The effects of the invasive seaweed *Asparagopsis armata* on native rock pool communities: Evidences from experimental exclusion

Carla O. Silva [a], Marco F.L. Lemos [a], Rui Gaspar [b], Carlos Gonçalves [b], João M. Neto [a,b,*]

[a] *MARE – Marine and Environmental Sciences Centre, ESTM, Instituto Politécnico de Leiria, Peniche, Portugal*
[b] *MARE – Marine and Environmental Sciences Centre, Department of Life Sciences, University of Coimbra, Coimbra, Portugal*

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ABSTRACT

Biological invasions represent a threat to ecosystems, through competition and habitat destruction, which may result in significant changes of the invaded community. *Asparagopsis armata* Harvey 1855 is a red macroalgae (Rodophyta) globally recognized as an invasive species. It is found from the intertidal to shallow subtidal areas, on rock or epiphytic, forming natural vegetation belts on exposed coasts. This study evaluated the variations on native intertidal seaweed and macroinvertebrate assemblages inhabiting rock pools with and without the presence of the invasive macroalgae *A. armata*. To achieve this, manipulation experiments on Atlantic (Portugal) rock pools were done. Three rock pools were maintained without *A. armata* by manual removal of macroalgae, and three others were not experimentally manipulated during the study period and *A. armata* was freely present. In this study the variations between different rock pools were assessed. Results showed different patterns in the macroalgae composition of assemblages but not for the macrobenthic communities. *Ellisolandia elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders 2013 was the main algal species affected by the invasion of *A. armata*. Invaded pools tended to show less macroalgal species richness, showing a more constant and conservative structure, with lower variation of its taxonomic composition than the pools not containing *A. armata*, where the variability between samples was always higher. Despite the importance of the achieved results, further data based on observation of long-term series are needed, in order to further understand more severe effects of the invader *A. armata* on native macroalgal assemblage.

1. Introduction

The extent and significance of biological invasions in coastal marine ecosystems has become increasingly evident in recent years and has been recognized as one of the main causes of biodiversity loss and changes for native populations, community dynamics, and major ecosystem processes (Grosholz, 2002). Contrarily to the presence of an non-indigenous species (NIS) (also exotic species, introduced species, alien species, foreign species, or non-native species), which may be present in a community for long time without significantly affecting it, the increasing rate of biological invasions (by invasive exotics) is affecting ecosystems with strong ecological impacts on resident assemblages (Olabarria et al., 2009; Piazzi et al., 2001; Sánchez et al., 2005).

Displacement of native flora by invasive exotic macroalgal species has been largely reported as provoking changes of species' composition and their trophic food webs (Piazzi et al., 2001; Sánchez et al., 2005; Stæhr et al., 2000). Together with climate change, NIS macroalgae are

becoming one of the most important threats to marine biodiversity (Stachowicz et al., 2002). The impacts associated with these introductions are typically expressed as community dominance through the monopolization of space and changing competitive relationships in native assemblage (Schaffelke & Hewitt, 2007). However, recent studies indicate that ecological impacts have only been quantified from a small fraction of known introduced seaweed (<7%) (Thomsen et al., 2017).

Invasive exotics have been shown to alter benthic habitats and biotic communities, resulting in potential ecosystem impacts in a wide geographical range. Important examples are: *Sargassum muticum* (Yendo) Fensholt 1955 in the Galician coast (northwestern Spain), commonly associated with the replacement of native species, an increase of filamentous epiphytic algae and changes on the composition of flora and fauna. It also strongly affects several abiotic factors such as sedimentation, light penetration, water movement, nutrient cycle and oxygen levels (Sánchez et al., 2005; Gestoso et al., 2012; Olabarria et al., 2009); *Asparagopsis armata* Harvey 1855 in western Atlantic coast of the

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Iberian Peninsula (Rubal et al., 2018); *Codium fragile* spp. has been reported as a fast growing species that can have detrimental effects on subtidal kelp communities in the northeast Atlantic Ocean, by damaging and replacing native kelp (Laminaria spp.) (Chapman 1998); due to its large blades, the presence of *Grateloupia turuturu* Yamada 1941 can strongly affect biodiversity by outcompeting native macroalgal assemblages for light and space in Mediterranean (Cecere et al., 2011).

Previous studies have compared also faunal assemblages associated with invasive and native species. Most of these studies considered that the introduction of invasive macroalgae have not produced substantial modifications in the composition of faunal assemblages (e.g., loss of diversity) suggesting a weak impact in native faunal diversity. Thomsen et al. (2009) stated that there was no evidence for severe effects of invasive macroalgae on fauna density and assemblages. Other studies, such as Cacabelos et al. (2010), stated that epifaunal assemblages associated with the native *Laminaria ochroleuca* Bachelot Pylaie 1824 and with the invasive algal species *Sargassum muticum* (Yendo) Fensholt 1955 differed, but only for epifaunal organisms, since the number of taxa and diversity did not clearly differ between the two algae. Viejo (1999) also demonstrated that the composition of the epifaunal assemblages associated to the invasive *Sargassum muticum* and the local *Cystoseira nodicaulis* (Withering) M. Roberts 1967 were very similar. However, Navarro-Barranco et al. (2018) showed differences in macrofauna composition between native *Halopteris scoparia* (Linnaeus) Sauvageau 1904 and the invasive species *Asparagopsis taxiformis* (Delile) Trevisan 1845, using presence/absence data. Species richness, abundance and diversity of peracarids were significantly lower in invaded assemblages than in *H. scoparia* ones. The spread and establishment of invasive species is of growing concern and eradication can be very difficult to succeed.

