Patterns of distribution of the invasive alga *Asparagopsis armata* Harvey: a multi-scaled approach

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**Abstract**

Human activities are contributing to the homogenization of the world’s biota by transporting thousands of species to areas outside their native range. Some of these species can lead to profound changes in the structure and function of natural ecosystems in areas where they are introduced, with dramatic economic and ecological impacts. The red alga *Asparagopsis armata* is considered an invasive species in Europe, but can be particularly abundant in the Azores (NE Atlantic), where there is virtually no information on its ecology. Here, we investigate the patterns of spatial distribution and impacts of *A. armata* in the Azores, as a first step to understand its potential spread. Adopting a hierarchical design, we surveyed the distribution of *A. armata*, and associated assemblages, at a range of spatial scales (from islands (10s of km apart), locations (kms apart), sites (10s of m apart) to quadrats (m apart)). Results showed that the abundance of *A. armata* varied significantly among locations and that there was substantial variability in its abundance among islands, locations and quadrats and little variability among sites. At the scale of locations, the abundance of *A. armata* did not correlate with any of our predictor variables (sea urchin density, Latitude, Longitude and sea temperature). However, at the quadrat scale, there was a significant and negative correlation between the abundance of *A. armata* and diversity of associated macrophytes, as well as, with the abundance of the conspecific *A. taxiformis* and the abundance of most of the remainder macroalgal groups. The potential role of biotic and abiotic factors in generating the observed patterns is discussed. This study further highlights the suitability of the analytical tools used here to examine patterns of distribution over a range of spatial scales and its applicability in the field of aquatic invasions.

**Key words:** Azores, hierarchical analysis, invasion, macroalgae, shallow-water macroalgal communities

**Introduction**

Human activities are contributing to the homogenisation of the world’s biota by transporting thousands of species to areas outside their native range (Hallegraeff and Bolch 1992; Ruiz et al. 2000). Some of these species can overcome the ecological barriers of the new habitat and become
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established. Such non-indigenous species are considered invasive, due to their dominance and rate of spread in the new habitat (Lonsdale 1999) and can potentially have significant ecological and economic impacts (Williamson 2006; Simberloff et al. 2013).

In the Azores (NE Atlantic archipelago), several non-indigenous species have been reported in terrestrial (Silva et al. 2008), freshwater (Raposeiro et al. 2012) and marine (Cardigos et al. 2006) ecosystems. Among the later, the red alga *Asparagopsis armata* Harvey, 1855 was first confirmed in the Azores in 1952 (Tittley and Neto 2005). This species is probably the most conspicuous and widespread of all the non-indigenous marine species reported so far, occurring in all the nine islands of the archipelago (Neto 1994; Cardigos et al. 2006). It has a diplohaplontic heteromorphic life cycle (Feldmann and Feldmann 1939, 1942; Chihara 1961, 1962), in which the free-living, filamentous diploid sporophyte (“Falkenbergia” stage) produces haploid spores via meiosis, and these develop into erect, usually benthonic, male or female haploid gametophytes that produce male or female gametes. Fertilization occurs on the female reproductive structures and gives rise to a diploid zygote that develops into a multicellular carposporophyte, which remains dependent on the female thallus (Feldmann and Feldmann 1939). The benthonic gametophytes are seasonal in the Azores, where they generally peak in abundance in late spring or early summer (Neto 1997, 2000).

