent, although varying in intensity, through time, providing support for this general spatial configuration. The overall richness of taxa increased towards lower latitudes. These findings indicated that kelp beds in southern Europe are currently restricted to northern Portugal, though supporting less diverse macroalgal assemblages compared with those located in central and southern Portugal.

Additional keywords: latitudinal gradient, macroalgal assemblage structures, subtidal.

Received 22 June 2014, accepted 26 January 2015, published online 10 July 2015

Introduction

Macroalgal assemblages, including large brown algae such as kelp and fucoid species, are important habitat-formers, space occupiers and food providers in nearshore temperate habitats (Schiel and Foster 1986). Kelps, in particular, are 'foundation' species (Dayton 1975) with a high ecological, social and economic value, due to their role in supplying primary production, and their ability to support diverse associated assemblages (e.g. Smale *et al.* 2013; Bennett *et al.* 2016). For example, the average net primary productivity of some kelp forests is ~1000 g C m^{-2} $year^{-1}$ (Reed and Brzezinski 2009), but can be as high as 3000 g C m^{-2} $year^{-1}$ for *Macrocystis* and *Laminaria* species (Gao and Mckinley 1994).

As predominantly cool-water species, kelps are negatively affected by high temperatures, which can critically decrease their reproduction, growth and overall survival (Steneck *et al.* 2002; Wernberg *et al.* 2010). Therefore, kelp abundances are generally expected to decline with global warming (Wernberg *et al.* 2010; Díez *et al.* 2012; Tuya *et al.* 2012; Raybaud *et al.* 2013; Voerman *et al.* 2013; Brodie *et al.* 2014), although large species-specific variations in thermal tolerance and acclimatisation capacity (Biskup *et al.* 2014) could drive opposite patterns of distribution changes for different species (Smale *et al.* 2015). There is also evidence that kelp species can expand their ranges of distribution poleward as ice retreats, making new habitat available in polar regions (Krause-Jensen and Duarte 2014).

It has been suggested that latitudinal variation in ocean climate, especially year-round differences in seawater temperatures and primary production (see satellite data reported by Tuya *et al.* 2012) drive transitions in the distribution of seaweeds along the Portuguese coast (Peliz and Fiúza 1999; Lemos and Pires 2004; Tuya *et al.* 2012). It has also been suggested that a reduction in the intensity of upwelling events and warming in the last decades have caused temporal changes in species distributions (Lima *et al.* 2006, 2007). Within this context, there is a general perception, and some empirical evidence, suggesting that kelps that once dominated the entire Portuguese coast are becoming restricted to the cooler northern region (Assis *et al.*

2009; Tuya *et al.* 2012). More intense herbivory could have added a further contribution to such distributional shifts as there is emerging evidence for increasingly intense grazing by sea urchins and fishes in southern compared with northern Portugal (D. Pinho, I. Bertocci, F. Arenas, J. N. Franco, D. Jacinto, J. J. Castro, R. Vieira, I. Sousa-Pinto, T. Wernberg and F. Tuya, unpubl. data) and globally (Ling *et al.* 2009; Vergés *et al.* 2014).

Given the logistic difficulties of manipulating environmental variables, such as temperature, over large scales, the alternative option of assessing patterns of spatial and temporal variation of macroalgae along latitudinal gradients is relevant for indirectly examining their possible responses under present and predicted environmental changes (Harley *et al.* 2006; Wernberg *et al.* 2012). Such studies are scarce on the Portuguese continental coast, despite some recent advances (Assis *et al.* 2009; Tuya *et al.* 2012). Tuya *et al.* (2012), in particular, described changes in patterns of distribution of dominant macroalgal assemblages across the same locations used in this study. However, their analyses were restricted to a single time and, therefore, could not assess whether such patterns were limited to the particular time examined or were generalisable over multiple years. This information would be important, given the variability that is often documented in kelp systems as a consequence of processes variable over similar time scales, such as extreme storms (Smale and Vance 2016) or temperatures (e.g. Wernberg *et al.* 2013) or as a consequence of annual population dynamics (e.g. Fernández 2011). This study extends that of Tuya *et al.* (2012) by repeating the sampling over multiple years, which allows a new hypothesis about the temporal consistency of the spatial patterns to be tested. Moreover, the study by Tuya *et al.* (2012) was primarily focused on landscape-level changes expressed as main habitat types, identified according to five morpho-functional groups of organisms: kelp canopy, foliose algal turfs, filamentous algae, barren areas and filter-feeder patches. In contrast, the primary focus of the present study was on the species-level structure of macroalgal assemblages and on patterns of distribution, abundance and richness of their constituent taxa.

Materials and methods

Study area

The study was conducted at three regions of continental Portugal (Fig. S1 of the Supplementary material): Viana do Castelo (VIA, 41.5°N), Peniche (PEN, 39.2°N) and Sines (SIN, 37.8°N). This coastline is characterised by intertidal and shallow subtidal limestone, sandstone, shale or granitic reefs interspersed within extensive sandy habitats (Tuya *et al.* 2012). The continental Portuguese coast is an interface between 'cold' and 'warm' water regions, where macroalgal species of both boreal and Lusitanian origin (Southward *et al.* 1995; Lima *et al.* 2007) overlap. Many species have their southern or northern distributional range edges along this coast (Ardré 1971; Lima *et al.* 2007), whereas other species show latitudinal clines in their abundance (Boaventura *et al.* 2002; Pereira *et al.* 2006). The Portuguese coast is situated in the North Atlantic Upwelling System of the western coast of the Iberian Peninsula. Normally, winds and ocean nearshore currents exhibit strong seasonal variability, with clearly distinguished summer and winter patterns. Northern and north-western prevailing winds during summer are responsible for nearshore upwelling events, with concomitant nutrient inputs towards the ocean surface and promotion of primary productivity (Prego *et al.* 2007).

