

## Structure and temporal dynamics of a seaweed assemblage dominated by the invasive lineage 2 of *Asparagopsis taxiformis* (Bonnemaisoniaceae, Rhodophyta) in the Alboran Sea

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### Abstract

*Asparagopsis taxiformis* is a rhodophycean species composed of six genetic lineages, one of which is considered a relevant invasive component of Mediterranean flora. This study describes seasonal changes in the structure and biomass of the native community associated with *A. taxiformis* on the coast of Granada (southern Spain). The native community was represented by 18 Rhodophyta, 3 Chlorophyta, and 4 Ochrophyta species. Biomass was dominated by *A. taxiformis* and *Halopteris filicina*. In January, *A. taxiformis* represented only 16% of the whole community biomass, but 2 months later, more than 90% of the community biomass was formed by the invasive species. During the study period, species richness, the Shannon diversity index, and species evenness showed low and generally stable values. Given that *A. taxiformis* gametophytes are present throughout the year, they likely pose a constant stress to the development of the native community. This survey provides baseline information on the macroalgal community structure, which may be useful to further studies on the actual impact of the invasive lineage of *A. taxiformis*.

**Keywords:** Alboran Sea, Biomass, Evenness, Invasive, Gametophyte, Shannon index, Species richness.

### Introduction

Successful programs for the management of biological invasions should rely on accurate knowledge of the biology of the invasive species. The impact and effects of non-indigenous species on biodiversity cannot be generalized, and they vary greatly depending on the composition and structural complexity of the recipient community and the ecology of the invader (Sakai *et al.*, 2001; Pyšek *et al.*, 2012). Even though assessing the effect of invasive species on native communities and monitoring their conservation status is a complex task, it can lead to savings in both time and money over the long term.

In general, biological invasions are detrimental to native communities because of the decrease in diversity and consequent alteration of native trophic networks (Simberloff *et al.*, 2013; Maggi *et al.*, 2015). In the case of invasive macroalgae, these effects are magnified due to their role as the base of the trophic networks and as

ecosystem engineers (Boudouresque & Verlaque, 2010). Furthermore, once they are established, their impact is believed to be irreversible (Streftaris & Zenetos, 2006).

Over the last two decades, studies have investigated the effects of several invasive macroalgae in marine environments (see the review by Williams & Smith, 2007, and the meta-analysis by Maggi *et al.*, 2015). Several of these studies have described the effects of invasive seaweeds on native macroalgal assemblages in the Mediterranean Sea. These include *Caulerpa cylindracea* Sonder (Piazzi *et al.*, 2001) and *Caulerpa taxifolia* (M. Vahl) C. Agardh (Verlaque & Fritayre, 1994; Balata *et al.*, 2004), and the filamentous rhodophyta *Womersleyella setacea* (Hollenberg) R. E. Norris, *Acrothamnion preissi* (Sonder) E. M. Wollaston (Piazzi & Cinelli, 2000) and *Lophocladia lallemantii* (Montagne) F. Schmitz (Cebrián & Ballesteros, 2010; Marbà *et al.*, 2014).

*Asparagopsis taxiformis* (Delile) Trevisan de Saint Leon is one of the nine species listed as invasive in the

Mediterranean Sea (Bordalba & Duarte, 2010). This species is characterized by the alternation of erect gametophytes (n, GMP) up to 26 cm in length, with filamentous tetrasporophytes (2n, TSP) that form pompom-like structures and live free floating or entangled in benthic algae. These filaments are born from microscopic carposporophytes (2n) that remain attached to the GMP. Studies on the genetic composition of worldwide populations have shown that *A. taxiformis* is a species complex composed of six cryptic lineages (Andreakis *et al.*, 2007, 2016; Dijoux *et al.*, 2014) with different geographical distributions. Only two of these lineages have invasive characteristics (Andreakis *et al.*, 2007; Bolton *et al.*, 2011). Recent studies have shown that these cryptic lineages present different morphological (Zanolla *et al.*, 2014) and photosynthetic characteristics (Zanolla *et al.*, 2015). In the Mediterranean basin, lineage 2 (IL2) is regarded as invasive. These populations are thought to have an Indo-Pacific origin and are the result of multiple introduction events (Andreakis *et al.*, 2007). In 2008, Altamirano *et al.* reported both life stages on Andalusian coasts, and confirmed its invasive status in the area (in the sense suggested by Boudouresque & Verlaque, 2010).

