

ORIGINAL ARTICLE

Spatial variability of *Posidonia oceanica* (L.) Delile epiphytes around the mainland and the islands of Sicily (Mediterranean Sea)

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Abstract

This paper investigates patterns of variability in epiphytes of *Posidonia oceanica* leaves at various spatial scales around Sicily, including geographical differences among the Mediterranean basins, differences between the small islands and mainland, and the variability among and within replicated meadows in each of the previous conditions. Data on percentage cover of the most common epiphytic organisms were analysed by univariate techniques. Encrusting red algae, encrusting brown algae, filamentous algae, encrusting bryozoans, erect bryozoans, hydroids and Foraminifera were the most abundant taxa. Significant differences in the abundance of taxa were detected among geographical regions, while no significant differences were found between the islands and mainland. At smaller scales, variability was concentrated mostly among leaves 100s of centimetres apart and among meadows a few kilometres apart. These results suggest that both geographical and local processes are important in structuring the epiphytes of *P. oceanica* leaves in this area of the Mediterranean.

Problem

Seagrass meadows are among the most important marine ecosystems, contributing significantly to the productivity of shallow coastal areas of both temperate and tropical waters (Pergent *et al.* 1994; Cambridge & Hocking 1997). In the Mediterranean Sea, *Posidonia oceanica* (L.) Delile is the more widespread seagrass, forming broad meadows that may extend from the surface to about 40 m depth.

Epiphytes of seagrass leaves (ESL) play an important role in ecosystem functioning. The algal epiphytes may contribute significantly to the primary production of the meadow (Mazzella *et al.* 1992; Moncreiff *et al.* 1992; Nelson & Waaland 1997; Lepoint *et al.* 1999), while whole assemblages including both algae and invertebrates are an important food resource for many organisms (Buia *et al.* 1992; Klumpp *et al.* 1992). Moreover, ESL are considered sensitive indicators of natural and anthropogenic distur-

bance, as changes in the abundance and composition of assemblages occur in relation to variation in environmental conditions (May 1982; Borum 1985; Frankovich & Fourqurean 1997).

In *P. oceanica*, ESL are also more sensitive to environmental changes than the plant host (Panayotidis 1980). Delgado *et al.* (1999) illustrated an increase in the biomass of *P. oceanica* epiphytes sampled close to the sites of discharge of nutrient and organic matter. Recently, a study conducted in the north-west Mediterranean showed different patterns of spatial variability in the epiphytes of *P. oceanica* between disturbed and undisturbed locations, even if no effects were observed on the structure of entire assemblages (Piazzì *et al.* 2004a).

Understanding the spatial and temporal patterns of variability in populations and assemblages is important to discriminate between natural changes and human-induced effects (Underwood 1993; Benedetti-Cecchi 2001; Fraschetti

et al. 2005). Although ESL have been investigated repeatedly in space and time (Casola *et al.* 1987; Mazzella *et al.* 1989; Kendrick & Burt 1997; Reyes *et al.* 1998; Trautman & Borowitzka 1999; Vanderklift & Lavery 2000; Lavery & Vanderklift 2002; Esposito *et al.* 2003; Saunders *et al.* 2003), a detailed quantification of natural variability over a broad range of spatial scales, including differences between the small islands and continental coasts, has never been undertaken.

Numerous ecological processes can be responsible for geographical patterns of variability in *P. oceanica* ESL. Differences in hydrodynamic conditions, exposure to Atlantic currents and gradients in water temperature, may generate latitudinal gradients and differences among the basins in the Mediterranean Sea (Margalef 1985). *Posidonia oceanica* shows genetic disjunctions among the meadows of the different Mediterranean regions (Procaccini & Mazzella 1998), confirming that different populations thrive in different geographical areas. Differences could be expected on this basis for epiphytic assemblages also. A previous study showed differences in the structure of epiphytic assemblages of rhizomes among the Mediterranean regions (Piazza *et al.* 2002), while no comparable information is available to date on ESL.