Satellite-derived data indicated a latitudinal gradient of sea surface temperature and primary production in the study regions (Tuya *et al.* 2012).

Data collection

Algal assemblages were sampled in 2011, 2012 and 2013, when macroalgal diversity and standing biomass is normally the highest (i.e. spring–summer). In each year, five reefs (hundreds of metres long, several kilometres apart, depth between 8 and 12 m) were randomly selected within each region and six replicate quadrats (50 × 50 cm, some metres to tens of metres apart) were randomly laid out on each reef. Destructive sampling was carried out by scraping all vegetation within each quadrat. Sampling design and resolution were similar to those of previous studies aimed at describing assemblage-level dynamics of macroalgal systems dominated by small subsurface kelps (e.g. Wernberg *et al.* 2003; Tuya *et al.* 2012) and were considered appropriate given the present main goal of assessing changes in the structure of the entire algal assemblage, rather than the kelps alone. Collected material was stored in separate bags, kept in sea water for transportation to the laboratory, and there immediately frozen until ready for sorting. Once defrosted, samples were sorted and identified to the lowest possible taxonomic level (species in most cases). The biomass (fresh weight) of each taxon was measured after rinsing with fresh water and removing the excess water by shaking and drying algal material with absorbent paper.

Data analysis

Differences in macroalgal assemblage structure among regions were tested with three-way permutational multivariate analysis of variance (PERMANOVA: Anderson 2001) based on Bray–Curtis dissimilarities calculated from untransformed data. The model included the following factors: Time (three levels, random), Region (three levels, fixed and crossed with Time) and Reef (five levels, random and nested within Time and Region). For significant ($P < 0.05$) fixed-factor effects, pairwise tests were carried out as *post hoc* multivariate comparisons.

Multivariate patterns were visualised through non-metric multidimensional scaling (nMDS) ordination plots of centroids for each reef in each region and time of sampling. Because Bray–Curtis is a semimetric index (Legendre and Anderson 1999), centroids cannot be obtained simply as arithmetic averages of these dissimilarities (Anderson 2001). Thus, we first calculated principal coordinates from the Bray–Curtis dissimilarity matrix. This places the observations into a Euclidean space without altering the Bray–Curtis measure. Centroids were then obtained as arithmetic averages of the principal coordinates over the five replicate quadrats in each reef, region and time of sampling (McArdle and Anderson 2001). A matrix of Euclidean distances between each pair of centroids was calculated and used as the input for the nMDS.

The SIMPER procedure (Clarke 1993) was performed to determine the contribution of different taxa to dissimilarities

Table 1. Permutational multivariate analysis of variance (PERMANOVA) and *post hoc t*-tests examining the effects of time, region and reef on whole macroalgal assemblages associated with kelp species
Significant effects are shown in bold

Source of variation	d.f.	m.s.	Pseudo-*F*	*P*	Denominator
Time (T)	2	33 337.0	3.35	**0.001**	Reef (T × R)
Region (R)	2	80 513.0	3.41	**0.001**	T × R
T × R	4	23 589.0	2.37	**0.001**	Reef (T × R)
Reef (T × R)	36	9937.0	5.35	**0.001**	Residual
Residual	225	1858.2			

Pairwise comparisons: T × R

	2011	2012	2013
VIA *v.* PEN	$t=2.577$, $\boldsymbol{P=0.001}$	$t=2.610$, $\boldsymbol{P=0.001}$	$t=1.907$, $\boldsymbol{P=0.001}$
VIA *v.* SIN	$t=2.433$, $\boldsymbol{P=0.001}$	$t=1.915$, $\boldsymbol{P=0.002}$	$t=2.137$, $\boldsymbol{P=0.01}$
PEN *v.* SIN	$t=1.855$, $\boldsymbol{P=0.002}$	$t=1.534$, $\boldsymbol{P=0.029}$	$t=1.693$, $\boldsymbol{P=0.01}$

within each region. A taxon was considered important if its contribution to the total dissimilarity of that region was ≥3%, with a cut-off cumulative contribution of 80%. Data on the biomass of these taxa, as well as species richness, Pielou's evenness index (J) and the total algal biomass of each replicate were analysed by analysis of variance (ANOVA), based on the same design previously described. Before each ANOVA, the assumption of homogeneity of variances was checked with Cochran's *C* test. When possible, data were log-transformed to reduce heterogeneity of variances. When this was not successful, untransformed data were analysed and results were considered significant at $P<0.01$ to compensate for the increased probability of Type I error (Underwood 1997). For significant fixed-factor effects, Student–Newman–Keuls (SNK) tests were used for *a posteriori* comparisons of means. In the case of total biomass, the non-significant (at $P>0.25$) random interaction 'Time × Region' was pooled to increase the power of the test involving the factor 'Region' (Underwood 1997).