*A. taxiformis* is already included in several governmental management programs, such as the “Mediterranean Action Plan” of the United Nations Environmental Programme, the Spanish “Monitoring Marine Invasive Species in Mediterranean Marine Protected Areas”, or more recently, the “European Framework Directive on Marine Strategy”, which incorporated this species in the “Black List of Marine Invasive Species” (Streftaris & Zenetos, 2006; Bordalba & Quesada, 2010; Otero *et al.*, 2013). However, it is striking that there is no information of the effects of this invasive species on the native community in the Mediterranean Sea or elsewhere (but see Streftaris & Zenetos 2006 & Tamburello *et al.*, 2013).

The main objective of the present study was to analyse the structure of the native macroalgal community in a southern Spanish locality in an area invaded by *A. taxiformis* over a period of one year. The community structure and its temporal variability were described and assessed using the Shannon index, species richness, and species evenness.

## Material and Methods

### Study site and sampling design

*Asparagopsis taxiformis* colonizes Andalusian coasts (southern Spain) forming dense belts at a depth of 1 m to 17 m (Altamirano *et al.* 2008; present study). We studied a population located in Marina del Este, Granada (Spain, 36°43'N, 3°43'W), a 400-m semiexposed coast inhabited by *A. taxiformis* on rocky substrate at a depth of 1 to 12 m. All observations and samplings were conducted by SCUBA diving at a depth of 9.5 m between January and November 2011. The genetic lineage of the population was corroborated using the *cox2-3* intergenic spacer, as

previously described by Andreakis *et al.* (2004).

We determined the minimum sampling area using 40 x 40-cm quadrats subdivided into 10 x 10-cm squares ( $n = 3$ ) and increased the sampling area through iteration of contiguous squares. The minimum area was obtained when no statistical differences were found in biomass, species richness ( $S$ ) and diversity ( $H'$ ) when increasing the sampling area (Cain & Castro, 1959). A 25 x 25-cm area was obtained and used for routine quantitative sampling. We randomly sampled replicates at least 7 m apart, ensuring that the same area was not sampled in subsequent months. The number of replicates was determined and considered as significantly representative using the Elliot formula with  $p = 0.2\%$ . When using three replicates to represent the population, this value indicates that the associated error is lower than 20% and can be accepted (Plante & Le Loeuff, 1982).

### Sample sorting and data analysis

In each sampling we recorded the presence of GMP and TSP. However, most of the biomass comprised GMP due to the scarce and discontinuous presence of TSP. All algal material from the 25 x 25-cm quadrats was scraped, brought to the laboratory for sorting into species level and dried in an oven at 60°C for 48 h to obtain its dry weight (DW). Using these data, species richness ( $S$ ) was determined as the number of identified taxa. The Shannon-Weaver diversity index ( $H'$ ) and Evenness ( $J$ ) (Krebs, 1999) were also determined. When calculating these indexes *A. taxiformis* was excluded from the input data.

A one-way ANOVA was used to analyse variations in  $H$ ,  $S$  and  $J$  over time, given that the sampling procedure ensured independent replicate quadrats. The association between the all-species biomass and *A. taxiformis* was estimated using the Pearson correlation coefficient. Statistical analyses were performed using Sigmaplot software (Systat Software Inc., version 11.0).

## Results

Over the study period, 25 macroalgal taxa (18 Rhodophyta, 3 Chlorophyta, and 4 Ochrophyta, see Appendix 1) were identified at Marina del Este. Of these, 22 were identified up to species level. Table 1 shows their temporal variation in distribution and biomass.

