



## Effects of structural complexity on epifaunal assemblages associated with two intertidal Mediterranean seaweeds

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### ABSTRACT

Brown foundation seaweeds are key elements increasing substrate heterogeneity and shaping the biodiversity in rocky coastal ecosystems. They are, however, vulnerable species that are declining due to multiple anthropogenic and climate change stressors, leading to a shift to less structural complex habitats. We investigate the role of structural attributes of two intertidal macroalgae, *Ericaria amentacea* and *Laurencia obtusa*, in shaping the abundance and diversity of their associated epifaunal assemblages. For this aim, we measured seaweeds' biomass, thallus volume and length (used here as proxy of substrate complexity), and explored which seaweeds' substrate attribute explained better variation of epifaunal assemblages. Results showed that *E. amentacea* was more complex than *L. obtusa* and hosted a higher number of epifaunal individuals. However, unlike that expected, the epifaunal assemblage of *L. obtusa* was more structured with higher Shannon–Wiener diversity and Pielous' evenness. Our findings indicate that, besides seaweed's substrate attributes, other mechanisms such as wave action and chemical defense might play a role in structuring epifaunal assemblages. We suggest that a shift from *E. amentacea* to *L. obtusa* population could have effect on structure and abundance of associated epifaunal assemblages. Certainly, further investigations are needed to clear up the consequences of these changes.

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## 1. Introduction

Habitat complexity is a key determinant in structuring biotic assemblages (both composition and structure) in both terrestrial and marine environments, with structurally complex habitats hosting a high level of biodiversity than simpler ones (Kovalenko et al. 2012). The positive effects of habitat complexity in biodiversity seem to imply different mechanisms, including an increase of the area available for settlement, protection from physical disturbance, and organic matter (Kovalenko et al. 2012).

Macrophytes (seaweeds, seagrasses, and mangroves) play an important role in marine environments, contributing to biodiversity and energy flow along the world's coastline. Many of them are considered ecosystem engineers or foundation species (Piazzi et al. 2018; Sciuto et al. 2018; Ellison 2019), which are organisms that affect the availability of resources to other species directly or indirectly by modifying, maintaining, and creating habitats (Christie et al. 2009).

Among macrophytes, seaweeds act as biological “formers” of habitat structure, contributing to increase the habitat complexity of rocky shores. Many studies have shown that seaweeds shape their associated communities differently depending on algal architecture, life cycle, chemical defences

or physical factors (Chemello and Milazzo 2002; Jormalainen and Honkanen 2008; Vázquez-Luis et al. 2008; Pitacco et al. 2014; Veiga et al. 2014; Chiarore et al. 2019; Mancuso et al. 2021a, 2021b, 2022). Seaweeds with high structural complexity, expressed as a variety of substrate attributes (such as fractal dimension, degree of branching, thallus width and height, and wet weight), can support well-structured molluscs communities (Hacker and Steneck 1990; Gee and Warwick 1994; Chemello and Milazzo 2002; Bitlis 2019; Mancuso et al. 2021a).

In the Mediterranean Sea, foundation seaweeds are mainly comprised of species of the genus *Cystoseira* C. Agardh (Fucales, Phaeophyceae) recently divided into three genera *Cystoseira*, *Gongolaria* Boehmer and *Ericaria* Stackhouse (Orellana et al. 2019; Molinari Novoa and Guiry 2020) and hereafter referred to as *Cystoseira sensu lato*. Of these genera, the genus *Ericaria* Stackhouse (Fucales) (Molinari Novoa and Guiry 2020) include ten species that considerably improve the structural complexity and productivity of rocky coasts from the infralittoral zone down to the upper circalittoral zone (Giaccone et al. 1994; Bulleri et al. 2002; Falace and Bressan 2006; Ballesteros et al. 2009). *Ericaria* populations can support diverse associated communities (Schiel and Foster 2006; Cheminée et al. 2013; Mineur et al. 2015), and

some species, such as *Ericaria amentacea* (C.Agardh) Molinari & Guiry, are considered useful indicators of water and ecosystem quality according to the Water Framework Directive (WFD, 2000/60/EC), and are used for the CARLIT index (CARtography of Littoral and upper-sublittoral benthic communities) (Ballesteros et al. 2007; Mangialajo et al. 2007; Nikolić et al. 2013).

Declines of *Ericaria* populations have been reported along the Mediterranean Sea's coasts, particularly near urban areas, as a result of multiple anthropogenic stressors combined with the effects of climate change (Benedetti-Cecchi et al. 2001; Thibaut et al. 2005; Arevalo et al. 2007; Mangialajo et al. 2008; Strain et al. 2014; Mineur et al. 2015; Mancuso et al. 2018; Blanfuné et al. 2019). Loss of these valuable seaweeds typically results in a drastic loss of habitat complexity, leading to a shift to less structured communities dominated by turf-forming algae, sea urchin barrens or mussels beds (Benedetti-Cecchi et al. 2001; Connell et al. 2014; Strain et al. 2014; Agnetta et al. 2015; Mineur et al. 2015; Krumhansl et al. 2016), even while eroding essential ecosystem services and economic value of coastal areas (Mineur et al. 2015; Buonomo et al. 2018; De La Fuente et al. 2019). Understanding how the biodiversity associated with seaweeds changes in response to algal complexity allows us to predict how shift from essential foundation seaweeds such as *Ericaria* species to macroalgae with a lower structural complexity may affect the habitat structure.

In this study we quantify the structural attributes of two intertidal co-occurring seaweeds, *E. amentacea* and *Laurencia obtusa* (Hudson) J.V.Lamouroux, with notable differences in structure, and investigate the role of structural complexity in shaping the abundance and diversity of their associated epifaunal assemblages. *Laurencia obtusa* is an erected red alga that can be easily found near or in association with *Ericaria amentacea* in the lower intertidal zone (Chemello 2009). In comparison to *E. amentacea*, *L. obtusa* appears to be less vulnerable to environmental and anthropogenic stressors, as it can survive in habitats lacking of furoids (Mangialajo et al. 2008). This aspect suggests that this species can easily persist in habitats depleted of *Ericaria amentacea*. Understanding the ability of these two seaweeds to support epifaunal assemblages can aid in understanding the effects of possible habitat shift from *E. amentacea* to *L. obtusa*. Then, we hypothesize that *E. amentacea* had greater structural complexity and supported a more diverse epifaunal assemblage compared to *L. obtusa*, with significant implications for biodiversity conservation.

