

# 1 Macroalgae niche modelling: A two-step approach 2 using remote sensing and *in situ* observations of a 3 native and an invasive *Asparagopsis*

4 Enrique Casas<sup>1</sup> | Marc Fernandez<sup>2,3,4</sup> | Artur Gil<sup>3,5</sup> | Chris Yesson<sup>6</sup> | Afonso Prestes<sup>2,3</sup> | Ignacio  
5 Moreu-Badia<sup>2,3</sup> | Ana Neto<sup>2,3</sup> | Manuel Arbelo<sup>1</sup>

6 <sup>1</sup> Departamento de Física, Universidad de la Laguna, 38200 San Cristóbal de La Laguna, Spain

7 <sup>2</sup> Faculty of Sciences and Technology, Department of Biology, University of the Azores, Ponta Delgada,  
8 Portugal

9 <sup>3</sup> cE3c – Centre for Ecology, Evolution and Environmental Changes & Azorean Biodiversity Group,  
10 University of the Azores, Ponta Delgada, Portugal

11 <sup>4</sup> MARE - Marine and Environmental Sciences Centre, Agência Regional para o Desenvolvimento da  
12 Investigação Tecnologia e Inovação (ARDITI), Funchal, Madeira, Portugal.

13 <sup>5</sup> IVAR – Research Institute in Volcanology and Risk Assessment, University of the Azores, Ponta  
14 Delgada, Portugal

15 <sup>6</sup> Zoological Society of London, Institute of Zoology, London, UK

## 16 Correspondence:

17 Enrique Casas, Grupo de Observación de la Tierra y la Atmósfera, Universidad de la Laguna, S/C de  
18 Tenerife, Spain.

19 Email: [ecasasma@ull.edu.es](mailto:ecasasma@ull.edu.es)

20 ORCID: 0000-0002-6055-692X

21 **Abstract:** We are facing a global loss of biodiversity due to climate change. This will lead to  
22 unpredictable changes in ecosystems, affecting the goods and services they provide and  
23 facilitating the introduction of non-indigenous marine species. This represents one of the major  
24 threats to marine biodiversity and therefore, there is a strong need to assess, map and monitor  
25 these alien species. The appearance of non-indigenous species is especially dangerous in fragile  
26 ecosystems, and it is of great importance to better understand the invasion mechanisms of these  
27 invasive species. This is the case for invasive alga *Asparagopsis armata*, present in the Azores  
28 Archipelago. In this study, we propose a methodology to define the realized ecological niche of  
29 this invasive alga, alongside the native *Asparagopsis taxiformis*, to understand better its  
30 distribution and potential impact on native communities and ecosystem services. These  
31 objectives comply with the EU Biodiversity strategy for 2020 goals and the need to map and  
32 assess ecosystems and their services. The lack of reliable high-resolution data makes this a  
33 challenging task. Within this scope, we propose a combination of Remote Sensing, Unmanned  
34 Aerial Vehicle based imagery together with in-situ field data to build ecological niche modelling  
35 approaches as a cost-effective methodology to identify and characterize vulnerable marine  
36 ecosystems. Our results show that this combination can help achieve monitoring, leading to a  
37 better understanding of ecological niches and the consequences of non-indigenous species  
38 invasion in fragile ecosystems, like small islands, when faced with limited data.

39 **Keywords:** *Asparagopsis armata*; *Asparagopsis taxiformis*; Ecological Niche Modelling; Remote  
40 Sensing; Unmanned Aerial Vehicle

41

42

43

44

## 45 1. INTRODUCTION

46 The global decline in marine biodiversity coupled with the rapidly changing climate leads  
47 to shifts in marine organisms' distributions (Poloczanska et al., 2013; Sunday et al., 2012). This  
48 may lead to unpredictable changes in the provision of associated ecosystem services, with  
49 potentially severe impacts on society and the economy, such as reducing fisheries or loss of  
50 recreational opportunities (Beaumont et al. 2008) and the apparition of non-indigenous-marine-  
51 species (NIMS). Macroalgae are amongst the most invasive NIMS (Schaffelke et al. 2006). They  
52 are considered one of the greatest threats to native marine biodiversity and the ocean's resource  
53 value (Marine and Diuersity, 1994; M. Vitousek et al., 1997).

54 The NE Atlantic is a hot spot of ocean warming, with temperature increases measured  
55 between 0.3° and 0.8° C per decade (MCCIP, 2010). The Azores Archipelago, located in this region,  
56 composes nine volcanic islands along with many islets, positioned in three main groups on the  
57 mid-Atlantic ridge (França et al. 2003). The geologically recent formation of the islands, coupled  
58 with its isolated location make the marine and coastal environment of the Azorean Archipelago  
59 of high interest, particularly given its biodiversity-rich coastal ecosystems (Santos et al., 1995).  
60 However, small islands are known to be vulnerable to climate change (Veron et al. 2019), and the  
61 threat of alien species invasion for small islands is well documented (Tompkins and Webb, 2017;  
62 IPCC, 1995).

63 This is the case of the invasive *Asparagopsis armata*. *A. armata* was introduced to the Azores  
64 in the early 20th century in the Atlantic and Mediterranean. It is widely distributed in the eastern  
65 North Atlantic Ocean, including Canaries and Macaronesia (Dijoux et al. 2014), where it is also  
66 considered invasive (Martins et al. 2019). It shows a tropical-to warm-temperate distribution,  
67 presenting biomass peaks in spring and summer (Andreakis et al. 2004).

68 NIMS have been linked to the reduction of ES provision, which is often termed Ecosystem  
69 Disservices (EDS), functions or properties of ecosystems that cause effects that are perceived as  
70 harmful, unpleasant or unwanted (Von Döhren and Haase 2015). The relation between the NIM  
71 *A. armata* and its related ES and EDS has only been recently studied, but it is known to affect  
72 natural ecosystem functioning and to provide EDS (Katsanevakis et al. 2014). One disservice could  
73 be the potential impact on other native seaweeds, such *Asparagopsis taxiformis*. *A. taxiformis* is  
74 considered a cosmopolitan species in warm-temperate to tropical waters (Ní Chualáin et al. 2004).  
75 However, distinct geographical lineages indicate regional differentiation within this species (Ní  
76 Chualáin et al., 2004; Andreakis et al., 2004).

77 There is a strong need to monitor native and invasive seaweed distribution, but this can be  
78 time-consuming, resource intensive, and often limited to small areas (Werdell and Roesler 2003).  
79 Moreover, in NE Atlantic, we can find a lack of regional-scale distribution data resulting in a  
80 more challenging detection of ecological impacts over local communities (Smale et al., 2013;  
81 Rodrigues, 2015). Knowledge of the socio-economic effects of invasive seaweed is poor, and  
82 economic impacts derived from seaweed invasion are mainly based on mitigation costs, rather  
83 than long term socio-economic impacts (Schaffelke and Hewitt 2007).

84 Methods such as remote sensing (RS) could be the answer to achieve cost-effective  
85 methodologies to map and monitor seaweed distribution at regional and global scales (Green et  
86 al., 1996; Topouzelis et al., 2018; Wabnitz et al., 2008; Traganos and Reinartz, 2017). RS has been  
87 used to map seaweeds (Dogan et al., 2013; Casal et al., 2013; Hoang et al., 2016), although studying  
88 heterogeneous coasts constitutes a much more difficult task because of the lack of suitable satellite  
89 imagery with adequate spectral and spatial resolutions (Brodie et al. 2018). Previous studies have  
90 attempted to map the coastline of São Miguel with low-cost Unmanned Aerial Vehicle (UAV)  
91 imagery, to obtain red-green-blue (RGB or "real colour") images with very high resolution  
92 (Kellaris et al. 2019).

93 An alternative approach to direct monitoring is the characterization of species' (realized)  
94 niches, which can help assess invasion capabilities of NIMS. Given a set of environmental  
95 variables known to directly influence a certain species physiology, the environmental

96 fundamental niche can be understood as the physiological responses of that species to those  
97 environmental variables, where its growth rate is identified as positive.

98 Assuming all environmental drivers are identified, we can predict geographic areas where  
99 the species of interest could establish and thrive, (assuming no significant competitive  
100 interactions (Clark et al. 2007), and no dispersal limitations (Barve et al. 2011)). Assessing a  
101 species' fundamental niche based on field observations is virtually impossible, but the realized  
102 niche can be retrieved with in-situ data. Realized niche can be described as the fundamental niche  
103 after a series of constraints are applied. These constraints can be identified as (i) the accessibility  
104 to geographic locations and (ii) the interactions between species (biotic interactions) in that area.  
105 Furthermore, the geographic scope of the study area can influence our interpretations if the full  
106 environmental range of the species is not seen in the area of study. However, the realized niche  
107 of a species, assessed for a certain geographic area with different accessibility characteristics and  
108 biotic interactions, can be used to determine the invasiveness capabilities for any NIMS in a given  
109 geographic area.

110 Our goal is to infer the realized ecological niche of the invasive red alga *Asparagopsis armata*,  
111 and its native co-generic species *Asparagopsis taxiformis* around São Miguel Island using presence  
112 records from all over Azores Archipelago. This will allow a better understanding of this species'  
113 potential geographic spread and its socio-economic consequences.