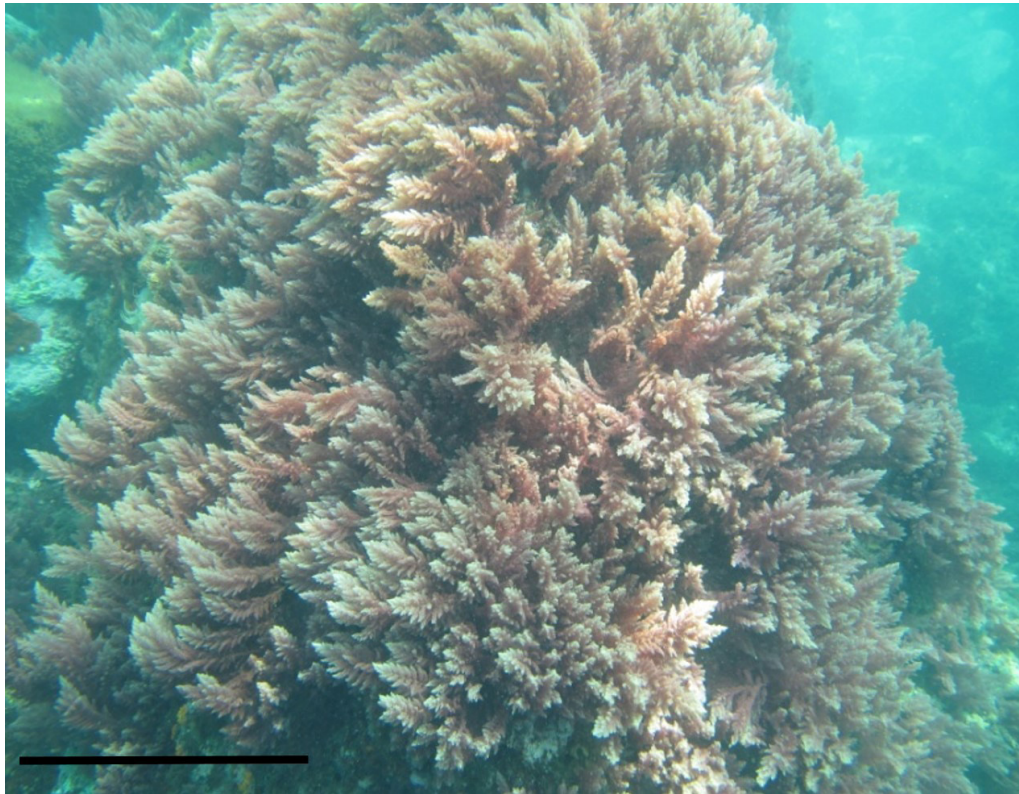
We observed that gametophytes of *A. taxiformis* inhabited rocky substrate at a bathymetric depth of 0 m to 12 m over the entire study period (Fig. 1). In contrast, the presence of tetrasporophytes was only recorded in June, September and November (Table 1). Genetic surveillance revealed that all gametophytes and tetrasporophytes sampled corresponded to lineage 2.

With the exception of *A. taxiformis*, the three most frequent and abundant species were *Halopteris filicina*, *Peyssonnelia squamaria* and *Dictyota dichotoma*, which were present almost in every sampling (Table 1).

**Table 1:** Temporal variation in species distribution and biomass (SD) (gDW m<sup>-2</sup>) in areas invaded by *A. taxiformis*.

Year	2011									
Species/Month	01	02	03	04	05	06	07	08	09	11
<i>A. ciliolatum</i>	+			+						
<i>A. hubbsii</i>				+			+	+		
<i>A. taxiformis</i>	5.8 (0.4)	49.4 (11.6)	67.5 (3.6)	56.5 (6.2)	113.6 (45.3)	95.8 (19.7)	42.5 (6.5)	19.4 (10.2)	90.3 (35.5)	84.0 (49.8)
<i>C. tetragonum</i>					+	+				
<i>C. ustulatus</i>			+							
<i>C. codii</i>				+	+					
<i>Ceramium</i> sp.								+		
<i>C.officinalis</i>									+	+
<i>F. hillebrandii</i>						+			+	+
<i>G. spathulatum</i>			+							
<i>G. pusillum</i>			+							
<i>J. rubens</i>	+			+		+			+	+
<i>M. lichenoides</i>				+			+		176.56 (10.3)	
<i>O. simpliciusculus</i>	+									
<i>P. squamaria</i>	+	1.5 (0.6)	6.8 (6.1)	+	8.2 (2.0)	+	+	+	21.3 (18.5)	
<i>P. cartilagineum</i>	+		+	+	+	+		+		+
<i>Polysiphonia</i> sp.			+							
<i>R. pseudopalmata</i>			+	+	+		+	+	+	+
<i>S. coronopifolius</i>								+		
<i>C. laetevirens</i>			+							
<i>C. prolifera</i>				+						
<i>C. effusum</i>	+									
<i>C. sinuosa</i>	+									
<i>D. dichotoma</i>			+	+				+	+	
<i>Dictyota</i> sp.			+			+				
<i>H. filicina</i>	42.6 (1.5)	+	2.0 (2.3)	2.8 (2.9)	16.4 (13.1)	+	+	7.3 (9.1)	36.3 (25.0)	+