## 2. Materials and methods

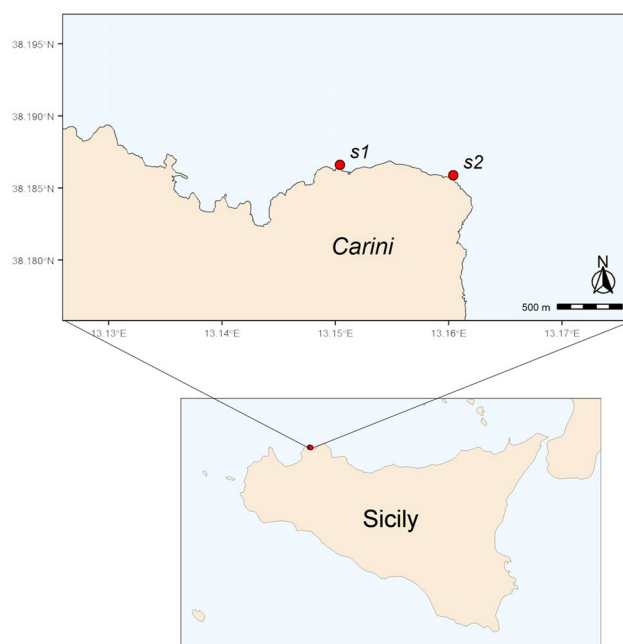
### 2.1. Study site and species

The study was carried out between June and July 2012 in two sites on the rocky shore of Carini (site 1 Lat: 38.186385, Long: 13.151703, and site 2 Lat: 38.186446, Long: 13.157194), about 30 km west from Palermo (northern Sicily, Italy; Figure 1). The sites were characterized by similar environmental conditions (such as wave exposure, temperatures, salinity) and the presence of vermetid reefs with a conspicuous co-occurring presence of *E. amentacea* and *L. obtusa*.

*Ericaria amentacea* is a brown seaweed (Fucales) characterized by caespitose thalli up to 40–50 cm in height formed by creeping axis from which several cylindrical erect axes, up to 2–15 cm in height, arise. The apices of the cauloids are not very prominent. Branches of any order with spinose appendages with primary branches are cylindrical (to 40 cm high) with short secondary branches (Gómez-Garreta et al. 2002; Mannino and Mancuso 2009; Cormaci et al. 2012). Like other *Cystoseira sensu lato* species, *E. amentacea* displays seasonal changes in vegetative development, with new branches developing from perennial axes in May and reaching their maximum in July, then withering away in late August, leaving the basal cauloids to persist in a quiescent state during the cold winter season (Gómez-Garreta et al. 2002). In exposed coasts, *E. amentacea* typically thrives forming monospecific belts in the infralittoral fringe (the transitional area between the littoral and sublittoral zone). *Ericaria amentacea*, endemic to the Mediterranean Sea (Council of Europe 1979), is strictly protected in Appendix I of the Bern Convention on the Conservation of European Wildlife and Natural Habitats because to its structuring influence on shallow Mediterranean communities.

*Laurencia obtusa* is a red alga (Ceramiales) with erect thalli that generate small arborescent bushes up to 15 cm tall and 2–6 cm wide that are attached to the substrate by a stolon-like base. Apex of branches of any order truncated with an apical depression from which branched trichoblasts emerge (Rodríguez-Prieto et al. 2015).

Differences in structural complexity exist between *E. amentacea* and *L. obtusa*. *Ericaria amentacea* is taller than *L. obtusa*, with several long primary branches and spinose appendages that give it a complex appearance. *Laurencia obtusa* thalli, on the other hand, have a pyramidal form with open branches that become shorter towards the apex.



**Figure 1.** The two study sites (red dots) at the rocky-shore of Carini (northern Sicily, Italy).

## 2.2. Sampling and analysis of the epifauna

For each site, quadrats of 10×10 cm were haphazardly placed (~ 1 m apart) on homogeneously (100% coverage) algal patches of *E. amentacea* ( $n=6$ ) and *L. obtusa* ( $n=6$ ). To avoid loss of organisms, seaweeds were covered by plastic bags, then detached from the rocky substratum with chisel and hammer and subsequently closed very quickly inside the bag (Conlan et al. 2021). After collection, samples were transported in laboratory and washed under running tap water through a 1 mm mesh allowing the collection of the associated epifauna. After sorting, the epifauna was stored in 70% seawater ethanol solution and subsequently counted and identified to species, or the nearest possible taxonomic level. Epifaunal taxonomy and nomenclature were updated according to the most recent literature (Conlan et al. 2021; WoRMS Editorial Board 2021).

## 2.3. Seaweeds structural attributes

For each *E. amentacea* and *L. obtusa* individual collected within each square sample, thallus volume (TV), thallus length (TL) and biomass (DW) were measured, then average values per square sample ( $n=6$  per algal species) were used to explore their relationships with the diversity indices calculated for the epifaunal assemblages. Thallus volume was measured as the variation of volume, in ml, after the immersion of a thallus into a graduated cylinder filled with seawater. Thallus length is the length of thallus from the base to the apical portion of the frond, while biomass was calculated as dry weight (DW, gr) after drying in a stove at 60°C for 48 h (Stein-Taylor et al. 1985). Total values of TV, TL and DW for each sampling quadrat were used in the following analyses. The amount of epiphytes was negligible among the two seaweeds and so was not taken into account in this study.

## 2.4. Data analysis

Differences in substrate attributes (TV, TL and DW) between *E. amentacea* and *L. obtusa* were investigated using a two-way analysis of variance (ANOVA). The analysis was performed using seaweeds (fixed and orthogonal with 2 levels: *E. amentacea* and *L. obtusa*) and sites (random and orthogonal with 2 levels: s1 and s2). Cochran's test was used to check for the homogeneity of variances (Underwood 1997).

The epifaunal assemblages of each seaweed were characterized according to the total abundance of individuals (N), species number (S), Shannon-Wiener diversity index (H') and Pielou's Evenness index (J). A two-way ANOVA was used to test differences in the epifaunal indices (N, S, H', J) using the same factors described before for the substrate attribute analysis.

Differences in the epifaunal community structure (which takes into account species identity and relative abundance) and composition (presence/absence, which only takes into account species identity) among sites and seaweed species were assessed by Permutational Multivariate Analysis of Variance (PERMANOVA). The analyses were based on a Bray-Curtis distance matrix of square-root transformed

epifaunal abundances (structure) and on a Jaccard distance matrix of presence/absence data (composition) using 9999 permutations. Permutational analysis of multivariate dispersion (PERMDISP) was used to test differences in multivariate dispersion (Anderson et al. 2008). A principal coordinate analysis (PCoA) plot was generated to visualize the variation of the epifaunal community structure (based on a Bray-Curtis distance matrix) and composition (based on a Jaccard distance matrix).

SIMPER analysis (Clarke 1993) was performed to identify those taxa that contributed to the dissimilarity of the epifaunal assemblages between seaweeds ( $\delta i\%$ ). The ratio  $\delta i/SD_{(\delta i)}$  was used to measure the consistency of the contribution of a particular taxon to the average dissimilarity in the comparison between seaweeds. A cut-off value of 90% was used to exclude low contributions.

