



UNIVERSIDADE DOS AÇORES
FACULDADE DE CIÊNCIAS E TECNOLOGIA
Licenciatura em Biologia
UNIDADE CURRICULAR DE PROJETO

SPATIAL AND TEMPORAL DISTRIBUTION OF MACROALGAL ASSEMBLAGES
ASSOCIATED WITH THE INVASIVE *ASPARAGOPSIS ARMATA* ON INTERTIDAL
ROCKY SHORE IN AZORES

Sob orientação de:

Prof^a Doutora Ana I. Neto

Doutora Eva Cacabelos

Orientanda:

Leire Lopetegui Eguren

Ponta Delgada

2016/2017

Spatial and temporal distribution of macroalgal assemblages associated with the invasive *Asparagopsis armata* on intertidal rocky shore in Azores

LEIRE LOPETEGUI, EVA CACABELOS & ANA I. NETO

Departamento de Biologia, Universidade dos Açores, 9501-801 Ponta Delgada, São Miguel, Azores, Portugal

Abstract

Rapid globalization and the increasing trends of trade, travel, and transport in recent decades have accelerated marine biological invasions. The Rhodophyta *Asparagopsis armata* is considered one of the most invasive species in European subtropical and temperate waters. *A. armata*, first recorded in the Azorean Archipelago in 1928, is now well established and very common in all Azorean islands, mainly between 5 and 20 m depth. Although having a wide distribution in the archipelago, little is known about its spatial and temporal variation and its impact on the invaded littoral communities. The present study aims to fill this gap and define spatial and temporal variations of the seaweed assemblages associated with the invasive *Asparagopsis armata* on low intertidal rocky shore. Three locations along the south coast of São Miguel Island were compared (Caloura, Lagoa and São Roque) in a monthly sampling between November 2016 and April 2017. According to our predictions, of temporal and spatial variability in the number of macroalgal taxa, there was an interactive effect between location and time. Environmental factors were proposed to account for this. A positive correlation between the abundance of *Asparagopsis armata* and the high diversity was found in Caloura, contrasting the venerable generalization of more diverse communities are more resistant to invasion. However, further studies taking into account its higher biomass peak (late spring) are needed in order to confirm this positive correlation.

Keywords: Azores Island, invasion, *Asparagopsis armata*, intertidal assemblages, algal community

Introduction

Biological invasions are considered to be one of the most important direct drivers of biodiversity loss and a major pressure on several types of ecosystems, with both ecological and economic impacts (Millennium Ecosystem Assessment, 2005). Invasion of alien marines in their ecosystems may displace native species, therefore, causing the loss of native genotypes, modifying habitats or changing community structure. Furthermore, it affects food web properties and ecosystem processes and impedes the provision of ecosystem services. Moreover, it impacts human health and causes substantial economic losses (Katsanevakis *et al.*, 2014).

Littoral and sublittoral communities are particularly sensitive to anthropogenic pressures due to the exposition to a wide range of environmental conditions at the extreme edge of both the marine and terrestrial environment (Crowe *et al.*, 2000; Martínez *et al.*, 2012). Marine macroalgae dominate the rocky intertidal and shallow subtidal in most oceans, describing particularly important ecological functions, contributing to marine primary production. This intertidal assemblages, as many natural ones, are complex and intrinsically variable in space and time (Veiga

et al., 2013), and more knowledge about this variability is crucial to understand the ecological processes structuring them (Martins *et al.*, 2008). Intertidal macroalgal assemblages inhabiting the low-shore of the Azorean coast were studied to identify their spatial and temporal patterns of variability. Both macroalgal species/taxa and functional groups, considered to be good descriptors of benthic communities in previous ecological studies (Steneck & Dethier, 1994; Veiga *et al.*, 2013).

Natural colonization for marine organisms occurs mainly through oceanic currents (Cardigos *et al.*, 2006). However, besides natural pathways, various anthropogenic factors concur as additional vectors of entrance for marine species in areas outside their natural biogeographic range (Bax *et al.*, 2003). Rapid globalization and the increasing trends of trade, travel, and transport in recent decades have accelerated marine biological invasions. These have taken action on increasing the amount of introductions through various pathways, such as shipping, navigational canals, aquaculture and aquarium trade (Hulme, 2009; Katsanevakis *et al.*, 2013). Some of these anthropogenic activities such as hull fouling, ballast water, solid ballast, recreational boating and dive practices, fisheries and aquaria trade are relevant for the Archipelago of the Azores (Cardigos *et al.*, 2006) that is geologically recent and separated from the nearest continental coasts by at least 1,300 km (Morton *et al.*, 1998). Considering the small dimension of these volcanic islands and that the transatlantic boat-traffic stopping over has significantly increased over the last decade, this archipelago has a high potential of introductions.

