

Epifauna associated to the introduced *Gracilaria vermiculophylla* (Rhodophyta; Florideophyceae: Gracilariales) and comparison with the native *Ulva rigida* (Chlorophyta; Ulvophyceae: Ulvales) in an Adriatic lagoon

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Abstract

The composition and structure of epifaunal assemblages associated with the non-native *Gracilaria vermiculophylla* (Rhodophyta; Florideophyceae: Gracilariales) was analyzed and compared to those associated with the native *Ulva rigida* (Chlorophyta; Ulvophyceae: Ulvaceae). In a shallow coastal lagoon of the northwestern Adriatic Sea, we collected samples of each species from two different sites over a 5-year period. Epifaunal assemblages differed according to the habitat attributes provided by each type of seaweed. Amphipods comprised most of the epifaunal abundance on *U. rigida*, while gastropods comprised it on *G. vermiculophylla*. The architecturally more complex *G. vermiculophylla* supported higher species richness and diversity of associated macrofauna. Differences in structural complexity of the two seaweeds (irregularly branched *vs* flat sheet-like thalli) allow different (taxonomically and functionally) epifaunal assemblages.

Keywords: *Gracilaria vermiculophylla*, *Ulva rigida*, macrofauna, habitat architecture, Adriatic Sea

Introduction

Gracilaria vermiculophylla (Ohmi) Papenfuss (Florideophyceae: Gracilariales), is an invasive Rhodophyta recently recorded in the Po Delta lagoons (Sfriso et al. 2010). The species, which is native to Japan and Korea, was first recorded on the northern coasts of the Atlantic Sea in 2002 (Rueness 2005; Thomsen et al. 2007) and has rapidly colonised many European coasts and the lagoons of the Northern Adriatic Sea (Sfriso et al. 2012). In the Adriatic Sea, the most probable introduction vectors were clam farms, which imported the Manila clam *Ruditapes philippinarum* (Adams & Reeve, 1850) (Sfriso et al. 2012). This coarsely branched seaweed is particularly well adapted to low-energy, shallow soft bottom environments, like lagoons, harbours and inlets (Rueness 2005).

In the marine environment, seaweeds are of great ecological importance, particularly as primary producers and as habitat formers, providing space, shelter and food for a variety of associated epifaunal

organisms. Several papers have dealt with the role of marine seaweeds in structuring epifaunal assemblages, some of them comparing how different species of macroalgae influence the abundance, richness and diversity of associated assemblages (Chemello & Milazzo 2002). Seaweeds are three-dimensional biogenic habitats with a structural complexity that changes between and within macroalgal species. We may expect that patterns of composition and abundance of associated epifaunal organisms are influenced by the arrangement of structural elements within the habitat (Gee & Warwick 1994).

This study, carried out in a low-energy lagoon in the Northern Adriatic, focused on assemblages of epifauna associated with the invasive *G. vermiculophylla*, in comparison with the epifauna associated to the most common native seaweed *Ulva rigida* C. Agardh, 1822 (Chlorophyta; Ulvophyceae: Ulvaceae). No spatial and/or temporal studies of species composition and abundance of the macrofauna associated with seaweeds have been conducted in the Northern Adriatic

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lagoons. Our main goal was to analyse the composition and abundance of epifaunal assemblages associated with two habitat-forming algae, the non-native *G. vermiculophylla* and the native *U. rigida*. The two species have differences in structure; thus, distinctly different macrofaunal responses might be expected, with the more structurally complex *G. vermiculophylla* harbouring more abundant and diverse assemblages of invertebrates. In this study, we took advantage of the presence of the two seaweeds in the same environment (an Adriatic shallow lagoon) to test the following hypotheses: (i) the composition of macrofaunal (> 0.5 mm) assemblages associated with the two seaweeds differ because they have different structure; (ii) at a small spatial scale of observation, higher levels of habitat architecture (e.g. seaweed structure) support higher community abundance and diversity; (iii) patterns of composition and community structure of macrofaunal assemblages associated with the two seaweeds are consistent over a long time frame (5 years).