114 For this purpose, we use a combination of RS, UAV imagery and in-situ field data together  
115 with ecological niche modelling approaches to monitor and forecast the potential distribution of  
116 these important seaweeds. This will help to take the first step towards a deeper comprehension  
117 of the ES loss and ecosystem disservices related to NIMS establishment within local communities.

## 118 2. METHODS

### 119 2.1. STUDY AREA

120 The study area (Fig. 1) comprise Pico, Flores, Terceira and São Miguel islands within the  
121 Azores Archipelago. They are located in west (Flores) and the central Azores (Terceira and Pico),  
122 which are affected by the Gulf stream. São Miguel island belongs to the eastern region, where the  
123 Azores current has the most substantial influence over the whole archipelago. The Azores  
124 Archipelago is a confluence zone with notable influence over the oceanographic and biological  
125 characterization of the North Atlantic region (Caldeira and Reis 2017). It is considered a highly  
126 productive marine region with highly seasonal variations of nutrient cycles (Amorim et al. 2017).  
127 In concordance with global climate change patterns (Karl et al. 2000), temperature and  
128 precipitation levels in the Azores have been measurably on the rise (Santos et al. 2004).

129

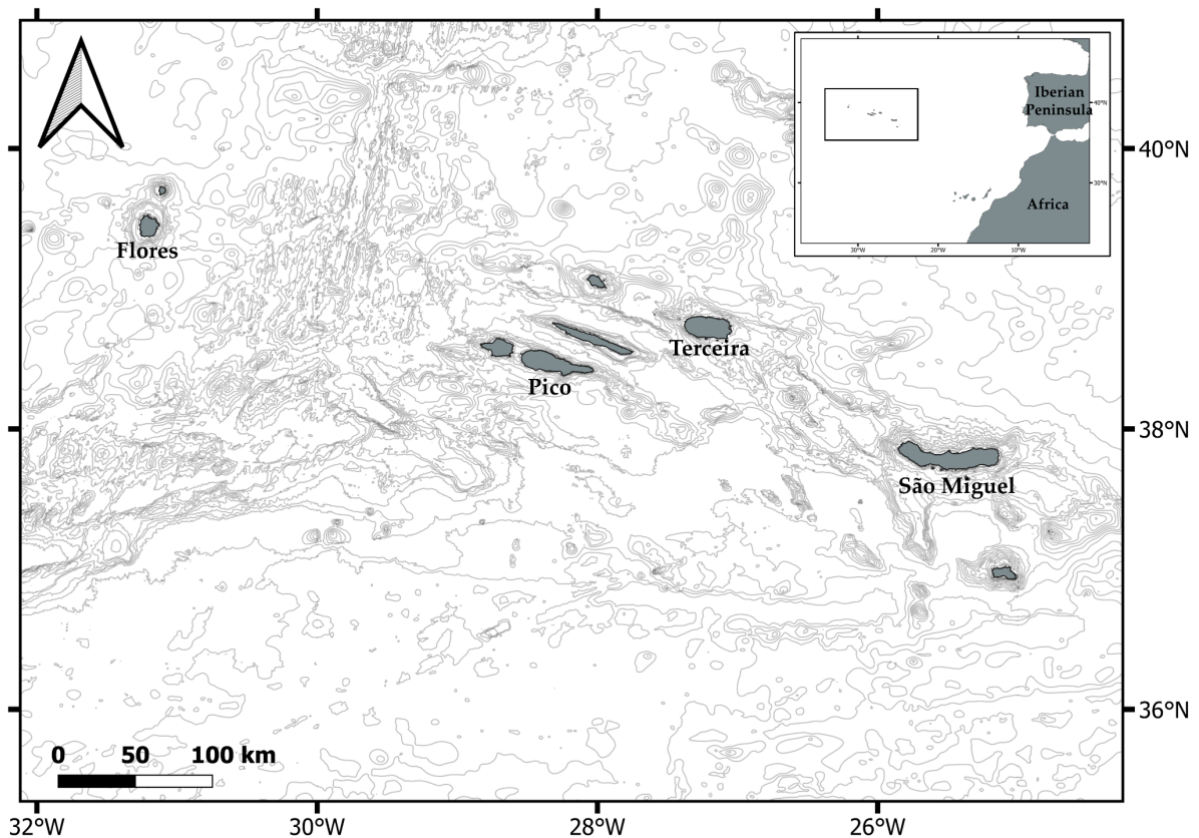


Fig. 1 Azores Archipelago.

## 2.2. ENVIRONMENTAL VARIABLES

Two sets of environmental variables were produced for this study, along with two different modelling approaches. An initial set of 6 environmental variables characterizing the abiotic conditions of São Miguel island were considered. These variables were derived from a DEM, taken from the EMODnet Bathymetry portal. We generated: Aspect, Depth, Fetch, Roughness, Slope and Topographic Position Index (TPI), restricted to a 3 km buffer from the shoreline. Aspect, roughness, slope and TPI were processed using *Aspect*, *Roughness*, *Slope* and *Topographic Position Index* Raster tools in *QGIS 3.4.1 Madeira*, at an output spatial resolution of 100m x 100m. Depth values were obtained directly from the DEM at a resolution of 100m x 100m. The Fetch (a measure of coastal exposure derived from spatial proximity to shorelines) was calculated using *R studio 1.1.463B* (Yesson et al. 2015).

The second set of environmental variables used in a presence/absence approach contained photoperiod, depth and temperature values. Depth and temperature values were obtained via in situ measures recorded with a *MARES Mission Puck 3* dive computer by scuba divers in 2016, 2017 and 2018 in Pico, Terceira, Flores and São Miguel islands. Photoperiod values corresponding to these survey's day were calculated using the *daylength* function in the *geosphere* R package (Forsythe et al. 1995). Table 2 shows both sets of variables.

We undertook a Variance Inflation Factor (VIF) analysis to test for spatial correlation of the environmental variables, to set aside those predictors spatially correlated. We ran the analysis using the VIF function implemented in the R *sdm* package (Naimi et al. 2014). This analysis showed that roughness and TPI were highly correlated (with VIF values greater than 10), so TPI was removed from subsequent analysis.

Table 2 Environmental variables			
Variables	Source	Spatial resolution	Model
Aspect (°)	Processed from EMODnet Digital Elevation Model with <i>Aspect</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100m x 100m	Presence/Background
Depth_1 (m)	Extracted directly from Digital Elevation Model available in EMODnet Bathymetry portal Digital Elevation Model ( <a href="http://emodnet-bathymetry.edu">http://emodnet-bathymetry.edu</a> )	100m x 100m	Presence/Background
Fetch (m)	Calculated using <i>R studio 1.1.463</i> as implemented in (Yesson et al. 2015)	100m x 100m	Presence/Background
Roughness (m)	Processed from EMODnet Digital Elevation Model with <i>Roughness</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100m x 100m	Presence/Background
Slope (°)	Processed from EMODnet Digital Elevation Model with <i>Slope</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100m x 100m	Presence/Background
TPI (m)	Processed from EMODnet Digital Elevation Model with <i>Topographic Position Index</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100m x 100m	Presence/Background
Depth_2 (m)	In situ measures	N/A	Presence/Absence
Temperature (°C)	In situ measures	N/A	Presence/Absence
Photoperiod (hours)	Calculated using <i>daylength</i> function in <i>geosphere</i> R package (Forsythe et al. 1995)	N/A	Presence/Absence

### 157 2.3. SPECIES OCCURRENCE DATA

158 Distribution models are based on statistical approaches that study the linkage of occurrence  
 159 data and environmental variables (Marcelino and Verbruggen 2015).

160 Occurrence data can be considered as georeferenced locations where the species have been  
 161 found, while absence data are georeferenced points where the species has been surveyed and not  
 162 found. Absence data are rarely available (Loiselle et al. 2003) but pseudo-absence or background  
 163 data can be used as an alternative (Marcelino and Verbruggen 2015). Due to the characteristics of  
 164 the data acquisition, while undertaking Ecological Niche Modelling (ENM) for invasive species,  
 165 it is a common procedure to use only presence data (Marcelino and Verbruggen 2015). For our  
 166 modeling approaches, we constructed two different occurrence datasets. (i) Presence-only data  
 167 derived from remote sensing imagery classification to run Presence/background models with our  
 168 first set of environmental variables to be used with MAXENT and (ii) Presence/absence dataset  
 169 obtained from a sampling survey in 2016, 2017 and 2018 in 4 islands of Azores Archipelago. A  
 170 series of spots were revisited during those years to assess the presence of the species and the  
 171 abiotic conditions (Table 2). This dataset was used to run the generalized linear models (GLM)  
 172 detailed below.