The Rhodophyta *Asparagopsis armata* native to southern Australia and New Zealand (Horridge, 1951), nowadays is widespread throughout the world, is one of the species that has been introduced in the Archipelago of the Azores probably through boat hulls or rafting vectors (Cardigos *et al.*, 2006). This invasive species was first recorded in the Archipelago of the Azores in 1928 (Schmidt, 1931). Currently it is well established and very common in all Azorean islands, mainly between 5 and 20 m depth (Neto, 2000). *A. armata* possesses long hooked stolons (Bonin & Hawkes, 1987), which become entangled among other marine organisms thus permitting thalli to sprawl loosely over large areas (Andreakis *et al.*, 2003). As many invasive plants, *A. armata* exhibits seasonal development patterns having as a consequence a temporal variation in its biomass (Klein & Verlaque, 2009), with its maximum occurrence in spring (Neto, 1997).

Despite its positive impact on ecosystem services such as water purification, biotic materials and biofuels, it is most commonly known because it negatively affects food fisheries and aquaculture, ocean nourishment, lifecycle maintenance and it also has a negative impact on multiple-species (Katsanevakis *et al.*, 2014).

Although having a wide distribution in the archipelago, little is known about its spatial and temporal variation and its impact on the invaded littoral communities. The present study aims to define spatial and temporal variations of the seaweed assemblages inhabiting low intertidal rocky shores, investigating the possible impact of the invasive *Asparagopsis armata* on Azorean systems. Moreover, we will analyse if the spatio-temporal variability pattern of the macroalgal assemblages obtained by using species/taxa will be consistent with that obtained by using functional groups.

Materials and methods

Study sites

For spatial variation analysis, three sites along the south coast of São Miguel Island, where the invasive species *Asparagopsis armata* was found in previous years, were compared (Caloura, Lagoa and São Roque, Fig. 1). The three sites, characterized by compact bedrock of hard basaltic rock, are within bays, enclosing relatively shallow waters, and of easy access for shore work. For seasonal variation, work was undertaken in the period between November 2016 and April 2017, resulting in 6 months of sampling.

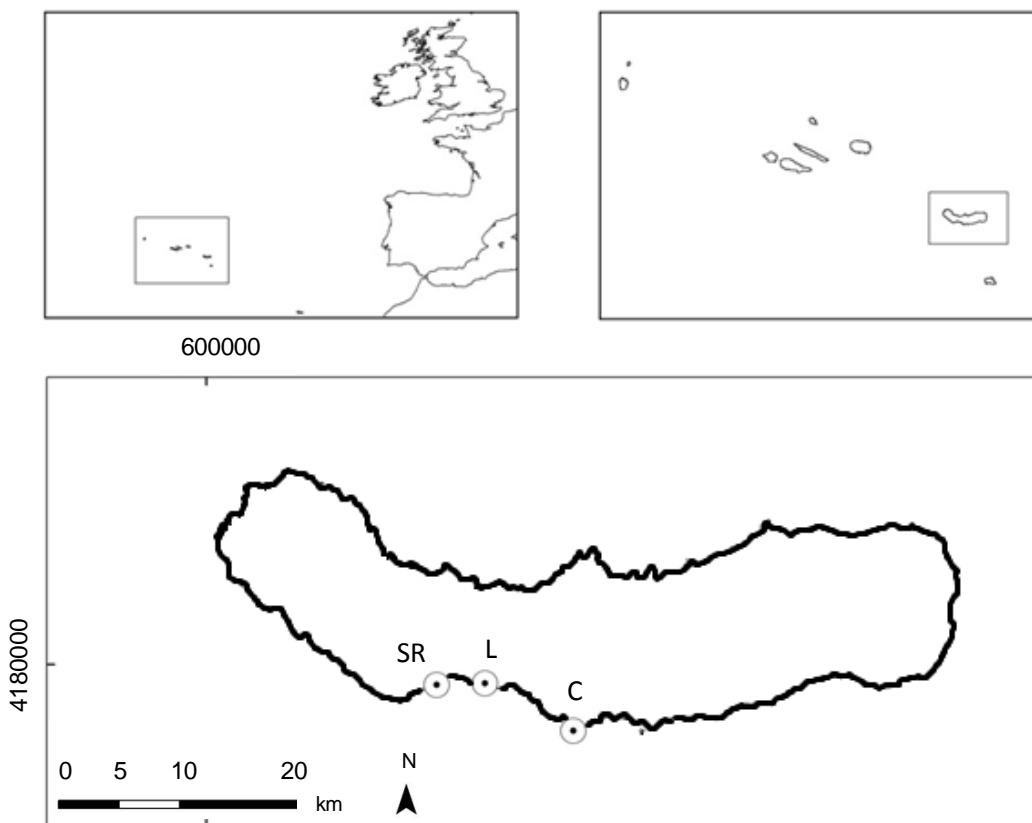


Figure 1. Island of São Miguel with the three location of sampling São Roque (SR), Lagoa (L), Caloura (C) (modified from Cacabelos *et al.*, 2012)

Sample collection

The three sites were surveyed monthly using a non-destructive method. In each site 9 photographs were taken at random at the very low-shore, using a 25 x 25 cm quadrat frame. Back at the laboratory, photographs were organized according to the month and site of the sample.

To measure the frequency of occurrence of each taxa, identification was made in Coral Point Count with Microsoft Excel extensions (CPCe) Program (Kohler & Gill, 2006). After automatic

frame-image sequencing, photographs were overlaid by a matrix of fifty randomly distributed points, and the fauna/flora taxa or substrate type lying beneath each point was visually identified up to the highest possible taxa (species, genus or functional group).