Finally, each taxon was assigned to one of three bioclimatic groups: 'cold water' Atlantic boreal, 'warm water' Lusitanian and 'widely distributed' species (according to Alvarez *et al.* 1988; Lüning 1990). The proportion of 'cold water' and 'warm water' algae in each region was calculated.

Results

In total, 127 macroalgal taxa (109 identified to species, 16 to genus, one to order and one just as a morphological group) were identified from the 270 quadrats. The main contribution to the richness of taxa was from Rhodophyta, with the orders Ceramiales and Gigartinales being particularly rich (36 and 11 taxa respectively). Ochrophyta were mostly represented by Fucales and Dictyotales (5 and 4 taxa respectively), whereas the order Ulvales (4 taxa) was the main contributor to Chlorophyta. When grouped according to their climate affinity, macroalgal assemblages at VIA showed the highest proportion of 'cold water' taxa (28.1%, 18 taxa), followed by PEN (10.9%, 10 taxa) and SIN (7.3%, 6 taxa). The opposite pattern was observed for 'warm water' taxa, ranging from SIN (25.6%, 21 taxa) to PEN (19.6%, 18 taxa) to VIA (15.6%, 10 taxa) (Table S1 of the Supplementary material).

At the assemblage-level, temporally variable differences in macroalgal structure among regions were evidenced as a significant interaction 'Time × Region', with the three regions clearly separated in 2011, whereas PEN and SIN were more similar to each other than to VIA in 2012 and 2013. This pattern was not masked by significant variation among reefs within each region (Table 1, Fig. 1).

The richness of algal taxa increased from north to south (Table 2, Fig. 2*a*). In contrast, evenness did not show any differences (Table 2). The total standing algal biomass was greatest at VIA, followed by PEN and SIN, which had a similar biomass (Table 2, Fig. 2*b*). The most characteristic species, according to the SIMPER analyses, in each region are listed in Table 3. In addition, two other 'kelp' species, *Phyllariopsis brevipes* and *Saccorhiza polyschides* (both belonging to the order Tilopteridales, but functionally similar to laminarian kelps) were mostly found at VIA (mean ± s.e. fresh weight of 4.98 ± 1.21 g and 14.79 ± 4.00 g, respectively), being almost absent at PEN (0.08 ± 1.21 g and 0.01 ± 3.00 g) and SIN (0.11 ± 1.21 g and 1.01 ± 4.00 g) (Table S1).

Three species (*Laminaria hyperborea*, *Peyssonelia harveyana* and *Phyllophora crispa*) showed temporally variable differences in abundance between regions, as indicated by the significant 'Time × Region' interaction (Table 4, Fig. 3). *L. hyperborea* was recorded only in VIA in 2012 and 2013, with a progressive decrease in biomass through the years. *P. harveyana* was predominantly present in SIN in 2013 and, with lower biomass, in 2012, whereas it had a very low abundance in PEN in 2012 and was completely absent at all other regions and times. The biomass of *P. crispa* was larger in VIA compared to PEN and SIN in 2011 and 2013, whereas in 2012 it was equally abundant in VIA and PEN, but absent in SIN.

Four species showed temporally consistent differences between regions (Table 4, Fig. 3). In particular, *Dilsea carnosa* appeared only at VIA (Fig. 3); *Lithophyllum incrustans* presented a progressively decreasing abundance from PEN to SIN to VIA; the biomass of *Pterosiphonia complanata* was larger at PEN than at the other two regions, where it was minimal; *Sphaerococcus coronopifolius* was recorded at SIN only.

Three species were characterised by temporally variable fluctuations in biomass, independently of regions (Table 4).