173

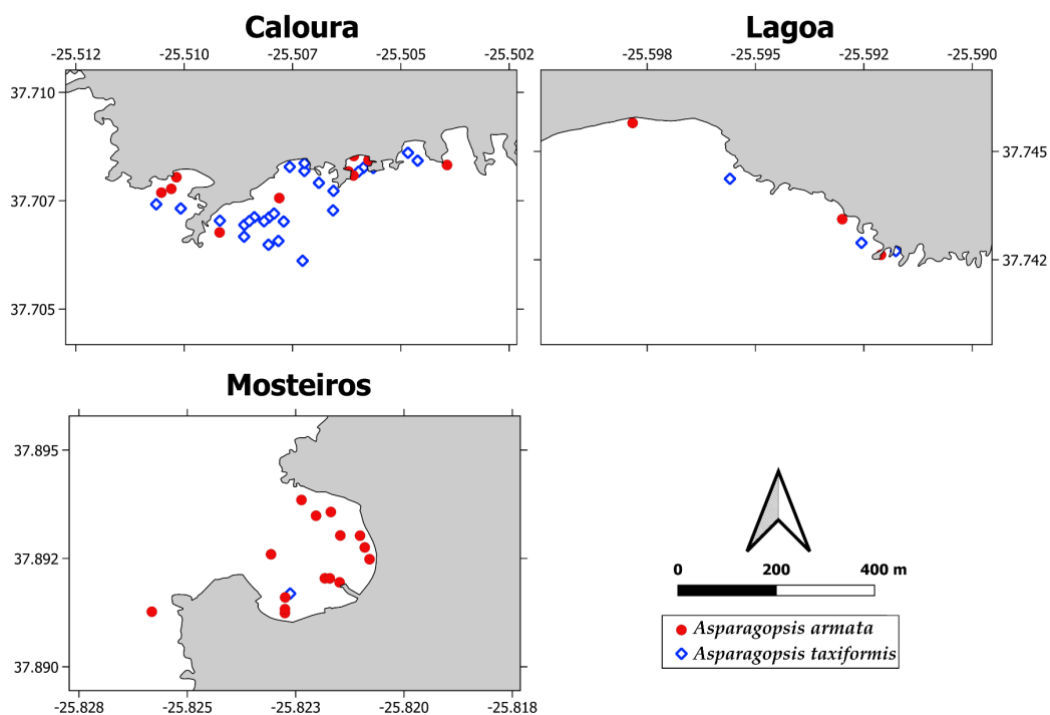
174

### 175 2.3.1. Remote sensing derived presence data

176 Occurrence data was supplemented by data inferred from a UAV survey (Kellaris et al.  
 177 2019). Images were taken with an unmanned aerial vehicle (UAV) in three São Miguel island  
 178 regions, using a DJI Phantom 3 Professional quadcopter drone that carries a visible light camera.  
 179 The survey was carried out at low tide, considering optimal conditions (low cloud coverage and  
 180 low wave speed) at 114m altitude, achieving a spatial resolution of  $4.93 \text{ cm}^* \text{ pixel}^{-1}$ . Surveys were  
 181 carried out in May and June 2018, in Caloura, Mosteiros and Lagoa coasts (Fig. 2), along with  
 182 ground-truth surveys by kayak and scuba divers to test the image classification. Support Vector  
 183 Machine (SVM) image classification was used as our source of occurrence data. The DroneDeploy  
 184 software (DroneDeploy, San Francisco, CA, USA) was used to design the flight plan with image  
 185 overlaps set to 85% frontlap, 80% sidelap and Pix4Dmapper (Pix4D SA, Lausanne, Switzerland)  
 186 was used to construct photomosaics.

187 This classification presented an accuracy of 0.998 with a standard deviation of  $6.42e^{-4}$  in  
 188 Kappa statistics (Kellaris et al. 2019). We used the *Point Sampling Tool* plugin in *QGIS 3.4.1* to  
 189 extract presence sites from these classified UAV images. First, we constructed a 100m x 100m  
 190 square rectangle grid and the UAV survey areas with *Create Grid* tool and then used *Centroids*  
 191 to obtain a point grid consisting of those squares' centroids. With these centroids, we extracted the  
 192 UAV classification output to obtain presence and absence of the target algae. We selected 100m x  
 193 100m resolution for our sample point grid to match the spatial resolution of our environmental  
 194 variables and our presence records.

195 A random subset selection of presence points for *A. armata* and *A. taxiformis* using the *Subset*  
 196 *Features* geostatistical Analysis tool in *ArcGIS 10.4*, to avoid spatial correlation between presence  
 197 records. This resulted in 29 and 30 presence records for *A. armata* and *A. taxiformis*, respectively  
 198 (Fig. 2).



199

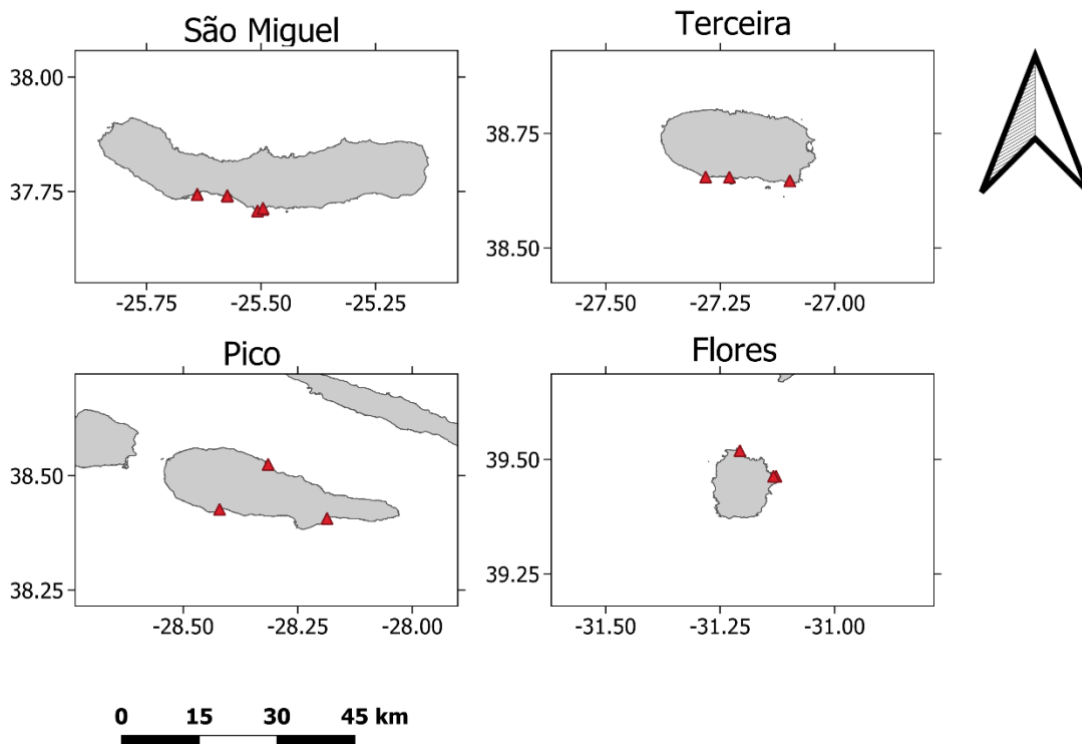
200 **Fig. 2** Presence data derived from UAV classification images in Caloura, Lagoa and Mosteiros  
 201 bays (São Miguel island).

202

203

## 204 2.3.2. Survey sampling data

205 Four islands (from 65 to 513 km apart) were selected among the three island groups (eastern,  
 206 central, and western) of the archipelago, chosen to be representative of the three groups and span  
 207 the entire length of the archipelago. Sampling surveys were carried out in 2016, 2017 and 2018  
 208 (Fig. 3). Within each island, 3 sites were randomly selected, with no prior identification of the  
 209 algae's presence, with surveys conducted depths of 5-, 10- and 15-meters depth. Within each site,  
 210 three 50 × 50 cm quadrats were placed on the seabed and visually sampled by scuba divers using  
 211 the method of Dethier et al. (1993), recording depth and temperature values with a MARES  
 212 *Mission Puck 3* dive computer.



213

214 **Fig. 3** Sampling sites (red triangles) in different islands of the Azores Archipelago during 2016,  
 215 2017 and 2018.

216 Each location was surveyed repeatedly for a total of 73 different sampling days over three  
 217 years. Quadrant position was randomly chosen in each survey and by the end of the process, 1265  
 218 observations were recorded. The species presence/absence data set consisted of 70 records in  
 219 2016, 955 records in 2017 and 240 records in 2018 (Table 3). This set of presence data was  
 220 constructed considering photoperiod and sampling sites' values along with sampled temperature  
 221 and depth (categorized as deeper or shallower than 10 m) and used to run three different kinds  
 222 of presence/absence models.

223

224

225

226

227

228

229

230

**Table 3** Presence records per surveyed year

	2016	2017	2018
<b>January</b>	0	60	0
<b>February</b>	0	60	0
<b>March</b>	0	60	0
<b>April</b>	0	60	0
<b>May</b>	0	160	60
<b>June</b>	0	315	60
<b>July</b>	0	60	60
<b>August</b>	0	60	60
<b>September</b>	0	60	0
<b>October</b>	0	50	0
<b>November</b>	60	10	0
<b>December</b>	10	0	0

231

232 **2.4. ECOLOGICAL NICHE MODELLING APPROACHES**

233 Species distribution models (SDMs) are widely used in ecology and conservation with a vast  
 234 variety of methodologies and approaches (Elith et al. 2006). An SDM algorithm is a mathematical  
 235 expression that can be used to estimate species distribution using environmental predictor  
 236 variables. Among the most commonly used methods, we can find regression algorithms that  
 237 make use of absence and presence data, such as: Generalized linear models (GLM), Generalized  
 238 additive models (GAM), multivariate adaptative regression splines and boosted regression trees;  
 239 or algorithms that only use presence data together with background data such as SVMs (Drake  
 240 et al. 2006) and MAXENT (Kearney et al. 2008).