Assemblages of islands can differ from those inhabiting locations on the mainland for a variety of reasons, including isolation from important sources of colonists, type of habitats available for colonization and exposure to human disturbance. These issues have been investigated mostly for terrestrial biota (Whittaker 1998), while a few studies have been carried out on marine assemblages (*e.g.* Piazza *et al.* 2004b; Rindi & Guiry 2004). In the Mediterranean Sea, Benedetti-Cecchi *et al.* (2003) have highlighted differences in shallow rocky shore assemblages between two islands of the Tuscan Archipelago and two locations on the mainland. On the contrary, no significant differences have been detected between deep rocky assemblages of islands and continental coasts in the same geographic area (Piazza *et al.* 2004c).

In addition to large-scale patterns of variability, small-scale spatial heterogeneity is also a prominent feature of benthic assemblages (Fraschetti *et al.* 2005). Several processes can account for this type of variability, including vagaries in the dispersal, supply and settlement of propagules, post-recruitment biological processes (Coleman 2002 and references therein) and disturbances (Airoldi & Cinelli 1997). In addition to providing a better understanding of relevant ecological processes, proper quantification of small-scale spatial variability in assemblages is also important for the detection of human impacts. Some studies have shown that certain types of anthropogenic disturbances may alter natural patterns of variability over small spatial

scales (*e.g.* Terlizzi *et al.* 2005), although this is not a general phenomenon (Chapman *et al.* 1995).

This paper examines the general hypothesis that variability in ESL occurs at different spatial scales. This hypothesis was tested with a multifactorial sampling design that generated quantitative data on variability among: (i) geographical areas 100s of kilometres apart, (ii) habitats (islands and mainland), (iii) meadows 10s of kilometres apart, (iv) sites 100s of metres apart, (v) plots 2–5 m apart and (vi) shoots 10s of centimetres apart. Sicily is particularly suited for this purpose because it is surrounded by small islands, it separates different Mediterranean basins and it is large enough to be considered a continental habitat.

Material and Methods

This study was carried out between July and September 2000 in three geographical areas around Sicily, the northern coast (Tyrrhenian Sea), the southern coast (Sicily Strait) and the western coast (at the boundary between the two basins) (Fig. 1). Two habitats were sampled in each geographical area, represented by islands and by locations on the mainland, with three replicate meadows in each combination of geographical area \times habitat. Five sites were randomly selected in each meadow at 10 m depth and five plots were randomly selected in each site. Five vertical (orthotropous) shoots 10s of centimetres apart were collected in each plot by scuba diving and fixed in 4% formalin seawater. Sampling was completed within 1 month.

Epiphytes were examined on the more external leaf of each shoot (the oldest one), to ensure that the analysis focused on a mature assemblage (Reyes *et al.* 1998;

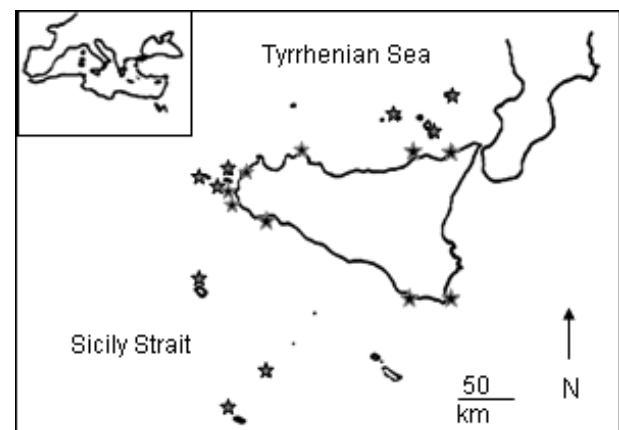


Fig. 1. Map of Sicily. Symbols indicate locations of the studied *Posidonia oceanica* meadows. Grey pins: islands; black pins: mainland coasts.

Vanderklift & Lavery 2000; Buia *et al.* 2003). The first 10 cm of the internal face from the tip of the leaves was sampled under a dissecting microscope supplied with a grid of 100 squares. The abundance of each taxon was obtained by examining five field views of 1 cm² and recording the presence or absence of that taxon within nine squares per field view, for a total of 45 (9 × 5) squares examined (Piazzì *et al.* 2004a). The abundance of each taxon was determined as the ratio between the squares in which the taxa were present *versus* the total of the squares (45) and then expressed as percentage. The macroalgal epiphytes were lumped into morphological groups (filamentous, red crustose, brown crustose, green crustose, red corticated, brown corticated, foliose and articulated calcareous algae) according to Steneck & Dethier (1994); animals were analysed at the level of phylum. Bryozoans were distinguished as erect and crustose forms.