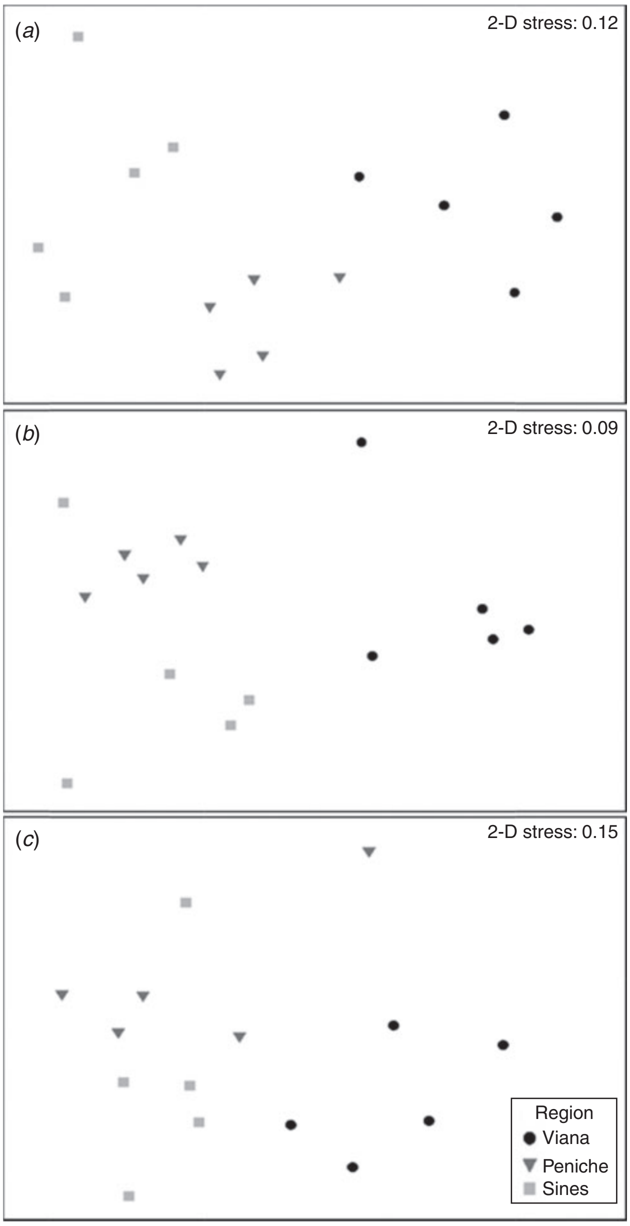

Fig. 1. Two-dimensional non-metric multidimensional scaling plot showing similarities in the structure of algal assemblages between centroids of reefs within each region over the 3 sampling years (*a*, 2011; *b*, 2012; *c*, 2013).

Dictyota dichotoma showed a decrease in biomass from 2011 to 2012, but it recovered in 2013 (Fig. 3). The average biomass of *Plocamium cartilagineum* was similar in 2011 and 2012, but decreased in 2013 (Fig. 4). *Rhodymenia pseudopalmata* had a larger biomass in 2011 (though mostly present in VIA only) than in 2012 and 2013 (Fig. 4).

The remaining four species (*Chondrus crispus*, *Codium adhaerens, Crypropleura ramosa* and *Halopteris scoparia*) did not show significant terms besides 'Reef' (Table 4, Fig. 4), although some regional trends were evident. *C. crispus* was exclusively found in VIA, with a larger biomass in 2013, intermediate values in 2011 and very low values in 2012. Both *C. adhaerens* and *C. ramosa* were mostly collected in VIA in 2011 and, with much lower values, in 2013, whereas these two species were present with very low to null biomass in all other regions and times. Finally, *H. scoparia* was absent in 2011 in all regions, whereas in the other 2 years it was found only in PEN and SIN, with the largest values in the southernmost region, particularly in 2013 (Fig. 4).

Discussion

The three regions encompassing a latitudinal gradient across continental Portugal differed in the presence and biomass of kelps and associated macroalgal assemblages, although the differences were not fully consistent over three sampling periods. Nevertheless, in agreement with previous studies (Tuya *et al.* 2012), VIA was clearly separated from the other two regions in terms of the structure and biomass of macroalgal assemblages. This region had the larger algal biomass, but the lowest species richness, in contrast with SIN, which had the highest richness and smallest biomass.

The kelp *L. hyperborea* was the most characteristic species in assemblages from VIA, as expected because of its affinity for cold water and its southern distribution limit located in the north of the Iberian Peninsula (Pérez-Ruzafa *et al.* 2003). Similarly, species such as *D. carnosa* and *P. crispa*, which have a boreal distribution in the Atlantic and reach their southernmost limits in continental Europe on the Iberian Peninsula, were also characteristic of the shallow subtidal rocky habitats of VIA. In contrast, reefs in SIN were dominated by species that were either widely distributed or abundant in 'warm' environments, such as the Mediterranean Sea. These included, for instance, *D. dichotoma*, *C. adhaerens* and *S. coronopifolius*.

The broad latitudinal gradient in ocean climate, i.e. decreasing Chlorophyll *a* concentration and increasing sea surface temperature, from northern to southern Portugal (Tuya *et al.* 2012) appeared to drive the distribution of macroalgal assemblages, although caution is warranted with this interpretation as cause–effect relationships cannot be unambiguously unravelled by our non-manipulative approach. In fact, kelps occurred in VIA only, where they made up 38.4% of the total sampled biomass. Reproduction of laminarian kelps, in particular, is negatively affected by high temperatures and reduced availability of nutrients (Bartsch *et al.* 2008; Pereira *et al.* 2011) and such response could be responsible, at least in part, for the absence of kelps in PEN and SIN. In addition, a cold-water 'pocket' spanning northern Portugal and southern Galicia in Spain has long been recognised as having an important influence on marine biota along this coast (Southward *et al.* 1995; Peliz and Fiúza 1999), leading to the hypothesis that the abundance of kelps would decrease with increasing ocean temperature (e.g. Díez *et al.* 2012; Voerman *et al.* 2013). Nevertheless, empirical evidence of such latitudinal decrease in kelp abundance is scarce in Portugal (but see Tuya *et al.* 2012; Assis *et al.* 2013).