The rhodophyta seaweed *Asparagopsis armata* is native from Southern Australia and New Zealand (Horridge, 1951). In Europe, this macroalgae was introduced in the Atlantic and Mediterranean in the 1920s. The species is now widely distributed from the British Isles to Senegal, including the Azores, Canary, and Madeira Islands (Cacabelos et al., 2020), where it is considered an invasive exotic species. This seaweed is regarded as invasive because it spreads avidly in receiving habitats in short time, colonizing a wide area, displacing native species and producing a significant change in terms of community composition (Chualáin et al., 2004; Soler-Hurtado & Guerra-García, 2011). *Asparagopsis armata* presents lateral basal branches with retrorse spines (harpoon-like branches), which become entangled among other marine organisms thus permitting thalli to sprawl loosely over large areas (Andreakis, 2006). It is found from the intertidal to shallow subtidal areas, on rock or epiphytic, forming compact vegetation belts on exposed coasts. In spite of its wide distribution and spread rate, little is known about its potential ecological impacts on marine communities.

In this study, the main aim was to evaluate the effect of *A. armata* on intertidal seaweed and macroinvertebrate assemblages using a removal experiment in which the presence of this exotic species was manipulated. It is predicted that with the presence of *A. armata* in certain pools, the remaining assemblages would be distinct, in terms of composition and structure, from those found in rock pools where *A. armata* was experimentally removed.

2. Materials and methods

2.1. Study area

The study was carried out from February 2018 to December 2018 in Portinho da Areia Norte (WGS84: 39.369587, −9.377899) at the south part of the Peniche peninsula, central western coast of Portugal (Fig. 1). It belongs to an exposed coast to high wave action, the national coastal water type A5, but very near of the transition southward to coastal water type A6 (Bettencourt et al., 2004). In January 2018, 6 tide pools were randomly selected in the rocky intertidal area, with relatively similar size and invaded by *A. armata*. All pools were located at approximately the same tide level, which allow them to be isolated from the sea about the same time during a tidal cycle. The tidal rock pools position (semi-exposed sites) allowed seawater renewal every tidal cycle. Four hours was the duration time of rock pools, from formation to its complete disappearance. Two hours before and 2 h after the low tide moment was the full period to the complete exposure.
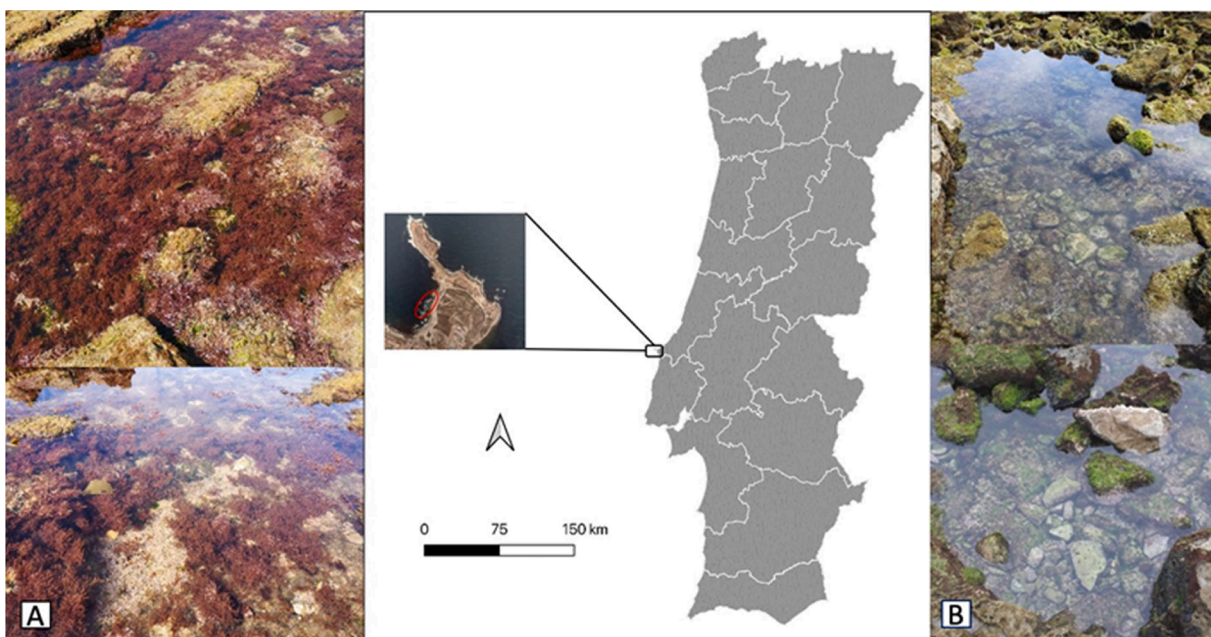

Fig. 1. Map of Peniche peninsula, western coast of Portugal, showing the location and photos of the sampling areas: A – Rock pools (A) with *A. armata*; B – Rock pools (C) without *A. armata*.

2.2. Field sampling and laboratory procedures

From the six intertidal rock pools used on experimental manipulations, three were maintained without *A. armata* (C pools) by regular manual removal of macroalgae so that the effect of its absence could be assessed in the community. Three other rock pools were not experimentally manipulated during the study period and *A. armata* was freely present (A pools). The manipulation period lasted for 10 months and community samples were collected twice per season, in a total of eight data points. The manipulation was maintained over the course of the experiment by periodically removing new *Asparagopsis* recruits, every 2–3 weeks.

When rock pools were isolated from the sea water, during ebbing, physical and chemical parameters were measured for Initial water pool conditions. The water temperature (°C), conductivity (μS cm^{-1}), oxidation–reduction potential (ORP) (mV), salinity, dissolved oxygen (DO) (%), and pH parameters were registered in situ (YSI Professional Plus handheld multiparameter probe). This procedure was repeated before the rock pools disappear, in all rock pools, for the assessment of final conditions. While the rock pools were formed, biological samples were collected inside each selected pool by removing the inner material, using a paint scraper, from a 0.1×0.1 m sampling square, randomly placed on the rocky surface, and immediately sorted for taxonomic identification and abundance quantification of biological material.