*Asparagopsis armata* is thought to be native to southern Australia and New Zealand (Horridge 1951). In Europe, it is widely distributed throughout the Atlantic and Mediterranean coasts, from the British Isles to Senegal, including the Azores, Canary and Madeira Islands (Ni Chualáin et al. 2004; Andreakis et al. 2007), where it is considered an invasive species (South and Tittley 1986; Sala and Bouderesque 1997; Bouderesque and Verlaque 2002). Despite its wide distribution and spread rate, compared to other invasive seaweeds (i.e., *Caulerpa* spp.), little is known about its potential ecological and/or economic impacts (but see Pacios et al. 2011; Guerra-García et al. 2012; Katsanevakis et al. 2014; Nyberg and Wallentinus 2005). Analyses of its distribution across multiple spatial scales are even scarcer, although crucial to understand the drivers of its distribution, assess its potential impact and contribute for future management and mitigation strategies (Underwood 1993; Bishop et al. 2002). Grazers can play an important role in structuring macroalgal assemblages (Lubchenco and Gaines 1981; Hawkins and Hartnoll 1983). The alga *A. armata* is generally perceived as being relatively unpalatable to most herbivores although some studies report that sea hares, abalones and some fish can indeed feed on *A. armata* (Sala and Bouderesque 2002; Katsanevakis et al. 2014; Greff et al. 2017). Unlike the above, we still know little about the potential role of sea-urchins, which are regarded as key structuring agents of subtidal communities in temperate and tropical regions (Paine and Vadas 1969; Morrison 1988), in controlling the distribution of this species.
Table 1. Predictor variables at sampled locations.

| Island       | Location     | Latitude (decimal degress) | Longitude (decimal degress) | Seawater temperature (°C) | Sea urchin density (n.m-2) (mean ± SE) |
|--------------|--------------|---------------------------|----------------------------|---------------------------|----------------------------------------|
| Flores       | Boqueirão    | 39.4630                   | 31.1277                    | 17                        | 0.00 ± 0.00                            |
|              | Ponta Delgada| 39.5216                   | 31.2066                    | 17                        | 0.00 ± 0.00                            |
|              | São Pedro    | 39.4630                   | 31.1330                    | 17                        | 0.35 ± 0.19                            |
| Pico         | São Roque    | 38.5244                   | 28.3144                    | 17                        | 0.00 ± 0.00                            |
|              | Santa Cruz   | 38.4061                   | 28.1858                    | 17                        | 0.40 ± 0.57                            |
|              | São Caetano  | 38.4261                   | 28.4205                    | 17                        | 0.15 ± 0.15                            |
| Terceira     | Monte Brasil | 38.6541                   | 27.2300                    | 16                        | 0.05 ± 0.07                            |
|              | Negrito      | 38.6547                   | 27.2816                    | 15                        | 0.00 ± 0.00                            |
|              | Salga        | 38.6461                   | 27.0977                    | 16                        | 0.00 ± 0.00                            |
| São Miguel   | Galera       | 37.7072                   | 25.5075                    | 19                        | 0.00 ± 0.00                            |
|              | Caloura      | 37.7127                   | 25.4955                    | 19                        | 0.00 ± 0.00                            |
|              | Lagoa        | 37.7400                   | 25.5733                    | 20                        | 0.00 ± 0.00                            |

Three aspects are generally perceived as being important in determining the successful establishment of non-indigenous species in their new habitat: the biology of the non-indigenous species (species invasiveness), the number and frequency of introductions (propagule pressure) and the susceptibility of the recipient native community to invasion (community invasibility) (Lonsdale 1999; Vaz-Pinto et al. 2014a). Here we investigate the patterns of distribution of A. armata in the Azores at a range of spatial scales and assess its potential interaction with the remaining macroalgal and sea urchin communities. This is a preliminary first step to explore the influence of potential factors (e.g. competition and grazing pressure) driving its distribution and successful establishment in the Azores.

Materials and methods

Study site and community structure

The study was done in the Azorean archipelago, which comprises 9 volcanic islands organised into 3 groups (eastern, central and western) located between 37° to 40°N and 25° to 31°W (Table 1). Sampling was performed within shallow-water communities (5 m depth), which, in this region, are mostly dominated by macroalgae. The most abundant organisms at this depth include articulated corallines (e.g. Ellisolandia elongata (J.Ellis and Solander) K.R. Hind), encrusting corallines (e.g. Lithophyllum sp.), coarsely branched algae (e.g. Halopteris scoparia (Linnaeus) Sauvageau, Asparagopsis taxiformis (Delile) Trevisan) and corticated foliose algae (e.g. Zonaria tournefortii (J.V. Lamouroux) Montagne, Dictyota spp.) (Martins et al. 2013). This is also the depth at which the gametophytic phase of the invasive A. armata attains its highest biomass during its seasonal peak in abundance in late spring/early summer (Neto 2000, 2001).