Materials and methods

Study site

The Marinetta Lagoon (Figure 1) is a microtidal, shallow water body (average depth 1 m) located in the northernmost part of the Po River Delta. The lagoon is connected to the Adriatic Sea by a quite narrow mouth (about 100 m wide), and has a surface area of

11.5 km². It is grossly divided into two parts by the terminal trait of the Po di Levante, a secondary deltaic branch of the Po River. The lagoon receives fresh water through the Po di Levante, whose discharge is controlled by a sluice and is regulated according to rainfall patterns. The western part of the lagoon has sandy bottoms, and part of it is utilised to rear the Manila clam *Ruditapes philippinarum*, while the eastern part of the lagoon is characterised by shelly–muddy bottoms and by reduced hydrodynamism; the annual salinity range is 29–11 (Vincenzi et al. 2014), depending on fresh water discharge from the Po di Levante and, thus, from precipitation.

Field methods

In the Marinetta Lagoon, we chose two sites dominated by the two seaweeds. Site G (45°02'47.78"N; 12°22'09.73"E) had a depth of 100 cm, and was dominated by *Gracilaria vermiculophylla*. Site U (45.03'19.11"N; 12°22'46.45"E) was shallower (40 cm depth) and was dominated by *Ulva rigida*. The main environmental conditions (salinity, dissolved oxygen, sediment texture) at the two sites were similar, with site G slightly more confined (*sensu* Guelorget & Perthuisot 1983) than site U (Mistri 2010).

Seaweeds and associated macrofauna samples were collected according to McIntyre et al. (1984), by pulling a cylinder (radius: 15 cm) with one end closed by a net of 0.5-mm mesh horizontally for

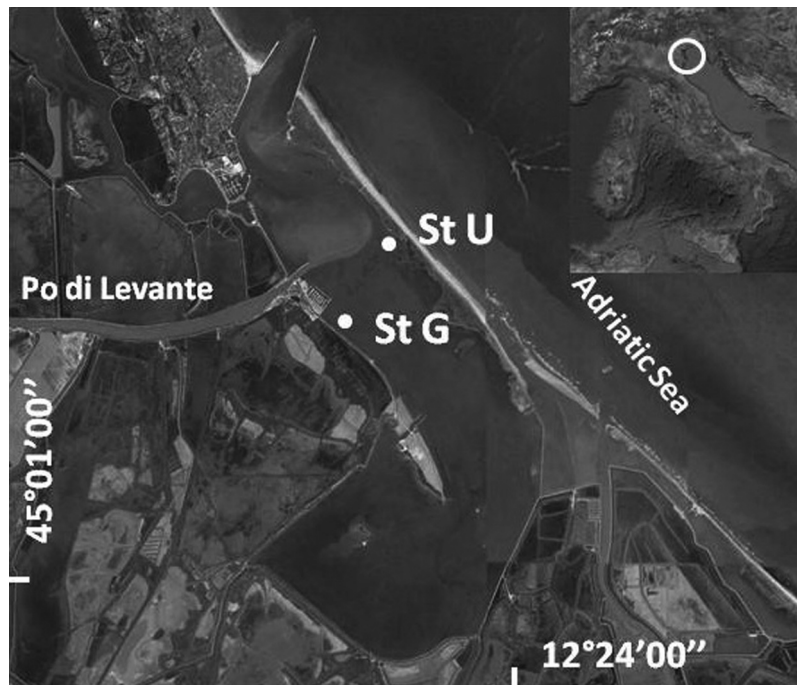


Figure 1. Marinetta Lagoon and study sites (StU: site U; StG: site G).

100 cm of path length (volume of water sampled: 70 L) through the seaweed mat. Each sample was carefully placed into a plastic bag and taken to the laboratory for further sorting. Using this procedure, we were able to sample motile organisms associated with seaweeds. Each site was sampled in triplicate with seasonal frequency, from 2006 to 2010. In the laboratory, the seaweeds were washed and then sieved through 0.5-mm mesh to recover macrofaunal organisms. We also scrutinized the entire thalli of seaweeds to find the epibionts attached to them. Then, all organisms collected were identified to the lowest possible taxonomic level. Each species was assigned a feeding strategy, based on literature data; four major trophic groups were distinguished: suspension feeders (SF), deposit feeders (DF), predators (P) and herbivores (H).

Dry weight (DW) of seaweeds was calculated after drying them for 48 h at 60°C.

