COMPARATIVE ANALYSIS OF EPIPHYTIC FORAMINIFERA IN SEDIMENTS COLONIZED BY SEAGRASS *POSIDONIA OCEANICA* AND INVASIVE MACROALGAE *CAULERPA* SPP.

GUILLEM MATEU-VICENS[1,4], ANTONIO BOX[2], SALUD DEUDERO[2] AND BEATRIZ RODRÍGUEZ[3]

ABSTRACT

Mediterranean shallow-water soft bottoms are characterized by extensive meadows of the endemic seagrass *Posidonia oceanica* (L.) Delile that support abundant benthic biota including numerous epiphytic foraminiferal taxa. The biomass of the epiphytic communities varies with the *P. oceanica* cycle, especially influencing those taxa with higher abundances in summer, when the foliar surface is maximum. During the past decades exotic macrophyte species have invaded habitats formerly dominated by *P. oceanica*. Two of these taxa are the green algae *Caulerpa taxifolia* (Vahl) Agardh, 1817 and *C. racemosa* (Forsskål) Agardh, 1873, that, along with the non-invasive *C. prolifera* (Forsskål) Lamouroux, 1809, produce defensive, secondary metabolites such as caulerpenyne that affects turnover rates of *P. oceanica* leaves. As a consequence of different architectural features of the algal substrate, replacement of *P. oceanica* by *Caulerpa* spp. results in the change from a complex three-dimensional, long duration substrate into a simpler, two-dimensional one with a shorter life span.

Epiphytic foraminifers can be clustered into functional groups according to their shape, structure, behavior and life span. The foraminiferal dead assemblage includes a total of 110 species, that included 43 species in sediments colonized by *P. oceanica*, 82 species in sediments with *C. prolifera*, 78 in sediments invaded by *C. taxifolia*, and 55 in sediments invaded by *C. racemosa*. Taxonomic composition of all assemblages is similar, though differences occur in the relative abundance of each taxon. Sediments in *P. oceanica* meadows are characterized by flat, encrusting, long life-span species (e.g., *Planorbulina mediterranensis* d'Orbigny, 1826), whereas in *Caulerpa* spp. habitat, temporarily motile, shorter life-span taxa (e.g., *Lobatula lobatula* (Walker and Jacob, 1798) and *Rosalina bradyi* Cushman, 1915) tend to dominate. Multivariate analysis shows that only the thanathocoenosis of *P. oceanica* sediments is representative of the *P. oceanica* epiphytic foraminiferal assemblage (*Planorbulinatum mediterranensae* Colom, 1942). Hence, differences among the foraminiferal assemblages in sediments colonized by different phytal substrates occur prior to taphonomic and dissolution processes and may be applicable to paleoecological interpretations.

INTRODUCTION

Mediterranean inner shelf environments (to 30–40 m) are characterized by extensive meadows of the seagrass *Posidonia oceanica* (L.) Delile, which are estimated to occupy a total area of 50,000 km^2 (Bethoux and Copin-Montéagut, 1986). *Posidonia oceanica* densities reported from western Mediterranean localities range between 150 shoots m^{-2} and 800 shoots m^{-2}, exceeding 1,500 shoots m^{-2} under exceptionally favorable conditions (Marbà and others, 2005; Papadimitriou and others, 2005). This plant exhibits seasonal growth, with maximum rates during May–June and decreasing to a stop in September (Ribes, 1998); leaves have life spans between 19 and 30 weeks (Hughes and others, 1991). *Posidonia oceanica* leaves when fully grown reach up to 80 cm long × 1 cm wide, which, along with the rhizomes, provide substrates suitable for colonization.

Posidonia oceanica meadows support abundant benthic biota, including numerous epiphytic taxa such as bryozoans, hydrozoans, and foraminifers (Pergent and others, 1995; Fornós and Ahr, 1997; 2006; Pardi and others, 2006). Many of these organisms possess calcareous skeletons that contribute to the production of carbonate sediments. The biomass of the epiphytic communities is closely linked to the *P. oceanica* cycle, especially influencing those taxa with higher abundances in summer, when available foliar surface is maximum (Ribes, 1998). Additionally, several algal species occur within the *P. oceanica* meadows, providing additional substrate for epiphytic biota, including many foraminiferal taxa (Langer, 1993).

In the past few decades, *Posidonia oceanica* has increasingly interacted with exotic species that are now widespread in environments formerly colonized exclusively by seagrass. As many as 84 introduced macrophytes are currently reported in the Mediterranean (Boudouresque and Verlaque, 2002). In highly altered areas, meadows are currently formed by the association of *P. oceanica* and the invasive macrophytes.

Caulerpa taxifolia (Vahl) Agardh, 1817 is considered one of the most invasive species in the Mediterranean (Phillips and Price, 2002). This species presents pinnate, fern-like fronds (up to 25 cm long × 2 cm wide) that extend upwards from horizontal stolons (up to 3 m long). This macroalga was accidentally released from the Monaco Aquarium in 1984 (Meinesz and Hesse, 1991) and rapidly spread across the western Mediterranean basin (Meinesz and others, 2001). In the Balearic Islands, the first report of *C. taxifolia* was in 1992 at a depth of 6 m in Cala d'Or Bay, Mallorca Island (Pou and others, 1993). This species is still restricted to Cala d'Or Bay and no expansion had been observed.

Caulerpa racemosa (Forsskål) Agardh, 1873 is another invasive macroalga in the Mediterranean Sea. It is generally considered a lessepsian species that has spread throughout

[1] MARUM – Center for Marine Environmental Sciences, University of Bremen, Leobenerstrasse, 28359 Bremen, Germany.
[2] Laboratori de Biologia Marina, Departament de Biologia, Universitat de les Illes Balears, Ctra. de Valldemossa kM 7.5, 07122 Palma de Mallorca, Spain.
[3] Laboratori de Micropaleontologia, Departament de Ciències de la Terra, Universitat de les Illes Balears, Ctra. de Valldemossa kM 7.5, 07122 Palma de Mallorca, Spain.
[4] Correspondence author: E-mail: gmateu@marum.de

the Mediterranean basin (Verlaque and others, 2004). First reported in the Balearic Islands in 1998 in Palma Bay, Mallorca Island (Ballesteros and others, 1999), *C. racemosa* is now found throughout the Balearic Islands archipelago. This macroalga has fronds up to 11 cm long with uncrowded, vesiculate, radially-arranged ramuli.

Caulerpa prolifera (Forsskål) Lamouroux, 1809, which is considered a non-invasive species, occurs throughout the Mediterranean, with the exception of Lyon Gulf and Adriatic Sea (Sánchez-Moyano and others, 2001). *Caulerpa prolifera* fronds may reach up to $15-25$ cm long $\times$ 2 cm wide, extending upwards from horizontal stolons as much as 1 m long. Growth and spatial distribution of *C. prolifera* are highly influenced by water temperature since it is an alga with subtropical affinity (Sanchez-Moyano and others, 2004). These macroalgae cover soft bottoms at depths of 1 to 20 m, mainly in areas of low water flow and weak hydrodynamics (Sanchez-Moyano and others, 2001; Sanchez-Moyano and others, 2004).

Caulerpa spp. are characterized by the presence of secondary metabolites, such as caulerpenyne, whose main function is chemical defense against herbivores and epiphytes (Box and others, 2008; Sureda and others, 2008a, 2008b). However, epiphytes, including foraminifers (Blanc-Vernet, 1969; Sarma and Ganapati, 1972; Davaud and Septfontaine, 1995; Prado and Thibaut, 2008) have been reported attached to these algae. *Caulerpa* spp. have a marked seasonal biomass cycle with higher biomass corresponding to higher water temperatures (Terrados and Ros, 1992; Meinesz and others, 1995; Piazzi and others, 2001; Sanchez-Moyano and others, 2004).

