

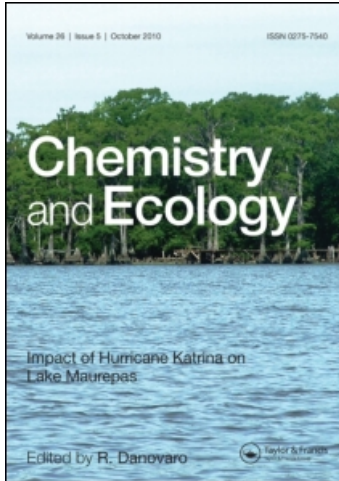
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Inconsistent responses to substratum nature in *Posidonia oceanica* meadows: An integration through complexity levels?

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The endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile can colonise either sand or rock, but mostly builds its own substratum through the formation of the so-called matte (a terrace of interlaced rhizomes and roots trapping sediment). We studied two shallow water meadows in the Ligurian Sea (NW Mediterranean) to examine the influence of the substratum nature on three different levels of ecological complexity: individual (the plant), population (the meadow) and community (the leaf epiphytes). Responses to substratum nature showed inconsistency among the three complexity levels in that leaf surface area (plant level) was lower and shoot density (meadow level) was higher on rock, whereas no major differences were found in epiphyte cover and quali-quantitative composition (community level). We argued that responses are integrated through complexity levels up to dampening substratum influence.

Keywords: seagrass; *Posidonia oceanica*; plant phenology; meadow density; epiphyte community; Mediterranean Sea

1. Introduction

Seagrass meadows are highly structured habitats, hosting diverse associated communities [1–4]. The complex ecosystems they form are characterised by the interplay of numerous abiotic and biotic factors [5], among which the nature of the substratum is of primary importance [6]. Most seagrass species thrive on loose sediments, to which they anchor and from which they take nutrients [7].

Posidonia oceanica (L.) Delile, a key species endemic to the Mediterranean Sea [8], is unique among seagrasses in that it can thrive on either rock or sand [9]. Another peculiarity of *P. oceanica* is that fully developed meadows are able to build their own substratum – a terraced structure, named matte, which consists of intertwined roots and rhizomes as well as sediment trapped among them [10].

While *P. oceanica* modifies the substratum in which it develops, the substratum in turn influences plant morphology and meadow density [11,12]. The combination of plant morphology with meadow density produces a canopy that is the prime responsible for habitat complexity, which

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plays a fundamental role in structuring the seagrass associated communities [13–15]. The epiphyte community is the most peculiar to *P. oceanica*, with many species exclusive of its leaves [16]. As epiphytes interact with their host through nutrient exchange [17,18], it can be envisaged that substratum influence on plant and meadow may reverberate to the epiphyte community.

The integrated study of plant, meadow and epiphyte community is generally encouraged to assess the status of *P. oceanica* ecosystems [19]. Such an approach follows a well established logic in ecological research, where three complexity levels are usually recognised: individual, population and community [20]. In seagrass studies, the individual level may obviously be represented by the plant, the population level by the meadow and the community level by the epiphytes. There are no studies, however, that take into account the influence of the substratum nature on such three complexity levels.

In the present paper, the plant phenology, the meadow density and the epiphyte cover and qualitative composition of *P. oceanica* growing on three different substrata, i.e. sand, matte and rock, are contrasted in two distinct shallow water beds of the Ligurian Sea (NW Mediterranean).

2. Materials and methods

Sampling was carried out in May and June 2006 in the two meadows of Cervara and Prelo (see Figure 1). Those meadows are probably the result of the fragmentation of a single meadow that once lined the eastern side of the Portofino Promontory [21] and degraded due to coastal development [22]. At present, upper and lower limits of the two meadows show a similar regression [23] but the surviving parts are in a comparatively good state of health [24]. A preliminary survey in the two meadows revealed the occurrence of the three substratum typologies (sand, matte and rock) at a depth of 5 m. For each substratum, shoot density was measured in three replicate quadrats (40 cm × 40 cm) randomly located [25]. Three orthotropic shoots of *P. oceanica* were randomly sampled within each quadrat.