The documented regional pattern in the distribution of kelp is also consistent with the general decrease in the intensity of upwelling events recorded since 1941, which has been responsible for increased temperatures and reduced nutrient availability of Portuguese coastal waters (Lemos and Pires 2004). This is

Table 2. ANOVA examining the effects of time, region and reef on the richness of algal taxa, the Pielou's evenness index and the total algal biomass

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Denominators for F as in Table 1, unless specified otherwise

Source of variation	d.f.	Total richness of algal taxa		Pielou's evenness index		Total algal biomass	
		m.s.	F	m.s.	F	m.s.	F
Time (T)	2	1012.07	17.66***	0.19	2.83	9.60	5.22**^{A}
Region (R)	2	1950.86	108.96***	0.08	0.56	12.03	6.54**^{A}
T × R	4	17.90	0.31	0.14	2.02	2.28	1.24^A
Reef (T × R)	36	57.30	4.41***	0.07	3.17***	1.79	4.70***
Residual	225	12.99	0.02		0.38		
Cochran's C test		$C = 0.122$, $P < 0.01$		$C = 0.010$, $P < 0.05$		$C = 0.087$, $P > 0.05$	
Transformation		None		None		Ln(x)	
SNK test: Region		SIN > PEN > VIA s.e. = 0.435				VIA > PEN = SIN s.e. = 0.143	

^{A}Tested over the pooled term (= T × R + Reef (T × R)); m.s.$_{\text{Pooled}}$ = 1.83 with d.f. = 40.

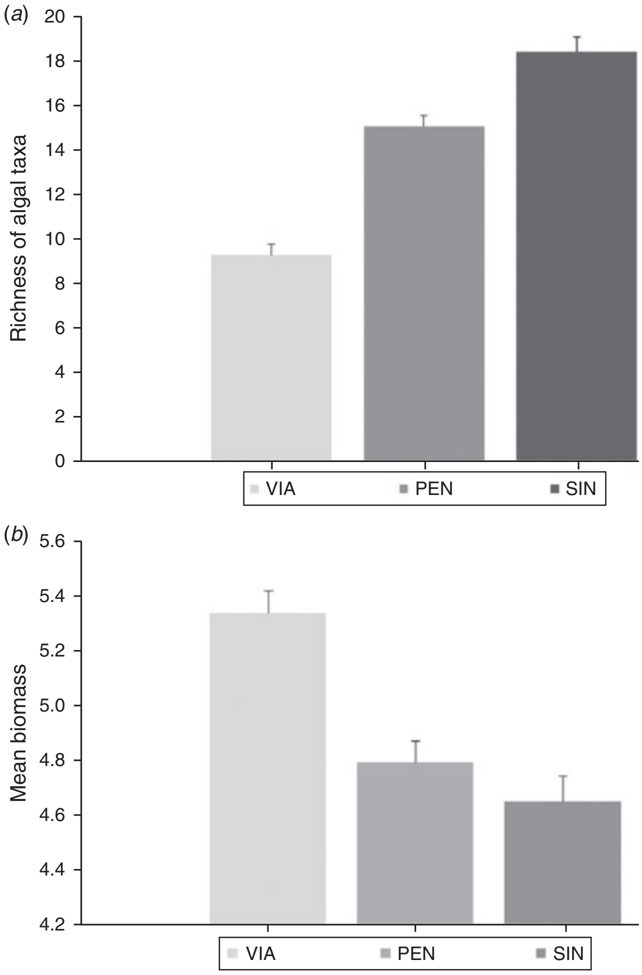

Fig. 2. (*a*) Total richness and (*b*) biomass (mean + s.e.) of algal taxa at each region (VIA, Viana do Castelo; PEN, Peniche; SIN, Sines). Data were averaged across six quadrats, five reefs and three periods.

Table 3. SIMPER results outlining the most representative species for each region according to their contribution (δ_i) to within-region dissimilarities

Species	Average biomass	δ_i	δ_i%	Cumulative δ_i%
Viana do Castelo				
Laminaria hyperborea	85.67	4.30	33.61	33.61
Dilsea carnosa	36.60	2.25	17.59	51.20
Phillophora crispa	16.61	1.37	10.75	61.94
Cryptopleura ramosa	7.96	0.77	6.04	67.98
Plocamium cartilagineum	9.53	0.75	5.90	73.89
Chondrus crispus	19.70	0.66	5.15	79.04
Rhodymenia pseudopalmata	8.94	0.57	4.43	83.47
Peniche				
Lithophyllum incrustans	21.40	8.01	32.30	32.30
Plocamium cartilagineum	35.31	7.33	29.54	61.84
Dictyota dichotoma	17.18	2.83	11.43	73.26
Pterosiphonia complatata	10.22	2.42	9.76	83.02
Sines				
Dictyota dichotoma	29.66	4.98	29.08	29.08
Lithophyllum incrustans	12.15	3.71	21.60	50.78
Sphaerococcus coronopifolius	22.33	2.06	12.04	62.83
Plocamium cartilagineum	5.84	1.13	6.61	69.43
Codium adhaerens	14.93	0.94	5.51	74.94
Halopteris scoparia	8.85	0.80	4.69	79.63
Peyssonelia harveyana	4.94	0.64	3.71	83.34

another mechanism that might have negatively affected the presence of kelps across continental Portugal during the last decades. Such oceanographic patterns could be exacerbated by the presence of the Nazaré Canyon (39.6°N), extending across the Portuguese continental margin from the coast to abyssal depths (Slagstad and Wassmann 2001). This canyon represents a geographical discontinuity between PEN and SIN in the south and VIA in the north (Lima *et al.* 2007, Tuya *et al.* 2012). Large extensions of sandy bottoms between VIA and the southern regions would also act as physical barriers, since these habitats are unsuitable for most seaweeds. Moreover, patterns of distribution of kelp and associated organisms along the Portuguese coast could be influenced by latitudinal variation in the intensity of grazing and the abundance of macro-herbivores. Preliminary findings (Pinho *et al.*, unpubl. data) suggest that grazing by sea urchins and herbivorous fishes is more intense in southern than in northern Portugal.