Data analysis

Obtained data from CPCe Program were combined to produce Microsoft Excel spreadsheets to matrix analyze. A 2-way fully crossed model analysis of variance (ANOVA) with Time (random, 6 levels) and Site (random, 3 levels) was used to investigate spatial and temporal patterns of variability in univariate data, such as the number of taxa and functional group and the abundance of *Asparagopsis armata* and more relevant taxa or functional groups. Homogeneity of variances were assessed using PERMDISP test and data transformation applied when necessary. If homogeneity was not achieved after transformation, untransformed data were analysed and the more stringent criterion of $p < 0.01$ was used to reject null hypotheses.

Temporal and spatial changes in the structure of macroalgal assemblages were analysed with the same design using the multivariate analogue PERMANOVA (Anderson, 2001). Analyses were based on Bray-Curtis similarity matrix (giving more weight to changes in species abundances) and also on Jaccard similarity matrix (based on changes in species composition, i.e. presence/absence data). Non-metric multidimensional scaling (MDS) to visualize multivariate results was used. To detect what functional groups contributed most to similarity within and dissimilarity among the locations, an analysis of similarity percentages (SIMPER) was carried out. Percentage cover of functional groups contributing most to dissimilarity among locations were analysed by using an ANOVA as mentioned before. The software PRIMER 6 & PERMANOVA was used for data analysis (Clarke & Warwick, 2001).

Results

A total of 30 macroalgal taxa were identified and grouped on 8 functional groups.

Number of taxa

A 2-way fully crossed model analysis of variance (ANOVA) with Time (random, 6 levels) and Location (random, 3 levels) based on observational data (number of taxa) detected a significant interaction between time and location (Table 1, Fig. 2A).

Pair-wise comparisons showed that the number of taxa was greater in Caloura than in São Roque over all sampling times (T). However, Caloura had a greater number of species than Lagoa only in T3, and Lagoa number of taxa was greater than that of São Roque in T2, T5 and T6 (Table 1).

Table 1. Two-way fully crossed analysis of variance, ANOVA (with location as a random factor with 3 levels and time as a random factor with 6 levels) considering the species and a pair-wise comparison of assemblages at different locations in different time levels. df: degrees of freedom, MS: mean squares, C: Caloura, L: Lagoa, SR: São Roque. T1; November 2016, T2; December 2016, T3; January 2017, T4; February 2017, T5; March 2017, T6; April 2017.

Source	df	MS	Pseudo-F
Time	5	8.207	1.459
Location	2	88.019	15.645***
Time x Location	10	5.626	2.776**
Res	144	2.026	
Tot	161		

Pair-wise comparisons		
T2 C>SR**; L>SR**	T5 C>SR***; L>SR***	
T3 C>L**; C>SR***	T6 C>SR***; L>SR***	

p<0.01, *p<0.001.

PERMDISP $F_{2,159}=10.738$, p<0.001. Transformation: None.

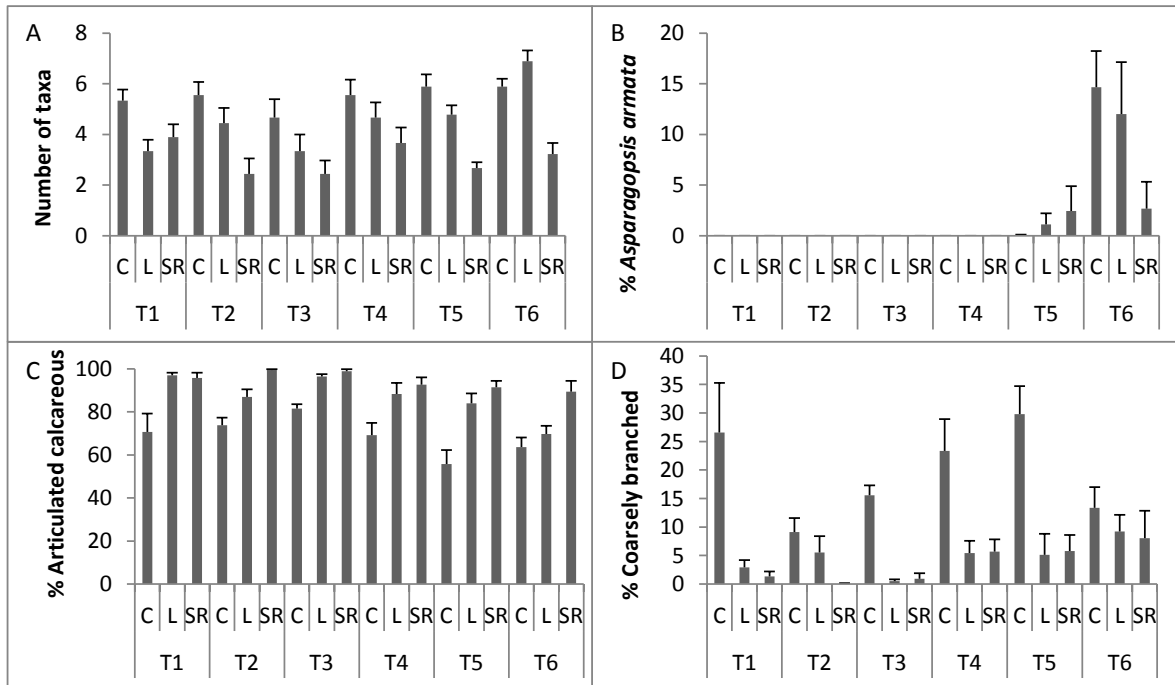


Figure 2. Mean (+SE, n=9) number of taxa (A) and abundance of *Asparagopsis armata* (B), the Articulated calcareous (C), Coarsely branched (D) functional groups obtained in each localization along the 6 time levels. See Table 1 for abbreviations.