Two effects, competitive and allelopathic, are exerted on *Posidonia oceanica* (Dumay and others, 2002; Wallentinus and Nyberg, 2007) by *Caulerpa* spp. They compete with the seagrass for light and nutrients, while their caulerpenyne production reduces growth and longevity of *P. oceanica* leaves. The result is a higher turnover of the seagrass induced by the presence of the invasive algae (Pergent and others, 2008).

Additionally, important differences can be observed concerning the architectural features of each phytal substrate. In *Posidonia oceanica* two strata are clearly distinguished, the rhizome and the blades, each with characteristic associated communities (Langer, 1988). In contrast, *Caulerpa* spp. have a much simpler structure. The replacement of *P. oceanica* by *Caulerpa* spp. results in a structural change from a complex three-dimensional system to one that is almost two-dimensional (Wallentinus and Nyberg, 2007). Consequently, the resulting architectural differences determine the type of substrate and the available surface for epiphytic colonization that, in turn, affect the type and amount of sediment that is produced and accumulated.

Foraminiferal assemblages associated with different phytal substrates, especially seagrass meadows, have been widely studied (e.g., Brasier, 1975; Baden, 1990; Langer, 1993; Ribes and others, 2000; Wilson, 2007). Epiphytic foraminifers have been examined not only in taxonomic studies but also from an ecological perspective, which has contributed new tools for environmental and paleoenvironmental analysis. Langer (1993) split epiphytic foraminifers into four categories corresponding to functional groups based on their shape, structure, and behavior. Morphotype A is that of sessile, flat, encrusting taxa with long life spans (>1 yr). Morphotype B represents temporarily motile species with life spans of 2–5 months. Morphotype C corresponds to permanently motile species that may extrude their pseudopodia from the canal system through multiple apertures, and which have life spans of 3–4 months. Finally, morphotype D groups together permanently motile taxa that have a single aperture and a very short life span. Each of these morphotypes prefers a specific phytal substrate. Morphotypes A and B are abundant on flat surfaces such as seagrass blades, morphotype C is ubiquitous, and morphotype D mostly occurs in sediment-rich parts of plants such as the rhizome. These morphotypes cannot be regarded as guilds (*sensu* Wilson, 2006). Nevertheless, the applicability of Langer's classification has been demonstrated in both ecological (Wilson, 1998; Ribes and others, 2000; Murray, 2006; Wisshak and Rüggeberg, 2006; Fujita, 2008) and paleoecological (Brachert and others, 1998; Moissette and others, 2007; Mateu-Vicens and others, 2008a, 2008b) studies.

In the Balearic Islands of the western Mediterranean, foraminiferal assemblages of *Posidonia oceanica* seagrass have been studied in detail (Colom, 1942; Mateu, 1970; Mateu and others, 1984; Gazá, 1988; Abril, 1993; Moreiro, 1993). However, there is a lack of information related to other phytal substrates such as *Caulerpa racemosa*, *C. taxifolia*, and *C. prolifera*. Indeed, few in the Mediterranean studies detail the foraminiferal biocoenosis of *C. prolifera* (Blanc-Vernet, 1969; Blanc-Vernet and others, 1979) and none refer to the invasive caulerpal species.

Our study at Mallorca Island compares foraminiferal assemblages in sediments colonized exclusively by *Posidonia oceanica* seagrass with those in a meadow of *P. oceanica* with *C. racemosa*, *C. taxifolia* or *C. prolifera* mats. Its goal is to determine whether the progressive substitution of a complex phytal substrate (*P. oceanica*) by a simpler substrate (*Caulerpa* spp.) is recorded by the content and distribution of epiphytic foraminiferal dead-assemblages in the sediment.

MATERIAL AND METHODS

STUDY AREA AND SAMPLING DESIGN

This investigation was carried out in Mallorca, one of the Balearic Islands in the western Mediterranean. Two different areas (Fig. 1) were selected, Cala d'Or (39°22′44.61″N, 3°14′23.07″E) and Portals Vells (39°28′20.21″N, 2°31′16.53″E). Both are enclosed bays of similar bathymetry (6–8 m). Samples were collected over soft bottoms colonized by invasive *Caulerpa taxifolia* and *C. racemosa*, as well as by established *C. prolifera* and the seagrass *Posidonia oceanica*. Other macroalgal species also were recorded (Table 1), but they were much less common and their canopy was negligible compared to those of *P. oceanica* and *Caulerpa* spp. Densities of *P. oceanica* in the invaded meadows were consistently lower than 50 shoots m^{-2}, whereas at least 700 shoots m^{-2} were present where *P. oceanica* dominated the substrate (Fig. 2).

FIGURE 1. Map showing the Porto Colom and Portals Vells study areas in the Balearic Archipelago, western Mediterranean.

Sampling was performed by scuba divers who inserted metacrilate (plastic) corers (3.5 cm diameter × 5 cm long) into the sediment. At Cala d'Or, 10 samples were collected from sediment in areas dominated by *Caulerpa taxifolia* (samples CT1–CT4), *C. prolifera* (samples CP1–CP4) and *Posidonia oceanica* (samples PO1 and PO2). At Portals Vells, three *C. racemosa* samples (CR1–CR3) and two *P. oceanica* samples (PO3 and PO4) were collected. Samples at both study sites were collected at least 100 m apart to avoid pseudoreplication.

SAMPLE PROCESSING

For each sample, granulometric analysis was carried out by sieving 100 g of sediment within a range: >2 mm, 2–1 mm, 1–0.5 mm, 0.5–0.25 mm, 0.25–0.125 mm, 0.125–0.063 mm, and <0.063 mm, and classified according to Wentworth grain-size scale. Subsequently, mean values of different sediment fractions for each type of phytal substrate were calculated. Then, the 0.500–0.125 mm fractions were combined and foraminiferal taxonomic analysis was performed by picking up to 300 specimens per sample (enough to detect 95% of the species with >1% abundance according to Dennison and Hay, 1967). To minimize the noise produced by taphonomic processes, reworked (damaged) shells were discarded and only intact or rose Bengal-stained (Walton, 1952) specimens were considered. The rose Bengal method was not used to distinguish dead from living specimens because, after death, stainable organic matter can remain in a test for up to a few months (Boltovskoy and Lena, 1970; Murray and Bowser, 2000). Instead, we used the stain to discern the taphocoenosis from the dead (thanatocoenosis) assemblage.