Sampling design

A spatially structured hierarchical design (Underwood and Chapman 1996) was adopted to examine the patterns of distribution of A. armata and
associated macroalgal assemblages at 4 islands separated by 65 to 515 km. Islands were randomly selected, but stratified to include at least one island per group (eastern, central and eastern), so that sampling spanned the entire length of the archipelago.

For each island, 3 exposed locations, separated by kilometres (5–40 km) were randomly selected. Within each location, 2 sites (10s of m apart) were randomly selected and within each site, 10 50 × 50 cm quadrats (metres apart) were haphazardly placed on the seabed at about 5 m depth. The assemblage in each quadrat was visually sampled using the method of Dethier et al. (1993), where a score of 0 (absent) to 4 (filled = 4%) was given to each taxa within each of the 25 10 × 10 cm subquadrats. Organisms filling overall less that ¼ (= 1%) of a single subquadrat were recorded as rare and later ascribed an arbitrary score of 0.5%. All sampling was done within a month (20th May to 23rd June 2017) during the peak of *A. armata* abundance.

At each location, we also recorded sea temperature at the seabed using a portable thermometer, latitude and longitude (Table 1). The density of conspicuous macroinvertebrate grazers, such as sea-urchins (e.g. *Sphaerechinus granularis*) was also recorded in 10 randomly laid 1 × 1 m quadrats per site to assess the relationship between the density of these species and the percentage cover of *A. armata* (Table 1).

**Data analysis**

To examine patterns of spatial variation in the distribution of the invasive alga *A. armata*, a 3-way fully nested permutational ANOVA (PERMANOVA, Anderson 2001) was used. Factors were island (random, 4 levels), location (random, 3 levels) and site (random, 2 levels) with 10 replicates. Logistical constraints meant that at one of the sampling sites, only 8 replicate quadrats (instead of 10) were sampled. For this reason, we used permutational ANOVA, rather than a traditional ANOVA, since the latter is more affected by unbalanced designs (Underwood 1997). Permutational ANOVA was run on Euclidean distances with 999 permutations. Prior to analysis, PERMDISP was used to check data for heterogeneity of variances. Since heterogeneity of variances persisted, even after attempts to transform the data, we ran the analyses on the untransformed data, but used a more conservative P-value (α = 0.01) to determine significance. All analyses were run on the PRIMER-E v6 + PERMANOVA add-on (Clarke and Gorley 2006).

Mean squares (MS) estimates were used to assess the variation associated with each scale. This was done by dividing the difference between the MS of the term of interest and the MS of the term hierarchically below by the product of the levels of all terms below that of interest (Underwood and Chapman 1996; Fletcher and Underwood 2002). Estimates of spatial variations were reported as actual variances, to guarantee independence and allow comparisons with other studies, but also as relative percentages, to ascertain the relative contribution of each scale to the overall variability.
Table 2. Fully nested permutational ANOVA comparing Asparagopsis armata abundance at a hierarchy of spatial scales (islands, locations and sites) and the associated estimates of variance ($\omega^2$) and their relative (%) contribution to each scale.

| Source                  | df | MS       | F        | P      | $\omega^2$ | %  |
|-------------------------|----|----------|----------|--------|------------|----|
| Island                  | 3  | 33537.00 | 3.02     | 0.056  | 377.95     | 33 |
| Location (Island)       | 8  | 88756.00 | 38.09    | 0.001  | 545.40     | 47 |
| Site (Island × Location)| 12 | 291.33   | 1.34     | 0.207  | 7.43       | 1  |
| Residual                | 214| 217.68   |          |        |            | 19 |