Community structure

For macroalgal taxa, a multivariate analysis (PERMANOVA) based on Bray Curtis similarity matrix of assemblage showed a significant interaction between time and location (Table 2, Fig. 3). Inspection of pair-wise comparisons showed differences in the structure of assemblages between Caloura and São Roque over all sampling times, while differences with Lagoa were only observed

in T3 and T5. Macroalgal assemblages from Lagoa differed from those of São Roque in T2, T5 and T6 (Table 2).

Table 2. Two factor PERMANOVA test with Bray Curtis similarity matrix (with site as a random factor with 3 levels and time as a random factor with 6 levels) considering the complete macroalgal assemblage and a pair-wise comparison of assemblages at different locations in different time levels. See Table 1 for abbreviations.

Source	df	MS	Pseudo-F
Time	5	11625	2.9602
Location	2	21206	5.3998
Time x Location	10	3927.1	6.3659**
Res	144	616.9	
Tot	161		

Pair-wise comparisons	
T2 C≠SR***; L≠SR***	T5 C≠L***, C≠SR***; L≠SR***
T3 C≠L**; C≠SR***	T6 C≠SR***; L≠SR***
T4 C≠SR**	

p<0.01, *p<0.001.

PERMDISP $F_{2,159}=13.048$, p<0.001. Transformation: None.

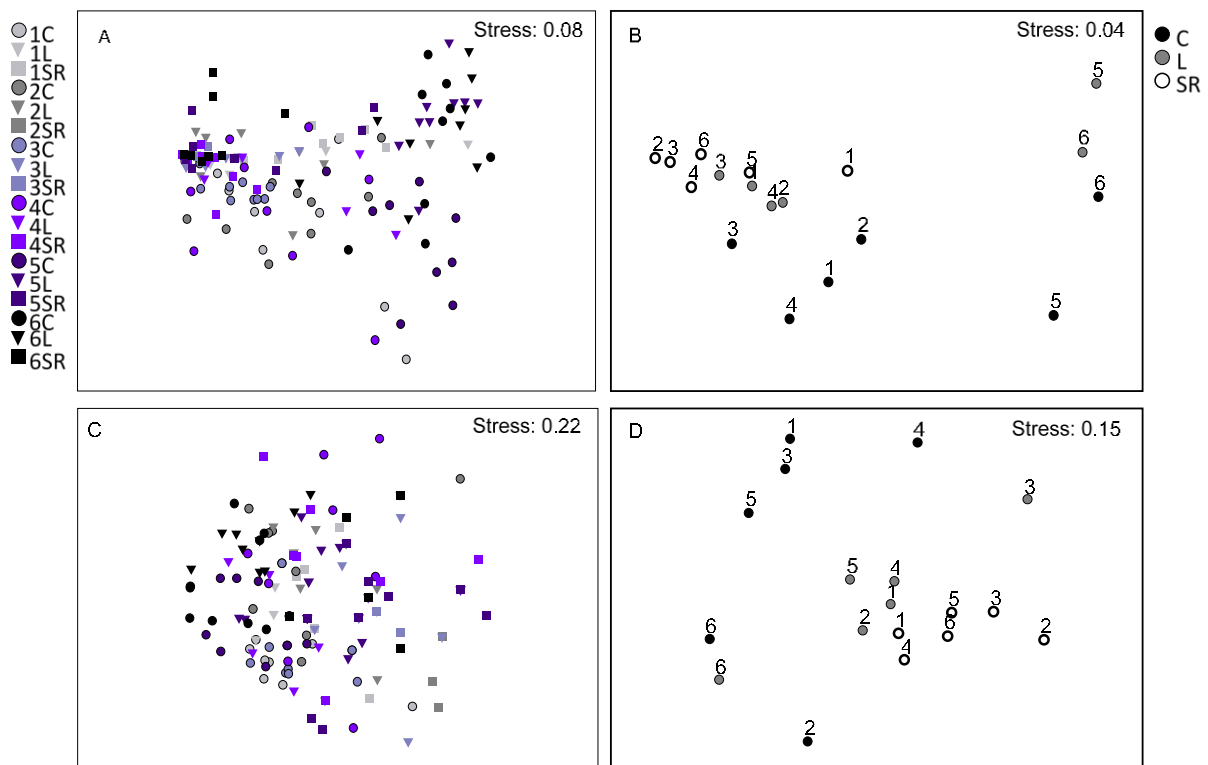


Figure 3. Non-metrical multidimensional scaling (MDS) plot based on Bray Curtis (A, B) and Jaccard (C, D) matrix representing composition and structure of the macroalgal assemblages in A) and C) the replicates of each location and B) and D) the centroids for each locations and the time levels. See Table 1 for abbreviations.