+: indicates biomass < 0.5 gDW m<sup>-2</sup>

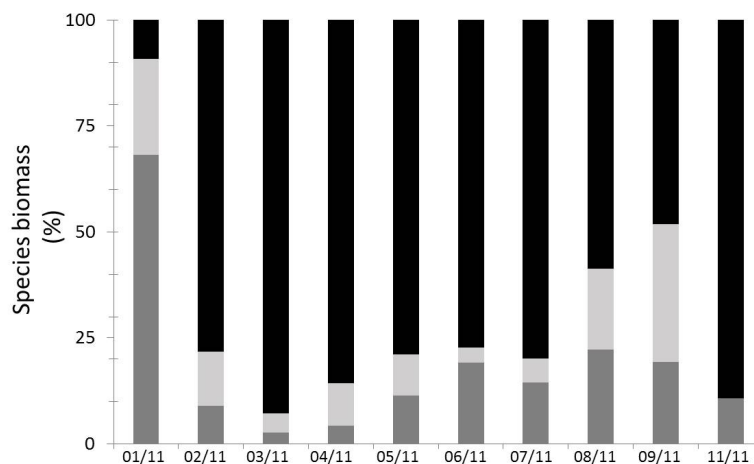


**Fig. 1:** *Asparagopsis taxiformis* lineage 2 at Marina del Este, Granada, Spain. Scale bar: 0.5 m.

*Mesophyllum lichenoides*, *Rhodomenia pseudopalmata*, and *Corallina officinalis* were the second most frequent taxa.

*Asparagopsis taxiformis* alone comprised more than 90% of the total biomass sampled in March and December 2011 (Fig. 2). However, although *Halopteris filicina* typically accounted for 3% to 21% of total biomass, this

figure rose to 62% in January. The remaining species sampled formed a minority group. Appendix 1 contains a list of these species and Table 1 shows their seasonality. Their contribution to biomass typically ranged from 0% to 8%, except for the increase observed in September (28%; see Fig. 2). The most abundant species within this minority group was *M. lichenoides*.



**Fig. 2:** Biomass percentage (%) over the study period of *Asparagopsis taxiformis* (black), *Halopteris filicina* (dark grey), and the other species (light grey) listed in Appendix 1. Time indicates months (January–November 2011).



A significant negative correlation was found between the biomass of *A. taxiformis* IL2 and *H. filicina* ( $R = -0.35$ ;  $n=27$ ;  $P = 0.032$ ), but no covariation was found between the biomass of the invasive taxon and the group formed by the remaining species ( $R = 0.20$ ;  $n = 27$ ;  $P = 0.413$ ).

The most significant decrease in  $S$  was recorded in February. This figure was 82% lower than that recorded in May, whereas no differences were observed in the other months ( $F: 3.37$ ;  $df: 8$ ;  $P < .05$ ; see Fig. 3). In June, July, and November, *A. taxiformis* was the only species whose biomass was more than  $0.05 \text{ gDW m}^{-2}$ ; thus, a value of zero was obtained for  $H'$  and  $J$ . These indexes had significantly higher values in April, May, and September, but did not reach significance in the remaining months (ANOVA output for diversity values:  $F: 6.58$ ;  $df: 8$ ;  $P < .05$ ; ANOVA output for evenness values:  $F: 3.24$ ;  $P < .005$ ; see Fig. 3).

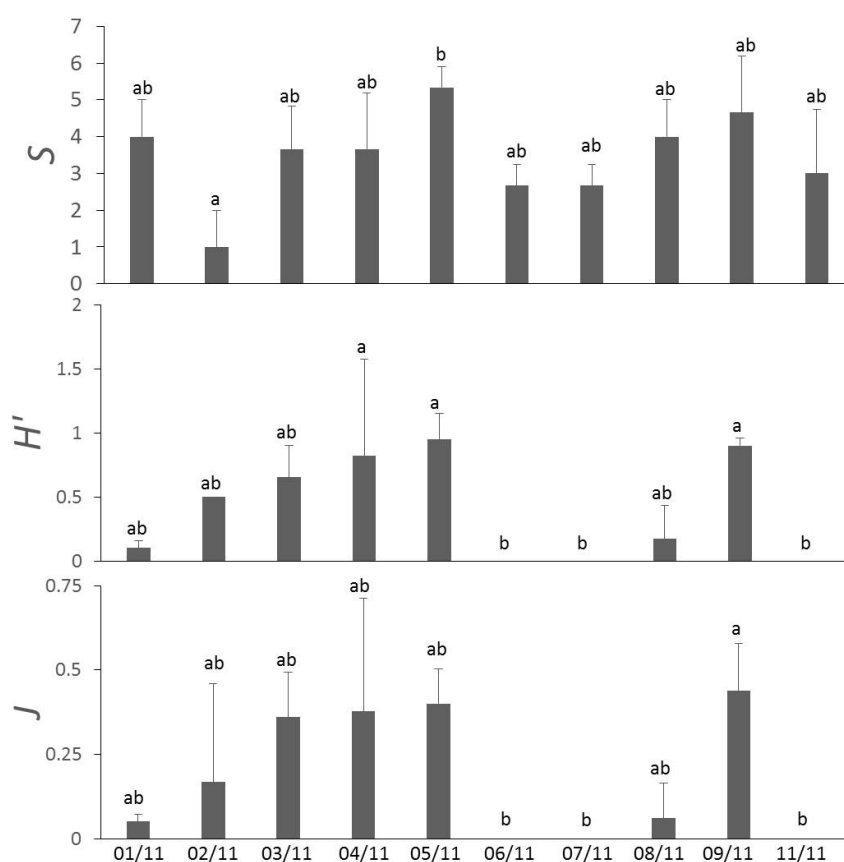
## Discussion

This study is the first attempt to quantify yearly changes in the structure and biomass of the native community associated with the introduced species *Asparagopsis taxiformis*.