241 In this context, we propose a two-step approach to characterize the species ecological niche.  
 242 A “geographic approach” focuses on how species distribution is affected by topographical  
 243 variables and an “environmental approach” to understand the species’ temporal dynamics.

244 On the one hand, in-situ observations provide a robust dataset of the species’ presence and  
 245 absence over time, with extensive temporal coverage but limited geographic extent. This  
 246 continuous monitoring of the species allowed us to study how changes in dynamic variables,  
 247 such as SST or photoperiod, affect species distribution, although providing little information  
 248 regarding the species’ response to different abiotic environmental characteristics. On the other  
 249 hand, a remote sensing-based dataset lacks temporal coverage, but its geographic extent, with  
 250 surveys in three different bays of the island, allows us to characterize how species distribution is  
 251 affected by terrain variables changes.

252

253 **Presence/background approach**

254 First, to characterize the algae distribution response, we worked with MAXENT, using the  
 255 first set of 6 topographic variables with presence data derived solely from remote sensing. These  
 256 variables were used to assess the response of *A. armata* and *A. Asparagopsis* to different  
 257 topographic characteristics. Environmental variables were not used for this model as their spatial  
 258 resolution was too coarse in comparison to the topographic data. As presence records were  
 259 retrieved from three different coasts limited to São Miguel island, the extent for model validation  
 260 was limited to this island as well. This analysis will provide estimates of the species’ topographic  
 261 preferences, to be then used along with results of presence/absence models.

262 MAXENT has been broadly used to model species distribution. It is based on a maximum  
 263 entropy approach, predicting the species occurrence by minimizing the estimated relative  
 264 entropy from presence data only (Phillips et al. 2006) which has been shown to perform well with  
 265 limited datasets. Samples With Data (SWD) tables were constructed using the *Point Sampling Tool*



266 plugin in *QGIS 3.4.1 Madeira*, extracting environmental variables corresponding to each presence  
 267 record. Localities where the algae were not present in the UAV classification maps were selected  
 268 as background (or pseudo absence) data. The KUENM package (Cobos et al. 2019) with R studio  
 269 1.1.463 was used to undertake an automated calibration process using MAXENT software  
 270 creating a certain number of candidate models, taking into consideration all possible  
 271 combinations of setting parameters. A single set of variables was used, comprising all six  
 272 topographic variables, Beta multiplier range values were selected from 0.1 to 9.7 (with increasing  
 273 steps of 0.4) and all possible combinations of setting parameters were used in the automated  
 274 process. Then, partial ROC, omission rates and Akaike's Information Criterion (AIC) were  
 275 assessed to find statistically significant models (Cobos et al. 2019).

276

### 277 **Presence/absence approach**

278 Secondly, we undertook a species habitat suitability characterization using the  
 279 presence/absence dataset to study how these species' distributions responds to dynamic  
 280 environmental variables. Before final model selection, GAM, RF and GLM algorithms were  
 281 constructed, and performances compared, based on this initial assessment the GLM algorithm  
 282 was selected to undertake the presence/absence approach.

283 The extent considered for model validation should be set according to geographic areas  
 284 where the species had accessibility. In this particular case, a more limited extent was taken into  
 285 consideration (Barve et al. 2011)

286 The relatively recent arrival of *A. armata*, would point to a more limited extent being  
 287 considered, in keeping with its short term expansion capabilities (Barve et al. 2011). However,  
 288 resource availability limited the study area to 4 islands of the archipelago (Fig. 3)

289 To study the different responses to changes in temperature, photoperiod and depth, the sites  
 290 were revisited over three years to characterize the physiological response to annual variability of  
 291 those abiotic factors, along with potential preferences over any particular location.

292 Four variables were used to calibrate the models: (i) Temperature, (ii) Photoperiod, (iii)  
 293 Depth and (iv) Sampling site. Recorded temperatures reached minimum levels of 15 and 23° C  
 294 for the 3-year period, with photoperiod values ranging between 9.53 and 14.76 hours and  
 295 registered depths of 5, 10 and 15 meters, then classified in two classes (<10 m and >10 m).

296

## 297 **2.5. MODEL EVALUATION**

298 Both models' performance was evaluated using Area Under the Curve (AUC) values and by  
 299 assessing how predictors contribute to explain and determine the species distribution.  
 300 For the MAXENT model (Presence/background), variable contributions were calculated using a  
 301 Jackknife approach implemented in *MAXENT 3.4.1* and 40 models were run using a 20%  
 302 bootstrap random subsample selection test.

303 After assessing and evaluating our models, two suitability maps were constructed  
 304 graphically explaining how *A. armata* and *A. taxiformis* geographic distribution is affected and  
 305 explained by topographic environmental variables, and spatial explicit species geographic  
 306 distribution maps were constructed. Then, species response to environmental variables was  
 307 characterized and species realized ecological niche was inferred with the combination of both  
 308 outputs.

309

310

## 311 **3. RESULTS**

312 Direct observations of *Asparagopsis armata* span 426 sites totalling 1265 observations. The  
 313 native *Asparagopsis taxiformis* was seen in 793 sites within the same 1265 observations (Fig. 3).

314 Presence/background data was also generated from classified drone imagery 29/30 presence  
315 records for *A. armata*/*A. taxiformis* respectively and 2355/2356 background records.

### 316 3.1. Presence/background approach

317 A total of 493 MAXENT models were generated for *A. armata* and *A. taxiformis* for parameter  
318 optimization. Model selection criteria were based on: (i) Partial Receiver Operating Characteristic  
319 (ROC), with values lower than 1 showing statistical significance, (ii) Omission rates, with values  
320 lower than 5% related to the best performance and (iii) Lowest delta AIC pointing to the single  
321 best model finding the best trade-off between data fitting and model complexity, avoiding both  
322 overfitting and underfitting (Peterson et al. 2008; Snipes and Taylor 2014; Cobos et al. 2019).  
323 Model parameters are presented in table 4.

324

	<i>A. armata</i>	<i>A. taxiformis</i>
<b>Beta Multiplier</b>	1.1	1.2
<b>Hinge features threshold</b>	0.45	0.5
<b>Beta threshold</b>	1.63	1.86
<b>L/Q/P* features</b>	1.4	1.5

\*Linear, quadratic and product features

325

326 Depth was the most crucial variable for the *A. taxiformis* model, followed by Roughness, and  
327 all other variables were excluded after Jackknife analysis. The species was associated with 5 and  
328 20 m of depth and low values of roughness, suggesting a preference for smoother bottoms. In  
329 contrast, for *A. armata*, Depth, and Fetch were the variables with a higher relative contribution to  
330 habitat prediction, with Depth the most important again (Table 5). For *A. armata*, we found  
331 response to depth similar to *A. taxiformis*, with preferences for shelter and shoreward areas (lower  
332 Fetch). The maximum preference appears to values closer to 100 m, dramatically decreasing when  
333 fetch reaches values greater than 10000 m. All other variables were discarded for modeling  
334 processes as they were negatively impacting model performance.

335

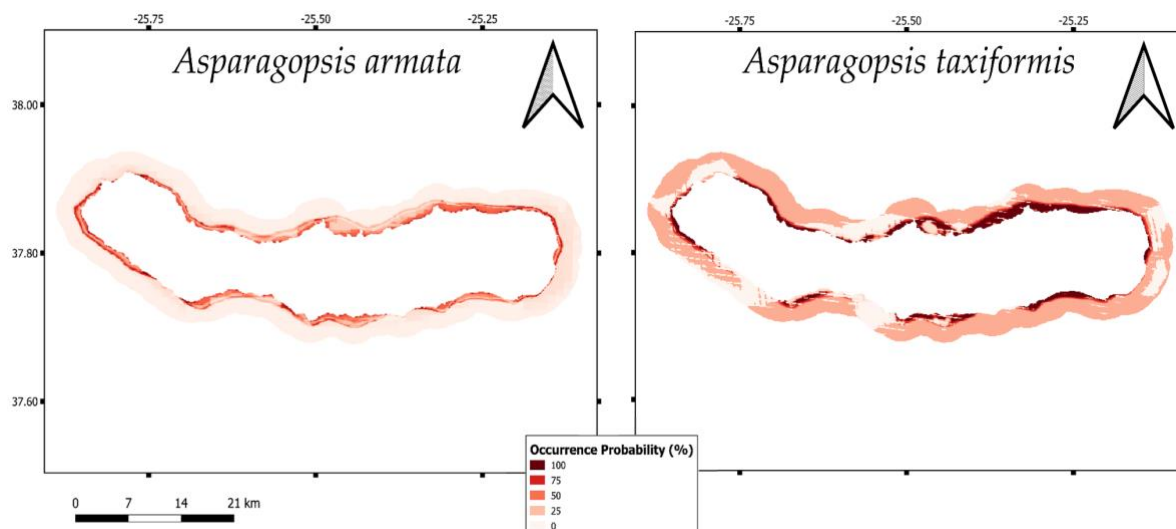
336

		Variable contribution (%)	Variable Permutation Importance (%)
<i>A. armata</i>	Depth	72.1	55.3
	Fetch	27.9	44.7
<i>A. taxiformis</i>	Depth	62.5	63.75
	Roughness	37.5	36.25

337

338 When optimal parameter settings were characterized, we run the MAXENT model 40 times.  
339 Both *A. taxiformis* and *A. armata* models had an excellent performance, with a mean AUC value  
340 of 0.806 and 0.823.