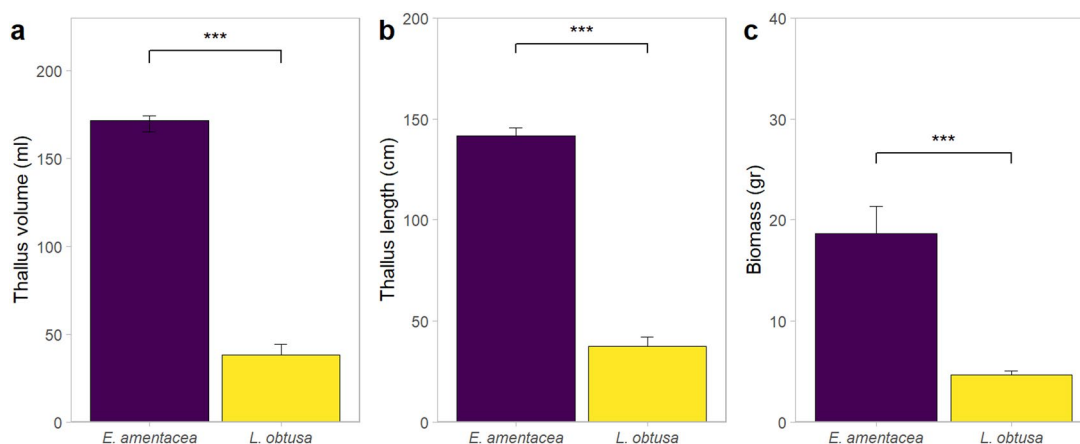
Finally, for each seaweed, linear regression (LM) analysis was used to test which substrate attributes (TV, TL and DW) explained better the variation of epifauna descriptors (N, S, H' and J). Adjusted R-squared (adj.R-squared) was used to check quality of relationship between substrate attributes and epifaunal descriptors.

Statistical analyses were performed using R open access statistical software 3.5.1 (R Core Team 2018). See the "Data availability and reproducible research" section for further details.

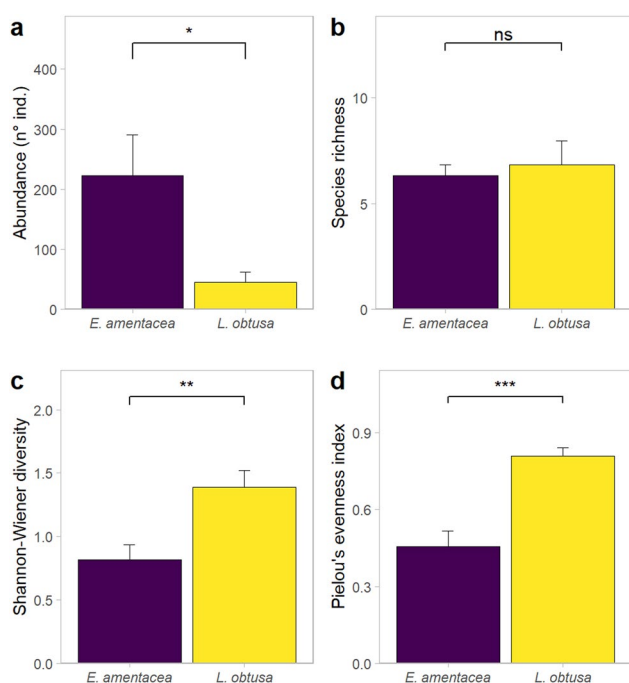
## 3. Results

Thallus volume (TV), thallus length (TL) and biomass (DW) were significantly higher in *E. amentacea* (average values  $\pm$  SE of TV =  $172 \pm 10.1$  ml, TL =  $142 \pm 3.8$  mm and DW =  $19 \pm 2.7$  gr) compared to *L. obtusa* (average values  $\pm$  SE of TV =  $38 \pm 6.1$  ml, TL =  $37 \pm 4.6$  mm and DW =  $5 \pm 0.4$  gr) (Figure 2, Table S1), while no significant differences were found between the two sites (Table S1).

Overall, 3215 individuals made up the epifauna collected, of which 2669 on *E. amentacea* and 546 on *L. obtusa*. Of these, Crustacea were the dominant group on both seaweeds in terms of number of individuals (*E. amentacea*=2527, *L. obtusa*=355), while Mollusca constituted the smaller part of the analyzed epifauna (*E. amentacea*=64, *L. obtusa*=168). In particular, among Crustacea amphipods were the most represented group with *Protohyale camptonyx* (Heller, 1866) being the most abundant species ( $190 \pm 63.1$  individuals) followed by *Jassa slatteryi* Conlan 1990 ( $17.1 \pm 3.4$  individuals) on *E. amentacea*, while *P. camptonyx* ( $13.8 \pm 8.6$  individuals) was followed by the species *Elasmopus pocillimanus* Costa, 1853 ( $7.6 \pm 5$  individuals) on *L. obtusa* (Table S2, Table S3). On the contrary, Mollusca were the dominant group on both seaweeds in terms of number of taxa (Mollusca 19 taxa compared to the 9 taxa of Crustacea), and were more abundant on *L. obtusa* (Mollusca 16 taxa: Crustacea 8 taxa) than on *E. amentacea* (Mollusca 10 taxa: Crustacea 9 taxa) (Table S2, Table S3). On *E. amentacea* the most abundant molluscan taxa were *Rissoa* sp., *Tricolia* sp., *Ocenebra edwardsii* and *Pisania striata* ( $0.2 \pm 0.1$  individuals), whereas *Rissoa similis* was the most abundant species on *L. obtusa*, with a mean value of  $5.6 \pm 2$  individuals respectively (Table S2, Table S3).



**Figure 2.** Variation of thallus volume (a), thallus length (b) and biomass (c) between *Ericaria amentacea* and *Laurencia obtusa*. Bar plots show mean  $\pm$  SE ( $n=6$ ). For more details see Table S1.



**Figure 3.** Abundance (a), species richness (b), Shannon-Wiener diversity (c), and Pielou's evenness index (d) of the epifaunal assemblage associated with *E. amentacea* and *L. obtusa*. Bar plots show mean  $\pm$  1 standard error ( $n=6$ ). Significant codes: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , ns  $p > 0.05$ . See Table S4 for further details.

Overall, *E. amentacea* clearly supported far higher epifaunal abundance than *L. obtusa* with average values of 277 and 48 respectively (Figure 3). However, species richness was comparable between the two seaweeds, while Shannon-Wiener diversity and Pielou's evenness were higher in *L. obtusa* compared to *E. amentacea* (Figure 3, Table S4).