TABLE 1. Checklist of non-invasive algal species reported from the substrates colonized by *Caulerpa prolifera, C. racemosa, C. taxifolia*, and *Posidonia oceanica*. X indicates occurrence.

|	Algal-colonized substrates			
Algal species	*Caulerpa prolifera*	*Caulerpa racemosa*	*Caulerpa taxifolia*	*Posidonia oceanica*
Acetabularia acetabulum (L.) Silva, 1952	X	X		
Amphiroa rigida Lamoroux, 1816				X
Corallina mediterranea Areschong, 1852				X
Dilophus fasciola (Roth) Howe, 1914	X		X	X
Dyctiota dichotoma (Hudson) Lamoroux, 1809	X	X	X	X
Flabellia petiolata (Turra) Nizamuddin, 1987	X	X	X	X
Halimeda tuna (Ellis & Solander) Lamoroux, 1816	X			
Halopteris filicina (Grateloup) Kützing, 1843				X
Halopteris scoparia (L.) Sauvageau, 1904		X		
Jania rubens (L.) Lamoroux, 1812	X	X	X	X
Padina pavonica (L.) Thivy, 1960	X	X	X	X
Peyssonellia spp.	X	X	X	X
Polysiphonia sp.	X		X	X
Valonia utricularis (Roth) Agardh, 1823			X	
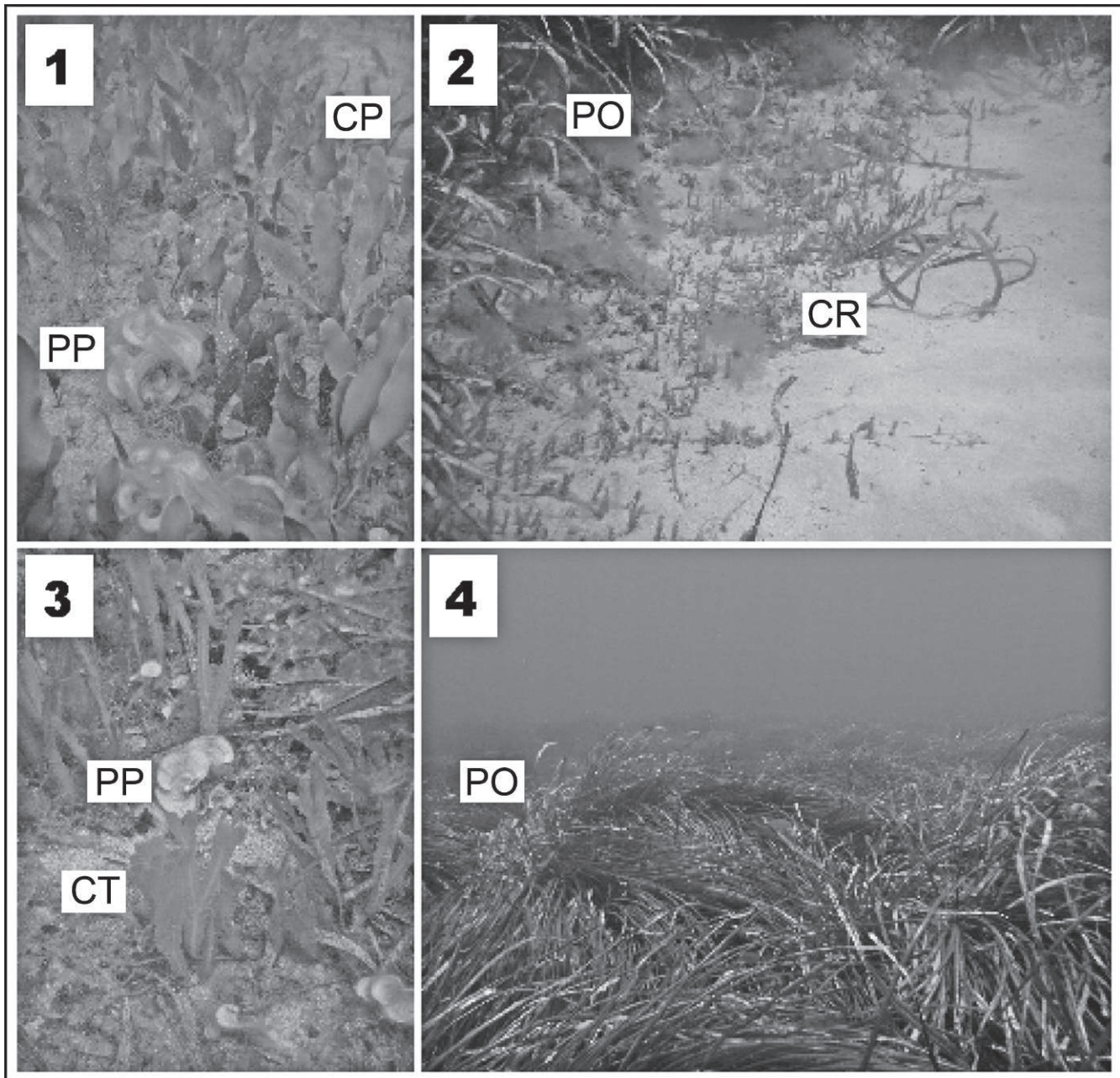
FIGURE 2. Images of the sampling areas. 1. Substrate dominated by *Caulerpa prolifera*. 2. *C. racemosa* encroaching on *Posidonia oceanica* patches. 3. *C. taxifolia*-covered substrates. 4. *P. oceanica* meadow showing a high-shoot density. CP, CR, CT, PP, and PO refer to *C. prolifera*, *C. racemosa*, *C. taxifolia*, *Padina pavonica*, and *P. oceanica*, respectively.

Foraminiferal species were assigned to genera based on Loeblich and Tappan (1987). They were then assigned to the morphotypes of Langer (1993) to analyze their relationships to the algae/seagrass life cycle.

STATISTICAL ANALYSIS

Differences in foraminiferal assemblages of species, genera, and morphotypes among sites dominated by *Caulerpa* spp. or *Posidonia oceanica* were analyzed using PRIMER 6.0 software. TAXDTEST was performed to compare the taxonomic composition in the different studied foraminiferal assemblages with a reference master list (up to 136 species) that summarizes the *Posidonia oceanica* foraminiferal biocoenosis from the Balearic Islands (Colom, 1942, 1964; Mateu, 1970; Gazá, 1988; Abril, 1993; Moreiro, 1993), Catalonia (Mateu, 1970) and southern France (Blanc-Vernet, 1969) before invasive species were reported in those areas. The DIVERSE routine was applied to obtain the Shannon index and the number of species per sample. Transformation [Log $(x + 1)$] was applied to generic abundances, while Multi-Dimensional Scaling (MDS) and CLUSTER representations were used to correlate groups of samples with habitat types. ANOSIM was applied at the
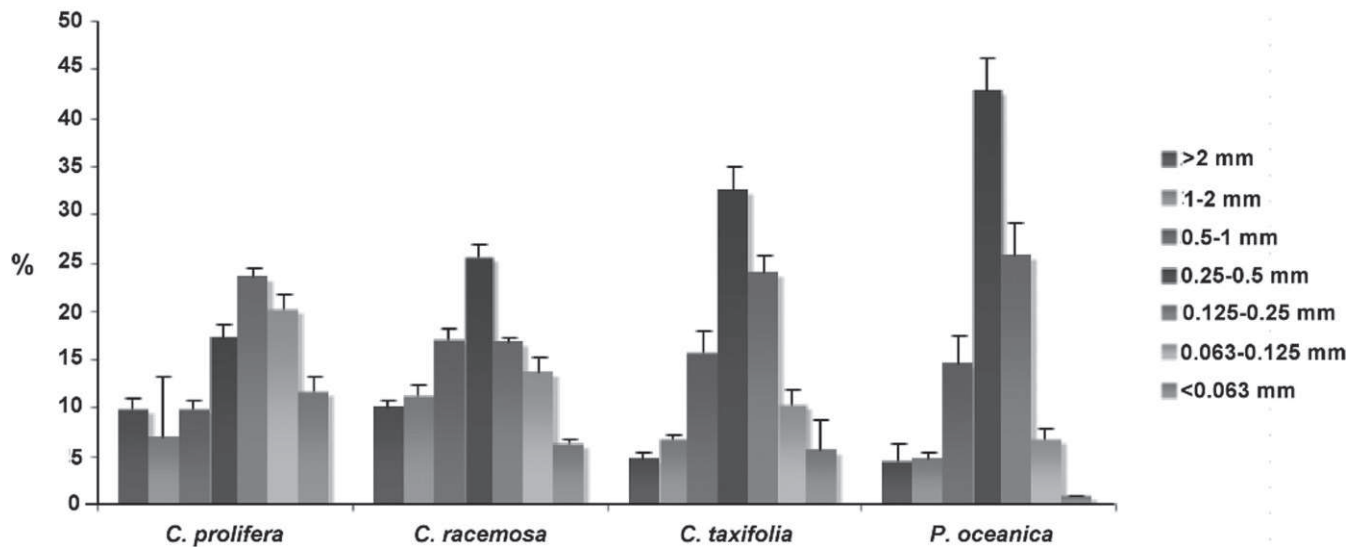
FIGURE 3.   Sediment textures for *Caulerpa* spp. and *Posidonia oceanica*.

generic and morphotype levels to analyze differences between habitats.