Multivariate analysis based on presence/absence of taxa (Jaccard) also showed a significant ($p < 0.001$) interaction between both time and location (Table 3, Fig. 3).

Table 3. Details of the two factor PERMANOVA test based on Jaccard matrix (with site as a random factor with 3 levels and time as a random factor with 6 levels) considering the species and a pair-wise comparison of assemblages at different locations in different time levels. See Table 1 for abbreviations.

Source	df	MS	Pseudo-F
Time	5	7390.8	1.5434
Location	2	17373	3.6279
Time x Location	10	4788.7	3.0464***
Res	144	1571.9	
Tot	161		
Pair-wise comparisons			
T1 C≠L***; C≠SR***		T4 C≠L**; C≠SR***	
T2 C≠L*; C≠SR***; L≠SR*		T5 C≠L***; C≠SR***; L≠SR**	
T3 C≠L**; C≠SR***; L≠SR***		T6 C≠L*; C≠SR***; L≠SR***	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

PERMDISP $F_{2,159} = 0.00596$, $p = 0.956$. Transformation: None.

For functional groups, multivariate analysis based on Bray Curtis similarity matrix showed a significant value in the interaction of two factors (Table 4, Fig. 4).

Table 4. Details of the two factor PERMANOVA test with Bray Curtis similarity matrix (with site as a random factor with 3 levels and time as a random factor with 6 levels) considering the functional groups of the species and a pair-wise comparison of assemblages at different locations in different time levels. See Table 1 for abbreviations.

Source	df	MS	Pseudo-F
Time	5	1539.7	2.9298
Location	2	7916.9	15.065
Time x Location	10	525.53	2.2074**
Res	144	238.08	
Tot	161		
Pair-wise comparisons			
T1 C≠L**; C≠SR***		T4 C≠SR**	
T2 C≠L*; C≠SR***; L≠SR**		T5 C≠L**; C≠SR***	
T3 C≠L***; C≠SR***; L≠SR**		T6 C≠SR**; L≠SR**	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

PERMDISP $F_{2,159} = 23.574$, $p < 0.001$. Transformation: None.

The MDS representation based on Bray Curtis similarity matrix, showed a bigger variation (in functional groups) in Caloura than in the other locations (Fig. 4). The smallest variation in functional groups along time it is observed in São Roque (Fig. 4).

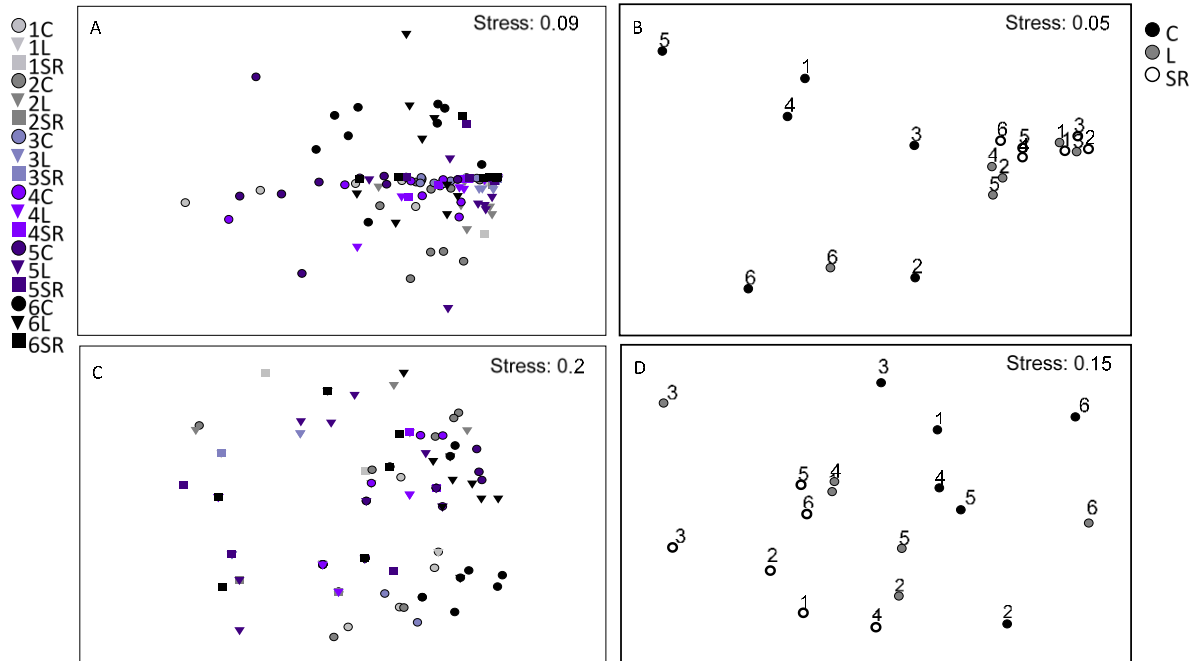


Figure 4. Non-metrical multidimensional scaling (MDS) plot based on Bray Curtis (A, B) and Jaccard (C, D) matrix representing composition and structure of the functional groups in A) and C) the replicates of each location and B) and D) the centroids for each locations and the time levels. See Table 1 for abbreviations.