Table 4. ANOVA examining the effects of time, region and reef on the most representative species for each region

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Denominators for F are as in Table 1

Source of variation	d.f.	*Chondrus crispus*		*Codium adhaerens*		*Cryptopleura ramosa*		*Dictyota dichotoma*		*Dilsea carnosa*		*Halopteris scoparia*		*Laminaria hyperborea*	
		m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F
Time (T)	2	2295.25	0.75	1604.36	2.01	418.81	1.8	20 950.31	5.69**	1920.20	0.34	1097.82	1.37	77 461.21	3.71
Region (R)	2	11 638.96	5.07	6688.19	4.17	1878.44	4.33	11 130.59	1.34	40 197.29	20.93	1997.32	2.24	220 169.62	2.84
T × R	4	2295.99	0.75	1604.36	2.01	433.70	1.87	8281.38	2.25	1920.20	0.34	891.29	1.11	797.19	3.71*
Reef (T × R)	36	3063.31	3.78***	797.19	232.1	5.18***	3679.26	5.46***		5661.08	3.52***	801.00	14.51***	20 854.44	3.22***
Residual	225	810.40		421.50		44.85		673.61		1608.89		55.19		6479.82	
Cochran's C test		$C = 0.594$, $P < 0.01$		$C = 0.476$, $P < 0.01$		$C = 0.370$, $P < 0.01$		$C = 0.209$, $P < 0.01$		$C = 0.323$, $P < 0.01$		$C = 0.464$, $P < 0.01$		$C = 0.332$, $P < 0.01$	
Transformation		None		None		None		None		None		None		None	
SNK test										Region s.e. = 4.619 VIA > PEN = SIN				T × R s.e. = 26.365 2011: VIA = PEN = SIN 2012: VIA > PEN = SIN 2013: VIA > PEN = SIN	

		Lithophyllum incrustans		*Peyssonelia harveyana*		*Phyllophora crispa*		*Plocamium cartilagineum*		*Pterosiphonia complanata*		*Rhodymenia pseudopalmata*		*Sphaerococcus coronopifolius*	
		m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F
Time (T)	2	5.41	1.44	435.16	8.86***	4221.88	8.05**	9166.51	3.54*	186.23	0.6	1223.35	3.37*	2096.38	0.72
Region (R)	2	89.47	16.51*	725.77	1.66	7811.24	1.66	23 201.88	5.43	3017.30	19.06	2084.61	3.08	14 957.60	7.13*
T × R	4	5.42	1.48	437.97	8.91***	4691.49	8.96		4276.12***	1.65	158.29	677.22	1.87	2096.38	0.72
Reef (T × R)	36	3.75	5.28***	49.13	3.14***	523.55	1.39	2589.01	2.53***	308.4596	11.97***	362.53	3.11***	2912.79	6.94***
Residual	225	0.71		15.64		55.19		1025.02		25.77		1164.42			
Cochran's C test		$C = 0.081$		$C = 0.454$, $P < 0.01$		$C = 0.536$, $P < 0.01$		$C = 0.359$, $P < 0.01$		$C = 0.413$, $P < 0.01$		$C = 0.4140$, $P < 0.01$		$C = 0.4852$, $P < 0.01$	
Transformation		Ln(x)		None		None		None		None		None		None	
SNK test		Region s.e. = 0.238 PEN > VIA = SIN		T × R s.e. = 1.278 2011: VIA = PEN = SIN 2012: VIA = PEN = SIN 2013: SIN > VIA = PEN		T × R s.e. = 4.175 2011: VIA > PEN = SIN 2012: VIA = PEN = SIN 2013: VIA = PEN = SIN				Region s.e. = 1.325 PEN > VIA = SIN				Region s.e. = 4.826 SIN > VIA = PEN	