RESULTS

Sediment textures (Fig. 3) represent a gradient from relatively well sorted, medium-to-fine sands in areas dominated by *Posidonia oceanica* to very poorly sorted predominantly sands in areas dominated by *Caulerpa prolifera*. Sediments in *C. taxifolia* areas more similar to those of *P. oceanica*, whereas those in *C. racemosa* areas more similar to those of *C. prolifera*.

We recorded 110 foraminiferal species distributed as follows (Table 2): 43 species in sediments exclusively colonized by *P. oceanica*, 82 species for sediments with *C. prolifera*, 78 species for sediments invaded by *C. taxifolia*, and 55 species for sediments invaded by *C. racemosa*. In the *P. oceanica* thanatocoenosis, the most conspicuous taxa are *Lobatula lobatula* (Walker and Jacob), *Planorbulina mediterranensis* d'Orbigny, and *Nubecularia lucifuga* Defrance, whereas most of the common foraminiferal species in *Caulerpa* spp. are more or less equally distributed. Nevertheless, *L. lobatula* and *Rosalina bradyi* Cushman show high abundances in samples from *Caulerpa* spp. areas. Similarly, *Quinqueloculina berthelotiana* d'Orbigny is very frequent in some samples from *Caulerpa taxifolia* (CT3 sample), as are *Nubecularia lucifuga* and *N. massutiniana* Colom in some samples from *C. prolifera* (CP1, CP2, and CP3 samples) and in *C. racemosa* (Table 2) areas.

In the TAXDTEST analysis (Fig. 4), the variation in taxonomic distinctness (Λ^+) obtained for the *P. oceanica*-associated thanatocoenosis fits within the theoretical values calculated from the reference master list of the *P. oceanica* biocoenosis. Assemblages from sediments colonized by *Caulerpa* spp. present Λ^+ values that indicate significant differences from the theoretical *P. oceanica* community.

At the generic level, only *Posidonia oceanica* samples cluster; foraminiferal assemblages do not group by dominant *Caulerpa* species (Fig. 5). Similarly, ANOSIM analysis shows significant differences between *P. oceanica* and *Caulerpa* spp. for abundances of foraminiferal genera. Greatest differences correspond to *P. oceanica* and *C. taxifolia* (R = 0.833, sl = 0.029). There are no significant differences between foraminiferal genera abundances among the caulerpal species (Table 3).

There are notable differences between thanatocoenoses of Langer (1993) morphotypes in relation to *Posidonia oceanica* and *Caulerpa* spp. (Fig. 6). Moreover, significant differences are also observed between assemblages from *C. racemosa* and those from *C. prolifera* (R = 0.96, sl = 0.029) and *C. taxifolia* (R = 1, sl = 0.029) (Table 3). In assemblages from *P. oceanica* areas, Morphotype A (long-lived sessile forms) dominates and short-lived forms of Morphotype D are relatively uncommon. In assemblages from areas dominated by *C. prolifera* and *C. taxifolia*, morphotypes B and D (medium- to short-lived mobile forms) predominate. In *C. racemosa* areas, Morphotype B tends to be the most common and Morphotype C is very rare.

DISCUSSION

SEDIMENT TEXTURES

Seagrasses with clearly differentiated foliar and rhizomatic strata play a major role in carbonate production and sediment deposition and stabilization (Boudouresque and Jeudy de Grissac, 1983; Gacia and Duarte, 2001; Perry and Beavington-Penney, 2005). Plant canopy reduces flow velocity and inhibits resuspension processes below the plant canopies (Gacia and others, 1999, Gacia and Duarte, 2001), which in turn might favor mud accumulation (Bosence and others, 1985). Some of the mud originates from disaggregation of epiphytic carbonate-producing organisms that detach from decaying seagrass blades or, especially in low-latitude settings, by disintegration of associated calcareous green algae (Perry and Beavington-Penney, 2005). As observed by Fornós and Ahr (1997, 2006), however, we

TABLE 2. Checklist of foraminiferal taxa reported from each sample corresponding to the substrates colonized by *Posidonia oceanica, Caulerpa prolifera, C. taxifolia*, and *C. racemosa*. *Morphotype of Langer, 1993.

	Family	Species	Morph*	CP1	CP2	CP3	CP4	CR1	CR2	CR3	CT1	CT2	CT3	CT4	PO1	PO2	PO3	PO4
Agglutinated	Hemisphaeramminidae	*Daitrona* sp.	A								1	1						
	Textulariidae	*Textularia agglutinans*	D			1	1	3	1	3	1	1		1				
		Textularia candeiana	D			1		2		1		2						1
		Textularia gramen	D									3	1	1				
		Textularia pseudoturris	D					2		3								
Porcellaneous	Fischerinidae	*Vertebralina striata*	D	7	6	2	5	5	3	4	3	3	1	2	6	2	4	3
	Hauerinidae	*Affinetrina planciana*	D								3	5		3				
		Cycloforina contorta	D												1			
		Cycloforina rugosa	D					2			1		1					
		Cycloforina villafranca	D						1			1		1				
		Lachlanella bicornis	D							2	1	1	3					
		Lachlanella variolata	D						1		2		2					2
		Massilina secans	D		6	1	2		4	2			5	2		1	1	2
		Miliolinella grata	D	2	1	1	2											
		Miliolinella labiosa	D	2	3	2	3		1	2	1		1					
		Miliolinella semicostata	D	1	2	3												
		Miliolinella suborbicularis	D					6		3	5		3	3			2	2
		Miliolinella subrotunda	D	1		3	2											
		Miliolinella webbiana	D					2			2							
		Pseudotriloculina (Miliolinella) sidebottomi	D			2	1	3			2							
		Pseudotriloculina cuneata	D	1		2	1	1			10	3		3				
		Pseudotriloculina laevigata	D	4	1	1	1				1				2	4	3	2
		Pseudotriloculina oblonga	D	1			1	7		4	1							
		Pseudotriloculina rotunda	D	5		1	2			1	5	2	2	6				
		Quinqueloculina annectens	D	1		4									1			
		Quinqueloculina berthelotiana	D	5	7	13	11	5	10	7	7	8	43	15	8	9	11	6
		Quinqueloculina cf. *Q. juleana*	D			4												
		Quinqueloculina costata	D	2		4	2				3		1	5				
		Quinqueloculina disparilis	D	6	7	13	10	2	1	2	2		1	4				
		Quinqueloculina jugosa	D				1	2	1	2								
		Quinqueloculina laevigata	D	1		2		1	1	1	1		4	4				
		Quinqueloculina laticollis	D		1	2	1											
		Quinqueloculina seminula	D					2	1	1	1		3	2	9	7	9	5
		Quinqueloculina stalkeri	D		1	3												
		Quinqueloculina stelligera	D	7	8	15	12											
		Quinqueloculina ungeriana	D	5	9	14	7	1	2	1	2		3	2				
		Quinqueloculina vienensis	D		2	3												
		Quinqueloculina vulgaris	D	3	5	16	9		2	2	6	11	37	12	2	3		
		Quinqueloculina vulgaris var. *cornuta*	D		1	2	2	8	4	6	2	1	2	2				
		Siphonaperta hauerina	D								1							
		Siphonaperta agglutinans	D	1				1			7	5		4				1
		Siphonaperta aspera	D	7		1	2	1			2							
		Siphonaperta dilatata	D	1							9			3				
		Siphonaperta irregularis	D	1			2				1							
		Siphonaperta lucida	D								1							
		Siphonaperta osinclinatum	D	1														
		Siphonaperta quadrata	D		1			5	4		1							2

TABLE 2. Continued.