The percent cover of the most abundant groups and taxa was analysed by five-way ANOVA. The factors

considered were: Geographic Area (three levels, fixed), Habitat (small islands *versus* mainland coasts, fixed and crossed with Geographic Area), Meadow (three levels, random, nested in the interaction Geographic Area × Habitat), Site (five levels, random, nested in Meadow) and Plot (five levels, random, nested in Site). Five leaves from five different shoots were considered for each Plot. Homogeneity of variances was tested by Cochran's C-test (Underwood 1997) and data were ln(x + 1) transformed when necessary. Student–Newman–Keuls (SNK) test was performed to check for *a posteriori* comparisons of mean values after significant effects in ANOVA (Underwood 1997). In addition to hypothesis testing, ANOVA was also used to estimate the variance components associated with the random factors (Meadow, Site, Plot, Leaf) in the model of analysis (Sokal & Rohlf 1981; Underwood 1997). These data were used for qualitative comparisons of patterns of variability across scales.

Six separated ANOVA for the most abundant groups were conducted to evaluate variability among meadows in each habitat and region, in order to determine possible patterns of variability related to the different distances among meadows in the regions studied.

Results

In Table 1, the most frequent species and/or genus included in the morphological groups are reported. Seven taxa were sufficiently abundant to be used in univariate analyses (Fig. 2) (Table 2). Significant differences were detected among the geographic areas for encrusting brown algae, filamentous algae, encrusting bryozoans and Foraminifera. SNK tests indicated that encrusting brown algae, filamentous algae and Foraminifera were significantly more abundant on the western coast of Sicily when compared with the northern and southern coasts that did not differ significantly (SE for comparisons: encrusting brown algae = 4.027; filamentous algae = 0.151; Foraminifera = 0.760). A significant geographic Area × Habitat interaction was detected for hydroids (Table 2, SNK test). Multiple comparison tests within this interaction indicated that hydroids were more abundant on islands compared with the mainland only on the southern coast of Sicily, while the two habitats did not differ in the other geographic areas (SE = 0.166). In contrast, the SNK test was not able to discriminate any alternative to the null hypothesis for encrusting bryozoans. With the exception of hydroids, there was no significant effect of habitat for any of the other taxa considered. Spatial variability within habitats was, in contrast, large and significant at all the scales investigated (meadow, site and plot) and for all the taxa examined (Table 2).

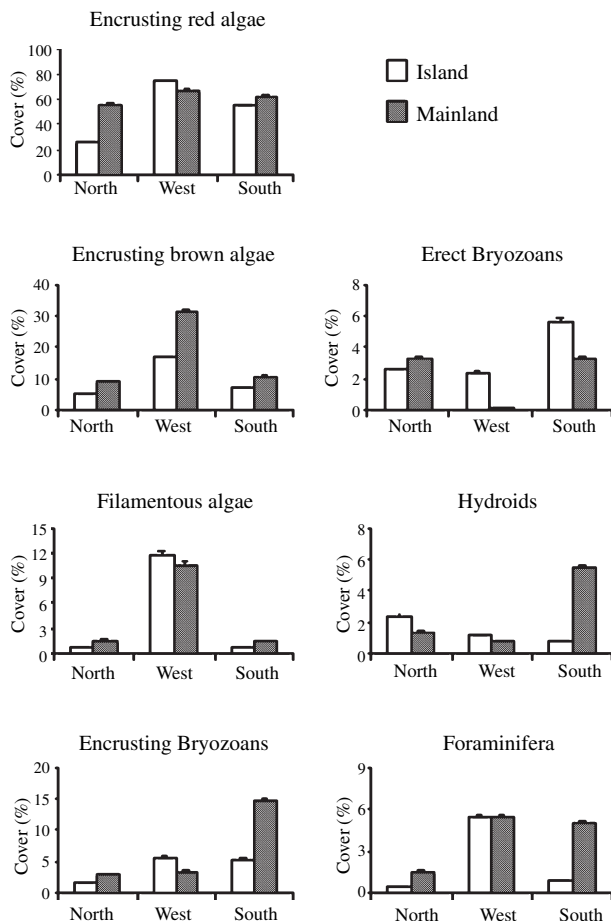


Fig. 2. Percent cover (mean ± SE, n = 3) of the most abundant groups of epiphytes of *Posidonia oceanica* leaves.