In all cases, sampling consisted of complete removal of all algae and macroinvertebrates present in randomly chosen plots. In the laboratory, each sample was washed in tap water. Water was then sieved (mesh size: 0.5 mm) to retain the macrofaunal invertebrates and macroalgae were separated. Macroalgae were identified to species, dried to constant weight (60 °C, 48 h), and weighed to the nearest 0.01 g. Macroalgae biomass was determined as dry weight (DW). Macroinvertebrates were preserved in formalin (4%) and inked with rose Bengal for later counting and identification, to the lowest possible taxonomic level (usually species). Taxonomic references were updated according to the World Register of Marine Species (Appeltans et al., 2013) and in the case of algae according to AlgaeBase (Guiry and Guiry, 2015).

2.3. Statistical analyses

2.3.1. Physical-chemical parameters analysis

The environmental parameters (temperature, conductivity, oxidation–reduction potential, salinity, dissolved oxygen and pH) were used to ordinate the sampling pools by performing principal coordinate (PCO) analyses. Euclidean similarity measure was used in the calculation of similarity matrices, after square root transformation, followed by normalization. Then, to see differences between samples, average for factor "pool*season" was selected.

2.3.2. Macroalgae data analysis

Macroalgae biomass was converted to dry-weight per unit (g DW m^{-2}). Bray Curtis similarity measure was used in the calculation of similarity matrices, after fourth root transformation of data.

The statistical significance of variance was tested using 9999 permutations of residuals under a reduced model, with a significance level of α-level of 0.05. PERMANOVA was applied including two fixed factors, 'Pools' (two levels: A - with *A. armata* and C - without *A. armata*) and 'Season' (nested in four levels: Wi (winter), Sp (spring), Su (summer) and Au (autumn)). *Asparagopsis armata* was not included in this analysis in order to identify effects on native diversity. To test whether differences of assemblages between pools were due to different multivariate dispersion between groups rather than in the location of centroids, the PERMDISP procedure was done.

To identify the taxa which contribute mostly to the communities' structural variation between sites, Similarity Percentage Analysis (SIMPER) was applied. Dissimilarities between groups were assessed using two-way crossed designs with factors 'Pools' and 'Season' (as for

PERMANOVA), with a 95% cut off for macroalgae. Principal Coordinate Analysis (PCO) was used as an ordination method to visualize patterns in data. Vectors based on Pearson correlations (greater than 0.5 to target variables with high correlations) were used.

2.3.3. Macrofauna data analysis

Abundance data of invertebrates was converted to density (ind. m^{-2}). The Bray-Curtis similarity measure was used in the calculation of similarity matrices, after the fourth root transformation of data (to reduce natural species dominance). PERMANOVA was performed to test differences between pools and seasons, followed by pair-wise tests. The statistical significance of variance components was tested using 9999 permutations of residuals under a reduced model, with an a priori chosen significance level of α = 0.05. The Similarity Percentages- species contributions (SIMPER) analysis was used to determine which macrofauna species contributed most for the dissimilarity between pools and stations. Dissimilarities between groups were assessed using two-way crossed designs with factors 'Pools' and 'Season' (as for PERMANOVA), with an 85% cut off for macroinvertebrate. Principal Coordinate Analysis (PCO) was used as an ordination method to visualize patterns in data. Vectors based on Pearson correlations (greater than 0.5 to target variables with high correlations) were used.

The diversity of macrobenthic fauna was assessed by different ecological indices: 1) Margalef richness index (d) (Margalef, 1968); 2) Shannon-Wiener diversity index (log$_e$); 3) Pielou evenness index (J') (Pielou, 1969); and 4) Simpson domination index (1-λ) (Simpson, 1949), using the following algorithms:

(1) d=(S-1)/log(N);
(2) H'=Σpilog(pi);
(3) J'=H'/log(S)
(4) 1-λ = 1-Σ(Ni*(Ni-1)/(N*(N-1))

where S is the number of species, N is the total number of individuals, pi is the proportion of abundance of species.

All multivariate analyses were carried out with PERMANOVA + for PRIMER software (PRIMER v6 & PERMANOVA + v1, PRIMER-E Ltd.).

Two-way analysis of variance (ANOVA) was applied to ecological indices. Considered factors were: 1) Pools, with two levels; and 2) Season with four levels, using SigmaPlot software for Windows, version 12.0.

3. Results

3.1. Environmental data

The physico-chemical parameters exhibited no significant differences between the initial and final rock pools conditions. Although, at the end of emersion period, the environmental variables were markedly different between seasons (*P*(perm) = 0.0001) (Table 1).

The PCO analysis indicated that the first two axes explained a total of 80.3% and 82.2% variation for the initial rock pool conditions and final rock pool conditions, respectively Fig. 2, A and B). In the Initial conditions, immediately after the rock pools got isolated from the sea due to ebbing tide, parameters that strongly correlated with the first axis (PCO1; r > ± 0.80) were temperature (r = 0.80) and conductivity (r = −0.91). With PCO2 were DO (%) (r = 0.95) and ORP (mV) (r = -0.86). In the Final conditions, before rock pools were inundated by flooding tide, pH showed the strongest correlations (r = 0.97) with PCO1 and conductivity (r = 0.83) with PCO2. The Initial conditions imposed a higher dispersion of rock pools in general, either for type of pool or season. Contrarily, in the end of the rock pool existence period, the Final water conditions allowed a distribution of rock pools under a clear pattern, with pools "A" and "C" grouped together by season, and seasons clearly apart from each other. The water rock pools converged to similar conditions on the end of the experiment on every season, imposing a

Table 1

Summary of PERMANOVA of physico-chemical parameters from the sampling rock pools after it was isolated (Initial) and before it was flooded (Final).