The native community at Marina del Este presented characteristics that are commonly observed in communities strongly affected by invasive organisms. Low species richness and diversity values, combined with the continuous presence of the invader -which typically formed more than 50% of the total algal biomass- indicate that *A. taxiformis* IL2 likely impoverishes the communities in which it settles.

In general, the bulk of the biomass in the macroalgal assemblage was always distributed between *A. taxiformis* and *Halopteris filicina*. The latter species is one of the most abundant and widely distributed algal species on Mediterranean coasts (Seoane-Camba, 1965). Analytically, its unbalanced proportion is explicit in the low values of evenness estimated.

The significant negative correlation found between the biomass of *A. taxiformis* IL2 and *H. filicina* could be due to the negative impact of this invasive species on *H. filicina*. Future studies could address the various mechanisms hypothesised to underlie this negative correlation. These mechanisms include: a) the presence of the invader precluding the development of *H. filicina*; and b) allelopathic substances from *A. taxiformis* inhibiting the growth of *H. filicina*. This process may be similar to the manner in which *Caulerpa taxifolia* inhibits the productivity of



**Fig. 3:** Temporal variation in species richness ( $S$ ), Shannon-Weaver diversity index ( $H'$ ), and evenness ( $J$ ) of the macroalgal community in areas invaded by *A. taxiformis*. Values are expressed as means  $\pm$  SD ( $n = 3$ ). Different letters denote significant differences ( $P < 0.05$ ). Time is designated as month/year (January-November 2011).

some species of autochthonous algae (Ferrer *et al.*, 1997). It is noteworthy that *H. filicina* and *A. taxiformis* simultaneously reach their peak biomass score in June (Zanolla, preliminary data). However, in this month, species richness in areas dominated by *H. filicina* (but where *A. taxiformis* was present) was double that estimated for areas dominated by *A. taxiformis*. Thus, a low number of species was observed when *A. taxiformis* was dominant, but not when *H. filicina* was dominant, suggesting that *A. taxiformis* has a negative impact on the native community. Spatial differences between assemblages can be ruled out as affecting the obtained results, because sampling was conducted in areas within the same bathymetric range and on identical types of substrate. Depth is the most important factor affecting community composition in Marina del Este (Cebrián & Ballesteros, 2004). Thus, algal assemblages at a given depth and on the same type of substrate are homogeneous (personal observation). Further support for the hypothesis of a possible negative effect of *A. taxiformis* on the native assemblage is suggested by the decrease of between 5 to 7 species in this study when compared to the catalogue of flora described by Cebrián & Ballesteros (2004) at the same bathymetric range (8-10 m) when *A. taxiformis* was absent.

Another feature of the native community structure is that species richness (*S*) and diversity (*H'*) barely change over the year, suggesting that there is no seasonal replacement of species in Marina del Este. This feature may be related to the weak environmental gradients to which the area is exposed (Zanolla *et al.*, 2017a). It is noteworthy that diversity (and thus evenness) values dropped to zero in the months when *A. taxiformis* IL2 reached its highest biomass scores.

Species richness (composition) and species evenness (dominance) influence the temporal and spatial variability of community properties and compositional stability, thus influencing the probability of the community being invaded (Wilsey & Potvin, 2000; Smith *et al.*, 2004). The dominance structure of natural assemblages is altered by species introduction and invasion by exotic species, which often show an initial dominance (Williams & Smith, 2007). The literature is replete with cases in which successful invasions result from exotic species with ecological traits that are different from and similar to those of the dominant native species (Symstad, 2000; Fargione *et al.*, 2003). Our study was similar to the latter case, given that *A. taxiformis* and *H. filicina* belong to the same functional and structural group, and that a negative correlation was found between the presence of *A. taxiformis* and the abundance of *H. filicina*. Nevertheless, manipulative studies with the two species (additive and substitutive design) should be conducted to identify any emergent effects between them.