Data analysis

Non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was used to test hypotheses about differences of epifaunal assemblages. This approach partitions the variability in the original dissimilarity matrix according to the full multifactorial design, with tests of individual terms obtained using permutations. Analyses followed a three-factor orthogonal design, with two habitats (*G. vermiculophylla* and *U. rigida*; fixed), four seasons (spring, summer, fall and winter; fixed), and 5 years (2006–2010; random). P-values were provided using unrestricted (9999) permutation of raw abundance data. When low unique values in the permutation distribution were available, asymptotical Monte Carlo P-values were used instead of permutational P-values. In addition, responses of assemblages were visualized by non-metric multidimensional scaling (nMDS) on the basis of Bray–Curtis dissimilarity matrices on fourth-root transformed density data. The SIMPER (similarity percentage) procedure was used to identify the percentage contribution of each taxon to the Bray–Curtis dissimilarity between the averages of groups. Taxa were considered important if their contribution to percentage dissimilarity was > 2%. Multivariate analyses were conducted using Primer v. 6 and PERMANOVA (Primer-E Ltd., Plymouth, UK).

Changes in number of species (S), number of individuals (N) and diversity (Shannon–Wiener's H') were analysed using analyses of variance (ANOVA). When significant differences between main factors or their interactions were found, Tukey's HSD (honest significant difference) tests were used as a posteriori comparison. The

homogeneity of variances was examined using Levene's test, and data were transformed when necessary to remove heteroscedasticity (Underwood 1997).

Results

In our field survey, seaweed highest average biomass was 85.9 (\pm 28 standard deviation, SD) g DW 70 L⁻¹ for *Gracilaria vermiculophylla*, and 65.7 (\pm 15.2 SD) g DW 70 L⁻¹ for *Ulva rigida* (Figure 2). *G. vermiculophylla* and *U. rigida* biomass significantly influenced total macrofaunal abundance, and at both sites, significantly positive patterns (site G: $r = 641$; site U: $r = 0.709$; both $P < 0.05$) were shown. For this reason, the density of each macrofaunal taxon was expressed as the number of animals per g DW of seaweed.

Figure 3 shows the average taxonomic composition of faunal community at the two sites. Three groups (in decreasing order of overall abundance: Amphipoda, Mollusca and Polychaetes) accounted for over 95% of all individuals observed. At site U, amphipods comprised most of the epifaunal abundance, accounting for 61% of the total. Bivalves were the second most numerous epifauna at 21% of total. At site G, conversely, gastropods (34% of total) were the most numerous epifauna, followed by amphipods (25.7%), bivalves (25.6%) and polychaetes (11%). At both sites, an increase in abundance of the invasive species *Arcuatula senhousia* (Benson in Cantor, 1842) (Mollusca: Mytilidae) was registered through time, with more than 10 individuals (ind) g DW in the warmer months of 2010 at site U.

Epifaunal assemblages differed to the habitat attributes provided by each type of seaweed. In fact, the composition of epifaunal assemblages varied significantly between the two sites (PERMANOVA; Table I); there were significant differences over time, particularly between warm and cold seasons of each year (pairwise tests not reported for brevity). Only in spring 2009 and 2010, the epibenthic assemblages at the two sites did not show significant differences in composition (pairwise test, $t = 1.91$ and $t = 1.84$ respectively, both $P = 0.07$). The non-metric multidimensional scaling (nMDS) plot (Figure 4) shows a clear separation of epifaunal communities from the two sites, with *G. vermiculophylla* points on the right and *U. rigida* on the left side of the plot. Dissimilarity between the two sites was 71.24%. The contribution from epifaunal species abundance to the average Bray–Curtis dissimilarity between the sites U and G (through SIMPER analysis; Table II) showed that differences were mainly due to the average higher proportion of the amphipods *Gammarus aequicauda* (Martynov, 1931)