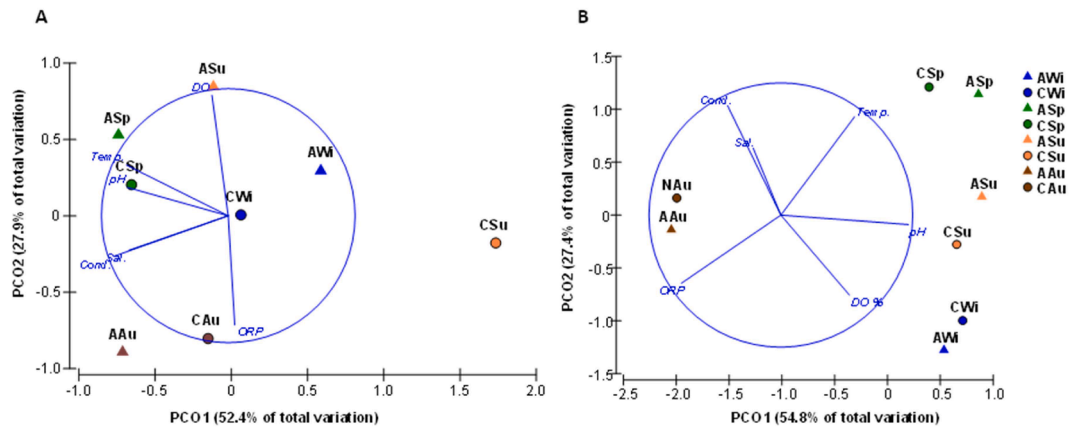| Source of variation	Initial				Final			
	df	MS	Pseudo-F	P(perm)	df	MS	Pseudo-F	P(perm)
Pools	1	3.891	0.667	0.582	1	1.058	0.234	0.9636
Seasons	3	9.480	1.626	0.090	3	28.037	6.213	**0.0001**
Pools × Seasons	3	4.977	0.853	0.544	3	2.303	0.510	0.9496

Fig. 2. . Principal Coordinates Ordination (PCO) of the physico-chemical parameters: (A) Initial rock pool conditions; (B) Final rock pool conditions. Vectors are the raw Pearson correlations of variables with the PCO axes. Key: upward triangles = Rock pool "A"; circles = Rock pool "C"; Wi = winter; Sp = spring; Su = summer; Au = autumn.

seasonally more consistent pattern, with different rock pools ("A" and "C") showing to be more similar between them and also higher differences comparing to other seasons. The season was a markedly evident factor.

The selected rock pools presented different shapes, volumes and depth, which could affect assemblage composition and bias the final results, but no physico-chemical significant variability existed between pool A and C initial conditions.

3.2. Assemblage composition

In the studied assemblages, 50 macroalgal taxa were identified plus *Asparagopsis armata* and its tetrasphorophyte phase (*Falkenbergia rufolanosa* (Harvey) F. Schmitz 1897); in total: 37 Rhodophyta, 7 Chlorophyta and 8 Ochrophyta (Appendix A). In both rock pools A and C there were 48 and 44 macroalgae taxa, respectively. The group Rhodophyta showed higher species richness (34 and 30 taxa for rock pool A and rock pool C, respectively). Chlorophyta and Ochrophyta had the same number of taxa (7) in pool C and pool A. Rock pools C and A from summer

season obtained the highest mean number of species (15.4 ± 0.66 and 15.4 ± 0.93, respectively), whereas pool C in winter obtained the lowest number (6.25 ± 0.74) (Fig. 1A). Mean biomass highest value was found for rock pool C in winter (9.13 ± 2.84 g DW m^{-2}), when *Asparagopsis armata* mean biomass was 1.95 ± 0.65 g DW m^{-2} while the lowest value (0.17 ± 0.07 g DW m^{-2}) was found for pool A in summer, with 0.70 ±

Table 2

Summary of PERMANOVA analyses for macroalgae based on biomass data.

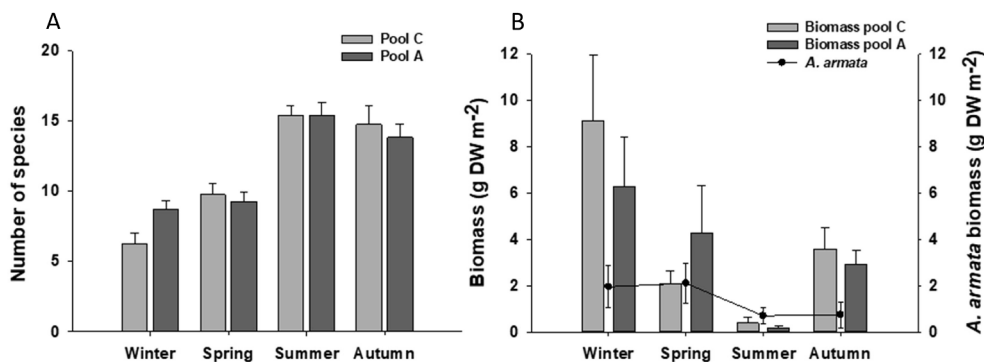| Source	df	MS	Pseudo-F	P(perm)
Stations	1	3636	2.5185	**0.0192**
Seasons	3	14861	10.294	**0.0001**
Stations × Seasons	3	2967.9	2.0558	**0.0046**
Groups	t		P(perm)	
Winter A #C	1.198		0.2208	
Spring A #C	1.9789		**0.0025**	
Summer A #C	1.4354		**0.0257**	
Autumn A #C	0.9784		0.4438	

Fig. 3. . Mean number of species (±SE) (A) and macroalgae mean biomass (g DW m^{-2} ± SE) with *Asparagopsis armata biomass* mean (SE) (B) per rock pool for all seasons.

0.33 g DW m^{-2} of *A. armata* biomass (Fig. 3).

PERMANOVA (Table 2) revealed statistically significant differences in macroalgae biomass between pools (P(perm) = 0.0192), between seasons (P(perm) = 0.0001) and also the interaction Pools*Seasons (P(perm) = 0.0046). But such patterns were not consistent in time. The pairwise on the "pools" revealed only significant differences between spring and summer season (P(perm) = 0.0025 and 0.0257), respectively. The lack of significant differences on the PERMDISP analysis indicated that the dispersion of samples did not provide a significant contribution (F = 1.4, p = 0.3) to the differences detected by PERMANOVA, indicating that there is only a location effect.