In the laboratory, for each shoot, two descriptors commonly used to estimate ecological status of *Posidonia oceanica* meadows were estimated [19]: the leaf surface area and the epiphyte community. Leaf surface area per shoot (cm² shoot⁻¹) was preferred over its ‘pure’ individual components (leaf length, width and number) as a synthetic parameter of plant phenology [25]. Both sides of each leaf blade were analysed using a binocular stereomicroscope to recognize and estimate the individual cover of the following taxa: the algae *Hydrolithon-Pneophyllum* spp, *Myrionema orbiculare*, *Giraudia sphacelarioides*, other algae; the hydroids *Monothecha obliqua*,

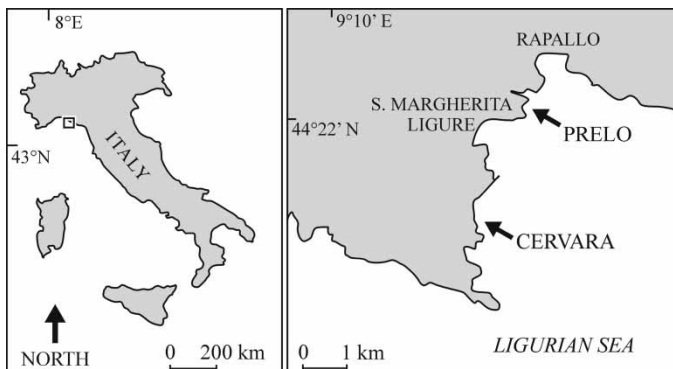


Figure 1. Geographical setting of the two studied meadows: Cervara and Prelo.

Sertularia perpusilla; the bryozoans *Electra posidoniae*, *Aetea truncata*, *Fenestrulina joannae*, other bryozoans; serpulids; and other animals [26].

Statistical analyses were performed under the null hypothesis of no differences among substrata. Leaf surface area, shoot density, total epiphyte cover, and epiphyte community dominance (measured with Simpson's λ [27]) were analysed by 2-way ANOVA, using substratum as fixed factor and meadow as random factor orthogonal to substratum; prior to the analysis, Cochran's C test was performed to verify the assumption of variance homogeneity, and $\ln(x)$ transformation was applied when necessary [28]. Student-Newman-Keuls (SNK) test was applied a posteriori to significant differences. Epiphyte community structure was analysed by non-metric multidimensional scaling (nMDS) and 2-way analysis of similarity (ANOSIM) of fourth root transformed percentage cover data; the similarity percentages procedure (SIMPER) was performed to identify the taxa mostly contributing to differences among substrata [29], adopting the cut-off criterion of cumulative 70% dissimilarity value.

3. Results

3.1. Individual (plant) level

Leaf surface area was lower on rock than on the other two substrata in both meadows (see Figure 2a), but a significant interaction between substratum and meadow was found (see Table 1). The SNK test showed that in both meadows the common pattern among substrata was for the highest values on sand and matte and the lowest on rock, with no significant differences between the two former substrata.