341 The model prediction estimates show a more homogeneous geographic distribution for *A.*  
342 *armata* without a clear preference in any region with lower habitat suitability values in São Miguel  
343 island. For *A. taxiformis*, we can observe higher suitability values over the north-northeast part of  
344 the Island (Fig. 4).



345

346

Fig. 4 MAXENT predicted potential geographic distribution in São Miguel island.

347

### 3.2. Presence/absence approach

348

349

350

351

352

353

354

355

Model performance for the presence/absence approach was relatively similar across all methods (Table 8). Simpler models should be preferred over complex ones (Guisan et al. 2002) therefore, based on models' similar performance and taking into consideration GLM more straightforward explanation and results in interpretation, we focus on the GLMs to present variable species response. Model evaluation was carried out with a cross-validation method implemented in the *Biomod* R package, with ten different runs.

Species	Model	Mean Value	Standard Deviation
<i>A. armata</i>	GAM	0.89	0.01
<i>A. armata</i>	GLM	0.88	0.02
<i>A. armata</i>	RF	0.91	0.02
<i>A. taxiformis</i>	GAM	0.74	0.02
<i>A. taxiformis</i>	GLM	0.74	0.02
<i>A. taxiformis</i>	RF	0.76	0.01

356

357

358

359

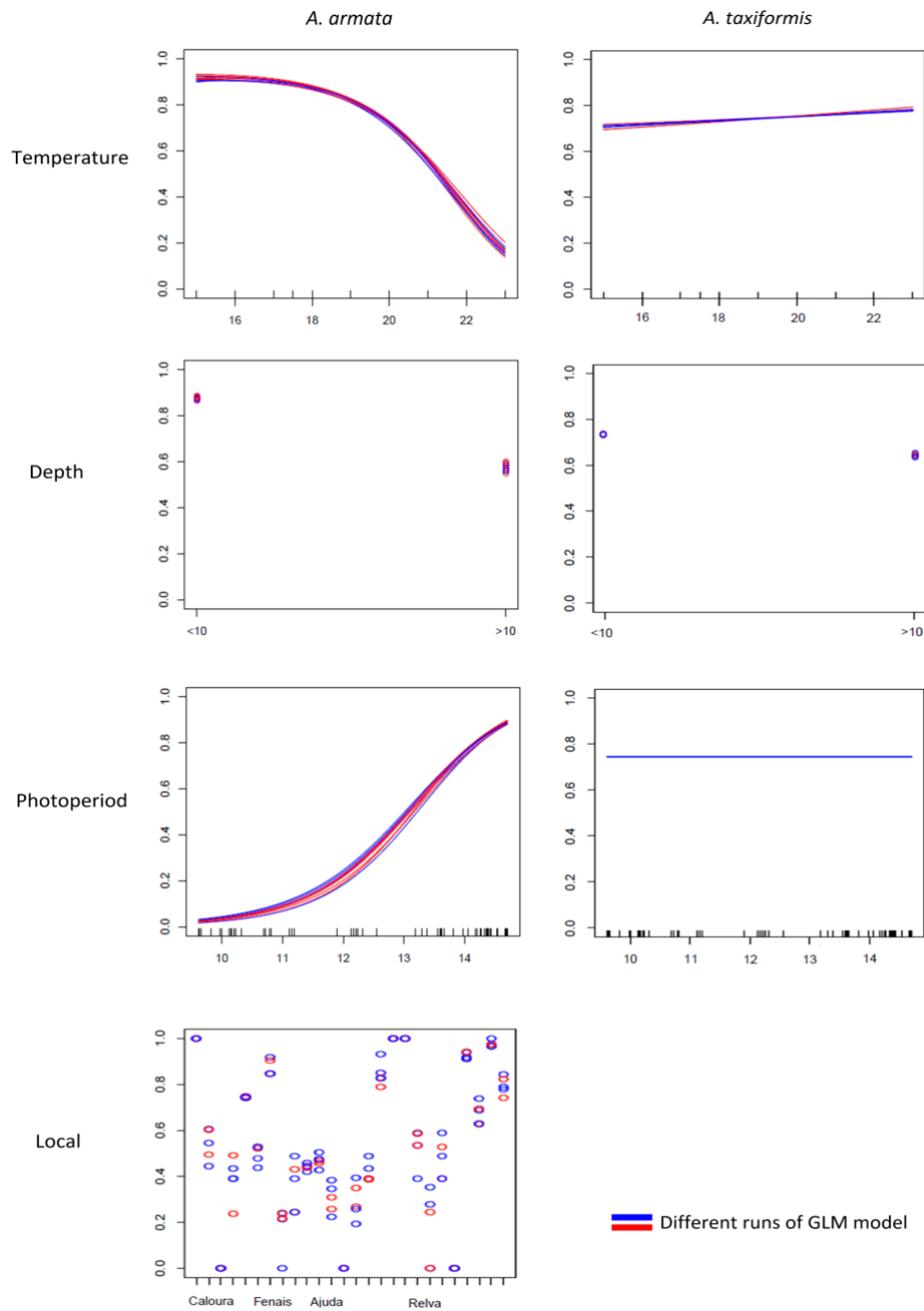
360

361

362

363

Photoperiod and temperature have the greatest influence on the *A. armata* model. At the same time, Depth barely affects the species response and sampling site, slightly affecting *A. taxiformis* distribution, has negligible influence over *A. armata* (Fig. 5 and Fig. 6). Maximum suitability is expected when medium-high values of photoperiod (starting at 13 hours per day) meet low to medium temperature values (around 15.5-18.5°C). High values of temperature are unsuitable for *A. armata*. The results are less clear for *A. taxiformis* (Fig. 5 and Fig. 6), which shows a relative weak response to photoperiod.

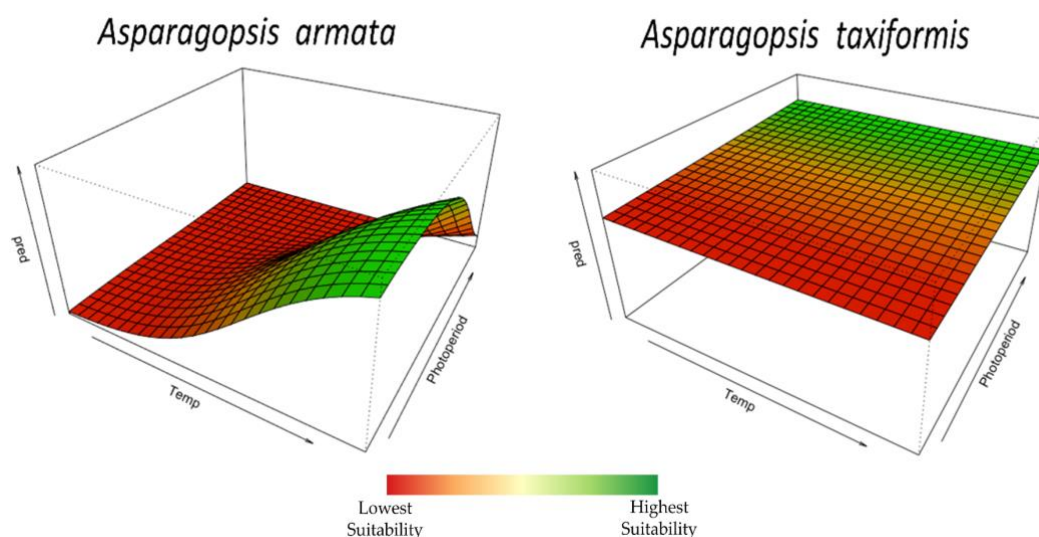


364

365

366

**Fig. 5** Species response to depth, photoperiod and temperature environmental predictors for 10 different runs for GLM model.



367  
368 **Fig. 6** *A. taxiformis* and *A. armata* response to photoperiod and temperature environmental predictors.

369

#### 370 4. DISCUSSION

371 In NE Atlantic, *Asparagopsis armata*'s known northern and southern distribution boundaries  
372 can be found in UK and Senegal, respectively. Along with this known geographic distribution,  
373 we can find optimal growth temperatures between 10 and 21°C, with lethal limits at 5 and 27°C  
374 (Mata et al. 2006). In the Azores Archipelago, these limits are very unlikely to be reached.  
375 Photoperiod values range from 9.5 to 14.76 hours, with the temperature reaching its minimum at  
376 15 °C with an annual maximum at 24°C. All possible fundamental abiotic environmental  
377 requirements for the species to be present are not met in the Azorean archipelago. As expected  
378 from mechanistic modeling approaches, the species' fundamental niche is extremely unlikely to  
379 be captured by a modeling effort based only on Azores distribution data.