	Family	Species	Morph*	CP1	CP2	CP3	CP4	CR1	CR2	CR3	CT1	CT2	CT3	CT4	PO1	PO2	PO3	PO4
Porcellaneous	Hauerinidae	*Triloculina marioni*	D	1		2	1	2	2			3		1				
		Triloculina plicata	D			1	1		1	3								
		Triloculina sp.	D	2		3												
		Triloculina tricarinata	D			3	2								4	1	3	2
		Wellmanelinella striata	A					5		2	1	2		1				
	Nubeculariidae	*Nubecularia lucifuga*	A	31	87	7	36	31	62	47	8	5	12	5	33	38	40	62
		Nubecularia massutiniana	A	16	26		23		56	28	6	5	8	11	11	12	6	9
	Peneroplidae	*Peneroplis pertusus*	D	2	1		2				6	9	8	12	21	26	24	12
		Peneroplis planatus	D	5	6	5	4	4	7	5	8	13	11	8				
	Sigmoilinitidae	*Sigmoilinita costata*	D	3			1											1
	Soritidae	*Sorites orbiculus*	A		3	2	2		4	2	7	7	2	5	16	9	13	6
	Spiroloculinidae	*Adelosina cliarensis*	D						2	1	1		1					
		Adelosina duthiersi	D							1	2	1						
		Adelosina laevigata	D			2				1	6	2	5					
		Adelosina pulchella	D	1	1			3		1		2						
		Adelosina striata	D	4			3	1					1					1
		Spiroloculina excavata	D								2		2	2				1
		Spiroloculina ornata	D	4	2	7	5	9	5	9	1	1	1	1				
		Spiroloculina ornata var. *tricarinata*	D	1	1	2	2	2	1	1	1	2	1	3		3	1	1
		Spiroloculina scita	D	2	1	2												
Calcareous-Perforate	Acervulinidae	*Acervulina inhaerens*	A								4	3		3				
		Sphaerogypsina globulus	A	1														
	Asterigerinatidae	*Asterigerinata mamilla*	B	7	1		3				1							
	Cibicididae	*Annulocibicides gymnesicus*	A	1				2		1					1		1	
		Cibicides refulgens	B	10	1	1	4	1	2	2	15	7	2	8	4	3	4	3
		Cibicidoides pseudoungerianus	B	3			1											
		Dyocibicides sp.	A	1									1		4	8	6	3
		Lobatula lobatula	B	28	40	60	43	65	46	56	64	93	61	73	68	51	60	44
	Cymbaloporidae	*Cymbaloporetta* sp.	B									2		1				
	Discorbidae	*Discorbis mira*	B	1														
		Discorbis nitida	B															
	Discorbinellidae	*Discorbinella bertheloti*	B					1		1								
	Elphidiidae	*Cribroelphidium decipiens*	C				2											
		Cribroelphidium excavatum	C	6							1							
		Elphidium advenum	C	5	5	4	6		1	1	11	10	7	12				
		Elphidium aff. *E. translucens*	C								3	2	1	3				
		Elphidium complanatum	C	1	1										3	3	2	1
		Elphidium crispum	C	4	6	3	3				2	1	1	3				
		Elphidium depressulum	C		1						2	1	2	2				
		Elphidium macellum	C	7	5	7	7				1	3	3	1	3	4	1	1
		Elphidium macellum var. *aculeatum*	C	1	1						1	4	3		3	3	4	2
		Elphidium maioricensis	C				1				2	1	2		5	2	6	3
		Elphidium pulvereum	C	1														1
	Eponididae	*Eponides repandus*		1														
	Glabratellidae	*Glabratella hexacamerata*		1														
	Homotrematidae	*Miniacina miniacea*	A										5	2				
	Mississippinidae	*Stomatorbina concentrica*											3		1			
	Nonionidae	*Astrononion stelligerum*	B	9			3						1					8
	Planorbulinidae	*Planorbulina* (*Cibicidella*) *variabilis*	A	4	3	16	4	6	8	7	4	4	6	4	16	10	9	8
		Planorbulina acervalis	A			2		4	6	8	2	5	4	5	8	9	5	4
		Planorbulina mediterranensis	A	11	5	31	20	17	28	19	11	15	18	14	56	86	79	51

TABLE 2. Continued.

Family	Species	Morph*	CP1	CP2	CP3	CP4	CR1	CR2	CR3	CT1	CT2	CT3	CT4	PO1	PO2	PO3	PO4
Polymorphinidae	Globulina gibba									1							
Rosalinidae	Rosalina bradyi	B	23	17	16	19	41	27	39	21	27	18	23				13
	Rosalina floridensis	B	2	2		1	1		1	1	2					1	2
	Rosalina globularis	B	6	4	4	13	13	6	10	8	8	7	6	11			12
	Rosalina globularis var. anglica	B	8	1		2	2	1	1	2	2					1	2
	Rosalina macropora	B		6	2	3	3			6	5		5		6		1
	Rosalina mediterranensis	B	5			14	14									7	14
	Rosalina obtusa	B	5	5		4	4	1	8	1	1	1					2
	Rosalina posidonicola	B	1			4	4										4
	Rosalina vilardeboana	B	7	5	4	2				1	2	3					
Rotaliidae	Ammonia beccarii	B	1	2	1							1	1				1
	Ammonia tepida	B	2	1													
Spirillinidae	Sejunctella sp.	A	1														
	Spirillina vivipara	A	4														
Trichohyalidae	Buccella frigida		1														

found that substrates of areas covered by *Posidonia oceanica* are sand dominated, while mud is almost insignificant, *Caulerpa* spp.-dominated zones are muddier, though still sand-dominated.

Similar textures have been observed on seagrass-dominated substrates elsewhere (e.g., Edel Province in Shark Bay, Australia [Read, 1974] and Inhaca Island, Mozambique [Perry and Beavington-Penney, 2005]) and different causes were invoked to explain the minimal mud fractions. In Edel Province, despite low-energy conditions, seagrass cover was not dense enough to trap enough fine sediment to form a mud-rich facies. At Inhaca Island, the sparseness of fine sediments seems to be independent of seagrass-blade density and epiphytic carbonate production; apparently the fine sediment gets winnowed. Latitude can also factor into the amount of mud produced in different settings. In low latitudes, calcareous green algae and other mud-producing biota are very prolific, whereas in mid latitudes, such is the Mediterranean, these organisms are less abundant and rarely or weakly calcify (Perry and Beavington-Penney, 2005).