The study area has experienced a high anthropogenic impact (Sedano *et al.*, 2014). A leisure port had been built by the end of the 1970s, which in turn increased urban growth during the 1980s. Marina del Este beach was created as a result of this coastal urban development. In

addition, *Asparagopsis armata* Harvey has been reported as an invasive species in Andalusian coastlines since 1965 (Seoane-Camba, 1965). This species inhabits the infralittoral zone of Marina del Este (García Jiménez *et al.*, 1996). A study of macroalgal assemblages at the study site in 1997 found that *A. armata* was the most abundant seaweed at depths of 0 m to 5 m, but did not find *A. taxiformis* (Cebrián & Ballesteros, 2004). In combination with the results of the study by Altamirano (1999), who reported the first record of *A. taxiformis* in the Alboran Sea (i.e., in the Chafarinas Islands), the foregoing information could provide the timeline and route of the invasion of *A. taxiformis* IL2 in the Alboran Sea. We suggest that the invasive process began somewhere in the eastern to central Mediterranean Sea and moved westerly after 1997. *A. armata* is currently confined to a depth of 1 m to 3 m, where both invasive species are sympatric. It has even been replaced by *A. taxiformis* in several Andalusian locations (personal observation). However, *A. armata* was not found during the present study, which may be due to the complete turnover of this invasive species by *A. taxiformis*. Thus, processes such as invasional meltdown (Simberloff & Von Holle, 1999), plus a highly altered recipient ecosystem (i.e., unbalanced species composition, poor species richness) may have facilitated the settlement of *A. taxiformis* IL2 in the region. All these factors have been extensively cited as facilitators of macroalgal invasions (Occhipinti-Ambrogi, 2007; Andreakis & Schaffelke, 2012), to which should be added the intrinsic characteristics of the invader, such as broad phenotypic plasticity (Zanolla *et al.*, 2015), effective vegetative propagation mechanisms (Zanolla *et al.*, 2017a), the production of novel genetic variants through sexual reproduction (Zanolla *et al.*, 2017b) and genetic characteristics that have rapid adaptive and expansive potential (Zanolla *et al.*, 2018).

The coastlines of southern Spain define the northern limit of the Alboran Sea, which is one of the most biodiverse marine areas of Europe and North Africa (García Raso *et al.*, 2010). The EU has recently included this area within the Special Areas of Conservation ES6140016 (Order 369/2015, 4<sup>th</sup> August, Boletín Oficial de la Junta de Andalucía, 2015). Taking into account the results of the present study, we recommend the development of management programs to eradicate this invasive species or to control the use of ballast water in this area.