The epifaunal structure and composition differed significantly among seaweeds (PERMANOVA results model- $F_{1,23} = 4.766$  and  $3.094$  for structure and composition, respectively,  $p < 0.001$ ; Table S5). PERMDISP analysis revealed no significant dispersion of samples within seaweeds. Principal coordinate analysis (PCoA) ordination plot clearly separated the structure of the epifaunal assemblage of the two seaweeds, while partial overlap was observed for the epifaunal composition (Figure 4). The first two axes of the PCoA explained

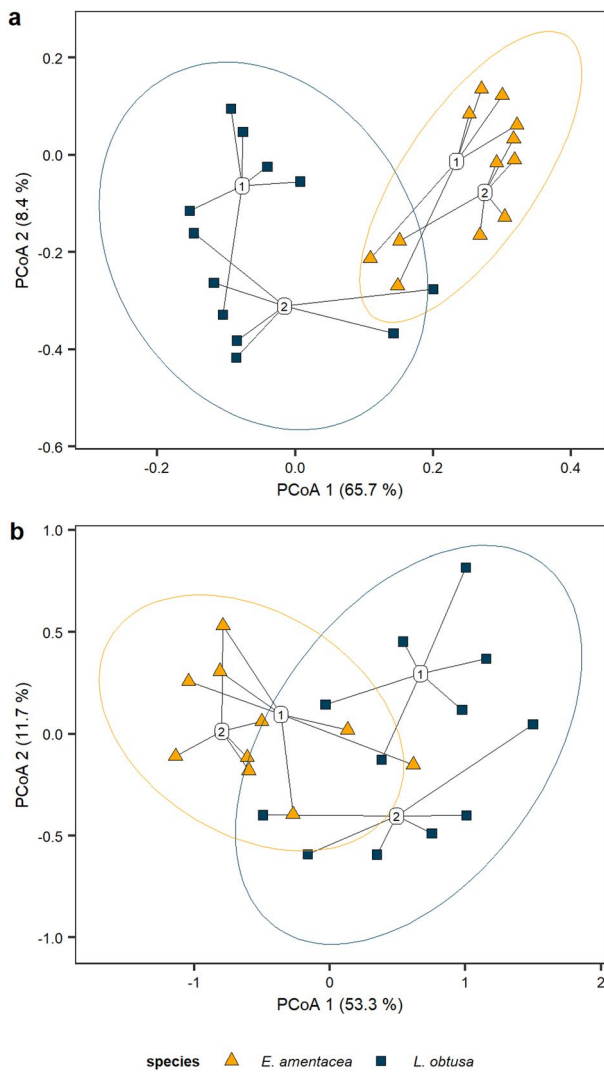
74.1% of variance for structure and 65% for composition. The first axis accounted for the larger part of the variance (structure = 65.7% and composition = 53.3%) and highlighted a shift, in both structure and composition, from *E. amentacea* to *L. obtusa* (Figure 4). The second axis explained lower variation (structure = 8.4% and composition = 11.7%) and tends to highlight differences of the epifaunal assemblage of each species between sites especially for composition (Figure 4).

Overall, three peracarid taxa (*P. camptonyx*, *J. slatteryi* and *E. pocillimanus*), Tanadiacea ind. and a gastropod mollusc (*R. similis*) mainly contributed 90% to the dissimilarity between *E. amentacea* and *L. obtusa* (SIMPER analysis; Table 1). *Protohyale camptonyx* alone contributed to 65% of the difference between the two seaweeds, being more abundant in *E. amentacea* than *L. obtusa* (Table 1, Figure 5). The other taxa contributed to other 23% of the observed differences, with the peracarid *J. slatteryi* and Tanadiacea ind. more abundant on *E. amentacea* compared to *L. obtusa*, whereas the gastropod *R. similis* and the amphipod *E. pocillimanus* were more represented on *L. obtusa* than *E. amentacea* (Table 1, Figure 5).

*Laurencia obtusa* showed a strong correlation between substrate attributes and epifaunal assemblage, while the substrate descriptors of *E. amentacea* were not related with any epifaunal descriptors (Table 2). In *L. obtusa*, linear regression analysis revealed that thallus length (TL) was the substrate attribute that best predicted (adj.R-squared  $> 0.5$ ) the variance of abundance (Figure 6) and Pielou's evenness of the epifaunal assemblage, whereas thallus volume (TV) best explained variation of species richness (Table 2).

#### 4. Discussion

According to our initial hypothesis, we found that *E. amentacea* was structurally more complex than *L. obtusa*, as shown by both the proxy of algal complexity used here (thallus volume, thallus length and biomass). We also found differences in the abundance and the diversity of the epifaunal assemblages between *E. amentacea* and *L. obtusa*. However, while *E. amentacea* had a higher number of epifaunal



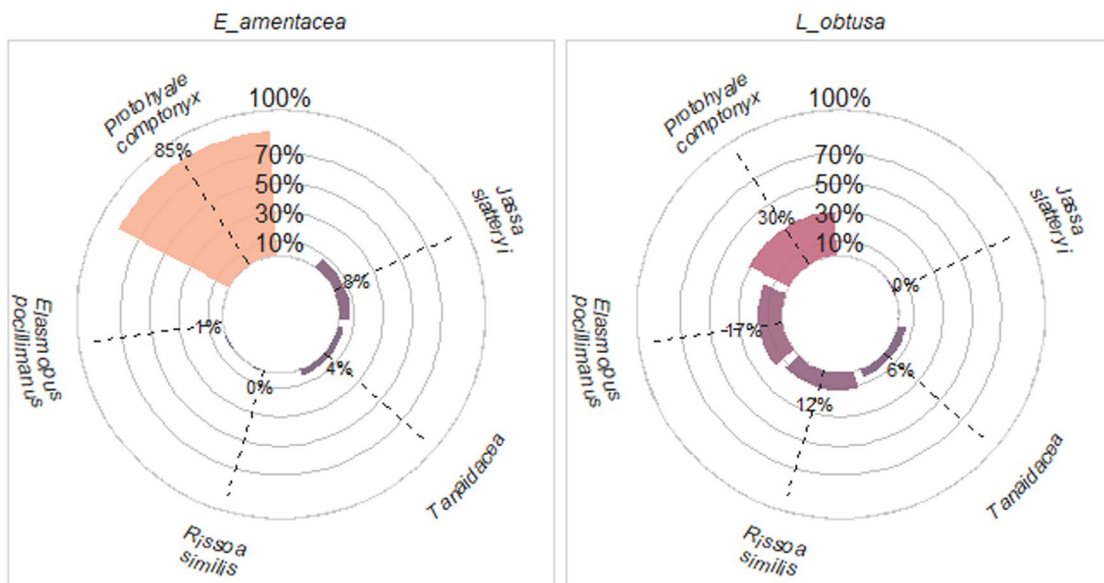
**Figure 4.** Structure (a) and composition (b) of the epifaunal assemblages associated with the two seaweeds. The circles show the 90% confidence interval for each seaweed.

individuals than *L. obtusa*, contrary to our hypothesis, *L. obtusa* had a more diversified epifauna assemblage (both in term of diversity and evenness) than *E. amentacea*. This was mainly due to the different abundances of the two epifaunal components between *L. obtusa* and *E. amentacea*, with *L. obtusa* hosting more molluscan taxa than *E. amentacea*, while the number of amphipod taxa were comparable between algal species.