Multivariate analyses based on Jaccard matrix (Table 5) confirms the results obtained in the Bray Curtis matrix, where a significant value is observed in the interaction between location and time (Table 4 and 5, Fig. 4).

Table 5. Details of the two factor PERMANOVA test based on Jaccard matrix (with site as a random factor with 3 levels and time as a random factor with 6 levels) considering the functional groups and a pair-wise comparison of assemblages at different locations in different time levels. See Table 1 for abbreviations.

Source	df	MS	Pseudo-F
Time	5	6711.1	1.8678
Location	2	15813	4.4012
Time x Location	10	3593	2.7241***
Res	144	1319	
Tot	161		
Pair-wise comparisons			
T1 C≠SR**			T5 C≠SR**
T2 C≠SR**			T6 C≠SR***; L≠SR***
T3 C≠L***; C≠SR***; L≠SR**			

*p<0.05, **p<0.01, ***p<0.001.

PERMDISP $F_{2,159}=7.607$, p<0.01. Transformation: None.

The SIMPER analysis showed the Articulated calcareous was the functional group that most contributed to the similarity within locations (Table 6). In Caloura however, the Coarsely branched functional group also contributes to the internal similarity until the level of cut-off (95 %).

Table 6. SIMPER analysis results of similarity between each location replicate (cut-off level of 95%).

Location	Functional group	Abundance	Contrib %	Cum %
Caloura	Articulated calcareous	69.07	79.87	79.87
	Coarsely branched	19.62	15.64	95.51
Lagoa	Articulated calcareous	87.04	95.79	95.79
São Roque	Articulated calcareous	94.56	98.92	98.92

The Articulated calcareous, the Coarsely branched and the Filamentous were the functional groups that most contributed to the dissimilarity between Caloura and Lagoa (Table 7). The Articulated calcareous and the Coarsely branched were the functional groups that contributed significantly to the dissimilarity between Caloura and São Roque (Table 7). Apart from the Articulated calcareous and Coarsely branched functional groups, the species *Asparagopsis armata* also contributed to the dissimilarity between Lagoa and São Roque.

Table 7. SIMPER analysis results of dissimilarity between each location (cut-off level of 75%).

Location	Dissimilarity average	Functional group	Contrib %	Cum %
Caloura - Lagoa	27.09	Articulated calcareous	39.17	39.17
		Coarsely branched	32.37	71.54
		Filamentous	6.25	77.8
Caloura - São Roque	28.38	Articulated calcareous	46.41	46.41
		Coarsely branched	31.5	77.91
Lagoa - São Roque	13.82	Articulated calcareous	42.36	42.36
		Coarsely branched	22.18	64.54
		<i>Asparagopsis armata</i>	9.49	74.03

Relevant functional groups

A 2-way fully crossed model analysis of variance (ANOVA) with Time (random, 6 levels) and Location (random, 3 levels) based on the biomass of *Asparagopsis armata* detected a significant interaction between time and location (Table 8, Fig. 2B). The percent cover of *A. armata* significantly increased in the last month (Time 6) of this study, where the species showed its greatest biomass (Fig. 2B).

The pair-wise comparisons between locations in the time level 6 (when *A. armata* appears), found differences between Caloura and São Roque (Table 8). The abundance of the invasive species is significantly higher in Caloura comparing to São Roque (Fig. 2B).

Table 8. Details of the 2-way fully crossed analysis of variance, ANOVA (with site as a random factor with 3 levels and time as a random factor with 6 levels) considering the species *Asparagopsis armata* and a pair-wise comparison of assemblages at different locations in time level 6. See Table 1 for abbreviations.

Source	df	MS	Pseudo-F
Time	5	415.56	6.287**
Location	2	39.742	0.60126
Time x Location	10	66.098	2.4688*
Res	144	26.773	
Tot	161		

Pair wise comparisons

Location	C>SR*
*p<0.05, **p<0.01, ***p<0.001. PERMDISP $F_{2,159}=3.589$, p=405. Transformation: None.	

Apart from the *Asparagopsis armata*, percentage cover of functional groups contributing most to dissimilarity among locations (SIMPER) were also individually studied.

For the Articulated calcareous functional group, there was a significant effect of both time and location, but there was not found interaction between both factors (Table 9, Fig 2C). The abundance of articulated calcareous species showed significant differences between Caloura and Lagoa, Caloura and São Roque, Lagoa and São Roque; and between the time levels 4 and 5, 3 and 5, and 3 and 4 (Table 9).

Table 9. Details of the 2-way fully crossed analysis of variance, ANOVA (with site as a random factor with 3 levels and time as a random factor with 6 levels) considering the percentage cover of Articulated calcareous and a pair-wise comparison of percentage covers at different locations and time levels. See Table 1 for abbreviations.

Source	df	MS	Pseudo-F
Time	5	0.5327	5.6881*
Location	2	4.4606	47.634***
Time x Location	10	0.0936	1.5299
Res	144	0.0612	
Tot	161		

Pair-wise comparisons

Location	C≠L**; C≠SR***; L≠SR*
Time	T4≠T5*; T3≠T5*; T3≠T4*
*p<0.05, **p<0.01, ***p<0.001. PERMDISP $F_{2,159}=2.1402$, p=0.141 Transformation: ArcSin.	