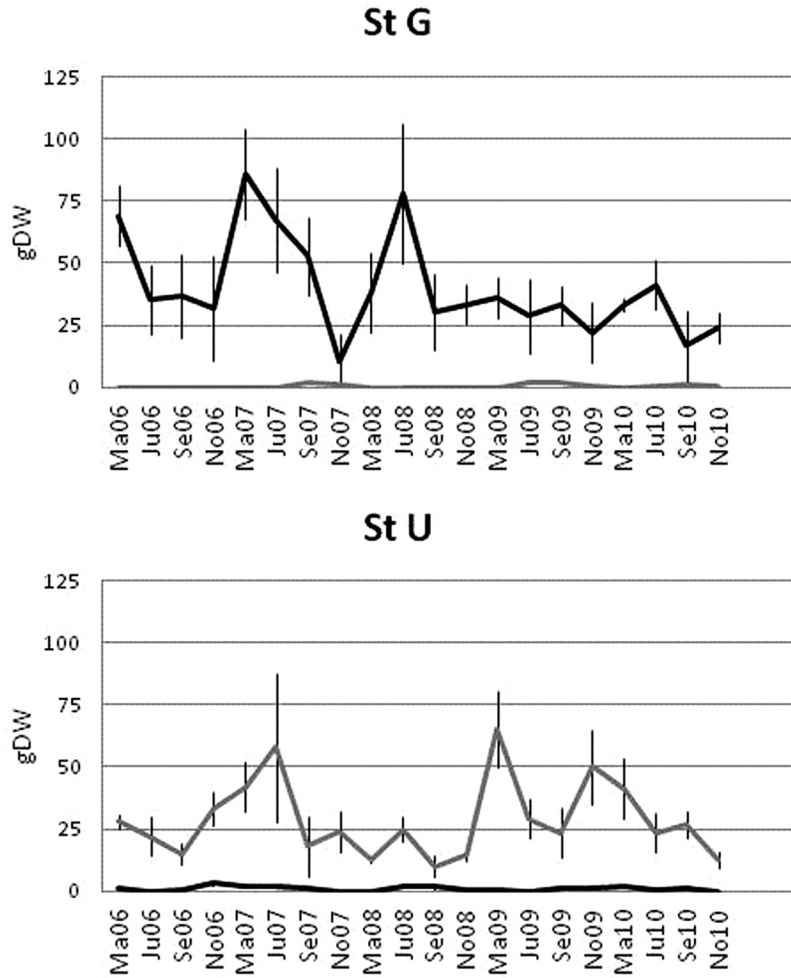


Figure 2. Average amount of macroalgae (as gDW) at the study sites (site G: StG; site U: StU; black: *Gracilaria vermiculophylla*; Grey: *Ulva rigida*; bars are SD). Ma06: March 2006; Ju06: June 2006; etc.

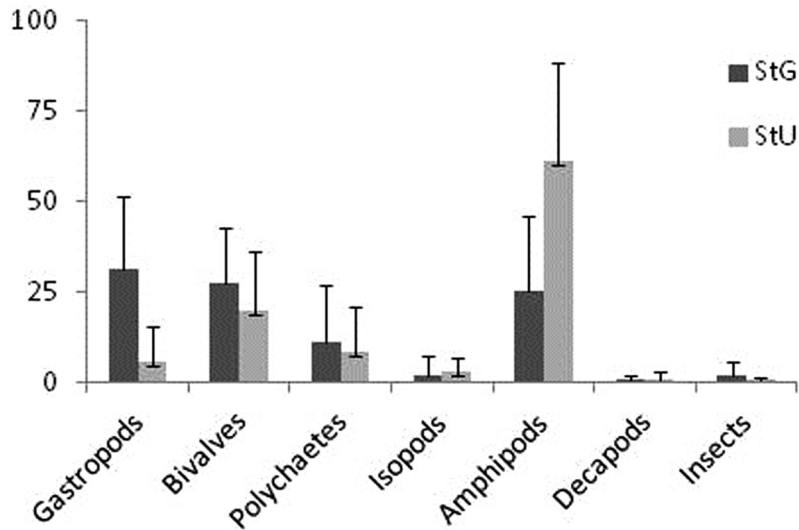


Figure 3. Average composition of epifaunal assemblages at each sampling site (site G: StG; site U: StU; bars are SD).

Table I. PERMANOVA: result of main test from unrestricted permutation of raw data.