Many studies highlighted the role of the seaweed structural complexity in shaping their epifaunal assemblage, with complex algae supporting higher abundance and greater number of epifaunal species compared to less complex macroalgae (Gee and Warwick 1994; Chemello and Milazzo 2002; Bedini et al. 2014; Pitacco et al. 2014; Veiga et al. 2014; Lolas et al. 2018; Veiga et al. 2018; Bitlis 2019; Chiarore et al. 2019; Poursanidis et al. 2019; Mancuso et al. 2021b, 2021a, 2022). For example, foundation seaweeds of the genera *Cystoseira*, *Ericaria*, *Gongolaria* (in the past all ascribed to the genus *Cystoseira*), seem to have more structured epifaunal assemblage compared to other less structurally complex macroalgae (Chemello and Milazzo 2002; Mancuso et al. 2021a, 2022). Our results show that although the volume, biomass and length of the thalli of *E. amentacea* were higher compared to *L. obtusa*, the epifaunal assemblage was less structured (low diverse and less evenness) compared to *Laurencia*.

**Table 1.** Results of the SIMPER analysis showing taxa that contributed to 90% of dissimilarity between habitats. **av E. amentacea** = average abundance in *Ericaria amentacea*, **av L. obtusa** = average abundance in *Laurencia obtusa*,  **$\delta i/SD(\delta i)$**  = average to sd ratio, **cum.  $\delta i\%$**  = cumulative contribution. SIMPER analysis was based on square-root transformed abundance of epifaunal taxa.

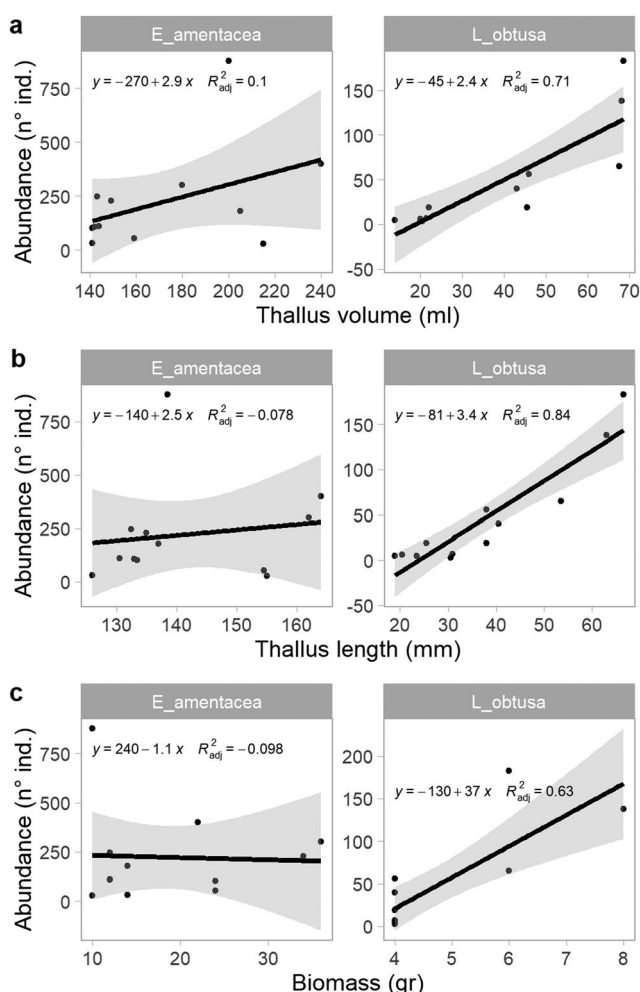
Taxa	av <i>E. amentacea</i>	av <i>L. obtusa</i>	$\delta i/SD(\delta i)$	cum. $\delta i\%$
<i>Protohyale comptonyx</i>	190.00	13.83	2.21	65
<i>Jassa slatteryi</i>	17.08	0.17	1.07	74
Tanaidacea ind.	9.17	2.58	0.78	81
<i>Rissoa similis</i>	0.08	5.58	0.63	85
<i>Elasmopus pocillimanus</i>	1.58	7.58	0.52	88



**Figure 5.** Relative abundances of the epifaunal taxa mainly contributing to the differences between *Ericaria amentacea* and *Laurencia obtusa*.

**Table 2.** Relationships (reported as adjusted R squared from LM) between thallus volume (TV), thallus length (TL) and biomass (DW) of *Ericaria amentacea* and *Laurencia obtusa*, and the abundance (N), species richness (S), Shannon-Wiener diversity (H) and Pielou's Evenness (J) of its associated epifauna. Values in bold are adj.R-squared major than 50%.

Structural features	N		S		H		J	
	Species							
	<i>E. amentacea</i>	<i>L. obtusa</i>	<i>E. amentacea</i>	<i>L. obtusa</i>	<i>E. amentacea</i>	<i>L. obtusa</i>	<i>E. amentacea</i>	<i>L. obtusa</i>
TV	0.1	<b>0.71</b>	-0.09	<b>0.56</b>	0.11	0.2	0.14	<b>0.62</b>
TL	-0.08	<b>0.84</b>	0.22	0.31	0.02	0	0.16	<b>0.69</b>
DW	-0.1	<b>0.63</b>	0.18	0.06	0.04	-0.08	0.14	0.45



**Figure 6.** Relationship between thallus volume (a), thallus length (b) and biomass (c) of *Ericaria amentacea* and *Laurencia obtusa* and the abundances of associated epifauna. Black lines and grey areas are linear regression and 95% confidence interval respectively.

Similar results have previously discovered comparing the epifaunal assemblages between *Gongolaria barbata* (Stackhouse) Kuntze (previously *Cystoseira barbata* (Stackhouse) C. Agardh) and *L. obtusa*, with *G. barbata* supporting lower abundances of epifauna compared to *L. obtusa* (Russo 1997). Russo (1997) hypothesised that, more than structural features of the seaweeds, allelochemicals may act as a defense against colonization by epibiota which represent a food source for most epifauna and that few epifauna species eat the host alga itself. Secondary metabolites released by seaweeds can act as chemical defense with the ability of shaping seaweed associated epifauna (Paul et al. 2006; Cacabelos et al. 2010; Máximo et al. 2018; Gache et al. 2019).