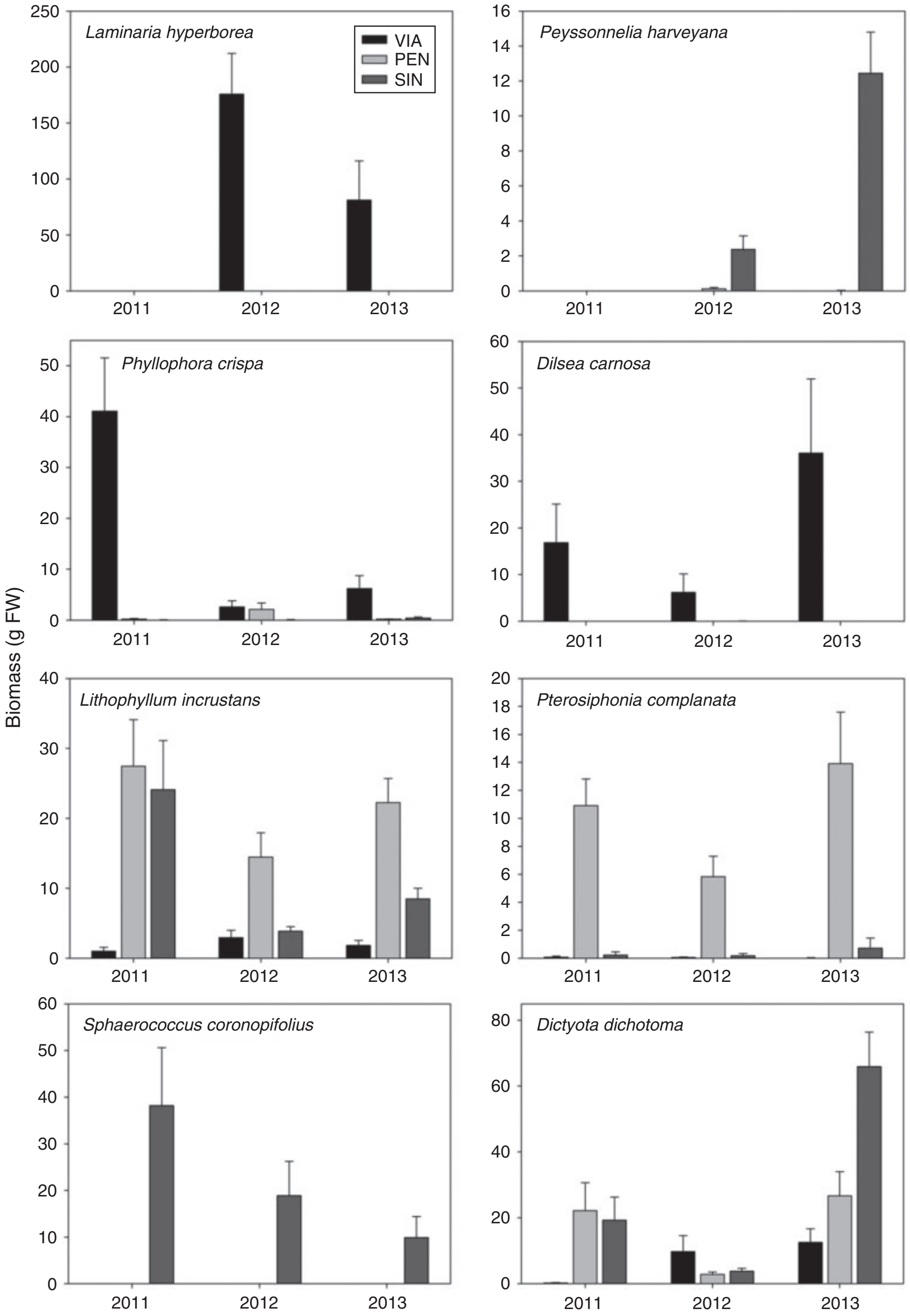

Fig. 3. Biomass (mean + s.e.) of individual algal species at each region and time of sampling. Data were averaged across six quadrats and five reefs. Abbreviations are as in Fig. 3.

Only three kelp species (*L. hyperborea*, *P. brevipes* and *S. polyschides*), out of the total seven described for the Portuguese coast (Rodrigues 1963; Araújo *et al.* 2003), were found in the present study. These three species were, by far, more abundant at VIA than at PEN and SIN (as was obvious, however, for *L. hyperborea* which has its southern distribution limit in north Portugal), analogously to *Laminaria ochroleuca* reported by Tuya *et al.* (2012). Because of their potential role as habitat-formers, a positive relationship might be expected between the abundance of kelps and the richness of associated taxa, though such association might be stronger for fauna than for algae, which could compete more with canopy-forming species for