SIMPER analysis identified taxa that contributed for the differentiation between invaded (Rock pools A) and non-invaded (Rock pools C) rock pools, with 60.2% dissimilarity between groups.

The top three species at the *A. armata* invaded sites (Rock pool A) that most contributed to this dissimilarity percentage (Table 3) were *Vertebrata thuyoides* (Harvey) Kuntze 1891 /*Vertebrata fruticulosa* (Wulfen) Kuntze 1891 (5.91%), *Ulva* spp. (5.86%) and *Lithophyllum incrustans* Philippi 1837 (5.09%). At rock pools without the invasive macroalgae (Rock pool C), the species that most contributed to this dissimilarity were *Ellisolandia elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders 2013 (21.73%), *Mesophyllum lichenoides* (J. Ellis) Me.Lemoine 1928 (4.12%), and *Jania rubens* (Linnaeus) J.V. Lamouroux 1816 (3.41%). Some species were equally abundant along all sampling areas (as *Gastroclonium ovatum* (Hudson) Papenfuss 1944 and *Amphiroa* spp.)

Regarding the macroinvertebrates, in both rock pool types, five groups contributed to about 90% of total density. They were Gastropoda, Malacostraca, Bivalvia, Polyplacophora, and Polychaeta, with the higher species richness belonging to Gastropoda (17 and 12 taxa for pool C and A, respectively) (Appendix B). The macroinvertebrates highest mean number of species was registered in rock pool C in autumn (13.83 ± 1.23) and the lowest values were recorded in pool C in winter (6.73 ± 0.93) (Fig. 4A). Regarding the mean density of macroinvertebrates, in the opposition of the *A. armata* biomass found in rock pools, the highest value was found for rock pool C in autumn (1743.3 ± 285.3 ind m^{-2}), while lower values were found for rock pool C in winter (251.8 ± 37.8) (Fig. 4B).

Concerning density, PERMANOVA did not detect any significant

differences between macroinvertebrate assemblages from control and *A. armata* invaded rock pools (P(perm) = 0.5095), only a significant temporal variability was confirmed for factor 'Season' (Table 4). However, macroinvertebrates density in summer was slightly higher in the invaded rock pools (A) (1686.7 ind. m^{-2} ± 311.3) than in the non-invaded rock pools (C). In Autumn, the pools C, without the invasive macroalgae, presented higher macroinvertebrate densities (as already mentioned) than pools A for the same season (1473.3 ind. m^{-2} ± 319.7) (Fig. 4).

The SIMPER analysis showed 55.5% dissimilarity in mean abundance composition between pools C, without invasive *A. armata*, and pools A, with *A. armata* (Table 5). For rock pools A, the top three dominant taxa that most contributed to this dissimilarity percentage were *Skeneopsis planorbis* (O. Fabricius, 1780) (8.02%), *Rissoa parva* (da Costa, 1778) (6.73%), and *Melarhaphe neritoides* (Linnaeus, 1758) (6.46%) (Table 7). For rock pools C, where *A. armata* was experimentally removed, the species that most contributed to dissimilarity were *Amphipholis squamata* (Delle Chiaje, 1828) (6.33%), Polychaeta (5.17%), and *Mytilus* sp. (2.43%). Although most species contributing to differences between pools with and without *A. armata* were mainly present at the former ones, Polyplacophora, Polychaeta, and Ophiuroidea showed higher abundances in rock pools C, without the invasive species.

A Principal Coordinates Analysis (PCO) based on the Bray-Curtis resemblance matrix was applied to visualize differences and similarities between samples. The PCO for the macroalgae biomass and macrofauna density, in general, did not show clear differences between the studied rock pools and seasons. For macroalgae it provided a tenuous distinction between pools and in some cases between seasons of the same rock pool (pools in spring and in autumn, Fig. 5A). The first two principal component axis explain 32.7% and 19.1% of the samples variability, for macroalgae biomass (A) and invertebrate's density (B) respectively.

For both macroalgal assemblages, six taxa showed a moderate to strong correlation with the first two PCO axes (Pearson's coefficient >0.5, Fig. 5A). The macroalgae taxa with higher value of correlation (greater than 0.5) were related to rock pool A, in autumn season, while macrofauna taxa with higher correlation are distributed between rock pools from spring and autumn season. For this assemblages, 5 taxa were the ones influencing more the relative distribution of different rock pools along seasons (Fig. 5B).

Concerning macrofauna, no significant differences were detected by PERMANOVA, showing that both rock pools type did not differ in the abundance of macrofauna species. The calculated diversity indices, in general, presented higher values in Winter and Spring for pools A, and the opposite trend in Summer and Autumn (Table 6).

Univariate analyses did not detect significant differences between the rock pools A (with *Asparagopsis armata*) and C (without *Asparagopsis armata*) for the diversity benthic macrofauna indices, except for factor 'season' concerning the number of taxa (S), the total number of individuals (N) and for the Margalef index (Table 7).

4. Discussion

This study aims to evaluate the variation observed on intertidal seaweed and benthic macroinvertebrate assemblages inhabiting rock pools with and without the presence of the invasive macroalgae *A. armata*.

Several studies have been made using invasive exotic species and assessing the induced changes in native macroalgal assemblages (De Leij et al., 2017; Olabarria et al., 2009; Sánchez et al., 2005). Nevertheless, to the present knowledge, in the literature, there are no studies showing the impact of *A. armata* on macroalgae and macroinvertebrate community assemblages.