At the scale of quadrats, the Pearson Product-Moment Correlation (PPMC) was used to measure the strength of a linear association between the percentage cover of the invasive A. armata and the percentage cover of the associated flora. For this purpose, the algal assemblage was grouped into 7 morpho-functional groups adapted from Steneck and Dethier (1994): articulated coralline algae (e.g. Ellisolandia elongata, Jania rubens), canopy-forming algae (e.g. Sargassum spp., Cystoseira spp.), coarsely branched algae (Asparagopsis taxiformis, Halopteris spp., Plocamium cartilagineum), corticated foliose algae (e.g. Dictyota spp., Zonaria tournefortii), encrusting algae (including both calcareous and non-calcareous species), filamentous algae (e.g. Cladophora spp., Polysiphonia spp.) and coenocitic algae (e.g. Codium spp.). We also correlated: (i) the percentage cover of A. armata with the cover of A. taxiformis, to explore the possibility of competition between the invasive (A. armata) and the congeneric species complex (A. taxiformis); and (ii) the percentage cover of A. armata and total species number (richness) to explore the potential relationship between the extent of susceptibility of the existing community to invasion by A. armata.

At the scale of locations, we used PPMC to measure the strength of a linear association between the percentage cover of A. armata and sea temperature, latitude, longitude and the density of sea urchins. For this purpose, the percentage cover of A. armata, as well as, the densities of sea urchins were averaged among all quadrats (n = 20) within each location. This analysis was done only at the scale of locations since this was the only spatial scale at which there was significant variation in the abundance of A. armata (see Table 2).

PPMC derived P-values were corrected for multiple comparisons using the Holm-Bonferroni Sequential correction (Holm 1979) separately for analyses done at the scale of quadrats and locations.

**Results**

Across the islands, the percentage cover of A. armata ranged from 0.15 ± 0.10 to 77.30 ± 4.98 (mean ± SE) (Figure 1). Despite the substantial variation between the islands, significant variation in the percentage cover of A. armata was only found at the scale of locations (i.e., km) (Table 2). The largest variation in the abundance of A. armata among locations ranged between 70.35 ± 4.49 in São Miguel, compared with 0.15 ± 0.10 in Pico Island.
Inspection of the components of variation showed that variability in the abundance of \( A. \text{armata} \) was mostly associated with the scale of locations, islands and, to a smaller extent, quadrats (Table 2). Variability in the abundance of \( A. \text{armata} \) at the scale of sites was negligible.

At the quadrat scale, after the correction of P-values for multiple comparisons, the abundance of \( A. \text{armata} \) was negatively and significantly correlated with the abundance of the congeneric \( A. \text{taxiformis} \), algal richness and the cover of articulated coralline, coarsely branched, corticated foliose and encrusting algae (Table 3). The only groups of algae that did not correlate with \( A. \text{armata} \) were canopy-forming algae and filamentous algae (Table 3).
At the scale of locations, none of our predictor variables (temperature, latitude, longitude and sea urchin density, see Table 1) significantly correlated with the abundance of *A. armata* (Table 3).

**Discussion**

Characterization of spatial scales of variation is a preliminary step to the experimental testing of a hypothesis. It allows the identification of the appropriate scales of variation, ensuring that attention in focused on the most relevant processes (Underwood and Chapman 1996; Benedetti-Cecchi 2001; Martins et al. 2008). The present study shows that, in the Azores, the abundance of the invasive alga *A. armata* varies mostly at the scale of locations (i.e. km). This result suggests that processes operating at the km scale are potentially the main drivers of the distribution of this invasive alga, a pattern that is widely common among subtidal taxa (Fraschetti et al. 2005; Tuya and Haroun 2006; Martins et al. 2013). Unlike in the Azores (our study), Tuya and Haroun (2006), only found significant variation in the cover of *Asparagopsis* spp. at the scale of sites in the Canaries. It should be noted, however, that these authors collapsed the two congeneric species (*A. armata* and *A. taxiformis*) into a single group for analysis, and so comparability between studies is not straightforward.

Despite the observed significant variation in the distribution of *A. armata* among locations, none of our studied variables significantly correlated with its abundance at this spatial scale. Therefore, variations in sea temperature among locations, factors associated with changes in latitude and longitude, as well as variation in the abundance of grazers (sea urchins) among locations are unlikely to explain the observed variability in the cover of *A. armata*. Although not directly measured in this study, changes in exposure to wave action among locations, are also unlikely to explain the observed variation in the abundance of *A. armata* (Tuya and Haroun 2006; Martins et al. 2013). The ability of this species, however, to disperse with water currents, either during its tetrasporophyte stage ("*Falkenbergia rufolanosa*") or gametophyte stage attached to floating objects, suggests that shoreline configuration and local currents may play an important role in determining its distribution at the location (km) scale (Archambault and Bourget 1999). However, the exact process which determines the distribution of *A. armata* in the Azores still requires further investigation.