Source	df	SS	MS	Pseudo-F	P(perm)	P(MC)
Habitat (H)	1	50760	50760	11.863	0.0119	0.0004
Season (S)	3	22604	7534.6	1.8449	0.0449	0.0301
Year (Y)	4	47357	11839	17.71	0.0001	0.0001
H × S	3	9964.2	3321.4	1.1623	0.3298	0.3185
H × Y	4	17116	4278.9	6.4006	0.0001	0.0001
S × Y	12	49007	4084	6.109	0.0001	0.0001
H × S × Y	12	34293	2857.7	4.2747	0.0001	0.0001
Residuals	80	53481	668.52			
Total	119	2.85E+05				

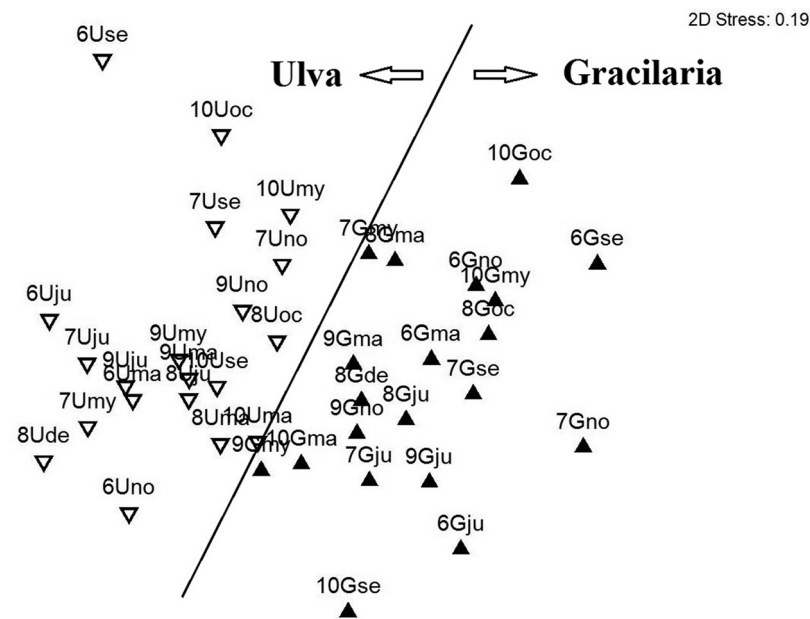


Figure 4. Ordination plot of epifaunal assemblages. Point acronyms: year (7: 2007; 8: 2008; etc.); site (G and U), and time (ma: March; ju: June; etc.) of sampling (black triangle: *Gracilaria vermiculophylla*; white triangle: *Ulva rigida*).

Table II. Summary of differences in abundance of major epifaunal taxa found on *Gracilaria* versus *Ulva* habitats.

Species	<i>Gracilaria</i> avg abundance	<i>Ulva</i> avg abundance	Avg dissimilarity	% contribution to overall dissimilarity	% cumulative contribution
<i>Gammarus aequicauda</i>	1.14	4.79	20.38	28.61	28.61
<i>Ecrobia ventrosa</i>	2.64	0.63	12.03	16.88	45.5
<i>Arcuatula senhousia</i>	1.96	2.21	11.69	16.41	61.91
<i>Microdeutopus gryllotalpa</i>	0.56	1.5	7.91	11.11	73.02
<i>Hydroides dianthus</i>	0.49	0.67	4.17	5.86	78.88
<i>Ficopomatus enigmaticus</i>	0.19	0.42	2.36	3.32	82.19
<i>Cerastoderma glaucum</i>	0.3	0	1.83	2.57	84.76
<i>Idothea baltica</i>	0.2	0.24	1.82	2.55	87.31
<i>Monocorophium insidiosum</i>	0.3	0	1.67	2.35	89.66
<i>Mytilus galloprovincialis</i>	0.02	0.24	1.44	2.03	91.68

and *Microdeutopus gryllotalpa* Costa, 1853, together with *A. senhousia*, at site U, and the gastropod *Ecrobia ventrosa* (Montagu, 1803) at site G. At site U, eight taxa contributed to a cumulative similarity

of 91.7%, while there were 10 taxa at site G (Table II).

Average species richness (S), abundance (N) and diversity (H') at the two sites are shown in Figure 5.