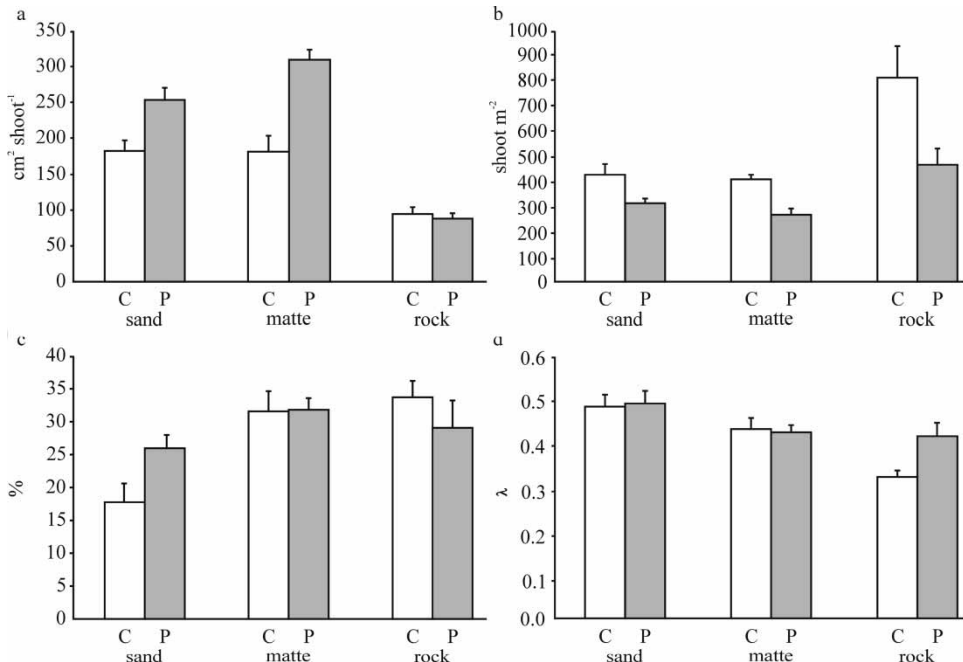


Figure 2. Average (+SE) values of leaf surface area (a), shoot density (b), total epiphyte cover (c) and epiphyte community dominance, expressed as Simpson's λ (d), according to substratum nature (sand, matte and rock) in Cervara (C) and Prelo (P) meadows.

Table 1. Two-way ANOVA on leaf surface area on three different substrata (Su) in two meadows (Me). Bold numbers indicate $p < 0.05$. SNK = Student-Newman-Keuls test. s = sand, m = matte, r = rock. C = Cervara, P = Prelo.

Source of variation	df	MS	F	<i>p</i>
Su	2	4.9641	9.79	0.0926
Me	1	1.1214	16.00	0.0002
Su × Me	2	0.5069	7.23	0.0018
Residual	48	0.0701		
Transformation		ln(x)		
Cochran's C test		C = 0.3636, not significant		
SNK test				
(a) Su(Me)		Cervara	Prelo	
Substratum		s = m > r	s = m > r	
(b) Me(Su)		sand	matte	rock
Meadow		C < P	C < P	C = P

3.2. Population (meadow) level

Shoot density showed the highest values on rock in both meadows (see Figure 2b). Analysis of variance showed significant differences among substrata and between meadows with no significant interaction effects between substratum and meadow (see Table 2). The SNK test confirmed that shoot density on rock was significantly higher than on sand and matte.

Table 2. Two-way ANOVA on shoot density on three different substrata (Su) in two meadows (Me). Bold numbers indicate $p < 0.05$. SNK = Student-Newman-Keuls test. s = sand, m = matte, r = rock. C = Cervara, P = Prelo.

Source of variation	df	MS	F	<i>p</i>
Su	2	0.6358	28.33	0.0341
Me	1	0.8358	25.00	0.0003
Su × Me	2	0.0224	0.67	0.5292
Residual	12	0.0334		
Transformation		ln(x)		
Cochran's C test		C = 0.3531, not significant		
SNK test				
Substratum		s = m < r		

3.3. Community (epiphyte) level

Total epiphyte cover reached lower values on sand (see Figure 2c), but no statistical differences were found among substrata nor between meadows (see Table 3).

Table 3. Two-way ANOVA on total epiphyte cover on three different substrata (Su) in two meadows (Me).

Source of variation	df	MS	F	<i>p</i>
Su	2	563.9423	4.20	0.2532
Me	1	21.8759	0.16	0.6076
Su × Me	2	191.1970	1.42	0.1077
Residual	48	64.3837		
Transformation		none		
Cochran's C test		C = 0.3654, not significant		

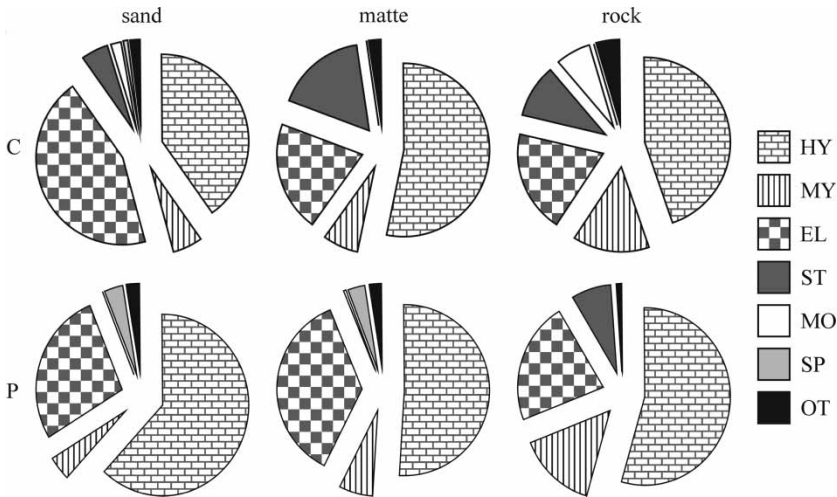


Figure 3. Contribution to the total epiphyte cover (brought to 100%) by different taxa on three substrata (sand, matte and rock) in Cervara (C) and Prelo (P) meadows. HY = *Hydrolithon-Pneophyllum* spp, MY = *Myrionema orbiculare*, EL = *Electra posidoniae*, ST = *Sertularia perpusilla*, MO = *Monothecha obliqua*, SP = serpulids, OT = others (taxa with a percentage cover smaller than 1%).