In the case of the Coarsely branched functional group, there was found a significant interaction of time and location (Table 10, Fig. 2D).

Pair-wise tests showed significant differences between Caloura and Lagoa, and Caloura and São Roque in time levels 1, 3, 4 and 5. At time level 2, the significant difference was found only between Caloura and São Roque. And in time level 6 there was not found significances differences between the three sites (Table 10, Fig. 2D).

Table 10. Details of the 2-way fully crossed analysis of variance, ANOVA (with site as a random factor with 3 levels and time as a random factor with 6 levels) considering the Coarsely branched functional group and a pair-wise comparison of percentage covers at different locations in different time levels. See Table 1 for abbreviations.

Source	df	MS	Pseudo-F
Time	5	8.91	1.8304
Location	2	141.24	28.997***
Time x Location	10	4.87	1.9384*
Res	144	2.51	
Tot	161		
Pair-wise comparisons			
T1 C>L***, C>SR***		T4 C>L**; C>SR**	
T2 C>SR***, L>SR*		T5 C>L**; C>SR***	
T3 C>L***; C>SR***		T6 -	

*p<0.05, **p<0.01, ***p<0.001.

PERMDISP $F_{2,159}=0.1572$, p=883. Transformation: Square root.

Discussion

According to our predictions of temporal and spatial variability in the number of taxa found in the macroalgal assemblages, there was an interactive effect between location and time. This is in accordance with Coleman (2002), whose observations of benthic assemblages, particularly on marine macroalgae, also showed great variation in patterns of distribution and abundance.

The composition of the studied algal community was similar to that described previously for lower shore intertidal community by Martins *et al.* (2008), mainly composed by coralline and coarsely branched algae. However, the cover percentages from both studies were different. Our mean percentage covers varied from 56 to 99% for articulated calcareous and from 0,5 to 27% for coarsely branched, whereas Martins *et al.* (2008) had percentages between 35-78% and 13-59% respectively. The spatio-temporal variability pattern obtained by using macroalgal species/taxa was consistent with that obtained by using functional groups, as observed e.g. by Veiga *et al.* 2013 in other Portuguese coasts, and therefore, the use of this approach in monitoring of marine assemblages is a valuable tool for environmental conservation and management.

The number of functional groups found and the studied once (Articulated calcareous, Coarsely branched and *Asparagopsis armata*) were also highly variable among locations and time levels. The spatial differences could be due to the environmental factors that operate in each of the locations, such as shore level, coastal slope and wave action (Wallenstein & Neto, 2006). Moreover, in this kind of open systems, oceanic currents influence recruitment and this has been cited as a key process in structuring marine populations (Martins *et al.*, 2008). The temporal variability could be explained by a seasonal pattern of wave height storm frequency and light intensity (Rubal *et al.*, 2011).

The fact that we only observed *Asparagopsis armata* on the associated algal community in the last month of the study reflects the results by Neto (1997) that indicated a maximum occurrence of

this species in spring for the Azores. Due to the period in which the study was done, only the initial phase of the proliferation was observed. However, the location of Caloura showed a significantly higher abundance of *A. armata* than the other locations. Caloura also presented a higher number of taxa (related to higher diversity) than the remaining locations. This positive correlation between a high abundance of *A. armata* and a high macroalgal diversity contrast the venerable generalization of more diverse communities are more resistant to invasion (Elton, 1958). However, some studies conclude that the effect of diversity on invasion success is largely due to its effects on resource (space) availability (Stachowicz *et al.*, 2002) and that natively rich ecosystems are likely to be hotspots for exotic species, the so-called “invasion paradox” (Fridley *et al.*, 2007; Cacabelos *et al.*, 2012).

In this study, we suggest that apart from the invasion resistance of the community, the direct driver to resist an invasion is the temporal stability of the macroalgal assemblage. It is known that the temporal stability of an ecosystem may lay in the taxa diversity and their compensatory dynamics (Prestes *et al.*, 2017) and that the increased temporal stability found in more diverse communities may itself be considered an enhancement of ecosystem function (Stachowicz *et al.*, 2002).

In conclusion, it is known that *Asparagopsis armata* has a negative impact on multiple-species (Katsanevakis *et al.*, 2014), and adding to this the high interspecific competition for space known to occur in the Azorean shore (Neto, 1997), further studies taking into account its higher biomass (late spring) are needed to study and analyze the direct effect of this invasive species in the intertidal macroalgal community across a range of spatial and temporal scales in order to prevent the global erosion of coastal biodiversity of the Azores.

With this study, we improve our ability to understand and predict the consequences of biodiversity loss due to human-related factors such as biological invasions, base knowledge to implement conservation and management actions aimed at preserving the functioning of marine systems.

Acknowledgements

We wish to thank Afonso Prestes for his help in the samplings and João Faria for helping us with the CPC program.