In the present study, *A. armata* had a significant impact on the native intertidal macroalgal assemblage, and, although less evident, also over
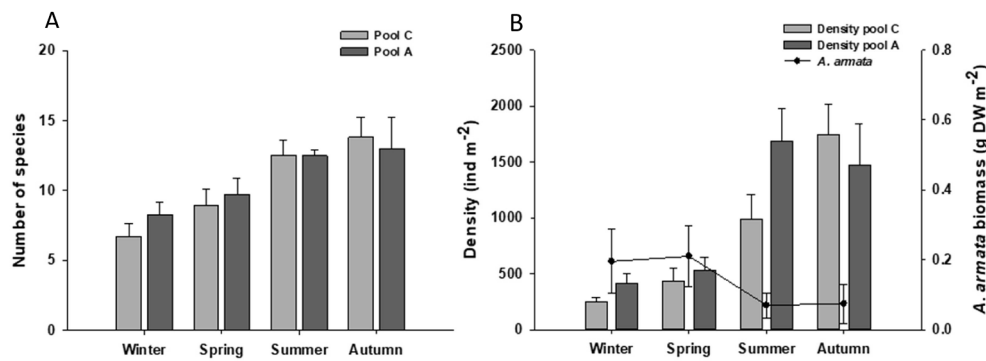
Table 3
Contribution of individual taxa to the average Bray-Curtis dissimilarity in macroalgae assemblage. Bold, higher values; rock pool C, without *Asparagopsis armata*; and rock pool A, with *A. armata*.

Taxa	Pool C	Pool A	Average Dissimilarity	Contribution %
	Average abundance			
Ellisolandia elongata	**1.79**	1.26	13.08	21.73
Vertebrata thuyoides/ Vertebrata fruticulosa	0.39	**0.42**	3.56	5.91
Ulva spp.	0.32	**0.54**	3.53	5.86
Lithophyllum incrustans	0.23	**0.24**	3.06	5.09
Mesophyllum lichenoides	**0.22**	0.18	2.48	4.12
Chondracanthus acicularis	0.19	**0.30**	2.27	3.77
Jania rubens	**0.19**	0.14	2.05	3.41
Ulva clathrata	0.16	**0.17**	1.91	3.18
Ceramium spp./*Gayliella* spp.	0.25	**0.30**	1.69	2.80
Champia parvula	0.18	**0.21**	1.63	2.71
Osmundea pinnatifida/ Laurencia pyramidalis	0.12	**0.15**	1.51	2.52
Crouania attenuata	0.11	**0.14**	1.47	2.45
Cladophora spp.	**0.11**	0.10	1.39	2.30
Polysiphonia spp. or Other Rhodomelaceae	0.10	**0.11**	1.32	2.19
Peyssonelia spp.	**0.11**	0.06	1.27	2.11
Caulacanthus ustulatus	**0.10**	0.08	1.25	2.07
Gastrocolonium ovatum	0.08	0.08	1.11	1.84
Amphiroa spp.	0.07	0.07	1.05	1.74

Fig. 4. . Mean number of species (SE) (A) and macroinvertebrate mean density (ind m^{-2} ± SE) with *Asparagopsis armata biomass* mean (SE) (B) per rock pool for all seasons.

Table 4

Summary of PERMANOVA analyses for macroinvertebrates based on abundances data.

Source	df	MS	Pseudo-F	P(perm)
Pool	1	1331.5	0.93382	0.5095
Season	3	6842.7	4.7988	**0.0001**
Pool × Season	3	12674	0.88883	0.6316

Table 5

Contribution of individual taxa to the average Bray-Curtis dissimilarity in macroinvertebrate assemblage. Bold, higher values; Rock pool C, without *Asparagopsis armata*; and Rock pool A, with *A. armata*.

Taxa	Pool C	Pool A	Average Dissimilarity	Contribution %
	Average abundance			
Skeneopsis planorbis	2.62	**3.05**	4.45	8.02
Rissoa parva	1.53	**1.87**	3.74	6.73
Melarhaphe neritoides	1.52	**1.68**	3.59	6.46
Amphipholis squamata	**3.18**	3.1	3.51	6.33
Bittium reticulatum	1.65	**1.75**	3.16	5.69
Amphipoda	1.51	**1.88**	2.89	5.2
Polychaeta	**1.92**	1.65	2.87	5.17
Dynamene magnitorata	1.26	**1.62**	2.8	5.04
Cymodoce truncata	1	**1.1**	2.69	4.84
Parvicardium scriptum	0.68	**1.07**	2.44	4.39
Gibbula sp.	0.66	**1.07**	2.36	4.25
Musculus costulatus	0.57	**1**	2.18	3.93
Gibbula pennanti	0.56	**0.59**	2	3.6
Mytilus sp.	**0.54**	0.42	1.35	2.43
Lepidochitona sp.	**0.46**	0.33	1.34	2.42
Gibbula umbilicais	**0.45**	0.31	1.31	2.37

macroinvertebrate assemblages. Results indicated that physico-chemical parameters did not have a strong contribution on pool type differentiation in terms of environmental conditions, with most of the variation occurring between seasons. Both rock pool types, with *A. armata* (A) and without it (C), presented similarities for the environmental conditions, which made them closer to each other within the same season then between seasons. This similarity between pairs of rock pools A or C from the same season was more evident in the end of the exposition time, immediately before the flooding tide inundates the intertidal rock pools, than right after their formation with ebbing tide. These results support the idea that individual morphological differences between the selected rock pools were not responsible for the different responses given by biological assemblages present in those two rock pool types. The effect of the presence of *A. armata*, either physically or by the

chemical compounds exudated into the water column, could be more determinant to the observed differences.