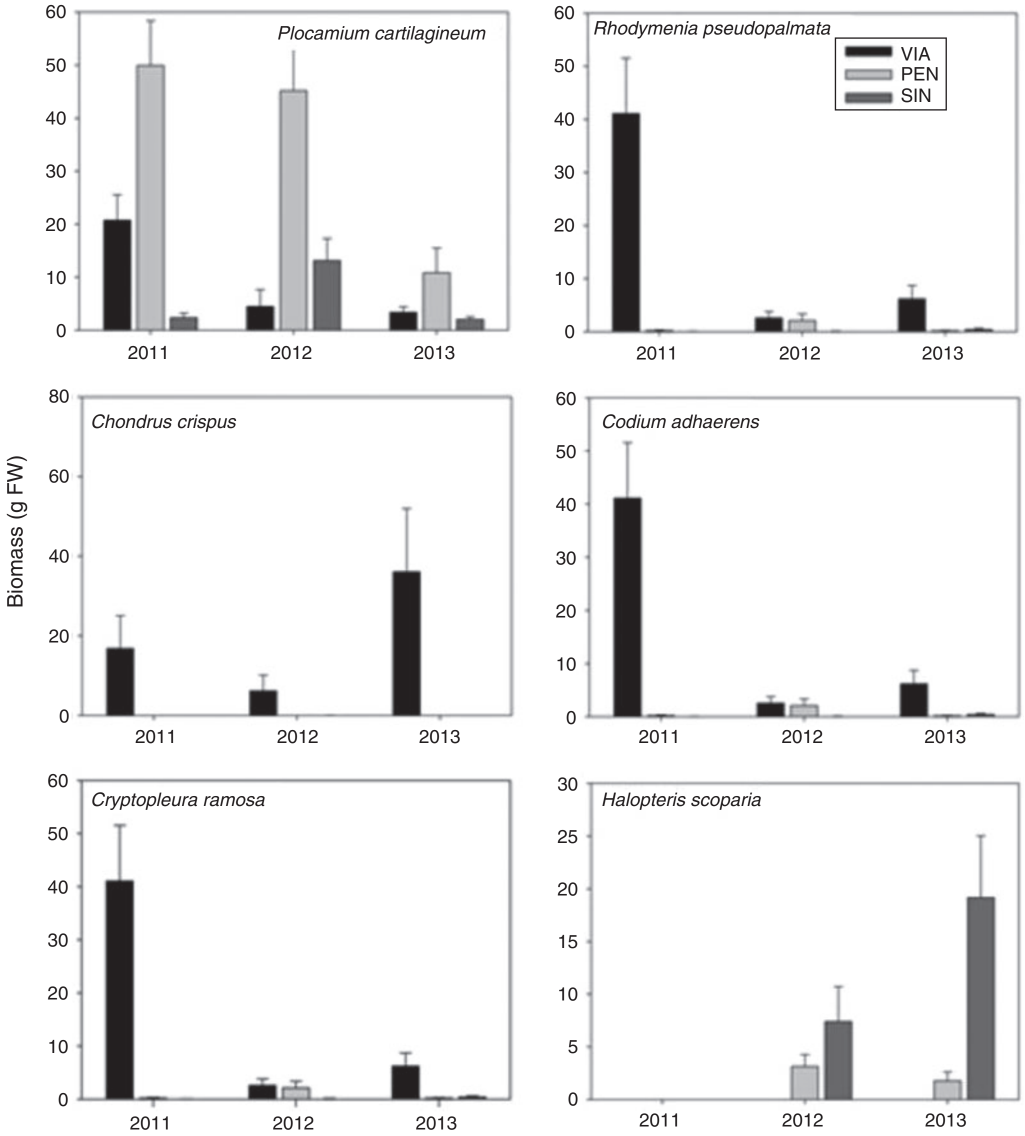

Fig. 4. Biomass (mean + s.e.) of individual algal species at each region and time of sampling. Data were averaged across six quadrats and five reefs. Abbreviations are as in Fig. 3.

resources, such as light and space (e.g. Maggi *et al.* 2012; Thomsen *et al.* 2014). Instead, the opposite pattern occurred in this study, with a progressively increasing richness moving south as kelp abundance decreased. This suggests that diverse macroalgal assemblages can be maintained independently of the presence of large biomasses of kelp. Indeed, there is evidence from other systems of a negative relationship between kelp biomass and species richness of associated seaweeds, particularly those with ephemeral life-histories (e.g. Wernberg and Goldberg 2008 and references therein). The ecological mechanisms responsible for such a relationship cannot be inferred from the present study, but they could reflect two main classes of responses. First, contrasting life-histories could have coevolved so that ephemeral forms reproduce, recruit and grow when the biomass of a dominant habitat-former is at a minimum, as suggested for epiphytal fauna (Wernberg *et al.* 2004). Second, some seaweeds could indirectly and mechanistically benefit from resources released by the natural reduction of the dominant species during certain phases of their life-cycles (Shepherd 1981). Moreover, the flora of transitional areas, such as PEN, includes elements from different climate regions, being, therefore, characterised by a larger diversity compared to the northern region.

Despite the limited available amount of quantitative data on subtidal macroalgal assemblages in Portugal, there is a perception by local and scientific communities that the abundance and distribution of kelps have declined in recent times (Assis *et al.* 2009). Similarly, declines in kelp distribution have been described and predicted all along the coasts of western Europe as a consequence of climate change (Díez *et al.* 2012; Raybaud *et al.* 2013; Voerman *et al.* 2013; Brodie *et al.* 2014). These trends could negatively affect the associated biodiversity and all goods and services that are supported by kelp forests. Therefore, the knowledge of kelp's ecology and patterns of abundance and distribution is a key requisite to support management and conservation actions aimed at preventing their further reduction and, eventually, disappearance under the predicted increase of natural and anthropogenic pressures. A contribution to achieve this goal can be provided, particularly in the context of assessments of climate-related effects, by studies, such as the present one, that examine shifts in the distribution of species across environmental gradients.

Acknowledgements

This study is part of a M.Sc. thesis by D. Pinho at the University of Porto. Financial support was provided by the European Regional Development Fund (ERDF) through the 'Programa Operacional Factores de Competitividade' (POFC-COMPETE) within the 'Quadro de Referência Estratégico Nacional (QREN)' and the Portuguese Fundação para a Ciência e a Tecnologia (FCT) through the projects 'Efeitos do clima oceânico na macroecologia e resiliência a perturbações dos povoamentos de kelps' – OCEANKELP (PTDC/MAR/109954/2009) and PEst-C/MAR/LA0015/2011 and a Ph.D. grant (SFRH/BD/84933/2012) to J. N. Franco. F. Tuya was supported by the MINECO 'Ramón y Cajal' program, T. Wernberg by the Australian Research Council and I. Bertocci by FCT within the Programa Ciência 2008 – Fundo Social Europeu.

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