380 On the contrary, our approach aimed to understand better and characterize the realized  
381 niche of the species within the archipelago. Aside from the abiotic environmental requirements  
382 present in any given geographic area, other particularities such as biotic interactions and species  
383 accessibility play an essential role when shaping the realized niche of a species. Such  
384 particularities are not explicitly captured by the model itself (Barve et al. 2011). However, the  
385 species' inferred realized niche identifies its suitability to the abiotic environmental variables  
386 available in a given geographic area.

387 For the specific set of variables considered in the model, *A. armata*'s distribution is best  
388 explained by two key variables: (i) Photoperiod and (ii) Temperature. The realized niche of the  
389 species, given the variables considered, can be found when specific values of photoperiod (13  
390 hours) meet temperatures between 15.5 and 18.5 °C.

391 Compared to its co-generic species, *A. armata*'s niche is much narrower than the *A.*  
392 *taxiformis*'. *A. taxiformis* is far less affected by changes in depth than *A. armata* and shows a  
393 generalist profile, in concordance with findings from the southern coast of Spain (Zanolla et al.  
394 2018), where they found different cohorts overlapping in time. *A. taxiformis* distribution cannot  
395 be explained with confidence by any of the environmental variables considered. However, there  
396 appears to be a geographic preference to locations such as Caloura beach. *A. armata*'s optimal  
397 temperatures and photoperiod values are expected to be met earlier in the year in latitudes closer  
398 to the equator, and later as we get farther north as Kraan and Barrington (2005) results show for  
399 the Irish coasts.

400 *A. armata*'s optimal environmental conditions in Azores Archipelago can be expected to be  
401 achieved in the early summer with explosive blooms when optimal conditions are met, and  
402 starting to decay after summer (Mata et al. 2006). Therefore, we could predict intense blooms  
403 when the water stays relatively cold in early-summer period (with high photoperiod values).  
404 When these criteria are met, we can expect suitable areas for *A. armata*'s gametophytic stage to  
405 overlap with *A. taxiformis*'. However, niche preferences of the two species are quite different to  
406 allow for a significant overlap. Nevertheless, other algal blooms may occur at various times over  
407 the year, not necessarily overlapping year on year, pointing out that photoperiod alone may not  
408 be a reliable predictor of blooms by itself (Martins et al. 2019).

409 *A. armata* does not show distribution preferences over any region of the São Miguel coast  
410 and this is something we might expect from a geographically wide-ranging invasive species. This  
411 feeds the narrative that *A. armata* shows opportunistic characteristics with explosive blooms  
412 when climatic conditions are met in late spring-early summer, growing all over the coast  
413 regardless of the environment's geographical characteristics. Conversely, *A. taxiformis* shows a  
414 specific preference over the north-northeast coast when analyzing its geographic distribution. *A.*  
415 *taxiformis* models are not very robust, and we may be lacking essential predictor variables. Other  
416 studies have shown the importance of variables such as primary productivity, surface salinity,  
417 nutrient concentrations, Chlorophyll-a, and pH for invasive seaweeds (Karl et al. 2000; Miller et  
418 al., 2019; Guerra-García et al., 2012). Variables such as SST or sea surface salinity are freely  
419 available from remote sensing datasets but at a much broader spatial resolution than the data  
420 used in this study. Spatial resolution strongly affects model predictive capabilities (Guisan et al.  
421 2007).

422 The relationship between the spatial resolution of species occurrence data and  
423 environmental variables is a crucial aspect for consideration. For instance, coarse resolution  
424 environmental variables may fail to identify the habitat where the species occurs, and changes in  
425 spatial resolution of environmental variables can alter our understanding of presence patterns  
426 (Guisan et al. 2007), especially when considering highly dynamic oceanographic processes.

427 On the contrary, when considering coarse-scale occurrence datasets, such as historical  
428 collections with inherent spatial uncertainties, the use of finer-scale environmental data is not  
429 advised (Graham et al. 2004).

430 Our case study worked with two datasets of two different natures, with presence records of  
431 high spatial resolution and low location uncertainties. The spatial resolution of our remote-  
432 sensing derived occurrences made this dataset unfit to be used with coarser freely available  
433 environmental variables (Guisan et al. 2007). However, it proved to be important when  
434 undertaking ecological modeling of invasive algae. Considering this limitation, along with its  
435 poor temporal resolution (our records being limited to a small window of time where abundance  
436 peaks were expected), we decided to model our species response to solely topographic variables,  
437 at a convenient native resolution of 100m x 100m. UAV imagery allowed us to get a wide  
438 "screenshot" where representative values of the species' topographic preferences could be easily  
439 and cost-effectively retrieved, compared to the logistic and human resources demanded for an  
440 extensive sampling field survey.

441 On the other hand, while lacking the capacity to assess topographic preferences, the in-situ  
442 dataset allowed us to determine species preferences for specific conditions of photoperiod and  
443 temperature, independent of the topographic characteristics, (which remained constant over the  
444 3 years of sampling). In contrast to the remote-sensing dataset, the in-situ dataset provide the  
445 temporal resolution needed to study dynamic variables. The in-situ dataset was unfit to be used  
446 with coarse resolution environmental data (Guisan et al. 2007) but convenient to characterize  
447 species response to abiotic dynamic factors.

448 Due to the limitations of environmental variable availability (outlined above), two different  
449 models were run in two separate steps of a sole modeling approach. Firstly, we assessed the  
450 species physiological response to dynamic variables, characterizing the realized niche related to

451 those abiotic factors, in an attempt to locate the time of potential peaks of abundance in the  
452 archipelago. In a second step, we sought to characterize species response to topographic  
453 variables, which is intrinsically linked to expected abundance peaks.

454 With the outputs of these two modeling steps, we inferred the realized niche of the species,  
455 identifying, on the one hand, the periods of the year where invasive *A. armata* could pose a real  
456 threat to native *A. taxiformis*. On the other hand, studying the species' topographic preferences  
457 where this peak of abundance is expected, providing spatially explicit assessments of its invasion  
458 mechanics. This spatially explicit information aims to be a convenient tool to better understand  
459 the species' invasiveness capabilities and anticipate the expected locations where explosive  
460 blooms may occur.

461 It is essential to consider that the presence/background model was constructed with  
462 observations from the South and West Coasts of São Miguel island, with no data in the North or  
463 East coast of São Miguel (due to weather constraints limiting survey sampling capabilities). This  
464 sampling procedure may have introduced a bias in the presence records. For this reason, the  
465 presence/background model was not projected to other islands of the archipelago (Stolar and  
466 Nielsen 2015).

467 Image classifications used in the present study indicated overfitting in the training data.  
468 Nevertheless, remote sensing-based occurrence data proved a convenient tool to predict potential  
469 geographic distribution, allowing us to infer species niche when working in parallel with *in*  
470 *situ* datasets.

471 While not explicitly captured in the model, the biotic interactions affecting species'  
472 establishment can be considered an intrinsic characteristic of any given geographic area. This  
473 local competition will ultimately affect a species' realized niche. This study aimed to assess the  
474 invasiveness trait of *A. taxiformis* in the Azores Archipelago by defining and studying its realized  
475 niche. Given the nature and the purpose of this modeling approach, caution is advised when  
476 considering extending these results to the whole species potential distribution (Malanson et al.  
477 1992).

478 While the two-step approach modeling with different datasets provided good results,  
479 demonstrating its potential application when facing data scarcity scenarios, other approaches  
480 might be helpful in the present study. For example, it could be interesting to broaden study areas,  
481 even attempting to undertake a complete UAV image classification of the whole island,  
482 considering different times of the year. This will permit construction of a species niche model  
483 based entirely on remote sensing-based data sets although depending on the time of the year this  
484 approach may not be feasible due to weather constraints (Kellaris et al. 2019). Nonetheless,  
485 although solely relying on UAV imagery may not be possible, it remains an excellent  
486 complementary tool.

487 Furthermore, once the realized niche of the invasive species is identified and possible  
488 locations for the species to appear anticipated, UAV imagery could represent a ready-to-use tool  
489 to reaffirm and validate the hypothetical locations more likely to be invaded, and so be used as  
490 an early alarm system.

491 As stated, our results may lack the capabilities to drive firm conclusions about the  
492 geographic distribution of the species outside the Azorean archipelago. For these purposes,  
493 historical presence datasets, with a much broader spatial resolution (and location uncertainties)  
494 could be used with other sets of freely available remote-sensing derived environmental variables  
495 to assess the potential distribution of these species in a wider geographic area, with coarser  
496 resolutions. This approach would allow us to get closer to the fundamental niche of the species.  
497 However, some problematic issues would need to be considered, such as the presence of potential  
498 different genetic lines of the species, that could be included in the same occurrence dataset. Other  
499 genetic lines of the species may represent different adaptations to various environments and  
500 hence, dissimilarities in niche characteristics. This issue may affect not only the model  
501 performance but the proper identification of its niche. Nonetheless, this approach would allow

502 us to compare the potential distribution of the species with the assessed realized niche in the  
503 Azores Archipelago, and help better understand the invasive capabilities of *A. armata*.