Table 1. Most frequent species and/or genus included in the morphological groups.

Encrusting red algae
<i>Hydroliton farinosum</i> (J. V. Lamouroux) Penrose et Y. Chamberlain
<i>Hydroliton boreale</i> (Foslie) Y. Chamberlain
<i>Pneophyllum fragile</i> Kützting
<i>Pneophyllum coronatum</i> (Rosanoff) Penrose
Encrusting brown algae
<i>Myrionema orbiculare</i> J. Agardh
Filamentous algae
<i>Antithamnion</i> spp.
<i>Ceramium</i> spp.
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh
<i>Giraudia sphacelarioides</i> Dérbès & Solier
<i>Cladophora</i> spp.
Encrusting bryozoans
<i>Electra posidoniae</i> Gautier
<i>Fenestulina joannae</i> (Calvet)
<i>Lichenopora radiata</i> (Audouin)
<i>Disporella hispida</i> (Fleming)
Erect bryozoans
<i>Aetea</i> sp.
<i>Valkeria</i> sp.
Hydroids
<i>Sertularia perpusilla</i> (Stechow)
<i>Aglaophenia</i> sp.
<i>Plumularia</i> sp.
Foraminifera
<i>Elphidium crispum</i> (Linnaeus)
<i>Planorbulina</i> sp.

Variance components indicated that most of the variability occurred at the scale of leaf, with the exception of the encrusting red algae that displayed larger variation at the scale of meadow. Variability at this scale was also important for encrusting brown algae, encrusting bryozoans, erect bryozoans and Foraminifera, while variability at the scale of plot was important for filamentous and encrusting red algae; variability at the intermediate scale of site was negligible in most cases (Table 3).

Separate ANOVA for each habitat and region showed the same patterns of ANOVA including all the factors; significance at the meadow level was detected independently from the relative distance among the meadows.

Discussion

Results show that epiphytes of *Posidonia oceanica* leaves do not vary significantly between the small islands and mainland, while significant differences were detected among the geographical regions. High spatial variability is present at the largest and the smallest scales investigated

and particularly among the meadows, plots and leaves. This descriptive study does not provide for a clear identification of the causes of the variability in ESL; thus only conjectures are possible.

Large-scale processes that could account for geographical pattern in the Mediterranean Sea include differences in temperature, in oceanographic conditions like latitudinal gradients in the influence of Atlantic waters and historical processes.

Differences among meadows can be also related to local differences in environmental characteristics of sampled locations. The significance at the meadow level in each geographical area, both in island and mainland habitat, shows that variability among meadows is independent of distances; thus the different distances among meadows in the geographical areas considered did not confound our results.

Patterns of small-scale variability similar to those documented in the present study have been detected by Piazza *et al.* (2004a) on the epiphytes of *P. oceanica* leaves and in other species of seagrasses (Vanderklift & Lavery 2000), suggesting that this is a pervasive feature in these kinds of systems. Variability in ESL at the scale of metres may be mostly influenced by differences in shoot density and in the characteristics of the canopy, which affect light intensity and water movement (Gambi *et al.* 1989). Other factors may be relevant though, like local hydrodynamic flows that affect dispersal, settlement and recruitment of propagules (Trautman & Borowitzka 1999; Vanderklift & Lavery 2000). Moreover, the role of biotic interaction such as grazing pressure and influence of established assemblages on potential recruitment cannot be ignored (Mazzella & Russo 1989). Experimental studies are necessary to elucidate the causes of the spatial patterns of leaf epiphytes of Mediterranean meadows.

The present study, although limited to the analysis of morphological groups and not to species, may give several suggestions in order to use seagrass epiphytes as bioindicators in the studies of impact. In fact, the lack of significant differences between the small islands and locations on the mainland suggests that the former habitat may be used as a reference condition for long-term experimental monitoring of ESL. On the contrary, our results clearly indicate the necessity of stratifying studies by geographic area. This aspect may be of higher importance in case that species composition will also be included, as indicated in Esposito *et al.* (2003). Finally, the future analyses of ESL should consider sampling designs that allocate a large number of replicates at the scales of shoots and plots, while a minimum of two sites would be sufficient to represent an entire meadow in relation to the low values of variance components at this scale.