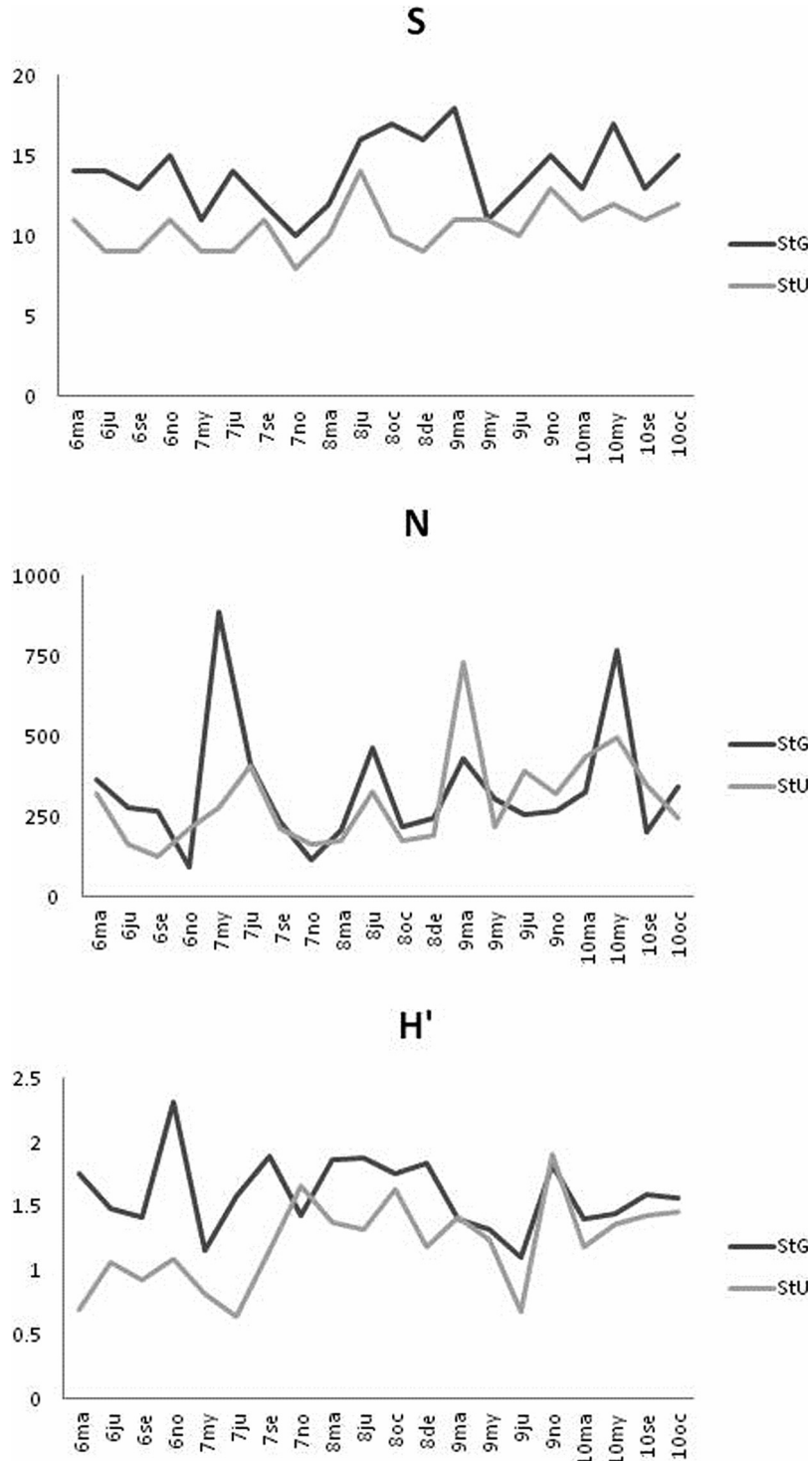


Figure 5. Epifaunal community descriptors (average values) at the two sites (site G: StG; site U: StU): S, number of species; N, abundance (as N ind g DW⁻¹), and H', diversity. March 2006: 6ma; June 2006: 6ju; etc.