Table 4. Two-way ANOVA on Simpson's Index λ on three different substrata (Su) in two meadows (Me).

Source of variation	df	MS	F	<i>p</i>
Su	2	0.0590	4.75	0.1740
Me	1	0.0131	2.49	0.1213
Su \times Me	2	0.0124	2.37	0.1048
Residual	48	0.0053		
Transformation		none		
Cochran's C test		C = 0.2449, not significant		

On the three substrata and in both meadows, the main epiphytes were the encrusting red algae *Hydrolithon-Pneophyllum* spp and *Myrionema orbiculare*, and the bryozoan *Electra posidoniae*. The hydroid *Sertularia perpusilla* was only occasionally important; all the remaining epiphytes occurred with very small percentage cover (see Figure 3). Despite slightly lower values on rock (see Figure 2d), epiphyte community dominance (expressed by Simpson's λ) was not statistically different among the three substrata nor between the two meadows (see Table 4).

MDS configuration showed a separation between the epiphyte community on rock and that on sand in both meadows; the epiphyte community on matte of Prelo meadow appeared more similar to that on sand, whereas the one of Cervara was more similar to that on rock (see Figure 4).

The 2-way crossed ANOSIM revealed significant differences among substrata ($r = 0.441$; $p = 0.1\%$) and between meadows ($r = 0.428$; $p = 0.1\%$). Pairwise test showed that differences between sand and rock ($r = 0.708$; $p = 0.1\%$) and between matte and rock ($r = 0.527$; $p = 0.1\%$) were comparatively higher than those between matte and sand ($r = 0.177$; $p = 0.1\%$). SIMPER showed that dissimilarities among substrata were mostly due to comparatively rare taxa, such as serpulids, other animals and other algae (see Table 5).

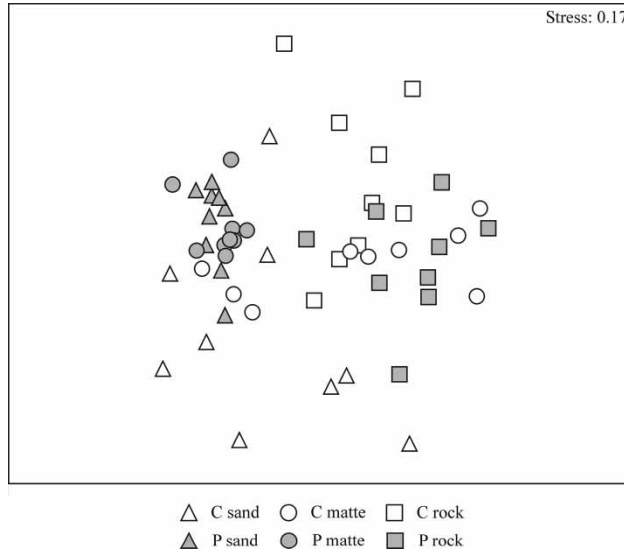


Figure 4. nMDS ordination plot comparing epiphyte community structure (percentage cover data) on three substrata (sand, matte and rock) in Cervara (C) and Prelo (P) meadows; each symbol represents one of the 9 replicate samples taken in each substratum and meadow.

Table 5. Results of SIMPER analysis, showing the taxa contributing most to the dissimilarity among substrata (sand, matte and rock). Cut off at 70% cumulative percentage.

	Sand-rock average dissimilarity = 33.56%		Contribute %	Cumulative %
	Average % Sand	Average % Rock		
<i>Sertularia perpusilla</i>	0.44	2.84	20.67	20.67
Serpulids	0.53	0.00	14.22	34.89
<i>Myrionema orbiculare</i>	1.08	4.57	12.46	47.35
Other animals	0.14	0.32	8.83	56.18
<i>Hydrolithon-Pneophyllum</i> spp	11.56	15.39	8.58	64.76
Other algae	0.16	0.37	8.36	73.12