References

- Anderson M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46
- Andreakis N., Procaccini G. & Kooistra W.H.C.F. (2003) *Asparagopsis taxiformis* and *Asparagopsis armata* (Bonnemaisoniales, Rhodophyta): genetic and morphological identification of Mediterranean populations. *European Journal of Phycology* 39 (3): 273-283
- Bax N., Williamson A., Aguero M., Gonzalez E. & Geeves W. (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27 (4): 313-323

- Bonin D.R. & Hawkes M.W. (1987) Systematics and life histories of New Zealand Bonnemaisoniaceae (Bonnemaisoniales, Rhodophyta): I. The genus *Asparagopsis*. New Zealand Journal of Botany, 25 (4): 577-590
- Cacabelos E., Olabarria C., Viejo R.M., Rubal M., Veiga P., Incera M., Gestoso I., Vaz-Pinto F., Mejia A., Engelen A.H. & Arenas F. (2012). Invasion of *Sargassum muticum* in intertidal rockpools: Patterns along the Atlantic Iberian Peninsula. Marine Environmental Research 90: 18-26
- Cardigos F., Tempera F., Ávila S., Gonçalves J., Colaço A. & Santos R.S. (2006) Non-indigenous species of the Azores. Helgoland Marine Research 60: 160-169
- Clarke K.R. & Warwick R.M. (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology Progress Series 216: 265-278
- Coleman M.A. (2002). Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. Journal of Experimental Marine Biology and Ecology 267, 53-74
- Crowe T.P., Thompson R.C., Bray S. & Hawkins S.J. (2000) Impacts of anthropogenic stress on rocky intertidal communities. Journal of Aquatic Ecosystem Stress and Recovery 7 (4): 273-297
- Horridge G.A. (1951) Occurrence of *Asparagopsis armata* Harvey on the Scilly Isles. Nature 167: 732-733
- Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK
- Fridley J.D., Stachowicz J.J., Naeem S., Sax D.F., Seabloom E.W., Smith M.D., Stohlgren T.J., Tilman D. & Von Holle B. (2007). The invasion paradox: reconciling pattern and process in species invasions. Ecology 88: 3-17
- Horridge G.A. (1951). Occurrence of *Asparagopsis armata* Harv. on the Scilly Isles. Nature 167: 732-733
- Hulme P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10–18
- Katsanevakis S., Zenetos A., Belchior C. & Cardoso A.C. (2013) Invading European Seas: assessing pathways of introduction of marine aliens. Ocean and Coastal Management 76: 64-74
- Katsanevakis S., Wallentinus I., Zenetos A., Leppäkoski E., Çinar M.E., Oztürk B., Grabowski M., Golani D. & Cardoso A.C. (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. Aquatic Invasions 9 (4): 391-423
- Klein J.C. & Verlaque M. (2009) Macrophyte assemblage associated with an invasive species exhibiting temporal variability in its development pattern. Hydrobiologia 636: 369-378
- Kohler K.E. & Gill S.M. (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers & Geosciences 32: 1259-1269
- Martins G.M., Thompson R.C., Hawkins S.J., Neto A.I. & Jenkins S.R. (2008). Rocky intertidal community structure in oceanic islands: scales of spatial variability. Marine Ecology Progress Series 356: 15-24

- Martínez B., Arenas F., Rubal M., Burgues S., Esteban R., García-Plazaola I., Figueroa F.L., Pereira R., Saldaña L., Sousa-Pinto I., Trilla A. & Viejo R.M. (2012) Physical factors driving intertidal macroalgae distribution: physiological stress of a dominant furoid at its southern limit. *Oecologia* 170 (2): 341-353
- Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington DC, 86 pp
- Morton B., Britton J.C. & Martins A.M.F. (1998) Coastal ecology of the Açores. Sociedade Afonso Chaves, Ponta Delgada, 249 pp
- Neto A.I. (1997) Studies on algal communities of São Miguel, Azores. PhD thesis. Universidade dos Açores, Ponta Delgada, 309 pp
- Neto A.I. (2000) Observations on the biology and ecology of selected macroalgae from the littoral of Sao Miguel (Azores). *Botanica Marina* 43 (5): 483-498
- Prestes A.C.L., Cacabelos E., Neto A.I. & Martins G. (2017). Temporal stability in macroalgal assemblage standing stock despite high species turnover. *Marine Ecology Progress Series* 567: 249-256
- Rubal M., Veiga P., Vieira R. & Sousa-Pinto I. (2011). Seasonal patterns of tidepool macroalgal assemblages in the North of Portugal. Consistence between species and functional group approaches. *Journal of Sea Research* 66: 187-194
- Schmidt O.C. (1931) Die marine vegetation der Azoren in ihren Grundzuegen dargestellt. *Bibliotheca Botanica* 102: 1-116
- Stachowicz J.J., Fried H., Osman R.W. & Whitlatch R.B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* 83: 2575-2590
- Steneck R.S. & Dethier M.N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476-498
- Veiga P., Rubal M., Vieira R., Arenas F. & Sousa-Pinto I. (2013). Spatial variability in intertidal macroalgal assemblages on the North Portuguese coast: consistence between species and functional group approaches. *Helgoland Marine Research* 67: 191
- Wallenstein F.M. & Neto A.I. (2006). Intertidal rocky shore biotopes of the Azores: a quantitative approach. *Helgoland Marine Research* 60: 196-206