Biological interactions (e.g. competition, predation) can also play an important role in determining the distribution of species (i.e. Connell 1961; Dayton 1971; Menge 1976; Steneck et al. 1991; Benedetti-Cecchi et al. 2001) and are often associated with distributional changes occurring at the smaller spatial scales of quadrats (but see also i.e. Ritchie et al. 2009; Wisz et al. 2013 for evidence of the role of biotic interactions in determining the distribution of species and assemblages at larger spatial scales). In agreement.
to this, we found a number of significant and interesting correlations between the abundance of A. armata and the remaining biota at the scale of quadrats.

First, we found a negative correlation between the abundance of A. armata and algal richness. This result is in agreement with the idea that more diverse communities should be less susceptible to invasion because of a more complete utilization of resources; a concept that is known as “biotic resistance” proposed by Elton (1958). Despite the intuitive nature of this concept, observational studies attempting to relate the frequency of invasion to community diversity are scale-dependent, showing variable, and even contrary results, with more diverse communities having more, not fewer, non-indigenous species (e.g., Lonsdale 1999), constituting the so-called “invasion paradox” (Fridley et al. 2007). Moreover, experimental approaches appear to suggest that species identities, particularly the identity of macroalgal functional groups, may be more important than richness in determining the ability of macroalgal communities to resist invasion (Arenas et al. 2006). It is thus unclear whether this pattern is evidence of biotic resistance or something else. Another potential explanation for the negative correlation between the abundance of A. armata and diversity is that the former may have a strong negative influence in the remaining macroalgal assemblage, in turn, leading to a lower diversity. This view is supported by the fact that the abundance of A. armata was negatively correlated with the abundance of most macroalgal morpho-functional groups (see Table 3). Such a result, where the abundance of invasive species is negatively correlated with the abundance of native taxa, is also supported by the study of Vaz-Pinto et al. (2014b). Again, future experimental exclusions of A. armata from invaded patches (such as those done to test the effects of other invaders; e.g. Piazzi and Ceccherelli 2006; Bulleri et al. 2010) must be carried out if we are to better understand the nature of this relationship.

Second, there was a negative correlation between the abundance of A. armata and A. taxiformis. Morphologically, the two congeneric species are very similar and they can easily be misidentified unless for the presence of harpoon-like hooks in A. armata (Andreakis et al. 2004). Even though the two species of Asparagopsis differ in their response to sea temperature (Ni Chualáin et al. 2004), the lower and upper critical limits of temperature of both species are unlikely to be met in the Azores (mean monthly SST ranging between 15–23 °C, Amorim et al. (2017). As such, the negative correlation between the two Asparagopsis spp. may be tentatively interpreted as evidence that they are competing, as already suggested by Tittley and Neto (2005). In fact, A. taxiformis was an uncommon component of the marine algal flora of the Azores (Tittley and Neto 2005), but it probably occurs nowadays across almost all Azorean Islands (Cardigos et al. 2006).
Although *A. armata* may have displaced *A. taxiformis* in the past (Tittley and Neto 2005), recent observations suggest otherwise (Tittley and Neto 2005; Cardigos et al. 2006). The nature of the relationship between the two *Asparagopsis* spp. in the Azores thus needs to be experimentally tested taking in consideration that there are different lineages of *A. taxiformis*, including a worldwide invasive lineage (Dijoux et al. 2014). Such study should also assess if competition between the two species varies with seasonal changes in temperature.