FORAMINIFERAL ASSEMBLAGES

The focus of our study is the analysis of foraminiferal assemblages within sediments from areas dominated by indigenous and invasive macrophytes. In the Mediterranean, epiphytic foraminifers are very diverse and abundant, and the sediments beneath the seagrasses and algae are rich in dead foraminiferal shells washed from the plants (Colom, 1942; 1964; Blanc-Vernet, 1969; Fornós and Ahr, 1997; 2006); similar observations have been reported from seagrass beds in the Caribbean (Steinker and Clem, 1984). As a consequence, in the absence of transport and reworking, these sediment assemblages are ecologically representative (Mateu, 1970) of the original epiphytal assemblages. In contrast, Wilson and Ramsook (2007) documented that sediment assemblages associated with *Thalassia testudinum* meadows in the Caribbean differ considerably from their original biocoenosis due to the the fragility of planorbulinids and differential transport.

Controversy continues regarding how representative dead assemblages are with respect to the original biocoenosis. According to Murray (2000), dead assemblages summarize the information of previous living assemblages, modified to a lesser or greater extent by taphonomic processes. Dead assemblages that pass into the fossil record (Murray, 1976) constitute a better analog of the original biocoenosis than the total assemblages (Murray and Alve, 1999).

Our results reveal differences in foraminiferal composition at species, generic, and morphotype levels. At species level, TAXDTEST analysis clearly shows that the assemblage found in *Posidonia oceanica* sediments are statistically indistinguishable from the *P. oceanica* epiphytic biocoenosis. The *P. oceanica* foraminiferal dead assemblage is characterized by high abundances of shells of *Planorbulina mediterranensis, Lobatula lobatula* and *Nubecularia lucifuga,* accompanied by common occurrences of *Astrononion stelligerum* (d'Orbigny, 1839), *Rosalina* spp., *Planorbulina acervalis* Brady, 1884, *P. variabilis* (d'Orbigny, 1826),
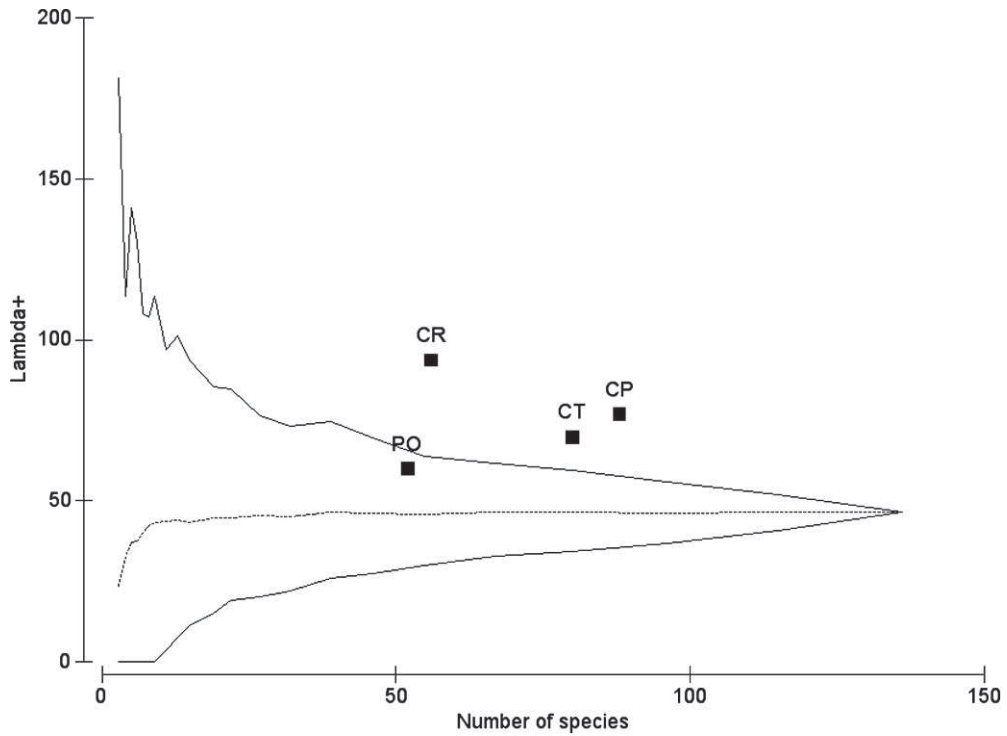
FIGURE 4. TAXDTEST representation of habitat species composition comparing a master list of foraminifers that live epiphytically on *Posidonia oceanica* with results from the four studied habitats. CP, CR, CT, and PO refer to *Caulerpa prolifera*, *C. racemosa*, *C. taxifolia*, and *Posidonia oceanica* respectively.
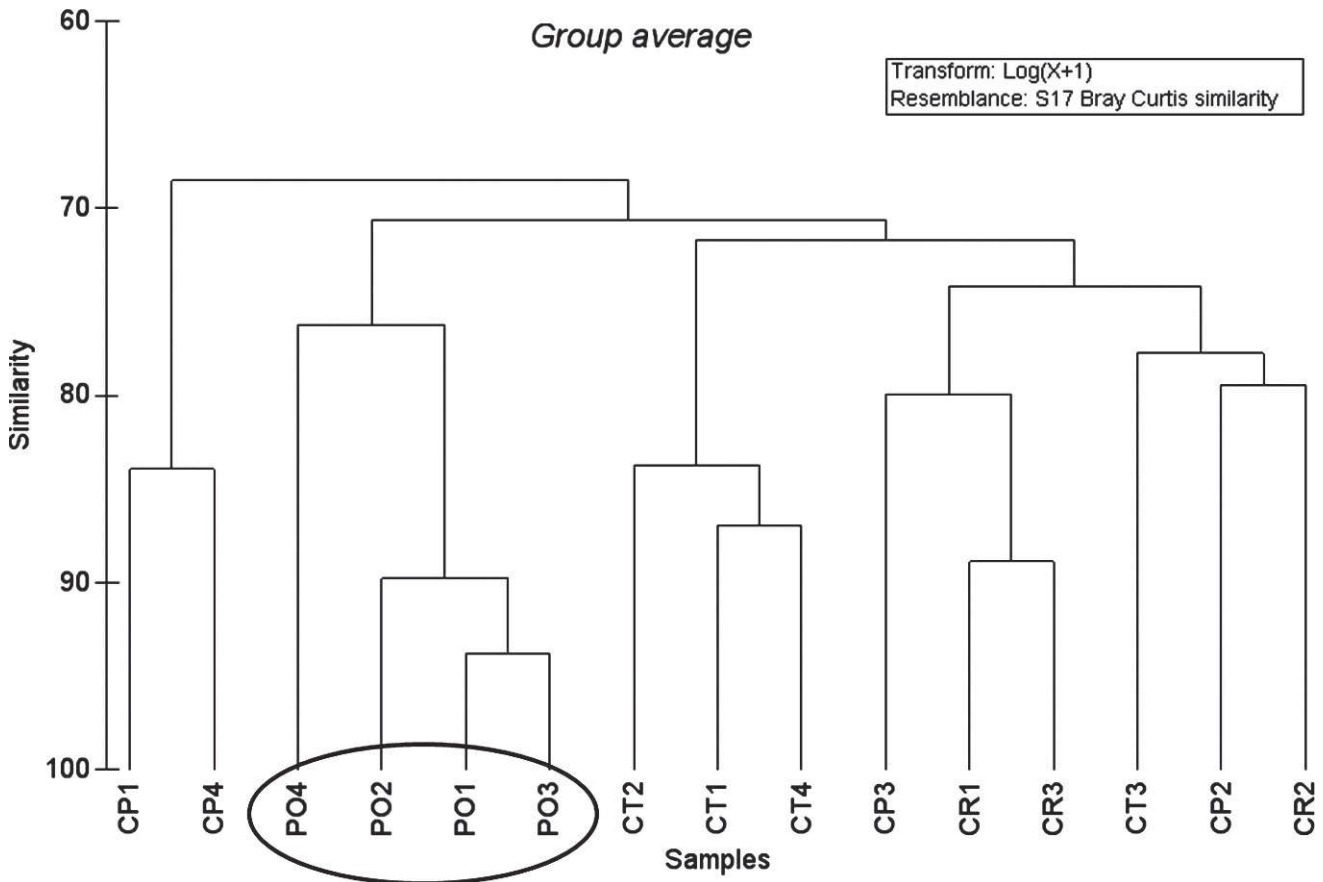

FIGURE 5. Cluster representation of samples based on generic abundances. *Posidonia oceanica* samples are encircled to highlight high similarity. CP, CR, CT, and PO refer to *C. prolifera*, *C. racemosa*, *C. taxifolia* and *P. oceanica* respectively; numbers (e.g., CT1) are sample numbers.