504 Eventually, as a consequence of ocean warming, optimal day lengths (photoperiod) will no  
505 longer match optimal temperatures for the species to thrive. Optimal photoperiod values will  
506 occur along with less suitable SST values (warmer sea surface). These conclusions are in  
507 concordance with the leading results in (Martínez et al. 2018), showing that rising values of Sea  
508 Surface Temperature (SST) are related to the ecological niche narrowing of temperate seaweeds,  
509 with solid distribution range contractions and shifts in distributions. While that may appear  
510 positive, as an invasive species may no longer find suitable habitat in the Azores with the  
511 consequent apparition of ecosystem disservices, it should be noted that many natives will suffer  
512 the same fate with severe socio-economic impacts. This is further evidence of the vital need to  
513 monitor not only invasive but native species in coastal ecosystems as a tool to inform  
514 policymakers and provide proof of socio-economic advantages derived from natural ecosystem  
515 protection and restoration.  
516

## 517 5. CONCLUSIONS

518 Further steps need then to be taken, and explicit spatial maps of both ES and EDS provided  
519 by *A. armata* and *A. taxiformis* should be produced as a critical tool for marine and coastal  
520 conservation, following the EU Biodiversity strategy for 2020. The Outermost Regions (ORs) of  
521 Europe, such as Azores Archipelago, are expected to undertake this MAES procedure, but a lack  
522 of reliable and high-resolution data usually makes this kind of assessment and valuation  
523 infeasible.

524 In this context, ecological niche modeling characterization represents one of the first steps of  
525 MAES in the region, helping to identify and characterize impacts and losses of ES related to  
526 Coastal ecosystems in remote and data-scarce scenarios. Future MAES procedures and spatially  
527 explicit ES assessments will strongly depend on ecological and socio-economic data, which in  
528 combination with ecological niche modeling methodologies will set a feasible scenario for MAES  
529 in the Macaronesian bioregion.

530 **Acknowledgements:** This study is a contribution to the research project 'ASPAZOR – Ecosystem impacts  
531 and socio-economic benefits of *Asparagopsis armata* in the Azores' (Ref. ACORES-01-1045-FEDER-00060)  
532 funded through FEDER (85%) and regional funds (15%) via 'Programa Operacional Açores 2020'. CY is  
533 supported by Research England

534  
535 **Author Contributions:** Using the initials of every co-author, as in: EC, MF, AG, CY, AP, IM, AN, MA.  
536 EC, MF, AG, CY and AN conceived the main research idea. MA contributed to the integration and  
537 development of the MAES approach into the main research idea. EC, MF, AG, IM and AP contributed to the  
538 production, collection and selection of field and modeling data. EC and MF developed the theory  
539 and performed the computations. EC, CY and MF verified the analytical methods.  
540 All authors discussed the results and contributed to the final manuscript.

541 **Conflicts of Interest:** The authors declare no conflict of interest. The funding sponsors had no role in the  
542 design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript,  
543 and in the decision to publish the results.  
544



545 **References**

- 546 Amorim P, Perán AD, Pham CK, et al (2017) Overview of the Ocean Climatology and Its  
547 Variability in the Azores Region of the North Atlantic Including Environmental  
548 Characteristics at the Seabed. *Front Mar Sci* 4:1–16.  
549 <https://doi.org/10.3389/fmars.2017.00056>
- 550 Andreakis N, Procaccini G, Kooistra WHCF (2004) *Asparagopsis taxiformis* and *Asparagopsis*  
551 *armata* (Bonnemaisoniales, Rhodophyta): Genetic and morphological identification of  
552 Mediterranean populations. *Eur J Phycol* 39:273–283.  
553 <https://doi.org/10.1080/0967026042000236436>
- 554 Barve N, Barve V, Jiménez-Valverde A, et al (2011) The crucial role of the accessible area in  
555 ecological niche modeling and species distribution modeling. *Ecol Modell* 222:1810–1819.  
556 <https://doi.org/10.1016/j.ecolmodel.2011.02.011>
- 557 Beaumont NJ, Austen MC, Mangi SC, Townsend M (2008) Economic valuation for the  
558 conservation of marine biodiversity. *Mar Pollut Bull* 56:386–396.  
559 <https://doi.org/10.1016/j.marpolbul.2007.11.013>
- 560 Brodie J, Ash L V., Tittley I, Yesson C (2018) A comparison of multispectral aerial and satellite  
561 imagery for mapping intertidal seaweed communities. *Aquat Conserv Mar Freshw*  
562 *Ecosyst* 28:872–881. <https://doi.org/10.1002/aqc.2905>
- 563 Caldeira RMA, Reis JC (2017) The Azores Confluence Zone. *Front Mar Sci* 4:1–14.  
564 <https://doi.org/10.3389/fmars.2017.00037>
- 565 Casal G, Kutser T, Domínguez-Gómez JA, et al (2013) Assessment of the hyperspectral sensor  
566 CASI-2 for macroalgal discrimination on the Ría de Vigo coast (NW Spain) using field  
567 spectroscopy and modelled spectral libraries. *Cont Shelf Res* 55:129–140.  
568 <https://doi.org/10.1016/j.csr.2013.01.010>
- 569 Clark JS, Dietze M, Chakraborty S, et al (2007) Resolving the biodiversity paradox. *Ecol Lett*  
570 10:647–659. <https://doi.org/10.1111/j.1461-0248.2007.01041.x>
- 571 Cobos ME, Peterson AT, Barve N, Osorio-Olvera L (2019) kuenm: an R package for detailed  
572 development of ecological niche models using Maxent. *PeerJ* 7:e6281.  
573 <https://doi.org/10.7717/peerj.6281>
- 574 Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover  
575 estimations: “objective” is not always better. 93–100
- 576 Dijoux L, Viard F, Payri C (2014) The more we search, the more we find: Discovery of a new  
577 lineage and a new species complex in the genus *Asparagopsis*. *PLoS One* 9:1–13.  
578 <https://doi.org/10.1371/journal.pone.0103826>
- 579 Dogan S, Regeer EJ, Mol EMM, Braam AW (2013) Gedwongen opname na medea-dreigement  
580 bij gesimuleerde psychose. *Tijdschr Psychiatr* 55:209–213.  
581 <https://doi.org/10.1007/s00338-003-0367-5>
- 582 Drake JM, Randin C, Guisan A (2006) Modelling ecological niches with support vector  
583 machines. *J Appl Ecol* 43:424–432. <https://doi.org/10.1111/j.1365-2664.2006.01141.x>

- 584 Elith J, H. Graham C, P. Anderson R, et al (2006) Novel methods improve prediction of species'  
585 distributions from occurrence data. *Ecography (Cop)* 29:129–151.  
586 <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- 587 França, Z., Cruz, J. V., Nunes, J. C., & Forjaz, V. H. (2005). *Geologia dos Açores: uma perspectiva*  
588 *actual. Açoreana* 10 (1); 11-140. Reedição PIC. VULCMAC. Interreg III B. Ponta Delgada  
589 (2005). ISBN: 972-97466-5-6. *Publicação*, (15)
- 590 Forsythe, W. C., Rykiel Jr, E. J., Stahl, R. S., Wu, H. I., & Schoolfield, R. M. (1995). A model  
591 comparison for daylength as a function of latitude and day of year. *Ecological Modelling*,  
592 80(1), 87-95 [https://doi.org/10.1016/0304-3800\(94\)00034-f](https://doi.org/10.1016/0304-3800(94)00034-f)
- 593 Graham CH, Ferrier S, Huettman F, et al (2004) New developments in museum-based  
594 informatics and applications in biodiversity analysis. *Trends Ecol Evol* 19:497–503.  
595 <https://doi.org/10.1016/j.tree.2004.07.006>
- 596 Green EP, Mumby PJ, Edwards AJ, Clark CD (1996) The cost-effectiveness of remote sensing for  
597 tropical coastal resources assessment and management. *Coast Manag* 24:1–40.  
598 <https://doi.org/10.1080/08920759609362279>
- 599 Guerra-García JM, Ros M, Izquierdo D, Soler-Hurtado MM (2012) The invasive *Asparagopsis*  
600 *armata* versus the native *Corallina elongata*: Differences in associated peracarid  
601 assemblages. *J Exp Mar Bio Ecol* 416–417:121–128.  
602 <https://doi.org/10.1016/j.jembe.2012.02.018>
- 603 Guisan A, Edwards Jr TC, Hastie T (2002) Generalized linear and generalized additive models in  
604 studies of species distributions: setting the scene. *Ecol Modell* 8:55–57.  
605 <https://doi.org/10.1111/j.1365-3040.1985.tb01209.x>
- 606 Guisan A, Graham CH, Elith J, et al (2007) Sensitivity of predictive species distribution models  
607 to change in grain size. *Divers Distrib* 13:332–340. [https://doi.org/10.1111/j.1472-](https://doi.org/10.1111/j.1472-4642.2007.00342.x)  
608 [4642.2007.00342.x](https://doi.org/10.1111/j.1472-4642.2007.00342.x)
- 609 Hoang, T. C., O'Leary, M. J., & Fotedar, R. K. (2016). Remote-sensed mapping of *Sargassum* spp.  
610 distribution around Rottnest Island, Western Australia, using high-spatial resolution  
611 WorldView-2 satellite data. *Journal of Coastal Research*, 32(6), 1310-1321  
612 <https://doi.org/10.2112/JCOASTRES-D-15-00077.1>
- 613 IPCC (1995) A report of the intergovernmental panel on climate change
- 614 Karl TR, Knight RW, Baker B (2000) Evidence for an increase in the rate of global warming?  
615 *Geophys Res Lett* 27:719–722
- 616 Katsanevakis S, Wallentinus I, Zenetos A, et al (2014) Impacts of invasive alien marine species  
617 on ecosystem services and biodiversity: A pan-European review. *Aquat Invasions* 9:391–  
618 423. <https://doi.org/10.3391/ai.2014.9.4.01>
- 619 Kearney M, Phillips BL, Tracy CR, et al (2008) Modelling species distributions without using  
620 species distributions: the cane toad in Australia under current and future climates. 423–  
621 434. <https://doi.org/10.1111/j.2008.0906-7590-05457.x>
- 622 Kellaris A, Gil A, Faria J, et al (2019) Using low-cost drones to monitor heterogeneous  
623 submerged seaweed habitats: A case study in the Azores. *Aquat Conserv Mar Freshw*