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## References

- Altamirano, M., 1999. Nuevas citas para la flora marina del Archipiélago de las Islas Chafarinas. *Acta Botánica Malacitana*, 24, 185-233.
- Altamirano, M., Muñoz, A.R., De La Rosa, J.C., Barrajón-Mínguez, A., Moreno-Robledo, C. *et al.*, 2008. The invasive species *Asparagopsis taxiformis* (Bonnemaisoniales, Rhodophyta) on Andalusian coast (Southern Spain): reproductive stages, new records and invaded communities. *Acta Botánica Malacitana*, 33, 1-11.
- Andreakis, N., Procaccini, G., Kooistra, W.H., 2004. *Asparagopsis taxiformis* and *Asparagopsis armata* (Bonnemaisoniales, Rhodophyta): genetic and morphological identification of Mediterranean populations. *European Journal of Phycology*, 39(3), 273-283.
- Andreakis, N., Kooistra, W.H.C.F., Procaccini, G., 2007. Microsatellite markers in an invasive strain of *Asparagopsis taxiformis* (Bonnemaisoniales, Rhodophyta): insights in ploidy level and sexual reproduction. *Gene*, 406, 144-151.
- Andreakis, N., Schaffelke, B., 2012. Invasive marine seaweeds: pest or prize? p. 235-262. In: *Seaweed biology*. Wiencke, C., Bischof, K. (Eds). Springer, Berlin, Heidelberg.
- Andreakis, N., Costello, P., Zanolla, M., Saunders, G.W., Mata, L., 2016. Endemic or introduced? Phylogeography of *Asparagopsis* (Florideophyceae) in Australia reveals multiple introductions and a new mitochondrial lineage. *Journal of Phycology*, DOI:10.1111/jpy.12373-15-166.
- Balata, D., Piazzzi, L., Cinelli, F., 2004. A comparison among assemblages in areas invaded by *Caulerpa taxifolia* and *C. racemosa* on a subtidal Mediterranean rocky bottom. *Marine Ecology*, 25.1, 1-13.
- Bolton, J.J., Andreakis, N., Anderson, R.J., 2011. Molecular evidence for three separate cryptic introductions of the red seaweed *Asparagopsis* (Bonnemaisoniales, Rhodophyta) in South Africa. *African Journal of Marine Science*, 33 (2), 263-271.
- Bordalba, N.M., Quesada, C.M.D., 2010. *Spanish document aiming at the identification of important ecosystems and assessment of ecological status and pressures to Mediterranean marine and coastal biodiversity*. Contract RAC/SPA, Nº 73-2009, 56 pp.
- Boudouresque, C.F., Verlaque, M., 2010. Is global warming involved in the success of seaweed introductions in the Mediterranean Sea? p. 31-50. In: *Seaweeds and their role in globally changing environments*. Israel, A., Einav, R., Seckbach, J. (Eds). Springer, Netherlands.
- Cain, S.A., Castro, G.D., 1959. *Manual of Vegetation Analysis*. Harper, New York, 325pp.
- Cebrián, E., Ballesteros, E., 2004. Zonation patterns of benthic communities in an upwelling area from the western Mediterranean (La Herradura, Alboran Sea). *Scientia Marina*, 68 (1), 69-84.
- Cebrián, E., Ballesteros, E., 2010. Invasion of Mediterranean benthic assemblages by red alga *Lophocladia lallemandii* (Montagne) F. Schmitz: depth-related temporal variability in biomass and phenology. *Aquatic botany*, 92 (2), 81-85.
- 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 (7):e103826.
- Fargione, J., Brown C.S., Tilman D., 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the USA*, 100, 8916-8920.
- Ferrer, E., Garreta, G., Ribera, M.A., 1997. Effect of *Caulerpa taxifolia* on the productivity of two Mediterranean macrophytes. *Marine Ecology Progress Series*, 149 (1), 279-287.
- García Jiménez, C.M., Retamero, A., Barrajón, A., 1996. Valores ecológicos del paraje natural de los acantilados de Maro- Cerro Gordo. *Quercus*, 123, 35-43.
- García Raso, J.E., Gofas, S., Salas, C., Manjón-Cabeza, E., Urra, J., *et al.*, 2010. *El mar más rico de Europa: biodiversidad del litoral occidental de Málaga entre Calaburras y Calahonda*. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, 137 pp.
- Krebs, C.J., 1999. *Ecological Methodology*. Benjamin/Cummings, Menlo Park, California, 620 pp.
- Maggi, E., Benedetti-Cecchi, L., Castelli, A., Chatzinikolaou, E., Crowe, T.P. *et al.*, 2015. Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels. *Diversity and Distributions*, 21, 1-12.
- Marbà, N., Arthur, R., Alcoverro, T., 2014. Getting turfed: The population and habitat impacts of *Lophocladia lallemandii* invasions on endemic *Posidonia oceanica* meadows. *Aquatic Botany*, 116, 76-82.
- Occhipinti-Ambrogi, A., 2007. Global change and marine communities: alien species and climate change. *Marine Pollution Bulletin*, 55, 342-352.
- Otero, M., Cebrián, E., Francour, P., Galil, B., Savini, D., 2013. *Monitoring marine invasive species in Mediterranean marine protected areas (MPAs): a strategy and practical guide for managers*. Malaga, Spain: IUCN, 136 pp.
- Plante, R., Le Loeuff, P., 1982. *Le benthos marin et les stratégies d'échantillonnage*. p. 235-240. In: *Stratégies d'échantillonnage en écologie*. Frontier, S. (Ed). Masson, Paris.
- Piazzzi, L., Cinelli, F., 2000. Effets de l'expansion des Rhodophyceae introduites *Acrothamnion preissii* et *Womersleyella setacea* sur les communautés algales des rhizomes de *Posidonia oceanica* de Méditerranée occidentale. *Cryptogamie Algologie*, 21 (3), 291-300.
- Piazzzi, L., Ceccherelli, G., Cinelli, F., 2001. Threat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. *Marine Ecology Progress Series*, 210, 149-159.
- Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., *et al.*, 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, 18 (5), 1725-1737.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J. *et al.*, 2001. The population biology of invasive species. *Annual Reviews of Ecology and Systematics*, 32, 305-32.
- Sedano, F., Marquina, D., Espinosa, F., 2014. Usefulness of meiofauna at high taxonomic levels as a tool to assess harbor quality status. Marina del Este Harbor (Granada, Spain) as a case study. *Revista Ciencias Marinas y Costeras*, 6, 103-113.
- Seoane-Camba, J., 1965. Estudios sobre las algas bentónicas en la costa sur de la Península Ibérica litoral de Cádiz. Consejo Superior de Investigaciones Científicas, Patronato Juan de la Cierva. *Investigaciones Pesqueras*, 29, 3-216.
- Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, 1 (1), 21-32.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle,