TABLE 3. Results of pairwise ANOSIM analysis applied to the foraminiferal genera and morphotypes observed in the different thanatocoenoses. Generic Global R = 0.611, significance level (sl) = 0.001; Morphotypes Global R = 0.748, sl = 0.001.

Pairwise test	Genera	Morphotypes
P. oceanica vs. *C. prolifera*	R=0.729, sl=0.029	R=0.844, sl=0.029
P. oceanica vs. *C. taxifolia*	R=0.833, sl=0.029	R=1.000, sl=0.029
P. oceanica vs. *C. racemosa*	R=0.778, sl=0.029	R=0.889, sl=0.029
C. prolifera vs. *C. taxifolia*	R=0.427, sl=0.086	R=0.104, sl=0.257
C. prolifera vs. *C. racemosa*	R=0.296, sl=0.614	R=0.963, sl=0.029
C. taxifolia vs. *C. racemosa*	R=0.556, sl=0.086	R=1.000, sl=0.029

Peneroplis pertusus (Forskål, 1775), *Sorites orbiculus* Ehrenberg, 1839, and a few species of *Quinqueloculina* and *Siphonaperta*. Similarly, leaves of Caribbean *Thalassia testudinum* seagrass are dominated by planorbulinids (Wilson, 1998; 2006), whose shells also occur in the surrounding sediments (Wilson and Ramsook, 2007).

In contrast, the *Caulerpa* spp. thanathocoenoses, especially *C. prolifera* and *C. racemosa* associations, are dominated by *Lobatula lobatula* and *Nubecularia lucifuga*, and to a lesser extent by *Rosalina bradyi*, while *Planorbulina mediterranensis* are common but not abundant. Our results are in agreement with Blanc-Vernet's (1969) observations in the Port of Alon and in Brusc Bay, where the seasonal

occurrence of *Caulerpa* sp. does not induce substantial changes in the foraminiferal association.

Compositional differences that we observed are consistent with the ecological and behavioral features synthesized in the four morphotypes described by Langer (1993). We found both the *P. oceanica* biocoenosis and thanathocoenosis to be dominated by morphotype A (Table 2, Fig. 6), which resembles Brasier's (1975) primary weed dwellers with their relatively long life spans that are well-adapted to the seagrass annual foliar cycle. In foraminiferal assemblages from areas dominated by *Caulerpa* spp., morphotype A generally co-occurs with morphotype B in nearly the equal abundance (except for samples CP2 and CR2 that favor morphotype A).
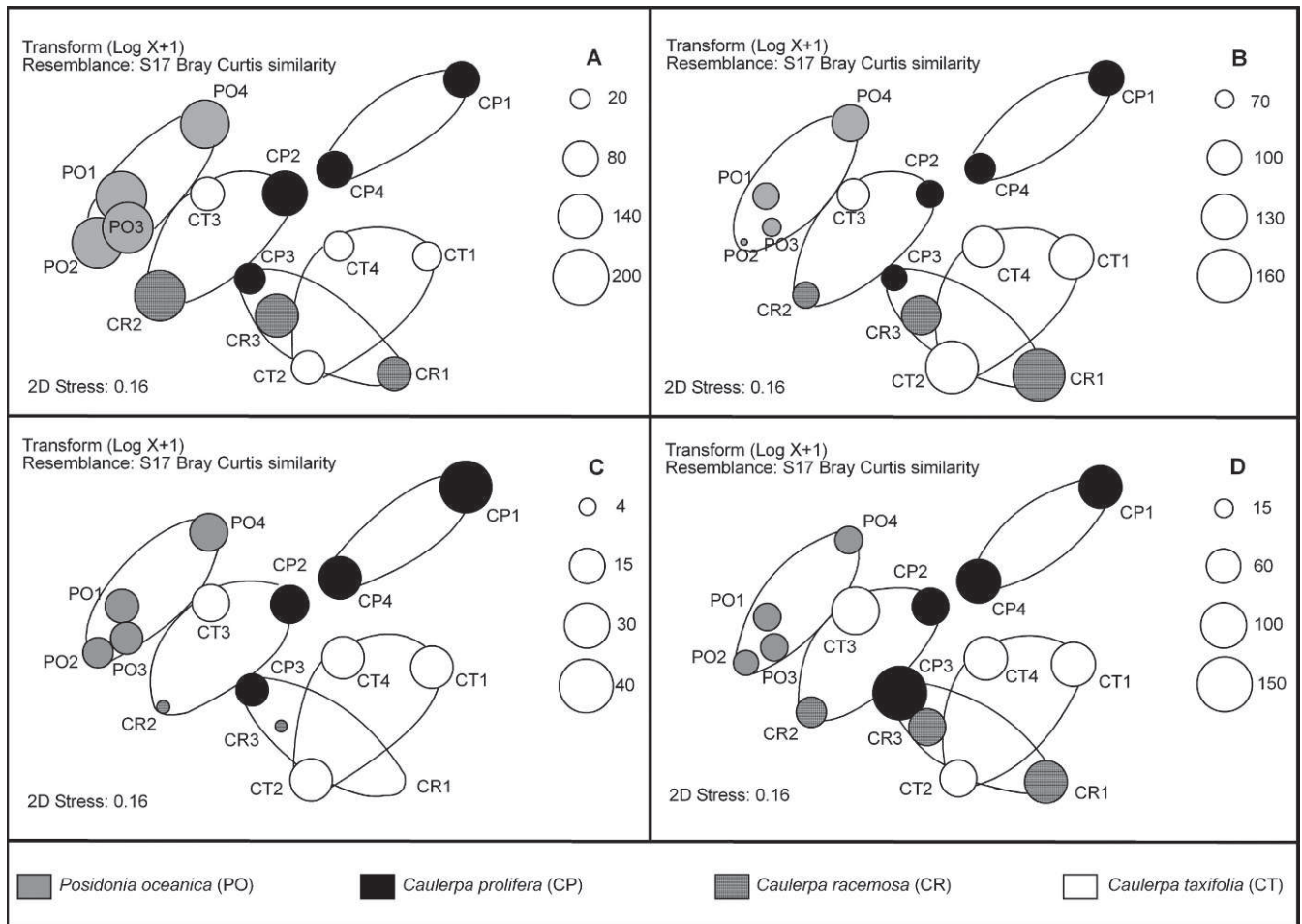

FIGURE 6. MDS representation of generic abundances for each sample from the studied habitats: A) Langer (1993) morphotype A; B) Langer morphotype B; C) Langer morphotype C; and D) Langer morphoptype D. Abbreviations as in Figure 5.