	Sand-matte average dissimilarity = 25.93%		Contribute %	Cumulative %
	Average % Sand	Average % Matte		
<i>Sertularia perpusilla</i>	0.44	2.69	16.63	16.63
<i>Myrionema orbiculare</i>	1.08	2.06	10.96	27.59
<i>Hydrolithon-Pneophyllum</i> spp	11.56	16.43	10.78	38.37
Serpulids	0.53	0.23	10.74	49.11
<i>Fenestrulina joannae</i>	0.12	0.23	9.78	58.89
Other algae	0.16	0.14	9.42	68.31
Other animals	0.14	0.28	9.13	77.45

	Rock-matte average dissimilarity = 28.63%		Contribute %	Cumulative %
	Average % Rock	Average % Matte		
<i>Sertularia perpusilla</i>	2.84	2.69	20.98	20.98
Serpulids	0.00	0.58	14.05	35.04
Other animals	0.32	0.28	10.49	45.53
Other algae	0.37	0.14	8.90	54.43
<i>Fenestrulina joannae</i>	0.16	0.23	8.88	63.31
<i>Myrionema orbiculare</i>	4.57	2.06	7.69	71.00

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4. Discussion

The responses to substratum influence provided by the three complexity levels within the *Posidonia oceanica* ecosystem (individual, population and community) turned out to be inconsistent among levels. Differences among sand, matte and rock exhibited reverse patterns if plants or meadows were considered, or no pattern at all if only the epiphyte community was analysed.

The plant level showed reduced leaf surface area on rock as compared to sand and matte. This may reflect the obvious need for better anchorage and also the lower nutrient availability on rock: although seagrasses can take nutrients from water through the leaves, the uptake from sediments through the roots is considered of major importance [30]. Reduced size in above-ground organs can be expected under these conditions [31]. The stunted growth of *Posidonia oceanica* individual shoots on rock is an expression of the growth and size plasticity of seagrasses [11,32]. It may represent a stress-tolerating strategy [33], if we equate the above mentioned shortage of anchoring possibility and nutrients on rock to a stress condition. These results were consistent with other studies in Ligurian Sea meadows [24,34].

At the meadow level, shoot density showed again differences among the three substrata, but in this case rock exhibited higher values than sand or matte. There was therefore an inverse pattern between leaf surface area and shoot density, with the highest leaf surface area and the lowest shoot density on matte and sand, and exactly the opposite on rock. This might suggest that *P. oceanica* meadows increase shoot density on rock as a strategy to compensate for reduced leaf surface area. Similar strategies are adopted by other seagrasses, such as *Zostera marina* and *Cymodocea nodosa*, revealing a trade-off between obtaining maximum light energy and simultaneously optimizing nutrient uptake [32,35].

Finally, no major differences were observed at the community level. Total epiphyte cover and community dominance were the same over the three substrata, whereas differences in taxonomic composition of epiphytes were comparatively small and mostly concerned rare taxa. Despite seasonal and depth-related variations, the epiphyte community of *Posidonia oceanica* leaves is known to be mostly composed of a recurrent number of strictly exclusive species that define a rather homogenous assemblage [36–39].

Due to the recommended use of *Posidonia oceanica* as an indicator of changed environmental quality in relation to several human-induced stresses [40–42], caution should be used when interpreting responses measured at different complexity levels, as our data indicate that they may be inconsistently different and cannot be, therefore, generalised.

However, these inconsistent responses might also be interpreted as a clue of a stress-dampening mechanism as one moves from the lowest (i.e. individual) to the highest (i.e. community) level of ecological complexity. The reduced plant size in response to an unfavourable environmental condition (rocky substratum, in our case) results compensated at meadow level by the increased shoot density. The substratum influence on plant and meadow does not reverberate to the epiphyte community. When leaf surface area and shoot density integrate in the canopy, the community most strictly related to the canopy (i.e. the epiphytes) remains substantially the same, so that substratum differences are virtually no more detectable at the community level. Most epiphytes are exclusive to their host, to which they are connected by intimate relations [13,18] and it was therefore expectable that stressed plant might harbour somehow altered communities. Our results, on the contrary, suggest that the leading factor for epiphyte community composition and structure is just the amount of available space and that seagrass leaves are anything but a mere passive surface to settle – an idea recalling more fouling than species-specific epiphytic assemblages [43].

Should further research confirm that responses to a stressor are integrated rather than anarchically inconsistent, a combination of different descriptors would therefore be mandatory when using the indicator potential of *Posidonia oceanica* [19] in order to unveil at which level specific stressors may affect its ecosystem.

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