It should also be noted (and formerly investigated) that variation in species interactions, occurring at smaller spatial scales, may also influence patterns of distribution at larger spatial scales (i.e. locations) (Ritchie et al. 2009; Wisz et al. 2013). If *A. taxiformis* effectively competes with the invasive *A. armata*, as is suggested by the negative correlation found between the two (see results and also Zanolla et al. 2018), it is possible that variation in the abundance of *A. taxiformis* at the scale of locations ($F_{8,12} = 10.978$, $P < 0.001$) can also impact the cover of *A. armata* at this spatial scale. This could easily happen via space pre-emption since *A. taxiformis* recruits earlier than *A. armata* in the Azores (authors personal observation).

In summary, this is the first step to understanding the processes driving the distribution and the potential ecological consequences of the invasive alga *A. armata* in the Azores. We report that *A. armata* was found throughout the archipelago and showed a high variation in abundance at the scale of locations (km). Seawater temperature, latitude and longitude, urchin density were not found to influence *A. armata* abundance. A negative correlation was found, however, between *A. armata* and macroalgal species richness and certain functional groups at the quadrat scale. Future studies to better understand the nature of the relationship between *A. armata* and the macroalgal community should benefit from an experimental approach where the presence of *A. armata*, alone or in combination with other components of the assemblage, is manipulated. A more in-depth investigation of the dispersive tetrastorophyte stage (“Falkenbergia rufolanosa”) of the alga may also help explaining the spatial variability in the distribution of the gametophytic stage of the alga.

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References

Amorim P, Perán AD, Pham CK, Juliano M, Cardigos F, Tempera F, Morato T (2017) Overview of the ocean climatology and its variability in the Azores region of the North Atlantic including environmental characteristics at the seabed. *Frontiers in Marine Science* 4: 56, https://doi.org/10.3389/fmars.2017.00056

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46

Andreakis N, Procaccini G, Kooistra WHCF (2004) *Asparagopsis taxiformis* and *Asparagopsis armata* (Bonnemaisoniaceae, Rhodophyta): genetic and morphological identification of Mediterranean populations. *European Journal of Phycology* 39: 273–283, https://doi.org/10.1080/0967026400200136436

Andreakis N, Procaccini G, Maggs C, Kooistra WHCF (2007) Phylogeography of the invasive seaweed *Asparagopsis* (Bonnemaisoniaceae, Rhodophyta) reveals cryptic diversity. *Molecular Ecology* 16: 2285–2299, https://doi.org/10.1111/j.1365-294X.2007.03306.x

Archambault P, Bourget E (1999) Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. *Journal of Experimental Marine Biology and Ecology* 238: 161–184, https://doi.org/10.1016/S0022-0981(99)00146-4

Arenas F, Sánchez I, Hawkins SJ, Jenkins SR (2006) The invasibility of marine algal assemblages: Role of functional diversity and identity. *Ecology* 87: 2851–2861, https://doi.org/10.1890/0012-9658(2006)87[2851:tiomaa]2.0.co;2

Benedetti-Cecchi L (2001) Variability in the abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series* 215: 79–92, https://doi.org/10.3354/meps215079

Benedetti-Cecchi L, Bulleri F, Acunto S, Cinelli F (2001) Scales of variation in the effects of limpets on rocky shores in the northwest Mediterranean. *Marine Ecology Progress Series* 209: 131–141, https://doi.org/10.3354/meps209131

Bishop MJ, Underwood AJ, Archambault P (2002) Sewage and environmental impact on rocky shores: necessity of identifying relevant spatial scales. *Marine Ecology Progress Series* 236: 121–128, https://doi.org/10.3354/meps236121

Bouderesque CF, Verlaque M (2002) Biological pollution in the Mediterranean Sea: invasive versus introduced macrophytes. *Marine Pollution Bulletin* 44: 32–38, https://doi.org/10.1016/S0025-326X(01)00150-3

Bulleri F, Balata D, Bertocci I, Tamburello L, Benedetti-Cecchi L (2010) The seaweed *Caulerpa racemosa* on Mediterranean rocky reefs: from passenger to driver of ecological change. *Ecology* 91: 2205–2212, https://doi.org/10.1890/09-1857.1

Cardigos F, Tempera F, Ávila S, Gonçalves J, Colaço A, Santos RS (2006) Non-indigenous marine species of the Azores. *Helgoland Marine Research* 60: 160–169, https://doi.org/10.1007/s10152-006-0034-7