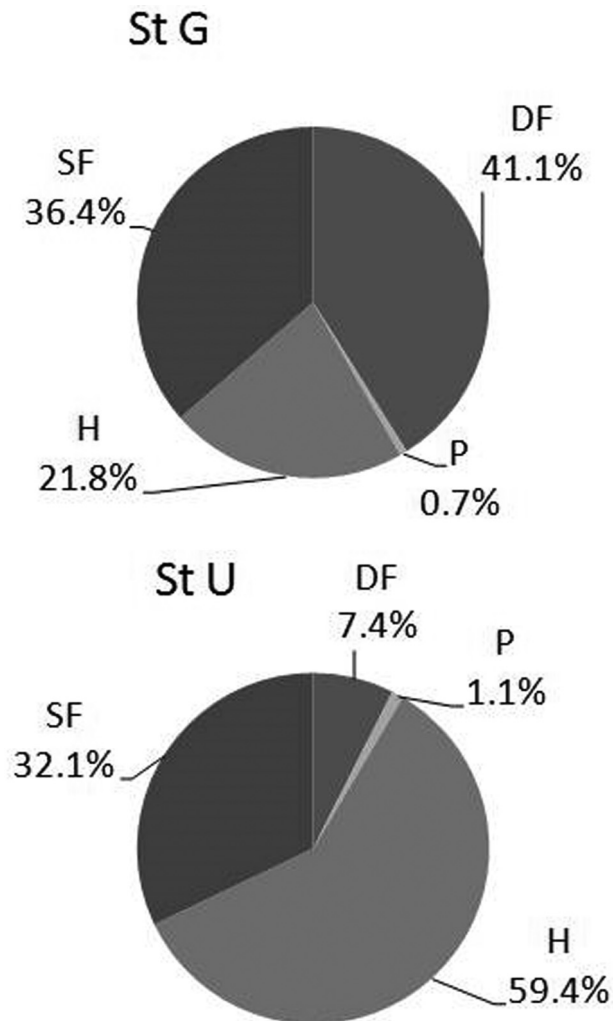


Figure 6. Average composition of feeding strategies at the two sites (site G: StG; site U: StU): suspension feeders (SF), deposit feeders (DF), predators (P) and herbivores (H).

Epifaunal assemblages at site G showed a significant higher species richness and diversity (ANOVA; both $P = 0.001$) with respect to site U.

In Figure 6, the average community composition by trophic groups is shown. Site G was dominated by deposit feeders (41.1%) and by suspension feeders (36.4%), while site U was dominated by herbivores (59.4%) followed by suspension feeders (32.1%), thus reflecting the numerical dominance of different taxa (gastropods at G, and amphipods at U) at the two sites.

Discussion

During our study period, macroalgal mats at the two sites in Marinetta Lagoon were present in relatively small amounts (compared to blooms reported, for example, in Ye et al. 2011), and probably for this

reason, adverse effects on the biota (e.g. Raffaelli et al. 1998) have not been observed. The results of this study indicated that our initial hypotheses were partially supported. Macrofaunal assemblages associated with *G. vermiculophylla* and *U. rigida* differed. Macrofaunal assemblages associated with the non-native *G. vermiculophylla* were more diverse (its morphology created a three-dimensional mosaic of structures and interstitial spaces for different types of invertebrates to occupy), but not more abundant. Patterns of community structure were consistent over time, but community composition changed, mostly due to the spread of the non-indigenous bivalve *Arcuatula senhousia*.

The importance of seaweed communities as habitats in temperate coastal waters is principally attributed to their complex, three-dimensional structure (Norkko et al. 2000). In Marinetta Lagoon, the

seaweeds *G. vermiculophylla* and *U. rigida* provide extensive vegetative structure on sand and mudflats that are otherwise devoid of macrophyte structure (Sfriso et al. 2012). This study has shown that large numbers of epifaunal individuals are associated with them. The most likely sources for colonisation are ambient benthic fauna, and pelagic larvae. Three groups (Amphipoda, Mollusca and Polychaetes) dominated, in terms of abundance, the epifaunal assemblages inhabiting *G. vermiculophylla* and *U. rigida* thalli. Our results also show that epifaunal abundances increase with increasing mass of seaweeds, probably reflecting the area provided by them. Byers et al. (2012) also observed that the abundance of *G. vermiculophylla* epifauna increased with algal biomass in estuarine mudflats of south-eastern USA.

Multivariate analysis indicated that structure of epifaunal assemblages differed between seaweeds. Previous works obtained similar results when comparing how different species of macroalgae modulated species richness and diversity of assemblages associated (Chemello & Milazzo 2002). Other studies found differences in composition and structure of epifaunal assemblages associated with native and invasive seaweed species, with native species generally supporting higher species richness and diversity (Wikström & Kautsky 2004). In our study case, however, other factors rather than the origin of species (i.e. native *vs* invasive) probably play an important role. On average, species richness and diversity of macrofauna living on the native *U. rigida* was significantly lower than those on the architecturally more complex, invasive *G. vermiculophylla*. Thomsen et al. (2013) found that *G. vermiculophylla* had a strong positive effect on habitat-associated invertebrates in Odense Fjord (Denmark).