Understanding how patterns in abundance, distribution and diversity of species change in relation to the spatial

Table 2. Analysis of variance on mean percentage cover of epiphytes of *Posidonia oceanica* in Sicily.

source of variation	d.f.	encrusting red algae		encrusting brown algae		filamentous algae		encrusting bryozoans		erect bryozoans		hydroids		Foraminifera	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
geographic area (=A)	2	341,948	4.2	131,826	5.4*	772.9	22.6***	23,973	4.9*	65.8	0.8	66.5	3.2	7614	8.8**
habitat (=H)	1	107,398	1.3	64,057	2.6	0.9	0.0	8792	1.8	68.2	0.8	69.9	3.4	3242	3.8
A × H	2	130,715	1.6	15,969	0.7	50.5	0.3	12,977	2.7	65.2	0.8	119.2	5.8*	1692	2.0
meadow (A × H) (=M)	12	80,658	27.3***	24,330	15.9***	34.2	6.0***	4857	17.2***	86.4	22.3***	20.6	6.4***	865	14.6***
site (M) (=S)	72	2957	2.7***	1533	2.7***	5.7	2.8***	282	2.3***	3.9	2.6***	3.2	2.5***	59	2.1***
plot (S) (=P)	370	1088	5.5***	563	2.2***	2.0	2.8***	120	2.0***	1.5	2.4***	1.3	2.4***	28	2.3***
residuals	4050	200		252		0.7		59		0.6		0.5		12	
total	4499														
Cochrane's test (C)		0.011		0.014		0.011		0.019		0.010		0.015		0.020	
transformation		None		None		ln(x + 1)		None		ln(x + 1)		ln(x + 1)		None	
SNK test				W > N = S		W > N = S		N = W = S				M: N = W = S		W > N = S	
												I: S > N = W			
												N: I = M			
												W: I = M			
												S: I > M			

*P < 0.05; **P < 0.01; ***P < 0.001.

N = north; W = west; S = south; M = Mainland; I = Island.

Table 3. Variance components analyses conducted on untransformed data and expressed as percentage.

variance components	encrusting red algae	encrusting brown algae	filamentous algae	encrusting bryozoans	erect bryozoans	hydroids	Foraminifera
meadow	48.81	23.16	6.56	21.06	19.77	7.57	18.08
site	5.87	4.93	6.27	3.68	4.22	5.36	3.39
plot	13.95	7.90	20.75	7.02	12.67	12.62	9.04
leaf	31.36	64.01	66.40	68.24	63.34	74.45	69.49

scale of observation has important implications, from the identification of the mechanisms that generate and maintain biological diversity (Underwood & Chapman 1996; Willis & Whittaker 2002), to the prediction of how local and regional environmental changes will affect diversity at multiple levels of organization (Lockwood & McKinney 2001; Scott *et al.* 2002), to the analysis of relationships between species richness and ecological function (Waide *et al.* 1999). The study of spatial patterns of biodiversity in benthic organisms has received considerable attention, and a synthesis of these studies suggests that small-scale processes are at least as important as large-scale processes in many assemblages (Fraschetti *et al.* 2005). Our results show that this also applies to ESL, a system common to many marine coastal areas.

Conclusions

Although a number of studies have investigated epiphytes on the leaves of seagrasses at different spatial and/or temporal scales, few have focused on geographical patterns and on differences between the small

islands and continental coasts. In the present paper, we compared leaf epiphytes of *Posidonia oceanica* meadows between the two habitats represented by islands and locations on the mainland coasts in different geographical areas around Sicily. This was performed by means of a multifactorial sampling design that enabled the quantitative assessment of variability at a hierarchy of spatial scales, ranging from 10s of centimetres to 100s of kilometres. Significant differences were detected among geographic areas for encrusting brown algae, filamentous algae, encrusting bryozoans and Foraminifera. A significant geographic area × habitat interaction was detected only for hydroids, while spatial variability within each habitat was large and significant, particularly among shoots 10s of centimetres apart and meadows a few kilometres apart.

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