We suggest that further studies focused on the effects of metabolites released by *L. obtusa* and *E. amentacea* in shaping their associated epifauna would allow us to better clarify this aspect. However, we hypothesize that the lower abundances of molluscs in *E. amentacea* can be also related to the high wave actions due to the position of the alga. *Ericaria amentacea* grow in the external border of the vermetid reef where waves impact in a disruptive way, while *L. obtusa* is located just behind *E. amentacea* where the wave action, despite high, tends to be laminar (Donnarumma et al. 2021). Moreover, due to the structural characteristics (short cauloids and long fronds) thalli of *E. amentacea* make a whip effect under wave action, which could cause the detachment of molluscs from its canopy. The molluscs' low speed - but also their behaviour (when disturbed they tend to retract themselves into the shell) - would make them unable to return back quickly on the algae, whereas amphipods' high mobility and the presence of pereopods would allow them to stay easily attached and closer to the thallus.

Epifauna might choose algal species based on nutritional quality, chemical content, and architectural complexity, however it considers the host as a refuge from predators rather than a source of food (Nicotri 1980; Brawley 1992; Gee and Warwick 1994; Jormalainen et al. 2001). According to Duffy and Hay (1991) and Duffy et al. (2001), predation could be the most important factor in regulating the densities of phytal invertebrates. More-compact and complex macroalgae may better protect from visual predation (Edgar 1983; Jacobi and Langevin 1996). Meso-herbivores living on seaweeds with chemical defenses against fish may be resistant to their chemical defenses, making them less predated (Duffy and Hay 1994). Additionally, some amphipods' mimetic ability (body color similar to algal fronds) allows them to avoid predators (Stachowicz and Hay 1999; Norderhaug 2004). *Ericaria amentacea* thalli, consisting of numerous and dense primary branches covered by many spinose appendages, may offer more protection from predators than *L. obtusa* thalli, an openly branched alga with shorter branches towards apex. Thus, the high abundance of amphipods on *E. amentacea* could be also related to the capacity of the alga to protect their hosts from predation. Also in this case, further research aiming to investigate the effect of predation on the epifauna inhabiting seaweeds can help to clarify this aspect.

Substrate attributes of the two seaweeds were differently related with the abundance and species richness of the epifaunal assemblage, with *L. obtusa* structural features explained higher variance of epifaunal assemblage compared to that of *E. amentacea*. Contrary to what expected, the structural

features of *E. amentacea* were not able to explain variation of epifauna. This is in contrast with other studies which have highlighted the role of the structural features of *Cystoseira sensu lato* in shaping their associated biota (Russo 1997; Chemello and Milazzo 2002; Pitacco et al. 2014; Lolas et al. 2018; Bitlis 2019; Chiarore et al. 2019; Poursanidis et al. 2019; Mancuso et al. 2021b, 2021a, 2022). Conversely, the relationship between the substrate features of *L. obtusa* and its associated epifauna were coherent with other findings which highlighted the contribution of thallus height and biomass to the epifaunal assemblage variation (Janiak and Whitlatch 2012; Pitacco et al. 2014; Veiga et al. 2018; Bitlis 2019; Chiarore et al. 2019).

Overall, our findings confirm only in part the role of seaweed substrate properties in defining the epifaunal assemblage and highlight that other mechanisms like as chemical defence and wave action may be involved in epifaunal selection, implying that further investigation is necessary. Furthermore, our results imply that the loss of *E. amentacea*, resulting in a significant drop in habitat structural complexity, would affect the epifauna in terms of total abundance rather than diversity. However, this second assumption would not be a speculative observation, but rather food for thought about the necessity of additional ad hoc research.

## Authors contributions

M.F.P.: Methodology; Investigation; Data curation; Formal analysis; Visualization; Writing - Original Draft, Review & Editing; Identification of seaweeds. L.B.S.: Identification of amphipods; Writing - Review & Editing. C.R.: Identification of molluscs; Writing - Review & Editing. M.A.M.: Conceptualization; Project administration; Resources; Supervision; Data curation; Writing - Original Draft, Review & Editing; identification of seaweeds.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## Data availability statement

Data are not currently provided. Upon acceptance, all data will be provided on Mendeley Data DOI: 10.17632/zsh48fddh5.1