- D.A., *et al.*, 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution*, 28 (1), 58-66.
- Smith, M.D., Wilcox, J.C., Kelly, T., Knapp, A.K., 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos*, 106, 253-262.
- Streftaris, N., Zenetos, A., 2006. Alien marine species in the Mediterranean-the 100 "Worst Invasives" and their impact. *Mediterranean Marine Science*, 7 (1), 87-118.
- Symstad, A.J., 2000. A test of the effects of functional groups richness and composition on grassland invasibility. *Ecology*, 81, 99-109.
- Tamburello, L., Benedetti-Cecchi, L., Masini, L., Bulleri, F., 2013. Habitat heterogeneity promotes the coexistence of exotic seaweeds. *Oecologia*, 172 (2), 505-513.
- Verlaque, M., Fritayre, P., 1994. Mediterranean Algal Communities Are Changing in the Face of the Invasive Alga *Caulerpa taxifolia* (Vahl) C Agardh. *Oceanologica Acta*, 17, 659-672.
- Williams, S.L., Smith J.E., 2007. A Global Review of the Distribution, Taxonomy, and Impacts of Introduced Seaweeds. *Annual Reviews of Evolution and Systematics*, 38, 327-359.
- Wilsey, B.J., Potvin, C., 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology*, 81, 887-892.
- Zanolla, M., Carmona, R., De La Rosa, J., Salvador, N., Sherwood, A.R. *et al.*, 2014. Morphological differentiation of cryptic lineages within the invasive genus *Asparagopsis* (Bonnemaisoniales, Rhodophyta). *Phycologia*, 53 (3), 233-242.
- Zanolla, M., Altamirano, M., Carmona, R., De La Rosa, J., Sherwood, *et al.*, 2015. Photosynthetic plasticity of the genus *Asparagopsis* (Bonnemaisoniales, Rhodophyta) in response to temperature: implications for invasiveness. *Biological Invasions*, 17 (5), 1341-1353.
- Zanolla, M., Altamirano, M., De La Rosa, J., Niell, F.X., Carmona, R., 2017a. Size structure and dynamics of an invasive population of lineage 2 of *Asparagopsis taxiformis* (Florideophyceae) in the Alboran Sea. *Phycological Research*, 66 (1), 45-51.
- Zanolla, M., Carmona, R., Altamirano, M., 2017b. Reproductive ecology of an invasive population of lineage 2 of *Asparagopsis taxiformis* (Bonnemaisoniales, Rhodophyta) in the Alboran Sea (Southern Mediterranean Sea). *Botanica Marina*, 60 (6), 627-638.
- Zanolla, M., Altamirano, M., Carmona, R., De la Rosa, J., Souza-Egipsy, V. *et al.*, 2018. Assessing global range expansion in a cryptic species complex: insights from the red seaweed genus *Asparagopsis* (Florideophyceae). *Journal of Phycology*, 54, 12-24.



**Appendix 1.** Macroalgal species found in Marina del Este during the study period.

Species
<u>Rhodophyta</u>
<i>Acrosorium ciliolatum</i> (Harvey) Kylin
<i>Antithamnion hubbsii</i> E.Y. Dawson
<i>Asparagopsis taxiformis</i> (Delile) Trevisan de Saint León
<i>Callithamnion tetragonum</i> (Withering) S.F. Gray
<i>Caulacanthus ustulatus</i> (Mertens ex Turner) Kützing
<i>Ceramium codii</i> (H. Richards) Mazoyer
<i>Ceramium</i> sp.
<i>Corallina officinalis</i> Linnaeus
<i>Falkenbergia hillebrandii</i> (Bornet) Falkenberg
<i>Gelidium spathulatum</i> (Kützing) Bornet
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux
<i>Mesophyllum lichenoides</i> (J. Ellis) Lemoine
<i>Ophidocladus simpliciusculus</i> (P.L. Crouan & H.M. Crouan) Falkenberg
<i>Peyssonnelia squamaria</i> (S.G. Gmelin) Decaisne
<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon
<i>Polysiphonia</i> sp.
<i>Rhodymenia pseudopalmata</i> (J.V. Lamouroux) P.C. Silva
<i>Sphaerococcus coronopifolius</i> Stackhouse
<u>Chlorophyta</u>
<i>Cladophora laetevirens</i> (Dillwyn) Kützing
<i>Cladophora prolifera</i> (Roth) Kützing
<i>Codium effusum</i> (Rafinesque) Delile
<u>Ochrophyta</u>
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux
<i>Dictyota</i> sp.
<i>Halopteris filicina</i> (Grateloup) Kützing