- 624 Ecosyst 1–14. <https://doi.org/10.1002/aqc.3189>
- 625 Kraan S, Barrington KA (2005) Commercial farming of *Asparagopsis armata* (  
626 *Bonnemaisoniaceae*, Rhodophyta) in Ireland, maintenance of an introduced species?  
627 103–110. <https://doi.org/10.1007/s10811-005-2799-5>
- 628 Loiselle BA, Howell CA, Graham CH, et al (2003) Avoiding pitfalls of using species distribution  
629 models in conservation planning. 17:1591–1600
- 630 M. Vitousek P, Mooney HA, Lubchenco J, Melillo JM (1997) Human Domination of Earth's  
631 Ecosystems. *Science* (80-) 277:494–499. <https://doi.org/10.1126/science.277.5325.494>
- 632 Malanson GP, Westman WE, Yan YL (1992) Realized versus fundamental niche functions in a  
633 model of chaparral response to climatic change. *Ecol Modell* 64:261–277.  
634 [https://doi.org/10.1016/0304-3800\(92\)90026-B](https://doi.org/10.1016/0304-3800(92)90026-B)
- 635 Marcelino VR, Verbruggen H (2015) Ecological niche models of invasive seaweeds. *J Phycol*  
636 51:606–620. <https://doi.org/10.1111/jpy.12322>
- 637 Marine G, Diuersity B (1994) Conserving biological diversity in the sea. 9:446–447
- 638 Martínez B, Radford B, Thomsen MS, et al (2018) Distribution models predict large  
639 contractions of habitat-forming seaweeds in response to ocean warming. *Divers Distrib*  
640 24:1350–1366. <https://doi.org/10.1111/ddi.12767>
- 641 Martins GM, Cacabelos E, Faria J, et al (2019) Patterns of distribution of the invasive alga  
642 *Asparagopsis armata* Harvey: a multi-scaled approach. *Aquat Invasions* 14:In press
- 643 Mata L, Silva J, Schuenhoff A, Santos R (2006) The effects of light and temperature on the  
644 photosynthesis of the *Asparagopsis armata* tetrasporophyte (*Falkenbergia rufolanosa*),  
645 cultivated in tanks. *Aquaculture* 252:12–19.  
646 <https://doi.org/10.1016/j.aquaculture.2005.11.045>
- 647 Miller DAW, Pacifici K, Sanderlin JS, Reich BJ (2019) The recent past and promising future for  
648 data integration methods to estimate species' distributions. *Methods Ecol Evol* 10:22–37.  
649 <https://doi.org/10.1111/2041-210X.13110>
- 650 Naimi B, Hamm NAS, Groen TA, et al (2014) Where is positional uncertainty a problem for  
651 species distribution modelling? *Ecography (Cop)* 37:191–203.  
652 <https://doi.org/10.1111/j.1600-0587.2013.00205.x>
- 653 Ní Chualáin F, Maggs CA, Saunders GW, Guiry MD (2004) The invasive genus *Asparagopsis*  
654 (*Bonnemaisoniaceae*, Rhodophyta): Molecular systematics, morphology, and  
655 ecophysiology of *Falkenbergia* isolates. *J Phycol* 40:1112–1126.  
656 <https://doi.org/10.1111/j.1529-8817.2004.03135.x>
- 657 Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis  
658 applications in ecological niche modeling. *Ecol Modell* 213:63–72.  
659 <https://doi.org/10.1016/j.ecolmodel.2007.11.008>
- 660 Phillips SB, Aneja VP, Kang D, Arya SP (2006) Maximum entropy modeling of species  
661 geographic distributions. *Int J Glob Environ Issues* 6:231–252.  
662 <https://doi.org/10.1016/j.ecolmodel.2005.03.026>

- 663 Poloczanska ES, Brown CJ, Sydeman WJ, et al (2013) Global imprint of climate change on  
664 marine life. *Nat Clim Chang* 3:919–925. <https://doi.org/10.1038/nclimate1958>
- 665 Rodrigues, M. (2015). A spatial typology for settlement pattern analysis in small islands.  
666 *GeoFocus. Revista Internacional de Ciencia y Tecnología de la Información Geográfica*,  
667 (15), 3-26
- 668 Santos, F. D., Valente, M. A., Miranda, P. M. A., Aguiar, A., Azevedo, E. B., Tomé, A. R., &  
669 Coelho, F. (2004). Climate change scenarios in the Azores and Madeira Islands. *World*  
670 *Resource Review*, 16(4), 473-491.
- 671 Santos, R. S., Hawkins, S., Monteiro, L. R., Alves, M., & Isidro, E. J. (1995). Marine research,  
672 resources and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater*  
673 *Ecosystems*, 5(4), 311-354.
- 674 Schaffelke B, Hewitt CL (2007) Impacts of introduced seaweeds. *Bot Mar* 50:397–417.  
675 <https://doi.org/10.1515/BOT.2007.044>
- 676 Schaffelke B, Smith JE, Hewitt CL (2006) Introduced macroalgae - A growing concern. *J Appl*  
677 *Phycol* 18:529–541. <https://doi.org/10.1007/s10811-006-9074-2>
- 678 Smale DA, Burrows MT, Moore P, et al (2013) Threats and knowledge gaps for ecosystem  
679 services provided by kelp forests: A northeast Atlantic perspective. *Ecol Evol* 3:4016–  
680 4038. <https://doi.org/10.1002/ece3.774>
- 681 Snipes M, Taylor DC (2014) Model selection and Akaike Information Criteria: An example from  
682 wine ratings and prices. *Wine Econ Policy* 3:3–9.  
683 <https://doi.org/10.1016/j.wep.2014.03.001>
- 684 Stolar J, Nielsen SE (2015) Accounting for spatially biased sampling effort in presence-only  
685 species distribution modelling. *Divers Distrib* 21:595–608.  
686 <https://doi.org/10.1111/ddi.12279>
- 687 Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of  
688 animals. *Nat Clim Chang* 2:686–690. <https://doi.org/10.1038/nclimate1539>
- 689 Tompkins E, Webb A (2017) Small islands
- 690 Topouzelis K, Makri D, Stoupas N, et al (2018) Seagrass mapping in Greek territorial waters  
691 using Landsat-8 satellite images. *Int J Appl Earth Obs Geoinf* 67:98–113.  
692 <https://doi.org/10.1016/j.jag.2017.12.013>
- 693 Traganos D, Reinartz P (2017) Mapping Mediterranean seagrasses with Sentinel-2 imagery.  
694 *Mar Pollut Bull* 0–1. <https://doi.org/10.1016/j.marpolbul.2017.06.075>
- 695 Veron S, Mouchet M, Govaerts R, et al (2019) Vulnerability to climate change of islands  
696 worldwide and its impact on the tree of life. *Sci Rep* 9:1–14.  
697 <https://doi.org/10.1038/s41598-019-51107-x>
- 698 Von Döhren P, Haase D (2015) Ecosystem disservices research: A review of the state of the art  
699 with a focus on cities. *Ecol Indic* 52:490–497.  
700 <https://doi.org/10.1016/j.ecolind.2014.12.027>

- 701 Wabnitz CC, Andréfouët S, Torres-Pulliza D, et al (2008) Regional-scale seagrass habitat  
702 mapping in the Wider Caribbean region using Landsat sensors: Applications to  
703 conservation and ecology. *Remote Sens Environ* 112:3455–3467.  
704 <https://doi.org/10.1016/j.rse.2008.01.020>
- 705 Werdell PJ, Roesler CS (2003) Remote assessment of benthic substrate composition in shallow  
706 waters using multispectral reflectance. *Limnology Oceanogr* 48:557–567.  
707 [https://doi.org/10.4319/lo.2003.48.1\\_part\\_2.0557](https://doi.org/10.4319/lo.2003.48.1_part_2.0557)
- 708 Yesson C, Bush LE, Davies AJ, et al (2015) The distribution and environmental requirements of  
709 large brown seaweeds in the British Isles. *J Mar Biol Assoc United Kingdom* 95:669–680.  
710 <https://doi.org/10.1017/s0025315414001453>
- 711 Zanolla M, Altamirano M, Carmona R, et al (2018) Assessing global range expansion in a cryptic  
712 species complex: insights from the red seaweed genus *Asparagopsis* (Florideophyceae). *J*  
713 *Phycol* 54:12–24. <https://doi.org/10.1111/jpy.12598>
- 714