## References

- Agnetta D, Badalamenti F, Ceccherelli G, Di Trapani F, Bonaviri C, Gianguzza P. 2015. Role of two co-occurring Mediterranean sea urchins in the formation of barren from *Cystoseira* canopy. *Estuar Coast Shelf Sci.* 152:73–77.
- Anderson MJ, Gorley RN, Clarke KR. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. Plymouth, UK: PRIMER-E, Plymouth.
- Arevalo R, Pinedo S, Ballesteros E, Arévalo R, Pinedo S, Ballesteros E. 2007. Changes in the composition and structure of Mediterranean rocky-shore communities following a gradient of nutrient enrichment: descriptive study and test of proposed methods to assess water quality regarding macroalgae. *Mar Pollut Bull.* 55(1–6):104–113.
- Ballesteros E, Garrabou J, Hereu B, Zabala M, Cebrian E, Sala E. 2009. Deep-water stands of *Cystoseira zosteroides* C. Agardh (Fucales, Ochrophyta) in the Northwestern Mediterranean: insights into assemblage structure and population dynamics. *Estuar Coast Shelf Sci.* 82(3):477–484.
- Ballesteros E, Torras X, Pinedo S, García M, Mangialajo L, de Torres M. 2007. A new methodology based on littoral community cartography dominated by macroalgae for the implementation of the European Water Framework Directive. *Mar Pollut Bull.* 55(1–6):172–180.
- Bedini R, Bonechi L, Piazzini L. 2014. Mobile epifaunal assemblages associated with *Cystoseira* beds: comparison between areas invaded and not invaded by *Lophocladia lallemandii*. *Sci Mar.* 78(3):425–432.
- Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F. 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Mar Ecol Prog Ser.* 214:137–150.
- Bitlis B. 2019. Mollusk fauna associated with *Cystoseira barbata* (Stockhouse) C. Agardh, 1820 in the Sea of Marmara (Turkey). *Oceanol Hydrobiol Stud.* 48(2):174–183.
- Blanfuné A, Boudouresque CF, Verlaque M, Thibaut T. 2019. The ups and downs of a canopy-forming seaweed over a span of more than one century. *Sci Rep.* 9(1):1–10.
- Brawley SH. 1992. Mesoherbivores. In: John DM, Hawkins SJ, Price JH, editors. *Plant-animal interactions in the marine benthos*. Oxford: Clarendon Press; p. 235–263.
- Bulleri F, Benedetti-Cecchi L, Acunto S, Cinelli F, Hawkins SJ. 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *J Exp Mar Bio Ecol.* 267(1):89–106.
- Buonomo R, Chefaoui RM, Lacida RB, Engelen AH, Serrão EA, Airoldi L. 2018. Predicted extinction of unique genetic diversity in marine forests of *Cystoseira* spp. *Mar Environ Res.* 138:119–128.
- Cacabelos E, Olabarria C, Incera M, Troncoso JS. 2010. Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. *Estuar Coast Shelf Sci.* 89(1):43–52.
- Chemello R, Milazzo M. 2002. Effect of algal architecture on associated fauna: some evidence from phytal molluscs. *Mar Biol.* 140(5):981–990.
- Chemello R. 2009. Marine bioconstructions in the Mediterranean Sea. A state-of-the-art on the vermetid reef. *Biol Mar Mediterr.* 16:2–18.
- Cheminée A, Sala E, Pastor J, Bodilis P, Thiriet P, Mangialajo L, Cottalorda JM, Francour P. 2013. Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes. *J Exp Mar Bio Ecol.* 442:70–79.
- Chiarore A, Bertocci I, Fioretti S, Meccariello A, Saccone G, Crocetta F, Patti FP. 2019. Syntopic *Cystoseira* taxa support different molluscan assemblages in the Gulf of Naples (southern Tyrrhenian Sea). *Mar Freshwater Res.* 70(11):1561–1575.
- Christie H, Norderhaug KM, Fredriksen S. 2009. Macrophytes as habitat for fauna. *Mar Ecol Prog Ser.* 396:221–233.
- Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecol.* 18(1):117–143.
- Conlan KE, Desiderato A, Beermann J. 2021. *Jassa* (Crustacea: amphipoda): a new morphological and molecular assessment of the genus. *Zootaxa.* 4939(1):zootaxa.4939.1.1.
- Connell SD, Foster MS, Airoldi L. 2014. What are algal turfs? Towards a better description of turfs. *Mar Ecol Prog Ser.* 495:299–307.
- Cormaci M, Furnari G, Catra M, Alongi G, Giaccone G. 2012. Flora marina bentonica del Mediterraneo: phaeophyceae\*. *Boll dell'Accademia Gioenia di Sci Nat.* 45:1–508.
- Council of Europe. 1979. Convention on the Conservation of European Wildlife and Natural Habitats Convention relative à la conservation de la vie sauvage et du milieu naturel de l'Europe. Annexe I – Espèces De Flore Strictement Protégées 1–24.
- De La Fuente G, Asnaghi V, Chiantore M, Thrush S, Povero P, Vassallo P, Petrillo M, Paoli C. 2019. The effect of *Cystoseira* canopy on the value