Chihara M (1961) Life cycle of the Bonnemaisoniaceous algae in Japan (1). *Science Reports of the Tokyo Kyoiku Daigaku* 10: 121–154

Chihara M (1962) Life cycle of the Bonnemaisoniaceous algae in Japan (2). *Science Reports of the Tokyo Kyoiku Daigaku* 11: 27–53

Clarke KR, Gorley RN (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth, 190 pp

Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351–389, https://doi.org/10.2307/1948498

Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover estimations: ‘objective’ is not always better. *Marine Ecology Progress Series* 96: 93–100, https://doi.org/10.3354/meps096093

Dijoux L, Viard F, Payri C (2014) The more we search, the more we find: discovery of a new lineage and a new species complex in the genus *Asparagopsis*. *PLoS ONE* 9: e103826, https://doi.org/10.1371/journal.pone.0103826

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London, 196 pp, https://doi.org/10.1007/978-1-4899-7214-9

Elton CS (1961) Life cycle of *Chthamalus stellatus*. *Comptes Rendus des Séances de l'Académie des Sciences, Paris* 1007: 2851–2861, https://doi.org/10.1016/S0022-0981(02)00142-9

Feldmann J (1942) Récherches sur les Bonnemaisoniacées et leur alternances de générations. *Annuelles des Sciences Naturelles Botanique* 11: 75–175

Fletcher DJ, Underwood AJ (2002) How to cope with negative estimates of components of variance in ecological field studies. *Journal of Experimental Marine Biology and Ecology* 273: 89–95, https://doi.org/10.1016/S0022-0981(02)00142-9
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Frascetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series* 296: 13–29, https://doi.org/10.3354/meps296013

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88: 3–17, https://doi.org/10.1890/0012-9658(2007)88[3:TRPRP]2.0.CO;2

Greff S, Zubia M, Payri C, Thomas OP, Perez T (2017) Chemogeography of the red macroalgae *Asparagopsis*: metabolomics, bioactivity, and relation to invasiveness. *Metabolomics* 13: 1–17, https://doi.org/10.1007/s11306-017-1169-z

Guerra-Garcia JM, Ros M, Izquierdo D, Soler-Hurtado MM (2012) The invasive *Asparagopsis armata* versus the native *Corallina elongata*: differences in associated peracarid assemblages. *Journal of Experimental Marine Biology and Ecology* 416: 121–128, https://doi.org/10.1016/j.jembe.2012.02.018

Hallegraeff GM, Bolch CJ (1992) Transport of diatom and dinoflagellate resting spores in ships’ ballast water: implications for plankton biogeography and aquaculture. *Journal of Plankton Research* 14: 1067–1084, https://doi.org/10.1093/plankt/14.8.1067

Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: An Annual Review* 21: 195–282

Holm S (1979) A simple sequential rejective multiple test procedure. *Scandinavian Journal of Statistics* 6: 65–70

Horridge GA (1951) Occurrence of *Asparagopsis armata* Harvey on the Scilly Isles. *Nature* 167: 732–733, https://doi.org/10.1038/167732c0

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions* 9: 391–423, https://doi.org/10.1080/19381038.2013.861577

Lonsdale WM (1999) Global patterns of plant invasions and the concept of plant invasibility. *Ecology* 80: 1522–1536, https://doi.org/10.1890/0012-9658(1999)80[1522:GPOPIA]2.0.CO;2

Ludwig M, Checo J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* 12: 405–437, https://doi.org/10.1146/annurev.es.12.110181.002201

Martins GM, Patarra RF, Álvaro NV, Prestes ACL, Neto AI (2013) Effects of coastal orientation and depth on the distribution of subtidal benthic assemblages. *Marine Ecology Progress Series* 45: 15–24, https://doi.org/10.3354/meps07247

Martins GM, Patarra RF, Álvaro NV, Prestes ACL, Neto AI (2013) Effects of coastal orientation and depth on the distribution of subtidal benthic assemblages. *Marine Ecology Progress Series* 45: 15–24, https://doi.org/10.3354/meps07247

Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* 46: 335–393, https://doi.org/10.1146/annurev.es.12.110181.002201

Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series* 296: 13–29, https://doi.org/10.3354/meps296013
Ritchie EG, Martin JK, Johnson CN, Fox BJ (2009) Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores. *Journal of Animal Ecology* 78: 724–731, https://doi.org/10.1111/j.1365-2656.2008.01520.x

Ruiz GM, Rawlings TK, Dobbs FC, Drake LA, Mullady T, Huq A (2000) Global spread of microorganisms by ships. *Nature* 408: 49–50, https://doi.org/10.1038/35040695

Sala E, Boudouresque CF (1997) The role of fishes in the organization of a Mediterranean sublittoral community. In: algal communities. *Journal of Experimental Marine Biology and Ecology* 212: 25–44, https://doi.org/10.1016/S0022-0981(96)002745-1

Silva L, Land EO, Luengo JLR (2008) Invasive terrestrial flora and fauna of Macaronesia: top 100 in Azores, Madeira and Canaries. Arena, Ponta Delgada, 546 pp

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Gailil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what’s what and the way forward. *Trends in Ecology and Evolution* 28: 58–66, https://doi.org/10.1016/j.tree.2012.07.013

South GR, Tittley I (1986) A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean. Huntsman Marine Laboratory and British Museum (Natural History). St. Andrews and London, 76 pp

Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476–498, https://doi.org/10.2307/3545860

Steneck RS, Hacker SD, Dethier MN (1991) Mechanisms of competitive dominance between crustose coralline algae: a herbivore-mediated competitive reversal. *Ecology* 72: 938–950, https://doi.org/10.2307/1940595

Tittley I, Neto AI (2005) Marine algal (seaweed) flora of the Azores: additions and amendments. *Botanica Marina* 48: 248–255, https://doi.org/10.1515/BOT.2005.030

Tuya F, Haroun RJ (2006) Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian archipelago: a multi-scaled approach. *Marine Ecology Progress Series* 311: 15–28, https://doi.org/10.3354/meps311015

Underwood AJ (1993) The mechanisms of spatially replicated sampling programmes to detect environmental impact in a variable world. *Australian Journal of Ecology* 18: 99–116, https://doi.org/10.1111/j.1442-9993.1993.tb00437.x

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, 504 pp

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107: 212–224, https://doi.org/10.1007/BF00327905

Vaz-Pinto F, Rodil IF, Mineur F, Olabarria C, Arenas F (2014a) Understanding biological invasions by seaweeds. In: Pereira L, Neto JM (eds), Marine algae: biodiversity, taxonomy, environmental assessment and biotechnology. CRC Press, Boca Raton, pp 140–177, https://doi.org/10.1201/b17540-5

Vaz-Pinto F, Torrentegi O, Prestes ACL, Álvaro NV, Neto AI, Martins GM (2014b) Invasion success and development of benthic assemblages: Effect of timing, duration of submersion and substrate type. *Marine Environmental Research* 94: 72–79, https://doi.org/10.1016/j.marenvres.2013.12.007

Williamson M (2006) Explaining and predicting the success of invading species at different stages of invasion. *Biological Invasions* 8: 1561–1568, https://doi.org/10.1007/s10530-005-5849-7

Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Dambgaard CF, Dormann CF, Forchhammer MC, Grytnes JA, Guisan A, Heikkinen RK, Høye TT, Kühn I, Luoto M, Maiorano L, Nilsson MC, Normand S, Öckinger E, Schmidt NM, Termansen M, Timmermann A, Wardle DA, Aastrup P, Svenning JC (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15–30, https://doi.org/10.1111/j.1469-185X.2012.00235.x

Zanolla M, Altamirano M, Niell F, Carmona R (2018) There is more than meets the eye: primary production of the invasive seaweed *Asparagopsis taxiformis* (Bonnemaisoniaceae, Rhodophyta) is provided by six cohorts with distinctive characteristics. *Aquatic Botany* 153: 24–28, https://doi.org/10.1016/j.aquabot.2018.11.007