The relationship we observed between the two seaweed species and their associated epifauna may be a general pattern, in which more complex thalli like those of *G. vermiculophylla* encourage a more diversified associated epifauna than do simple and flat-thalloid algae like *U. rigida*. Cardoso et al. (2004), for example, found richer macrofaunal communities associated to complex *G. verrucosa* than to flat *Ulva intestinalis* Linnaeus, 1753 thalli in Mondego Estuary. Schreider et al. (2003) indicated morphological complexity as a key factor in structuring macrobenthic assemblages associated to the brown seaweeds *Sargassum globulariaefolium* J. Agardh, 1889 and *Hormosira banksii* (Turner) Decaisne, 1842. It has been suggested that structural differences in habitat can affect numbers of epifauna (Gee & Warwick 1994). In the present study, however, structural complexity of seaweeds

generally did not influence abundances of epifauna, because there was no difference in abundance of epifauna between the complex *G. vermiculophylla* and the architecturally simpler *U. rigida*. Cacabelos et al. (2010) hypothesized that complexity of seaweeds might not be a consistent predictor of number of species of amphipods.

Habitat architecture may influence the composition of the associated fauna through (i) decrement of mortality rate due to predation (“refuge effect”), (ii) decrease of hydrodynamic features (“shelter effect”) and (iii) collectors of species (“filter effect”), strictly related to hydrodynamic processes and the larval supply (Chemello & Milazzo 2002). In our study, differences in epifaunal assemblages can be attributed to different seaweed architectures. It is known (Orth 1992) that structural complexity of seaweeds may stabilise predator–prey interactions due to the refuge effect. During sampling campaigns, we often collected pipefish (*Syngnathus abaster* Risso, 1827), and gobies [*Knipowitschia panizzae* (Verga, 1841), and *Pomatoschistus* spp.] together with seaweeds, and mostly in the *U. rigida* habitat. In the Po Delta lagoons, Syngnathidae and Gobiidae are very common and highly related with seaweed-dominated communities (Franzoi et al. 1993). It is known that those fish prey on small-sized invertebrates (Ceccherelli et al. 1994), including phytal amphipods and polychaetes (Franzoi et al. 1993). The more diverse and species-rich assemblages of the most complex *G. vermiculophylla* habitat may reflect lower predation pressure. Likely due to shelter and collector effects provided by the finely branched *G. vermiculophylla*, smaller-sized organisms (e.g. *Ecrobia ventrosa* and *Monocorophium insidiosum* Crawford, 1937) may have selected their host on the basis of its architectural complexity. Similar results were found by Johnston and Lipcius (2012), and Thomsen et al. (2013).

Considering feeding preferences, herbivorous species such as *Gammarus aequicauda* and other amphipods that feed mainly on the microphytobenthic film (phytal fauna do not generally feed on the host-plant tissues; Gee & Warwick 1994) were found to select the thin sheet-like thalli of *U. rigida*. It is known (Wikström & Kautsky 2004) that epiphytic load may play an important role in determining the structure of phytal assemblages. Among suspension-feeding organisms, some (e.g. *Cerastoderma glaucum* Bruguière, 1789) were found almost exclusively associated to *G. vermiculophylla*, while others (e.g. *Mytilus galloprovincialis* Lamarck, 1819, *Ficopomatus enigmaticus* Fauvel, 1923) seemed to select *U. rigida*.

This study carried out at a local scale demonstrated that the two seaweeds supported diversified

epifaunal assemblages. The structural complexity of the algae seemed to be of major importance for the structure of epifaunal assemblages. The habitat heterogeneity hypothesis assumes that structurally complex habitats offer more niches and diverse ways of exploiting environmental resources, allowing more species to coexist (MacArthur & Wilson 1967). In Marinetta Lagoon, the invasive *G. vermiculophylla* and the native *U. rigida* determine the three-dimensional physical structure of the habitat, which is otherwise made up of bare mudflats, providing a heterogeneous habitat for a variety of associated animals. Differences in structural complexity of the two seaweeds (irregularly branched *vs* flat, sheet-like thalli) allowed different (taxonomically and functionally) epifaunal assemblages.

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