- of midlittoral habitats in NW Mediterranean, an emergy assessment. *Ecol. Modell.* 404:1–11.
- Donnarumma L, D'Argenio A, Sandulli R, Russo GF, Chemello R. 2021. Unmanned aerial vehicle technology to assess the state of threatened biogenic formations: the vermetid reefs of mediterranean intertidal rocky coasts. *Estuar Coast Shelf Sci.* 251:107228.
- Duffy JE, Hay ME. 1991. Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology.* 72(4):1286–1298.
- Duffy JE, Hay ME. 1994. Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology.* 75(5):1304–1319.
- Duffy JE, Macdonald KS, Rhode JM, John D, Duffy J, E, Macdonald KS, Rhode JM, Parker JD. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. 82:2417–2434.
- Edgar GJ. 1983. The ecology of south-east tasmanian phytal animal communities. IV. Factors affecting the distribution of amphitoid amphipods among algae. *J Exp Mar Bio Ecol.* 70(3):205–225.
- Ellison AM. 2019. Foundation species, non-trophic interactions, and the value of being common. *ISCIENCE.* 13:254–268.
- Falace A, Bressan G. 2006. Seasonal variations of *Cystoseira barbata* (Stackhouse) C. Agardh frond architecture. *Hydrobiologia.* 555(1):193–206.
- Gache C, Bertucci F, Guerra AS, Calandra M, Berr T, Lafaye J, Jorissen H, Nugues M, Cossy J, Lecchini D. 2019. Effects of *Asparagopsis taxiformis* metabolites on the feeding behaviour of post-larval *Acanthurus triostegus*. *J Fish Biol.* 95(5):1355–1358.
- Gee J, Warwick R. 1994. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Mar Ecol Prog Ser.* 104:141–150.
- Giaccone G, Alongi G, Pizzuto F, Cossu AVL. 1994. La Vegetazione marina bentonica fotofila del Mediterraneo: 2. Infralitorale e Circalitorale: proposte di aggiornamento. *Boll. dell'Accademia Gioenia Di Sci. Nat.* 27:111–157.
- Gómez-Garreta A, Barceló M, Gallardo T, Pérez-Ruzafa I, Ribera MA, Rull J. 2002. Flora phycologica iberica. Vol. 1. Fucales: Universida. ed. Murcia.
- Hacker SD, Steneck RS. 1990. Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology.* 71(6):2269–2285.
- Jacobi CM, Langevin R. 1996. Habitat geometry of benthic substrata: effects on arrival and settlement of mobile epifauna. *J Exp Mar Bio Ecol.* 206(1–2):39–54.
- Janiak DS, Whitlatch RB. 2012. Epifaunal and algal assemblages associated with the native *Chondrus crispus* (Stackhouse) and the non-native *Grateloupia turuturu* (Yamada) in eastern Long Island Sound. *J Exp Mar Bio Ecol.* 413:38–44.
- Jormalainen V, Honkanen T, Heikkilä N. 2001. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Mar Ecol Prog Ser.* 220:219–230.
- Jormalainen V, Honkanen T. 2008. Macroalgal chemical defenses and their roles in structuring temperate marine communities. *Algal Chem Ecol.* 9783540741:57–89.
- Kovalenko KE, Thomaz SM, Warfe DM. 2012. Habitat complexity: approaches and future directions. *Hydrobiologia.* 685(1):1–17.
- Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Connell SD, Johnson CR, Konar B, Ling SD, et al. 2016. Global patterns of kelp forest change over the past half-century. *Proc Natl Acad Sci U S A.* 113(48):13785–13790.
- Lolas A, Antoniadou C, Vafidis D. 2018. Spatial variation of Molluscan fauna associated with *Cystoseira* assemblages from a semi-enclosed gulf in the Aegean Sea. *Reg Stud Mar Sci.* 19:17–24.
- Mancuso FP, D'Agostaro R, Milazzo M, Badalamenti F, Musco L, Mikac B, Lo Brutto S, Chemello R. 2022. The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and biodiversity of native algal forests in the Mediterranean Sea. *Mar Environ Res.* 173:105515.
- Mancuso FP, D'Agostaro R, Milazzo M, Chemello R. 2021a. The invasive *Asparagopsis taxiformis* hosts a low diverse and less trophic structured Molluscan assemblage compared with the native *Ericaria brachycarpa*. *Mar Environ Res.* 166:105279.
- Mancuso FP, Milazzo M, Chemello R. 2021b. Decreasing in patch-size of *Cystoseira* forests reduces the diversity of their associated molluscan assemblage in Mediterranean rocky reefs. *Estuar Coast Shelf Sci.* 250:107163.
- Mancuso FP, Strain EMA, Piccioni E, De Clerck O, Sarà G, Airoldi L. 2018. Status of vulnerable *Cystoseira* populations along the Italian infralittoral fringe, and relationships with environmental and anthropogenic variables. *Mar Pollut Bull.* 129(2):762–771.
- Mangialajo L, Chiantore M, Cattaneo-Vietti R. 2008. Loss of furoid algae along a gradient of urbanisation, and structure of benthic assemblages. *Mar Ecol Prog Ser.* 358:63–74.
- Mangialajo L, Ruggieri N, Asnaghi V, Chiantore M, Povero P, Cattaneo-Vietti R. 2007. Ecological status in the Ligurian Sea: the effect of coastline urbanisation and the importance of proper reference sites. *Mar Pollut Bull.* 55(1–6):30–41.
- Mannino AM, Mancuso FP. 2009. Guida all'identificazione delle Cistoseire (Area Marina Protetta "Capo Gallo-Isola delle Femmine). Palermo.
- Máximo P, Ferreira L, Branco P, Lima P, Lourenço A. 2018. Secondary metabolites and biological activity of invasive macroalgae of Southern Europe. *Mar Drugs.* 16(8):265.
- Mineur F, Arenas F, Assis J, Davies AJ, Engelen AH, Fernandes F, Malta E, Thibaut T, Van Nguyen T, Vaz-Pinto F, et al. 2015. European seaweeds under pressure: consequences for communities and ecosystem functioning. *J Sea Res.* 98:91–108.
- Molinari Novoa EA, Guiry MD. 2020. Reinstatement of the genera *Gongolaria* Boehmer and *Ericaria* Stackhouse (Sargassaceae, Phaeophyceae). *Not. Algarum.* 172:1–10.
- Nicotri ME. 1980. Factors involved in herbivore food preference. *J Exp Mar Bio Ecol.* 42(1):13–26.
- Nikolić V, Žuljević A, Mangialajo L, Antolić B, Kušpilić G, Ballesteros E. 2013. Cartography of littoral rocky-shore communities (CARLIT) as a tool for ecological quality assessment of coastal waters in the Eastern Adriatic Sea. *Ecol Indic.* 34:87–93.
- Norderhaug KM. 2004. Use of red algae as hosts by kelp-associated amphipods. *Mar Biol.* 144(2):225–230.
- Orellana S, Hernández M, Sansón M. 2019. Diversity of *Cystoseira sensu lato* (Fucales, Phaeophyceae) in the eastern Atlantic and Mediterranean based on morphological and DNA evidence, including *Carpodesmia* gen. emend. and *Treptacantha* gen. emend. *Eur J Phycol.* 54(3):447–465.
- Paul N, de Nys R, Steinberg P. 2006. Seaweed-herbivore interactions at a small scale: direct tests of feeding deterrence by filamentous algae. *Mar Ecol Prog Ser.* 323:1–9.
- Piazzoli L, Bonaviri C, Castelli A, Ceccherelli G, Costa G, Curini-Galletti M, Langeneck J, Manconi R, Montefalcone M, Pipitone C, et al. 2018. Biodiversity in canopy-forming algae: structure and spatial variability of the Mediterranean *Cystoseira* assemblages. *Estuar Coast Shelf Sci.* 207:132–141.
- Pitacco V, Orlando-Bonaca M, Mavrič B, Popović A, Lipej L. 2014. Mollusc fauna associated with the *Cystoseira* algal associations in the Gulf of Trieste (Northern Adriatic Sea). *Medit Mar Sci.* 15(2):225.
- Poursanidis D, Chatzigeorgiou G, Dimitriadis C, Koutsoubas D, Arvanitidis C. 2019. Testing the robustness of a coastal biodiversity data protocol in the Mediterranean: insights from the molluscan assemblages from the sublittoral macroalgae communities. *Hydrobiologia.* 826(1):159–172.
- R Core Team. 2018. R: a language and environment for statistical computing.
- Rodriguez-Prieto C, Ballesteros E, Boisset F, Alfonso-Carrillo J. 2015. Algae fanerogame del Mediterraneo. In: Il Castello, editor.
- Russo A. 1997. Epifauna living on sublittoral seaweeds around Cyprus. *Hydrobiologia.* 344(1/2/3):169–179.
- Schiel DR, Foster MS. 2006. The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. *Annu Rev Ecol Evol Syst.* 37(1):343–372.
- Sciuto F, Rosso A, Sanfilippo R, Alongi G, Catra M, Serio D, Bejaoui S, Leonardi R, Viola A. 2018. First data on ostracods and foraminifera living in *Cystoseira* associations in western Ionian Sea. *Medit Mar Sci.* 18(3):393–405.



- Stachowicz JJ, Hay ME. 1999. Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. *Ecology*. 80(2):495–509.
- Stein-Taylor JR, Littler MM, Littler DS, America, P.S. of. 1985. *Handbook of phycological methods: volume 4: ecological field methods: macroalgae*. Cambridge: Cambridge University Press; 448 p.
- Strain EMA, Thomson RJ, Micheli F, Mancuso FP, Airoidi L. 2014. Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Glob Chang Biol*. 20(11):3300–3312.
- Thibaut T, Pinedo S, Torras X, Ballesteros E. 2005. Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Mar Pollut Bull*. 50(12):1472–1489.
- Underwood AJ. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge: Cambridge University Press; 504 p.
- Vázquez-Luis M, Sanchez-Jerez P, Bayle-Sempere JT. 2008. Changes in amphipod (Crustacea) assemblages associated with shallow-water algal habitats invaded by *Caulerpa racemosa* var. *cylindracea* in the western Mediterranean Sea. *Mar Environ Res*. 65(5):416–426.
- Veiga P, Rubal M, Sousa-Pinto I. 2014. Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species. *Mar Environ Res*. 101:115–123.
- Veiga P, Torres AC, Besteiro C, Rubal M. 2018. Mollusc assemblages associated with invasive and native *Sargassum* species. *Cont Shelf Res*. 161:12–19.
- WoRMS Editorial Board. 2021. *World Register of Marine Species (WoRMS)*.