As many invasive macrophytes, *A. armata* exhibits seasonal development patterns having therefore a temporal variation in biomass (Klein & Verlaque, 2009). In this study, during 2018, *A. armata* reached a peak of biomass in spring, which accumulated and started to decompose in the rock pools. A sharp biomass fall was observed in the summer suggesting spring as an important growing period for the species. A seasonal patterns already documented for congener species in other places (e.g., *Asparagopsis taxiformis*, Azores, NE Atlantic archipelago) (Neto, 2000), with its possible disappearance from the high intertidal zone during summer, being found mainly in lower abundances in the low intertidal zone or in the shallow subtidal during this period of the year (Fa et al., 2000), is similar to this study. In the present work, the effect of *A. armata* on the macroalgal assemblage was detected in spring and summer seasons. During summer, with lower *A. armata* biomass, a higher macroalgal richness was evident. This result agrees with the concept known as "biotic resistance" proposed by Elton (1958) that states that communities with higher diversity should be less susceptible to invasion because of a more complete utilization of resources. On the other hand, in spring, when *A. armata* registered higher biomass in the invaded pools, a higher biomass of native macroalgae was registered. In fact, increased light intensity, daylight duration and temperature during the spring and summer stimulates the growth of many native sub-canopy algae (Vye et al., 2018). This fact might increase competition for primary resources with *A. armata*. Also, rock pools with *A. armata* tended to present lower species richness, which may contribute to increased variability within invaded rock pools in the intertidal zone (Loreau et al., 2001). High densities of *A. armata* inhabiting the tide pools could be responsible for a decrease in the macroalgae diversity through competitive interactions. These hypotheses are not mutually exclusive and experimental evidences from this study and others (Britton-Simmons, 2004; Stæhr et al., 2000; Thomsen et al., 2016) may explain the observed field patterns.

One macroalgal species, recognized to dominate native macroalgal assemblages by producing massive coverage (Streftaris & Zenetos, 2006), but also known to be significantly affected by the presence of the invasive *A. armata* is *Ellisolandia elongata*. This species contributed substantially to the total dissimilarity between different pool types. *Ellisolandia elongata* decreased in biomass when *A. armata* was present, which is supported by previous studies made by Guerra-García et al. (2012), that report *E. elongata* as the main algal species affected by the presence of *A. armata*. It's known from several studies that the presence of invasive macroalgae is responsible for habitat modifications (Vázquez-Luis et al., 2008; Vázquez-Luis et al., 2009; Guerra-García et al., 2012), which may provide to each specific species different advantages to different pool type. After all, the different expression of species attributes under different regimes of disturbance (such as wave-exposure or sand-deposition) and stress gradients produces much of the
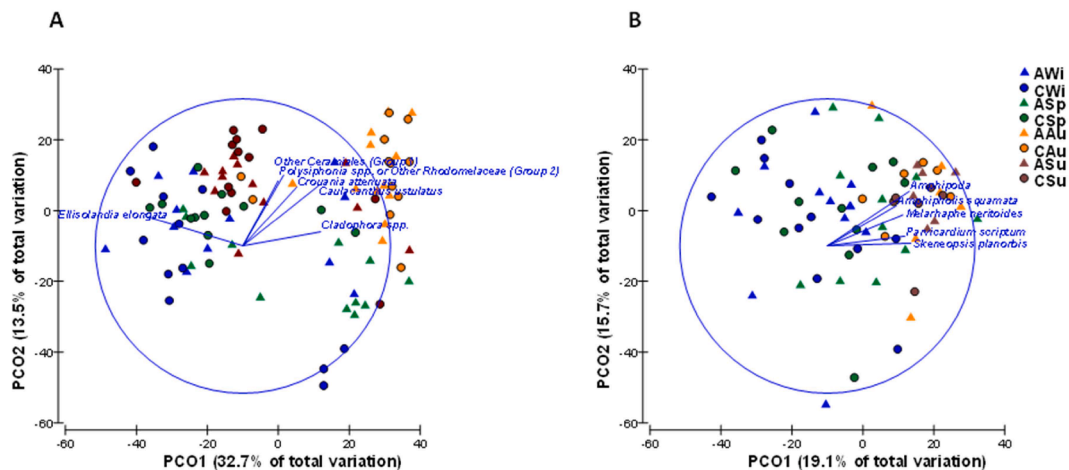
Fig. 5. . Principal Coordinate analysis (PCO) plot based on macroalgae biomass (A) and macrofauna density (B) per rock pool for all seasons with the representation of the species with vectors longer than 0.5. A and C = Rock pools A and C. Wi, Sp, Au and Su = Winter, Spring, August and Summer.

Table 6
Variation of Margalef (d), Pielou (J'), Shannon (H'(log$_e$)), and Simpson (1-Lambda') diversity indices per pool within seasons (Wi = Winter; Sp = Spring; Su = Summer; Au = Autumn).

Pools	C				A			
Season	wi	Sp	Su	Au	Wi	Sp	Su	Au
d	1.04 ± 0.15	1.33 ± 0.16	1.70 ± 0.17	1.72 ± 0.17	1.31 ± 0.09	1.26 ± 0.17	1.57 ± 0.05	1.66 ± 0.27
J'	0.74 ± 0.06	0.77 ± 0.04	0.72 ± 0.05	0.64 ± 0.04	0.77 ± 0.03	0.80 ± 0.02	0.66 ± 0.03	0.66 ± 0.05
H'(log$_e$)	1.36 ± 0.17	1.65 ± 0.18	1.83 ± 0.16	1.65 ± 0.09	1.62 ± 0.05	1.63 ± 0.11	1.65 ± 0.08	1.66 ± 0.22
1-Lambda'	0.63 ± 0.07	0.70 ± 0.06	0.74 ± 0.05	0.69 ± 0.04	0.72 ± 0.02	0.74 ± 0.03	0.71 ± 0.03	0.69 ± 0.07

Table 7
Results of ANOVAs testing for differences in the total number of taxa (S), total number of individuals (N), Shannon's diversity index (H'), Margalef richness (d), Pielou eveness (J') and Simpson domination (1-D). Significant differences are indicated in bold.