In *Caulerpa* spp., most morphotype A specimens are *Nubecularia lucifuga*. This porcelaneous species has a thick, imperforate wall that is relatively resistant to abrasion (Heap and Sbaffi, 2008) and it is less susceptible to transport than is the delicate, perforate test of *Planorbulina* (Kotler and others, 1992; Martin, 1999). Therefore, *Nubecularia* tend to accumulate on the *Caulerpa* spp. substrate in greater numbers than *Planorbulina*. Moreover, the porcelaneous wall structure of *Nubecularia* hinders detection of the rose Bengal stain, increasing the difficulty of distinguishing living or recently living individuals from dead (empty) tests.

Different reasons are invoked to explain the *Nubecularia lucifuga* abundances in areas dominated by *Caulerpa prolifera* and *C. racemosa*. The non-invasive *C, prolifera* is well adapted to low-energy environments and, at very shallow depths in the warmer eastern Mediterranean, often hosts *Nubecularia* and *Planorbulina* (Blanc-Vernet, 1969). In our study areas, similar environmental conditions occur at least during summer, which might favor the proliferation of these foraminifers. Moreover, as stated above, in *Caulerpa prolifera*-dominated areas, sparse shoots of *P. oceanica* could contribute to production and accumulation of shells of *N. lucifuga* and, to a lesser extent, *P. mediterranensis*.

The appearance of *Caulerpa racemosa* in the western Mediterranean is recent. This alga invades low-energy areas formerly dominated by *P. oceanica* and where abundant *Nubecularia* specimens accumulated. Thus, despite the occurrence of the invasive macrophyte and the reduction on the availability of the epiphytic substrate, and in the absence of strong hydrodynamics, the elapsed time has not been long enough for a radical change in the foraminiferal association of the sediment. In contrast, *C. taxifolia* has been modifying the habitat for a longer period, enough to alter the foraminiferal assemblages in the sediment. Additionally, *C. taxifolia*-dominated substrata contain less mud (Fig. 3), indicating higher hydraulic energy that, in turn, might have contributed to the microfaunal changes in the sediment.

Species of morphotype B also prefer attachment on flat surfaces such as seagrass or algal blades. As a consequence, one might expect the two ecological groups to compete for the substrate, but taxa belonging to morphotype B have a much shorter life span than those of morphotype A. Caulerpal algae show marked seasonal cycles with high biomass corresponding with high temperatures and substantial decrease in and breakup of fronds in winter (Terrados, 1995; Box, 2008), which reduces dominance of morphotype A. Similarly, secondary metabolites of *Caulerpa* spp. induce a decrease of leaf mean-length and rapid turnover of *P. oceanica*, which further reduces the dominance of morphotype A with respect to morphotype B.

Morphotype C corresponds to keeled, epiphytic elphidiids. Our results are in agreement with previous observations (Langer, 1993) documenting very low percentages of this morphotype in flat seagrass and algal blades such as *Posidonia oceanica*, *Caulerpa prolifera*, and *C. taxifolia*. This morphotype dominates on arborescent algae. The total absence of morphotype C in the *C. racemosa*-associated assemblage shows that this alga is an inadequate substrate for these foraminifers.

Representatives of Morphotype D, which mostly includes seagrass rhizome and sediment dwellers, are not as frequently encountered as morphotypes A and B, especially in *Posidonia oceanica*-associated sediments. The relatively higher abundance of this morphotype in areas of *Caulerpa* spp. is likely associated with the more poorly sorted, muddier sediments found there. Additionally, it is extremely difficult to distinguish epiphytic from infaunal specimens of morphotype D. especially hauerinids and textulariids.

The occurrence of non-invasive algae in the study area (Table 1) is not considered to affect the composition of the foraminiferal dead assemblages at meadow scale. The much higher densities and canopies of *Posidonia oceanica* (Fig. 2) determine most of the carbonate production within the meadow (Canals and Ballesteros, 1997). Thus, the presence of *Caulerpa* spp. and the associated allelopathic effects are likely factors influencing the foraminiferal assemblage characteristic of *P. oceanica* meadows. Our results show that sediment assemblages in areas dominated by *C. prolifera* and *C. taxifolia* are more diverse than those associated with *C. racemosa* and *P. oceanica*. It has been shown that the presence of invasive species can cause changes in the invertebrate community (Deudero and others, 2009) and increase the presence of more opportunistic and generalist species (Box, 2008).

Two different reasons can be invoked for the lower diversity found in sediments associated with *Caulerpa racemosa* and *Posidonia oceanica*. *Caulerpa racemosa* offers little surface for epiphytic colonization. For *P. oceanica* sediments, strongly adapted taxa but lower species richness might be related to an advanced stage of ecological succession, as Blanc-Vernet (1969) argued that *P. oceanica* meadows are indicative of a climax community. The resulting lower diversity of the associated biocoenosis (sensu Rejmánek, 1989; Meiners and others, 2002; Sax, 2002) includes the foraminiferal assemblage that is characterized by dominance of sessile *Planorbulina mediterranensis*. The higher foraminiferal diversity reflected in sediments associated with *C. prolifera* and *C. taxifolia* might be associated with new microhabitats available for foraminiferal colonization, especially by short-lived taxa. Moreover, the greater abundance and diversity of morphotype D forms associated the *Caulerpa* spp. might reflect the poor sorting of sediments in these areas. Consequently, in agreement with Langer (1993), imbricated microhabitats, along with characteristic seasonal patterns of the different phytal substrates, are the main controls for species diversity.

The foraminiferal assemblages we found are consistent with Semeniuk's (2000) observations regarding the heterogeneous distribution at local- and micro-scale of epiphytic species associated with algal patches within a seagrass meadow. This heterogeneity, along with the textural patterns associated with the studied phytal substrates, could lead to noticeable sedimentological differences before taphocenotic and dissolution processes occur. Such differences are in agreement with the mosaic facies concept, which refers to carbonate factories, especially in shallow-

water environments, as patchworks or mosaics in a range of settings influenced by many environmental factors (Wright and Burgess, 2005). Resultant facies distributions within carbonate-producing environments are more complex than an arrangement of facies belts more or less parallel to the coastline. Thus, our approach to the foraminiferal assemblages could be useful in facies analysis and paleoecological interpretation. For example, one might infer a seagrass meadow based on the relative abundances of foraminiferal morphotypes A and B and absence of any evidence of transport.

CONCLUSIONS

Foraminiferal assemblages from sediments associated with *Posidonia oceanica* and *Caulerpa* spp. are similar in terms of taxonomic composition, but have significant differences in the relative abundances of diagnostic taxa. In sediments colonized by *P. oceanica*, dominant foraminifers are long-living, flat, encrusting, sessile species of morphotype A (e.g., *Planorbulina mediterranensis*). In sediments associated with *Caulerpa* spp., tend to be dominated by comparatively short-lived, temporarily motile taxa corresponding to morphotype B (e.g., *Lobatula lobatula* and *Rosalina bradyi*) and D (hauerinids and textulariids). Dominance by one of these morphotypes is related to the productivity cycle of the phytal substrate (seagrass or alga) and to the interaction in terms of competition and allelopathy between *P. oceanica* and *Caulerpa* spp.

Lower diversity in *Posidonia oceanica*-associated assemblages are interpreted to represent a mature, stable ecosystem dominated by a few, well-adapted foraminiferal species. The presence of *Caulerpa* spp. alters the ecosystem dynamics and offers new substrates with different seasonal patterns that induce higher diversity.

Finally, differences between *Posidonia oceanica* and *Caulerpa* spp. foraminiferal assemblages are recorded in the sediments regardless of subsequent taphocenotic and dissolution processes. Therefore, taking these observations into account has potential utility in paleoecological interpretations by providing a means to recognize seagrass- and algal-dominated environments in the fossil record.

ACKNOWLEDGMENTS

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