Source of variation	df	S			N			H'		
		MS	F	P	MS	F	P	MS	F	P
Pools	1	2.22	0.18	0.68	0.19	1.99	0.16	0.007	0.04	0.85
Season	3	123.35	9.83	**0.001**	2.10	22.53	**0.001**	0.30	1.4	0.24
Pools*Season	3	4.13	0.33	0.804	0.10	1.07	0.37	0.09	0.41	0.75
Residual	61	12.55			0.09			0.21		
	68	16.93			0.18			0.20		

Source of variation	df	d			J'			1-λ		
		MS	F	P	MS	F	P	MS	F	P
Pools	1	0.005	0.02	0.88	0.001	0.05	0.81	0.005	0.18	0.68
Season	3	1.13	4.84	**0.004**	0.04	2.61	0.06	0.02	0.78	0.51
Pools*Season	3	0.08	0.35	0.79	00.005	0.27	0.85	0.006	0.23	0.88
Residual	61	0.23			0.02			0.03		
	68	0.26			0.02			0.03		

spatial and temporal heterogeneity observed in natural assemblages (Sousa, 1984). As species differ in their adaptations to particular environments, the outcome of interactions depends on the species identity (Viejo et al., 2008), which, in the end, produce their realized niches or patterns (Hutchinson, 1957).

Concerning macrofauna, no significant differences were detected by PERMANOVA, showing that rock pool types did not differ in the abundance of macrofauna species. Also, PCO results (Fig. 5B) did not portray differences among different pools and only the factor season was significant in the PERMANOVA test.

These results are similar to previous studies that have compared faunal assemblages with other invasive species to those associated with other native canopy species. Most of these studies considered that the introduction of invasive macroalgae have not produced substantial modifications in the composition of faunal assemblages (e.g., loss of

diversity) suggesting a weak impact in native faunal diversity. Thomsen et al. (2009) stated that there was no evidence for severe effects of invasive macroalgae on fauna density and assemblages. Other studies, such as Cacabelos et al. (2010), stated that epifaunal assemblages associated with the native *Laminaria ochroleuca* and with the invasive algal species *Sargassum muticum* differed, but only for epifaunal organisms, since the number of taxa and diversity did not clearly differ between the two algae. Viejo (1999) also demonstrated that the composition of the epifaunal assemblages associated to the invasive *Sargassum muticum* and the local *Cystoseira nodicaulis* (Withering) M. Roberts 1967 were very similar. The presence of comparable amounts of epiphytes on different macroalgae could be equally used as habitat and food by macrofaunal assemblages (Cacabelos et al., 2010). Contrarily to *A. armata* where no plant epiphytes were found (Guerra-García et al., 2012).

However, Navarro-Barranco et al. (2018) showed differences in macrofauna composition between native *Halopteris scoparia* (Linnaeus) Sauvageau 1904 and the invasive species *Asparagopsis taxiformis*, using presence/absence data. Species richness, abundance and diversity of peracarids were significantly lower in invaded assemblages than in *H. scoparia* ones.

Either due to the production of secondary metabolites (terpenes, phenolic compounds, etc.) (Carpenter et al., 2000; Greff et al., 2017) that affect the palatability or its acceptability by herbivores (Paul et al., 2006a; Silva et al., 2020); the presence of halogenated compounds that lower densities of biofilm bacteria found on the surface of *A. armata* fronds (Paul et al., 2006b); or the habitat complexity modification, the number of macrofaunal species, although not significantly different, was in this study always higher on rock pools A during Winter and Spring, when *A. armata* biomass was higher. The opposite pattern was observed for the low biomass period of Summer and Autumn, where the number of macrofauna species was higher on rock pools C without the invasive macroalgae. The same pattern was observed for ecological indices, with diversity showing higher values in Winter and Spring for rock pools invaded by *A. armata* and the opposite situation on Summer and Autumn (higher diversity values for rock pools C) (Table 4). Specifically, there was a tendency of Gastropoda, Bivalvia, and Crustacea to prefer invaded pools and Polyplacophora, Polychaeta, and Ophiuroidea to prefer the native macroalgal assemblage pools (Table 5).

Moreover, the lack of significant difference found between rock pool types may be due to the pattern in which *A. armata* is usually present in the studied area. The general low abundance of *A. armata* at this intertidal level and its pseudoperennial character (high cover percentages are only recorded during a few months of the year) (Arenas and Fernández, 2000) appear to or may limit competitive processes with native species. The effects of the native and the invasive species on macrofaunal assemblages at larger spatial and temporal scales are yet to be determined but may include effects on spatial patterns in β-diversity and detrital food webs, and the population dynamics of species associated with macrophytes at some or all stages of their life-history. Further work, following the trajectory of macroalgal and macrofauna communities over a longer duration, would increase information to assess the full community dynamics with and after *A. armata* removal. The trends here observed, may point to a progressive replacement of *E. elongata* by *A. armata*, which may directly or indirectly have considerable impacts on the ecology of rocky intertidal zone. In fact, a few studies assessed the relative importance of some of the biological mechanisms preventing invasions in marine habitat (Arenas et al., 2006; Bulleri et al., 2016), but it's also important to address the response of communities to habitat modifications imposed by invaders. The experimental exclusion of *A. armata* from the studied rock pools, and the difference found on macroalgae assemblages from pools with and without this invasive species may also be an important indication about the recovery potential of these marine ecosystems.

5. Conclusions

In this case, rock pools with and without *Asparagopsis armata* were not significantly different in terms of the environmental conditions measured in the water column (e.g., temperature, dissolved oxygen, pH). Although not quantified in this study, it is well documented from other works that the presence of *A. armata* is responsible for chemical modifications of the surrounding pool water due to exudated compounds; also, of direct effects resulting from shading by fronds; and to modifications of habitat complexity where it stands.

Even though, results suggest that there was a significant effect of *A. armata* on macroalgae assemblages, with statistically significant differences detected on abundance and taxonomic composition of native macroalgal communities; and less evident on macroinvertebrate communities, but detected as higher values for number of species, abundance and diversity in rock pools with *A. armata* for Winter and Spring

seasons, and the opposite for the rest of the year.

Investigation didn't last long enough for irrefutable conclusions but the spreading of this species ought to drive to a reduction of species composition from native macroalgae assemblages, with consequences also on macroinvertebrate communities and the associated food webs. Native macroalgal assemblages found in pools C (without *A. armata*), were more diverse than from pools A, foreseeing the importance of management actions seeking habitat recovery.

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